TROPICAL FORESTRY PAPERS 37

Leucaena

A Genetic Resources Handbook

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OXFORD FORESTRY INSTITUTE
DEPARTMENT OF PLANT SCIENCES
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FORESTRY RESEARCH PROGRAMME

TFP 37 *Leucaena* Genetic Resources Handbook Hughes OFI

Photographs

Front Cover
Medium-sized tree of *Leucaena esculenta*, the *guaje rojo* or *guaje colorado*, cultivated for its edible unripe seeds and pods, in the village of San Pablo Etla, in the Valley of Oaxaca at 1650m in south-central Mexico. In November, the tree has a heavy crop of glossy reddish-brown unripe pods. *L. esculenta* is one of the most important and widely cultivated species of *Leucaena* in Mexico.

Back Cover
Leucaena species in their native ranges in Mexico and Central America generally form small to medium-sized trees. **A.** *Leucaena diversifolia*, Yajalón, Chiapas, Mexico near the southern limit of its natural distribution; **B.** *L. salvadorensis*, San Juan de Limay, Estelí, Nicaragua - in March, at the peak of the dry season, the tree is almost leafless and in full flower; **C.** *L. greggii*, Iturbide, Nuevo León, Mexico, small tree in dry mattorral in full flower in May; **D.** *L. esculenta*, Etla, Oaxaca, Mexico, tree in full flower in early November; **E.** *L. matudae*, Mezcala, Guerrero, Mexico, showing its typical small branchy habit and dry thorn scrub forest habitat, here in November at the start of a seven-month dry season.

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List of Acronyms

BRAHMS	Botanical Research and Herbarium Management System
CATIE	Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica
CONSEFORH	Conservation and Silviculture of Dry Zone Forest Species Project, Siguatepeque, Honduras
CSIRO	Commonwealth Scientific and Industrial Research Organisation, Australia
DFID	Department For International Development, UK
IUCN	International Union for the Conservation of Nature
LEUCNET	International Leucaena Research and Development Network
MADELENA	Proyecto de Madera y Leña, CATIE, Costa Rica
MUSICA	Multiscale Information and Cartographic Assistant
NifTAL	Nitrogen Fixation for Tropical Agriculture, University of Hawaii, USA
NSSL	National Seed Storage Laboratory, USA
OFI	Oxford Forestry Institute, UK
SISTEM+	Species Information, Seed, Trials and Environment data Managament
USDA	United States Department of Agriculture, USA

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1 Introduction

1.1 *Leucaena* = *Leucaena leucocephala*?

Most foresters and agronomists who work in the tropics will, at some point, have set eyes on a *Leucaena* tree. In the majority of cases they will have observed a tree of one of a handful of genetically uniform varieties of one species, *Leucaena leucocephala*. It is a ubiquitous, small, seedy tree that occurs in most tropical countries. Whether that tree is viewed as a valuable asset providing basic products to smallholder farmers, as a salvation for sloping lands, as the 'alfalfa of the tropics' to commercial beef producers, or cursed as an undesirable alien weed depends on the perspective of the observer. *Leucaena* means different things to foresters, agronomists, pasture production scientists, veterinarians, botanists, ecologists and conservation biologists. However, for almost all, *Leucaena* means *Leucaena leucocephala*. Apart from those who live in the native home of *Leucaena* in Mexico and Central America and a small number of specialists, few are fully aware of the diversity of species which exists within *Leucaena*. There are 22 recognised species. They span 40 degrees of latitude and 2500m in altitude and grow under varied climatic and soil conditions. They have diverse sizes, tree forms, growth rates, site adaptabilities, phenologies, wood and leaf qualities and weedy attributes. They are highly crossable and form hybrids with ease. Several show high levels of within species diversity. All this diversity has remained poorly known and, until recently, largely untapped. The aim of this *Handbook* is to document what is known about diversity within *Leucaena* and present it as a whole to a wider audience.

The overwhelming early focus on *L. leucocephala* was perhaps not surprising - in many respects it is an extremely useful and adaptable tree. It can provide a multiplicity of basic products and services including firewood and poles, livestock fodder and green manure, food from leaves, pods and seeds, as well as shade and soil conservation. It can produce exceptional wood and fodder yields on some sites and may be cultivated and managed in diverse agricultural, agroforestry and forestry systems. Multiple uses, fast growth, ease of propagation and management, and exceptional fodder quality, have been key factors promoting its adoption. These characteristics combined with abundantly available seed led to promotion of *L. leucocephala* by national and international development agencies and its widespread use in tropical reforestation. At the peak of its popularity, in the late 1970s and early 1980s it was heralded by some as a 'miracle tree' and was the focus of several books, reviews, a comprehensive bibliography, national and international workshops, videos and a dedicated journal - *Leucaena Research Reports*.

The myth of the 'miracle tree' was brought sharply and starkly into focus with the spread of the psyllid defoliator, *Heteropsylla cubana*, across Asia between 1984 and 1989, and into Africa in 1992. In many parts of Asia the destruction of *L. leucocephala* by the psyllid was a disaster for livestock production and hindered progress on broader soil conservation and land rehabilitation programmes. No other single factor has halted promotion and use of *L. leucocephala* and prompted the search for new diversity and alternatives with such urgency as the psyllid. With extended use, a number of other limitations of *L. leucocephala* have become apparent including lack of cold and drought tolerance and poor growth on acid soils, weediness, low wood durability and poor seedling vigour hindering establishment.

Unfortunately, the great diversity of users and uses of *Leucaena* has not been matched by diversity of the material planted. The limitations associated with blanket planting of *L. leucocephala* are in part attributable to the exceptionally narrow genetic base of the material used in cultivation. Early and abundant production of seed through self pollination, giving true bred material, was crucial to the spread and universal adoption of *L. leucocephala*. However, it also meant that seed was spread extremely easily from country-to-country, region-to-region, organisation-to-organisation, and farmer-to-farmer, resulting in wide use of, and reliance on, an extremely narrow genetic base. Within three decades, since the release and promotion of the '*Giant*' or '*Salvador*' varieties of *L. leucocephala* from Hawaii, one or a few self pollinated varieties have become dominant across the tropics despite repeated reminders of their genetic vulnerability. The most widely cultivated variety, K8, represents largely selfed progeny of material originally collected from one or a few cultivated trees in the central Mexican State of Zacatecas.

Initial, often casual introduction of narrowly based genetic material of forestry plantation species is not unusual. Subsequent improvement is usually achieved by seeking, collecting, evaluating, selecting and using genetic diversity within species through traditional provenance studies and later selection and breeding programmes. Research on closely related species has in general been of lower priority. Such an approach has been the norm throughout the OFI programme on Central American forest genetic resources of species such as *Pinus caribaea, Cordia alliodora* and *Gliricidia sepium* and considerable genetic gains have been achieved in this way. *Leucaena* improvement has followed a similar approach. Three subspecies, each with very different characteristics have been recognized within *L. leucocephala* providing the basis for substantial genetic improvement. Limited variation amongst accessions of *L. leucocephala* subsp. *glabrata* has also been identified and is now the basis for development of new intervarietal hybrids. However, it is clear that there is even greater scope to improve *Leucaena* using species other than *L. leucocephala* particularly through use of interspecific hybrids. These lesser-known species are without doubt the most important source of new diversity.

While the pantropical cultivation and use of *L. leucocephala* for wood and leaf products is well known and amply documented, the indigenous use of *Leucaena* as a minor food plant in Mexico and Central America, although documented in many ethnobotanical studies, has been less widely studied and appreciated. In its native home, use of *Leucaena* has concentrated not on the familiar leaf and wood products, but on the unripe pods and seeds which are used as a minor food for human consumption (Chapter 4). In sharp contrast to the lack of diversity used in routine commercial exotic plantings, indigenous use has relied on, harnessed, and indeed fostered, diversity through a complex process of incipient domestication that has involved at least 13 species. It is not uncommon to find two, three, or sometimes four species of *Leucaena* cultivated in a single orchard in south central Mexico. Diversity is valued to promote year round production of pods and improve access to a wider range of pod types. Until recently, the full extent, importance and implications of indigenous domestication have not been realized, particularly by *Leucaena* growers and breeders elsewhere. Indigenous domestication has spawned an abundance of spontaneous hybrids. Spontaneous hybridization in a pre-Columbian *Leucaena* orchard in Mexico provides the most likely explanation for the origin of *L. leucocephala* and possibly other tetraploid species. Indigenous use has also been crucial for the conservation of *Leucaena* genetic resources. Despite large scale clearance of the majority of natural populations, many species remain abundant as a result of indigenous use. In the absence of adequate *in* or *ex situ* measures, conservation has relied on farming communities in Mexico and Central America who have been, and continue to be, the primary custodians of *Leucaena* genetic resources. An important objective of this *Handbook* is to point out and describe in detail how indigenous use and domestication have crucially influenced the recent evolution of *Leucaena* (Chapters 4 and 5) and in large part secured the conservation of its genetic resources (Chapter 8), and why this is important for *Leucaena* growers and breeders elsewhere.

1.2 Building foundations: taxonomy and genetic resources

Taxonomy provides the foundations for all efforts to conserve, utilize and improve economically important plant genetic resources. In an ideal world taxonomic research to discover, delimit and describe species, understand their relationships and map their distributions should precede efforts to assemble seed collections. In practice this is never the case. The two proceed hand-in-hand. Field exploration and seed collection expeditions provide insights into taxonomy and material for taxonomic research, which subsequently suggests how collection strategies might be refined, or what new collections of previously unknown or poorly known species are needed. This has been very much the case for *Leucaena*.

Systematic exploration and collection of *Leucaena* started in 1961. By the early 1980s two large seed collections of *Leucaena* had already been assembled, by the University of Hawaii and CSIRO in Australia, and new seed collections were contemplated. At the same time a substantial programme of applied research was underway to investigate the agronomy, silviculture, artificial crossability, *Rhizobium* affinities, cytology, fodder quality and site adaptability of species of *Leucaena*. In spite of this intense applied research activity and ever expanding promotion of *Leucaena* planting, basic taxonomic knowledge remained lacking. There was no up-to-date taxonomic revision of the genus, new species were being discovered, old neglected species rediscovered, and the origin of the most widely cultivated species *L. leucocephala* remained unknown. In short, it was clear that the utilization, breeding and conservation of *Leucaena* genetic resources were resting on shaky foundations.

The last decade has seen a period of intense research activity to investigate diversity in *Leucaena*. Intensive field exploration, collection of seed and botanical specimens, and ethnobotanical survey have been carried out in the natural populations of *Leucaena* throughout its range in 11 countries in Latin America. Molecular techniques have been applied for the first time to examine species relationships, the origins of tetraploid species and hybrids, and patterns of genetic diversity within species. A botanical database of *Leucaena* containing data on 2800 herbarium specimens has been built. Taxonomic research to delimit species, analyze their relationships and resolve synonymy has been completed and compiled as a new taxonomic monograph of the genus. Spontaneous hybrids have been analyzed and identified and new species and subspecies discovered, described and named. Progress has been made to understand the origins of three of the four economically important tetraploid species. The conservation status of *Leucaena* species has been assessed systematically for the first time. Comprehensive new seed collections (comprising more than 1000 seedlots) including all taxa and bulk provenance and individual family collections have been assembled. In short, our knowledge of the genus, its systematics and genetic resources has been transformed; shaky foundations have been reinforced and it is timely to draw together this accumulation of new findings.

1.3 Scope and objectives of the *Handbook*

This *Handbook* was originally conceived as a means of communicating and disseminating more widely and effectively, the results from the substantial programme of research on the systematics and genetic resources of *Leucaena* carried out by OFI over the last decade. An interim draft version was circulated as an unpublished report entitled *Leucaena genetic resources: the OFI seed collections and a synopsis of species characteristics* in 1993. That precursor has now been substantially expanded and upgraded throughout to produce the current *Handbook*. In particular, the 1993 draft has been updated to conform with the revised taxonomy presented in the new taxonomic monograph (Hughes, in press - due 1998). Alongside simply presenting results of the OFI work, the *Handbook* attempts to assemble, synthesize and present other data from previous research on all aspects of *Leucaena* genetic resources into a single, readily accessible source book for all those concerned with their cultivation, utilization, improvement and conservation.

The title - *A Genetic Resources Handbook* - may suggest to many a book concerned primarily with the cultivation and domestication of species of *Leucaena* used as exotics. This is not the case. It is as much directed towards forestry, conservation and wider rural development agencies, seed banks and others in Central America and Mexico seeking to promote the sustainable use and conservation of *Leucaena in situ*, as those who are planting, improving and hybridizing species of *Leucaena* elsewhere. All efforts to conserve, utilize and domesticate plant species, whether as natives or exotics, rely on the ability to identify species, and the sort of basic knowledge of taxonomy, species distributions, hybridization, and patterns of genetic diversity, which are the focus of this *Handbook*. Chapters on ethnobotany, indigenous domestication and conservation focus specifically on Mexico and Central America. It is published in both Spanish and English in recognition of this dual role.

Much of the original justification for research on the genetic resources of *Leucaena* was based on the perceived need for new genetic material to overcome the known limitations associated with widespread cultivation of *L. leucocephala*. The rationale has been that other species or hybrids could be found and introduced to replace or complement *L. leucocephala* or extend use of *Leucaena* to a wider range of sites. There have been repeated calls over the last few years for use of greater genetic diversity in *Leucaena* plantings to reduce risks. Much has been achieved towards this goal. This *Handbook* describes that diversity and underpins that view. However, this research has been undertaken at a time of changing perspectives on the role of exotic species particularly in non industrial forestry and agroforestry, of growing concerns about the risks associated with new species introductions, and growing emphasis on use of native species. **It is not the intention of this handbook to promote indiscriminate introductions of new species or hybrids.** The 'Common' shrubby *L. leucocephala* subsp. *leucocephala* has become a well known weed of open habitats in more than 20 countries scattered across all continents except Europe and Antarctica (Section 3.9). Several other species of *Leucaena* also show weedy attributes and most should be considered 'conflict species' and regarded with caution when considering introductions. The introduction of any alien species to a new area requires careful consideration of potential benefits and risks in relation to local conditions. Assessment of benefits and risks depends on accurate knowledge of species characteristics. This *Handbook* provides a tool to those attempting to reduce ill considered and unnecessary introductions through more careful assessment of their merits and potential hazards.

It is also important at this point to make it clear **what this publication is not**. Firstly, it is not the aim of this *Handbook* to provide a comprehensive review of data on the agronomy, silviculture, management, end use characteristics or utilization of *Leucaena* species. Only a preliminary summary of information on species characteristics is provided (Chapter 3). A full and detailed review of these topics is beyond the scope of this *Handbook*. It would anyway be premature because the summary presented is no more than an appetizer to the rich feast of data, so far largely unpublished, that will be forthcoming shortly from current research being undertaken to evaluate and characterize species in field trials and laboratory analyses. For example many important new data on environmental adaptation, forage quality and animal production of different species of *Leucaena* are presented in the forthcoming proceedings of a *Leucaena* workshop held in Hanoi, Vietnam in February 1998. Inevitably the *Handbook* therefore combines durable facts with 'facts' which are changing annually as new research results emerge. I would hope that a complementary volume on the evaluation, genetic improvement and utilization of *Leucaena* genetic resources might be compiled by those working within the International *Leucaena* Research and Development Network (LEUCNET) as more complete and accurate data are digested and analyzed. This *Handbook* provides the essential foundations for such efforts.

Secondly, this *Handbook* **is not a *Manual* of procedures** for how to grow *Leucaena*, how to establish a trial, or how to select a species or provenance for planting. There are many such manuals, both general, and specific to *Leucaena*, covering nursery procedures, silviculture and agronomy, for both wood and fodder production, and for trial establishment and analysis. The only parts which resemble a *Manual* of 'how-to' procedures are those of immediate relevance to genetic resources, on species identification and seed handling. Chapter 10 provides a set of tools to enable readers to accurately identify species of *Leucaena*. Basic information on seed collection, predation, handling, storage, germination and inoculation is presented in Chapter 7.

Finally, this *Handbook* **is not a taxonomic monograph**. A new taxonomic monograph of *Leucaena* has recently been completed (Hughes, in press - due 1998). The taxonomy used here follows that monograph. In addition, a botanical database - the *BRAHMS Leucaena Monograph* - has also been compiled. This is a botanical specimen database which includes data on more than 2800 specimens lodged in 26 herbaria. Detailed field notes, common names, phenology and wild/cultivated codes, and duplicate records are included and the majority of specimens (2393) have accurate geographical data (Lat/Long). Full nomenclatural data including name status (accepted, basionym, heterotypic synonym, excluded *etc.*), synonymy and protologues are included in the database. Type collections are linked to names. Associated research material (nodules, wood, photos, bruchids, seed, dried leaves *etc.*) is cited. Copies of this database are available from the author.

As already noted, there are many different users of *Leucaena* genetic resources. They often occupy different and in many ways very separate worlds and use their own technical jargon. For example crop breeders working on forage improvement refer to accessions, lines, composites, and improved varieties or cultivars, while tree breeders talk about provenances, families, bulk seedlots, and progeny trials. My background is in forestry and botany, but I have attempted to make this *Handbook* relevant and understandable to all with an interest in *Leucaena*.

There are two main ways to access information in the *Handbook*. Species accounts arranged alphabetically provide summaries of species data and characteristics, along with botanical drawings and distribution maps (Chapter 11). The remaining chapters are generic by topic - systematics, ethnobotany, hybrids, conservation, *etc.* Each chapter stands alone for those who care to dip in in this way. For those who want an even shallower dip, summary boxes of salient points are included in each chapter. For those who explore the *Handbook* more thoroughly, I hope they will excuse the inevitable duplication that this attempt to improve accessibility entails. Less immediately palatable data on species names, OFI seed collection passport data and seed distribution are consigned to Appendices for reference. An index to scientific names is also provided.

1.4 Future priorities

The genetic resources of species of *Leucaena* have now been as thoroughly explored, collected and documented as for any tropical woody genus. The applied work currently underway to evaluate and characterize species and within species diversity in field trials and laboratory analyses, much of it carried out under the umbrella of the LEUCNET research network will add to and further consolidate this knowledge base. Although our understanding of species diversity in *Leucaena* is now more complete, there remains a great dearth of data on patterns and levels of diversity and geneflow within and between populations within species (Section 6.4). New research to assess the effects of habitat fragmentation and domestication on patterns of diversity and geneflow is needed to underpin effective conservation and improvement strategies. However, the main challenge now is to work out ways to use this diversity. A number of issues, so far somewhat neglected by *Leucaena* growers and breeders, but which are likely to dictate the agenda for future use and improvement, are briefly highlighted here.

Optimal use of *Leucaena* genetic resources in forestry and farming systems will depend as much on clear understanding and recognition of the socio-economic and environmental contexts as on technical or biological advances. As noted earlier, *Leucaena* is used for different products, in different agroforestry and farming systems, under widely varying socio-economic conditions. The socio-economic imperatives for large scale commercial beef production farmers in northern Australia are very different to those of small scale, smallholder subsistence farmers in the middle hills of Nepal. The socio-economic context dictates which products are used, what product qualities are desired, what farming systems with which crop and livestock combinations and hence 'associative traits' of trees are involved, what breeding objectives are appropriate, what dissemination pathways are in place for uptake of new germplasm, what levels of diversity are appropriate and acceptable to provide adequate security, and, in large part, whether *Leucaena* is perceived as a weed or an asset.

Hybrids, both spontaneous and artificial are extremely important in *Leucaena* (Chapter 5). Further research is needed to perfect technologies to design and produce high yielding, high quality, psyllid-resistant *Leucaena* hybrids. Nevertheless, the potential to do so is within our grasp given modest investment in research. High interspecific crossability, diversity of useful characteristics amongst species and relative ease of artificial hybridization, mean that new hybrids can be designed and created virtually at will to meet specified criteria. However, it will not be enough to breed high yielding, psyllid-resistant varieties or hybrids which produce high quality products. Effective mechanisms for their multiplication, dissemination, maintenance, development, or control may not be in place. For example, sterile, or near sterile triploid hybrids offer particular potential being highly productive and environmentally benign, but could be unattractive to smallholder farmers by simply creating inequitable and unsustainable dependencies on outside seed suppliers, in the absence of locally available and appropriate propagation technologies. Any new germplasm which is released must also be shown to be environmentally benign and designed to provide longterm security to farmers and growers. Risks of weediness and the need for security in relation to pests and diseases are key considerations. The narrow genetic base of the widely planted varieties of *L. leucocephala* is a recurrent theme throughout this *Handbook*. There can be no justification for new releases which perpetuate this flawed and genetically risky approach. Maintenance of diversity (species and intraspecific) is an essential part of the adaptive strategy of resource poor farmers to cope with heterogenous and uncertain ecological and socio-economic environments. Domestication is discussed in Chapter 9.

It is also the intention of this *Handbook* that the critical interdependencies between domestication of *Leucaena* as an exotic and its indigenous use, domestication and conservation, discussed in detail in later chapters, are more fully appreciated and recognized. The critical role played by farmers and rural communities in Mexico and Central America who have been and continue to be, not only the primary custodians of the genetic resources of *Leucaena*, but also important architects of *Leucaena* diversity through indigenous domestication, is rarely appreciated or acknowledged by the majority of *Leucaena* growers and breeders across the tropics. Genetic material from the natural populations in Latin America has, so far, been freely available to all throughout the tropics. Seed recipients have been able to obtain material without having to concern themselves with the political, financial and administrative inconvenience of seeking access to genetic resources from the natural populations. Nor have they had to consider the possibility of sharing benefits, however modest, derived from those genetic resources with those who provided, domesticated and conserved them. Future success in maintaining unrestricted exchange of *Leucaena* genetic resources is likely to depend on the formation of partnerships between providers (farmers, rural communities, conservation agencies, rural development agencies and governments in the countries of origin) and users (growers, seed producers and breeders) which clearly recognize the principle of fair and equitable sharing of benefits. *"As with plant genetic resources more generally, and as recognized by the Convention on Biological Diversity, more substantive recognition of the rights of those whose efforts have helped to maintain and create forest genetic diversity may be a prerequisite to maintaining it"* (Kanowski and Boshier, 1997: 218).

Some have questioned whether interest and confidence in *Leucaena* will recover from the destruction of *L. leucocephala* by the psyllid. There is no doubt that there is ample diversity within *Leucaena* and technologies available, or being developed, to harness that diversity, particularly through hybridization, to restore *Leucaena* as one of the most useful and popular agroforestry trees. It is also technically feasible to ensure that improved genetic material provides greater farmer security and is environmentally safe. However, the low status historically afforded to this (largely) non-food crop, of primary interest to the rural poor of the tropics, means that much of the onus for research and development of *Leucaena* has fallen on, and continues to rest with, a small number of individual scientists in a handful of often poorly resourced institutions. The formation of LEUCNET in 1994 is welcome and offers excellent prospective benefits for the successful restoration of *Leucaena*. However, this outcome remains elusive. Just how effective LEUCNET will be in marshalling resources, coordinating strategies and sustaining research and development effort remains to be seen. Without doubt the challenge for LEUCNET will be to embrace the full diversity of interests in *Leucaena* genetic resources to create truly collaborative, integrated programmes of mutual benefit. It will also need to face up to the full complexity of issues, particularly socio-economic and environmental, which will constrain genetic development and improvement of *Leucaena* in the future.

2 Systematics

2.1 The scope of systematic studies

The terms *systematics* and *taxonomy* are often used interchangeably to refer to the science of discovery, description, comparative biology and classification of species. Any systematic study comprises several components. Firstly, it involves the delimitation and description of species in answer to the basic question - what species are there in the study group? Species description precedes comparative study of morphological and molecular variation to analyze species relationships. A scheme of relationships, presented as a hierarchical branching diagram is used to construct a classification. Most analyses of relationships among taxa rely on cladistic methods, sometimes referred to as phylogenetic systematics. Cladistics is an objective and maximally informative systematic discovery procedure which reveals hierarchical order in character data. This allows natural (or monophyletic) groups supported by the maximum number of shared characters (synapomorphies) to be identified and recognized in classifications. The product of a systematic study is a classification presented in an efficiently retrievable form, such as a taxonomic account, monograph or biodiversity database. Taxonomic accounts tell us about the organization and history of diversity, providing data on what species there are, where these species occur, what characteristics and properties they have and how are they related. For economically important plant groups, such as *Leucaena*, clear knowledge and documentation of species diversity directs both the search for close relatives of widely planted species which are the source of new genetic diversity, and the setting of priorities for conservation. On a more prosaic level, classifications provide the scientific names that are the universal language for communication amongst agronomists, foresters, agroforesters, crop and tree breeders, natural resource managers, conservation biologists and ecologists, as well as the basis for developing identification tools. Systematics thus provides important foundations for all efforts to conserve, utilize and improve plant genetic resources.

Recent systematic study of *Leucaena* has involved: (i) investigation of generic relationships to establish whether *Leucaena* forms a natural group (Luckow, 1997; Hughes, in press); (ii) delimitation of species and their description to determine what species there are in the genus (Brewbaker, 1987a; Zárate, 1984a; 1987a; 1987b; 1994; Hughes, 1986; 1988; 1991; 1997a; Hughes and Harris 1994; in press); (iii) analysis of morphological (Hughes, in press) and molecular (Harris *et al.*, 1994a, 1994b) variation observed amongst species using cladistic methods, to provide a hypothesis of species relationships; (iv) the assembly of a new taxonomic monograph (Hughes, in press) which synthesizes (i)-(iii) and presents a taxonomic account including descriptions, keys, maps and drawings.

One of the principal aims of this *Handbook* is to clarify the taxonomy of what has often appeared to be a confusing group. To facilitate this it includes: this Chapter which discusses the results of recent taxonomic research; Chapter 10 on how to identify *Leucaena* species and hybrids including keys, spot characters and illustrations; descriptions and botanical drawings of all taxa and further notes on taxonomy under individual species accounts in Chapter 11; and updated identifications of all the OFI *Leucaena* seedlots listed in Appendix 2.

2.2 The genus *Leucaena* and its close relatives

A clear understanding of generic relationships is important to determine whether the genus *Leucaena*, as currently understood, forms a natural (monophyletic) group. If so, what are the shared attributes which characterize that group and hence allow *Leucaena* to be distinguished from closely related genera? Knowing where *Leucaena* fits into the bigger tree of life and hence what are its close relatives, may also indicate other genera with similar attributes to *Leucaena*. In other words, do species from closely related genera have similar potential uses? Are they also fast growing trees? Do their leaves also contain mimosine? Are they also attacked by psyllids? Analysis of generic relationships may thus provide pointers for new exploration and testing of species of *Gagnebina* or *Alantsilodendron* in Madagascar, *Dichrostachys* in Africa or *Schleinitzia* in the Pacific which might be used locally in similar ways to *Leucaena*. Finally, a clearer understanding of which are the closely related genera is needed in order to understand species relationships within *Leucaena*, providing the broader, higher level picture of character variation that will indicate the root for the network of species relationships (Fig 3).

Leucaena is placed in the tribe Mimoseae of the subfamily Mimosoideae of the family Leguminosae. At the time of Bentham's 1846 treatment it included another genus *Schleinitzia*, a genus whose species have been variously ascribed to *Leucaena, Piptadenia* and *Prosopis*, but which was judged to have closest affinities to *Leucaena* (Verdcourt, 1977; 1979; Nevling and Niezgoda, 1978; Lewis and Elias, 1981).

Within the Mimoseae, Lewis and Elias (1981) placed *Leucaena* with *Schleinitzia* in the informal '*Leucaena* group'.

Box 1 Systematics

- *Leucaena* first established by Bentham in 1842
- Family: Leguminosae
  Subfamily: Mimosoideae
  Tribe: Mimoseae
- Closely related genera are: *Desmanthus, Schleinitzia, Calliandropsis, Alantsilodendron, Gagnebina, Dichrostachys, Neptunia* and *Kanaloa*
- 22 species
  6 infraspecific taxa
  2 widespread spontaneous hybrids
- Most species are diploid, 2n = 52 or 2n = 56
  Four known tetraploid species: *L. leucocephala, L. diversifolia, L. pallida*, 2n = 104 and *L. confertiflora*, 2n = 112

Within the confines of this group *Schleinitzia* is readily distinguished from *Leucaena* by presence of small stipitate anther glands and its indehiscent (opening only along the margins), often winged, pods. However, more recent studies by Luckow (1993; 1995a) and Hughes (in press) indicate that *Schleinitzia* is more closely related to *Desmanthus* than to *Leucaena*. *Desmanthus* was placed by Lewis and Elias (1981) in the related '*Dichrostachys* group' comprising the genera *Dichrostachys, Desmanthus, Neptunia* and *Gagnebina*. This casts doubt on the informal groupings made by Lewis and Elias (1981) and suggests that *Schleinitzia* may not, after all, be the closest relative of *Leucaena*.

Even in the short time since the study of Lewis and Elias, three new genera, *Calliandropsis* (Hernández and Guinet, 1990), *Alantsilodendron* (Villiers, 1994) and *Kanaloa* (Lorence and Wood, 1994) (Table 1), with affinities to the *Leucaena* and *Dichrostachys* groups have been discovered and named, indicating just how rudimentary our knowledge of these groups remains.

What is clear is that the close relatives of *Leucaena* do at least lie amongst the genera listed in Table 1. A new cladistic analysis of morphological data (Hughes, in press) narrows down the possible schemes of relationships amongst these genera to two hypotheses (Fig 1) which provide equally informative explanations of the currently available morphological data. When this wider range of genera is considered, the analysis confirms the status of *Leucaena* as a distinct genus supported by two shared attributes, pollen surface smooth, finely perforate, lacking ornamentation, and hairy anthers (Fig 1) (Hughes, in press). Given that no other genus of Mimosoid legumes has flowers with hairy anthers, this second character can be useful to distinguish *Leucaena* from other genera (Chapter 10). Hairy anthers can be observed on open flower heads with the naked eye or with a simple x10 hand lens. Assuming the plant in question belongs to the Mimosoideae, if its anthers are hairy then it is definitely a *Leucaena*. However, three species of *Leucaena*, *L. pulverulenta, L. retusa* and *L. greggii* lack hairs on their anthers.

The generic boundaries of *Leucaena* were also questioned by Britton and Rose (1928) who described two segregate genera *Ryncholeucaena* and *Caudoleucaena*, each with a single species, *L. greggii* and *L. retusa* respectively. *Ryncholeucaena* was distinguished by its narrow linear pods and longitudinal seed alignment and *Caudoleucaena* by its long pointed floral bracts, narrow linear pods and oblique seed alignment. These two species also share several other unusual characters including long inflorescence stalks and yellow flowers. While all subsequent authors have treated these segregate genera as falling within *Leucaena* (Brewbaker, 1987a; Harris *et al.*, 1994a; Zárate, 1994), some have recognized their unusual

Generic Relationships of *Leucaena*

Figure 1 Two solutions depicting alternative schemes of generic relationships
(from Hughes, in press)

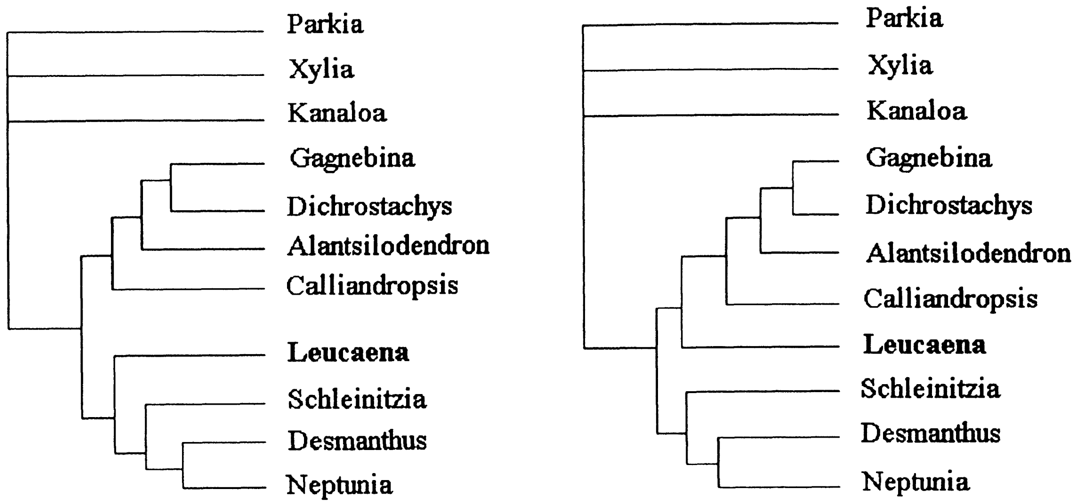


Table 1 Genera of the informal Leucaena and *Dichrostachys* group.

Informal Group (Lewis and Elias, 1981)	Genus	Number of species and distribution
***Dichrostachys* Group**	*Gagnebina*	4-5 spp. Madagascar, Mascarene and Comoros Islands
	Dichrostachys	Approx. 12 spp. Madagascar, NE Africa, 1 sp. pantropical, 1 sp. Australia
	Desmanthus	About 24 spp. New World, USA to Argentina (Luckow (1993)
	Neptunia	11 spp. Pantropical, mainly tropical America and Australia
***Leucaena* Group**	*Leucaena*	22 spp. New World from Texas to Peru
	Schleinitzia	3-4 spp. W Pacific basin (New Guinea, Melanesia, Micronesia and Polynesia)
Named since Lewis and Elias (1981)	*Calliandropsis*	1 species, endemic to central Mexico
	Alantsilodendron	8 spp., endemic to Madagascar
	Kanaloa	1 species, endemic to Kaho'olawe Island, Hawaii

characteristics and emphasized their possible close relationship to each other. Recent analyses of morphological (Hughes, in press) and molecular (Harris *et al.*, 1994a) data support inclusion of *L. retusa* and *L. greggii*, as closely related species within *Leucaena*.

2.3 Species delimitation

The genus *Leucaena* was established by Bentham (1842) with four species: *L. glauca*, *L. pulverulenta*, *L. diversifolia* and *L. trichodes*, all previously placed in *Acacia*. Following Bentham's later recognition of six (Bentham, 1846), then nine species (Bentham, 1875), four botanists, each with a different approach to species delimitation, Nathaniel Britton and Joseph Rose, James Brewbaker and Sergio Zárate, have figured prominently in the classification of *Leucaena*. The number of species recognized has varied from ten to 39.

After Bentham's (1875) revision, field exploration over the next 50 years, principally by the prolific plant collectors Edward Palmer, Cyrus Pringle, Joseph Rose and Karl Purpus, led to the description of many supposed new species and culminated in the revisions of Standley (1922), who recognized 15 species and Britton and Rose (1928), who alone added 24 species, bringing the total to 39. Britton and Rose (1928) based their delimitation of species on characters that are now viewed as unreliable, either because they present continuous patterns of variation across species (*e.g.* leaf, leaflet and pod dimensions) and are therefore not amenable to anything but arbitrary division, or because they vary within populations that are otherwise constant (*e.g.* leaf and pod pubescence). In the absence of rangewide sampling, they failed to detect the continuities and population variation that are now obvious. The result was a proliferation of supposed new species.

James Brewbaker and colleagues at the University of Hawaii made the first attempt to rationalize this proliferation of species. Their knowledge of *Leucaena* was gained from several seed collection expeditions and their work on genetic improvement of *Leucaena* species through hybridization from the 1960s onwards. They adopted an approach to species delimitation, based on observation of material in cultivation in Hawaii and on crossability, and reduced the number of species recognized initially to ten (Brewbaker and Ito, 1980), with gradual reacceptance of additional species to 16 as they were added to the Hawaii collection (Brewbaker, 1987a; 1987b; Brewbaker and Sorensson, 1994). The criteria used by Brewbaker and colleagues to delimit species (Brewbaker *et al.*, 1972, Brewbaker and Ito, 1980; Brewbaker, 1987a; Brewbaker and Sorensson, 1994) were never explicitly stated and no formal taxonomic account was produced. What is clear however, is that Brewbaker maintained a sceptical view of the validity of any species until he had collected material of it himself and observed its progeny in cultivation in the Waimanalo arboretum in Hawaii. Additional species were acknowledged only with some reluctance during the 20 years after his initial acceptance of ten.

Sergio Zárate of the Universidad Nacional Autónoma de México, worked on *Leucaena* initially for the Flora of Oaxaca, later collecting more widely with the Australian forage germplasm collector Bob Reid. From the 1970s onwards, he has continued to investigate the taxonomy, ethnobotany and indigenous domestication of the Mexican species of *Leucaena* as minor food plants (Zárate, 1982; 1984a; 1984b; 1987a; 1997), work which culminated in publication of a revision of the Mexican species (Zárate, 1994). This revision included two new species, four new subspecies and five new combinations, four of them based on species recognized by Britton and Rose. Zárate's approach to species delimitation relied on extensive use of subspecies. Zárate (1994) justified this by the frequent occurrence of interspecific hybridization in *Leucaena*, and the unusual *"abundance of incipient allopatric speciation"* (Zárate, 1994: 88), which he attributed to the complex biogeographical history of the region. Subspecies were viewed as a solution to these perceived difficulties. Zárate also apparently saw subspecies as a mechanism to indicate relationships reflected in his belief that *"a classification exclusively of distinct species is of no benefit either to the interested scientist, or for communication of this knowledge to the user community"* (Zárate, 1994: 88, translated from Spanish). Zárate further mentioned ease of identification (to species) with certainty, as more than compensating for the inconvenience caused by a system composed mainly of subspecies.

Although this marked variation in numbers of recognized species and in the importance given to subspecific ranks by different authors is partly attributable to the history of collection and species discovery, it is also a function of differing views about what constitutes good character evidence for species or infraspecific taxa. A new taxonomic monograph of *Leucaena* has recently been completed by Hughes (in press) providing the first complete taxonomic revision of the genus since that of Britton and Rose (1928). This revision recognizes 22 species with an additional six infraspecific taxa and two named hybrids. The aim (Hughes, 1997a; in press) has been to name, as species, all the diagnosable entities based on available character evidence. Such an objective must emphasize distinctions rather than similarities as pursued by Zárate (1994). The delimitation of *Leucaena* species by Hughes (1997a; in press) is based on the phylogenetic species concept using characters and character states defined on qualitative morphological variation. This is an explicit pattern based species concept (Rosen, 1979; Eldredge and Cracraft, 1980; Nelson and Platnick, 1981; Cracraft, 1983; Nixon and Wheeler, 1990) which recognizes species that possess constant and unique character states or unique combinations of character states. The result is that many of the species described by Britton and Rose are not recognized as distinct by Hughes (in press), and their names are now treated as synonyms (Table 2). In contrast, some of the subspecies recognized by Zárate

(1994) qualify as distinct species.

As noted in Chapter 5, there is ample evidence for hybridization within *Leucaena*; infraspecific taxa provide no solution to the problem of naming hybrids. Zárate's second contention that subspecies are an effective way to indicate groups of closely related taxa, is again little substitute for an informed analysis of species relationships and presentation of an explicit hypothesis of relationships in the form of a hierarchical branching diagram (see below). A number of species groups within *Leucaena*, such as the *L. shannonii* and *L. esculenta* alliances, initially presented difficulties in the delimitation of species. As additional characters have been discovered and particularly as "field" characters have been added, most of these problems have been solved.

Hughes (1997a; in press) used variation in a number of quantitative leaf and pod traits, rejected as species characters because they vary continuously across species and show overlapping variation when viewed across the genus as a whole, to recognize a number of subspecies and varieties. Subspecies were used for entities which are distinguished by several quantitative traits and which are clearly correlated with geography (*e.g. L. collinsii*; Figs 24 and 25). Varieties were used for entities which differ in several quantitative traits but which are not correlated with geography (*e.g. L. lanceolata*; Figs 38 and 39) or for which the geographic limits of the variants are poorly known. An exception to strict application of the phylogenetic species concept was the retention of *L. trichodes* and *L. macrophylla* as distinct species in the absence of clear character state differences pending more detailed examination of variation within this widely distributed group (see Section 11.11 for full discussion).

Molecular evidence, where available, has been found to support delimitation of species and subspecies. The cpDNA analysis of Harris *et al.* (1994a) and the isozyme analyses of Chamberlain *et al.* (1996) were directly applicable in this way. Additional evidence from isozymes of *L. leucocephala* (Harris *et al*, 1994b) as well as the analysis of variation in seed storage proteins (Chamberlain, 1993) provided some circumstantial evidence. No taxa based on molecular variation alone have been retained.

Accepted names and synonyms of species of *Leucaena* are presented in Table 2. This includes several new taxa and combinations published by Hughes (1997a) and follows the taxonomic monograph of Hughes (in press). A complete checklist of accepted names, synonyms, doubtful and excluded names, their place of publication and type specimens is included as Appendix 1.

2.4 Recent taxonomic confusion

It is not uncommon to encounter confusion over species names amongst *Leucaena* researchers and growers. The same species may be referred to using different names in different countries, by different researchers and in different seed collections. As a wider range of species are tested, brought into cultivation and used in hybridization this problem has been aggravated. This confusion is a major handicap to the smooth progress of international *Leucaena* research and communication. While confusion may be partly attributed to difficulties of identification, often due to hybridization (Chapter 5), it also reflects the differing approaches to species delimitation and hence numbers of species recognized by Britton and Rose, Brewbaker, Zárate and Hughes. This has resulted in use of names that are now considered to be synonyms and distribution of incorrectly named seedlots for trials. The most common sources of taxonomic confusion are discussed and clarified below. All taxonomic changes are discussed in detail in the individual species accounts (Chapter 11) and in Hughes (1997a; in press).

L. diversifolia: The known tetraploid and diploid taxa, treated in the past as subspecies of *L. diversifolia* (Brewbaker, 1987a; Pan and Brewbaker, 1988; Zárate, 1994), are now recognized as distinct species, *L. diversifolia* (tetraploid) and *L. trichandra* (diploid) (Hughes and Harris, 1995; Hughes, in press). The name *L. diversifolia* subsp. *diversifolia*, previously used by Brewbaker (1987a), Pan and Brewbaker (1988), Zárate (1994), and Harris *et al.* (1994a) and in the early distribution of OFI seedlots (Hughes, 1993), is now replaced simply by *L. diversifolia*. Previously the diploid taxon was recognized as *L. diversifolia* subsp. *stenocarpa* (Zárate, 1984a; 1994). This name was used by Hughes (1993), Harris *et al.* (1994a) and applied to the OFI *Leucaena* seed distributed up to 1996. However, Pan (1985), Pan and Brewbaker (1988) and Brewbaker and Sorensson (1994) used the name *L. diversifolia* subsp. *trichandra*. The correct name for the diploid taxon, which is now recognized as a distinct species, is *L. trichandra* (Hughes, in press).

L. pallida: Although Brewbaker (1985; 1987a), Zárate (1994) and Hughes (1993) all agreed that the four species described by Britton and Rose (1928), *L. dugesiana, L. oaxacana, L. pallida* and *L. paniculata* are all referable to the same species, there has been disagreement about the accepted name and whether it should be treated as a separate species, or a subspecies of *L. esculenta*. It was originally designated as *L. paniculata* in the CSIRO *Leucaena* seed collection (Bray, pers. comm), as *L. esculenta* subsp. *paniculata* by Zárate (1984a; 1994) and as *L. pallida* by Brewbaker and colleagues in Hawaii. Hughes (1993) originally followed Zárate (1984a) and used the name *L. esculenta* subsp. *paniculata* in the OFI seed distribution. The correct name for this taxon has now been clarified and justified as *L. pallida* by Hughes (in press), in line with the majority of recent agronomic literature (Brewbaker, 1987b; Brewbaker and Sorensson, 1994).

Table 2 Synopsis of *Leucaena* species, infraspecific taxa, and their synonyms recognized by Hughes (in press). A complete checklist of all accepted names, synonyms, their place of publication and type specimens is presented in Appendix 1.

Recognized species and authorities	Recognized infraspecific taxa	Synonyms (excluding basionyms)
L. collinsii Britton & Rose	subsp. *collinsii*	*L. esculenta* (Sessé & Moc. ex DC.) Benth. subsp. *collinsii* (Britton & Rose) S. Zárate
	subsp. *zacapana* C.E. Hughes	-
L. confertiflora S. Zárate	var. *confertiflora*	-
	var. *adenotheloidea* (S. Zárate) C.E. Hughes	*L. confertiflora* S. Zárate subsp. *adenotheloidea* S. Zárate
L. cuspidata Standley	-	*L. cuspidata* Standley subsp. *jacalensis* S. Zárate
L. diversifolia (Schltdl.) Benth.	-	*L. diversifolia* (Schltdl.) Benth. subsp. *diversifolia sensu* Pan (1988) *L. brachycarpa* Urban *L. laxifolia* Urban
L. esculenta (Sessé & Moc. ex DC.) Benth.	-	*L. confusa* Britton & Rose *L. doylei* Britton & Rose
L. greggii S. Watson	-	-
L. involucrata S. Zárate	-	-
L. lanceolata S. Watson	var. *lanceolata*	*L. microcarpa* Rose *L. brandegeei* Britton & Rose *L. cruziana* Britton & Rose *L. palmeri* Britton & Rose *L. pubescens* Britton & Rose *L. purpusii* Britton & Rose *L. sinaloensis* Britton & Rose *L. sonorensis* Britton & Rose *L. nitens* M.E. Jones
	var. *sousae* (S. Zárate) C.E. Hughes	*L. lanceolata* S. Watson subsp. *sousae* S. Zárate
L. lempirana C.E. Hughes	-	-
L. leucocephala (Lam.) de Wit	subsp. *leucocephala*	*L. glauca* (Willd.) Benth. *L. latisiliqua sensu* Gillis & Stearn
	subsp. *glabrata* (Rose) S. Zárate	
	subsp. *ixtahuacana* C.E. Hughes	

Recognized species and authorities	Recognized infraspecific taxa	Synonyms (excluding basionyms)
L. macrophylla Benth.	subsp. *macrophylla*	*L. macrocarpa* Rose *L. houghii* Britton & Rose *L. nelsonii* Britton & Rose *L. macrophylla* Benth. subsp. *nelsonii* (Britton & Rose) S. Zárate
	subsp. *istmensis* C.E. Hughes	-
L. magnifica (C.E. Hughes) C.E. Hughes	-	*L. shannonii* J.D. Smith subsp. *magnifica* C.E. Hughes
L. matudae (S. Zárate) C.E. Hughes	-	*L. esculenta* (Sessé & Moc. ex DC.) Benth. subsp. *matudae* S. Zárate
L. multicapitula Schery	-	-
L. pallida Britton & Rose	-	*L. dugesiana* Britton & Rose *L. oaxacana* Britton & Rose *L. paniculata* Britton & Rose *L. esculenta* (Sessé & Moc. ex DC.) Benth. subsp. *paniculata* (Britton & Rose) S. Zárate
L. pueblana Britton & Rose	-	-
L. pulverulenta (Schltdl.) Benth.	-	-
L. retusa Benth.	-	*Acacia sabeana* Buckley
L. salvadorensis Standley ex Britton & Rose	-	-
L. shannonii J.D. Smith	-	-
L. trichandra (Zucc.) Urban	-	*L. stenocarpa* Urban *L. diversifolia* (Schltdl.) Benth. subsp. *stenocarpa* (Urban) S. Zárate *L. guatemalensis* Britton & Rose *L. revoluta* Britton & Rose *L. standleyi* Britton & Rose *Acacia albanensis* Britton & Rose
L. trichodes (Jacq.) Benth.	-	*L. canescens* Benth. *L. pseudotrichodes* (DC.) Britton & Rose *L. colombiana* Britton & Killip *L. bolivarensis* Britton & Killip *L. trichodes* (Jacq.) Benth. var. *acutifolia* Macbride

L. magnifica* and *L. matudae: Both these species were originally described as subspecies (*L. shannonii* subsp. *magnifica* and *L. esculenta* subsp. *matudae* respectively) and OFI seed was distributed under these names up to 1996. Adoption of a uniform, pattern based species concept across the whole genus has meant that these two subspecies now qualify as distinct species based on unique morphological characters, or combinations of characters (Hughes, 1997a; in press).

L. leucocephala: Variation within *L. leucocephala* was first noted by agronomists evaluating different accessions for fodder production (*e.g.* Hutton and Gray, 1959; Brewbaker *et al.*, 1972). Two main variants, based primarily on habit, branchiness and vigour were recognized: firstly, a shrubby, low growing, highly branched, seedy, and often weedy, variant designated the '*Common* type'; secondly an erect, arborescent, lightly branched, less seedy variant designated the '*Giant*' or '*Salvador* type' (Hutton and Gray, 1959; Gray, 1967; Brewbaker *et al.*, 1972; Brewbaker, 1980; Brewbaker, 1987b). These variants were formally recognised as distinct subspecies by Zárate (1987a). The two subspecies recognized by Zárate (1987a) correspond directly to the agronomic types *viz*: subsp. *leucocephala* = '*Common* type'; subsp. *glabrata* = '*Giant*' or '*Salvador*' type. A third agronomic variant, the so called '*Peru* type' also belongs with subsp. *glabrata*. During recent exploration by Hughes and collaborators in northern Guatemala, an additional variant, which differed from both subsp. *leucocephala* and *glabrata*, was encountered and described as a third subspecies named *ixtahuacana* by Hughes (1997a).

L. collinsii* subsp. *zacapana: pre-1991, this taxon, native to the Motagua Valley system in south-east Guatemala was confused with *L. diversifolia*. Seed of *L. collinsii* subsp. *zacapana* distributed from OFI (Ident Nos 15/83 and 18/84) during the 1980s was misidentified as *L. diversifolia*. This name was also wrongly used by the regional, CATIE-based MADELENA project in all its research activities with this taxon in Central America.

2.5 Species relationships

Understanding of species relationships, based on analysis of comparative morphological and molecular data, provides the basis for classification. There are three published analyses of species relationships within *Leucaena* - Zárate's (1984a; 1994) division of the genus into two sections, an analysis of chloroplast DNA variation by Harris *et al.* (1994a) and a cladistic analysis of 29 morphological characters by Hughes (in press).

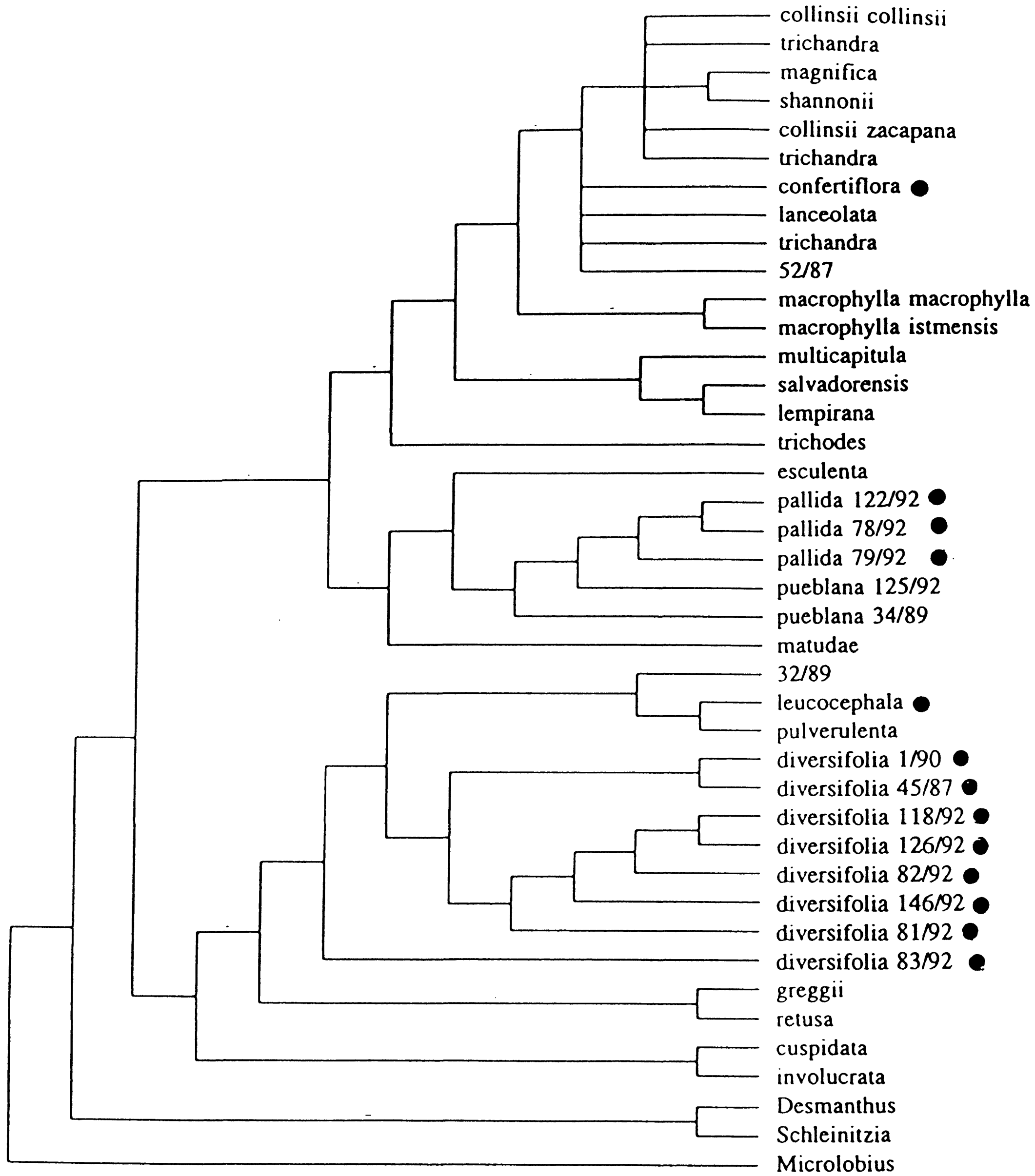
Zárate (1984a) suggested dividing the genus into two sections, based on three conspicuous leaf characters - leaflet size, number of pinnae, and shape of petiole gland. This informal division was claimed by Zárate (1984a: 27) to be *"somewhat natural"* although the problematic position of *L. shannonii* with its polymorphic leaflets which are intermediate between the two sections was recognized. The two sections were formally designated by Zárate (1994) as section Macrophylla, typified by *L. macrophylla*, comprising *L. macrophylla, L. lanceolata, L. shannonii, L. retusa* and *L. trichodes*, and section Leucaena, typified by *L. leucocephala*, comprising the remaining species.

Harris *et al.* (1994a) produced the first explicit hypothesis of relationships within *Leucaena* based on chloroplast DNA variation. This scheme of relationships shows three major groups (Fig 2) and does not support the sectional classification of Zárate (1994). Cytoplasmic DNA phylogenies may differ from species phylogenies particularly where there has been hybridization and introgression (Doyle, 1992). Given that there is considerable evidence that hybridization has been important in *Leucaena* (Chapter 5), the cpDNA tree (Fig 2) should be treated as a 'gene tree' and not a 'species tree'. This also means that it is difficult to compare directly the morphological tree with the cpDNA tree, or to combine the two as an integrated scheme of relationships. However, known maternal inheritance (Harris, unpubl.), while limiting the usefulness of cpDNA in estimating species relationships, makes it particularly useful for detecting cases of hybridization and for determining the maternal parent of tetraploid species originating as hybrids between two diploid species (allotetraploids) (see below).

The third scheme of species relationships (Fig 3) derived from cladistic analysis of 29 morphological characters (Hughes, in press) shows no support for the two sections designated by Zárate (1994). It shows broad, but not complete, agreement with the gene tree derived from cpDNA. Given the difficulties associated with treating the cpDNA tree as a species tree, the morphological analysis was used by Hughes (in press) as a basis for classifying species within the genus. This scheme is favoured over the sectional classification of Zárate (1994) because it is based on a larger number of characters: 29 rather than three. Hughes (in press) also showed that the characters used by Zárate are not satisfactorily partitioned into two states. Leaflet size and number of pinnae show continuous variation across species (Figs 17 and 18) and are not amenable to anything but arbitrary division. Also variation in petiole gland shape is divided into three basic types rather than two (Table 14; Fig 19). The scheme of relationships adopted by Hughes (in press) identifies a number of groups or 'alliances' of closely related species within the genus (Fig 3). These include:

- the *L. esculenta* alliance comprising *L. esculenta, L. pueblana, L. involucrata* and *L. matudae*.
- the *L. lanceolata* group comprising *L. lanceolata, L. multicapitula, L. trichodes, L. macrophylla* and a subgroup within it:
- the *L. shannonii* alliance of *L. shannonii, L.*

Figure 2 Analysis of chloroplast DNA and origins of tetraploid species



Scheme of relationships derived from analysis of chloroplast DNA variation. Tetraploid accessions are marked ●. Numbers refer to OFI seed accession numbers - see Appendix 2 for details (modified from Harris *et al.*, 1994a).

magnifica, L. lempirana and *L. salvadorensis*.

- the four species, *L. retusa, L. greggii, L. cuspidata* and *L. pulverulenta*, although not a group, are consistently placed at the base of the tree and are hypothesized to be closely related. There is evidence to support a close relationship between *L. retusa* and *L. greggii*.The relationships of *L. collinsii* and *L. trichandra* are unresolved in this analysis. Further discussion of species relationships is included in the individual species accounts (Chapter 11).

It remains to be seen what the predictive value of this classification (Fig 3) will be in terms of either new character data or species characteristics more widely. Two observations are of note at this stage. Firstly, it is known that condensed tannin content of leaves, an important determinant of nutritive value of livestock fodder, varies significantly across species (Stewart and Dunsdon, in press; Section 3.7). It is notable that very low (sometimes zero) condensed tannin levels are found for all the species of the *L. lanceolata* alliance and for no other species except the unresolved *L. collinsii*. Secondly, all species of the *L. lanceolata* alliance are moderately or highly susceptible to attack by the psyllid while the remaining species, with the notable exception of *L. pulverulenta*, are moderately or highly resistant (Section 3.4). These two applied traits are thus broadly congruent with this scheme of relationships.

2.6 Chromosome numbers and tetraploid species

Chromosome number (ploidy level) provides a special type of data where some species within a genus have multiple sets of chromosomes (polyploids). The occurrence of polyploidy within *Leucaena* has long been known following early chromosome counts (2n = 104) for *L. leucocephala* (Tjio, 1948; Frahm-Leliveld, 1957; Shibata, 1962; Gonzalez *et al.*, 1967). Subsequent studies showed that both diploids and tetraploids occur and that within each ploidy level there are two chromosome numbers (2n = 2x = 52; 2n = 2x = 56; 2n = 4x = 104; 2n = 4x = 112; Table 3). While the majority of species are diploid, there are four known tetraploids in *Leucaena*, *L. confertiflora* (2n = 112), *L. diversifolia*, *L. leucocephala*, and *L. pallida* (all 2n = 104). Tetraploid species may originate either as autotetraploids - where chromosome doubling occurs when mitotic chromosomal division is not accompanied by cell division, AA → AAAA - or as allotetraploids where chromosome doubling occurs as a result of hybridization between species with distinct genomes, AB → AABB. Allotetraploids are more common that autotetraploids in plants. Evidence suggests that three of the four known *Leucaena* tetraploids are allotetraploids derived from hybridization between two diploid species.

Evidence on the origins of the tetraploid species of *Leucaena* remains incomplete. As noted earlier the maternally inherited chloroplast DNA analysis provides the best source of evidence concerning the likely maternal parent species. In the cpDNA tree tetraploid species are likely to appear as sister (adjacent) species to their maternal progenitors (Fig 2). In a cladistic analysis of morphological data, hybrids, with their reticulating evolutionary histories, violate the fundamental assumption that Nature's hierarchy can be effectively represented by a dichotomous branching diagram. For this reason the four tetraploid species of *Leucaena* were omitted from the initial analysis of morphological data which was carried out including only the diploid species (Fig 3) (Hughes, in press). However, morphological analysis may still provide some additional data on hybrid (tetraploid) origins by including the tetraploid species one by one in the analysis (Hughes, in press).

The currently available evidence on the origin of the known tetraploid species of *Leucaena* is summarized below. Further molecular research that may cast light on these origins is in progress (Harris, unpubl.; Hartman and Cocking, 1996).

- ***L. leucocephala***: the cpDNA data suggest that *L. leucocephala* had *L. pulverulenta*, or a species with the cpDNA type of *L. pulverulenta*, as the maternal parent. The morphological analysis suggested that *L. leucocephala* is a hybrid between two distantly related species, one with large and one (*L. pulverulenta*) with small leaflets. Given the distribution of *L. pulverulenta* in NE and E Mexico, one of the two large leaflet species from that area, *L. lanceolata* or *L. macrophylla*, is the most likely male parent species. Low crossability of *L. macrophylla* (Section 5.2), suggests *L. lanceolata* as the most likely second parent species. The possibility that *L. leucocephala* arose in cultivation was suggested and discussed by Hughes and Harris (1995) and Harris *et al.* (1996). Such an origin is compatible with ethnobotanical evidence (Chapters 4 and 5). Given the existence of three recognized subspecies of *L. leucocephala* multiple origins with slightly differing parentage are likely.

- ***L. diversifolia***: although Pan (1985) and Pan and Brewbaker (1988) hypothesized *L. diversifolia* to be an autotetraploid derived from *L. trichandra*, the cpDNA data of Harris *et al.* (1994a) showed that this is not the case. *L. trichandra* and *L. diversifolia* have highly

Table 3 Chromosome numbers for species of *Leucaena*.

Species	Chromosome number 2n	Author
L. collinsii	52 (?56)	Pan and Brewbaker (1988); Sorensson (1988; 1989a)
L. confertiflora	112	Sorensson (1988); Sorensson and Brewbaker (1994); Palomino *et al.* (1992; 1995)
L. cuspidata	?	
L. diversifolia	104	Pan and Brewbaker (1988); Sorensson (1989a)
L. esculenta	52 (?56) (?112)	Hutton (1981); Pan and Brewbaker (1988); Sorensson (1989a); Palomino *et al.* (1995)
L. greggii	56	Sorensson (1988; 1989a)
L. involucrata	?	
L. lanceolata	52	Gonzalez *et al.* (1967); Pan and Brewbaker (1988); Sorensson (1989a)
L. lempirana	?	
L. leucocephala	104	Tjio (1948); Frahm-Leliveld (1957); Shibata (1962); Gonzalez *et al.* (1967); Hutton (1981); Pan and Brewbaker (1988); De Freitas *et al.* (1991); Sorensson (1989a)
L. macrophylla	?52	Sorensson (1989a)
L. magnifica	?52	Sorensson (1989a)
L. matudae	?52	Sorensson (1989a)
L. multicapitula	?52	Sorensson (1989a)
L. pallida	104 (?110, 112)	Pan and Brewbaker (1988); Sorensson (1989a); Palomino *et al.* (1992)
L. pueblana	?	
L. pulverulenta	56	Turner and Fearing (1960); Gonzalez *et al.* (1967); Hutton (1981); Pan and Brewbaker (1988); Sorensson (1989a)
L. retusa	56	Pan and Brewbaker (1988); Sorensson (1989a)
L. salvadorensis	?56	Sorensson (1988; 1989a)
L. shannonii	52	Hutton (1981); Pan and Brewbaker (1988); Sorensson (1989a)
L. trichandra	52 (?56)	Hutton (1981); Pan and Brewbaker (1988); Sorensson (1989a); Palomino *et al.* (1992)
L. trichodes	52	Gonzalez *et al.* (1967); Hutton (1981); Pan and Brewbaker (1988)

distinctive chloroplast genomes and were placed as distantly related on the cpDNA tree (Fig 2). The cpDNA data instead suggest that *L. diversifolia* also had *L. pulverulenta* as its maternal parent (Harris *et al.*, 1994a). *L. pulverulenta, L. leucocephala* and *L. diversifolia* have very similar chloroplast genomes (Hughes and Harris, in press). Morphological analysis placed *L. diversifolia* as sister species to *L. trichandra* indicating that species as a possible paternal parent.

▸ ***L. pallida***: Pan (1985) hypothesized *L. pallida* to be an allotetraploid derived from hybridization between *L. esculenta* and *L. trichandra* based on morphological intermediacy and geography. The analysis of cpDNA (Harris *et al.*, 1994a) was compatible with that hypothesis until *L. pueblana* was resurrected as a species distinct from *L. pallida* by Hughes (in press). When *L. pueblana* is recognized, this species becomes the likely maternal progenitor (Fig 2). This is compatible with the morphological analysis which placed these two species as sister species.

▸ ***L. confertiflora***: the origin of *L. confertiflora* remains unknown.

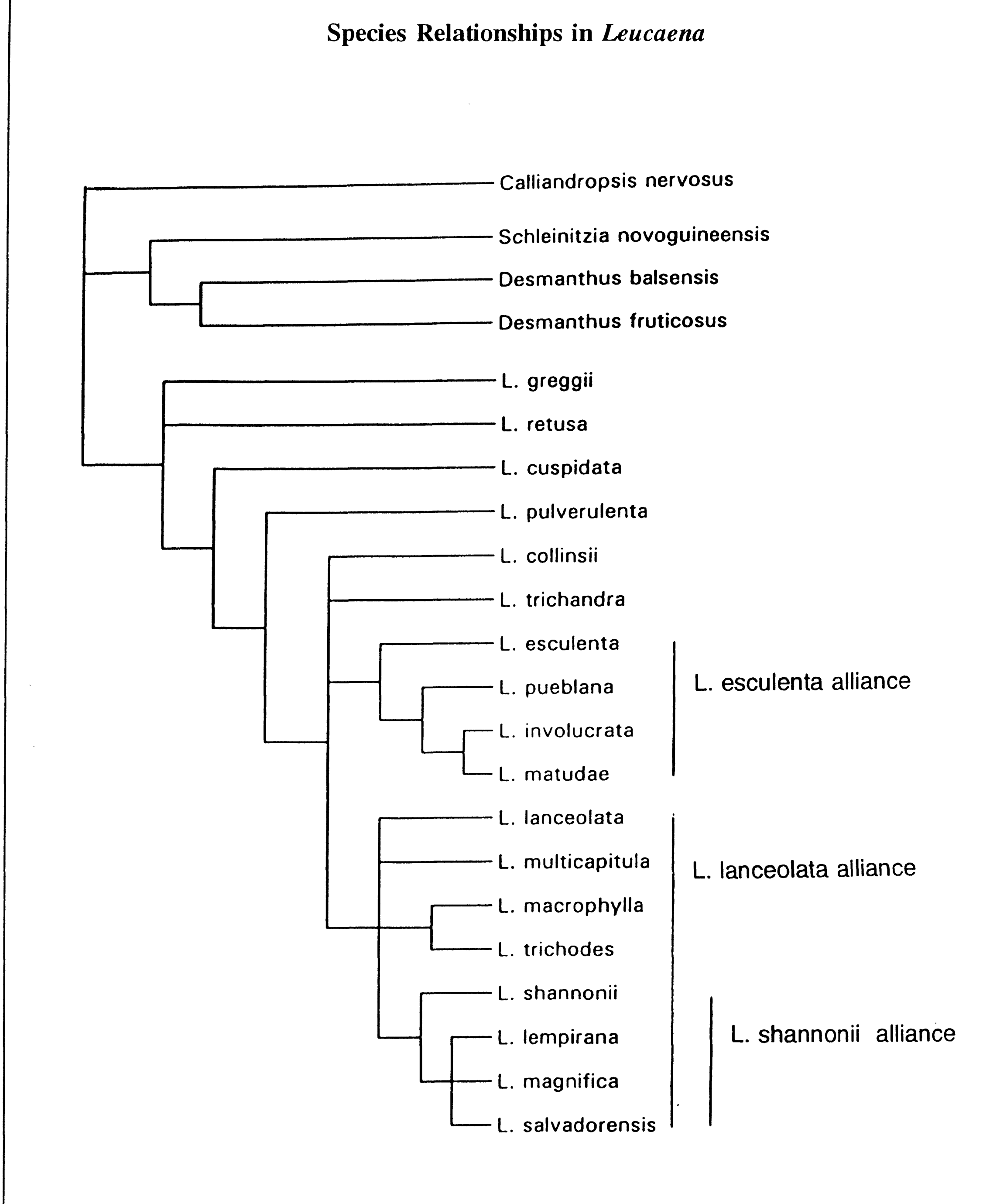


Figure 3 Scheme of relationships of diploid species hypothesized by cladistic analysis of 29 morphological characters showing three species groups within *Leucaena* (modified from Hughes, in press).

3 Species characteristics

3.1 *Leucaena leucocephala*

Tree size and form, site adaptability (including cold and drought tolerance and soil preferences), phenology, product quality (leaves and wood), psyllid resistance, growth rate and weediness are some of the characteristics which determine the potential of *Leucaena* species. As noted in Chapter 1, *L. leucocephala* has been widely planted throughout the tropics. At the peak of its popularity, in the late 1970s and early 1980s it was heralded by some as a 'miracle tree' and was the focus of several books, reviews, a comprehensive bibliography, national and international workshops, videos and a dedicated journal - *Leucaena Research Reports*. The characteristics of *L. leucocephala* are thus extremely well known and amply documented (Oakes, 1968; Gray, 1968; Pound and Martínez-Cairo, 1983; National Academy of Sciences, 1984; Brewbaker, 1987b; Hocking, 1993; Jones *et al*., 1992; 1997). *L. leucocephala* provides the benchmark for comparison in all trials and experiments evaluating the characteristics of other species of *Leucaena*.

In many respects *L. leucocephala* is an extremely useful, versatile and adaptable tree. It can provide a multiplicity of basic products and services including firewood and poles, livestock fodder and green manure, food for human consumption from leaves, pods and seeds (Chapter 4), as well as shade and soil conservation benefits (Fig 7). It can produce high wood and fodder yields on some sites and may be cultivated and managed in diverse agricultural, agroforestry and forestry systems. Multiple uses, fast growth, ease of propagation and management, and exceptional fodder quality (Jones, 1979; 1994b; Shelton and Brewbaker, 1994; Norton *et al*., 1995) have been key factors promoting its adoption. It is one of the foremost tropical fodder trees, sometimes being described as the 'alfalfa of the tropics' and was one of the first species to be used intensively for the production of green manure in alley cropping systems and live barrier slope stabilization.

On the other hand *L. leucocephala* lacks cold tolerance and grows poorly on acid soils, important limitations which restrict its use in tropical highland and many wet tropical lowland areas. It produces prodigious quantities of true bred seed through self pollination from an early age. While this meant that seed of *L. leucocephala* was spread extremely easily from farmer to farmer, area to area, and country to country, it also brought with it the problems of weediness (Section 3.9) and diversion of photosynthates away from wood and leaf production. The prodigious quantities of pods produced by *L. leucocephala* are thus both an advantage and a limitation.

Other limitations of *L. leucocephala* are low durability of its wood limiting use for poles for construction or fenceposts (Timyan, 1996) and poor seedling vigour hindering establishment (Bray, 1986; Jones and Bray, 1983; Lesleighter and Shelton, 1986; Bashir *et al*., 1986; Castillo *et al*., 1994; Sorensson *et al*., 1994). However, the most serious limitation of *L. leucocephala* is susceptibility to defoliation by the psyllid *Heteropsylla cubana* (Fig 7F-G) (Section 3.4). While the psyllid rarely causes tree mortality, severe and cyclical defoliation meant that farmers and communities who had come to rely on *L. leucocephala* for leaf products, such as dry season livestock fodder, were suddenly faced with shortages (*e.g.* Djogo, 1994). No other single factor has halted promotion and use and prompted the search for new diversity and alternatives with such urgency as the advent of the psyllid (*e.g.* Geiger *et al*., 1995).

Utilization of genetic diversity within species is the normal starting point in any crop or tree breeding programme. Variation within *L. leucocephala* was first noted by agronomists evaluating different accessions for fodder production (*e.g.* Hutton and Gray, 1959; Brewbaker *et al*., 1972). Two main variants, based primarily on habit, branchiness and vigour were recognized: firstly, a shrubby, low growing, highly branched, seedy, and often weedy, variant designated the '*Common*[1] type'; secondly an erect, arborescent, lightly branched, less seedy variant designated the '*Giant*' or '*Salvador* type' (Hutton and Gray, 1959; Gray, 1967; Brewbaker *et al*., 1972; Brewbaker, 1980; Brewbaker, 1987b). These variants were formally recognised as distinct subspecies by Zárate (1987a). The two subspecies correspond directly to the agronomic 'types': subsp. *leucocephala* = '*Common* type'; subsp. *glabrata* = '*Giant*' or '*Salvador* type'. A third agronomic variant, the so called '*Peru* type' was recognized (Gray, 1968; Brewbaker and Hutton, 1979; Brewbaker, 1980) based on material introduced to Australia from Argentina, but of supposed Peruvian origin, and characterized by the erect habit of the '*Giant* type' but the greater branchiness of the '*Common* type'. However, the '*Peru* type' also belongs within subsp. *glabrata*. The bred line '*Cunningham*', released and widely planted in Australia (Gray, 1967), is a cross between the '*Salvador*' and '*Peru*' types.

Despite this conspicuous diversity of shrubby and arborescent types within *L. leucocephala*, the considerable effort that has been devoted to field testing of large numbers of both '*Common*' and '*Giant*' accessions has revealed only limited useful variation. More than 100 accessions of the *Common*, subsp. *leucocephala* tested by Brewbaker and Sun (1996) were

[1] previously the shrubby *L. leucocephala* has been inappropriately referred to as the '*Hawaiian*' type (Brewbaker, 1997; Bray, 1997).

Box 2 Species diversity and characteristics

▸ Multiple uses, fast growth, ease of propagation and management and high fodder quality have been key factors prompting promotion and adoption of *L. leucocephala* in tropical agroforestry. With extended use important limitations associated with over-reliance on *L. leucocephala* have become apparent. These include: lack of cold tolerance; poor growth on soils with low pH, low P, low Ca, high salinity, high Al saturation or waterlogging; early and abundant seed production and weediness; low wood durability; high susceptibility to the psyllid defoliator *Heteropsylla cubana*.

▸ Significant genetic and useful diversity has been detected within *L. leucocephala* most notably amongst the three recognized subspecies. Limited variation amongst accessions of *L. leucocephala* subsp. *glabrata* has also been detected and is now the basis for development of new cultivars and most notably new intervarietal hybrids. However, it is clear that there is even greater scope to improve *Leucaena* using species other than *L. leucocephala*, particularly through use of interspecific hybrids. These lesser-known species are without doubt the most important source of new diversity.

▸ There is tremendous diversity in tree size and form, cold and drought tolerance, soil preferences, wood and leaf quality, psyllid resistance, and weed risk amongst species of *Leucaena*. Some species show potential for direct use. Exploiting hybridization promises almost unlimited scope to use this species diversity for *Leucaena* improvement. Much work remains to fully characterize this diversity. A large amount of data from field trials and laboratory analyses is now being assembled.

▸ Cool tolerant *Leucaena* species, such as *L. diversifolia* and *L. pallida* and their hybrids with *L. leucocephala* suitable for growing in frost-free tropical highland areas have been successfully identified. True frost tolerance is likely to be more elusive, although progress may be made through hybrids with *L. retusa* and *L. greggii*. The potential to incorporate other cool tolerant species such as *L. confertiflora*, (a tetraploid found at higher elevations (to 2550m) than any other species in central Mexico) in hybrids remains to be investigated.

▸ There is a wide range of psyllid resistance from highly-resistant to highly-susceptible across species within *Leucaena*.

▸ There is considerable variation in wood density and heartwood formation. A number of species have significantly higher wood density than *L. leucocephala* and offer scope for improved firewood quality and enhanced wood durability for poles.

▸ While leaves of all species of *Leucaena* have high crude protein contents, there is considerable variation in tannins, digestibility and palatability. Much work is currently underway to assess the nutritive value of lesser-known species. It remains to be seen if any (and if so which) of the lesser-known species or hybrids will be comparable in nutritive value to the very high quality feed of *L. leucocephala*.

▸ *L. trichandra* is the most variable species in the genus in yield, psyllid tolerance and leaf chemical composition. Provenance variation is critical in any evaluation of *L. trichandra*. Provenances from SE Guatemala show particular promise.

▸ *L. leucocephala* subsp. *leucocephala* is an invasive weed of open habitats in more than 20 countries. Several other species and hybrids are potentially as weedy as *L. leucocephala*. Most species of *Leucaena* show weedy traits and tendencies, while only five can be judged to have lower weed risks.

found to be of a single genotype. Most of the accessions of *Giant*, subsp. *glabrata* have also been found to be identical (Brewbaker *et al.*, 1972; Wheeler *et al.*, 1987; Arora, 1981). One accession, K636 from Coahuila, Mexico, was found to be significantly more psyllid-tolerant and less seedy than the widely used K8, K28, K67 and K72 varieties (Wheeler *et al.*, 1987; Bray, 1987; Glover, 1988; Wheeler, 1988; Castillo and Shelton, 1994). While variation among the three subspecies of *L. leucocephala* and within subsp. *glabrata* has been successfully identified and used to improve *Leucaena*, it is clear that there is even greater scope for genetic gain using species other than *L. leucocephala*.

Species diversity within *Leucaena* may be used either by cultivating lesser known species directly, or through artificial hybridization. The high crossability found among species within *Leucaena* (Sorensson and Brewbaker, 1994), the successful development of artificial hybridization techniques (Sorensson, 1995), and the diversity of useful characteristics encountered among species (this Chapter), led Brewbaker and Sorensson (1990; 1994) to consider the whole genus as the potential genepool available for use and genetic improvement. As stated by Brewbaker (1995: 76) *"exploiting hybridisation promises almost unlimited genetic diversity for leucaena improvement in agroforestry systems"*. Hybrids are discussed in detail in Chapter 5. Lesser known species have been the focus of research, particularly to produce hybrids, for at least three decades. However, it is only in the last decade that serious attempts have been made to characterize and use this diversity more fully. Several new species have also been discovered, and old neglected species rediscovered during this time and it is only now that the taxonomic backbone is better defined (Chapter 2) that assessment of species characteristics can proceed on a sound footing.

Despite growing interest in a wider spectrum of species, the characteristics of most species remain poorly known. In this chapter a synopsis of species characteristics is presented, summarized in Table 4, and discussed. A full and detailed review of the voluminous literature on many of these topics is beyond the scope of this Chapter. However, much of this literature relates to only one species, *L. leucocephala*, and here my aim is to provide a preliminary overview of species characteristics across the whole genus. Furthermore, this synopsis should be considered no more than a prelude to the very large amount of data, so far largely unpublished, that will be forthcoming shortly (*e.g.* in the 1998 Hanoi Workshop Proceedings) from current research to evaluate and characterize species in field trials and laboratory analyses.

3.2 Tree size and form

All *Leucaena* species form small to medium sized trees ranging from 3-5m in height (*e.g. L. greggii, L. retusa, L. confertiflora* and *L. cuspidata*) to 20-25m (*e.g. L. multicapitula, L. salvadorensis, L. esculenta, L. macrophylla* and *L. magnifica*) (Table 4) (Back cover A-E). Several lesser known species form trees to 20m height and 40-60cm dbh rivalling the larger trees of *L. leucocephala* subsp. *glabrata*. Tree form varies from consistently single stemmed (*e.g. L. macrophylla* subsp. *istmensis, L. magnifica* and *L. multicapitula*, under free growth) to strongly multiple stemmed (*e.g. L. confertiflora, L. cuspidata* and *L. matudae*). As noted earlier, *L. leucocephala* is distinguished by unusual heritable intraspecific diversity in tree size and form with its well known shrubby '*Common*' (subsp. *leucocephala*) and arborescent '*Giant*' types (subsp. *glabrata*) (Brewbaker, 1987b). Brewbaker (1987b) and Brewbaker and Sorensson (1994) have interpreted this as a general phenomenon within the genus, with *L. magnifica* an arborescent form of *L. shannonii*, *L. diversifolia* of *L. trichandra* and *L. multicapitula* of *L. trichodes*. However, as variation in other characters has been assembled, it has become apparent that not all these 'pairs' of shrubby and arborescent types are in fact closely related (see *e.g.* Hughes, 1997b for *L. multicapitula*; Hughes, in press, more generally). Most are now recognized as distinct species which simply vary in form and stature.

Species also vary in branchiness and crown architecture, but this will require closer evaluation in field trials. The planar, two-dimensional branching habit of some provenances of *L. trichandra* is unusual within the genus. All species are known to resprout after cutting and are amenable to management under regular lopping but the details in terms of resprout vigour, number of resprouts and possible frequency and intensity of lopping have only been studied for *L. leucocephala* (reviewed by Robinson and Thompson, 1988; Brewbaker, 1987b) and, to a lesser extent, *L. diversifolia* and *L. pallida*.

The potential of a wide range of *Leucaena* species to be used in agroforestry combinations, in similar ways to *L. leucocephala*, is demonstrated by their widespread incorporation in traditional indigenous agroforestry systems in Central America and Mexico (Chapter 4; Figs 9F-G, 10B-D). Several species are maintained over crops *e.g. L. esculenta, L. magnifica, L. pallida, L. trichodes* and to a lesser extent *L. salvadorensis*. Other species, such as *L. lanceolata* and *L. collinsii* subsp. *zacapana* are encouraged and maintained in bush fallows, and *L. diversifolia* is often used as shade over coffee. An important factor influencing the incorporation of tree species into agroforestry combinations is their ease of management. All *Leucaena* species are apparently easily managed by farmers by lopping.

3.3 Ecogeography

Leucaena species are distributed in their native ranges across some 40 degrees of latitude and 2500m in altitude indicating a diversity of climates, and particularly temperature regimes, experienced by different species

(Fig 10A). This distribution also encompasses significant variation in rainfall, length and intensity of dry season and soil type. While definitive statements about site tolerances of species must be based on field testing across environments, conditions within the native range provide a first indication of likely climatic limits and soil preferences and a working basis for assessing their potential. Site matching techniques have been used to predict where *L. leucocephala* can be grown successfully in the Neotropics (Lascano *et al.*, 1995). However, for other species of *Leucaena*, data on site preferences from trials are too patchy (see below) to draw conclusions as yet, and localised climate variation within Mexico and Central America may limit the accuracy of climatic interpolations on which to base predictions. The discussion here is based on the limited published literature and a crude assessment of broad ecogeographic conditions within the native ranges of different species which are mapped in Chapter 11. What is quite clear is that there is considerable scope to extend the range of sites where *Leucaena* can be planted beyond the areas where *L. leucocephala* performs well through use of other species, either directly or through hybridization.

L. leucocephala is essentially a tropical species requiring warm temperatures (25-30°C) for optimum growth, with poor cold tolerance and significantly reduced growth during cool winter months in subtropical areas (Brewbaker and Sorensson, 1987a; Williams, 1987). It is limited to areas below about 1500m altitude and 15-25° north or south of the equator. *L. leucocephala* sheds its leaves even with light frosts and heavy frost kills all above ground growth, although trees often resprout the following summer. Similarly *L. leucocephala* grows well only in subhumid or humid climates (650-3000mm) with moderate dry seasons of up to 6-7 months (Lascano *et al.*, 1995).

Cold tolerance. In any discussion of cold tolerance it is important to distinguish between cool tolerance and frost tolerance. Some subtropical and many tropical highland regions experience cool climates, often with reduced sunshine due to persistent cloud cover, but without frost. Furthermore, frost tolerance must distinguish between tolerance of occasional (once a year or once every few years) light frosts (as in large areas of the dry subtropics), and regular (every year over one or several months) frost occurrence. Several of the northern and higher altitude species of *Leucaena* experience frost in their native ranges. In particular, *L. retusa* and *L. greggii* tolerate regular, frequent and often sharp frosts with temperature minima as low as -15°C. These species are truly frost-tolerant, but are known to be slow growing even on frost free sites (Glumac *et al.*, 1987; Stewart *et al.*, 1991; 1993) and have little direct potential, although their use through hybridization, particular involving a 'bridge' species such as *L. pulverulenta* (Sorensson, 1995), is being investigated in Hawaii (Chapter 5). Several other species including *L. pulverulenta, L. pallida, L. esculenta, L. involucrata, L. cuspidata* and *L. confertiflora* experience moderate, infrequent frosts in their native ranges and may show limited frost tolerance. *L. diversifolia* is another highland species which grows in cooler conditions but does not experience frost. The remaining species grow, in their native ranges, in truly tropical, frost free conditions.

Cold tolerance of cultivated *Leucaena* has only been studied for a limited range of species but this has confirmed the exceptional frost tolerance of *L. retusa* and more limited cold tolerance of *L. pulverulenta* (Glumac *et.al.* 1987; Long, 1989). The ability of *L. diversifolia* and its hybrid with *L. leucocephala* to outperform *L. leucocephala* in cool stable climates, with low mean temperatures but no frost, was suggested by Brewbaker (1982) and has since been demonstrated by Brewbaker *et al.* (1988), Khajuria and Singh (1991), and Maasdorp (1992). The inability of *L. diversifolia* to withstand frost has been confirmed by Williams (1987). Surprisingly, the hybrid between *L. leucocephala* and *L. diversifolia* (KX3) was found to be remarkably frost tolerant in S.E. Queensland, Australia (Gutteridge and Sorensson, 1992) and survived frosts with temperature minima as low as -12°C. In subtropical areas that experience occasional light frosts (*e.g.* parts of southern Africa, large areas of South America, northern Mexico and the southern U.S.A.), frost-tender *Leucaena* species may survive and resprout following dieback and can be managed in this way with annual cutting (Foroughbakhch and Hauad, 1990). Austin *et al.* (1997) demonstrated that *L. pallida*, the *L. leucocephala* × *L. pallida* (KX2) hybrid, and *L. trichandra* also show good tolerance of cool, but frost free upland conditions in Hawaii. The level of cold tolerance of *L. esculenta, L. cuspidata* and *L. confertiflora* remains to be investigated in trials but indications are that *L. pallida* and *L. esculenta* are killed by moderate or severe frosts. For example, local residents reported that an unusually hard frost killed all above ground parts of *L. pallida* and *L. esculenta* at San Pedro Chapulco, Puebla, Mexico in 1972.

In summary, *Leucaena* species and hybrids suitable for growing in cool but frost free tropical highland areas include *L. diversifolia* and *L. pallida* and their hybrids with *L. leucocephala*. True frost tolerance is likely to be more elusive, although some progress may be made through hybrids with *L. retusa* and *L. greggii*. The potential to use *L. confertiflora* in hybrids with *L. leucocephala* remains to be investigated. *L. confertiflora* is a tetraploid, thereby opening up opportunities for hybridization, and is found at higher elevations (to 2550m) than any other species in central Mexico.

Drought tolerance. Most species of *Leucaena* grow in their native ranges in seasonally dry tropical forest (Fig 10A). Mean annual precipitation and length of dry season vary across species from 550-700mm with a 7-month dry season for *L. collinsii* subsp. *zacapana, L. matudae*, some *L. pallida*, and *L. pueblana* to 1500-3500mm with a 2 or 3-month dry season for *L. diversifolia* and *L. multicapitula*. Most species lie in between with annual rainfall 750-1500mm and a dry season of 4-5 months. *L.*

pallida has out performed other species under cold dry conditions in Botswana (Karachi and Lefofe, 1997). *L. leucocephala* does not perform well in drier environments, with less than 650mm annual rainfall, and a dry season of more than 4-6 months. Further testing will be required to assess drought tolerance of other species, particularly in relation to dry season leaf retention for livestock fodder production. It is unlikely that any species of *Leucaena* will perform as well as species of other genera, such as *Acacia* or *Prosopis*, with rainfall less than 500mm. They should not be tested in those areas.

Soils. *L. leucocephala* is known to be intolerant of soils with low pH, low P, low Ca, high salinity, high aluminium saturation and waterlogging (Brewbaker, 1987b) and has often failed under such conditions (Hutton, 1981; 1982; Oakes and Foy, 1984, Brewbaker, 1987b; Shelton, 1994; Blamey and Hutton, 1995). The possible approaches to use of *Leucaena* on acid soils were reviewed by Hutton (1995) and Blamey and Hutton (1995) who concluded that high production is not possible without significant selection and breeding. Recent testing of a wider range of species and seed sources has confirmed the poor survival and low acid soil tolerance of *Leucaena* species on several sites in Asia (Khoa *et al.*, 1997; Castillo *et al.*, 1997). Therefore it seems likely that the solution to tree planting on acid soils lies, not with expensive and time consuming breeding programmes to improve *Leucaena* but rather with exploitation of other legume genera, such as *Erythrina, Calliandra, Flemingia* and *Inga* which are naturally well adapted to acid soils. Considerable success has been reported with species from these genera in recent years (Kass, 1995; Lawrence *et al.*, 1995; Chamberlain and Pottinger, 1995; Shelton, 1994). Nevertheless, some attention has been given to looking for acid soil-tolerant species or hybrids of *Leucaena*. Research by Hutton and others, principally in South America, showed that *L. diversifolia, L. trichandra*, and to a lesser extent *L. shannonii* and *L. macrophylla*, exhibit some acid soil tolerance (Hutton, 1981; 1984; 1990; 1995; Oakes and Foy, 1984; Holden *et al.*, 1988). Hybrids between *L. leucocephala* and either *L. trichandra* or *L. diversifolia* were found to grow better on acid soils than the '*Cunningham*' variety of *L. leucocephala* (Hutton, 1990; 1995). The acid tolerance of *L. diversifolia* and particularly *L. trichandra* is not surprising given that these species frequently occur as understorey trees in pine forest in Central America, often on very thin, heavily leached, nutrient-poor lithosols developed from volcanic tuffa. Given that *L. trichandra* has the widest natural distribution and is the most variable species in the genus (Figs 66 and 65; Section 11.22) with known morphological variants (Hughes, in press), considerable genetic diversity as assessed by isozymes and RAPDs (Harris, unpubl.) and known variation in growth, psyllid resistance and tannin content of leaves (Stewart and Dunsdon, in press), it is also likely to show variation in acid soil tolerance. If acid soil tolerance is available within *Leucaena*, it is most likely to be found in *L. trichandra* and in any new testing of material or production of hybrids for acid soil tolerance it will be particularly important to include a wide range of provenances. The occurrence of *L. multicapitula* in lowland rain forest in Panama made researchers suspect that it also might be more acid tolerant than *L. leucocephala*. This requires further investigation but it has been shown by Alvarez *et al.* (1987) that low soil pH in the native range in Panama is compensated for by relatively abundant Ca and Mg in the rooting zone.

3.4 Psyllid resistance

The most serious limitation of *L. leucocephala* is susceptibility to the psyllid defoliator *Heteropsylla cubana* (Figs 7F-G). Psyllids are small jumping, sap sucking, plant lice, reminiscent of aphids, which damage *Leucaena* trees by feeding from the phloem of developing shoots and young foliage so that damage is concentrated in these regions (Figs 7F-G). While the psyllid only causes limited tree mortality, severe and cyclical defoliation, deformation, stunting and dieback mean that farmers and communities who had come to rely on *L. leucocephala* for leaf products, such as dry season livestock fodder or green manure, were suddenly faced with shortages and loss of income. For example, Djogo (1994: 376) states that *"the destruction of Leucaena by the psyllid was a disaster for cattle production systems in most parts of West Timor"* in Indonesia. Wider impacts have been loss of farmer confidence in external recommendations, consequent suspicion of new alternative species promoted by outsiders, and hindrance of progress on broader land conservation and rehabilitation programmes (*e.g.* Mella *et al.*, 1989; Geiger *et al.*, 1995). In Thailand, although *L. leucocephala* has long been grown throughout the country, Sampet *et al.* (1995: 201) considered that *"it is doubtful if interest in Leucaena will recover without substantial effort and funding"*. The psyllid is a classic example of a pest catching up with an exotic after many years of pest free existence, through its accidental movement to a new area (Beardsley, 1987).

Since the psyllid first started spreading in 1984, considerable research effort has been mobilised to examine the problem and provide options for its control and management. Indeed, the psyllid has been the focus of international workshops in Hawaii in 1987 (Withington and Brewbaker, 1987), Indonesia in 1989 (Napompeth and MacDicken, 1989) and Tanzania in 1994 (Ciesla and Nshubemuki, 1995). In the context of genetic resources, only one aspect of this broad programme of research - the search for psyllid resistance within *Leucaena* - is relevant and discussed in detail in this section. General overviews of the psyllid problem were provided by MacDicken (1987), Napompeth (1989), Bray (1994) and Geiger *et al.* (1995), and of the biology of *Heteropsylla cubana* by Beardsley (1987), Waterhouse and Norris (1987), Hodkinson (1989) and Muddiman *et al.* (1992). The dramatic spread of the psyllid westward from Central America in 1985, almost encircling the globe within a decade, is documented in detail by Muddiman *et al.* (1992) and Bray (1994). Attempts to document and quantify the impact of psyllid damage have been made by Mella *et al.* (1989), Oka (1989), Heydon and Affonso (1991), Darma *et al.* (1992), Intari *et al.* (1992) and Room *et al.* (1993).

The severity and scale of damage caused by the psyllid is extremely variable. In Latin America, where the psyllid is native, its distribution is extremely patchy. In some areas, such as the Yucatán Peninsula in Mexico, even though *L. leucocephala* is extremely abundant, psyllids are apparently rare or even absent (McClay, 1989; Waage, 1989), and even where it does occur it rarely causes significant damage (see below). Psyllid pressure has thus not been a significant consideration so far in testing of new *Leucaena* species in field trials in Latin America (*e.g.* McClay, 1989; Stewart *et al.*, 1991). The presumption is that the psyllid is controlled by predator and parasite pressure in these areas (McClay, 1989). The much more severe damage caused elsewhere, at least in the first two years following introduction of the psyllid, may be due to lack of control agents. As local, native control agents adapt and adjust, there is evidence in some areas that psyllid populations decline and damage reduces with time. However, severe damage in Asia has also been attributed, at least in part to the extremely narrow genetic base of the widely cultivated material, comprising essentially a handful of self pollinated varieties of one species, *L. leucocephala* (*e.g.* Brewbaker, 1985; Bray, 1994; Geiger *et al.*, 1995) (Sections 6.3 and 9.3).

The possibility of identifying and using psyllid-resistant genetic material within *Leucaena* was proposed by Sorensson and Brewbaker (1987a) and Bray (1987; 1994) as one option to deal with the psyllid problem, alongside other measures such as biocontrol (reviewed by Mitchell, 1987; Nakahara *et al.*, 1987; McClay, 1989; Waage, 1989 and others). As discussed by Bray *et al.* (1989) and Bray (1987; 1994), there are three options for the selection and breeding of psyllid-resistant *Leucaena*: (i) selection within *L. leucocephala*; (ii) use of psyllid-resistant species directly; (iii) development of psyllid-resistant interspecific hybrids. All three options depend on the ability reliably to detect and assess resistance. This is not necessarily straightforward. The ultimate test of resistance is to establish the reduction in yield of a particular genotype due to the presence of the psyllid, but clearly this is very difficult and time consuming. Most assessments of psyllid resistance have relied on observations of either numbers of psyllid adults and nymphs, or levels of damage, scored on simple rating schemes (Othman and Prine, 1984; Bray, 1987; Sorensson and Brewbaker, 1987a; Bray and Woodroffe, 1988; Wheeler, 1988). Although these rating schemes are qualitative and hence subjective, and give no indication of real loss due to psyllid infestation, they have been quite effective in general comparative assessments. The damage rating scheme of Wheeler (1988), on a 1 (no damage) - 9 (blackened stems with total leaf loss) scale, has been widely adopted. Some authors have subsequently grouped scores into broad categories of resistance (*e.g.* 1-3 = highly resistant, 4-6 = intermediate, 7-9 = susceptible, Sorensson and Brewbaker, 1987a or 1-2 = highly resistant, 3-4 = moderately resistant, 4-5 = moderately susceptible, 5-9 = highly susceptible, Mullen *et al.*, 1996; 1997). Assessment of damage is further complicated by the fact that psyllid populations vary over time in relation to seasons and climatic fluctuations, and from area to area, and damage may also be affected by age of tree and lopping. What is clear is that effective assessment of resistance depends on sufficient replication of each entry, susceptible controls and a 'saturated' psyllid environment (such as that created by stands of susceptible varieties) (Bray, 1994).

Despite these difficulties, the numerous assessments carried out over the last decade, with a few notable exceptions (see below) show broad agreement and now appear to provide a coherent and fairly comprehensive picture of psyllid resistance within the genus. The general lack of genetic diversity and useful variation within *L. leucocephala* is well known (Section 6.4). With few exceptions, assessments show *L. leucocephala* to be highly susceptible. Indeed, in most trials it was among the most susceptible species. Within *L. leucocephala* a few accessions from N.E. Mexico, and most notably K636, showed some psyllid tolerance (Wheeler *et al.*, 1987). This has been attributed not to resistance *per se*, but rather to more rapid recovery after defoliation and retention of some mature leaves during defoliation, which mean that K636 is more tolerant of heavy psyllid infestations than other varieties of *L. leucocephala* (Wheeler *et al.*, 1987; Bray, 1987; Pan, 1987; Glover, 1988; Wheeler, 1988; Castillo and Shelton, 1994). However, while some have promoted K636 on the basis of its superior psyllid tolerance and growth compared to other varieties (Uniquest, 1997), Pan (1987) reported that K636 had not performed satisfactorily in Taiwan, and Wheeler (1988) judged that tolerance was inadequate for intensive fodder management. This discrepancy of opinion may be due to differing psyllid pressure in different areas, and general decline in psyllid pressure two years after initial epidemics permitting mildly psyllid-tolerant varieties such as K636 to grow satisfactorily.

From the start of the psyllid outbreak, it was apparent that some species are much more resistant than others. Initial assessments were based on observation of existing collections growing in Florida, Hawaii, Australia and Taiwan and within a few years a broadly consistent pattern of resistance across the main species emerged. From the start it was established that *L. collinsii, L. esculenta* and *L. pallida*, and some accessions of *L. diversifolia* and *L. trichandra* showed good resistance, while other species including *L. leucocephala, L. pulverulenta, L. lanceolata* and *L. shannonii* were susceptible (Sorensson and Brewbaker, 1984; 1986; 1987a; Hollingsworth *et al.*, 1985; Glover, 1987; 1988;

Pan, 1987; 1988; Piggin and Parera, 1987; Bray and Woodroffe, 1988; Wheeler, 1988; Wheeler and Brewbaker, 1989; 1990; Austin *et al.*, 1990; 1997; Dzowela *et al.*, 1995; Castillo and Shelton, 1994; Gunasena and Wickramsinghe, 1995). The Leucaena Psyllid Trial, LPT, network provided data across sites for a limited number of species and accessions and showed that these general patterns were highly consistent across a wide range of sites and conditions (Wheeler and Brewbaker, 1990). The early results reported by Othman and Prine (1984) which showed some disagreement with this picture have been attributed to misidentification of material (Sorensson, 1989b). Results from the ICRAF trial at Chipata in Zambia also showed some unusual rankings for psyllid resistance (ICRAF, 1996). The reasons for this are uncertain but could be due to unusual drought stress, suboptimal application of the screening method or the arrival of the psyllid when the trees were already quite large.

Most early assessments of psyllid resistance were limited by incomplete coverage of species and limited numbers of accessions included in trials. More recently, all species and subspecies have been assessed based on the OFI seed collections. Sorensson (1989b) listed *L. confertiflora, L. greggii, L. matudae* and *L. retusa* as additional species showing high resistance and *L. salvadorensis, L. multicapitula* and *L. trichodes* as highly susceptible. Austin *et al.* (1995) also tested a wider range of accessions confirming the high resistance of *L. pallida* and susceptibility of *L. multicapitula* and *L. salvadorensis*. By far the most comprehensive assessment of psyllid resistance across the genus as a whole is that by Mullen *et al.* (1996; 1997) who looked at 116 accessions covering all known species at two sites. This assessment largely confirmed the known picture of resistance across species and provided the first data on some of the lesser known species. Notable amongst these are *L. confertiflora* which was highly resistant and *L. leucocephala* subsp. *ixtahuacana* which was slightly less susceptible than subsp. *glabrata* and subsp. *leucocephala*. As *L. confertiflora* is also tetraploid it might prove to be a useful parent in crosses with the other tetraploid species, *L. leucocephala, L. pallida* and *L. diversifolia*. Mullen *et al.* (1996; 1997) also confirmed that there is considerable variation within species such as *L. diversifolia, L. pallida* and *L. trichandra*. It is well established that *L. trichandra* is the most variable species (Section 6.4) and this is confirmed for psyllid resistance which ranged from 1.4-5.2 (damage scores of Wheeler, 1988) across the 12 accessions included, with material from S.E. Guatemala (*e.g.* accessions OFI 53/88, CPI46568, or K919) showing good resistance (Castillo and Shelton, 1994; Austin *et al.*, 1995; Mullen *et al.*, 1996; 1997). It is interesting to note that the psyllid is very abundant in the natural populations where the OFI 53/88 seed was collected, although not apparently causing any significant damage.

It is now clear that there is a complete range of psyllid resistance from highly resistant to highly susceptible across species within *Leucaena*. A set of highly resistant species have now been identified. Psyllid damage rating ranges and categories, based primarily on the data of Mullen *et al.* (1996; 1997) are presented in Table 4.

Psyllid resistance in interspecific hybrids is generally intermediate between the parent values (Sorensson and Brewbaker, 1986; 1987a; Wheeler and Brewbaker, 1990) and hybrids have been advocated as the best option to incorporate psyllid resistance for wider use by *Leucaena* growers (Wheeler and Brewbaker, 1990; Brewbaker and Sorensson, 1987a; 1994; Sorensson, 1995). Initially interest has focused on hybrids between *L. pallida* (resistant) and *L. leucocephala* (susceptible) (KX2), but many other hybrid combinations also show good psyllid resistance. Psyllid resistance of KX2 has been further enhanced beyond the F_1 by four cycles of recurrent selection in breeding programmes in Hawaii. Production and use of artificial hybrids is discussed in detail in Chapter 5.

In spite of several investigations and much speculation (Darma and Sutikno, 1989; Sorensson, 1989b; Wheeler and Brewbaker, 1990; Wheeler *et al.*, 1994; 1995), the mechanism of psyllid resistance remains unknown. There appear to be no obvious correlations between psyllid resistance and leaflet size (Sorensson, 1989b), mimosine (Wheeler and Brewbaker, 1990) nor condensed tannins (Wheeler *et al.*, 1994; Austin *et al.*, 1997). It is clear that the mechanism for resistance is complex; many mechanisms have been proposed involving possible psyllid attraction/repulsion factors such as volatiles, sap constituents (secondary metabolites such as saponins or phenols) and aspects of the plant surface micro-environment such as pubescence or waxy coatings.

3.5 Phenology

A clear understanding of the timing of phenological events (flowering, fruiting and leafing) is needed for efficient planning of seed collections and artificial hybridization. Phenology is also important in understanding natural or spontaneous hybridization events, interactions with pollinators, seed dispersal, seed predators and the psyllid defoliator, and the wider ecology, evolution and population dynamics of species. Phenology data for *Leucaena* are currently limited to species level summaries based on observational data obtained during seed collection expeditions; a few detailed species studies (*e.g.* Bendeck and Foroughbakhch, 1988 for *L. greggii*); herbarium specimen data (natural populations); observations at a handful of sites, such as Hawaii (Brewbaker, 1983) and Taiwan (Pan, 1988) where collections of *Leucaena* have been cultivated as exotics. There are no published studies of variation within species. The main features of any phenology pattern are frequency (continual, sub-annual, annual, supra-annual), amplitude (intensity of response), duration (short or extended), date and synchrony (Newstrom *et al.*, 1994). In *Leucaena*, flowering and fruiting may be annual (most species) or sub-annual/continuous (two species) and there is considerable variation among species in date and duration (Fig 4).

It is well known that *L. leucocephala* produces prodigious quantities of seed from the first year, more or less continuously through the year as moisture permits and across a wide range of different environments (Gonzalez *et al.*, 1967; Pan, 1988). Heavy clusters of 5-10 (-45) pods are produced on each flower head and this has been attributed to self fertility. One other species, *L. diversifolia*, and the hybrid between *L. leucocephala* and *L. diversifolia*, which are also self fertile, are similarly precocious and produce abundant seed over an extended period of the year. However these two species and their hybrid are exceptional; the majority of species of *Leucaena* have strictly annual, seasonal and short (but somewhat variable) duration (2-5 months) flowering periods and do not flower and fruit quite so abundantly nor so early.

With a few exceptions (see below) the species with seasonal flowering and fruiting patterns may be divided into two groups. A group of cool subtropical or subtemperate northerly or high altitude species (*L. cuspidata, L. greggii, L. pulverulenta* and *L. retusa*) flower in February - May and fruit between September and November. The remaining species occur primarily in seasonally dry tropical forest and flower and fruit predominantly during the dry season between October and April, in common with the majority of trees of the dry tropical forest (Janzen, 1967; Frankie *et al.*, 1974). Some of these species such as *L. collinsii, L. lanceolata, L. lempirana, L. macrophylla* and *L. shannonii* flower in the early part of the dry season (October - November) and ripen fruits within 3-6 months by the middle or end of the same dry season. Others have longer maturation periods: up to 8-9 months for *L. cuspidata* and 9-11 months for *L. salvadorensis*, which flowers in March-April with pods not ripening until February of the following dry season. Wheeler (1991) and Sorensson (1992a) reported similar variation amongst species, from 90 to 280 days from flowering to pod maturation in Hawaii. *L. multicapitula* and *L. trichodes* are exceptions to these general patterns. *L. multicapitula* flowers and fruits during the wet season over a period of only 2-3 months, while the apparently extended flowering of *L. trichodes* (Fig 4) is attributable to variation in different parts of its very extensive distribution in South America (Fig 68).

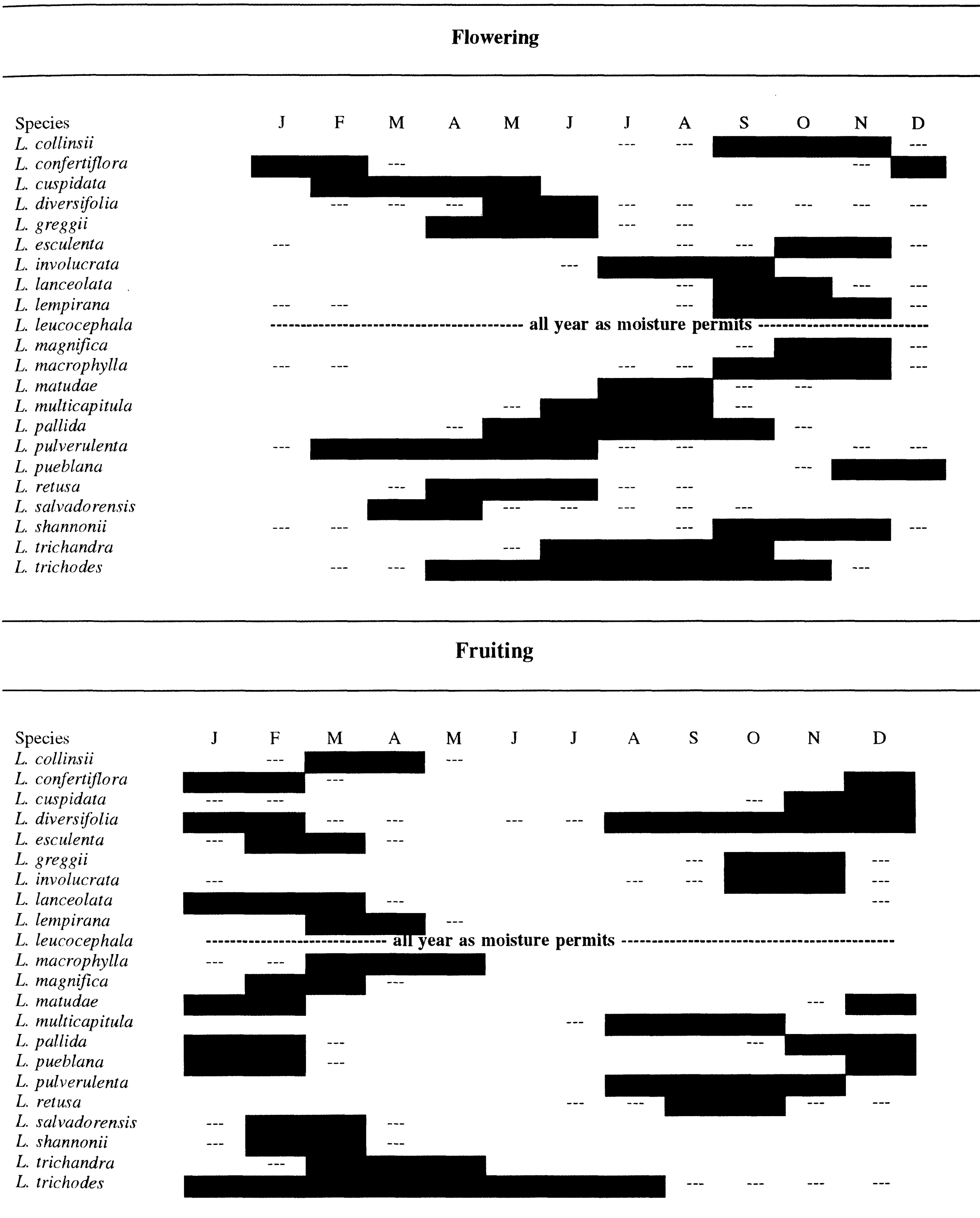
Phenological patterns may be very different when trees are grown outside their native ranges. For example in Taiwan, Pan (1988) found that flowering of all species occurred in June-August except for *L. esculenta* which flowered in November-January. In some environments, some species may not fruit at all (*e.g. L. esculenta* at low elevations in Hawaii).

Most species are strongly deciduous in their native ranges in response to the prolonged (4-6 month) dry season (or winter cold season for *L. confertiflora, L. greggii* and *L. retusa*), losing some or all of their leaves for between one and five months. However, leaf phenology is known to be strongly dependent on site and management such as lopping. Leafing patterns from wild populations are therefore likely to be a poor guide to the behaviour of cultivated populations. Dry season leaf retention is particularly important for fodder use and is an important criterion in assessment of species for use in seasonally dry areas. For example, Dzowela *et al.* (1995) showed considerable variation in dry season leaf retention, initiation of dry season growth and dry season coppice regrowth amongst a subset of *Leucaena* species growing under adverse conditions of cold and drought in Zimbabwe. Rosecrance (1990) found that leaflet drop due to environmental stress is related to leaflet size, with larger leaflets generally persisting longer than small ones.

3.6 Wood quality

Initial interest in use of *Leucaena* as an exotic focused on livestock fodder (see below), and it was not until the discovery and release of the 'giant' varieties of *L. leucocephala* that the potential of *Leucaena* for wood production became apparent (Pound and Martínez-Cairo, 1983). As with most aspects of *Leucaena* research, investigation of wood properties and utilization has concentrated until recently almost exclusively on *L. leucocephala* (Pottinger and Hughes, 1995). The wood properties of this one species have been thoroughly investigated and documented (Bawagan and Semana, 1978; Guevara, 1978; Relwani, 1981; Bawagan, 1983; Pound and Martínez-Cairo, 1983; Van Den Beldt and Brewbaker, 1985). This work shows wood of *L. leucocephala* to be of medium specific gravity (0.5-0.7), with pale yellow sapwood and light reddish brown heartwood, to machine easily, to dry without splitting or checking and to have generally acceptable pulping characteristics (*e.g.* Tang, 1981). Most authors have emphasized the potential to use wood of *L. leucocephala* for a wide range of products including domestic and industrial fuel - including dendrothermal energy generation (Denton, 1983) - poles, posts, sawn timber, furniture, parquet flooring, particle board, and pulp. However, the potential to use *L. leucocephala* for saw timber is greatly limited by its generally small dimensions - usually not greater than 30cm diameter - its branchiness, which limits lengths of clear bole available and means wood is often knotty, and its high proportion of juvenile wood. Nevertheless, there is growing use of small dimension sawn wood in a number of industries, such as flooring, which might include *L. leucocephala* in the future (*e.g.* Brewbaker and Sun, 1996). In practice, *Leucaena* wood is primarily used for fuelwood and charcoal for domestic household or local industrial use (*e.g.* lime or pottery kilns), and for small dimension poles. Use of short rotation *L. leucocephala* for poles is limited by lack of durability and susceptibility to attack

Figure 4 Variation in patterns of flowering and fruiting phenology of *Leucaena* species in their native ranges in Latin America. Black shading = main period; ----- = extended period of sporadic flowering or fruiting. Data are derived from field observations and herbarium specimens.



by termites and wood borers (Timyan, 1996). *L. leucocephala* provides fuelwood and charcoal of acceptable, although not highest, quality and it is a popular fuel, often competing with alternative local species, at least in areas where fuelwood is in short supply (National Academy of Sciences, 1980; 1984). The promised potential for large scale use of *Leucaena* in pulp production or dendrothermal energy plantations (Denton, 1983) has not come to fruition. Indeed, despite much discussion about its wood production potential, *L.*

leucocephala has not been become an established or widely cultivated plantation species that is able to compete with the species of *Pinus, Eucalyptus* or *Acacia* which dominate tropical plantation forestry.

Utilization depends on many different wood properties. For example fuelwood quality depends not only on wood density and heat production, but also ease of harvesting, transporting, drying and splitting, burning qualities such as smokiness, sparkiness and smell, rapid growth rates and coppicing ability. However, wood specific gravity is known to be a good index of strength, pulp yield, heat production and other properties (Panshin and de Zeeuw, 1971) and is one of the few physical properties that is amenable to relatively easy and precise measurement. That there is little variation in the heat produced by a unit weight of oven dry wood was confirmed by a study of calorific values which ranged from 4286 to 4531 kcal/kg across 11 species of *Leucaena* (Bezkorowajnyj *et al.*, 1996). In the few studies which compare wood properties across species, wood density has been the main trait assessed as an indicator of overall quality. Wood density may be affected by growth rate, growing conditions, tree age and tree spacing. In addition, density normally varies across the tree trunk and may change between heartwood and sapwood. Reported density figures for species thus vary and are often quoted as ranges. Density assessment requires standard material and sampling in order to compare species.

Knowledge of the wood properties of species other than *L. leucocephala* is limited to that derived from anecdotal information about wood use within the native ranges of species in Latin America, and a handful of studies of wood samples from species and provenance trials.

In sharp contrast to use of *Leucaena* as an exotic, which has been mainly as livestock fodder, fodder is little used in Mexico and Central America and, after food use of pods (Chapter 4), wood is the most important product. Wood of most species of *Leucaena* is used by farmers and rural communities in Mexico and Central America for firewood, posts and poles. Wood of a number of species is highly preferred by these users over *L. leucocephala* and indeed alongside other native tree genera, such as *Prosopis* and *Lysiloma*, which are known for their high wood quality. *L. collinsii* (both subspecies), *L. lempirana, L. magnifica, L. salvadorensis* and *L. trichandra* (in some areas) are all noted to produce excellent quality firewood. The observation of abundant early heartwood formation in species such as *L. collinsii, L. lempirana* and *L. salvadorensis* (Figs 8B-C), and the known preference of these species for house construction, including use for house corner posts is evidence of the high wood durability of these species compared to *L. leucocephala* (*e.g.* Hellin and Hughes, 1993). In many areas these species are maintained, protected, managed and sometimes cultivated in traditional agroforestry systems (Figs 8A and 10B) (Chapter 4) because they produce high quality wood. *L. collinsii* subsp. *zacapana* is managed on a four-year bush fallow coppice system for intensive high quality firewood production in the dry Motagua Valley of S.E. Guatemala. Similarly trees of *L. salvadorensis*, which produces wood of higher density and durability than *L. leucocephala*, are maintained and managed by pollarding specifically for poles in agroforestry systems in southern Honduras (Fig 8A) (Hellin and Hughes, 1993), and are preferred over most other species (Colindres *et al.*, 1995). *L. lempirana* wood is apparently similar and the species is managed for production of fence posts in cattle rearing areas of north central Honduras. In many parts of Mexico, wood use is subsidiary to food use for some species such as *L. esculenta* (Chapter 4), which means that trees are protected for pod production and the wood, although often of high quality, is little used. The only other species which is recognized for its wood within Mexico and Central America is *L. pulverulenta* which is reported to produce heavy, hard, very close grained wood with rich dark brown heartwood, reflected in its common name *lead tree*, which was used in the past for lumber, including railway sleepers, in southern Texas (Standley, 1922; Sargent, 1921; Isely, 1970; 1973).

Measurements of wood density and heartwood formation from samples collected from a species and provenance trial established by CONSEFORH in 1989 in Honduras provided the first data comparing wood quality across species within the genus. Assessments of wood density from this trial, at years one, two (Stewart *et al.*, 1991; 1993) and five (Gourlay *et al.*, in press) show close agreement in species rankings and demonstrate for the first time that there is significant variation in both wood density and heartwood formation within the genus. Data on wood density and heartwood formation (Gourlay *et al.*, in press) are presented in Table 4. These data show that the mean whole radius density across all species was 0.72 g/cm^3. A subset of species, including *L. collinsii, L. salvadorensis, L. shannonii* and *L. magnifica*, have wood density values consistently greater than 0.8 g/cm^3 and are significantly above average, with a maximum value of 0.95 g/cm^3 for *L. collinsii* subsp. *zacapana* (Fig 8C). These results reflect the preferred status of these species amongst farmers and rural wood users in Mexico and Central America (see above). Wood of *L. leucocephala*, at 0.58-0.64 g/cm^3, was slightly below the average for all species, while the lowest mean whole radius density of 0.56 g/cm^3 was found for *L. multicapitula* (Gourlay *et al.*, in press). Heartwood is denser than sapwood in most tree species, but this study shows the reverse to be the case for *Leucaena* (Gourlay *et al.*, in press). Wood specific gravity of all species of *Leucaena* thus compares favourably with that of other well known multipurpose tree species such as *Gliricidia sepium*: 0.5-0.6 g/cm^3 (Stewart, 1996) and *Calliandra calothyrsus*: 0.51-0.78 g/cm^3 (National Academy of Sciences, 1980). The species of *Leucaena* with higher wood densities match wood of species such as *Prosopis juliflora*: 0.7 g/cm^3 (National Academy of Sciences, 1980). Wood in the Honduran trial was produced under a strongly seasonal climate with a 5-6 month dry season. Wood density values on more favourable sites may be lower and may be subject to genotype-environment interaction. Examination of wood density across a range of sites will address this. The considerable variation in wood density across species indicates that trial assessments which measure only height and diameter may be misleading for those with an interest in wood production. Gourlay *et al.* (in press) also showed that there is considerable variation in heartwood formation among species. At 5 years of age heartwood formation ranged from zero (*L. esculenta* and *L. matudae*) to 59% for *L. salvadorensis* with an average across species of 41%.

The little that is known about wood quality characteristics of the other *Leucaena* species indicates that there is great variation in density and heartwood formation. This variation has scope to be used to improve firewood quality, with possible bio-energy potential. In general, in plantation forestry, faster growing trees have lower wood density than slow growing species on the same site. This does not appear to be the case for *Leucaena*. In the Honduran wood density studies, the highest wood biomass producer, *L. salvadorensis* (Stewart *et al.*, 1991), had amongst the highest wood densities, similar to that of *L. collinsii* subsp. *zacapana*. Within *Leucaena* it is apparently feasible to combine fast wood biomass production with high wood density, a combination of particular interest for fuelwood production. There is also particular scope to enhance durability of poles for local construction through use of lesser known species such as *L. magnifica* and *L. salvadorensis*. There is however, little indication that any of the lesser known species have the potential to compete as plantation species for the production of sawtimber, again because most are branchy with short clear boles. Utilization of small dimension wood for flooring or crafts could be greatly enhanced by use of species such as *L. collinsii* and *L. salvadorensis* with their early and abundant production of rich dark reddish brown heartwood. Wood quality of hybrids and the heritability of wood characteristics in *Leucaena* have yet to be investigated.

3.7 Leaf quality

Lack of nitrogen is one of the limiting factors in many tropical agricultural production systems reducing productivity of crops, pastures and animals (Gutteridge and Shelton, 1994). Most tropical grasslands are nitrogen-deficient and of poor quality for grazing animals (Bray, 1986), and, with few exceptions (mainly in the wet tropics), livestock live for considerable periods of the year on sub-maintenance diets (Robinson, 1985). The two largest sources of nitrogen are from artificial fertilisers and biological nitrogen fixation in legumes, with the latter being the cheapest source. All species of *Leucaena* are known to fix atmospheric nitrogen although the *Rhizobium* affinities are not completely understood (Halliday and Somasegaran, 1983) (Chapter 7). Biologically fixed nitrogen in the form of leguminous protein in leaves (or pods) can be consumed by animals to meet their protein requirements or may be returned to the soil as organic mulch or animal manure. Use of nitrogen-fixing tree leaves, either for livestock fodder or green manure, has been promoted as one solution to some of these problems (*e.g.* Robinson, 1985). *Leucaena leucocephala* has been one of the foremost tropical fodder trees, often being described as the 'alfalfa of the tropics' (Bray, 1986; Pound and Martínez-Cairo, 1983; National Academy of Sciences, 1984; Brewbaker, 1987b; Shelton and Brewbaker, 1994) and was also one of the first species to be used for the production of green manure in alley cropping systems (Kang *et al.* 1981; 1985).

Cursory examination of leaf morphology alone (see *e.g.* Figs 17 and 18) shows there to be considerable variation in numbers of pairs of pinnae, numbers of pairs of leaflets, leaflet size, length and thickness of leaf rachis and length and number of pinnular rachises, among species of *Leucaena*. This implies variable proportions of fibrous lignified (indigestible) tissue and photosynthetic (digestible) tissue that might be a guide to nutritive value (or decomposition rates). Furthermore, only some species show nyctinastic movements of the pinnular rachis, suggesting less fibrous and lignified material. *Leucaena* leaves are thus extremely diverse and variation in nutritive value and decomposition rates amongst species is to be expected.

Fodder quality. Unlike most of the species characteristics discussed in this chapter, such as psyllid resistance, cold or drought tolerance, wood quality or weediness, for which limitations associated with *L. leucocephala* are driving the search for new and superior diversity amongst other species (or hybrids), *L. leucocephala* is, in most respects, one of the highest quality and most palatable fodders trees of the tropics (Figs 7B-D) (Jones, 1979; 1994a; Pound and Martínez-Cairo, 1983; Brewbaker, 1987b; Shelton and Brewbaker, 1994; Norton *et al.*, 1995). Efforts to investigate nutritive value of other species of *Leucaena* have thus been driven not by poor leaf quality of *L. leucocephala*, apart from mimosine content (see below), but by other limitations, and most notably susceptibility to the psyllid (Section 3.4) which has drastically reduced leaf yields and hence the value of *L. leucocephala* as a forage crop. The emphasis is thus on finding species (or hybrids) which match, or at least do not differ significantly from, the very high fodder quality of *L. leucocephala*. Leaf quality of *L. leucocephala* compares favourably with alfalfa or lucerne (*Medicago sativa*) in feed value except for its higher tannin content (Jones, 1979) and mimosine toxicity to non-ruminants (Bray, 1995a). Leaves of *L. leucocephala* have high nutritive value (high palatability, digestibility, intake and crude protein content), resulting in extremely impressive animal production with 70-100% increases in animal live weight gains compared to pure grass pastures (Fig 7B) (Shelton and Brewbaker, 1994; Jones, 1994b; Esdale and Middleton, 1997). In addition, *L. leucocephala* is very persistent over several decades of cutting or grazing, is highly productive, recovers quickly from defoliation, combines well with companion grasses and can be grazed with minimal losses due to trampling or grazing (Jones, 1994b). As attention has turned to other species, and especially hybrids, which are psyllid-resistant, doubts have arisen about their nutritive values compared to *L. leucocephala* (Bray, 1987; Austin *et al.*, 1990; Bray *et al.*, 1990; Castillo *et al.*, 1994; Norton *et al.*, 1995).

Any assessment of fodder quality must recognize the great diversity of farming systems within which *Leucaena* fodder is, or might, be used. Important distinctions must be made between direct grazing and cut-and-carry stall-feeding systems, between use as sole feed and as a feed supplement, between ruminants and non-ruminants, and amongst different animal species within these categories. *Leucaena* fodder may be used in a wide variety of situations. Feed quality characteristics required for large scale beef production grazing systems, such as those in Australia, where production is measured in terms of live weight gains which are critical to economic returns from marginal pasture land, may be very different from those suitable for small scale cut-and-carry stall-feeding systems used by smallholder farmers in many parts of the tropics which demand more diverse products and services (draught power, manure, milk and meat) and which often involve greater diversity of livestock. The bulk of research on feed quality of *Leucaena* has been directed towards extensive commercial beef production grazing systems. Just how applicable this will be to a wider range of ruminants is open to question. It is well known that different ruminants (sheep, buffalo, goats, cattle and camels) show considerable differences in their ability to digest and utilize the nutrients from foliage of the same species and that certain species are good fodder for one type of livestock but not another (Robinson and Thompson, 1988).

Assessment methods. Nutritive value of any animal feed depends on a number of factors including palatability, chemical composition, digestibility and toxicity due to presence of secondary compounds. Furthermore, interactions occur between these factors but are often poorly understood. For example, the complex interactions between proteins and tannins mean that it is not clear whether tannins in Leucaenas are beneficial or disadvantageous in terms of digestibility and nutritive value, and what levels and types of tannins may reduce or enhance feed value (see below) (Norton, 1994; Wheeler *et al.*, 1995; Stewart and Dunsdon, in press). Nutritive value may also depend on time of year, part of the tree (leaf, shoot, age of leaf, position in tree crown), animal species (and breed), accustomization or adaptation of animals to new feeds, what other components are in the diet and on the state of leaf material (fresh/wilted/dried *etc.*). For example it is well known that initial palatability provides no indication of potential palatability (Robinson, 1985). This complexity means that assessment of the nutritive value of different tree species, which is our primary interest here, is not straightforward (reviewed by Wilson, 1969; Le Houerou, 1980; Torres, 1983; Robinson, 1985; Norton, 1994; Stewart and Dunsdon, in press). It is widely accepted that the standard 'objective' measures of nutritive value derived from proximate analyses are suspect in terms of actual value to the animal and that there is no substitute for feeding trials which assess animal production (live-weight gain, milk yield *etc.*) (Robinson, 1985; Norton, 1994). Nevertheless, although such trials may provide the only truly realistic assessment of nutritive value, they are costly and have not been carried out for any species of *Leucaena* other than *L. leucocephala*. The only indications of nutritive value of lesser known species of *Leucaena* remain those derived from leaf chemical composition and *in vitro* digestibility measurements and conclusions about nutritive value are therefore tentative. The nutritive value of leaves of *L. leucocephala* has been exhaustively investigated but the fodder quality of other species of *Leucaena* is, in general, still poorly known.

Mimosine. Early efforts to detect variation in leaf quality among species of *Leucaena* looked at variation in content of the mild toxin, mimosine. Most woody legumes contain secondary compounds which form one component of plant defence mechanisms. These compounds may be toxic to herbivores, may confer unpalatability or may reduce feed intake. In general ruminants (cattle, sheep, and goats) are less affected by secondary compounds than non-ruminants (pigs, horses and poultry) because of the capacity of rumen micro-organisms to degrade these compounds and render them less harmful (Jones, 1994a). The undesirable (toxic) effects of feeding *Leucaena* have been largely attributed to the non-protein amino acid, mimosine which is converted to DHP (3-hydroxy-4-1(H)-pyridone), a metabolite of mimosine, in the rumen. The toxic effects of mimosine were reviewed by Jones (1979; 1994a). The initial strategy used to avoid toxicity was to limit feed intake of *Leucaena* to less than 30% of the diet. At such levels the nutritive value far outweighs its potential toxicity and no detrimental effects are apparent (Bray, 1986). Attempts were also made to select and breed low mimosine lines and hybrids (see below). However, for ruminants, a much more effective and elegant solution has been found with the identification and use of rumen microbes which are capable of detoxifying mimosine and DHP (Lowry, 1983; 1987; Jones, 1985; reviewed by Jones, 1994a). This notable success story has largely solved the mimosine problem for ruminants. As a result interest in the quest for low mimosine *Leucaena* species and hybrids (Chapter 5) has waned. However, mimosine remains a significant problem for non-ruminants, restricting use of *Leucaena*, and is the main disadvantage of *Leucaena* in leaf meal production compared to alfalfa (Bray, 1995a). *Leucaena* leaf meal production, for incorporation in commercial poultry and pig feed, may provide a significant source of rural income in South East Asia, as in parts of Indonesia (Lowry *et al.*, 1984) and Thailand (Manidool, 1983). Furthermore, the quest for low mimosine lines and hybrids illustrates some of the problems associated with investigation and genetic improvement of fodder quality in *Leucaena* and bears further discussion here because of this.

Bray (1995a) catalogues the many factors (apart from genetic factors such as species) which can affect mimosine concentration. These include plant growth rate, stage of development, plant part (young growing shoots, expanded leaves, older leaves), season, and plant response to stress and treatment, such as drying of samples (Jones, 1980). This means that great care needs to be taken over sampling for measurement of mimosine and may explain the great variation in values obtained by different workers. For example, Hauad and Foroughbackch (1991) found that mimosine concentration of *L. leucocephala* varied from 3% to 9% from winter to summer in northern Mexico. Despite sampling problems, contradictory results, and widely differing absolute values amongst the several studies carried out (Brewbaker and Hylin, 1965; Megarrity, 1980; Brewbaker and Kaye, 1981; Chandrasekharan and Govindaswamy, 1985; Gupta *et al.*, 1986; Hauad and Foroughbackch, 1991; Hutton, 1985; Saunders *et al.*, 1987), a more or less consistent pattern of relative values in mimosine concentration can be detected across those species which have been tested. All species of *Leucaena* tested so far contain mimosine. There is a positive relationship between mimosine content and leaflet size; species with small leaflets (*L. collinsii, L. diversifolia, L. esculenta, L. greggii, L. pulverulenta*) generally have lower mimosine concentrations than the large leaflet species (*L. macrophylla, L. lanceolata, L. trichodes*). *L. leucocephala* has intermediate levels of mimosine. Nevertheless, the picture of mimosine variation in *Leucaena* remains incomplete with no published studies that include all species. Despite variation in mimosine concentrations across species, attempts to breed low mimosine hybrids between *L. leucocephala* and *L. pulverulenta* in Australia were unsuccessful (Bray, 1984; 1986; 1995a; Bray *et al*, 1984; 1988; Hutton, 1985). Although hybrids with lower mimosine than *L. leucocephala* were produced, they were also significantly lower in yield, and not worthy of commercialization (Bray, 1995a). Given the likely correlations and interactions among traits such as mimosine and growth rate, crude protein (Saunders *et al.*, 1987), tannin content and possibly pest resistance, hybrids which combine high nutritive value with high growth rates may be elusive (Bray, 1995a).

Nutritive value. Despite the limitations associated with analyses of leaf chemical composition and *in vitro* digestibility (see above), they do indicate that some species of *Leucaena*, such as *L. pallida* and *L. diversifolia*, may have lower nutritive values than *L. leucocephala* (*e.g.* Austin *et al.*, 1995; Shelton, 1995; Norton *et al.*, 1995; Stewart and Dunsdon, in press). Initial analyses indicate that there is considerable variation in leaf quality traits, especially tannin content and digestibility, across species (Stewart and Dunsdon, in press). Although statistically significant variation in crude protein content has been detected, all species of *Leucaena* have high crude protein contents (range 19-26%) compared to grasses and crop residues (2-11%), woody legumes in general (average 16%) and general acceptable levels for maintenance of ruminants (9%) or lactation and growth (15%) (Norton, 1994; Norton *et al.*, 1995). Crude protein contents of all *Leucaena* species are high enough to be used as supplements. Very high crude protein levels are not beneficial for sole feeds, resulting simply in rapid breakdown and release as ammonia. Given these generally high levels of crude protein, nutritive value of *Leucaena* species is likely to depend more on other factors such as tannins, and fibre content which influence digestibility. Published data indicate that there is significant variation in condensed tannin content across species from very low (virtually zero) to high levels (Table 4) (Wheeler *et al.*, 1995; Stewart and Dunsdon, in press). In line with other species characteristics dramatic variation in tannin content, from zero to very high, was found among different provenances of *L. trichandra* (Stewart and Dunsdon, in press). However, there is no universal agreement over the significance of tannin levels in terms of nutritive value. In general tannins reduce digestibility because they form tannin-protein complexes which render protein unavailable in the rumen. However, for high protein feeds such as *Leucaena*, protection of some protein against microbial degradation in the rumen may provide bypass protein for absorption in the small intestine. While high tannin levels (>6%) are likely to adversely affect digestibility, moderate levels could be beneficial in terms of overall protein absorption. However there is no guarantee, nor evidence that bypass protein is absorbed. Conversely, while very low levels, or complete absence, of tannin should be generally beneficial, it is possible that excess protein is rapidly degraded in the rumen into ammonia which is released in the form of urea (Norton *et al.*, 1995; Wheeler *et al.*, 1995). At present little or nothing is known about the structure and activity of tannins from *Leucaena* species, except that tannins vary amongst species and that quality of tannins may be as important as quantity.

Variation in tannins is likely to explain in part the variation recorded in digestibility across species. Stewart and Dunsdon (in press) showed that 45% of the variation in *in vitro* digestibility was accounted for by variation in tannin content. Species with high *in vitro* digestibility, such as *L. shannonii, L. multicapitula* and *L. collinsii* subsp. *zacapana* tend to have low tannin content (Stewart and Dunsdon, in press). In this context it is again important to distinguish between *in vitro*/*in sacco* digestibility, which measure degradation in the rumen and would tend to be reduced by tannins, and *in vivo* digestibility which measures degradation in the whole animal, about which the influence of tannins is unknown. As stated by Stewart and Dunsdon (in press), tannins in *Leucaena* species should be treated with caution until evidence is available on their specific nutritional effects. However, simply taking *L. leucocephala* as a benchmark, species with high, but not highest *in vitro* digestibility and low, but not lowest, tannin content, are likely to provide excellent nutritive value in *Leucaena*.

Although there are several studies which indicate lower relative palatability of species such as *L. esculenta* and *L. diversifolia* compared to *L. leucocephala* (*e.g.* Bray 1987; Austin *et al.*, 1991; Stewart and Dunsdon, in press), preference tests provide little indication of potential palatability. For example, although *L. salvadorensis* was shunned by sheep in preference tests (Stewart and Dunsdon, in press), it is well known that naturally regenerated seedlings are avidly browsed in Honduras by cattle (Hellin and Hughes, 1993). Evidence suggests that most species are probably palatable (*e.g.* Otsyina and Masangi, 1995).

Much new work is currently underway to assess the nutritive value of lesser known species of *Leucaena*. Any attempt at a more detailed assessment here would thus be misleading and rapidly superseded by new data. It remains to be seen if any (and if so which) of the lesser known species or hybrids will be comparable in nutritive value to *L. leucocephala*. The consequences of using fodder with variable characteristics are likely to be more critical for intensive beef production systems than for smaller scale more diverse livestock systems, where diverse feed values could have potential benefits. Much remains to be done before the actual feed value of these lesser known species will be understood with the same confidence associated with use of *L. leucocephala*. What is clear is that, as with other characteristics, species of *Leucaena* vary greatly in leaf chemical composition, tannin content and digestibility.

Green manure. *Leucaena* leaves have also been used for green manure in cropping systems. The value of *Leucaena* leaf litter as a fertilizer is recognized by farmers in Central America who, in some areas, retain trees over crops specifically to maintain soil fertility (Chapter 4). Similarly, farmers in Indonesia and the Philippines have recognized the soil improvement properties of *Leucaena* used as a shade tree over cacao or tea (Dijkman, 1950). In parts of Indonesia, and the Philippines, *L. leucocephala* has been used for several decades to create hedgerow terraces for erosion control, but with widely recognized benefits in terms of soil fertility (Perera, 1980; 1983). More recently *Leucaena* was one of the first species to be successfully adapted to formal alley cropping (Kang *et al.* 1981; 1985). Alley cropping refers to cultivation of leguminous trees in hedgerows which are regularly lopped with the prunings used to mulch and fertilize crops grown in the alleys between the hedgerows. Several studies have demonstrated the beneficial effects of *Leucaena* leaves on crop yields (Gill and Patil, 1982; Torres, 1983; Kang *et al.*, 1984; Bashir *et al.*, 1986; Muriethi *et al.*, 1994). These studies showed that in some areas returning *Leucaena* mulch to a maize crop increases maize yield sufficiently to offset the reduction caused by the presence of the *Leucaena* hedgerows. In coastal Kenya Muriethi *et al.* (1994) showed that maize yields could be maintained at 85% of those receiving recommended fertilizer inputs while still using up to half of the *Leucaena* prunings for cattle fodder, assuming the animal manure is returned to the soil. Such studies show the potential to use *Leucaena* to increase overall agricultural productivity in integrated tree-crop-livestock combinations. However, success with *L. leucocephala* in alley cropping has not been universal and is likely to be very site specific (Robinson, 1986). Indeed it is now widely recognized that alley cropping has been less widely adopted than anticipated due to unforeseen biophysical, but particularly socio-economic constraints and the more limited situations where alley cropping may be successful are now better understood (Carter, 1995).

All this research has concentrated on *L. leucocephala*. Its leaves, even with moderate yields, contain more than enough nitrogen to sustain a maize crop (Budelman, 1989). They are finely divided with small leaflets and decompose quickly (with a 7-day N half-life) providing a very rapid, short term influx of nutrients related to a low C/N ratio (Weeraratna, 1982). Careful timing of pruning is needed to ensure that nutrients are made available at the right time for crop growth. It has been suggested that leaves of *L. leucocephala* may decompose too rapidly resulting in leaching of nutrients away from the rooting zone before being taken up by the crop (Robinson, 1986). This also means that they have limited value as mulch for weed control which is recognized as one of the additional benefits of alley cropping, particularly in the humid tropics. Leaf decomposition characteristics of other *Leucaena* species remain unknown. However, it is well established that leaves of other well known legume trees such as *Gliricidia sepium, Calliandra calothyrsus, Erythrina poepigiana* and *Inga edulis* vary greatly in their nutrient contents, the percentage of nutrients released and hence the quality of prunings (reviewed by Palm, 1995). Given the great variation in leaflet size within *Leucaena* (Figs 17 and 18), some variation in decomposition, release of nutrients and quality might be expected among species of *Leucaena*. However, no species of *Leucaena* has thicker leathery leaflets which characterize species of genera such as *Inga* which are well known for their value as mulch (Lawrence *et al.*, 1995). It seems likely that optimal nutrient input/mulch regimes in alley farming will depend either on mixed green manure inputs based on several species with differing decomposition properties, and/or on more detailed investigation that allows closer matching of nutrient release profiles to crop demand through species selection (Palm, 1995).

The beneficial characteristics of *L. leucocephala* for use in bio-engineering to protect hill slopes and embankments from erosion were reviewed by Clark and Hellin (1996), but once again, there are no comparative data for other species of *Leucaena*.

3.8 Growth rates

High yield has been a major factor prompting the promotion and adoption of *L. leucocephala* following the discovery and distribution of the giant arborescent varieties, now assigned to subsp. *glabrata* (National Academy of Sciences, 1984; Brewbaker, 1987b). The '*Giant*' varieties have universally out yielded the pantropically naturalized '*Common*' shrubby varieties belonging to subsp. *leucocephala* by 20-100% in leaf production and up to 2.5 times in wood production (*e.g.* Bray *et al.*, 1988; Brewbaker *et al.*, 1972; Brewbaker, 1980; Chadrasekaran, 1982; Gray, 1967; Hu *et al.*, 1980; Hutton and Bonner, 1960; Hutton and Gray, 1959; Ramirez, 1987). Despite field testing of large numbers of accessions of *L. leucocephala* subsp. *glabrata*, very little variation in yield has been detected, beyond the higher psyllid tolerance, and hence higher yield, shown by K636 (*e.g.* Wheeler *et al.*, 1987).

On favourable sites (see above) *L. leucocephala* subsp. *glabrata* can indeed produce exceptionally high fresh leaf yields in the range 40-80 tonnes ha^{-1} yr^{-1} when moisture is not limiting, and 20-50 tonnes in seasonally dry or subtropical climates (Brewbaker, 1987b) comparable to other high yielding shrubby tropical legumes and the best herbaceous legumes. Height growth and wood yields from *L. leucocephala* over short (3-5yr) rotations also compare favourably with other species ranging from 3 to 4m height yr^{-1} and 10 to $60m^3$ ha^{-1} yr^{-1} (Brewbaker, 1987b; Dutt, 1981; Van Den Beldt and Brewbaker, 1983; 1985). On less favourable sites, as in cooler tropical highland areas or on acid soils (see above), or under high psyllid pressure, yields have often been disappointing, and under such conditions *L. leucocephala* is generally outperformed by other genera, or potentially other species or hybrids of *Leucaena*.

Little is known about growth rates of most species of *Leucaena*. Until recently field testing of lesser known species has been patchy, often based on small unreplicated plots or arboretum entries on a limited range of sites and including a small subset of species and provenances. Many early trials indicated that *L. leucocephala* out yielded most other species (*e.g.* Brewbaker *et al.*, 1972; Foroughbakhch and Hauad, 1990; Gupta *et al.*, 1986; Raina, 1984). However, even in some of these early pre-psyllid trials a number of species of *Leucaena* outperformed *L. leucocephala* on certain site types. The superior performance of *L. diversifolia* over *L. leucocephala* under cool tropical highland conditions (Brewbaker *et al.* , 1988; Khajuria and Singh, 1991; Maasdorp, 1992) is one example (see above). The spread of the psyllid means that the yield advantage of *L. leucocephala* over other species has been diminished relative to more psyllid-resistant species such as *L. pallida* and *L. diversifolia* (*e.g.* Glover, 1988; Otsyina and Msangi, 1995).

Within the last eight years a network of new field trials, based on the OFI seed collections, has been established (Appendix 3). These trials include a much wider range of species and provenances alongside the well known varieties of *L. leucocephala* and a selection of promising hybrids such as KX2 and KX3 (Table 12 in Chapter 9). Three foundation trials include the complete OFI collection and a wide range of other seed sources (Appendix 3). Results from most of these trials are preliminary, based on early assessments, and synthesis of results across sites is incomplete. Nevertheless, a number of preliminary conclusions are apparent:

- *L. retusa* and *L. greggii* are consistently slow growing under a wide range of site conditions (Glumac *et al.*, 1987; Gupta *et al.*, 1986; Foroughbakhch and Hauad, 1990; Stewart *et al.*, 1991, 1993; Víquez, 1995).

- the high forage yield potential of *L. pallida* and its hybrid with *L. leucocephala*, KX2, has been demonstrated and repeated in numerous recent trials (Castillo and Shelton, 1994; Austin *et al.*, 1995; 1997; Brewbaker and Sun, 1996; Shelton and Brewbaker, 1994; Sorensson, 1995; Sorensson and Brewbaker, 1986).

- A number of species have out yielded the well known giant varieties of *L. leucocephala* and the KX1, KX2 and KX3 hybrids in both wood or leaf biomass production on some sites. For example in the prototype trial established by CONSEFORH in Honduras in 1989 *L. collinsii*, *L. lanceolata, L. macrophylla* subsp. *istmensis* and *L. salvadorensis* were the highest wood biomass producers (Stewart *et al.*, 1991; 1993). Similar results were obtained by Víquez (1995) and Argel and Perez (1997) in trials in Costa Rica. Mullen *et al.* (1996) found that *L. esculenta, L. pallida* and *L. trichandra* (OFI provenance 53/88, see below) out yielded the psyllid-tolerant accession, K636, of *L. leucocephala* subsp. *glabrata*. Thus it cannot be assumed that the widely known varieties of *L. leucocephala* and hybrids will outperform other species, even in areas, such as Honduras, where psyllid pressure is not significant.

- Within the highly variable *L. trichandra* (Section 6.4), material from south east Guatemala (*e.g.* accessions such as CSIRO CPI46568, OFI 53/88, and University of Hawaii K919) has proved highly productive in a number of trials in Honduras (Stewart *et al.*, 1991, 1993), Australia (Bray, 1982; Mullen *et al.*, 1996), Hawaii (Austin *et al.*, 1995) and Tanzania (Otsyina and Msangi, 1995).

Once again many new data are currently being gathered and a clearer picture of yield variation will become available in the near future.

3.9 Weediness

The benefits to be gained from introduction of *Leucaena* to new areas are widely documented (Pound and Martínez-Cairo, 1983; National Academy of Sciences, 1984; Brewbaker, 1987b) and have been outlined above. It is well established that as natural habitats become progressively more fragmented and degraded, weeds, and particularly weedy agroforestry trees are in increasing demand to create robust utilitarian agroecosystems - the *"brave new ecosystems"* referred to by Cronk (1995) - to meet the needs of human populations (Hughes, 1988b; 1994; 1995). Many of the attributes which confer success in such agroecosystems are by definition also characteristics of weeds. It is therefore not surprising that as well as benefits, introduction of successful agroforestry trees, such as *L. leucocephala*, can also cause problems of weediness. Furthermore, the '*circa situm* conservation' (Chapter 8) benefits derived from greater use of local tree diversity to create and maintain agroecosystems may be lost through over-reliance on introduced species such as *L. leucocephala*. **Introductions should only be considered if no native species is suitable for the purpose for which the introduction is being made.** In this section, the status of *L. leucocephala* as a weed is reviewed and the risks associated with introduction of other species of *Leucaena* are assessed by taking *L. leucocephala* as a benchmark for comparison. Protocols for species introductions which incorporate a weed risk assessment are recommended and other measures which may reduce risks, such as use of seed predators as biocontrol agents, or development of sterile hybrids, are discussed.

***L. leucocephala*.** An invasive plant may be defined as 'an alien plant spreading naturally (without direct assistance of humans) in natural and semi-natural habitats, to produce a significant change in terms of composition, structure and ecosystem processes' (Cronk and Fuller, 1995). *L. leucocephala* subsp. *leucocephala*, the shrubby 'Common type' (see above) is a well known invasive (Fig 8D). It is spreading naturally and has been reported as a weed in more than 20 countries scattered across all continents except Europe and Antarctica *e.g.* in Africa in Tanzania (Sheil, 1994), Cameroon (Duguma, 1995), and South Africa (Henderson, 1989; Wells *et al.*, 1989; Neser, 1994); in S.E. Asia in the Philippines (Merrill, 1912), Java, Indonesia (Macdonald and Frame, 1988), Papua New Guinea (Verdcourt, 1979) and Malaysia (Corner, 1938); several Pacific islands including Guam (Debell and Whiteswell, 1993), Vanuatu (Cock, 1984), New Britain and Tonga (Verdcourt, 1979) and Hawaii, U.S.A. (Smith, 1985; 1989); on several Indian Ocean islands including Reunion, Mauritius and Rodrigues (Polhill, 1990); Australia (Lambert, 1996; Jones and Jones, 1996), the island of Fernando de Noronha off the coast of Brazil (Felfili and Da Silva, 1990), several islands of the Caribbean such as Haiti (Timyan, 1996) and Puerto Rico (Little and Wadsworth, 1964), in southern Florida (Gordon and Thomas, 1997), and Texas ('semi-weedy' in urban areas, Isely, 1970; 1973), in the Bahamas, and in the Yucatán Peninsula of Mexico where it is only doubtfully native (McClay, 1989; Hughes, in press; Section 11.10).

L. leucocephala subsp. *leucocephala* is a weed of open (often coastal) habitats, semi-natural, disturbed, degraded habitats, other ruderal sites (*e.g.* roadsides, abandoned fields and waste ground) and occasionally of agricultural land where it has been planted as a shade tree over cacao. In their system of invasive categories Cronk and Fuller (1995) assigned *L. leucocephala* to their category - '*a serious or widespread weed invading semi-natural or natural habitats which are of some conservation interest*'. In Florida it is classified as a Category II weed, defined as a species which has a local distribution but either rapidly expanding populations, or known potential to invade and disrupt native vegetation elsewhere (Gordon and Thomas, 1997). In this sense it is not one of the world's worst weeds and it is not known to invade undisturbed closed forest habitats. For example, in Australia, although a known weed it is not a proclaimed noxious weed (Parsons and Cuthbertson, 1992). However, in many areas it has formed dense monospecific thickets, as in Hawaii where it is reported to be replacing native *Metrosideros-Diospyros* open forest and possibly threatening *Erythrina sanwichensis* in parts of its range (Fig 8D) (Cronk and Fuller, 1995). *L. leucocephala* is present on at least five of the islands of the Fernando de Noronha archipelago where it is also competing with native island endemics, in this case *Ficus noronhae* and *Oxalis noronha* (Felfili and da Silva, 1990). On the Acra plains in Ghana, a number of rare endemic species of critical conservation concern, including *Commiphera dalzielii* and *Hunteria ghanensis*, occur in areas now severely invaded by introduced trees including *Azadirachta indica* and *L. leucocephala* (Hawthorne[1], pers comm.) Dense monospecific stands, even if not of immediate conservation concern, can render extensive areas of disturbed ground unusable and inaccessible (Cock, 1984).

The weediness of *L. leucocephala* subsp. *leucocephala* has been attributed to its abundant, precocious (within first year), year round seed production (Gonzalez *et al.*, 1967), lack of pollinator specificity, its ability to resprout after cutting or burning, the build up of a persistent seed bank in the soil, its ability to form dense impenetrable thickets and its self compatibility which means that it can spread from seed produced from an isolated tree. Conversely, it is thornless, has no known allelopathic effects, is highly palatable, is not shade-tolerant, is non-climbing in habit and seed dispersal is largely by gravity with only limited movement of seed on the ground by insects and rodents (although Jones and Jones (1996) suggest that some seed may survive passage through cattle), a set of traits which limit its invasiveness.

It has been suggested that *L. leucocephala* subsp. *glabrata* is likely to be less weedy than subsp. *leucocephala* (Shelton, 1996). I can see no basis for this and under the Pheloung (1995) system (see below), both subspecies obtain identical scores except that subsp. *glabrata* has not been recorded as a weed elsewhere

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thereby reducing its score. Other systems (*e.g.* Reichard and Hamilton, 1997) suggest stricter scoring for species which are in the same genus as known weed species. Subspecies *glabrata* is generally somewhat less precocious and seedy than subsp. *leucocephala*. There is also some variation in seediness amongst accessions. However, even the less seedy varieties such as K636, still produce prodigious quantities of seed at an early age. Indeed Hutton and Gray (1959) showed that the Salvador type (subsp. *glabrata*) produced more pods and seeds per plant than the Hawaiian type (subsp. *leucocephala*). The fact that subsp. *glabrata* is not recorded as a weed yet, is quite possibly because it has only been widely introduced in the last three decades, whereas subsp. *leucocephala* has been spreading for more than 150 years. As early as 1912 *L. leucocephala* subsp. *leucocephala* was *"so thoroughly naturalized, common and widely distributed that the casual observer would consider it a native species"* in the Philippines (Merrill, 1912). As noted above, it is well known that 'invasion trajectories' (introduction - naturalization - facilitation - invasive spread - interaction with other biota - stabilisation) typically span 100 years or more (Cronk, 1995; Hobbs and Humphries, 1995; Scott and Panetta, 1993; Lodge, 1993). Subsp. *leucocephala* has had several centuries to become a weed. It seems likely that, given time, subsp. *glabrata* may also naturalize and become weedy.

Other species of *Leucaena*. Given the current interest in introduction of a wider spectrum of species or hybrids of *Leucaena* to new areas, some researchers are asking whether these species are likely to be more or less weedy than *L. leucocephala* subsp. *leucocephala* in order to judge the advisability of new introductions. Many authors have highlighted the difficulties of predicting the outcome of species introductions (Cronk, 1995; Cronk and Fuller, 1995; Hughes, 1994; 1995) and as Cronk (1995: 4) suggested it is likely that *"whatever we predict about the future of weeds, the reality is likely to surprise us"*. This is because of three main factors. Firstly, the long term perspective required to take account of possible changes in land use, production goals and management practices is difficult to achieve. Secondly, it is well known that there is often a lag of up to 100 years between first introduction and emergence of an invasive problem. Thirdly, spontaneous hybridization between introduced species and native species or other introduced species may give rise to new and potentially weedy hybrids.

The weed risk assessment procedure devised and tested by Pheloung (1995) to regulate plant imports to Australia, and subsequently modified for use in New Zealand (Williams, 1996), is one of several systems developed recently (for others see Reichard and Hamilton, 1997; Tucker and Richardson, 1995). Such systems provide one way to compare the potential weediness of different species of *Leucaena*. Under the Australian system, plants are scored according to a set of 49 criteria including evidence of weediness elsewhere and biological attributes of the plant. Scores were calibrated using 370 known Australian introductions as the basis for assigning one of three categories - *reject, evaluate further* or *accept* (Pheloung, 1995). *L. leucocephala* subsp. *leucocephala* scored between 2 and 5 (Pheloung, 1995; Williams, 1996) (although I obtained a slightly higher score of 7) points, scores which fall within the *evaluate further* category. This means that should *L. leucocephala* be proposed for introduction to Australia today, further evaluation would be demanded prior to introduction under new quarantine procedures. Evaluation could consist of repeating the weed risk assessment with updated and more complete information, undertaking an environmental impact assessment and a cost-benefit analysis to justify the risk, and/or ensuring post-entry evaluation in the form of field studies supervised by an expert panel to examine more directly the weed potential and verify its potential benefits. Taking *L. leucocephala* as a benchmark for comparison, I have assessed other species of *Leucaena* under the same system.

One other species, *L. diversifolia*, also appears to have all the invasive traits of *L. leucocephala* and does not differ significantly in the weed risk assessment. It is also self compatible and seeds heavily at an early age. The remaining species of *Leucaena* differ from *L. leucocephala* and *L. diversifolia* in being self incompatible and somewhat less seedy and precocious although this is a matter of degree in that most are still relatively seedy from an early age (1-2 years). Only *L. cuspidata, L. greggii, L. matudae, L. retusa* and *L. salvadorensis* are known to be less precocious, seeding at 2-3 years of age. Further than this, four species, *L. lanceolata, L. pulverulenta, L. shannonii* and *L. trichodes* show marked weedy tendencies, spreading and colonizing ruderal sites such as roadsides and abandoned fields and forming dense thickets within their native ranges (Fig 8H) (*e.g.* Isely, 1970 for *L. pulverulenta* in Brownsville, Texas, U.S.A.). Given that known weediness elsewhere is a key factor in weed risk assessment (Pheloung, 1995), and probably the best predictor of weediness (Scott and Panetta, 1993), documentation of the weediness of these four species here (Chapter 11) will be important if they are proposed for new introductions elsewhere. Species are tentatively assigned to one of four weed risk categories taking *L. leucocephala* as a benchmark (Table 4): 0 = lower risk; 1 = significant risk; 2 = risk as for *L. leucocephala*; 3 = known weed.

Hybrids. As indicated above hybridization can pose new and unpredictable threats of weediness (reviewed by Abbott, 1992). This is very much the case for *Leucaena* with its high interspecific crossability and known frequency of spontaneous hybridization (Chapter 5). There are already several documented cases of spontaneous hybridization in *Leucaena* following introduction of species to new areas (Hughes and Harris, 1994, in press; Chapters 4 and 5). One of these hybrids between *L. leucocephala* and *L. diversifolia* has arisen spontaneously in Mexico, Guatemala, Jamaica, Dominican Republic, Papua New Guinea and the Philippines (Hughes and Harris, in press) following cultivation of the parents. This hybrid is self fertile, produces prodigious quantities of seed from an early age and shows weedy tendencies in secondary vegetation in Veracruz, Mexico (Fig 8E). It is potentially as weedy as *L. leucocephala*. This hybrid has also been created artificially and promoted, as KX3, by the University of Hawaii. Later generation segregants of this hybrid may be less seedy than the F_1 material that was initially distributed. As an increasing number of species are introduced and tested in field trials there will be many new opportunities for spontaneous hybrids, some of which may also pose threats of weediness (Chapter 5).

Protocols for introductions. It can be seen that, with five exceptions, **all species of *Leucaena* should be considered potentially weedy 'conflict species' and regarded with caution when considering introductions**. One species, *L. diversifolia*, and one hybrid, *L. leucocephala* × *L. diversifolia* (KX3), have clear potential to be as weedy, in time, as *L. leucocephala*. They are likely to invade open habitats and ruderal sites just like *L. leucocephala*. It is against this backdrop that potential importers must judge the advisability of new introductions. There is growing awareness of the environmental hazards posed by introduced species (Hughes, 1994; 1995). This has prompted calls for a more parsimonious approach to reduce ill considered and unnecessary introductions in general through more careful prior assessment of likely benefits and risks. **For most species of *Leucaena*, it seems possible that risk assessment will result in an *evaluate further* categorization**. Under new regulations in New Zealand and Australia this would indicate the need for more detailed cost-benefit analysis and post-entry evaluation. In future the onus will be on plant importers to demonstrate that proposed introductions of *Leucaena* species are safe, or if judged to carry environmental risks, that the economic benefits outweigh the risks. Detailed protocols for new species introductions are provided by Pheloung (1995) and Hughes (1995).

Trials. Introductions are normally made initially into small scale experimental field trials. It is often assumed that trials leave open the option of eradication if post-entry evaluation indicates cause for concern (IUCN, 1987; Cronk and Fuller, 1995). However, such trials, which are normal practice in forestry and agroforestry introduction programmes, will provide only limited information on invasive tendencies. Furthermore, to be effective in controlling invasives, trials would need to be heavily protected, isolated and closely monitored for several years and in some cases decades; these conditions are rarely met in practice. Trial assessments rarely look at reproductive ecology or seed dispersal and regeneration; there are many cases where a few trees surplus to trial requirements are distributed to farmers; often on-farm testing of species is recommended; often trials remain in a neglected state long after assessment is complete providing a long term source of possible invasives (Sheil, 1994); for *Leucaena* species with their abundant and precocious production of hard coated seed, most trials will leave behind a soil seed bank that may persist for many years; seedlings can emerge at least up to seven (and probably more) years after seeding (Jones and Jones, 1996); often seed is collected from trials by experimental station workers or visitors to plant in other areas or back in their gardens and farms. In Honduras putative hybrids derived in this way from a species trial have been observed growing on the farm of a station worker 30km distant. Thus, although trials provide some scope for monitoring and control, and should be pursued with improved monitoring procedures, it is a fallacy that movement of introduced species can be reliably controlled at the stage of initial field testing of new *Leucaena* species following current practice. Once established *Leucaena* may be hard to control or eradicate (Evenson, 1982; Sorensson, 1992b). Trees have the ability to resprout after fire or other damage. Although *Leucaena* species have highly palatable leaves, trees may be remarkably persistent even when repeatedly grazed close to the ground and are thus hard to control or eradicate through grazing management.

Bruchid seed predators. Introduction of host-specific seed destroying insects has been used successfully to limit the spread of a number of economically important invasive legume trees in South Africa, reducing the fear that they will become unmanageably weedy and making their continued planting and use acceptable (Neser and Kluge, 1986). By reducing seed production below a critical level, populations should eventually decline reducing the 'aggressiveness' of introduced species. Effective seed predation of *Acacia melanoxylon* (Neser, 1996) and *Prosopis* species (Zimmermann, 1991), two economically important alien invasives in South Africa, has been achieved by introducing host-specific bruchid beetles. A similar approach has been proposed for *L. leucocephala* in South Africa (Neser, 1994; 1996; Tribe, 1995). A *Leucaena* seed feeding bruchid beetle *Acanthoscelides macrophthalmus* (Fig 8G), was deliberately introduced to South Africa in 1989 for specificity studies and in 1996 the South African Plant Protection Research Institute applied for permission to release it. The accidental introduction of *A. macrophthalmus* to Queensland, Australia in 1996 (Jones, 1996), is viewed overall as a positive influence to restrict further spread of *Leucaena* there (Jones and Jones, 1996). Introduction of seed feeding bruchids might thus make wide scale use of *Leucaena* more generally acceptable, although the effectiveness of *A. macrophthalmus* in reducing seed production remains to be assessed. In their native ranges in Mexico and Central America, *Leucaena* seeds are predated by seven species of bruchid in two genera, *Stator* and *Acanthoscelides* (Section 7.3). While the two species of *Stator* are known omnivores that feed on a wide range of Mimosoid legume genera, the five species of *Acanthoscelides* feed exclusively on *Leucaena* and have not been recorded on any other host plant genus (Hughes and Johnson, 1996). Although different species of *Acanthoscelides* feed on different numbers of host plant species in their native range, host records cannot be taken to indicate specificity elsewhere. However, *A. macrophthalmus* is known to feed on seeds of 18 different species of *Leucaena* and may thus provide some insurance against possible weediness of species other than *L. leucocephala* in the future where it has been introduced in Australia and South Africa. The disadvantages of introducing seed destroying bruchids for *Leucaena* seed producers are obvious. However, Neser (1994; 1996) proposed that pods in seed orchards can be readily protected from bruchids by insecticide treatment (as pursued for *Acacia mearnsii* in South Africa) or, for smaller quantities, by protecting individual branches with sleeves until harvested. It has also been suggested that greater control over seed production might encourage use of improved genetic material.

Sterile varieties and hybrids. Another possible avenue to avoid weediness is through genetic selection for low seediness and ultimately through use of sterile hybrids. This is discussed in detail in Sections 5.7 and 9.4.

Table 4 Summary of species characteristics

Species	Max Tree Size ht(m)	dbh(cm)	Altitude (m) (native range)[1]	Cold Rating[2]	Rainfall range (mm)[3]	Drought Rating[4]	Psyllid resistance Damage score	category[5]	Weed risk[6]	Wood density[7] g cm^{-3}	Heartwood %[7]	Crude protein[8] % leaf dry matter	Condensed tannin[8]	*In vitro* dry matter digestibility[8] %
L. collinsii subsp. *collinsii*	5-15	20-40	450-800 (-1210)	0	800-1100	2	1-2	HR	1	0.75	45	21.1	0	55
L. collinsii subsp. *zacapana*	6-15	20-40	110-600 (-900)	0	600-900	3	2-4	MR-MS	1	0.91	48	21.3	9	64
L. confertiflora var. *confertiflora*	3-5	10-20	(1500-) 1750-2430	2	?500-1000	2-3	?1-3	HR	1	?	?	?	?	?
L. confertiflora var. *adenotheloidea*	3-5	10-20	2000-2550	2	?500-1000	2	1-3	HR	1	?	?	?	?	?
L. cuspidata	3-6	10-20	1600-2200 (-2400)	?2-3	400-1500	?1-2	?2	MR-HR	0	?	?	?	?	?
L. diversifolia	8-20	15-40	30-1500 (-1740)	1	1200-3500	0	2-5	MR	2	0.68	36	23.2	171	32
L. esculenta	12-20	30-60	(400-) 600-1800 (-2080)	2	800-1500	1	1-2	HR	1	0.7	0	18.9	323	37
L. greggii	3-7	10-20	500-1500	3	300-500	2-3	1-2	HR	0	0.71	?	19.2	144	33
L. involucrata	3-7	10-20	400-1500	?2-3	500-700	2-3	?4-5	MS	1	?	?	?	?	?
L. lanceolata var. *lanceolata*	4-10	10-20	0-700 (-1100)	0	800-1200	1	4-5	MS	1	0.72	33	21.8	139	48
L. lanceolata var. *sousae*	5-15	10-25	0-400	0	900-1500	1	3-4	MR	1	0.75	38	21.4	88	49
L. lempirana	8-18	20-40	150-500	0	1000-1500	1	5-6	HS	1	?	?	18.8	0	?
L. leucocephala subsp. *leucocephala*	3-8	10-20	0-250 (-500)	0	500-2000	1(-2)	5-9	HS	3	?	?	?	?	?
L. leucocephala subsp. *glabrata*	8-20	10-40	0-1000 (-2100)	0	650-3000	1(-2)	5-9	HS	2	0.64	19	23.8	181	47
L. leucocephala subsp. *ixtahuacana*	3-8	10-20	1350-2000	0	?750-1200	1(-2)	?4-5	MS	2	?	?	?	?	?
L. macrophylla subsp. *macrophylla*	4-12	10-25	(20-) 500-1900	1	750-1600	1	3-5	MS	1	0.69	21	22.4	118	40

Species	Max Tree Size ht(m)/dbh(cm)		Altitude (m) (native range)[1]	Cold Rating[2]	Rainfall range (mm)[3]	Drought Rating[4]	Psyllid resistance Damage score/category[5]		Weed risk[6]	Wood density[7] g cm^{-3}	Heartwood %[7]	Crude protein[8] % leaf dry matter	Condensed tannin[8]	*In vitro* dry matter digestibility[8] %
L. macrophylla subsp. *istmensis*	5-18	10-35	0-400 (-1500)	0	800-1200	1	3-5	MS	1	0.64	39	23.1	103	43
L. magnifica	10-20	20-50	600-950	0	800-1000	1-2	4-5	MS	1	0.83	37	21.2	0	52
L. matudae	6-10	15-30	500-860	0	500-750	3	1-2	HR	0	0.58	0	17.3	300	40
L. multicapitula	15-25	25-60	100-200 (-400)	0	1000-2500	0	5-7	HS	1	0.56	40	25.8	62	42
L. pallida	4-20	10-45	(850-) 1300-2200 (-2480)	2	500-1000	1-2	1-5	HR-MR	1	0.67	0	?	?	?
L. pueblana	3-15	5-25	580-2000	0-1	400-750	3	1-2	HR	1	?	?	?	?	?
L. pulverulenta	5-15	10-25	0-1400 (-1850)	2	600-1200	1-2	4-7	MS-HS	1	0.65	50	18.8	237	28
L. retusa	3-5	5-15	400-1900	3	400-800	2	1-2	HR	0	0.73	?	19.7	298	54
L. salvadorensis	10-22	20-70	(150-) 300-800 (-1080)	0	800-2000	2	3-5	MS	0	0.81	56	20.5	40	50
L. shannonii	4-10	10-35	(5-) 400-1000 (-1450)	0	800-1400	1-2	3-5	MS	1	0.86	50	24.7	54	59
L. trichandra	3-20	5-40	(200-) 700-2000 (-2500)	1	1100-2000	0-1	1-6	HR-MS	1	0.7	45	18.6	208 (range 0-495)	30
L. trichodes	8-15	20-35	0-1500 (-2300)	0	500-1200	1-2	3-5	MS	1	0.63	40	22.8	18	46

[1] Based on herbarium specimen records - range and extremes (outliers) based on frequency distribution of specimens
[2] 0 = tropical, no cold or frost tolerance; 1 = cool tolerance, tropical highland but no frost tolerance; 2 = slight frost tolerance, withstands occasional light frosts; 3 = frost tolerant, withstands regular moderate frosts down to -15°C
[3] Estimated from seed collection site data
[4] Drought tolerance categories based on mean annual rainfall and length of dry season within native range: 0 = intolerant; 1 = 1000-1500mm with 3-4 month dry season; 2 = 750-1000mm with 4-6 month dry season; 3 = 500-750mm with 6-7 month dry season
[5] Range in psyllid damage score: 1 = no damage - 9 = blackened stems with total leaf loss (Wheeler, 1988) and psyllid resistance category following Mullen *et al.* (1996; 1997): HR = highly resistant; MR = moderately resistant; MS = moderately susceptible; HS = highly susceptible
[6] Weediness risk: 0 = lower risk; 1 = significant risk; 2 = risk as for *L. leucocephala*; 3 = known weed (*L. leucocephala* subsp. *leucocephala*).
[7] Wood density and heartwood data means of one-several accessions at 5 years derived from Gourlay *et al.* (in press); wood density of *L. greggii* and *L. retusa* at two years from Stewart *et al.* (1993)
[8] Leaf quality data are from Stewart and Dunsdon (in press), averages of one-several accessions; condensed tannin measurements are max absorbance (optical density) at 540-560 mm per g dry matter

4 Ethnobotany and Indigenous Domestication

4.1 Sources of ethnobotanical data

Ethnobotany is the study of plant-human interactions and dependencies (Bye, 1993; Martin, 1995). It involves study of the biological, ecological and cultural bases of plant-human interactions over evolutionary time and socio-economic space. The rich cultural diversity and floristic wealth of Mexico and Central America has led to highly diverse and intricate plant-human interactions (Bye, 1993). There are three main categories of ethnobotanical data that provide evidence about the extent and importance of the food use of *Leucaena*:

- Present day use of unripe pods and seeds of species provides the most comprehensive, detailed and directly observable source of ethnobotanical data.

- Vernacular names and indigenous classification systems (folk taxonomies) provide a wealth of additional data on species characteristics and uses, and insights into the cultural significance and perception of *Leucaena* species.

- Archaeological and historical evidence provide data on prehistorical and historical use and importance of *Leucaena* as a food.

Within Mexico, and parts of Guatemala, use of *Leucaena* has concentrated not on the familiar leaf and wood products (Chapter 3), but on the unripe pods and seeds (Figs 22 and 9B-E), and to a lesser extent flower buds and galls, which are used as minor food plants for human consumption. Throughout south central Mexico and north west Guatemala unripe pods are harvested, shelled and the seeds either dried or eaten raw, cooked, or added fresh to cooked food. Unripe pods are a common sight in markets in this region. The Spanish name for *Leucaena* is *guaje*, derived from the indigenous nahua name *Huaxín*. '*Guaje*' may be used simply as a name, but '*guajes*' may also be used to refer to 'pods' or 'trees' of *Leucaena*; a '*guajal*' is an 'orchard' of *Leucaena* trees.

The use of the unripe seeds of species of *Leucaena* for food was noted in the earliest sixteenth century ethnobotanical documents of the Spanish conquest of Mexico (reviewed by Zárate, 1997) and by early botanical expeditions to the region (*e.g.* Sessé and Mociño, 1792, published 1894), and has been subsequently documented on numerous occasions (*e.g.* Standley, 1922; Whitaker and Cutler, 1966; Smith, 1967; Zárate, 1984a; 1984b; 1987a; 1994; 1997; McVaugh, 1987; Ramírez, 1991; Casas, 1992; Casas *et al.*, 1994; Casas and Caballero, 1996). However, more detailed published data on the use, classification and indigenous domestication of *Leucaena* species in Mexico are limited to three studies: La Montaña, Alcozauca, Guerrero (Casas, 1992; Casas *et al.*, 1994; Casas and Caballero, 1996), San Pedro Chapulco, Puebla (Zárate, 1984b) and the Tenejapa municipality of the Tzeltal region, Chiapas (Berlin *et al.*, 1974). These studies, in common with many ethnobotanical inventories, adopted a geographic focus, working in a limited area and within a single linguistic group. Here, I take a different approach to examine the ethnobotany of the genus *Leucaena* as a whole throughout its native distribution in Mexico and Central America. My aim is not to provide an exhaustive inventory or review, but rather an overview and assessment of published and new ethnobotanical data in the context of indigenous domestication and its probable influences on genetic resources.

Alongside published studies, new data on current use and marketing have been gathered and recorded during more than a dozen collection expeditions by the author to many parts of Mexico and Central America. Informal interviews with farmers, those harvesting and processing *Leucaena* pods and vendors in local and regional markets were conducted whenever the opportunity arose. Vernacular names were sought and recorded from local informants during all collection activities and were augmented by the large number of names recorded on herbarium labels. More systematic surveys were carried out in three villages where significant numbers of species occur together in cultivation: Santiago Acatepec, San Pedro Chapulco and Santa Catalina Oxolotepec, all in Puebla, central Mexico. Species identities, local names, uses, characteristics and preferences were recorded in detail in these villages. Formal quantitative surveys of the volume and value of the *guaje* trade in Mexico were not feasible given the time and resources available. Nor has it been possible to see and verify the identities of the plant remains retrieved from archaeological excavations of cave settlement sites except from published photographs (Smith, 1967: 241; 1986: 269); archaeological evidence cited here is derived solely from the published literature.

4.2 Present day use

Current practices of exploitation and management of *Leucaena* species in Mexico, because they can be observed and surveyed directly, provide the most detailed, informative and complete source of ethnobotanical data. Current use of partially domesticated taxa may also provide insights into past use and the likely progression of domestication. However, significant changes in the perception and use of food plants through time mean that the current picture may not be an accurate guide to the past. Transition from hunter-gathering to settled agriculture has undoubtedly resulted in a radical shift in diet and drastic changes in the importance of particular species (Bye, 1993). For example, acorns (*Quercus*), mesquite pods (*Prosopis*), nopales (*Opuntia*) and maguey (*Agave*) which were staple foods of hunter-gatherers in south central Mexico between 9,000 and 5,000 BC (MacNeish, 1967; Smith, 1967; Flannery, 1986), are now only minor components used to supplement new staples such as maize (*Zea mays*) and beans (*Phaseolus*). Seeds of *Leucaena* species, like other adventive, undomesticated or incipiently domesticated food plants (see below) might thus be expected to be less important now than in the past. Thus present day use, although highly informative, provides only a partial picture and must be assessed along with other evidence from indigenous classification systems and archaeology.

Seeds of 13 of the 22 species of *Leucaena* are used as food (Table 5). Food use is prevalent throughout south central Mexico and in the north west fringes of Guatemala, mainly in Huehuetenango (Fig 6) and is particularly common and intensive in the States of Chiapas, Oaxaca, Puebla, Guerrero and Morelos. Further north, seeds of a few species, and particularly *L. leucocephala*, are harvested and eaten sporadically.

Unripe pods of different species are harvested at different seasons (Table 5) by climbing trees and lopping the terminal branches or groups of pods, often crudely, with machetes, small knives or cutting poles (Fig 9A). Annual pollarding in this way apparently causes only limited damage to the trees which resprout and fruit annually. Unripe pods are often sold directly without further processing (Figs 9D and E). Alternatively the pods are shelled, sometimes where they are collected (Fig 9C) or back at home (Fig 9B) to remove the unripe green seeds which are then dried, stored and used for home consumption or transported, sometimes long distances, and sold in local and regional markets. Seeds may be eaten raw, are casually consumed during outdoor work and often added as a garnish to cooked food. Rural restaurants often provide *guajes* along with chile, salt and pepper. Alternatively seeds are cooked in stews or mixed with beans and maize tortillas. Milling of dried seeds to produce flour for making *guaje 'tortitas'* has been noted in parts of Guerrero by Casas (1992) and Casas and Caballero (1996). Although the seeds are by far the most important edible part, young leafy shoots, flower buds, open flower heads, and galls (*'polochoco'*; Casas, 1992) of *Leucaena* are also harvested and consumed raw or cooked on a small scale in some areas (Casas, 1992; Casas and Caballero, 1996).

Although there are no quantitative assessments of the volume of pods and seed harvested nor of the volume and value of the *guaje* trade, it is clear that large quantities are collected and marketed. I observed a store containing more than 150 'quintal' (=100kg) sacks of dried seeds of *L. esculenta* in Teloloapan, Guerrero in 1987, and individual farmers report harvesting several 100 kg of seed per year around San Martín Pachívia, Guerrero. Flannery (1986) measured the potential production of *guajes*, in this case *L. pallida*, from dry thorn scrub forest around Mitla, Oaxaca and found 1.4 trees/100m^2 which yielded an average of 19,910 pods/ha/yr or 24.9 edible kg/ha/yr of seeds.

As pointed out by Xolocotzi (1993: 734), the *"market is one of the most impressive survivals of ancient Mexico"* and market surveys are an informative source of ethnobotanical data on *Leucaena* pod and seed consumption. *Leucaena* pods are sold in markets throughout south central Mexico and in all markets in inland regions of Oaxaca, Puebla and Guerrero (Figs 9D-E). Pods of different species are sold at different times of year according to production season, and often more than one species may be sold at the same season. In large markets such as Oaxaca or Tehuacan, pods of *L. leucocephala* are available throughout the year.

In Central America, food use is virtually unknown except close to the Mexican border in Guatemala. Hence the species restricted to Central America (*L. lempirana, L. magnifica, L. multicapitula, L. salvadorensis* and *L. shannonii*) have no recorded use as food. Nevertheless, most of the Central American species are highly valued for their wood products including fence posts, house corner posts, and firewood, and trees of several of these species are protected when land is cleared (Figs 8A and 10B) and may be cultivated on a limited scale. For example the wood of *L. salvadorensis* is preferred by farmers for house corner posts, fence posts and firewood over most other species (Colindres *et al.*, 1995), and certainly over the introduced *L. leucocephala*, in parts of southern Honduras. Natural regeneration of *L. salvadorensis* is protected in fields and mature trees managed by lopping and pollarding in traditional agroforestry systems (Hellin and Hughes, 1993). Similarly, in parts of northern Honduras *L. lempirana* is sometimes protected and managed in fields when most other tree species are cleared for pasture. Like *L. salvadorensis*, the wood of *L. collinsii* subsp. *zacapana* is dense and produces a high percentage of heartwood at an early age (Stewart *et al.*, 1993; Pottinger and Hughes, 1995; Gourlay *et al.*, in press), properties which again make it particularly valuable to farmers and local communities in south eastern Guatemala. Again in these areas it is common to find trees protected and managed in traditional agroforestry systems, either scattered in crop land or as short rotation coppice in bush-fallow. Finally, trees of the highly restricted and endangered *L. magnifica* (Chapter 8; Section 11.12) are also protected in fields, again as a source of high quality wood products, but in this case also for soil improvement. Farmers in parts of Chiquimula, Guatemala (*e.g.* around Quetzaltepeque, Yerbabuena and El Rincón) apparently maintain trees of *L. magnifica* in their fields specifically to enrich their soil, claiming that the leaf fall from trees is a rich fertilizer. Thus, even in Central America, where

Table 5 **Present day use of *Leucaena* species as food plants**

Species and principal vernacular names	Production season	Harvesting	Marketing	Cultivation and management	Wider translocation
L. collinsii guash, chalíp	December - March	Throughout the central depression of Chiapas	Local and transported to neighbouring highland market towns *e.g.* San Cristobal de las Casas and Tenejapa, Chiapas; Todos Santos Cuchumatanes, Huehuetenango, Guatemala	Cultivated in backyards and informal *guajales* throughout central depression of Chiapas	Limited
L. confertiflora guaje Zacatzín, guaje de cerro	July-August	Locally intensive	Limited to local markets *e.g.* Tehuacan from San Pedro Chapulco	Cultivated in small *guajales* in a few villages *e.g.* San Pedro Chapulco and Santa Catalina Oxolotepec, Puebla	Limited to villages adjacent to natural populations *e.g.* San Pedro Chapulco and Santa Catalina Oxolotepec, Puebla
L. cuspidata efé, efé de Cerro	(August-) September - October	Locally intensive	Limited to local markets *e.g.* Ixmiquilapan, and Zimipan, Hidalgo from Cardonal and Tolantongo	Very occasionally in backyards *e.g.* Cardonal and Jacala, Hidalgo	Very limited
L. diversifolia guaje chiquito	November - February	Local and sporadic	Very limited and local	Sporadically but mainly as coffee shade in Veracruz and Chiapas	Limited, possibly introduced for coffee shade
L. esculenta guaje rojo, guaje colorado	(December-) January - February (-March)	Very widespread and intensive	Marketed almost throughout Mexico. In all local and regional markets throughout south central Mexico and in Mexico City	Very widely in backyards, fields and *guajales* throughout south central Mexico and sporadically elsewhere	Very widely, natural range now obscured due to wide cultivation (Section 11.5)
L. lanceolata guajillo	November - January	Local and sporadic	Not known, possibly local	Rarely and locally *e.g.* San Mateo del Mar by the Huave indians (Zizumba and Colunga, 1982)	Not recorded
L. leucocephala Guaje verde, guaje de castilla	Year-round, soil moisture permitting	Widespread and intensive	Widespread throughout Mexico and often transported long distances *e.g.* from Tehuantepec to Oaxaca and Mexico City	Very widely throughout Mexico in backyards and *guajales*, except where frost prohibits growth	Very widely, natural populations unknown
L. macrophylla guaje amarillo, guaje de caballo	December - March	Local and sporadic	Limited and largely local	Limited	Very limited
L. matudae guaje brujo	(September-) October - December	Locally intensive around Mezcala, Guerrero	Not known	Not recorded	Not recorded
L. pallida guaje colorado, guaje delgado	(June-) July -October - (-November)	Widespread and often intensive	Widespread in local and regional markets throughout Oaxaca and Puebla	Widely in Oaxaca and Puebla in backyards, *guajales* and on terrace boundaries	Probably widely distributed; natural range obscured by cultivation

Species and principal vernacular names	Production season	Harvesting	Marketing	Cultivation and management	Wider translocation
L. pueblana guaje	November - December	Local and sporadic	Not recorded	Not recorded	Not recorded
L. pulverulenta guajillo	(June-) July - September	Local and sporadic	Limited and largely local	Limited and sporadic	Uncertain but probably moved to new areas
L. trichandra Sasíb (Tzeltal)	(October-) November - February	Local and sporadic	Local markets only	Limited, sporadic and local	Not recorded

food use is not known, local species of *Leucaena* are well known and often highly preferred by farmers and rural communities who protect and manage them in traditional agroforestry systems.

4.3 Indigenous management and cultivation

The intensity of use of *Leucaena* for food varies greatly from area to area and for different species (Table 5) from casual gathering of pods from nearby wild populations (Fig 9B) for home consumption, to intensive harvesting of commercial quantities, often accompanied by cultivation in informal orchards or '*guajales*', and storage and transportation of pods and seeds for sale in local and regional markets. This variation in intensity of use is not readily categorized, but rather represents a continuum of increasing human intervention. The informal categories discussed below are thus arbitrary and overlapping; species, such as *L. esculenta*, which are intensively cultivated may also be the focus of casual harvesting from natural populations in the same area (Casas and Caballero, 1996).

Harvesting from wild populations. At one extreme pods are gathered from natural populations close to settlements and consumed locally. For species such as *L. cuspidata* and *L. matudae* this represents the full extent of their use. Pods of these species are rarely marketed, and then only in nearby market towns. Although such harvesting of pods can be locally very intensive, these species have been subject to only minimal management or alteration. In a few areas, trees are protected, encouraged and retained after land is cleared, but are rarely cultivated and then as individual trees in backyards and gardens (*e.g. L. cuspidata* in Cardonal and near Jacala, Hidalgo).

Protection and local cultivation and management. Species such as *L. collinsii* and *L. confertiflora* are used more intensively. For example, *L. collinsii* is widely cultivated throughout the central depression of Chiapas, often in small informal orchards or *guajales* and pods are transported over a wide area for sale in regional market towns up to 100km distant (*e.g.* markets of San Cristobal de las Casas and Tenejapa in Chiapas and Todos Santos de los Cuchumatanes in the highlands of Huehuetenango, Guatemala). Cultivated trees are derived from local wild populations and longer distance translocation does not appear to have occurred. The cultivation and use of *L. confertiflora* was studied by Zárate (1984b) in San Pedro Chapulco, Puebla. He showed that it is cultivated in small *guajales* in certain villages such as Chapulco (Fig 9F) and Azumbilla. *L. confertiflora* is also cultivated in other villages, such as Santa Catalina Oxolotepec, in the same region. Trees were established in these villages from material derived from wild populations nearby (<5km distant); pods are marketed up to 20km away in Tehuacan. Although the trees are in cultivation, pods of these species continue to be harvested from nearby wild populations as well.

Intensive cultivation and management. Three species, *L. esculenta, L. leucocephala* and *L. pallida* are much more widely and intensively used. Pods and seeds of these species are harvested on a large (commercial) scale and marketed (Figs 9D and E) regionally and in cities several hundred kilometres distant from areas of production. All three species are widely and intensively cultivated in backyards and fields, often in more or less formal orchards or *guajales* (Figs. 9F and G, 10C and D), sometimes on high quality agricultural land and even on irrigated land in some areas *e.g.* the extensive *L. esculenta* and *L. leucocephala guajales* of the Tehuacan Valley (Fig 9G). In some areas these species are so abundant as to form the dominant tree component in many villages, towns and traditional agroforestry systems (Fig10 D). All three species have apparently been widely introduced to new areas in Mexico outside, and often distant from, natural populations.

L. esculenta, the *guaje rojo* or 'red-podded *Leucaena*' (Figs 9 and 22C), is perhaps the most widely used, best known and studied species in terms of food use. Most historical reports which describe food use refer to this species (Zárate, 1997). This intense use has generated the greatest diversity of processing, storage and cooking methods as well as management and cultivation systems of any species. Casas (1992) and Casas and Caballero (1996) studied the use, cultivation and management of *L. esculenta* (and other species) in La Montaña area, Alcozauca in north west Guerrero. They showed that in that area pods are harvested from remnant natural populations, highly modified semi-natural populations, where *guaje* trees have been actively protected following clearance of forest for agriculture, and from cultivated trees in backyards and formal *guajales*. Such systems of management form part of a *"diversified strategy of subsistence .... integrating different forms of plant manipulation"* (Casas and Caballero, 1996). This study mirrors the wider picture for *L. esculenta* which is extensively cultivated throughout south central Mexico. It is also clear from the occurrence of isolated, often solitary, cultivated trees scattered across Mexico in outlying areas (*e.g.* in Guaymas, Sonora; Lagunita, Hidalgo; Tuxtla Gutierrez, Chiapas; Fig 33), that *L. esculenta* has been and continues to be introduced into cultivation in new areas, often involving translocation over long distances (up to several 1000 km), driven by the continued interest in pod production in areas where it is currently not found. Single isolated individuals, introduced into cultivation often do not produce pods, presumably due self incompatibility (Sorensson, 1993).

The characteristics and distribution of *L. pallida*, *guaje colorado* or *guaje delgado*, the 'coloured or narrow-podded *Leucaena*' (Figs. 22D and 54) are very similar to those of *L. esculenta* and it is also widely used and cultivated, especially in Oaxaca, Puebla and parts of Guerrero, often on terrace boundaries (Fig 9F). As the vernacular name suggests, pods of *L. pallida* are also coloured (reddish purple), but are narrower with smaller seeds than *L. esculenta.* It complements *L. esculenta* in two ways. Firstly, it withstands light frost (Chapter 3) and can be grown at slightly higher elevations. Secondly, the season of production (July - November) precedes and complements that of *L. esculenta* (December - February).

Several characteristics of *L. leucocephala*, *guaje verde* or *guaje de castilla*, the 'green-podded *Leucaena*' (Figs. 9D and 22A), make it a particularly attractive species for production of edible seeds. Firstly, unlike other species, it fruits virtually throughout the year, where soil moisture permits (Gonzalez *et al.*, 1967), thereby overcoming the seasonality of other species. Secondly, it produces very large quantities of seed, partly because of its year round fruiting, but also because of its heavy pod and seed set. It is quite common to find 5-15 pods per flower head (in extreme cases there may be up to 45), each with 15-20 seeds. Heavy pod set has been attributed to known self compatibility (Brewbaker, 1983). This means that even isolated individual trees may produce heavy pod crops and may be sufficient to supply household requirements for *guajes*. Finally, the seeds of *L. leucocephala* are almost as large as those of *L. esculenta* and are preferred because they are 'sweeter' than those of most other species. These attributes mean that *L. leucocephala* is now the most widely cultivated species of *Leucaena* in Mexico (Fig 44). It is found throughout Mexico below 2000 m elevation and there are few villages or towns without at least a few trees. Spread of cultivation continues even today with the establishment of new *guajales* (*e.g.* 1.5 ha in Santiago Acatepec, Puebla in 1992). Attempts to establish *L. leucocephala* at or beyond its drought and cold tolerance limits (*e.g.* by watering trees in dry areas or using potted trees to protect from frost as in villages in southern Puebla), are evidence of the strong desire and drive to cultivate this species.

There is only limited evidence to suggest that the genetic composition of populations of *Leucaena* species has been modified following passive or active selection to any significant degree. The only published study which looked for variation caused by selection within species is that by Casas and Caballero (1996) who measured phenotypic variation in pod characteristics in wild, managed and cultivated populations of *L. esculenta* near Alcozauca, Guerrero. They found high awareness of, and well developed cognitive systems to describe, infraspecific variation in pod and seed characters amongst local people (see below), indicating a potential for selection. They also found that pods from trees in managed and cultivated populations were significantly larger, with more seeds per pod, than pods from trees in wild populations. This study suffered from lack of control over site parameters (cultivated trees are generally on better sites) which provide an equally probable explanation for the variation encountered. Proof of genetic modification would require analysis of genetic diversity using molecular markers and/or common garden field experiments. Further than this, there is no evidence from archaeological remains to indicate modification of pod or seed size through time (see below).

4.4 Vernacular names and classification

Understanding the traditional names and classification systems of *Leucaena* species is a basic step in elucidating their significance and cultural perception in societies which use and cultivate them for food. Full linguistic analysis of all the vernacular names and folk taxonomies of *Leucaena* is beyond the scope of this chapter. There are 120 indigenous languages in Mexico, 54 of which are currently used (Bye, 1993), and around half of which probably have names for *Leucaena* species. Documentation of cognitive systems for *Leucaena* is therefore a large and on-going task. Martínez (1979) records 42 common names for *Leucaena*; at least 150 different vernacular names for *Leucaena* species have been recorded somewhere (a list is available from the author). This is a large number, for a genus of only 22 species. This reflects firstly, the cultural and language diversity across the range of *Leucaena*; some of the many different names for the same species are simply translations from other languages. Secondly it reflects the significance and importance of *Leucaena* as perceived throughout the region. In this section, two published indigenous classifications are discussed as examples of the importance/prominence of *Leucaena* species and indigenous recognition and awareness of species diversity, and the derivations of names are examined to see what can be learned about local perceptions.

It is well established that, in general, the number of folk names within a genus increases as one moves along the cultural significance continuum of 'useless - significant - protected - cultivated' (Berlin *et al.*, 1974; Berlin, 1992; Bye, 1993). Plants which are highly important may be lexically highly differentiated. At the extreme, folk taxonomies of certain food and medicinal plant groups may be 'over-differentiated' with recognition of entities within species that are not recognized by formal botanical taxonomies. In addition to assessing the degree of sophistication of *Leucaena* folk taxonomies, vernacular names may be interpreted and assessed in terms of their derivations and meanings, again in the context of evidence for food use and cultivation of *Leucaena*.

Hierarchical systems which employ vernacular generic names for *Leucaena* and which are subdivided into mutually exclusive lexemes corresponding to species have been documented for several ethnic groups and languages in Mexico. The Spanish generic name *guaje*, derived from the nahua name *huaxín*, is now very widely used throughout Mexico and parts of Central America in parallel to names in local languages. The numerous equivalents of *guaje* in local languages include: *nduva* (mixteco), *huaxín* (nahua), *laa* (zapotec), *napajteam* (huave), *thúk* (huastec), *sasíb* or *shasíb* (tzeltal), *chalí* or *chalíp* (maya; Huehuetenango, Guatemala), *uaxín* or *uaxím* (maya; Yucatán, Mexico), *tze* (mazateco), *liliak* (totonaco) and *na sa* (hapaneco). *Guaje*, although most widely applied to species of *Leucaena*, is also sometimes applied to species of other legume genera such as *Acacia, Albizia, Calliandra, Desmanthus* and *Desmodium* (Berlin *et al.*, 1974; Casas 1992; Luckow, 1993). Unripe pods and seeds of several species of *Desmanthus* (*D. fruticosus, D. pumilus* var. *pumilus* and *D. virgatus*) are also used for food (Casas, 1992; Luckow, 1993).

Two species level classifications of *Leucaena* are presented in Figure 5. It is immediately apparent that these classifications are highly differentiated at species level. The tzeltal classification (Berlin *et al.*, 1974) shows that *Leucaena* is finely divided compared to the other genera placed within *sasíb* even though only one species (*L. trichandra*) is common in Tenejapa. The other two species of *Leucaena* are occasionally cultivated at lower elevations within the area but their pods are often imported from adjacent areas and sold in the markets of Tenejapa and San Cristobal de las Casas. In contrast to the well known food use of all three species of *Leucaena* in Tenejapa, no cultural utility is known for *Acacia angustissima*, nor any of the three species of *Calliandra* (*C. calothyrsus, C. grandiflora, C. houstoniana*). The differentiation of *Leucaena* is thus a fine division indicative of intimate use compared to the other genera, which are botanically distinct and easily recognized, but which are closely related in tzeltal thinking in that they share similar shrubby habit, finely divided leaves, ruderal habitats and ecology, attributes which may have been the basis for their grouping (Berlin *et al.*, 1974).

The mixtec classification of *Leucaena* from Alcozauca, Guerrero (Casas, 1992; Casas and Caballero, 1996) is even more finely divided. Not only are species of *Leucaena* recognized using mixtec names, but four, albeit not mutually exclusive, infraspecific categories are recognized within the widely cultivated and intensively used species, *L. esculenta*. Again these are fine divisions indicative of intensive use and management as observed by Casas (1992) and Casas and Caballero (1996).

Given the widespread use of *Leucaena* seeds and pods for food, it is not surprising that the majority of vernacular names for species of *Leucaena* are derived from pod characteristics including size, shape, colour and season of production (Fig 22). Pod colour is the commonest trait that is used by local people to distinguish and name species as *e.g. guaje colorado, rojo, verde, blanco, amarillo* (coloured, red, green, white, yellow). Pod size is the second most important trait determining species recognition and names: *e.g. guaje delgado* (= narrow podded); *guaje chiquito, guajillo, guajito, guachito, guashillo, frijolillo* are all diminutive terms that are used for species with small pods (*e.g. L. diversifolia, L. trichandra, L. macrophylla, L. pulverulenta* and *Desmanthus virgatus*); *paka sasíb* (= *bac'il sasíb* but with broader pods) (Berlin *et al.*, 1974); *guaje de ratón* (= '*Leucaena* of the mouse' again in reference to the very small pods of *Desmanthus fruticosus* and *D. pumilus* var. *pumilus*, Figs. 22G and H). Complete lack of pod production by sterile hybrids between *L. leucocephala* and *L. esculenta* is well known amongst local *guaje* growers and users, who refer to it as *guaje macho*, the 'male *Leucaena*' (Hughes and Harris, 1994). Because of the lack of pod production, trees of this hybrid, where they arise, are often rogued by ring barking or cutting. The mixtec categories used to describe infraspecific variants within *L. esculenta* (Casas and Caballero, 1996) (Fig 5), refer not only to pod size, but also to flavour. Another example is *guaje manso* (= gentle/meek/mild/tame) which refers to the mild flavour of the seeds of *L. leucocephala* in Veracruz.

In addition to pod characteristics, indigenous names also reflect a strong awareness of other species characteristics and often indicate a clear differentiation between wild and cultivated or introduced species. Examples include references to where species grow (*guaje del rio* for *L. diversifolia* which grows near rivers or *guaje de tierra caliente* for *L. leucocephala* in Hidalgo which grows at lower, warmer elevations than *L. cuspidata*). Awareness of season of production is also reflected in some vernacular names. For example *lya gusgih* (Zapoteca de Mitla) = *guaje de lluvias* = rainy season *guaje* (Zárate, 1994). References to cultivated/introduced status are also frequent indicating the importance and significance of cultivation in local perceptions. For example: *huash de castilla* (*guaje de castilla*) meaning literally 'Castilian' (Spanish) *Leucaena* implying introduction from the 'home country' = *L. leucocephala* in Chiapas where it is widely cultivated vs *huash* or *huash de monte* meaning 'wild (from the forest/scrub/wild country) *Leucaena*' = *L. collinsii* subsp. *collinsii*, the native *Leucaena* in this area. Similarly, *guaje de castilla* = *L. leucocephala* vs *guaje de indio* = Indian *Leucaena* = *L. lanceolata/L. macrophylla* in coastal Guerrero, or *guaje de cerro/guache de cerro, efé de cerro* = mountain or 'hill *Leucaena*' = *L. cuspidata* or *L. confertiflora* vs *guaje de huerta* = 'orchard *Leucaena*' *i.e.* cultivated = *L. leucocephala*, or occasionally *Leucaena* hybrids, which are cultivated in *guajales* in backyards and around villages in parts of Hidalgo or Puebla. Finally, Zárate (1997) refers to *L. leucocephala* as the 'domestic *guaje*' from the name *calloaxin* derived from the Nahuatl *calli*, meaning *house*.

4.5 Archaeological and historical evidence

Evidence of the origins and prehistory of plant use and domestication rests with archaeological studies. *Leucaena* remains, in the form of seeds and pod fragments, have been found during archaeological excavations of a number of prehistoric cave settlement sites in Mexico. These include the Diablo and Lerma caves in the Sierra de Tamaulipas, Tamaulipas (MacNeish, 1967), several caves (Coxcatlán, El Riego, Venta Salada, Palo Blanco and Purrón) in the Tehuacan Valley, Puebla (Smith, 1967) and the Guilá Naquitz cave near Mitla, Oaxaca (Flannery, 1986; Smith, 1986) (Fig 6). All these sites are rich in botanical remains which are well preserved and largely identifiable, providing chronologies of debris resulting from plant use. The five major caves of the Tehuacan Valley provide the longest and most complete and continuous chronologies, spanning a 9000 year period; in short, they provide an uninterrupted history of the use of plants from 7000 BC to 1540 AD, a period spanning the transition from a gathering economy reliant on wild food plants to an agricultural economy based on domesticated crops. *Leucaena* remains were found in all the Tehuacan Valley cave sites, the earliest dating from the El Riego Phase (6800 - 5000 BC) and increasing in abundance during the Santa Maria Phase (900 - 200 BC). Pod fragments were identified as *L. esculenta* (from 900 BC) and *L. pueblana* (Smith, 1967). Without more detailed study of the plant material in the light of current taxonomy and knowledge of the species now found in the area, it is not clear whether some remains are attributable to any of the other species of *Leucaena* now found in the Tehuacan Valley (*L. leucocephala* in the lower valley and *L. pallida* and *L. confertiflora* at higher elevations).

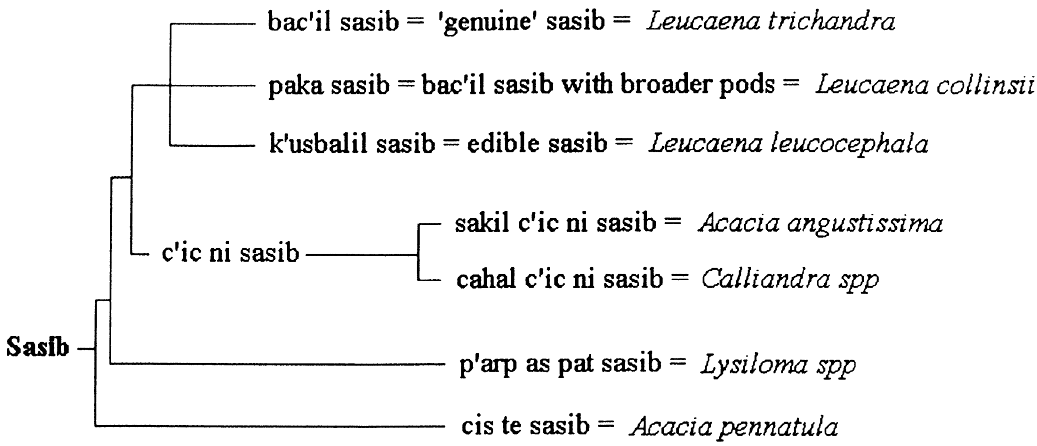
The marked increase in frequency of pods during the Santa Maria Phase (900 - 200 BC) has been interpreted as corresponding to the start of cultivation of *Leucaena* in the Tehuacan Valley (Smith, 1967). Given that *L. esculenta* and *L. leucocephala* are widely cultivated for pod production in traditional agroforestry systems in the Tehuacan Valley today (Fig 9G), this seems a reasonable hypothesis. Although *Leucaena* fragments were always present, they were never as abundant as staple foods, and seeds of *Leucaena* probably formed a small, but constant, element in the diet (Smith, 1967). *Leucaena* may be compared with other species which were used in similar ways, forming important dietary elements and which were simultaneously a wild food source and increasingly grown in cultivation. These include *mesquite* pods (*Prosopis laevigata*); *huizache* pods (*Acacia farnesiana* and *A. sericea*); *nopales* (pads) and *tuna* (fruits) (*Opuntia spp.*); *maguey* (food and fibre) (*Agave spp.*), amongst many others (Smith, 1967).

The Guilá Naquitz cave, near Mitla, Oaxaca, was a much smaller, seasonally occupied 'micro-band', or family settlement, with a short but informative chronology from 8750 - 6670 BC (Flannery, 1986). *Leucaena* pod fragments were found in all time zones of the excavation with between 5 and 247 pods in any one zone (Smith, 1986). These pods appear to be of *L. pallida*, but identification remains to be confirmed. Flannery (1986) attempted a crude assessment of the relative importance of different foods in the archaic forager diet based on the relative proportions of plant remains found in the Guilá Naquitz cave and on the relative abundance of plant species in the neighbouring natural vegetation. He concluded that *Leucaena* seeds were a regularly used, but never abundant food source, with hypothetical daily intakes of 50-100 g per day during the production season from July to September. Despite this low intake, Flannery (1986) postulated that *Leucaena* seeds formed an important source of protein - providing 3-8% of daily protein intake - making them the third largest protein source after acorns (*Quercus*) and nopales (*Opuntia*). Given that *Leucaena* seeds are often eaten raw on the spot during present day foraging trips, their abundance in the cave may be an under representation of their significance in the diet (Flannery, 1986).

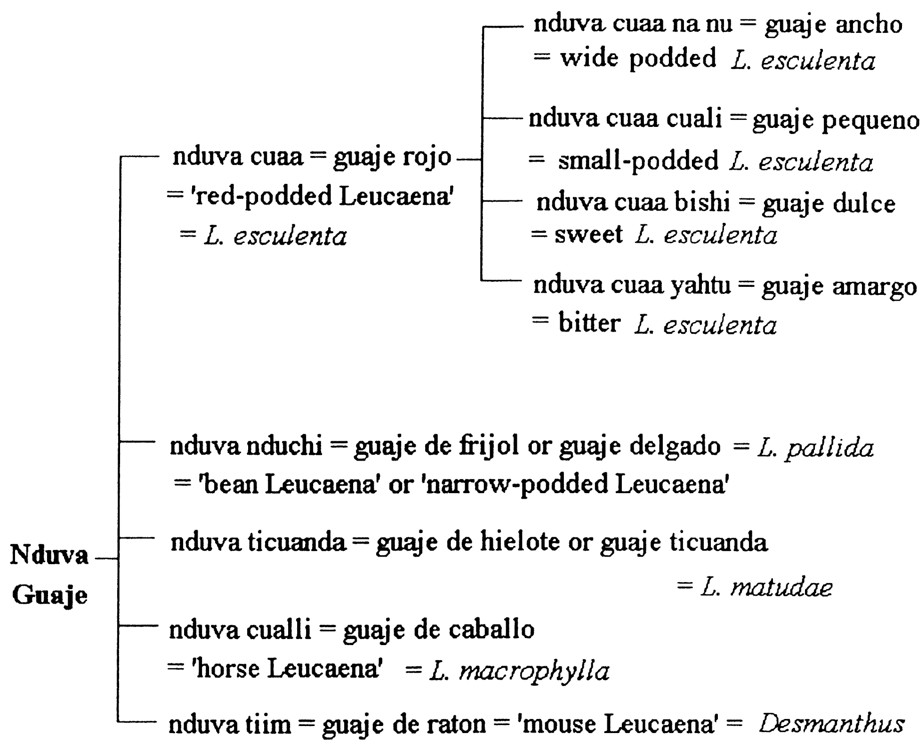
Archaeological data provide evidence to suggest that *Leucaena* seeds have provided a minor, but constant and reliable, food source for at least the last 7000 years. Increased frequency of pod fragments between 900 and 200 BC is possibly indicative of cultivation of *Leucaena* in the Tehuacan Valley 2000 years ago. Despite this long history of use, the record of pod fragments and seed of *Leucaena* over time provides no evidence, such as an increase in seed or pod size indicative of selection. In the case of *Leucaena*, cultivation has apparently preceded genetic change with a long period between first experimentation, cultivation and further domestication.

Documented historical evidence of the importance and prominence of *Leucaena* species was thoroughly reviewed by Casas (1992) and Zárate (1997). Illustrations and references to *Leucaena* and use of pods and seeds for food are abundant from the earliest glyphs to the records of the Spanish conquistadors. Although the Spaniards noted the wide food use of *Leucaena* across south central Mexico in sixteenth century accounts, and recorded *Leucaena* in cultivation, they apparently largely ignored *Leucaena* as a source of food for themselves. Traditional use was allowed to continue apparently largely unaffected by the conquest (Zárate, 1997). *Leucaena* provides the derivation of numerous place names including: the State and city of Oaxaca itself

Figure 5 Indigenous Classifications of *Leucaena*



Tzeltal classification of *Leucaena* species in the Municipality of Tenejapa, Chiapas (modified from Berlin *et al.*, 1974)



Mixtec classification of *Leucaena* species, La Montana, Alcozauca, Guerrero (modified from Casas and Caballero, 1996) derived from nahua *huaxín* (*Leucaena*) = *yacae* (= on the nose or point) *i.e.* 'on the point of the *guajes*'; Huajuapan derived from *huaxín* + *ua* (= possession) + *pan* (= place) *i.e.* 'place of *guajes*'; Oaxtepec derived from *huaxín* + *tepetl* (= cerro = hill), *i.e.* 'hill of *guajes*'; numerous small settlements such as Los Aguajes, Los Guajes, Cerro de Guajes. Such prominence of *Leucaena* in the derivation of place names is further indication of the importance of the genus.

4.6 Artificial sympatry and spontaneous hybridization

The ethnobotanical inventory of *Leucaena* is far from complete. However, evidence from surveys of present day use, indigenous classifications and archaeology indicate that species of *Leucaena* have been, and still are, of great importance as minor food plants in Mexico. Use of *Leucaena* seeds for human consumption is prevalent over a wide geographic area, involves at least 13 species and has probably been continuous over the last 7000 years. The wide geographic, taxonomic and historical extent of *Leucaena* use has resulted in a series of highly sophisticated and finely differentiated cognitive systems that derive primarily from variable pod characteristics.

Artificial sympatry. Use has been accompanied by increasing cultivation and translocation of species within Mexico, in some cases over long distances up to several 1000 km. This has resulted in wholesale disruption of species distributions bringing several species that would otherwise be isolated from each other into contact (artificial sympatry) with either natural populations of other species, or other cultivated species. While movement and cultivation of species within Mexico means that it may be difficult to map the precise limits of original natural populations of the widely cultivated species, it is possible to discern the general picture in most cases. Species are cultivated firstly in order to improve access to and ease of harvesting of local species; secondly, to obtain additional species which have desirable pod characteristics but are not native to the area; and thirdly, to extend availability by cultivating a selection of species which fruit in different seasons. By cultivating two or more species together these goals can be achieved, providing access to diverse pod types and opening up the potential for year-round production. In many cases species mixtures have apparently arisen in an *ad hoc* manner, more by accident than design. In other cases, multi-species orchards have been planted specifically to obtain diverse pod qualities and year-round production (Fig 10C).

Artificial sympatry between pairs of species is common and widespread (Table 6). Indeed, *L. leucocephala* is now so widely cultivated throughout Mexico and Central America that few species (only those such as *L. cuspidata, L. retusa* and *L. involucrata* which grow in areas too cold for *L. leucocephala*) are not now sympatric to a greater or lesser degree with *L. leucocephala*. Mixtures of more than two species also occur in a number of areas. For example in northern Oaxaca, southern Puebla and north west Guerrero, *L. esculenta, L. pallida* and either *L. leucocephala* or *L. confertiflora* are frequently found growing within single villages and sometimes within single *guajales*. All four species are planted together in some areas *e.g.* in the villages of Santiago Acatepec and San Pedro Chapulco, Puebla. In the vicinity of Chilapa de Díaz, Oaxaca, *L. confertiflora, L. esculenta, L. pallida* and *L. trichandra* are found together. Similarly, *L. collinsii, L. esculenta* and *L. leucocephala* are found cultivated together in backyards in the suburbs of Tuxtla Gutierrez in Chiapas, as are *L. esculenta, L. leucocephala* and *L. macrophylla* commonly in parts of Morelos (*e.g.* in the valley of the Rio Yautepec, between Oaxtepec, Yautepec and Jojútla de Juarez) and Guerrero (*e.g.* above Almaloya).

Spontaneous hybrids. This high level of artificial sympatry resulting from cultivation, as evidenced by diverse ethnobotanical data, has facilitated spontaneous hybridization (Hughes and Harris, 1994; in press; Section 5.5) and may also explain the origin of one or more of the tetraploid species (Sections 2.6 and 5.6). For example, hybrids between *L. leucocephala* and *L. esculenta*, identified by Hughes and Harris (1994), are largely sterile and, since natural vegetative propagation is not known within the genus, each individual must have arisen as a separate F_1 hybrid. Hybridization between *L. leucocephala* and *L. esculenta* is probably recent, following cultivation of the parent taxa in the last 2,000 years. Hybrids have now been found scattered quite commonly in parts of Morelos and Puebla (Fig 13), despite some roguing of trees which do not produce pods by local residents. They are also found in Dakar, Sénégal where both parent species are introduced in cultivation (Hughes and Harris, 1994). A similar spontaneous origin for hybrids between *L. leucocephala* and *L. diversifolia* was postulated by Hughes and Harris (in press). This hybrid apparently occurs spontaneously whenever the two parent species are brought together in cultivation. That this is the case for the hybrids in the Dominican Republic, Jamaica, Papua New Guinea and the Philippines, where both parent species are introduced, is not in doubt. In Mexico and Guatemala, both parent species are also cultivated, *L. leucocephala* for pod production (*e.g.* in informal *guajales* near Tuzanapan and Plan del Rio, Veracruz, Mexico), and *L. diversifolia* primarily for coffee shade (*e.g.* widely around Xalapa and Coatepec, Veracruz, Mexico; near Barillas, Huehuetenango, Guatemala; in Jamaica). At least five other putative spontaneous hybrids have been found in indigenous *guajales* (Table 7; Chapter 5), but their identities remain to be investigated in detail. That *L. leucocephala* was one parent in several of these hybrids, and has been proposed as a parent in other putative hybrids as well, may be attributed to the fact that it is the most widely cultivated species both in Mexico and Central America and pantropically, and is now sympatric with the majority of other species. Its extended, virtually year-round, flowering period (Gonzalez *et al.*, 1967)

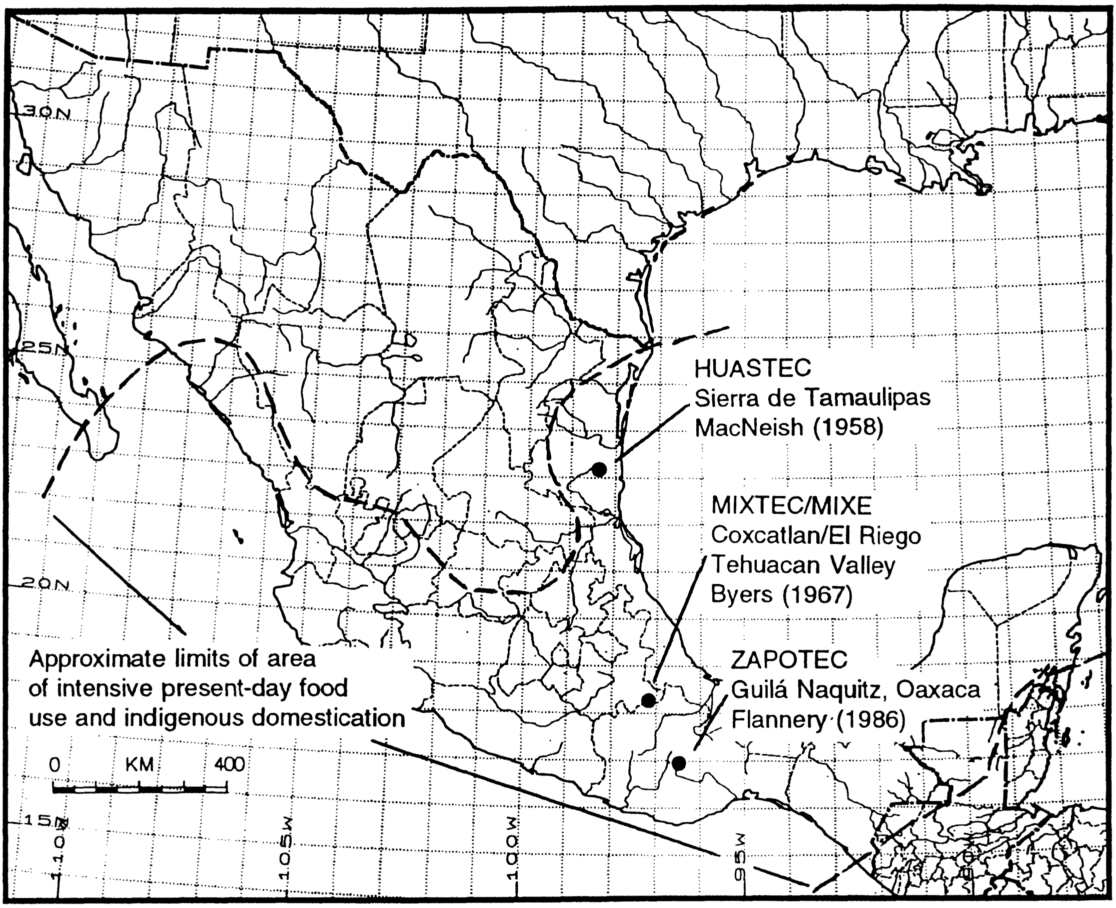


Figure 6 Map showing the approximate limits of intensive present day use and indigenous domestication, and locations of archaeological sites where *Leucaena* pod remnants have been found.

which overlaps with that of more seasonal species may also promote hybridization.

Tetraploid origins. The occurrence of four known tetraploid species of *Leucaena* and their possible origins are discussed in Section 2.6. Palomino *et al.* (1995) postulated recent origins for tetraploid *L. confertiflora, L. pallida* and *L. diversifolia* based on measurements of DNA content, but concluded that polyploidy had not been instrumental in the domestication process. However, the possibility that domestication may have been instrumental in the origin of tetraploids spontaneously in cultivation, must also be considered given the abundant evidence of human interference from ethnobotanical data. Two of the widely used and cultivated species, *L. pallida* and *L. leucocephala*, are tetraploid. Anthropogenic origins of one or both of these species are quite compatible with the ethnobotanical evidence. The case for *L. leucocephala* is particularly compelling. As described above, *L. leucocephala* has a set of characteristics (year-round pod production, very abundant pod and seed set (Gonzalez *et al.*, 1967), seed set on isolated trees due to self compatibility, and sweet seeds) that make it outstanding for pod production compared to other species of *Leucaena*. Thus a spontaneous origin of *L. leucocephala* would have been immediately noticed and seized upon by a *guaje*-conscious society. Such a scenario is compatible with other evidence about *L. leucocephala*. Firstly, there are no known populations of *L. leucocephala* (apart from weedy populations of subsp. *leucocephala* in the Yucatán Peninsula) that appear to be natural, although it is extremely widespread in cultivation (Fig 44). Despite numerous seed collection expeditions over the last 30 years by different researchers, a natural range for *L. leucocephala* remains unknown. Secondly, Harris *et al.* (1994b) analyzed isozyme variation amongst accessions from Mexico and Central America and found that there was only limited genetic variation within *L. leucocephala*, again suggesting a recent, possibly anthropogenic, origin with subsequent rapid spread in cultivation. As discussed above, that spread is continuing today. Finally, given that *L. pulverulenta*, which is restricted to north east Mexico (Fig 58), is the most likely maternal parent of *L. leucocephala* (Harris *et al.*, 1994a), an origin in that area is probable. Two of the three subspecies of *L. leucocephala* occur sympatrically

Table 6 Artificial sympatry amongst pairs of species of *Leucaena* following cultivation

Cultivated Species	Artificial Sympatry
L. esculenta	*L. confertiflora* - *L. esculenta* is occasionally cultivated close to *L. confertiflora guajales* (*e.g.* Chapulco and Santa Catalina Oxolotepec) or close to natural populations
	L. leucocephala - frequently throughout south central Mexico and sporadically elsewhere
	L. pallida - frequently cultivated together in Oaxaca, Puebla and NW Guerrero
	L. macrophylla - *L. esculenta* is widely cultivated through much of the range of *L. macrophylla* subsp. *macrophylla*
	L. pueblana - frequently in the mid- and upper Tehuacan Valley
	L. trichandra - *L. esculenta* is sporadically cultivated near the northern limits of *L. trichandra*
	L. collinsii - *L. esculenta* is cultivated and weakly naturalized in the vicinity of Tuxtla Gutierrez, Chiapas
L. leucocephala	all species except *L. involucrata, L. matudae* and *L. retusa*
	L. collinsii - *L. leucocephala* is cultivated throughout range of *L. collinsii* in the central depression of Chiapas and the Motagua Valley, Guatemala
	L. confertiflora - rarely, as close to the upper elevational limit for cultivation of *L. leucocephala*, but still present in some villages (*e.g.* San Pedro Chapulco, Puebla)
	L. cuspidata - *L. leucocephala* is rarely cultivated in lower villages in Hidalgo, near natural populations of *L. cuspidata*
	L. diversifolia - frequently in central Veracruz, occasionally in Chiapas, Mexico, Huehuetenango, Guatemala, Jamaica and elsewhere (Hughes and Harris, in press)
	L. greggii - *L. leucocephala* is very rarely cultivated near *L. greggii* populations as near frost limit for *L. leucocephala*
	L. lanceolata - *L. leucocephala* is sporadically cultivated throughout the range of *L. lanceolata*
	L. lempirana - *L. leucocephala* is occasionally cultivated in or close to natural populations
	L. macrophylla - *L. leucocephala* is frequently cultivated in or near remnant populations
	L. magnifica - *L. leucocephala* occasionally cultivated
	L. multicapitula - *L. leucocephala* is widely cultivated in and around remnant natural stands of *L. multicapitula*
	L. pueblana - *L. leucocephala* is frequently cultivated throughout the range of *L. pueblana*
	L. pulverulenta - these two species commonly occur together either both in cultivation (*e.g.* in parts of Tamaulipas and south Texas) or close to natural populations of *L. pulverulenta*
	L. salvadorensis - *L. leucocephala* is sporadically cultivated in and around remnant populations and indigenous agroforestry plantings of *L. salvadorensis*
	L. shannonii - *L. leucocephala* is sporadically cultivated in and around remnant populations of *L. shannonii*
	L. trichandra - *L. leucocephala* is sporadically cultivated in and around natural populations of *L. trichandra*
	L. trichodes - *L. leucocephala* is sporadically cultivated in and around natural populations of *L. trichodes*
L. pallida	*L. confertiflora* - *L. pallida* is occasionally cultivated close to *L. confertiflora guajales* (*e.g.* Chapulco and Santa Catalina Oxolotepec) or close to natural populations
	L. esculenta - frequently cultivated together in Oaxaca, Puebla and NW Guerrero
	L. leucocephala - occasionally cultivated with *L. pallida* although close to frost limits for *L. leucocephala*
	L. matudae - *L. pallida* is sporadically cultivated near upper elevational limit for *L. matudae*
	L. pueblana - *L. pallida* is cultivated in close proximity to natural populations of *L. pueblana* in the upper Tehuacan Valley
	L. trichandra - frequently *L. pallida* is cultivated in or around natural populations of *L. trichandra* close to the northerly limits of that species in Oaxaca

with *L. pulverulenta* today. This area coincides with the Huastec region which is known as an area of early agricultural development and an area where *Leucaena* seeds were apparently used in early times (MacNeish, 1958; 1965) and thus an area where *L. leucocephala* could have been noticed and propagated. Thus, although the evidence is circumstantial, and the hypothesis of an anthropogenic origin for *L. leucocephala* is highly speculative, it appears to offer the best explanation of the available evidence.

Few other genera present similarly high levels of artificial sympatry, although there are many documented examples of similar anthropogenic hybrid origins in other economically important plant genera following cultivation and domestication in Mexico (reviewed by Bye, 1993). One group which appears to be rather similar to *Leucaena* in terms of use, cognitive systems, translocation and high artificial sympatry is the large Neotropical Mimosoid legume genus *Inga*. Artificial sympatry of three or more species of *Inga* is common on farms in Honduras and a few farms have six species growing together (Lawrence and Zúniga, 1996), although, as yet, no *Inga* hybrids have been reported.

4.7 Indigenous domestication

The term '*domestication*' has been used in a wide variety of ways, but is normally taken to imply human-induced change in the genetics of a plant population to conform to human desires and appropriate development within the agro-habitat created for its production (Harlan, 1975). It is widely recognized that early domestication and early agriculture generally adopted plant species that were immediately available in the local flora. While some view domestication as a gradual progression or continuum from wild to fully domesticated, others invoke more sudden revolutionary changes - such as loss of seed distribution mechanisms or hybridization - to explain domestication. There appears to be no general consensus about the relative importance of different mechanisms, but for *Leucaena* it is now apparent that both gradual modification and sudden changes have been involved in its domestication. The gradualist continuum may comprise a series of transitions from casual gathering from wild populations, through systematic or selective harvesting and protection of trees when land is cleared, transplanting of naturally regenerated seedlings, more intensive cultivation and husbandry with the possibility of active selection, and ultimately complete removal from the wild state and dependence on husbandry for survival, *i.e.* loss of ability to survive in 'natural' ecosystems (Harlan, 1975). As Rindos (1984) pointed out, even management in terms of protection or tending entails some genetic change and thus a start towards 'domestication'. The reality of this 'domestication' continuum and of the greater complexity of the domestication process are now more widely accepted (Harris, 1989; Xolocotzi, 1993; Clement and Villachica, 1994; Leakey and Izac, 1996; Wiersum, 1996; Edwards and Schreckenberg, 1997). This has resulted in recognition of intermediate phases to describe the often important steps, such as cultivation, which precede the more significant genetic alteration which has often been considered an indicator of domestication. These intermediate phases have been described as *"incipient domestication"* (Zárate, 1984b: 237), *"pre-domestication cultivation"* (Xolocotzi, 1993) or *"semi-domestication"* (Clement and Villachica, 1994: 231).

There is little evidence to suggest that significant selection has occurred within cultivated species of *Leucaena*. Species are seen to be at variable stages of incipient domestication, semi-domestication or pre-domestication cultivation exactly as found for many Amazonian fruit and nut species by Clement and Villachica (1994) and many agroforestry species more generally (Wiersum, 1996). These different stages, which may be simultaneously observed today for different species and in different areas, support the view that the traditional dichotomy between hunter gatherers and agriculturalists, and between wild and domesticated, is blurred and forms a continuum that may be descriptive of, but does not necessarily explain, domestication (Harris, 1989; Clement and Villachica, 1994). The greater difficulty of domestication of woody perennials compared with annual crops due to long generation times, is well known and appreciated. For example avocado (*Persea americana*), although probably in cultivation in the Tehuacan Valley as early as 5,000 to 6,000 BC shows no influence of selection (increase in size) until 900-200 BC, an extremely slow rate of change compared to annual crops such as maize (Smith, 1967). If there has been genetic modification of *Leucaena* species due to human selection, then the phenotypic effects have been small and genetic effects remain to be detected.

Of far greater importance in domestication of *Leucaena* have been the sudden and dramatic changes brought about by spontaneous interspecific hybridization facilitated by juxtaposition of different species in indigenous cultivation. Indeed, in the case of *Leucaena*, it seems that hybridization, and the probable origin of *L. leucocephala* in cultivation, may be what constitutes domestication. Thus despite the fact that *Leucaena* seeds have been, and still are, plant foods of only minor dietary significance, and that species of *Leucaena* are in an early stage of incipient domestication with little evidence of selection or 'true domestication' in the classical sense, domestication in the broader sense that includes spontaneous hybridization, has entailed a number of profound effects on the evolution of the genus. The generation of a series of spontaneous hybrids, some of which are fertile and apparently spreading and being used, and possibly including one or more tetraploid species, represents a far more dramatic change than the usually slow change that results from indigenous selection.

Although erosion of genetic diversity caused by human intervention has been the dominant impact for many plant groups (Wilson, 1988), human actions that favour diversity and which may be conducive to rapid evolutionary change may also be important (Bye, 1993). It is clear that human actions have not only protected and conserved several *Leucaena* species through use (Chapter 8), but that indigenous domestication has also been instrumental for the evolution of new diversity in the genus in the form of a set of spontaneous hybrids.

Box 3 Ethnobotany and indigenous domestication

- Indigenous use has concentrated not on leaf and wood products but on unripe pods and seeds which are used as food for human consumption.

- 3 sources of ethnobotanical data are: present-day use, vernacular names and folk taxonomies, and archaeological evidence.

- The ethnobotanical inventory of Leucaena is far from complete. However, evidence from surveys of present-day use, indigenous classifications and archaeology indicate that species of *Leucaena* have been, and still are, of great importance as minor food plants in Mexico. Use of *Leucaena* seeds for human consumption is prevalent over a wide geographic area, involves at least 13 species, and has probably been continuous over the last 7000 years. The wide geographic, taxonomic and historical extent of *Leucaena* use has resulted in a series of highly sophisticated and finely-differentiated cognitive systems that derive primarily from variable pod characteristics related to food use.

- Use has been accompanied by protection, management, cultivation and translocation of species within Mexico in traditional 'orchards' that often incorporate two or more species in mixtures (artificial sympatry).

- There is only limited evidence for selection. *Leucaena* species are thus at various stages of incipient domestication.

- The main outcome of indigenous domestication has been to facilitate spontaneous hybridization by bringing together different species in cultivation. Seven putative hybrids which have apparently arisen in this way have been found. Ethnobotanical evidence is compatible with the hypothesis that *L. leucocephala*, and possibly other tetraploid species such as *L. pallida*, arose as spontaneous hybrids following cultivation of their parent species in indigenous orchards.

Figure 7 *Leucaena leucocephala*: potential and limitations

A. *L. leucocephala* subsp. *glabrata* mature tree to 20 m ht showing heavy pod production, and moderate drought tolerance, Cabo San Lucas, Baja California Sur, Mexico.

B. *L. leucocephala* grown in fodder hedgerows in extensive pasture production systems in Queensland, Australia. Combined *Leucaena*/grass pasture systems have resulted in exceptional cattle live weight gains (photo courtesy of M. Shelton).

C. *L. leucocephala* used for multiple products on a small farm in lower hills of Nepal - mature tree heavily lopped for livestock feed used in stall feeding fodder system, with smaller trees managed under regular lopping for firewood and live barriers. This picture was taken in 1984, prior to the arrival of the psyllid in Nepal.

D. *L. leucocephala* pollarded along terrace boundaries on small farms in Choluteca, southern Honduras.

E. *L. leucocephala* was introduced to the Comayagua Valley in central Honduras within the last 20 years. It is now one of the commonest trees on small farms, used around settlements and along field boundaries.

F. Adult psyllid, *Heteropsylla cubana*, the defoliator which spread from Central America around the globe between 1984 and 1994 (photo courtesy of P. Oui); scale bar = 0.5mm.

G. Young growing shoot of *L. leucocephala* showing typical wilting and defoliation damage caused by heavy psyllid infestation (photo courtesy of M. Cock).

H. Camptomeris leaf spot, caused by the fungal pathogen *Camptomeris leucaenae*. This fungus causes black leaf spotting, loss of leaflets and some dieback often associated with secondary pathogens and is a potentially serious disease of *Leucaena* causing reduced forage yields and quality.

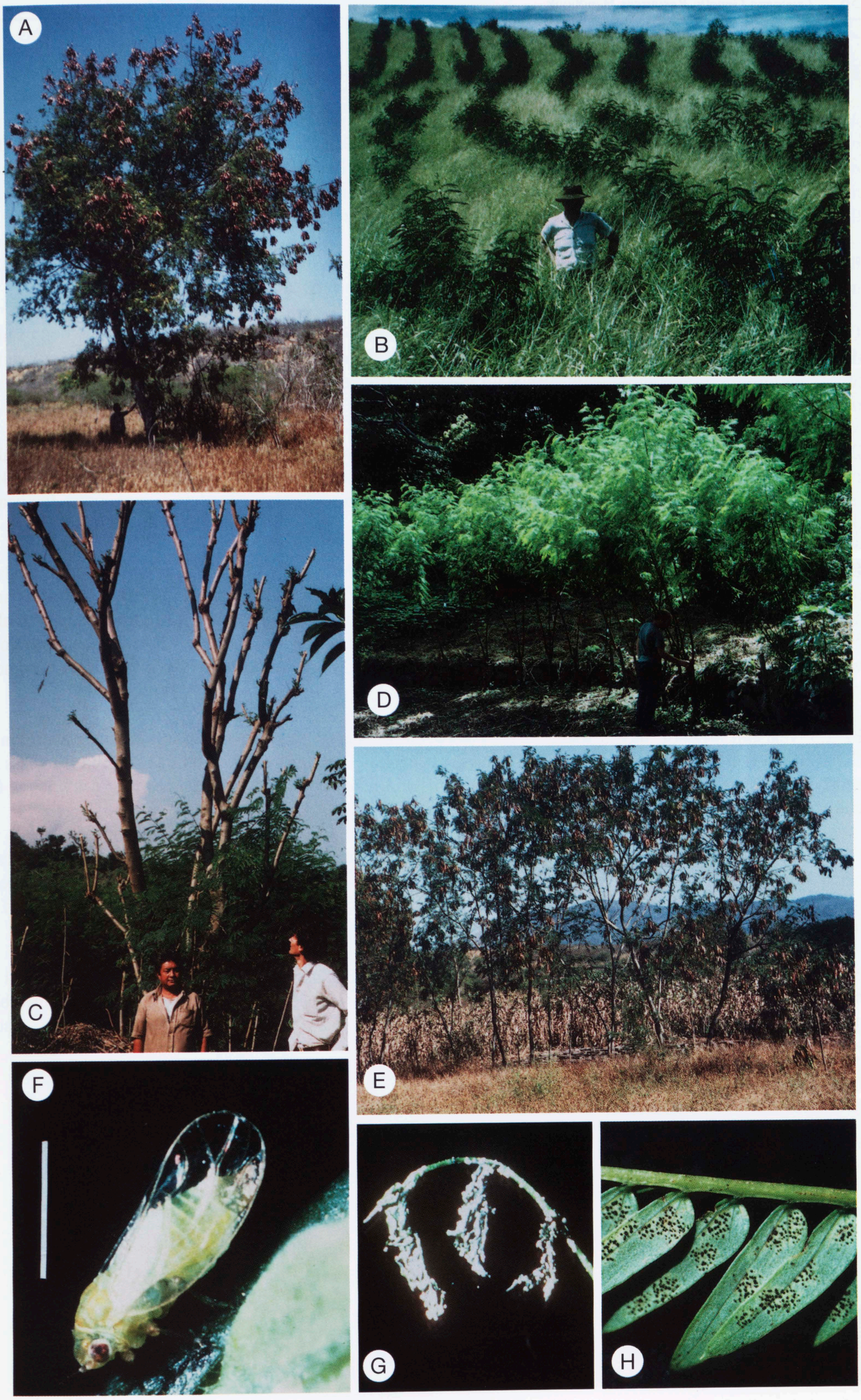

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Figure 8 Wood production and weediness of *Leucaena*

A. *Leucaena salvadorensis* managed by heavy lopping and pollarding for production of high quality poles which are used in local construction as house corner posts in San Ramón Arriba, Choluteca, Honduras. The wood of *L. salvadorensis* has high density and a high proportion of heartwood and is known to be more durable than wood of *L. leucocephala*. Trees are managed in traditional agroforestry systems over crops, in this case millet, showing the context and potential of *circa situm* conservation.

B. Poles of *L. salvadorensis* are renowned for use as corner posts in local house construction throughout its native range, here used in San Juan de Limay, Estelí, in northern Nicaragua.

C. Pole of *L. collinsii* subsp. *zacapana* showing the high wood quality of this species. It forms wood of high density (mean wood density at 5 years 0.91) with a high proportion of heartwood (48% at 5 years) and is highly preferred throughout its native range for poles and firewood. Here cut for local house construction use near Chiquimula, south east Guatemala.

D. Dense monospecific thickets of *Leucaena leucocephala* subsp. *leucocephala* above Diamond Head, Oahu, Hawaii, U.S.A. showing the potential of this taxon to become an invasive weed. This photograph was taken in 1986, soon after the arrival of the psyllid defoliator, *Heteropsylla cubana* in Hawaii and shows the heavy defoliation caused by the psyllid.

E. This small tree is a spontaneous hybrid between *L. leucocephala* and *L. diversifolia*, growing in secondary roadside vegetation between Xalapa and Veracruz, in Veracruz, Mexico. The hybrid is common in this area apparently arising spontaneously wherever the two parents are cultivated together. This hybrid, which has also be created artificially, as KX3, is self fertile and produces abundant seed from an early age. These traits, along with its invasive tendencies in secondary vegetation in Mexico, suggest that it has the potential to become a weed.

F. 2.5 year-old tree of the artificial hybrid between *L. leucocephala* and *L. esculenta* growing in a CONSEFORH field trial at La Soledad, Comayagua, central Honduras. This hybrid is triploid, seedless or nearly seedless, extremely fast growing, and highly psyllid-resistant, a set of traits that make it attractive for cultivation, assuming its propagation can be mastered.

G. Adult bruchid beetle of *Acanthoscelides macrophthalmus* emerging from a mature seed after feeding; scale bar = 2mm. This seed feeding bruchid has been recorded from 18 species of *Leucaena* and has recently been introduced to Australia (accidentally) and South Africa (intentionally) where its potential for biocontrol of *L. leucocephala* is being evaluated.

H. Some lesser known species of *Leucaena*, including *L. lanceolata, L. pulverulenta, L. shannonii* and *L. trichodes* show marked weedy tendencies within their native ranges, freely colonizing open and disturbed habitats. This photograph shows abundant colonization of secondary vegetation by *L. lanceolata* in Oaxaca, southern Mexico.

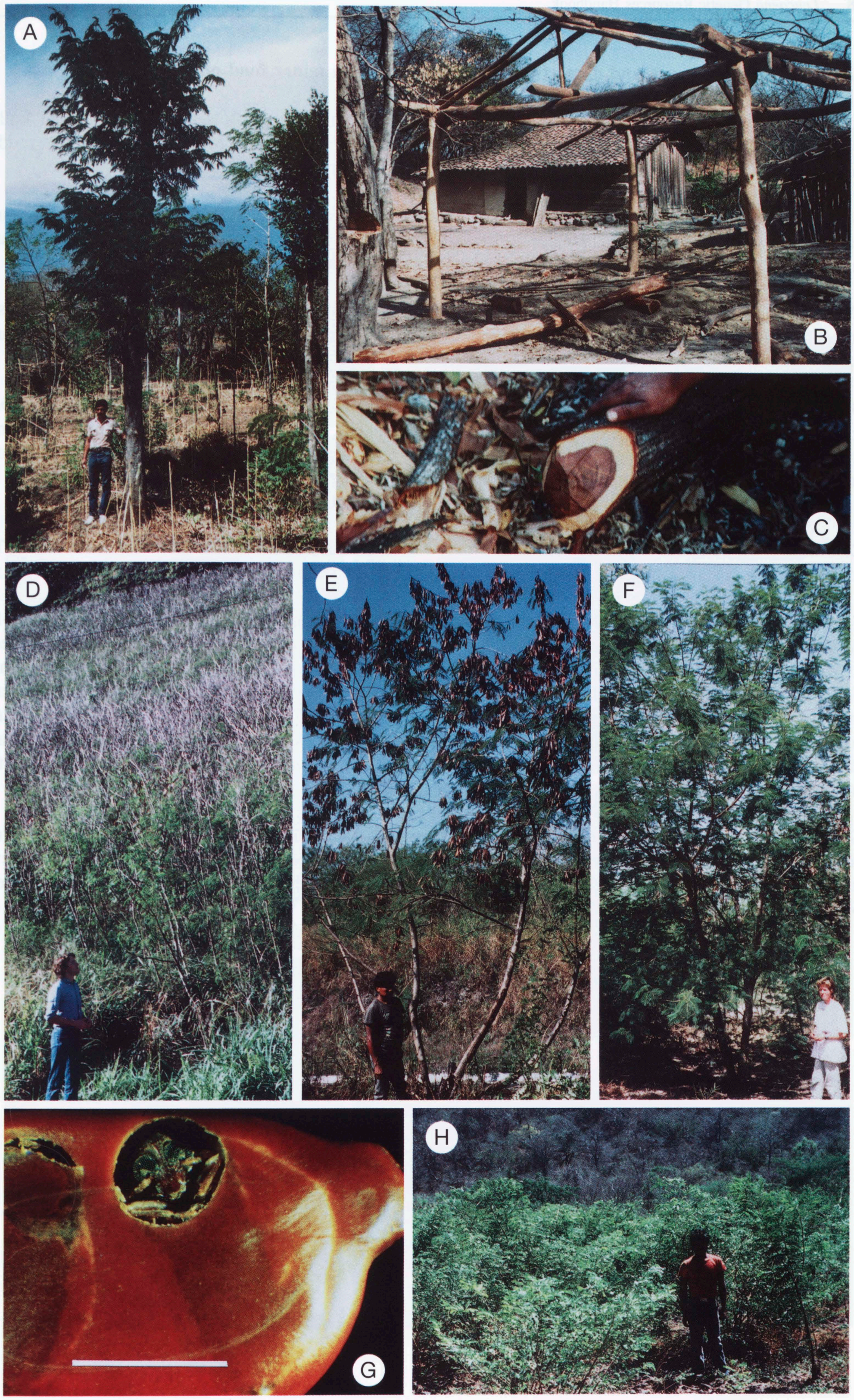

A
B
C
D
E
F
G
H

Figure 9 Indigenous use and domestication of *Leucaena* as a minor food plant in Mexico

A. Local farmer harvesting unripe pods of *L. esculenta* from an informal orchard in the Tehuacan Valley, Puebla, Mexico. *L. esculenta*, known as the *guaje rojo* or *guaje colorado* in Mexico because of its reddish pods, is one of the most important, widely used and cultivated species at mid elevations in Mexico.

B. Extraction and processing the unripe seeds of *L. esculenta* for food use, in mid February near San Martin Pachívia, Guerrero, Mexico. This household harvests several 100 kilograms of *L. esculenta* seed from nearby cultivated and semi-natural populations each year for sale in local markets.

C. Extraction and processing is sometimes done directly in the field to avoid transporting large quantities of pods. Unripe green seeds of *L. esculenta* being shelled after harvesting, in mid February, near San Martin Pachívia, Guerrero, Mexico.

D. Unripe pods of *L. leucocephala* subsp. *glabrata*, the *guaje verde, guaje blanco, guaje castilla*, or *k'usbalil sasíb* for sale in the market of San Cristobal de las Casas, Chiapas, Mexico. *L. leucocephala* is highly preferred for food use throughout south central Mexico. It is widely cultivated at lower elevations along the Pacific coast and in the central Depression of Chiapas, for example around Tuxtla Gutierrez, and the pods transported for sale, virtually year-round, to all the surrounding highland market towns such as San Cristobal.

E. Unripe pods of *L. esculenta* for sale in February in the central market of Oaxaca, southern Mexico. The local names, *guaje rojo* or *guaje colorado* are derived from the deep maroon unripe pod colour.

F. Small *Leucaena* orchard at 2000m in the village of San Pedro Chapulco, Puebla, Mexico. Here trees of *L. pallida* and *L. confertiflora* are grown in lines separating alleys where crops are grown. Unripe pods and seeds of these species are harvested in July-September, consumed locally and sold in nearby markets such as Tehuacan. The trees alternate within rows with *Agave* and *Opuntia*, two other important indigenous food plants in a typical traditional agroforestry system showing the context and environment under which *circa situm* conservation and indigenous domestication of *Leucaena* takes place. Crop production is marginal in this area due to low and variable rainfall, and tree products, such as *Leucaena* pods and seeds, provide an important source of both subsistence foods and income.

G. Extensive orchard of *L. esculenta* in the mid-Tehuacan Valley, Puebla, Mexico. *L. esculenta*, although considered to be introduced to the Tehuacan Valley, is now widely and commonly cultivated over crops, even in areas with irrigation. Here trees are in flower and with a few highly unripe pods over irrigated maize in November, shortly before the *L. esculenta* pod production season.


A
B
C
D
E
F
G

Figure 10 *Circa situm* conservation, indigenous cultivation, artificial sympatry and spontaneous hybrids

A. Map of part of Latin America showing the total distribution of the genus *Leucaena* in the New World. Data points are derived from 2393 herbarium specimen collection sites with verifiable localities (88% of the total specimens examined). The overall distribution shows the occurrence of species of *Leucaena* in seasonally dry tropical habitats and their virtual absence from the cold arid deserts of north central Mexico and the non-seasonal wet lowland forests of the southern Gulf of Mexico (Tabasco and northern Chiapas), the Petén region of Guatemala, the Atlantic zone of Honduras, Nicaragua, Costa Rica and Panamá and the perhumid forests of the Darién/Chocó coastal zone of Colombia and northern Ecuador. The number of taxa occurring per degree-square is mapped. This shows that the greatest diversity of species occurs in southern Mexico and to a lesser extent in northern Central America. The highest diversity of species, with 12 taxa in one degree-square, is in southern Puebla. Diversity in these areas is augmented by 'indigenous' cultivation and artificial sympatry.

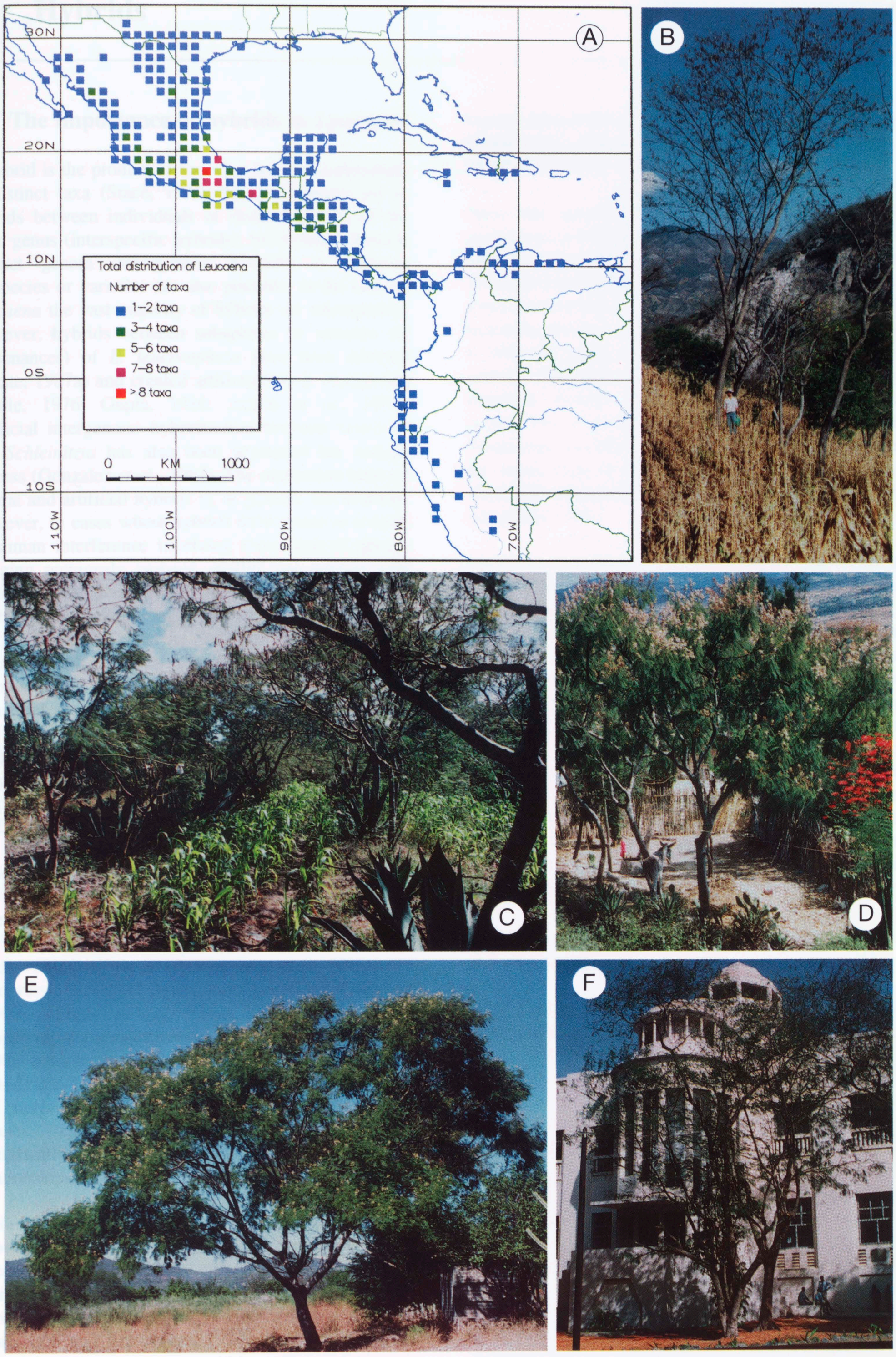
B. Wood of *L. collinsii* subsp. *zacapana* is highly preferred for poles and firewood being of high density and heartwood percentage. Because of this trees are often protected and managed over crops, here over millet near Chiquimula, south east Guatemala, in the early dry season in January after the crop has been harvested. Such traditional agroforestry systems are the venue for widespread *circa situm* conservation of *Leucaena* genetic resources.

C. A complex orchard of *Leucaena* at 1900m elevation in the village of Santiago Acatepec, Puebla, Mexico. Three species of *Leucaena, L. esculenta, L. leucocephala* and *L. pallida* occur in this one orchard. *L. confertiflora* occurs in nearby degraded thorn scrub mattoral. This is typical of the level of artificial sympatry found in the *Leucaena* orchards in this part of Mexico. Two hybrids, arising spontaneously as a result of artificial sympatry, have been found in this one orchard. Firstly there are seven individuals of the seedless triploid hybrid between *L. leucocephala* and *L. esculenta*. The seedlessness of this hybrid is well known among local people who are interested in food use of unripe pods and seeds. The hybrid is known as the *guaje macho* (male *Leucaena*) and trees are often rogued from this orchard because of this. The second hybrid, *Hughes 1625*, is as yet unidentified, but appears to have *L. leucocephala* as the female parent, with possibly two other species involved in its parentage. Orchards, or *guajales* of this type are the venue and workbench of indigenous domestication. In this type of traditional agroforestry system trees are intercropped with other indigenous food plants such as maize, *Opuntia* and *Agave*.

D. Typical indigenous cultivation of *L. esculenta* for food use in backyards around houses in the small village of San Pablo Guila, Oaxaca, southern Mexico.

E. Tree of a spontaneous hybrid between *L. leucocephala* and *L. esculenta*, near Izucar de Matamoros, southern Puebla, Mexico. The hybrid, here in full leaf and flower during the early dry season in December, flowers prolifically over an extended period but is sterile and seedless. It occurs widely but sporadically in six States in south central Mexico and being sterile, each hybrid tree has arisen independently. It is known locally by the name *guaje macho*, the male *Leucaena*, and trees are sometimes rogued because of their lack of pods, but may be retained as attractive ornamentals.

F. Tree of a spontaneous hybrid between *L. leucocephala* and *L. esculenta* outside the Musées de L'Institut Fondamental d'Afrique Noire, Dakar, Sénégal, Africa. *L. leucocephala* is common and naturalized throughout Dakar and *L. esculenta*, although known and recorded from there is apparently rare. Spontaneous hybrids have arisen following introduction of these two species, even though one parent species is rare (photo courtesy of C. Fagg).



A
B
C
D
E
F
30N
20N
10N
0S
10S
110W
100W
90W
80W
70W
Total distribution of Leucaena
Number of taxa
1–2 taxa
3–4 taxa
5–6 taxa
7–8 taxa
> 8 taxa
0
KM
1000

5 Hybrids

5.1 The importance of hybrids in *Leucaena*

A hybrid is the product of breeding between individuals of distinct taxa (Stace, 1975). Most references are to hybrids between individuals of distinct species of the same genus (interspecific hybrids), but hybrids between distinct genera (intergeneric hybrids) or between subspecies or varieties are also possible. In the case of *Leucaena* the vast majority of hybrids are interspecific. However, hybrids between subspecies or varieties (or provenances) of *L. leucocephala* have been detected (Zárate, 1987a) and created artificially (*e.g.* Hutton and Beattie, 1976; Gupta, 1986; Austin *et al.*, 1997). Artificial intergeneric hybridization between *Leucaena* and *Schleinitzia* has also been attempted but without success (Gonzalez *et al.*, 1967). The distinction between natural and artificial hybrids is, in general, not in doubt. However, in cases where hybrids have arisen as a result of human interference involving movement of species bringing previously isolated species into contact with each other (Section 4.6), the distinction is not so clear. Such hybrids, with assisted, but not strictly man made (artificial), origins, may be described as 'semi-natural' or results of 'assisted-hybridization' or simply as 'spontaneous'. In this chapter hybrids are distinguished as natural, spontaneous or artificial.

Evidence suggests that natural hybridization is both geographically widespread and frequent in diverse groups of plants (Stace, 1975; 1989; 1991; Rieseberg, 1995; McDade, 1995). Interspecific hybridization is accepted as an important process generating species of plants (Anderson, 1949; Stebbins, 1959; Stace, 1975; Grant, 1981; Rieseberg, 1995). As discussed by Abbott (1992), recent data have confirmed that stabilization of hybrids can lead to the origin of fertile homoploid hybrid taxa (Gallez and Gottlieb, 1982; Rieseberg *et al.*, 1990a), the introgressive origin of infraspecific taxa (Rieseberg *et al.* 1990b; Abbott *et al.*, 1992) and the origin of allopolyploid (amphidiploid) species (Soltis and Soltis, 1990b; Ashton and Abbott, 1992). Natural or spontaneous hybrids can be a major source of taxonomic confusion and may be difficult to distinguish from 'normal' species, complicating species delimitation and identification (Chapter 10) as well as analysis of species relationships.

Evidence of hybridization in *Leucaena* is provided by known polyploidy (Section 2.6), confirmed and unconfirmed reports of spontaneous hybridization (Hughes and Harris 1994; in press), evidence for cpDNA introgression (Harris *et al.*, 1994a), and high crossability (Sorensson and Brewbaker, 1994). Evidence from any one of these three sources would be sufficient to suggest that hybridization may have been important. Taken together there is overwhelming evidence that spontaneous hybridization, recent and possibly ancient, has been a significant process in the evolution of *Leucaena*.

Once the potential for artificial hybridization is considered, hybrids assume even greater importance as there are many more artificial than spontaneous hybrids. Artificial hybridization provides one method to move genes from species that have useful traits to others which lack them, thereby combining the desirable characteristics of different species. Artificial hybridization has been a central component of tree improvement for many important forestry and agroforestry genera such as *Acacia, Erythrina, Eucalyptus, Pinus, Populus* and *Salix* (Namkoong and Kang, 1990; Nikles, 1992) and has been the main focus of *Leucaena* breeding efforts to date (Brewbaker and Sorensson, 1990; Brewbaker *et al.*, 1989; Sorensson, 1995).

Thus, in *Leucaena*, both spontaneous and artificial hybrids are important sources of diversity. In this chapter, both types of hybrids are discussed and a number of actual hybrids and their characteristics and potential are described. Research on natural or spontaneous hybrids has largely been carried out by Hughes and Harris (1994; in press) in Oxford. Investigation of crossability and artificial hybridization has been carried out by Brewbaker and colleagues in Hawaii (Brewbaker and Sorensson, 1990; 1994; Pan, 1985; Sorensson, 1992a; 1993; 1995; Sorensson and Brewbaker, 1994), Australia (Bray, 1984; Hutton and Gray, 1959), Colombia (Hutton, 1988) and India (Gupta *et al.*, 1986). This chapter attempts to synthesize the data published by these research groups.

5.2 Crossability

Crossability refers to the ability of species to hybridize and is determined through artificial crossing experiments which involve different combinations of species in reciprocal crosses. Crossability amongst 15 of the 22 species of *Leucaena* has been investigated in a programme of hand crossing, involving more than 50,000 pollinations, carried out in Hawaii (Sorensson, 1993; Sorensson and Brewbaker, 1994) building on earlier work by Gonzalez (1966), Gonzalez *et al.* (1967), Hutton (1982) and Pan and Brewbaker (1988). This work has shown that *Leucaena* species hybridize as readily as certain other woody genera such as *Erythrina* (Neill, 1988) or *Salix* (Mosseler, 1990), and far more readily than most herbaceous plant genera. Ninety-one (77%) of the 120 possible two-way interspecific combinations between the 15 tested species produced viable seed (Sorensson and Brewbaker, 1994). It appears that species have evolved in geographical isolation from each other with few genetic barriers to hybridization.

Hybrids in *Leucaena* may be grouped by ploidy-specific mating type as diploid (diploid × diploid), tetraploid (tetraploid × tetraploid), or triploid (tetraploid × diploid). Mean crossability indices (viable seeds from cross pollination *cf* from intraspecific or compatible self pollinations expressed as a %), are highest amongst tetraploids (73%), with 32% amongst diploids and only 12% for triploid matings (Sorensson and Brewbaker, 1994). For this reason the three well known tetraploid species *L. leucocephala, L. diversifolia* and *L. pallida* which are completely interfertile have been considered the 'primary' genepool for improvement and have been the main focus of recent artificial hybridization efforts (Sorensson and Brewbaker, 1994; Sorensson, 1995). The only group which is somewhat less cross incompatible with other species are the three species *L. macrophylla, L. trichodes* and *L. multicapitula*. The unusual pollen of these three species which occurs in polyads (albeit of two different polyad types) (Hughes, 1997b) has been implicated in causing this incompatibility by Sorensson (1992a). Ploidy-specific crossability polygons modified from Sorensson (1993) and Sorensson and Brewbaker (1994) are presented in Fig 11.

5.3 Detection of hybrids

The first problem in any investigation of natural or spontaneous hybrids is how to distinguish hybrids from 'normal' species. Normally discrete species originate through mutation and selection acting on diverging lines. A 'normal' species is a unique product of evolution and occurs only once; it cannot be recreated experimentally. Hybrids on the other hand form only through the crossing of 'normal' species and can appear again and again, and a hybrid found naturally whether it is fertile or sterile, can theoretically be synthesized artificially (Wagner, 1969). Distinguishing between 'normal' species and hybrids is not always straightforward and often involves considerable research using diverse evidence from morphology, molecules and geography. Hybrids are usually detected and identified on the basis of a set of criteria including: (a) phenotypic intermediacy between putative parents; (b) reduced fertility; (c) segregation of F_2 progeny from a fertile hybrid; (d) overlapping distributions of the hybrid and the putative parents; (e) additivity of biochemical or nuclear molecular markers; (f) ecological intermediacy; (g) artificial re-synthesis of the hybrid; (h) possession of 'foreign' haplotype (Wagner, 1969; Gottlieb, 1972; Rosen, 1979; Stace, 1975; 1989; Humphries, 1983; Rieseberg and Ellstrand, 1993; Rieseberg and Morefield, 1995; McDade, 1995).

In practice, most hybrids are actually 'detected' prior to formal analysis of morphological intermediacy, based on one or more of the other criteria, and frequently, intuitive interpretation of morphological, geographical and fertility observations (Wagner, 1983). Confirming hybrid identity usually depends on cumulative evidence from several or all of the criteria, none of which alone provides a rigorous and unequivocal test, but when taken together are usually judged to support a hypothesis of hybridity beyond reasonable doubt (Gottlieb, 1972).

Many recent investigations of putative hybrids have employed secondary plant metabolites, isozymes and, more recently, DNA characters. The rationale for using molecular characters as markers for hybrid identification and characterisation is that there are an unlimited number of independent, selectively neutral DNA markers that are expected to show complete additivity in F_1 hybrids (Rieseberg and Brunsfeld, 1992). Combined analysis and comparison of DNA characters from both organellar (chloroplast, cpDNA and mitochondrial, mtDNA) and nuclear genomes provides some of the best evidence of hybridization (Avise, 1994). This is because primary (F_1) hybrids should combine the nuclear encoded DNA markers of each parent while organellar markers are expected to be those of the maternal or paternal parent, depending on the direction of hybridization and the mode of organelle inheritance (Soltis and Soltis, 1991). For *Leucaena*, research using a combination of chloroplast and nuclear DNA markers has had a major impact on the detection and characterisation of hybrids (Harris, 1995; Harris *et al.*, 1994a; 1994b; Hawkins and Harris, in press; Hughes and Harris, 1994; in press). *Leucaena* chloroplast DNA is inherited through the maternal parent (Harris *et al.*, 1993). Restriction fragment length polymorphism analysis (RFLP) of cpDNA characters has been successfully used to provide information about the maternal parent of a number of hybrids and tetraploid species of putative hybrid origin (Harris *et al.*, 1994a; Hughes and Harris, 1994; in press; Hawkins and Harris, in press). Although nuclear DNA markers are expected to show an additive profile of the two parents, in *Leucaena* nuclear ribosomal DNA profiles in hybrids are not always completely additive, suggesting that reliance on a single nuclear DNA marker can lead to errors. Reliable detection of hybrids in *Leucaena* is thus likely to depend on use of a set of taxon diagnostic nuclear DNA markers (Hughes and Harris, 1994). Because of their technical simplicity and potential to provide large numbers of nuclear markers scattered randomly across the genome, use of randomly amplified polymorphic DNA (RAPD) markers has also been investigated for hybrid detection in *Leucaena* (Harris, 1995; Hawkins and Harris, in press; Hughes and Harris, in press). Many limitations associated with use of RAPDs for detection of hybrids were highlighted in these studies, but when interpreted under strict criteria, RAPDs have been shown to provide useful additional evidence of hybridity (Hawkins and Harris, in press; Hughes and Harris, in press). There is little doubt that molecular markers will continue to be an essential tool to identify and characterise new putative hybrids as they are discovered.

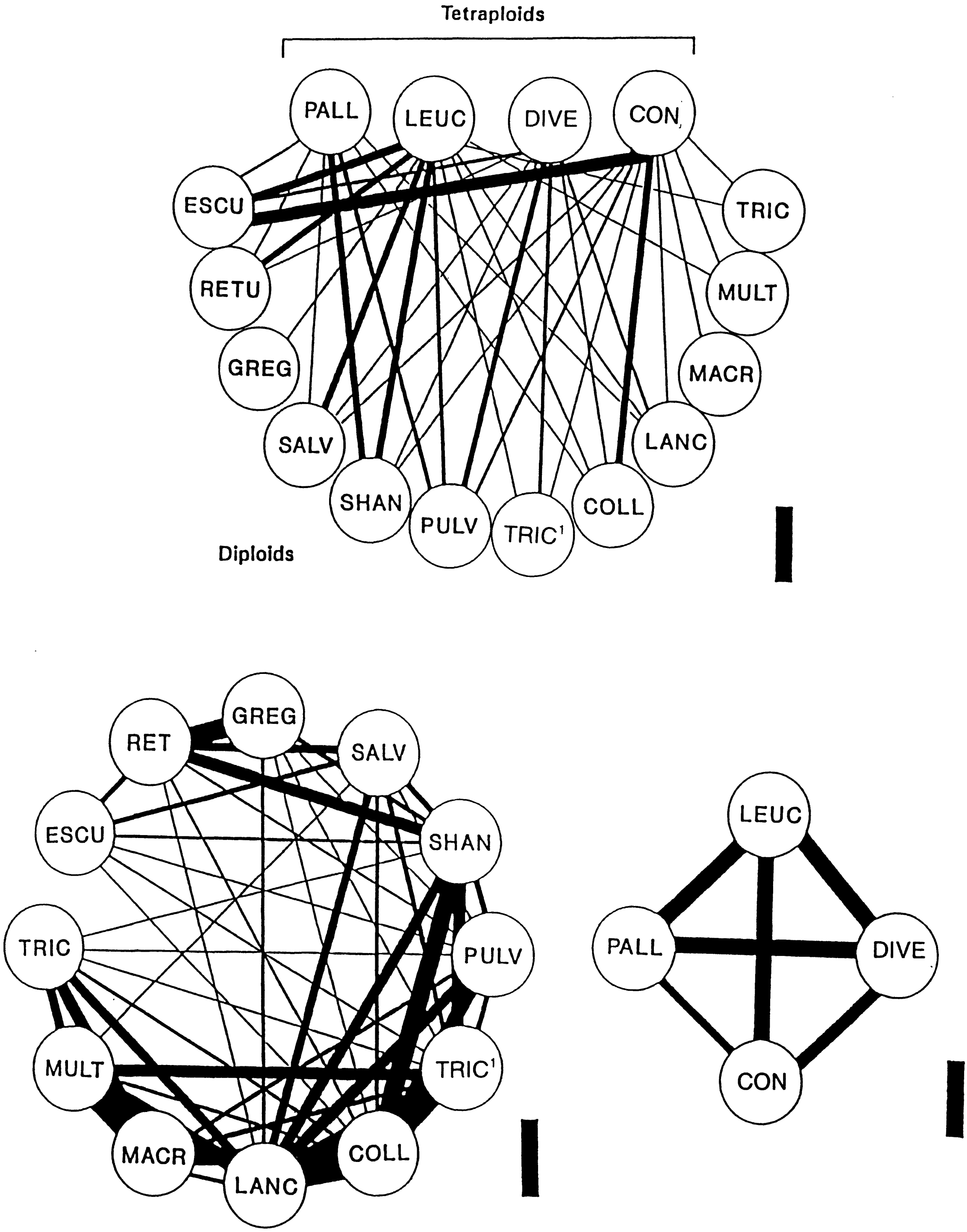


Figure 11 Relative ease of hybrid seed production among 15 species of *Leucaena*, using maximal data from reciprocal crosses for each interspecific mating, divided by ploidy-specific mating types: tetraploid × diploid, diploid × diploid, and tetraploid × tetraploid. Bar thickness indicates a crossability index (see text) of 100%. Diploid species: ESCU = *L. esculenta*, RETU = *L. retusa*, GREG = *L. greggii*, SALV = *L. salvadorensis*, SHAN = *L. shannonii*, PULV = *L. pulverulenta*, TRIC[1] = *L. trichandra*, COLL = *L. collinsii*, LANC = *L. lanceolata*, MACR = *L. macrophylla*, MULT = *L. multicapitula*, TRIC = *L. trichodes*; tetraploid species: PALL = *L. pallida*, LEUC = *L. leucocephala*, DIVE = *L. diversifolia*, CON = *L. confertiflora*; scale bar thickness indicates a crossability index of 100%. Modified from Sorensson (1993) and Brewbaker and Sorensson (1994).

For *Leucaena*, the task of detecting hybrids is made significantly easier by the existence of a large collection of artificial hybrids created at the University of Hawaii mainly by Sorensson (1993) (summarized by Sorensson and Brewbaker (1994)). The criterion of re-synthesis is not a realistic option in all hybrid studies, but provides strong evidence relative to other criteria (Gottlieb, 1972). For *Leucaena*, material derived from progeny of controlled crosses of known parentage is often available for direct comparison with putative natural or spontaneous hybrids.

In addition, Sorensson (1993) examined quantitative leaf morphology of a set of artificial hybrids and derived two models to predict hybrid leaf morphology based on the morphology of the two parent species. He used four leaf traits: number of pinnae per leaf, number of leaflets per pinna, leaflet length and leaflet width, all of which vary widely across species within the genus, and showed that hybrid morphology for all four traits could be predicted using a simple inheritance model. With rare exceptions leaf parameters are inherited on a geometric scale intermediate between the two parents. This simply means that hybrids between two diploid, or two tetraploid, species generally showed mid-parent values on a natural log scale expressed mathematically as:

$$\mathbf{2lnF_1 = lnP_1 + lnP_2}$$

where F_1 is the hybrid leaf trait value and P_1 and P_2 are the parental values.

Triploid hybrids were also intermediate, but resembled the tetraploid parent more closely, necessitating inclusion of a dosage effect for ploidy into the model:

$$\mathbf{3lnF_1 = 2lnP_1 + lnP_2}$$

where P_1 is the tetraploid parent. A dosage effect due to ploidy has been noted in hybrid studies more generally (Stace 1975; Wagner, 1969; 1983). Sorensson's model fitted the artificial hybrid combinations tested with only a handful of exceptions. The model provides a way to predict values for hybrid leaf traits based on parent values. Predicted values can then be compared with measured values for putative hybrids. For putative natural or spontaneous hybrids, the actual individual parent trees are usually not known, so all that can be estimated is a mean predicted value based on the mean values estimated amongst a set of individuals of the putative parents. The model of Sorensson (1993) suggests additive genetic control of quantitative traits of the bipinnate leaf of species of *Leucaena*. Sorensson's (1993) hybrid leaf model has been successfully used to assist in the identification of one spontaneous hybrid in *Leucaena* (Hughes and Harris, in press).

Many readers will no doubt have encountered trees which they suspect may be hybrids during the course of their work. The practical steps to investigate and identify unknown hybrids are discussed in Section 10.6.

5.4 Taxonomic treatment of hybrids

There are two ways to refer to or name recognized hybrids (Wagner, 1969; 1983; Stace, 1975). Designating hybrids according to the hybrid formula (*e.g. L. esculenta* × *L. leucocephala*) is maximally informative but cumbersome and inconvenient, especially if the hybrid is common and/or in cultivation. The alternative, that of naming a hybrid as for any other species (*e.g. L.* ×*brachycarpa*, where the '×' before the species name is used to indicate that a species is a hybrid) is more convenient and nomenclaturally stable, although less informative than the hybrid formula and carries with it the hazard of over burdening the literature with extra names. There is no consensus which is best and the two options appear to be have been used arbitrarily by different authors. Wagner (1969; 1983) suggested naming hybrids only if they are common, conspicuous or especially important for one reason or another (*e.g.* economically important in cultivation), and it is generally agreed that at least some such hybrids should be named (Stace, 1975). This compromise avoids the proliferation of names for very rare and sometimes ephemeral hybrids, but provides stable and convenient names for common and important ones.

In *Leucaena*, hybrids have been referred to almost universally by the hybrid formula, perhaps because of the emphasis on, and abundance of, artificial hybrids. Some hybrids have been widely referred to by the identity codes provided under the University of Hawaii system which designates artificial hybrids as KX1, KX2, KX3. Although these codes are now widely used and reasonably well known, they are no more informative than names or hybrid formulae. Furthermore, some hybrids have been numbered simply as K1000, K1001 *etc.* as for non hybrid accessions. In *Leucaena*, there is a good case for naming common, conspicuous or especially important hybrids. Two such hybrids are named in forthcoming publications (Hughes and Harris, in press; Hughes, in press) (see below).

5.5 Spontaneous hybrids

Most authors have suggested that natural hybridization is infrequent in *Leucaena*, precluded by geographic isolation of species in their natural range (Sorensson and Brewbaker, 1994, Brewbaker and Sorensson, 1994). In areas such as northern Central America (Guatemala and Honduras), where species of *Leucaena* (apart from *L. leucocephala*) are rarely cultivated or transported (*c.f.* Mexico), species distributions are indeed generally without overlap (strictly allopatric). In a few areas distributions of different species virtually meet but do not overlap (parapatric). Lack of intimate species mixtures (sympatry) in natural stands is striking in these areas.

The high crossability found in *Leucaena* means that when previously isolated species are brought together in cultivation, there is virtually unlimited scope for the production of spontaneous hybrids. Indeed, if two species are cultivated together the chances are three-to-one that they will be cross-compatible. It is clear that indigenous domestication and use of *Leucaena* species as minor food plants in many parts of Mexico has resulted in widespread movement of species, bringing previously isolated species into contact with each other (artificial sympatry) (Section 4.6) facilitating spontaneous hybridization in many areas. While a significant number of putative spontaneous hybrids have been reported from indigenous orchards or '*guajales*' of *Leucaena* in Mexico (Table 7), only two have so far been investigated in sufficient detail (Hughes and Harris, 1994; in press) to confirm their hybridity and identities beyond doubt.

As well as indigenous domestication, more recent introduction, cultivation and domestication of species of *Leucaena* as exotics (Chapter 9) has brought many previously isolated species into contact, again facilitating spontaneous hybridization. There are numerous observations of hybrids which are the result of crossing between species growing in research arboreta, field trials or wider cultivation of species of *Leucaena* as exotics (*e.g.* Bray, 1986; Lammers, 1940; Dijkman, 1950; Hutton, 1981; Hutton and Tabares, 1982; Hughes and Harris, 1994; in press; Timyan, 1996). However, few of these hybrids have been examined and documented in sufficient detail to ascertain the true extent of spontaneous hybridization in such situations.

An annotated list of putative spontaneous hybrids is presented in Table 7. There is no doubt that this list is incomplete as many more such hybrids have probably occurred than have been noted and recorded. Three spontaneous hybrids whose identities have been established beyond doubt are discussed in more detail below as examples of how such hybrids may occur, how they may be investigated, and what their characteristics and significance may be.

***L. leucocephala* × *L. pulverulenta*.** The first reports of the occurrence of putative spontaneous hybrids in *Leucaena* were between *L. leucocephala* and *L. pulverulenta* from parts of western Java, Indonesia where these two species have been in cultivation since around 1900 (Brewbaker, 1988; Dijkman, 1950; Lammers, 1940; Lowry *et al.*, 1984). This cross apparently occurs spontaneously with ease whenever the self incompatible *L. pulverulenta* (diploid, 2n=56) is grown near *L. leucocephala* (tetraploid, 2n=104) (Brewbaker, 1988). The *L. leucocephala* × *L. pulverulenta* hybrids are triploid and variably fertile. While F_1 hybrids (2n=80) are fertile, subsequent generation hybrids are extremely variable in chromosome number (2n=56-104; Gonzalez *et al.*, 1967) and may be completely sterile or very weakly fertile. Hybrid individuals were noticed by foresters in Indonesia because of their outstanding growth and lack of seed production. In Indonesia the hybrids are known by the common name '*lanang*' or 'male *Leucaena*', possibly due to their vigour and stature (Dijkman, 1950) or because they are seedless (see below). These hybrids have been cultivated in Indonesia as shade trees over tea and coffee for several decades (Section 9.4). The same hybrid has also been reported from southern Texas, U.S.A. by Correll and Johnston (1970) who stated simply that *"where L. leucocephala and L. pulverulenta have been planted together, some hybridization has occurred"*. Although the precise limits of the natural distribution of *L. pulverulenta* in northern Mexico and south Texas are poorly known due to cultivation, it seems likely that the Texan hybrids are also the result of cultivation of both, but certainly one of the parents, and are thus spontaneous rather than truly natural.

L. leucocephala* × *L. esculenta (Figs 10E-F and 8F). Putative hybrids between *L. leucocephala* and *L. esculenta* were reported from Mexico (Sorensson and Brewbaker, 1994) and Colombia (Hutton and Tabares, 1982). Following these unconfirmed reports, the identities of eight putative hybrids collected in five states in southern Mexico were investigated in more detail by Hughes and Harris (1994) and confirmed using a combination of geographical, morphological, molecular and ethnobotanical evidence. In all eight hybrid individuals examined in that study, molecular data indicated that the female parent was *L. leucocephala* but subsequently Hawkins and Harris (in press) encountered one hybrid individual with *L. esculenta* as the female parent. This concurs with data from artificial crossing (Sorensson and Brewbaker, 1994) which showed that crosses with *L. leucocephala* as the female parent produced more seed. These hybrids show broad, but not half-way, morphological intermediacy between the two parent species in a range of leaf, flower, shoot and bark characters (Figs 12). They are closer to *L. leucocephala* in quantitative traits due to the recognized dosage effect due to ploidy (see above; Hughes and Harris, 1994; Sorensson, 1993; 1995). Hybrids are easily recognized using leaf material alone (Fig 12), and by their striking lack of pod production despite virtual year-round and abundant flowering.

Hybrids between *L. leucocephala* (tetraploid 2n=104) and *L. esculenta* (diploid 2n=52) are triploid. All the hybrids observed in Mexico are seedless and seed sterility has been confirmed in artificial hybrids (see below). Given that vegetative propagation is not known to occur naturally in *Leucaena*, each hybrid tree observed in Mexico must have arisen as separate spontaneous F_1 hybrids. Despite this lack of persistence, this hybrid is relatively frequent and widespread, albeit sporadic in occurrence in six States in south central Mexico (Figs 10E and 13). It was collected first in Morelos in 1982 and more than 25 individuals have now been recorded with only limited field exploration. It is undoubtedly more common in Mexico than has been realized up to now. Given the wide present day sympatry of the two parent species (Fig 13) and the apparent ease with which the hybrid occurs under these circumstances, it is likely to become even more common in the future. It is named for these reasons using the epithet '*mixtec*' in the forthcoming taxonomic monograph (Hughes, in press).

The name '*mixtec*' refers to the role that human interference by the Mixtec and other pre-Columbian peoples of central Mexico played in the origin of this hybrid species. By bringing *L. esculenta* and *L. leucocephala* into cultivation and into artificial sympatry (Section 4.6), the opportunity was created for this hybrid to arise, almost certainly within the last 2000 years. It grows almost exclusively in suburbs of towns and villages, in gardens, backyards and orchards ('*guajales*') where the parent species are cultivated for pod production. Due to their lack of pod production, hybrids are widely recognized and known by local people in Mexico today by the name '*guaje macho*' (male Leucaena). Sometimes trees are rogued because of the lack of pods (due to interest in edible pod production in these areas; Chapter 4), but in other areas are retained as attractive ornamentals.

Hutton and Tabares (1982) showed that hybrids between *L. leucocephala* and *L. esculenta* have also arisen spontaneously outside Mexico, where the two species were cultivated in the research arboretum at CIAT, Colombia. The recent discovery of two *L. leucocephala* × *L. esculenta* hybrids in Dakar, Sénégal (Fig 10F) (Hughes and Harris, 1994) was a surprise. While *L. leucocephala* is commonly cultivated and weedy throughout Dakar, *L. esculenta* is apparently rare although it was recorded by Berhaut (1956) and cited by Lock (1989). Again this indicates the apparent ease with which this hybrid occurs. As *L. esculenta* is more widely introduced into areas where *L. leucocephala* is common and naturalized, hybrids between these two species may also become more common outside Mexico.

L. leucocephala* × *L. diversifolia (Fig 8E). An initial hypothesis of hybridity between *L. leucocephala* and *L. diversifolia* was postulated to account for scattered trees which were clearly different from, and morphologically intermediate between, these two species growing in parts of Veracruz, Mexico (Sorensson and Brewbaker, 1994; Zárate, 1994) and Huehuetenango, Guatemala where the only commonly growing species of *Leucaena* are *L. leucocephala* and *L. diversifolia*. Botanical specimens which closely resemble these putative hybrids were later encountered amongst collections from Jamaica, Dominican Republic, the Philippines and Papua New Guinea.

The identity and characteristics of these putative hybrids were investigated in detail by Hughes and Harris (in press) using combined geographical, morphological and molecular evidence. Hybridity and the identity of the putative parent species *L. leucocephala* and *L. diversifolia* were supported by four of the criteria normally used to verify hybrids. Hughes and Harris (in press) showed firstly, that the hybrids occur in areas where the two parent species are always present, and, in most cases, where no other species of *Leucaena* are found. Secondly, they exhibit a high degree of intermediacy in a set of quantitative leaf and pod traits (Fig 14) and RAPD markers. Finally, and most convincingly, they closely resemble artificial hybrids between the two putative parent species. Hughes and Harris (in press) showed that leaf morphology of the hybrids does not differ significantly from that predicted by the hybrid leaf expression models of Sorensson (1993).

Zárate (1994) noted the occurrence of what he believed were hybrids between *L. leucocephala* and *L. diversifolia* (treated by him as *L. diversifolia* subsp. *diversifolia*) from around Temascal, Oaxaca, Mexico and attributed these to *L.* ×*brachycarpa*. *L. brachycarpa* was originally named from Jamaica, and is now known to be the same as *L. diversifolia* (Hughes and Harris, in press; Hughes, in press; Harris, unpubl.). The occurrence of *L. leucocephala* × *L. diversifolia* hybrids in Jamaica, has perhaps contributed to the confusion surrounding the identity of *L. brachycarpa* and indeed all the material from Jamaica. For example, botanical specimens of the hybrid were misidentified as either *L. brachycarpa* or *L. leucocephala* by taxonomists. All three taxa occur in close proximity to Hope in the Parish of St. Andrew, Jamaica.

The *L. leucocephala* × *L. diversifolia* hybrid is named by Hughes and Harris (in press) using the specific epithet '*spontanea*' in reference to its spontaneous occurrence whenever the two parent species are brought together in cultivation. Material of this hybrid from scattered locations in Veracruz, Mexico, Guatemala, Dominican Republic, Jamaica, the Philippines and Papua New Guinea was examined by Hughes and Harris (in press). Timyan (1996) reported that the hybrid also occurs spontaneously in Haiti. It is abundant, as far as is known, only in parts of the State of Veracruz in Mexico (Fig 8E) and elsewhere appears sporadically as scattered individuals. All the known trees occur in disturbed areas, including gardens or backyards, coffee plantations and secondary vegetation on roadsides. As discussed by Hughes and Harris (in press), it is very likely that these hybrids arose following novel artificial sympatry of the two parent species in cultivation. That this is the case for the hybrids in the Dominican Republic, Jamaica, and the Philippines, where both parent species are introduced, is not in doubt. In Papua New Guinea, it is not clear whether hybrids arose spontaneously there, as suggested by Howcroft (1994), or were derived from spontaneous crosses which had arisen in the CSIRO trial plantings in Townsville, Queensland, Australia from which seed (accession CPI 33820), thought to be of *L. diversifolia*, was sent to Papua New Guinea in the late 1970s (Bray, pers. comm.). Bray suggests that this *"seed was harvested from field nurseries* (in Townsville) *and could well have contained any number of hybrids"*. The hybrids, of whatever origin, proved to be high yielding and have sometimes been called '*Mexican giant*' in Papua New Guinea (Howcroft, 1994). In Mexico and Guatemala, both parent species are also cultivated, *L. leucocephala* for pod production (Section 4.3) (*e.g.* in

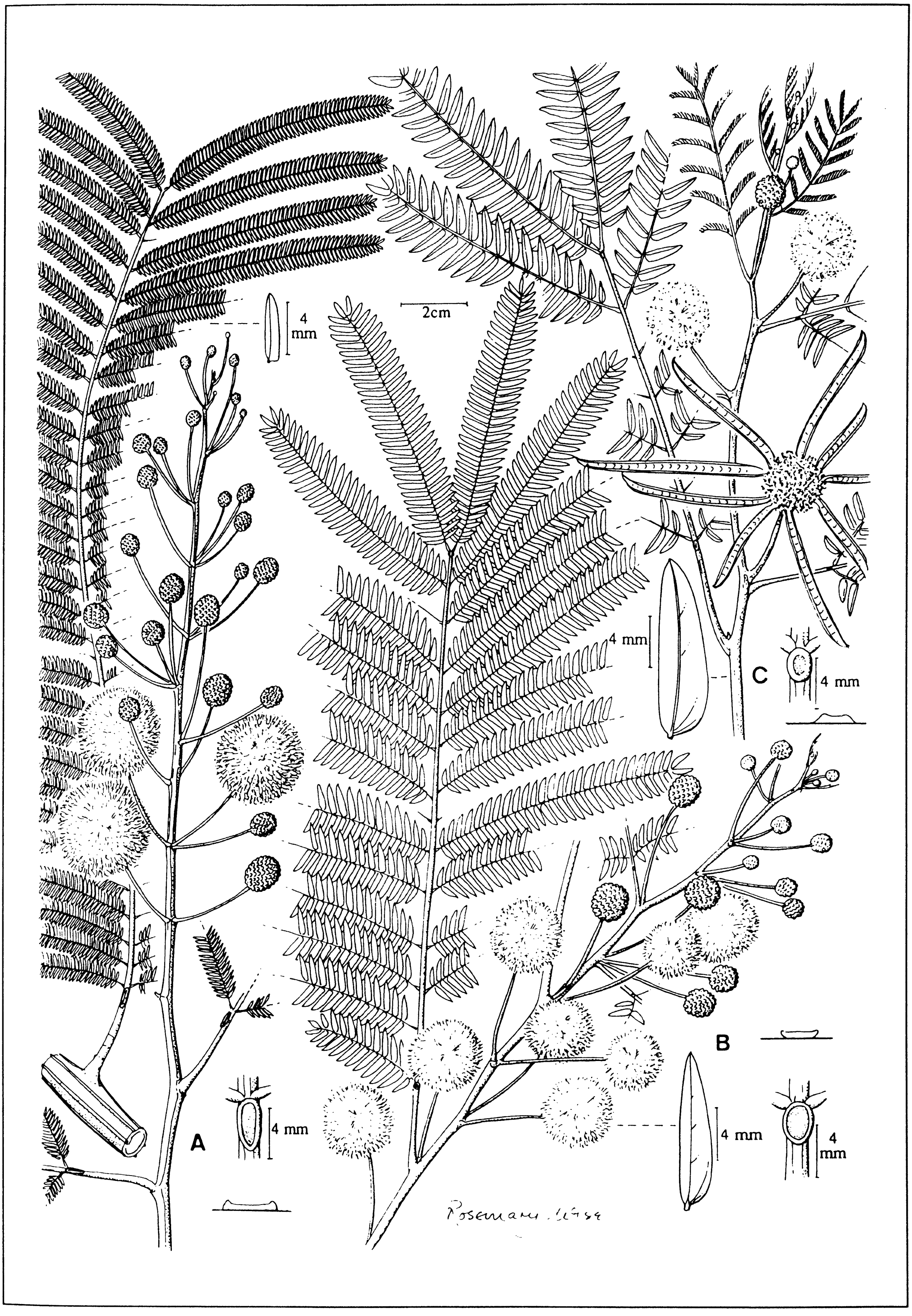


Figure 12. **A.** *L. esculenta*; **B.** *L. leucocephala* × *L. esculenta* hybrid; **C.** *L. leucocephala* subsp. *glabrata*. Drawing first published in *Plant Systematics and Evolution*.

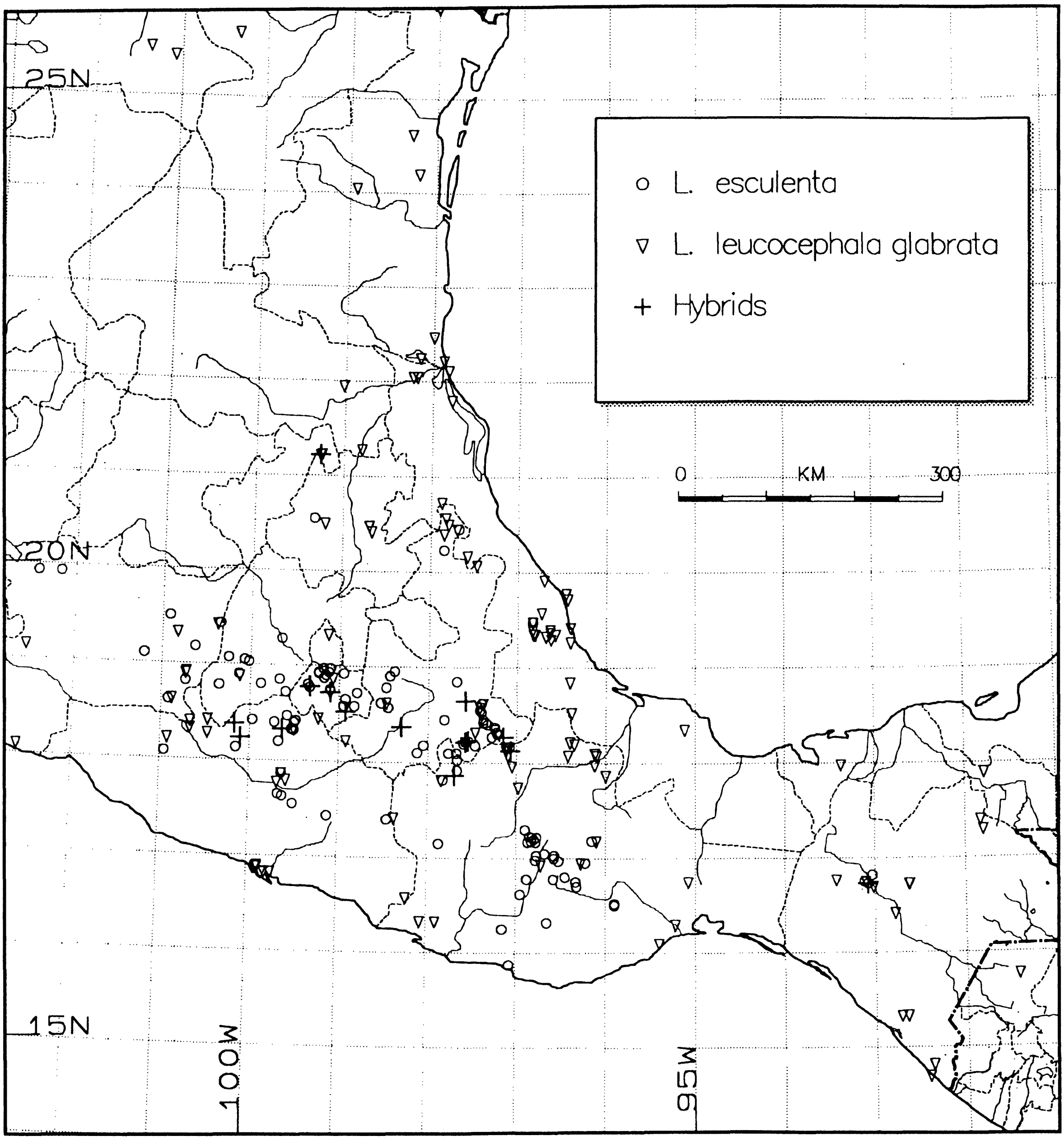


Figure 13 Map of south central Mexico showing the distribution of *L. esculenta, L. leucocephala* subsp. *glabrata* and *L. leucocephala* x *L. esculenta* hybrids in six States in southern Mexico

informal orchards ('*guajales*') near Tuzanapan and Plan del Río, Veracruz, Mexico), and *L. diversifolia* primarily for coffee shade (*e.g.* widely around Xalapa and Coatepec, Veracruz, Mexico; near Barillas, Huehuetenango, Guatemala; in Jamaica). In all areas hybrids have thus apparently arisen spontaneously following cultivation. Given the very wide present day cultivation of both *L. leucocephala* and *L. diversifolia*, particularly as exotics, it is extremely likely that this hybrid is more widespread and abundant than current botanical collections suggest, especially as wide cultivation of the parent species is not entirely recent. For example, a botanical specimen of this hybrid was collected in Jamaica in 1903. Although segregation has been observed in advanced generation artificial hybrids (see below), no such segregation has been observed among the spontaneous hybrids in Mexico nor Guatemala, suggesting that most may be F_1 hybrids, but later generation and backcross material are to be expected. Without doubt, continued spontaneous hybridization and cultivation of artificially produced hybrids (see below) mean that this hybrid is likely to

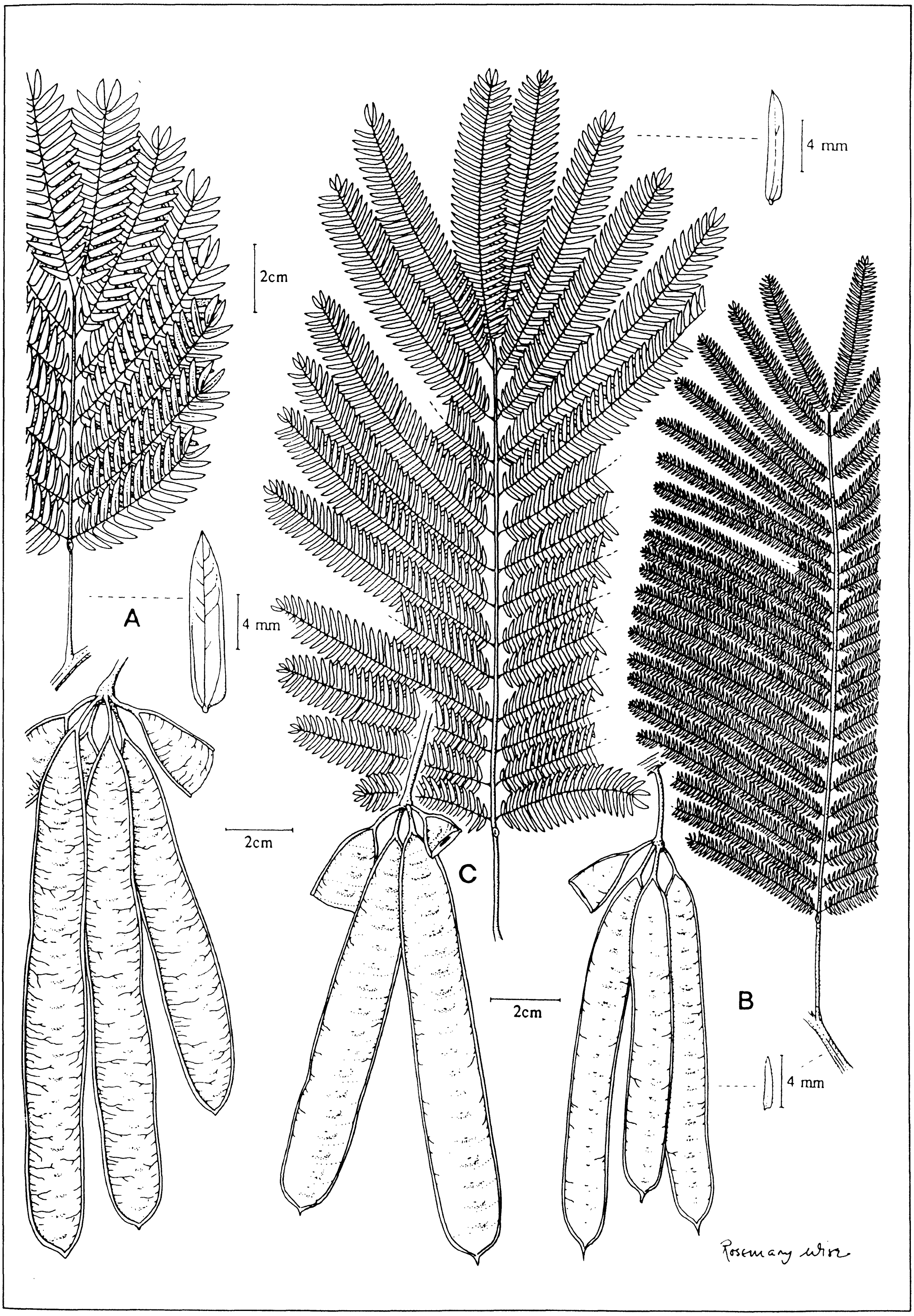


Figure 14 **A.** *L. leucocephala* subsp. *glabrata*; **B.** *L. diversifolia*; **C.** *L. leucocephala* × *L. diversifolia* hybrid. Drawing first published in *Plant Systematics and Evolution*.

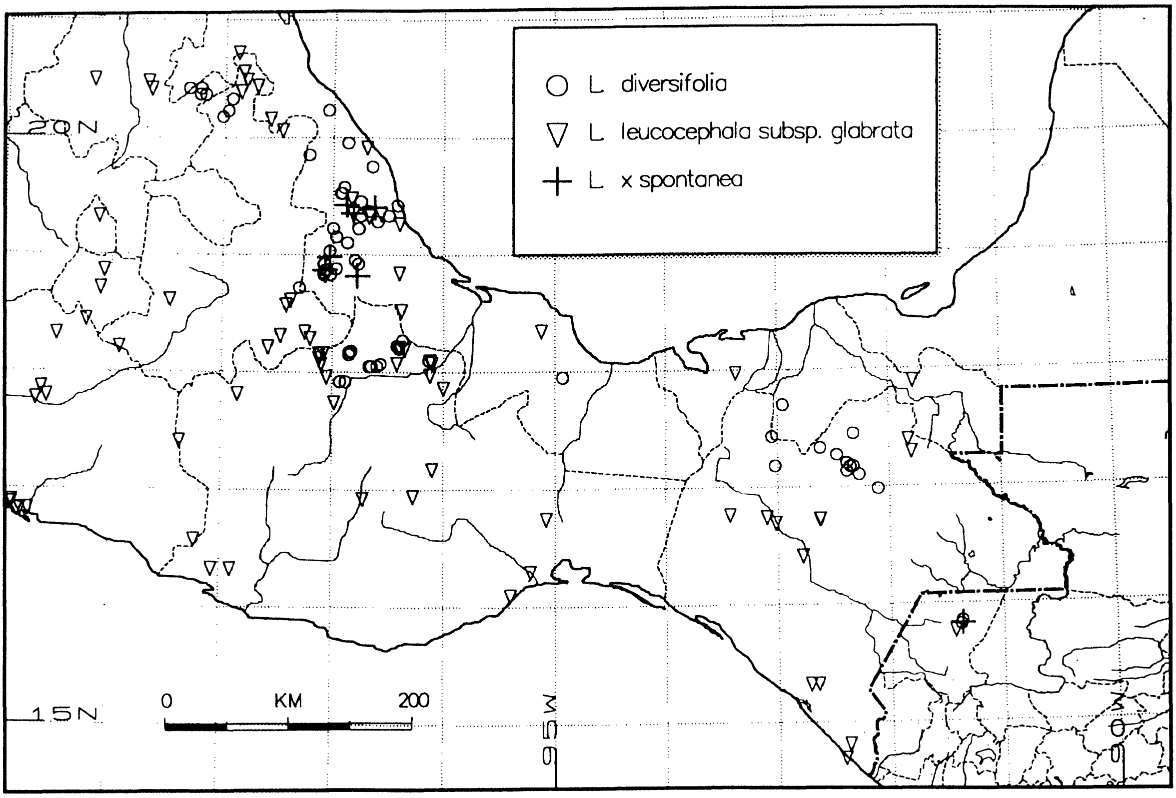


Figure 15 Map of part of southern Mexico spanning the Isthmus of Tehuantepec, showing the distributions of *L. leucocephala* subsp. *glabrata*, *L. diversifolia* and *L. leucocephala* × *L. diversifolia* hybrids

become even more common and widely distributed in the future.

Other spontaneous hybrids. Unconfirmed reports of putative hybrids from Mexico and Central America include *L. pulverulenta* × *L. diversifolia* (Zárate, 1982; 1994), and *L. pallida* × *L. esculenta* (Brewbaker, pers. comm.). Gutteridge and Sorensson (1992) reported use of a spontaneous hybrid between *L. leucocephala* and *L. trichandra* in frost tolerance trials in Queensland, Australia. Spontaneous hybrids between *L. leucocephala* and *L. trichandra* have been identified and propagated by grafting in Indonesia (Toruan-Mathius *et al.*, 1995). A further seven putative hybrids were discovered and collected by the author during field exploration (Table 7). Initial hypotheses of hybridity were postulated for these trees because of their unusual morphology (*i.e.* they could not be placed within any known species of *Leucaena*), their distribution and abundance (*i.e.* they all occur in areas of overlap between two or more species of *Leucaena* and are generally rare or infrequent) and, in several cases, their reduced fertility. The hybridity and parentage of these additional putative hybrids remain to be fully investigated and confirmed. In many cases their origins may be more complex than the three relatively straightforward hybrids discussed above. Some may be derived from crosses between more than two parent species. For example Hughes and Harris (1994) investigated the identity of an unusual putative hybrid tree (accession *Hughes* 1625) from the village of Santiago Acatepec, Puebla, Mexico where *L. leucocephala*, *L. esculenta*, *L. pallida* and *L. leucocephala* × *L. esculenta* hybrids are found in close proximity in cultivation, and *L. confertiflora* is found in degraded natural vegetation nearby. Molecular analysis using a combination of nuclear and chloroplast DNA markers, showed the maternal parent of this putative hybrid unequivocally to be *L. leucocephala*, but the paternal parent remained uncertain due to lack of species specific nuclear markers (Harris, unpubl.). Similar mixtures of three or four species of *Leucaena* growing in single villages in central Mexico are fairly common (Table 6; Chapter 4) and could account for some of the other putative hybrids *e.g.* from San Pedro Chapulco or Santa Catalina Oxolotepec (Table 6). Trees originally identified as *L. pallida* growing in the village of San Pedro Chapulco, Puebla, Mexico have since been hypothesized to be hybrids based on evidence from chloroplast DNA (Harris *et al.*, 1994a). The identity of this putative hybrid also remains uncertain. Several seedlots of this putative hybrid have been collected (*e.g.* OFI 52/87 and UH K804, K805, K806 and K953). As might be expected of hybrids, these accessions have performed differently in terms of growth, leaf chemical composition and psyllid resistance compared to other accessions of *L. pallida* in field trials (Austin *et al.*, 1995; 1997; Sorensson *et al.*, 1994; Shelton, pers. comm) and have also proved to be superior parents in subsequent artificial hybridization. There is clearly much still to be understood, and more to be found before the full intricacies of spontaneous hybridization facilitated by indigenous cultivation are revealed.

5.6 Significance of spontaneous hybrids

Spontaneous hybridization has a number of important implications for the conservation, management and utilization of *Leucaena* genetic resources. Spontaneous hybrids can present opportunities in the form of new hybrid species with traits attractive to farmers and breeders. However, they can also pose unpredictable risks in the form of new weeds, or contamination of native genepools. Spontaneous hybridization also means that there is a high chance of contamination of any open pollinated seed. Finally, such hybrids exacerbate confusion over identification.

New species. Hybrid origins have been proposed for three of the four known tetraploid species of *Leucaena*, *L. pallida* (Pan, 1985), *L. leucocephala* and *L. diversifolia* (Harris *et al.*, 1994a). The putative origins of *L. leucocephala* resulting from spontaneous hybridization, possibly in pre-Columbian cultivation between *L. pulverulenta* and *L. lanceolata*, and of *L. pallida*, are discussed in detail in Chapters 2 and 4. While such scenarios are based on circumstantial evidence and are speculative, pending more data, they appear to provide the most probable explanation for the origins of these two species. If correct, spontaneous hybrid origins for *L. leucocephala*, the most widely cultivated and economically important species in the genus (Sections 2.6 and 4.6), and possibly *L. pallida*, also prominent in recent domestication, would without doubt be the most significant results of spontaneous hybridization. However, even if these tetraploids arose in other ways, the contribution of spontaneous hybridization facilitated by indigenous cultivation has nonetheless been highly significant, giving rise to three confirmed hybrids which are now fairly common and widespread elements of the ruderal and urban flora of parts of south central Mexico as well as several other rarer and as yet unidentified hybrids. There is thus no doubt that spontaneous hybridization has resulted in new diversity in *Leucaena*, and will no doubt continue to do so in the future. For example, the widespread occurrence of sterile *L. leucocephala* × *L. esculenta* F_1 hybrids raises the possibility that speciation could occur via chromosome doubling and the formation of an allohexaploid species isolated from each of the parents as has happened in some other plant genera (*e.g.* Ashton and Abbott, 1992). In some cases useful and highly productive spontaneous hybrids may be accidentally or intentionally collected and used. The *L. leucocephala* × *L. diversifolia* hybrid planted in Papua New Guinea (see above), because it is self fertile, is one example of how seed of a valuable spontaneous hybrid may be unwittingly distributed and used.

New weeds. Spontaneous hybrids may also be unproductive and may present new and unpredictable threats of weediness (reviewed by Abbott, 1992; Abbott and Milne, 1995). Again the *L. leucocephala* × *L. diversifolia* hybrid provides an example of a potential weed. It is self fertile, produces prodigious quantities of seed from an early age, shows weedy tendencies on ruderal sites in Veracruz, Mexico, and, under the Australian Weed Risk Assessment system (Section 3.9), scored the same as the weedy *L. leucocephala*. The *L. leucocephala* × *L. diversifolia* hybrid is already widely distributed (see above), and may be expected to be as weedy as *L. leucocephala* (Fig 8E). Furthermore, multiple origins of a hybrid, as documented for *L. leucocephala* × *L. diversifolia* (Hughes and Harris, in press) provide insurance against extinction, particularly during the early stages of establishment and may increase the amount of diversity sampled from the parent species (Abbott, 1992) further enhancing the weedy risks associated with such hybrids.

Contamination of natural genepools. Hybridization, where accompanied by backcrossing to one or both parents can lead to infiltration of genes from one species to another. Such interspecific geneflow is known as introgression. Although there is no evidence for introgression following hybridization in *Leucaena*, backcrossing is likely to occur at least in the case of hybrids between *L. leucocephala* and *L. diversifolia* in Veracruz, Mexico. From a conservation standpoint, introgression can result in genetic contamination of native populations and consequent loss of adaptive gene complexes, or in extreme cases extinction of rare species (Levin *et al.*, 1996). Isolation from cross compatible species should thus be considered in conservation efforts, especially for rare species. For example *circa situm* efforts to conserve rare species such as *L. magnifica* (Chapter 8) could be compromised or displaced by cultivation of other species, such as *L. leucocephala* in or near the few small populations which remain of that species.

Seed production. Crossing amongst species of *Leucaena* cultivated as exotics in replicated field trials, research arboreta, and routine plantings also has important implications for use and conservation. Trials and research arboreta, because they can involve several to many species (in a few cases all species) planted in close proximity on a single site, are the ultimate form of artificial sympatry. It is well known that significant proportions of open pollinated seed derived from such plantings are crosses. For example Bray (1986: 350) states that *"much seed harvested in (and distributed from!) nurseries is of outcrossed origin"*; Brewbaker (pers. comm.) states that at the University of Hawaii Waimanalo Farm, *"any* (open pollinated) *seedling could have a variety of fathers"*. Howcroft (1994) reported that, in Papua New Guinea, not unexpectedly, spontaneous hybrids have occurred whenever species trials have been

Table 7 Putative spontaneous hybrids (*Hughes* accessions refer to botanical collections)

Putative hybrid	Status	Distribution	Characteristics
L. leucocephala* × *L. esculenta	Investigated in detail (Hughes and Harris, 1994); identity confirmed; sterile, triploid, anthropogenic origin; named using the epithet 'mixtec' (Hughes, in press)	Frequent but scattered sporadically in six States in south central Mexico; spontaneous in Sénégal and Colombia (Hutton and Tabares, 1982) following introduction of parent species.	Artificial hybrid created in Hawaii (K1000); seedless, fast growing and psyllid-resistant
L. leucocephala* × *L. diversifolia	Investigated in detail (Hughes and Harris, in press); identity confirmed, fertile, tetraploid, probable anthropogenic origin following cultivation of parent species; named using the epithet 'spontanea' (Hughes and Harris, in press)	Common in parts of Veracruz, Mexico, infrequent in Huehuetenango, Guatemala; spontaneous in Jamaica, Dominican Republic, Haiti (Timyan, 1996), Papua New Guinea and the Philippines following introduction of parent species	Artificial hybrid created in Hawaii (KX3) and promoted for tropical reforestation. Cool tolerant and moderately psyllid-resistant
***L. leucocephala* × ??**	Identity unknown. Single tree (*Hughes 1625* and *1788*). Investigated by Hughes and Harris (1994) without conclusion, although female parent likely to be *L. leucocephala*; possibly a three way hybrid; anthropogenic origin almost certain	Single tree in backyard in the village of Santiago Acatepec, Puebla, Mexico	Unknown
L. leucocephala* × ? *L. lanceolata	Identity unconfirmed; five trees (*Hughes 1745* and *1891*) derived from seed collected in a multi-species field experiment in Honduras; anthropogenic origin confirmed; weakly fertile	Five trees cultivated from seed on a farm near Villa Alícia, Siguatepeque, Honduras	Unknown, but fast growing
L. leucocephala* × *L. pulverulenta	Identity unconfirmed; reported by Dijkman (1950) from Indonesia and by Correll and Johnston (1970) from Texas; triploid, largely sterile, anthropogenic origin	Spontaneous in Western Java, Indonesia and in south Texas, USA where both parent species are in cultivation	Propagated by grafting in parts of Indonesia for tea shade in situations where seedless trees are preferred
L. leucocephala* × *L. trichandra	Identity unconfirmed; weakly fertile; probable triploid; anthropogenic origin	Apparently spontaneous in parts of Indonesia where both putative parents are introduced and cultivated (Toruan-Mathius *et al.*, 1995)	Cultivated from seed in Indonesia (accession RSB01) from grafted seed orchards
? *L. pallida* × ? *L. diversifolia*	Identity unknown; single tree (*Hughes 1317*) likely hybrid based on cpDNA analysis of Harris *et al.* (1994a); weakly fertile; anthropogenic origin likely	Single tree from near Huautla, Sierra Mazateca, Oaxaca, Mexico	Unknown
***L. pallida* × ??**	Identity unknown; single tree (*Hughes 1882*); probable anthropogenic origin; weakly fertile; several possible parent species growing in close proximity (*L. confertiflora, L. leucocephala, L. esculenta, L. pallida* and other putative hybrids)	Single tree, probably cultivated, in the village of San Pedro Chapulco, Puebla, Mexico.	Large tree, reputed to be >70 years old
? *L. pallida* × ? *L. confertiflora*	Identity unknown; fertile; several collections (*Hughes 1800* and *1801*) fertile, likely anthropogenic origin	Scattered trees in the village of Santa Catalina Oxolotepec, Puebla	Unknown

established. Hutton (1981) also documents spontaneous hybrids arising in the CIAT arboretum plots in Colombia. This is certain to be the case in many other countries also.

What is clear is that in order to guarantee the genetic identity and purity of open pollinated seedlots, seed must be produced in isolation from other species of *Leucaena* (Brewbaker, 1983; Wheeler, 1991). This poses obvious problems for the maintenance and regeneration of *ex situ* living collections (Bray, 1986) (Section 8.4) and routine seed production. Most *Leucaena* breeders and seed producers seem to accept that some contamination of open pollinated seed is inevitable, even with isolation of seed orchards, particularly given the pantropical and weedy distribution of *L. leucocephala*. If distribution of undesirable hybrids is to be avoided this relies on growers examining, detecting and roguing atypical seedlings.

Field trials and containment. The fate of spontaneous crosses, for example arising in trials, will always be unpredictable. Seed of most will no doubt fail to germinate, or seedlings will not survive. However, some may persist for many years in the soil seed bank and germinate later, for example after trials are cleared. Seed from trial plantings may also be collected deliberately by breeders, foresters or agronomists as a source of material for distribution to other researchers for new trials or to farmers for routine planting. Research station workers and other visitors to trials may also collect seed for planting back in their farms or gardens. For example, five putative hybrid trees derived from spontaneous crosses, possibly between *L. leucocephala* and *L. lanceolata*, in a species elimination trial, were found growing on the farm of a research station worker in Honduras 30km from the trial site. In this case the hybrids are apparently sterile or only weakly fertile and will almost certainly not persist.

Identification. Finally, spontaneous (and to a lesser extent artificial) hybrids will continue to present a difficult challenge to those who have to identify them and will tend to exacerbate existing confusion about identification of species. One example of the difficulties of identifying hybrids during seed collections from San Pedro Chapulco, Mexico was outlined above. In this case mis-identification of probable hybrids as *L. pallida* resulted in misinterpretation of trial results (*e.g.* those reported by Austin *et al.*, 1995; 1997 and Sorensson *et al.*, 1994, where one or more of the '*L. pallida*' accessions tested are probably in fact hybrids). Howcroft (1994) reported that there is considerable doubt about the identity of some taxa and putative hybrids in Papua New Guinea. Identification of hybrids is discussed in Section 10.6.

5.7 Artificial hybrids

Artificial hybrids are produced by hand crossing. This involves extracting pollen from the anthers of one species and applying it manually to the stigma of another, at the same time isolating the flowers from insects pre- and post-pollination and, for self fertile species, removing the stamens (emasculation) to avoid selfing. High crossability means that there are few genetic barriers to moving genes from one species to another via artificial hybridization. The high crossability of *Leucaena* species, combined with the diversity of useful traits encountered amongst species (Chapter 3) led Brewbaker and Sorensson (1990; 1994) to consider the whole genus as the potential genepool available for improvement and breeding. As stated by Brewbaker (1995: 76), *"exploiting hybridization promises almost unlimited genetic diversity for* Leucaena *improvement in agroforestry systems"*. The production of artificial hybrids has been the main focus of *Leucaena* breeding efforts to date (Brewbaker and Sorensson, 1990; 1994; Sorensson, 1995).

Tremendous progress in artificial hybridization has already been made in *Leucaena* (reviewed by Sorensson, 1995). A wide variety of hybrids have been produced, grown and evaluated. Many have shown useful combinations of traits; some show hybrid vigour (a phenomenon, known as heterosis, in which offspring of crosses perform better than the average of the two parents). A few hybrids have been widely tested, subsequently bred and introduced into cultivation with successful seed multiplication. Nevertheless, a number of technical problems have been encountered and there is much more to be done to fully realize the potential of artificial hybridization in *Leucaena*. Hybrid breeding and seed production are discussed in more detail in Chapter 9.

The first artificial hybrids in *Leucaena* were created amongst five species in Hawaii (Gonzalez *et al.*, 1967). At that time the primary interest was in breeding a low mimosine *Leucaena* (Section 3.7). This work provided the first indication of the high crossability within the genus. The hybrid between *L. leucocephala* and *L. pulverulenta* was studied with particular interest because of the low mimosine content of *L. pulverulenta*. However, the first artificial hybrid that reached widespread use was the intervarietal hybrid between the Salvador and Peru types of *L. leucocephala*. This hybrid combines the vigour of the Salvador type with the superior branching habit of the Peru type to produce the 'Cunningham' cultivar (Hutton and Beattie, 1976) which still is the mainstay of Australian *Leucaena* forage production systems, and which was subsequently introduced much more widely, becoming important in other countries such as Thailand (Manidool, 1983). Since these early efforts, hybridization programmes have expanded, mainly at the University of Hawaii, based on work by Brewbaker (1983), Pan (1985) and most notably Sorensson (1993) who undertook an ambitious crossing programme amongst 15 species spanning almost a decade. Continuous experimentation has refined techniques for isolation, emasculation, pollen manipulation (including collection, storage and analysis), pollination and seed protection (Brewbaker, 1983; Sorensson, 1988; 1995; Sorensson and Sun, 1990). A step-by-step guide to hand crossing was produced by Wheeler (1991) as part of a larger *Guide to Management of Leucaena Seed Orchards*. Most aspects of artificial hybridization are now routine, although further progress is being sought on pollen storage (which may limit some crosses due to non overlapping flowering times), manipulation of flowering and production of unreduced gametes (Sorensson and Brewbaker, 1987b; Sorensson, 1995; 1997). Lack of routine protocols for large scale vegetative propagation is also a major limitation in hybrid programmes (see below).

As noted earlier, there are three ploidy-specific types of hybrids, diploid (diploid × diploid), tetraploid (tetraploid × tetraploid) and triploid (tetraploid × diploid). Each has potential to contribute to breeding. However, by far the greatest emphasis so far has been on tetraploid hybrids used to modify *L. leucocephala* via hybridization and backcrossing with other tetraploid species. There has also been considerable interest in production of triploid hybrids which are generally seedless, and in production of tetraploid versions of 'triploid' hybrids via unreduced gametes (Sorensson and Brewbaker, 1987b; Sorensson, 1997). However, there has been comparatively little interest to date in use of diploid hybrids as raw broad based germplasm for further manipulation and domestication (Sorensson, 1995).

Tetraploid hybrids. Hybridization in *Leucaena* has been seen to date largely as a way to improve and broaden the genetic base of *L. leucocephala* by incorporating genes from lesser known species as a means of overcoming specific limitations (reviewed in Chapter 3), such as high mimosine, lack of cold tolerance or susceptibility to the psyllid (Brewbaker and Sorensson, 1990; 1994; Brewbaker *et al.*, 1989). This work has been concentrated on hybridization amongst three of the four known tetraploid species, *L. leucocephala, L. diversifolia* and *L. pallida* which are completely cross compatible and were considered to be the 'primary genepool' by Sorensson and Brewbaker (1994). The three hybrids, *L. pallida* × *L. diversifolia* (KX1), *L. leucocephala* × *L. pallida* (KX2) and *L. leucocephala* × *L. diversifolia* (KX3) have thus been the main focus of attention and illustrate both the potential and some of the difficulties of hybrid breeding. Two of these have shown particular promise.

***L. leucocephala* × *L. pallida* (KX2).** The artificial hybrid between *L. leucocephala* and *L. pallida* (designated KX2 by the University of Hawaii) has perhaps caused more interest than any other over the last five years (Austin *et al.*, 1995; 1997; Brewbaker and Sun, 1996; Shelton and Brewbaker, 1994; Sorensson, 1995; Sorensson and Brewbaker, 1986; Sorensson *et al.*, 1994; Castillo and Shelton, 1994; Castillo *et al.*, 1994). This interest has been driven primarily by its excellent psyllid resistance and exceptional forage yields which match previous yields obtained from *L. leucocephala* prior to the psyllid (Austin *et al.*, 1997). It has a spreading branchy habit, ideal for forage production, excellent psyllid resistance, some cool tolerance, excellent seedling vigour (clear hybrid vigour or heterosis) and is a shy seeder, a set of traits that make it attractive for fodder use (Austin *et al.*, 1995; 1997; Brewbaker and Sun, 1996; Shelton and Brewbaker, 1994; Sorensson, 1995; Sorensson and Brewbaker, 1986; Sorensson *et al.*, 1994; Wheeler and Brewbaker, 1990; Castillo *et al.*, 1994). However, doubts remain over the nutritive value of KX2 leaves, which have a lower edible fraction, higher condensed tannin and lower digestibility than *L. leucocephala* (Wheeler *et al.*, 1994).

KX2 segregates wildly and, although it is self incompatible, it may segregate self compatible individuals in later generations (Sorensson, 1995). Castillo *et al.* (1994) and Wheeler *et al.* (1994) also showed that KX2 hybrid populations are highly variable in leaf condensed tannin content. This suggests that there may be good scope for selecting high yielding, psyllid-resistant trees with moderate condensed tannin content and acceptable digestibility (Castillo *et al.*, 1994; Bray, 1995b). Five cycles of recurrent mass selection for early growth, psyllid resistance and low leaf condensed tannin levels in populations of as many as 1500 have been undertaken in Hawaii to obtain stable KX2 lines (Brewbaker and Sun, 1996) which are high yielding, with highly nutritious foliage and good psyllid resistance (Wheeler *et al.*, 1994). Advanced generation F_6 hybrids developed from 15 families, known by the varietal name 'Ohana' (Hawaiian for extended family) have been used to produce seed which is now available commercially in small quantities from the Hawaiian Agricultural Research Centre (Austin and Osgood, 1996).

***L. leucocephala* × *L. diversifolia* (KX3).** As well as occurring spontaneously in a number of countries (see above), the hybrid between *L. leucocephala* and *L. diversifolia* has been created artificially in Hawaii (Brewbaker *et al.*, 1988; Brewbaker and Sorensson, 1990; Sorensson, 1995) and has caused wide interest amongst those concerned with tropical tree planting. Both parent species are tetraploid and self fertile (Brewbaker, 1983; Sorensson, 1989a); the hybrid has been shown to be a self compatible tetraploid and is a prolific seeder (Brewbaker and Sorensson, 1990; 1994). Compared to most other hybrids, seed production of KX3 is thus straightforward. It is strongly arborescent in habit and can be very vigourous, particularly on mid elevation sites where cooler conditions do not favour the growth of *L. leucocephala* (Brewbaker and Sorensson, 1987a; Brewbaker *et al.*, 1988). It shows moderate, and possibly adequate psyllid resistance, for wood production, or for forage production under low-moderate psyllid pressure. Open pollinated seed of this hybrid was widely distributed from Hawaii in the last decade, particularly to Asian countries for experimental field testing as one entry in the Leucaena Psyllid Trial network (*e.g.* Glover, 1988). The prolific seeding of this hybrid means that it has the potential to spread and become weedy (Fig 8E) (Sections 3.9 and 5.6).

Although F_1 hybrids are reasonably uniform, segregation has been observed among advanced generation progeny of KX3 (de Freitas *et al.*, 1991; Sorensson, 1995). De Freitas *et al.* (1991) observed considerable variation in flower colour amongst F_2, F_3 and F_4 generation material and aneuploidy with 86-103 chromosomes as well as the normal 104. Segregation in F_2 and subsequent generations can produce both individuals of exceptional vigour and stunted trees of little value and early roguing of seedlings of open pollinated seed is needed. In order to create more stable lines of KX3, several generations of selfing and recurrent selection for habit, vigour and cool tolerance have been undertaken (Brewbaker and Sun, 1996).

Sterile triploid hybrids. Alongside tetraploid hybrids, many authors have discussed the attractions of sterile or near sterile, seedless or virtually seedless triploid hybrids (Brewbaker, 1988; Brewbaker and Sorensson, 1990; Brewbaker and Sun, 1996; Dijkman, 1950; Lammers, 1940; Lowry *et al.*, 1984; Sorensson, 1995). Interest in seedless hybrids has increased in recent years with growing awareness of the conservation and wider environmental problems posed by invasive weeds such as *L. leucocephala* (Hughes, 1994; 1995) (Section 3.9). The principal advantages of seedless hybrids are the elimination of weediness risks and concentration of photosynthates in leaf and wood rather than pod and seed production. Brewbaker and Sun (1996) estimated that 30-50% of photosynthate is used in pod and seed production by the self fertile and very seedy common varieties of *L. leucocephala* subsp. *leucocephala*. They postulated that seedlessness could therefore contribute to major increases in wood and leaf yields. However, seedless hybrids tend to have extended flowering periods due to inhibition of seed set (Stace, 1975; Brewbaker and Sorensson, 1990; Hughes and Harris, 1994) and may therefore devote significant resources to production of extra flowers. Nevertheless, several seedless triploids have proved to be extremely vigourous although diversion of photosynthates has not been proven (Sorensson, 1995). Seedless hybrids are thus viewed as environmentally benign for planting in conservation sensitive environments and agroforestry systems where weediness of seedy *L. leucocephala* can be a problem. Finally, seedless hybrids may prove to be attractive ornamentals with their extended flowering periods (Brewbaker and Sorensson, 1990).

The first sterile, or near sterile triploid hybrid to be used commercially was the *L. leucocephala* × *L. pulverulenta* hybrid which had arisen spontaneously in Indonesia (see above). Interest in this hybrid arose in Indonesia because of problems of natural regeneration and weediness of seedy *L. leucocephala* when planted as a shade tree over tea and coffee. The sparsely seeding hybrids were noticed and subsequently propagated by grafting (Dijkman, 1950). Wider interest in this hybrid elsewhere was driven by attempts to breed low mimosine lines by combining *L. pulverulenta*, with its known low mimosine content (Section 3.7), with *L. leucocephala*. With this in mind this hybrid was recreated artificially in Hawaii (Gonzalez *et al.*, 1967), Australia (Bray, 1984; 1986; Bray and Fulloon, 1987; Bray *et al.*, 1988), India (Gupta, 1990; Gupta *et al.*, 1986), and Colombia (Hutton, 1985). As well as having lower mimosine content, it proved to be extremely vigourous (Gonzalez *et al.*, 1967), significantly out yielding *L. leucocephala* (by 70% in leaf production and 100% in wood production) (Bray, 1986; Bray *et al.*, 1988). Quite apart from the obvious propagation difficulties, expectations that this hybrid might be a highly productive, high quality forage plant were short lived due to its overwhelming susceptibility to the psyllid (Section 3.4). Multiple breeding objectives (*e.g.* vigour, low mimosine, high nutritive value) which may change (*e.g.* to add psyllid resistance) can make the ideal hybrid a complex and elusive moving target. The *L. leucocephala* × *L. pulverulenta* hybrid remains an attractive fodder tree in areas with low psyllid pressure such as northern India (Gupta, 1990) where dry season leaf retention was also found to be superior to *L. leucocephala*.

A set of other sterile or near sterile triploid hybrids have been created and have proved to be fast growing, offering diverse combinations of useful traits. The *L. leucocephala* × *L. esculenta* hybrid has been artificially recreated in Hawaii, designated as 'accession' K1000, (Sorensson and Brewbaker, 1994; Brewbaker and Sun, 1996). The seed sterility of this triploid has been verified in artificial hybrids in Hawaii (Brewbaker *et al.*, 1989; Sorensson, 1995) and Colombia (Hutton, 1988) and has been attributed to chromosome irregularities observed at meiosis (Hutton and Tabares, 1982) and consequent low pollen viability of between 1-8% (Hughes and Harris, 1994) and 13% (Hutton and Tabares, 1982). The *L. leucocephala* × *L. esculenta* hybrid is an extremely vigorous and leafy tree (Fig 8F), shows outstanding psyllid resistance, and being seedless, poses no risk of weediness, making it one of the most attractive *Leucaena* hybrids for reforestation assuming the problems of propagation can be overcome (Brewbaker *et al.*, 1989; Brewbaker and Sun, 1996). The copious gum produced by some individuals of this hybrid has been noted to be similar in composition to gum arabic (Brewbaker and Sorensson, 1990; 1994).

Other seedless triploid hybrid combinations, such as *L. leucocephala* × *L. trichandra* or *L. diversifolia* × *L. pulverulenta* (Hawaii accession K1001) also have the potential to combine high psyllid resistance, cold tolerance and vigour (Sorensson, 1995). Triploid hybrids between *L. leucocephala* and *L. trichandra* apparently arose spontaneously in Indonesia (Toruan-Mathius *et al.*, 1995) and have been created in Hawaii (Sorensson, 1995). They set few seeds, have good *in vitro* dry matter digestibility, are highly psyllid-resistant and moderately cool tolerant (Sorensson, 1995; Toruan-Mathius *et al.*, 1995). In order to take advantage of the great genetic variability now known to characterize *L. trichandra* (Sections 3.8 and 6.3), choice of accession or provenance to be used in any crosses of this hybrid will be critical; superior accessions from south east Guatemala (Sections 3.8 and 6.3) should be included.

5.8 Conclusions

The history of *Leucaena* since Man first arrived in Mexico several millennia ago is one of progressive disturbance of natural populations, disruption of species distributions, cultivation, and of spontaneous hybridization. Anderson (1949) was amongst the first to note the close association between habitat disturbance and hybridization. He emphasized the importance of human movement of plants, bringing otherwise isolated species into contact with weedy, domesticated and incipiently domesticated species and ecological disturbance which may create the ecological niches in which hybrids may become established and thrive. Since Anderson's pioneering work on hybrids many examples of interspecific hybridization following introduction of one species into the range of another have been documented (reviewed by Abbott, 1992; Abbott and Milne, 1995). Ecological disturbance continues to accelerate virtually throughout Mexico and Central America; farmers there continue to exchange, cultivate and experiment with different species of *Leucaena*; it seems probable that spontaneous hybrids will become even more common than they are already as a result of indigenous domestication.

At the same time, introductions of *Leucaena* species outside Mexico and Central America have accelerated dramatically in the last decade, both geographically and in terms of numbers of species and provenances (Section 6.2; Appendix 3). There are few tropical countries where *L. leucocephala* is not now cultivated, and in many it is extensively naturalized and weedy (Section 3.9). This means that any other introduced species is likely to encounter at least *L. leucocephala*. Several spontaneous hybrids which have arisen amongst species of *Leucaena* when planted as exotics have already been documented. This unprecedented movement of larger numbers of species will undoubtedly spawn a new wave of spontaneous hybrids in coming years. Hybridization will be promoted by weak crossing barriers, unspecialized pollinators, long flowering periods of some species and habitat disturbance.

The potential of artificial hybridization to create new, adaptable, highly vigourous, high quality, and, if desired, seedless hybrids has already been demonstrated. Although only a handful of artificial hybrids are so far in routine use, and problems of hybrid seed production or vegetative propagation remain to be overcome, with modest investment in breeding, there are good prospects to realize this potential more fully. Planting of *Leucaena* is likely to be dominated by artificial hybrids in the future.

The words of Weiner (1994: 244 and 242) aptly sum up the domestication, ancient and modern, of *Leucaena* - *"We bring strangers together to make strange bedfellows, and we remake the beds they lie in, all at once...... Thus, our disturbances hybridize both the environment and the species. We are hybridizing the planet".* There is no doubt that we are, either directly or indirectly, hybridizing *Leucaena* and that hybrids, either spontaneous or artificial, will be increasingly prominent and important in the future. The end point of this process is difficult to envisage. There are few examples of other woody genera with high interspecific crossability whose species have been widely cultivated and introduced. Two genera that provide a possible vision of the future of *Leucaena* are *Salix* and *Populus*. *Salix* species are notorious for their high crossability (Mosseler, 1990) and proliferation of spontaneous hybrids following introduction and cultivation (Meikle, 1984; Cremer *et al.*, 1995). For example, in UK 64 hybrid combinations are known to occur (Stace, 1991) and there are several examples of loss of integrity of native *Salix* species following spontaneous hybridization with introduced species and cultivars (White, 1994). Ten of the UK *Salix* hybrids are between three species, one is a hybrid between four species (Stace, 1991) and the possibility of a single hybrid made up of all the species occurring in Britain has been mooted (Meikle, 1984). In Australia at least seven different two-way and two three-way hybrids have resulted so far from the 100 or so introductions of species and varieties of *Salix* (Cremer *et al.*, 1995). This has resulted in new hybrid species, new weeds, problems of identification (Meikle, 1984; Stace, 1991; Cremer, 1995), difficulties of containment of hybrids in the nursery trade, and growing concerns, in Australia, about the undesirable impacts of willows on riparian environments (Cremer *et al.*, 1995). The scale and impact of hybrids in *Salix* provide some likely scenarios for the future development of *Leucaena*.

Box 4 Hybrids

- Evidence that hybridization has been a significant process in the evolution of *Leucaena* is provided by known polyploidy, confirmed and unconfirmed reports of spontaneous (semi-natural) hybrids, evidence for cpDNA introgression, and high crossability. Once the potential for hybridization is considered then hybrids assume even greater importance as there are many more artificial than spontaneous hybrids. Artificial hybridization has been the main focus of *Leucaena* breeding efforts to date.

- 77% of the possible 120 two-way interspecific combinations between 15 tested species produced viable seed indicating high crossability in the genus. Species of *Leucaena* have apparently evolved in geographical isolation from each other with few genetic barriers to hybridization.

- Reliable methods have been developed to detect natural or spontaneous hybrids using a combination of morphological and molecular data.

- While natural hybridization appears to be infrequent in *Leucaena*, precluded by geographic isolation, it is clear that indigenous domestication in Mexico has resulted in wide movement of species, bringing previously isolated species into contact with each other thereby facilitating widespread spontaneous hybridization. More recent introduction and cultivation of *Leucaena* species as exotics across the tropics has mirrored this process also resulting in a series of spontaneous hybrids. Nine different spontaneous hybrids have been detected so far and the identities of three confirmed beyond doubt.

- Spontaneous hybrids present both opportunities, in the form of new hybrid species with traits attractive to farmers and breeders, risks in the form of new weeds, genetic contamination of native populations through introgression, and problems for seed production and identification.

- Exploiting artificial hybridization promises almost unlimited scope and genetic diversity for *Leucaena* improvement in agroforestry systems. The potential to create adaptable, highly vigourous, high product quality, psyllid-resistant, and if desired, seedless hybrids has been amply demonstrated. Interest in artificial hybrids has focused so far mainly on three of the four tetraploid species. There is also growing interest in the development of sterile triploid hybrids which may be highly productive, psyllid-resistant and, being seedless present no risk of weediness.

- Although only a handful of artificial hybrids are so far in routine use, if problems of hybrid seed production and vegetative propagation are overcome, there are good prospects to fully realize the enormous potential of hybridization. Planting of *Leucaena* hybrids and spontaneous hybridization mean that hybrids will become increasingly important in the future.

6 Germplasm collections

6.1 Introduction

Topics covered in this chapter include the history and status of the major *Leucaena* seed collections, the differing sampling strategies they employed and, related to this, a summary of what is known about patterns of variation within species. A short section on future collecting priorities is included. Discussions on seed multiplication strategies, domestication, and issues relating to access to genetic resources are discussed in Chapter 9. Practical aspects of seed collection, storage, and pretreatment are covered in Chapter 7. The major *Leucaena* seed collections are summarized in Table 8 and the specific origins of the handful of most widely cultivated accessions listed in Table 12, Chapter 9. The recently compiled *World Leucaena Catalogue* (Bray *et al.*, 1997) provides a comprehensive list of seed accessions with standardized passport data for all the major *Leucaena* collections and is an important source of more detailed information. Detailed data and information about the OFI *Leucaena* seed collections is included in Appendix 2.

6.2 History of introduction

The genetic resources of *Leucaena* have been under scrutiny as a source of useful plants for at least the last two millennia. Incipient domestication of *Leucaena* species for food use in Mexico (Chapter 4) meant that *Leucaena* seed was already being collected and transported within Mexico in pre-Columbian times. There is evidence to suggest that the distributions of widely used species such as *L. esculenta* were greatly extended within Mexico by this process. Seed of a wide range of *Leucaena* species continues to be transported around Mexico today as species continue to be introduced into cultivation in new areas.

Leucaena leucocephala. The first introduction of *Leucaena* outside Mexico and Central America was of the shrubby *'Common'* type of *L. leucocephala* belonging to subsp. *leucocephala*, which is reported to have been introduced to the Philippines before 1815 (Merrill, 1912). Communication between Spain and the Philippines during the Spanish occupation was via Mexico and relied on the annual Spanish government galleons that sailed between Acapulco and Manila from 1521 until 1815 (Merrill, 1912). During this period nearly 200 tropical American species including a number of well known legume trees such as *Acacia farnesiana, Gliricidia sepium, Pithecellobium dulce, Prosopis juliflora* and *Samanea saman* along with *Leucaena* were introduced (Merrill, 1912). *L. leucocephala* is recorded in Blanco's (1845) Flora of the Philippines (cited in Merrill, 1918) but beyond this the precise date of introduction is not known although some speculate that it may have been introduced before 1600 (Brewbaker *et al.*, 1972; Brewbaker and Hutton, 1979; Pound and Martínez-Cairo, 1983). By the early years of this century, in the Philippines, *L. leucocephala* was already *"so thoroughly naturalized, common and widely distributed that the casual observer would consider it a native species"* (Merrill, 1912), again indicating that it had been present there for some time. The source within Mexico, of the original *L. leucocephala* material introduced to the Philippines is not clear. *L. leucocephala* is indeed found today abundantly around Acapulco, the area alluded to as the source by Brewbaker *et al.* (1972) and Pound and Martínez-Cairo (1983), but all trees from that area and indeed from most of the western Pacific coast of Mexico, belong not to subsp. *leucocephala*, but to subsp. *glabrata* (Fig 44). However, it is quite possible that seed and/or pods of subsp. *leucocephala* were transported to Acapulco from elsewhere in Mexico by the Spanish who were undoubtedly aware of the indigenous use of *Leucaena* for human consumption (Chapter 4) although the Spanish themselves apparently had little interest in eating *Leucaena* seeds (Zárate, 1997). The exact motivation for introducing *Leucaena* from Mexico to the Philippines remains unknown. Food use, use as feed and bedding for horses, as suggested by Brewbaker *et al.* (1972) and Pound and Martínez-Cairo (1983), or accidental movement provide possible explanations. Although pods and seeds of *Leucaena* are used for food in parts of Asia, including Indonesia, Thailand, the Philippines and Vietnam, today (National Academy of Sciences, 1984; Brewbaker and Hutton, 1979; Whiting, 1982; Manidool, 1983; Pound and Martínez-Cairo, 1983; Wirjodarmodjo and Wiroatmodjo, 1983, Brewbaker, 1987b; Sampet *et al.*, 1995), it seems unlikely that this was introduced by the Spanish from Mexico. It seems more likely to have been discovered there independently in forms compatible with local culinary practices through use of young leafy shoots as vegetables and in soups (Manidool, 1983), young seedling sprouts (3-day old roots) and preparation of fermented *tempeh* from *Leucaena* seeds in parts of Java, Indonesia.

By the late 19th Century subsp. *leucocephala* had spread or been introduced widely through Asia and Africa and it is now pantropical and recorded from the majority of tropical and subtropical countries (*e.g.* Lock, 1989 for Africa; Nielsen, 1992b for Malesia). Herbarium records confirm that subsp. *leucocephala* has been widespread in the Caribbean, Africa and Asia at least since the latter part of the 19th Century. Recent isozyme studies of more than 100 accessions indicate that naturalized populations of subsp. *leucocephala* outside its native range in the Americas comprise a single genotype (Brewbaker and Sun, 1996).

L. leucocephala subsp. *leucocephala* is a colonizer of ruderal sites and secondary or disturbed vegetation in many places such as the Philippines where Merrill observed it to be already very abundant in 1912. This has been attributed to its precocious year-round flowering and fruiting, abundant seed production, self fertility, hard seed coat, and ability to resprout after fire or cutting. It is now naturalized and weedy in many areas (Section 3.9). On some Pacific islands, spread was accelerated by aerial seeding for rehabilitation of eroded lands (*e.g.* on Guam: Debell and Whitesell, 1993) and on some islands such as Hawaii it now forms extensive dense monospecific thickets.

It is clear that subsp. *leucocephala* was introduced much earlier than subsp. *glabrata* (see below) which was widely introduced across the tropics only in the last few decades. Thus, most pre-1950 agronomic investigation and most Flora treatments (*e.g.* Brenan, 1959, Fl. Tropical East Africa; Brenan and Brummitt, 1970, Fl. Zambesiaca; Ross, 1975, Fl. Southern Africa; Elias, 1974, USA; Barreto Valdéz and Yakovlev, 1982, Cuba; Merrill, 1912, Fl. Manila, Philippines; Nielsen, 1992b, Fl. Malesiana), and references to naturalization and weediness (Section 3.9; Cronk and Fuller, 1995), refer to subsp. *leucocephala.*

That spread of subsp. *leucocephala* preceded subsp. *glabrata* was confirmed during testing of accessions from around the world for forage during the 1950s, which revealed all non Mesoamerican accessions to be of subsp. *leucocephala* (Hutton and Gray, 1959; Brewbaker *et al.*, 1972; Batson *et al.*, 1984). *L. leucocephala* subsp. *glabrata* corresponds to the '*Giant*' or '*Salvador*' type (Zárate, 1987a) recognized by agronomists in the 1950s and 1960s. Its superior vigour, erect habit and branching characteristics compared to the previously tested shrubby '*Common*' type (subsp. *leucocephala*), were recognized following introduction to Hawaii in 1945 of material collected near Jocóro, in Morazán Province, El Salvador (Brewbaker *et al.*, 1972; Brewbaker, 1980). Its designation as the '*Salvador*' type refers to this original collecting locality. Following trials in Hawaii (Brewbaker *et al.*, 1972) and Australia (Gray, 1967), one variety, designated K8 was formally released by the University of Hawaii (Brewbaker, 1975), and a handful of others (K28, K67, K72 *etc.*) followed. Active promotion of the '*Giant*' varieties for reforestation by national and international development agencies and numerous NGOs from the mid 1970s onwards (*e.g.* National Academy of Sciences, 1984; Philippine Council for Agriculture and Resources Research, 1978; International Development Research Centre, 1983; Kaul *et al.*, 1983 in India) meant that subsp. *glabrata* was moved around the tropics very rapidly and extensively (Pound and Martínez-Cairo, 1983; Brewbaker 1987b). Only a handful of self fertile accessions of subsp. *glabrata*, several of which originate from cultivated material from El Salvador, have been widely introduced leading to concerns about genetic vulnerability of single 'variety' plantations (Brewbaker, 1980; 1985; see below).

A third agronomic variant, the so called '*Peru*' type was recognized (Gray, 1968; Brewbaker and Hutton, 1979; Brewbaker, 1980) based on material introduced to Australia from Argentina, but of supposed Peruvian origin, and characterized by the erect habit of the '*Giant*' type but the greater branchiness of the '*Common*' type. The '*Peru*' type apparently belongs within subsp. *glabrata*, although the original material has not been traced to verify this. The bred line '*Cunningham*', released and widely planted in Australia (Gray, 1967; Hutton and Beattie, 1976), is a cross between the '*Salvador*' and '*Peru*' types and is therefore also attributable to subsp. *glabrata*.

Other species. Although early (pre-1850) introductions of *Leucaena* were apparently confined to *L. leucocephala*, several other species were introduced to Asia, and a number of Caribbean islands for cultivation as shade trees over coffee or cacao in the second half of the nineteenth century. For example *L. pulverulenta*, *L. diversifolia*, and possibly *L. trichandra* were introduced by Dutch foresters to Indonesia in the late 1800s (Dijkman, 1950) and *L. diversifolia* to West Africa (Cameroon and Ivory Coast) and the Caribbean (Jamaica and Dominican Republic) at about the same time.

Introduction of the remaining species of *Leucaena* outside Latin America has occurred only in the last few decades. With the advent of genetic improvement, breeding and hybridization programmes, two major seed collections of *Leucaena* were assembled in Hawaii and Australia (see below). These collections included an increasing range of species which were grown initially in experimental trials in Hawaii and Australia. However, greater momentum for closer scrutiny of the full range of lesser known species and their wider introduction and use in hybridization came with the spread of the psyllid in the mid 1980s and early 1990s (Section 3.4). In 1987 NFTA established a network of trials, the Leucaena Psyllid Trial (LPT), to evaluate psyllid resistance and growth rates of various *Leucaena* species and hybrids (Glover, 1987). This involved the introduction of a number of accessions of *L. diversifolia, L. pallida* and their hybrids with *L. leucocephala* for the establishment of field trials initially in the Philippines, Thailand, Indonesia and Australia. The LPT programme expanded to include both more species, such as *L. collinsii, L. esculenta* and *L. trichandra* and hybrids, and more trials - 28 in total in 16 countries throughout Asia (Wheeler and Brewbaker, 1989; 1990). As the OFI seed collections were assembled and completed in 1993, seed of an even wider range of species has become available for the first time. A handful of early OFI *Leucaena* seedlots (*L. collinsii* subsp. *zacapana*, *L. leucocephala* subsp. *glabrata* and *L. shannonii*) were distributed as part of the international Dry Zone Hardwoods, DZH trial network (Hughes and Styles, 1984). The observed superior performance of *L. collinsii* subsp. *zacapana* on a range of sites was a notable result of this trial series (Stewart and Dunsdon, 1994). The completed OFI *Leucaena* seed collections have been used to establish a new trial network to test a wider range of species, provenances and hybrids on a wider range of sites across the tropics and this has led to a dramatic expansion in both the number of species introduced and the number of countries importing new material (Pottinger, 1995). By 1997, more than 80 trials had been established in more than 30 countries based on the OFI seed collections (Appendix 3) under the umbrella of LEUCNET (Shelton and Pottinger, 1995).

Protocols for introductions. Introductions of *Leucaena* species, in common with virtually all movement of plants around the globe, have been undertaken with minimal regulation (other than standard phytosanitary controls), little concern about the outcome, and lack of awareness about possible risks (Section 3.9; Hughes, 1994; 1995). However, the growing awareness of the problem of biological invasions in general (Williamson, 1996) and plant invasions in particular (Cronk and Fuller, 1995) means that regulation of species introductions in many countries is set to change. New protocols are adopting a guilty-until-proven-innocent approach with detailed risk assessment prior to permitting new introductions (Pheloung, 1995; Hughes, 1995). The implications of this for *Leucaena* and the risks associated with *Leucaena* species are considered in detail in Section 3.9.

6.3 Seed collections

With the emergence of *Leucaena* as an important forage plant, systematic seed collections started in the 1960s and since that time, three major collections of *Leucaena* species have been assembled by the University of Hawaii (UH), USA, The Commonwealth Scientific and Industrial Research Organization (CSIRO), Australia and the Oxford Forestry Institute (OFI), UK. The background, history, sampling strategies and status of these collections were reviewed by Hughes *et al.* (1995). This section is based largely on that review. A comprehensive catalogue of the major international and national seed collections of *Leucaena* has recently been compiled (Bray *et al.*, 1997).

University of Hawaii: Work to assemble the first germplasm collection of *Leucaena* was started by the University of Hawaii in 1962, initially based on miscellaneous seedlots acquired around the globe from a variety of cultivated non native sources of *L. leucocephala*. Systematic efforts to explore and collect seed from the natural populations of *Leucaena* began in the late 1960s with an expedition by Brewbaker in 1967 to Mexico and neighbouring countries in Latin America. This collection included a range of *Leucaena* species other than *L. leucocephala*, for the first time. Seed collections by researchers from Hawaii, led by Brewbaker, continued intermittently over the next 20 years with five more major expeditions in 1977, 1978, 1985, 1988 and 1997 sampling wild populations throughout Latin America (Brewbaker and Sorensson, 1994). By 1988, a large collection had been assembled and grown in Hawaii including more than 1000 accessions representing most taxa, although still dominated by *L. leucocephala* which accounted for 541 accessions. Seedlots are documented with basic passport data held on a spreadsheet using the "K" number series running chronologically from K1 onwards. Seed from the Hawaii collection has been widely distributed for testing and includes the well known and widely planted K8 and K636 varieties of *L. leucocephala* and the K156 variety of *L. diversifolia* (Table 12). This collection also forms the core of several other large germplasm collections (approx. 90% of the USDA collection and a significant proportion of the NSSL, ILCA and IGFRI collections). Identities are verified from living collections in Hawaii.

CSIRO: From the mid 1950s up to the mid 1970s CSIRO assembled a largely opportunistic collection of 200 accessions, mainly of *L. leucocephala* from non native sources. Extensive targeted collections were made, in Mexico and Colombia, in 1978-79 by Bob Reid, working with Sergio Zárate. As well as increasing the range of variation available both in terms of numbers of species and variation within species. Particular attention was devoted to *L. pulverulenta* (for breeding for low mimosine) and *L. leucocephala* (from marginal environments both dry and cool) (Bray, 1986). Passport data is documented under the CPI (Commonwealth Plant Introduction) numbering system in the purpose designed UNIX-based data management system of the Australian Tropical Forages Genetic Resource Centre.

Oxford Forestry Institute: In the mid 1980s, OFI started to assemble a new *Leucaena* seed collection prompted by the discovery, or rediscovery, of a number of little known and potentially valuable species in Guatemala and Honduras, that had apparently been overlooked by previous collecting expeditions and by the realization that several of these species were under threat of substantial genetic erosion or even extinction (Hughes, 1986; 1988a; Hellin and Hughes, 1993). The main objective of the OFI programme was to assemble a comprehensive collection including all *Leucaena* species, but concentrating on lesser known species other than *L. leucocephala*. Over the period 1984 to 1993, a series of annual expeditions to Mexico and Central America allowed collections to be made in collaboration with the Forest Authorities and tree seed banks in the region. These collections are now complete and are documented using a customized seed database, SISTEM+ (Filer, 1997) (Appendix 2). Identities are verified from botanical voucher specimens deposited in major herbaria in Central America, Mexico, U.S.A. and Europe (Appendix 2).

National Collections: National collections or collections at regional centres such as ILCA or CIAT, are largely derived from these three international collections. In addition, several contain small numbers of unique accessions from their local areas. A good example would be the *L. trichandra* collection RSB01 from Indonesia (Oka, 1989). Within Mexico and Central America a number of agencies maintain seed collections of local species from natural populations. The national tree seed banks in Guatemala, Honduras and Nicaragua are notable in this respect and regularly collect seed from natural stands of a wide range of native *Leucaena* species, for direct use in tree planting projects.

Sampling strategies. The three major international seed collections employed different sampling strategies reflecting the contrasting methods applied in agricultural crop germplasm collections and forest tree improvement. The Hawaii and CSIRO collections were assembled essentially as for any crop germplasm collection with short duration collection expeditions, sampling widely across localities and including small but variable numbers of parent trees, the resulting seedlots termed accessions. An accession can be progeny from a single parent tree or from several trees, but rarely includes more than ten parents. Although this approach makes little attempt to select particular trees within natural populations or to assemble representative population samples, it allows cost effective sampling of as many sites as possible within the time available, ensuring coverage of as broad a range of environments as possible by sampling in relation to soil changes and microclimate. Unreplicated arboretum style trials are used to initially screen the large number of accessions collected, relying on seed increase from superior accessions for further evaluation and breeding.

In contrast, forest tree improvement programmes which have largely worked with out crossing species, follow highly structured sampling strategies in seed collections from wild populations. Longer seed collection expeditions enable large numbers of parent trees to be sampled across populations, avoiding neighbouring trees, to assemble bulk collections termed provenances. These collections usually include a minimum of 25 parent trees and often up to 50-60, and are expected to be genetically diverse and amenable to subsequent selection and breeding. This permits seed source identity to be maintained and provenance variation to be utilized as a starting point in any improvement programme. The larger quantities of seed collected are sufficient to supply many trials and other plantings such as seed production stands. In many cases, individual tree seedlots are also collected at the same time. Such an approach, with maintenance of family identity, allows establishment of family-based half-sib progeny trials and seed orchards (out crossing species) and aims to maintain much stricter control over pedigree and a much broader genetic base within provenances. It also provides material for investigation of population genetics (*e.g.* Chamberlain *et al.*, 1996). This was the approach followed in the OFI collections.

Duplication. Table 8 summarizes the numbers of accessions in the main seed collections of *Leucaena*. It is immediately apparent that there is a significant degree of duplication, roughly estimated here as greater than 25%, across collections.This means that the total number of original or unique accessions is almost certainly considerably fewer than 3,000. Duplication can take several forms. Firstly, there may be internal duplication within collections, but this is quite limited within the major *Leucaena* seed collections. Secondly, duplication of seedlots between collections can occur when material is exchanged and distributed. For example, some material from the UH collection is represented in the CSIRO collection and vice versa, and the USDA collection is largely derived from the UH collection *etc.* Finally, duplication can arise through independent collection of material by different organisations from the same population. Just how common, or important, this latter aspect is, has not been investigated. The percentage duplication figures shown in Table 8 are approximate estimates and refer to the second type of duplication across different collections. A full analysis of all types of duplication and detailed identification of duplicate collections remain to be carried out for *Leucaena* although Bray *et al.* (1997) make a start on this process.

The domination of *L. leucocephala*, although diminished following the new OFI collections, remains significant with over 50% of all collections of that one species. Given the marked lack of genetic diversity that has been found within *L. leucocephala* (Sections 6.3 and 9.3; Harris *et al.*, 1994b), and particularly within the shrubby subsp. *leucocephala* (Brewbaker and Sun, 1996), a large fraction of these accessions are likely to be genetically uniform and therefore redundant. In contrast, the much higher level of genetic variation known to exist in other species such as *L. diversifolia*, *L. trichandra* (see below), and others, is only sparsely represented in the collections. A few species such as *L. confertiflora, L. cuspidata, L. involucrata, L. matudae* and *L. pueblana* are represented by only a handful of accessions.

The number of accessions in a collection gives little indication of either the level of genetic diversity sampled or the availability of seed. Levels of genetic diversity within accessions vary according to the number of parent trees sampled, and other factors (Section 6.4). Seed quantities for many of the accessions are very limited. For example more than 500 of the accessions held by the University of Hawaii have 100 or fewer seed in stock. CSIRO aims to maintain 200g of seed available of all its accessions but has succeeded in this only for self fertile types. A similar situation applies to the USDA and some other collections. The NSSL and Kew collections are in essentially 'permanent' long term storage and are 'not accessible'. This effectively means that a large fraction of the accessions listed in Table 8 are not available for use and testing without regeneration. Larger seed quantities are available for the remainder of the accessions and for the much of the OFI collection. With three major independent international germplasm collections each with their own numbering systems and a series of national and other collections partially derived from them, also with their own numbering systems, it is not surprising that considerable confusion surrounds the identity of material in many collections. A world *Leucaena* catalogue (Bray *et al.*, 1997) provides a complete list of accessions, standardised passport data, some cross referencing between collections and a rough assessment of overall duplication. However, there is no

Table 8 Major *Leucaena* seed collections showing numbers of accessions (modified from Hughes *et al.* (1995). A listing of all accessions and associated data is provided in (Bray *et al.*, 1997)

Species[1]	UH[2]	USDA[3]	OFI[2,4]	CSIRO	NSSL[5]	Kew[6]	ILCA	IGFRI[7]	TOTAL
L. collinsii	37	19	5(113)	10	-	4	4	11	198
L. confertiflora	2	-	5(18)	4	-	-	-	-	24
L. cuspidata	-	1	5(20)	2	-	-	1	-	24
L. diversifolia	54	53	16(88)	15	1	3	21	29	264
L. esculenta	55	23	2(34)	13	2	2	3	10	142
L. greggii	32	7	3(50)	9	-	-	1	30	129
L. involucrata	-	-	2	-	-	-	-	-	2
L. lanceolata	47	35	7(83)	41	1	3	3	35	248
L. lempirana	-	-	2(82)	-	-	2	-	-	84
L. leucocephala	541	493	19(78)	590	125	4	102	268	2201
L. macrophylla	17	6	4(30)	19	-	2	2	12	88
L. magnifica	5	-	3(55)	-	-	2	-	-	62
L. matudae	3	-	1(14)	-	-	-	-	-	17
L. multicapitula	3	-	2(20)	-	-	1	-	2	26
L. pallida	20	12	6(50)	15	-	-	10	1	108
L. pueblana	?	-	3	-	-	-	-	-	3
L. pulverulenta	18	14	3(33)	45	4	2	6	10	132
L. retusa	18	4	1(10)	13	1	-	2	12	60
L. salvadorensis	3	1	6(123)	-	-	3	1	10	141
L. shannonii	33	23	6(130)	12	1	2	4	55	260
L. trichandra	54	?	11(80)	15	?	2	?	?	151
L. trichodes	23	4	2(50)	15	-	2	1	11	106
SP.[8]	-	14	-	-	5	-	13	-	32
TOTAL	965	709	1166	818	140	34	174	496	4502
ESTIMATED %DUPLICATION[9]	10[10]	90[10]	0	30	100	100	100	100	>25

UH=University of Hawaii, USA; USDA = United States Department of Agriculture, USA; OFI = Oxford Forestry Institute, UK; CSIRO = Commonwealth Scientific and Industrial Research Organisation, Australia; NSSL = National Seed Storage Laboratory, USA; ILCA = International Livestock Centre for Africa, Ethiopia; IGFRI = Indian Grassland and Fodder Research Institute, India.

1 Botanical subspecies and varieties are combined within species
2 The large number of hybrid accessions held at UH and OFI are not included in this listing
3 G.A.White, USDA, personal communication, 1992
4 First number is provenances, second is total number of individual tree or half-sib family accessions
5 S.A.Eberhart, NSSL, personal communication, 1988. Long term, essentially permanent storage, 'not accessible'
6 Long term, essentially 'not accessible'; derived directly from OFI collections; all accessions are bulked seedlots derived from 20-50 parent trees
7 From Gupta, V.K. (1990). Genetics and Breeding of *L. leucocephala*. Unpubl. paper, IGFRI, Jhansi, India
8 Hybrids in the NSSL and ILCA collections are placed in this category
9 Duplication here refers to cases where the same seedlot is represented in two or more collections. Figures are broad estimates, not based on detailed investigation. Internal duplication is estimated to be low in all collections
10 Duplication between the UH and USDA collections is high (probably over 90%): the USDA collection being derived largely from the UH collection

accurate assessment of levels of duplication across collections, or levels of redundancy due to uniformity of genetic material. There is a clear need to rationalize individual collections.

6.4 Variation within species and sampling strategies

A clear understanding of the level and structure of variation between and within populations of species is needed to design seed collection sampling, subsequent genetic improvement, and genetic conservation strategies (Schnabel and Hamrick, 1990; Surles *et al.*, 1990). For example, data on genetic diversity within populations determines how many trees need to be sampled to incorporate all the alleles at a particular frequency. Similarly, data on variation between populations is needed to identify superior seed sources (provenances) and to maintain a broad genetic base for future breeding. Knowledge about absolute levels of diversity within populations is also important for out crossing species as heterozygosity and performance may be linked. Use of genetically diverse material may be necessary to prevent inbreeding depression during future generations. Given the importance of *Leucaena* in tropical agriculture and reforestation and the considerable efforts being made to collect, evaluate and hybridize species, it is surprising that there have been very few attempts to assess levels of diversity within species and their populations. Research has focused more on species diversity than diversity within species because of the known lack of diversity within *L. leucocephala* and the overwhelming focus on hybridization in genetic improvement (Chapter 5). Patterns of genetic variation among and within populations have remained little studied. Nevertheless, the few studies which have been carried out provide important pointers to patterns and levels of infraspecific genetic variation. In any study of the level and structure of variation within species of *Leucaena* a fundamental distinction must be made between self fertile species (*L. leucocephala, L. confertiflora* and *L. diversifolia*) and out crossing, self incompatible species (remaining species of *Leucaena*) (Sorensson and Brewbaker, 1994).

Agronomic traits. The traditional approach to assessment of forest or agricultural genetic resources has been to examine a combination of morphological and agronomic traits under controlled conditions in field trials or 'common-garden' experiments. Much of the evaluation work undertaken to date has concentrated on characterizing species rather than variation within species. However, a number of trials have included multiple accessions (provenances) providing preliminary indications of useful variation within species. These studies indicate that some species are much more variable than others. For example, high levels of diversity in growth, psyllid tolerance, leaf chemical composition (especially tannins which range from zero to very high), and leaf and pod morphology (Figs 17, 18 and 22) have been found amongst provenances of *L. trichandra* (Stewart *et al.*, 1991; 1993; Austin *et al.*, 1995; Hughes, in press; Stewart and Dunsdon, in press) and this species is apparently the most variable in the genus. *Leucaena diversifolia, L. lanceolata* and *L. pallida* also show significant variation amongst provenances, although not to the same degree as *L. trichandra*. In contrast, very limited variation has been detected in growth or other traits within other species such as *L. collinsii, L. salvadorensis* and most notably *L. leucocephala* (Brewbaker *et al.*, 1972; Wheeler *et al.*, 1987; Arora, 1981). These observations are to be expected given that, in general, the magnitude of genetic diversity is highly correlated to both the size of the geographic range and the environmental amplitude encompassed within that range. *L. trichandra* is the most widely distributed species of *Leucaena* (Fig 66) (after *L. leucocephala* which is widely cultivated), a distribution that encompasses a wide range in altitude, from 200 to 2300m, and site conditions. In contrast, species such as *L. collinsii* and *L. salvadorensis* occupy much more restricted distributions and environmental amplitudes.

Molecular studies. In addition to morphological and agronomic traits, the application of biochemical and molecular techniques has provided a powerful set of tools for the study of genetic diversity within and among plant populations. The most widespread and commonly used approach is the analysis of isozymes (Soltis and Soltis, 1990a). Isozyme analyses have been used to examine variation within *L. diversifolia* (Pan, 1985), *L. leucocephala* (Harris *et al.*, 1994b; Brewbaker and Sun, 1996) and most notably for species within the *L. shannonii* alliance (*L. shannonii, L. magnifica, L. salvadorensis* and *L. lempirana*) by Chamberlain *et al.* (1996). More recently other techniques including chloroplast DNA restriction fragment length polymorphisms (RFLPs) and randomly amplified polymorphic DNA sequences (RAPDs) have been used to study genetic diversity, but their application to examine diversity within species of *Leucaena* has been limited to a study of *L. leucocephala* by Harris *et al* (1994b) and the broader study of chloroplast DNA RFLP data by Harris *et al.* (1994a) (Section 2.6).

The *L. shannonii* alliance. The most detailed, thorough and complete study of variation between and within populations of species of *Leucaena* is that of Chamberlain *et al.* (1996) which examined isozyme variation within and between 10 populations of four species, *L. shannonii, L. magnifica, L. salvadorensis* and *L. lempirana*. Six enzyme systems were used to identify 10 polymorphic putative loci which were assessed on the basis of the average number of alleles per locus, the observed mean heterozygosity, expected mean heterozygosity and the percentage of polymorphic loci, as measures of genetic diversity within populations. Very low levels of variation were observed within two populations of the narrowly restricted endemic, *L. magnifica* which were each found to be monomorphic at five enzyme loci. This fits with the general picture of lower levels of within population variation in narrowly restricted endemic species than in widely distributed species (Loveless, 1992). Intermediate levels of variation, comparable to those found more widely for tropical, predominantly out crossed, insect pollinated species, were found within populations of *L. salvadorensis* and *L. lempirana*. Of the four species included by Chamberlain *et al.* (1996), *L. shannonii* populations showed the highest levels of variation and were polymorphic at all seven enzyme loci. *Leucaena shannonii*, which occupies an extensive disjunct distribution (Fig 64), also showed higher between population variation than the species with more restricted distributions (Figs 48 and 41). Traditional agronomic, morphological and isozyme data thus support the general trend of greater diversity within more widely distributed species. Additional isozyme data will be forthcoming in the near future through work in progress to examine variation within *L. salvadorensis* (Lopes, unpubl. data) and *L. diversifolia* and *L. trichandra* (Harris, unpubl. data).

Leucaena leucocephala. Patterns of variation within *L. leucocephala* are of particular interest because of its economic importance, the extreme lack of diversity and associated limitations (Chapter 3) of the cultivated (and naturalized) material across the tropics, and because of interest in understanding the origin of this tetraploid species for which no unequivocally wild populations have been found (Section 11.10). Unfortunately, the few studies carried out to date provide only limited insights into patterns of variation within and between populations. While morphology and agronomic traits clearly distinguish the three subspecies *leucocephala*, *glabrata* and *ixtahuacana*, the considerable effort that has been devoted to field testing of new accessions of *L. leucocephala* has revealed only limited useful variation. Although one accession of subsp. *glabrata* (K636 from Coahuila, Mexico) was found to be significantly more psyllid-tolerant and less seedy than the widely used K8, K28, K67 and K72 varieties, most accessions were found to be identical (Brewbaker *et al.*, 1972; Wheeler *et al.*, 1987; Arora, 1981). An initial report of isozyme variation in 12 individuals of *L. leucocephala* concluded that very little variation existed in this species (Schifino-Wittmann and Schlegel, 1990). Brewbaker and Sun (1996) found that more than 100 accessions of '*Common*' type subsp. *leucocephala* material outside Mexico, were of a single genotype. It is also well known that only a small number of accessions of the '*Giant*' or '*Salvador*' type subsp. *glabrata* (K8, K28, K72, K636) have been distributed, and that this subspecies also has a very narrow genetic base outside Mexico (Brewbaker, 1980; 1985). In contrast to these studies of introduced material, Harris *et al.* (1994b) concentrated on analysing variation among accessions collected from Mexico and Central America. 324 individuals from 12 populations were assessed for isozyme diversity using three enzyme systems which were found to be polymorphic. Harris *et al.* (1994b) analyzed the variation in 18 different multi-enzyme phenotypes across the 12 populations but did not characterize enzyme banding patterns in terms of loci and alleles. Phenotypes not only distinguished between subspecies, but also identified inter-population variation within subsp. *glabrata*. Data indicated high levels of inter-population variation compared to intra-population variation as might be expected for a self pollinated species. More intensive sampling would be required to reveal geographic patterns of variation within *L. leucocephala*. Recent work in Hawaii has revealed high levels of heterosis in intervarietal hybrids of *L. leucocephala*, again indicating that there is significant genetic variation amongst accessions.

Population disturbance. Few undisturbed natural populations of *Leucaena* species remain following wholesale disturbance of the seasonally dry tropical forest where most species occur (Chapter 8). Seed collections are thus derived almost in their entirety, not from undisturbed primary genepools, but from a variety of fragmented remnant populations, secondary vegetation and incipiently domesticated (cultivated) populations, all of which have been significantly disturbed in one way or another. Virtually none of the OFI *Leucaena* seed collections has sampled undisturbed pristine forest. As discovered by Chamberlain *et al.* (1996), two populations of *L. lempirana* were found to have high levels of variation in terms of percentage of polymorphic loci and mean number of alleles per locus, but low mean heterozygosity due to a significant deficiency in the number of heterozygotes indicating that both populations are in severe genetic disequilibrium. The genetic implications of population disturbance remain to be more fully investigated, but similar disequilibria may be common. Many of the OFI provenance seed collections encompassed large areas in order to include a sufficient number of sample trees. For example, the 60 parent trees included in the OFI collection of *L. salvadorensis* from San Juan de Limay in northern Nicaragua collected in 1991, were sampled from a series of remnant populations scattered over an area of more than 100 km^2. Optimal sampling strategies in terms of number of trees sampled and spacing between sampled trees have thus had to be modified pragmatically and opportunistically. The goal of sampling has, in many cases, been reduced simply to sampling as much of the genetic diversity as possible in the time available. This means that the material sampled may bear little relation to expected levels of genetic diversity sampled from natural populations. Further than this, underlying geographic patterns among populations across the distribution of more widespread species are also likely to be disrupted. A mosaic of local variants, as found for *Gliricidia sepium* (Dawson and Chamberlain, 1996), rather than predictable patterns of between- and within-population variation, is likely for most out crossing species of *Leucaena*.

6.5 Future collections: gaps and priorities

The genetic resources of *Leucaena* species have now been as thoroughly explored and collected as almost any other tropical woody genus. Characterisation and evaluation of these collections, now in progress within

Box 5 Genetic Resources: collection and utilization

- The genetic resources of *Leucaena* have now been as thoroughly explored and collected as almost any other tropical woody genus with three major international seed collections comprising over 3,000 seedlots. Although gaps in these collections remain, and new species might still be found, the priorities are evaluation of species and within-species diversity in field trials and rationalization of collections to reduce duplication, rather than new collections.

- Historical introductions and the major seed collections have been dominated, until the last two decades, by one species, *L. leucocephala*, despite the great lack of intraspecific diversity in that species. Most other species appear to be more variable than *L. leucocephala*, variation is greater in more widely distributed species and some, such as *L. trichandra*, show high levels of infraspecific diversity.

- The OFI seed collections include all the known taxa of *Leucaena*, multiple provenance collections (bulked from 20-50 parent trees) of most species and 1166 individual tree half-sib family collections, providing a broad genetic base for evaluation in field trials, establishment of seed production areas and seed orchards and future hybridization and tree improvement.

- Very little of the genetic diversity assembled in the three major collections outlined above is currently available for routine use by *Leucaena* growers. Deployment of *Leucaena* has been characterised by promotion following seed increase from an extremely narrow genetic base. An approach to deployment of self-fertile tetraploid seed that employs multi-line varieties as genetically diverse composite seedlots is long overdue. A much more proactive approach to and increased investment in seed production is required.

LEUCNET, is the most urgent priority, rather than new collections. Furthermore, current seed collections need to be rationalized to reduce or at least clarify duplication and eliminate holdings of redundant material, mainly of *L. leucocephala*. This rationalization and evaluation will help to highlight gaps and priorities for future seed collections.

Nevertheless, despite the numerous expeditions to explore and collect the genetic resources of *Leucaena* over the last three decades and the relative ease with which even the more inaccessible areas can now be explored, there are without doubt significant gaps in the coverage of collections. Only a small fraction of territory occupied by *Leucaena* has been explored by collectors and several species are represented by only a handful of collections (Table 8). Priorities for new seed collections are:

- Species such as *L. confertiflora, L. cuspidata, L. involucrata, L. matudae* and *L. multicapitula* which are currently represented by only a handful of accessions are priority species for new seed collections.

- As promising species and provenances are identified from trials, new collections to sample greater variation between and within populations may be justified. For example, trials indicate that provenances of *L. trichandra* from south east Guatemala (CPI46568 and OFI 53/88) are significantly more psyllid-tolerant and vigourous than others. New and more intensive seed collections of *L. trichandra* from south-east Guatemala are needed to provide a secure base for the genetic development of this species.

- As new hypotheses of the origin of *L. leucocephala* (Sections 2.6 and 4.6) emerge, it is clear that fresh field exploration in central and northern Veracruz is justified to map the distributions of *L. pulverulenta* and *L. lanceolata* (the two putative parent species) in detail and explore possible locations where *L. leucocephala* could have originated.

Data from botanical specimens of *Leucaena* lodged in herbaria in Central America, Mexico, the U.S.A. and Europe along with those assembled during recent OFI field work, provide the most detailed and complete source of information to guide future field exploration and collection. Data from more than 2800 botanical specimens from 22 herbaria have been assembled during the OFI *Leucaena* research programme in the form of a botanical database using the Botanical Research and Herbarium Management System, BRAHMS (Filer, 1996). Detailed locality data can be retrieved and sorted by species, collector, geographic area (Country, State, Department, Municipality or individual locality), or year of collection, making this a powerful tool for planning collecting expeditions. Such data are particularly useful for day-to-day planning of routes and printouts of all localities by species or region are an essential tool to take to the field. Copies of this database are being distributed to key herbaria and are available from the author. Customized printouts, sorted to user's specification can also be prepared on request.

However carefully planned, field exploration of biodiversity and plant collecting is a hit-or-miss affair. Serendipity and opportunism are as important as careful planning (Iltis, 1988) and future exploration could uncover further surprises. The discovery of several species of *Leucaena* new to science (*L. confertiflora, L. involucrata, L. lempirana* and *L. magnifica*), all of them collected within a few yards of motorable roads, or in the case of *L. confertiflora* in cultivation in the village of San Pedro Chapulco in a small orchard (Zárate, 1984a; 1994) in the last 20 years, indicates that there may still be more to find. Nine of the 22 species of *Leucaena* are narrowly restricted endemics, their distributions spanning fewer than five degree grid squares (Table 10). Species which occupy such a small range may be hard to find. Furthermore, the identities of many spontaneous hybrids and the full intricacies of indigenous domestication remain to be investigated (Chapters 4 and 5). This may be only the end of the beginning of field exploration and collection of *Leucaena*!

7 Seeds: collection, processing, storage and pretreatment

7.1 Introduction

In general, the collection, processing and storage of seed of *Leucaena* species is straightforward. Seed can be dried and stored at low temperature and reduced moisture content following conventional seed storage methods. However, seed predation by bruchid beetles, seed pretreatment to overcome dormancy caused by hard-seededness, and *Rhizobium* inoculation can complicate seed handling and require specific protocols.

Seeds of species of *Leucaena* vary in shape from circular or ellipsoid to rhomboidal in a few species, but are uniformly flattened and lens-shaped in cross-section with a rich reddish brown, glossy seed coat, or testa which is marked on both sides with a U-shaped pleurogram. The most notable variation is in size which ranges from 4.5 mm long with up to 80,000 seeds per kg for *L. diversifolia*, to 12 mm long for *L. cuspidata, L. esculenta* and *L. salvadorensis* with as few as 8,000-10,000 seeds per kg for *L. esculenta* (data for all species in Chapter 11). The pods of all species are passively dehiscent with the seeds discharged by gravity.

7.2 Collection, handling and storage

Collection. *Leucaena leucocephala* produces prodigious quantities of seed from the first year, more or less continuously through the year as moisture permits and across a wide range of different environments (Gonzalez *et al.*, 1967; Pan, 1988). Heavy clusters of 5-10 (-45) pods are produced on each flower head and this has been attributed to self fertility. One other species, *L. diversifolia*, and the hybrid between *L. leucocephala* and *L. diversifolia*, which are also self fertile, are similarly precocious and produce abundant seed over an extended period of the year. However these two species and their hybrid are exceptional; the majority of species of *Leucaena* have strictly annual, seasonal and short (but somewhat variable) duration (2-5 months) flowering periods and do not flower and fruit quite so abundantly nor early.

For most species, seasonal flowering and fruiting mean that timing of seed collections is critical to coincide with peak ripeness. Variation in flowering and fruiting times across species may be considerable (Fig 4, Section 3.5). Time to ripening also varies among species, *e.g.* from 90-280 days from flowering to mature pods in Hawaii (Wheeler, 1991; Sorensson, 1992a). In the natural populations, some species such as *L. collinsii, L. lanceolata, L. lempirana, L. macrophylla* and *L. shannonii* ripen fruits within 3-6 months while others have longer maturation periods, of up to 8-9 months for *L. cuspidata*, and 9-11 months for *L. salvadorensis*. All *Leucaena* species have dehiscent pods and for most species the optimal collection period is 2-4 weeks. Green seed expands to a maximum size a few weeks before ripening but remains soft at that stage. Final ripening involves a reduction in seed moisture content and hardening of the seed coat, and is indicated by reduction in seed size and change in colour from green to rich reddish brown.

Extraction and processing. Ripe pods may be sun-dried to promote dehiscence and lightly threshed by hand to extract the seed. Seed can be separated from the empty pods and cleaned by screening and winnowing and further dried in the sun. By sunning seed for a day or two after extraction, seed moisture content is reduced and the majority of bruchid beetles emerge at that stage (see below). Simple winnowing separates the majority of beetle-damaged seed from good seed, although other methods including flotation in salt water (Sorensson, 1993) and gravity table separation (Hughes, 1993) have also been used.

Storage. Storage of conventional seed requires reduction of metabolic activity. This is normally achieved by reducing seed moisture content and storage at low temperature. *Leucaena* seed can be stored under conditions of <10% moisture content at <+4°C for long periods (at least up to five years) while retaining high viability. In order to maintain low moisture content, seed must be stored in hermetically sealed containers. Seed viability in long term storage at lower temperatures (-20°C) has not been tested, but given the hard seed coat of most *Leucaena* species, seed can probably be stored safely for long periods (at least several decades). However, seed stored under poor conditions of high moisture content and temperature can rapidly lose viability. Seeds may be stored for short periods at ambient temperatures but it is always important to keep seeds dry and sealed in containers. Plastic bags of seed can cook rapidly if left in the sun.

Quarantine. Effective quarantine allows for the safe movement of germplasm without placing unnecessary restrictions. Although there is some information on actual and potential pests and pathogens of *Leucaena* (Boa and Lenné, 1995), there is currently little information on the likelihood of seed based transmission of them (Quiniones and Dayanm 1985). The possibility of introducing seed feeding beetles is an obvious hazard. Techniques, including insecticide treatments, to reduce the risk of moving seed beetles are discussed below. Seed may also treated with fungicides, such as *Captan* (recommended by Samuel *et al.*, 1994) to avoid transport of seed borne pathogens. One such disease is *Camptomeris* leaf spot (Fig 7H), caused by the fungus *Camptomeris leucaenae.*

Camptomeris causes leaf spotting and chlorosis, loss of leaflets, or whole leaves, and some dieback, often associated with secondary pathogens (Lenné, 1980). It is a potentially serious disease causing reduced forage yields and quality particularly in areas with >2000mm rainfall (Lenné, 1980; 1991). *Camptomeris* is widespread in Latin America and the Caribbean and has also been reported from Taiwan, the Philippines and India (Boa and Lenné, 1995). The mode of introduction of *Camptomeris* to these countries is not known, but movement on seed is a possibility (Lenné, 1980; Boa and Lenné, 1995). Fungicide treatment is designed to reduce the risk of spread of any seed borne diseases and *Captan* appears not to adversely affect germination or seedling growth (Samuel *et al.*, 1994).

7.3 Seed feeding beetles

The number of viable seeds of many plants, and particularly legumes, can be greatly reduced by seed feeding predators such as bruchid beetles. Typically, female adult bruchids lay eggs on young, unripe legume pods, larvae then chew into the pod and unripe seed, feed inside the seed, pupate and adults emerge when the pods and seeds are ripe leaving a round exit hole (Fig 8G). Seeds of all species of *Leucaena* are predated at some level in the natural populations by seed feeding bruchid beetles. The level of predation varies from less than 5% for some species such as *L. salvadorensis* to higher than 95% for species such as *L. pallida*. Where levels of predation are high, very large quantities of pods need to be collected in order to obtain a small quantity of clean seed.

Leucaena seed beetles are at the same time potentially hazardous and costly - to those concerned with efficient seed production in breeding programmes and seed orchards and safe international distribution of seed - and potentially beneficial and of great use - to those developing efficient biocontrol agents to mitigate the weedy or invasive tendencies of some *Leucaena* species (Hughes, 1996, Jones, 1996; Neser, 1994, 1996; Section 3.9). Knowledge of *Leucaena* seed beetles and a clear understanding of their host interactions is thus of some importance.

Leucaena bruchids and their host specificities were summarized by Hughes and Johnson (1996), building on earlier work by Johnson (1981; 1983; 1984; 1989; 1990), Johnson and Kingsolver (1976) and Johnson and Slobodchikoff (1979), and are shown in Table 9. This shows that in their natural ranges, species of *Leucaena* are predated by seven different species of bruchid in two genera, *Stator* and *Acanthoscelides*. The two species of *Stator* are known omnivores that feed on a wide range of Mimosoid legume genera, although they have been recorded from only a few species of *Leucaena*. In contrast, the 5 species of *Acanthoscelides* feed exclusively on *Leucaena*, and have not been recorded on any other host plant genus. Although this may indicate specificity to *Leucaena* within their native ranges, it cannot be taken to indicate specificity in relation to a wider and different range of host genera and species that would be encountered when bruchids are introduced elsewhere. Within *Acanthoscelides* the 5 species have been recorded from between two and 18 *Leucaena* host species. Two species, *A. macrophthalmus* and *A. mankinsii*, are notably ubiquitous being recorded from 18 and 15 species of *Leucaena* respectively. Thus within the genus *Leucaena* these bruchids are generalists and show little or no species level specificity. It is notable that *A. macrophthalmus* (Fig 8G), the species recently introduced accidentally to Australia (Jones, 1996) and proposed for release in South Africa (Neser, 1994; 1996), is the most ubiquitous of the 5 species based on host records. This means that it is likely to predate seeds of most, if not all, species of *Leucaena* which are planted in these countries.

Although the 5 *Acanthoscelides* species have so far been reported only sporadically from outside Latin America, and most notably, recently from Australia (Jones, 1996), *Leucaena* seeds may still be heavily predated in these areas by other generalist beetles. Records include the square necked grain beetle *Cathartus quadricollis* reported on *L. leucocephala* in the Dominican Republic (Pound and Martínez-Cairo, 1983), *Araecerus levipennis* (Coleoptera: Anthribidae) in Hawaii (Sherman and Tanashiro, 1956), *Araecerus fasciculatus* (Coleoptera: Anthribidae) on *L. leucocephala* in India (Singh *et al.*, 1981) and the Philippines (Braza and Salise, 1988).

Several measures can be taken to ensure that bruchid beetles are killed, and damaged seed removed, before seed is distributed. Exposure of seed to sun after extraction from pods for 1-2 days ensures that the majority of adult beetles emerge. Nevertheless, a small proportion of live adult beetles may remain inside the seed after sunning and drying. For this reason, it may be advisable to treat seed with insecticide. The OFI *Leucaena* seedlots were treated with Pirimiphos-methyl ("Actelic"), a persistent grain storage insecticide in order to kill any late emerging beetles. In addition, seedlots were cleaned using a gravity table separator to remove the majority, although not all, insect damaged seed. Reinfestation of mature seed by emerging adult beetles is not known to occur in *Leucaena*. These procedures are important to avoid shipment of live beetles and comply with phytosanitary requirements of quarantine authorities. An alternative method which avoids use of potentially hazardous insecticides, is the $C0_2$ method. High concentrations of CO_2 (>60%) (and hence reduced oxygen levels) applied for 8 weeks at temperatures of 28°C by filling plastic seed storage bags with CO_2 can kill beetles and have been used to control insect infestations in *Acacia* seed (Sary and Yameojo, 1993).

7.4 Seed pretreatment

In common with many legumes, seeds of most, but not all, species of *Leucaena* have hard, impermeable seedcoats and require pretreatment before sowing in order

Table 9 Summary of Bruchid-Host Interactions for *Leucaena* (from Hughes and Johnson, 1996)

Bruchid Seed Predator / *Leucaena* Host Species	*Acanthoscelides macrophthalmus*	*Acanthoscelides mankinsi*	*Acanthoscelides boneti*	*Acanthoscelides leucaenicola*	*Acanthoscelides suramerica*	*Stator pruinius*	*Stator limbatus*
L. collinsii subsp. *collinsii*	x	x					
subsp. *zacapana*	x		x				
L. confertiflora	x	x	x	x			
L. cuspidata		x					
L. diversifolia	x	x	x	x			
L. esculenta	x	x	x	x			
L. greggii	x						
L. involucrata							
L. lanceolata	x	x		x			
L. lempirana							
L. leucocephala subsp. *leucocephala*	x	x					
subsp. *glabrata*	x	x			x	x	x
L. macrophylla	x	x	x	x			
L. magnifica	x						
L. matudae							
L. multicapitula	x	x					
L. pallida	x	x	x	x			
L. pueblana	x	x					
L. pulverulenta	x	x		x			x
L. retusa	x						
L. salvadorensis	x	x					
L. shannonii	x	x	x				
L. trichandra	x	x	x	x			x
L. trichodes	x				x		

to obtain rapid, uniform and high final germination. Sharma *et al.* (1994) showed that this hard seed coat dormancy is associated with late stage seed maturation. The impervious seed coat inhibits water uptake of untreated seeds making germination slow and erratic, extending over months or years. Pretreatment requires that the seed coat be broken to allow water to enter and the seed to expand.

Three basic pretreatment methods, mechanical, hot water and sulphuric acid, have been used for legume seeds (*e.g.* Fordham, 1965; Doran *et al.*, 1983). As with all other aspects of *Leucaena* research, pretreatment methods have been amply investigated for *L. leucocephala*, but largely neglected for other species. For *L. leucocephala* variations of all three methods have been used successfully (Akamine, 1942; 1952; Takahashi and Ripperton, 1949; Gray, 1962; Pound and Martínez-Cairo, 1983; Van de Beldt and Brewbaker, 1985; Oakes, 1984; Alvarez-Racelis and Bagaloyos, 1977). In general, hot water treatments have found greatest favour, being effective, easy to arrange, and safe. Typically, soaking in water at 80°C for 3 minutes followed by washing in cool water has been perhaps the most widely used. Sulphuric acid has been largely abandoned as too hazardous for routine nursery use.

However, not all seeds of *Leucaena* are equally hard and impervious. Variation in hard seededness has been documented between species (Hawkins and Ochoa, 1991) and between varieties of *L. leucocephala* (Hopkinson, 1997). Variation in seed size (Section 7.1) also affects pretreatment. For this reason, **the standard hot water treatments used for *L. leucocephala* cannot be applied indiscriminately to other species**. Hawkins and Ochoa (1991) tested a range of different hot water treatments against controls and manual scarification for the majority of species of *Leucaena*. Their results suggested that no seed pretreatment is needed for *L. salvadorensis* and that untreated seed of this species could be sown directly and germinate rapidly. However, work in Australia has shown that seed of *L. salvadorensis* does need pretreatment (Mullen[1], pers. comm.). This discrepancy may be attributable to seed age with seed becoming progressively harder with age in storage. To a lesser extent the same applies to *L. esculenta* with untreated seed giving up to 79% of the expected germination with manual scarification (Hawkins and Ochoa, 1991). There is no doubt that hot water treatments are highly detrimental and can readily kill seed of *L. salvadorensis* and mechanical scarification methods (see below) should be used for these two species.

Hawkins and Ochoa (1991) showed that all other species require pretreatment. However, there was a great deal of variation between species in response to different treatments. For example *L. multicapitula* gave 62% germination with a 100°C hot water treatment, whereas *L. trichandra*, with seeds of similar size, gave only 8% germination with the same treatment. They showed that hot water treatments were generally poor, causing

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significant seed mortality and giving lower germination (depending on severity) than manual scarification. This means that hot water treatment times and temperatures need to be calibrated for each species individually. However, precise calibration of hot water treatments will only be justified for species that perform well in the trials and enter routine planting. Similar variation was detected between the '*Cunningham*' and K636 ('*Tarramba*') varieties of *L. leucocephala* subsp. *glabrata* by Hopkinson (1997) who showed that K636 is more resistant to boiling water than '*Cunningham*'. In many cases the severity of hot water treatments required to break dormancy is such as to cause significant damage and death of seeds, or, if less severe, results in incomplete softening. Successful hot water treatments require meticulous and firm control of the duration of soaking and the temperature during soaking, which in turn can depend on the ratio of the volumes of seed to water which can be difficult to achieve.

For these reasons, many are turning to mechanical scarification methods as an alternative. For small seedlots manual scarification can be easily applied to maximise germination. Indeed this is the method used in laboratory testing of seed to determine the viability of a seedlot and is the only universally reliable pre-sowing treatment that can be recommended to give optimal germination. Manual scarification can be carried out by cutting, piercing, nicking, chipping or filing the seed coat of individual seeds with a mounted needle, knife, scalpel, handfile, nail clippers or abrasive paper. It is only necessary to make a small cut to pierce the outer layer of the seed coat and care should be taken to avoid cutting deeply which causes damage to the cotyledons as this can increase the chance of damping off in the nursery. The hot wire or glow-burner method (Robbins, 1986; Poulsen and Stubsgaard, 1995) produces similar results to mechanical scarification by burning, but is faster (100 seeds in 2-3 minutes, reported by Poulsen and Stubsgaard, 1995) and is also recommended.

Manual scarification is suitable for laboratory testing and for small, or particularly valuable seedlots, such as those to be sown in a trial or seed orchard. Although time consuming, experience in the one nursery in Honduras has shown that seed for a complete, replicated species/provenance trial can be manually scarified in four man-days at low cost with dexterous and careful workers (Hawkins and Ochoa, 1991). If the full value of small research seedlots is to be realized then a small investment in manual seed scarification is needed.

However, for larger seedlots used in routine planting manual methods are impractical. A number of machines have been developed for large scale mechanical scarification. One of the most promising is the 'seed gun' (Poulsen and Stubsgaard, 1995) which slings seed against the wall of a rotating metal cylinder causing fine, virtually invisible cracks in the outer layer of the seed coat. Such methods have high capacity are fast and suitable for large quantities. However, As with hot water methods, these need careful calibration for each species or provenance/variety (Hopkinson, 1997) and machinery needs to be fully adjustable. Another advantage of mechanical methods, being dry, is that seed can be returned safely to storage after pretreatment. This means that pretreatment can be carried out centrally, say at a seed bank, before seed is packed and distributed to nurseries, allowing greater control over scarification (Lauridsen and Stubsgaard, 1987).

In summary, the glow burner, or hot wire method is particularly suited for small quantities. It is precise, gentle, highly replicable and results in optimal, *i.e.* the maximum possible, germination. For larger quantities, investment in a mechanical scarifier such as the 'seed gun' is recommended.

7.5 *Rhizobium* inoculation

Leucaena species have the ability to form a symbiotic association with root nodule bacteria, *Rhizobium*, which are able to convert nitrogen in the air into a form usable in the plant. This conversion is called biological nitrogen fixation, and is carried out by the *Rhizobium* inside the root nodules. Effective nodulation is dependent on availability and abundance of a suitable strain of *Rhizobium* in the soil. Compared to most woody legumes the *Rhizobium* affinities in the genus *Leucaena* are well studied (Halliday and Somasegaran, 1983). All *Leucaena* species tested to date have the ability to nodulate.

Leucaena is known to be specific in its *Rhizobium* requirements. There are cases of lack of nodulation following introduction of *L. leucocephala* to new areas due to lack of compatible *Rhizobia*, for example in Australia and the Llanos region of Colombia, although these appear to be isolated cases. Within the genus *Leucaena*, significant *Rhizobium* strain specificity has been found. This was exemplified by the lack of nodulation on *L. retusa* with a range of known '*Leucaena* strains'.

Despite this specificity, a number of strains that effectively nodulate a wide range of *Leucaena* species have been found. NifTAL strain TAL1145 has been shown by Somasegaran and Martin (1986) to be an elite strain for *L. leucocephala* and *L. diversifolia* with the greatest nitrogen fixation and competitive ability in mixed strain 'cocktails'.

Although *L. leucocephala* has already been widely introduced throughout the tropics, it is still prudent to inoculate *Leucaena* seed with preselected elite strains of *Rhizobium* when it is planted in a new area. For this reason, a mixed strain *Rhizobium* cocktail is included with all *Leucaena* seedlots distributed from OFI. Inoculum has been supplied by the NifTAL Project of the University of Hawaii. It is packed for easy use in a dry sterile peat-based medium. The inoculum contains a mixture of *Rhizobium* strains: TAL 583, 1145, 1770 and

1887. Inoculum used in this way has a limited storage life and should be stored in a refrigerator at +4°C until used. Exposure to direct sunlight or excessive heat will destroy the *Rhizobium*. Detailed procedures for application of the inoculum are presented in the NifTAL booklet "Legume inoculants and their use" (Anon, 1984). If problems arise and seedlings fail to nodulate, it is advisable to contact the NifTAL Project, University of Hawaii, 1000 Holomua Avenue, Paia, Hawaii, 96779-9744, USA; TELEX NifTAL 7430315 (ITT); FAX (808) 579-8516, who will be able to give advice and supply further inoculum if required.

Box 6 Seeds: collection, storage and pretreatment

- In general the collection, processing and storage of seed of *Leucaena* species is straightforward. Seed of all species can be stored at <+4°C and <10% moisture content following conventional seed storage methods

- Seeds of all species of *Leucaena* are predated in the natural populations by seed-feeding bruchid beetles. Beetles are both potentially hazardous and costly for efficient seed production but may be of use in biocontrol. Host records for *Leucaena* bruchids are well documented. Five species of *Acanthoscelides* bruchids are restricted to *Leucaena*; one of these, *A. macrophthalmus* (recently introduced to Australia and proposed for release in South Africa) has been recorded from 18 species of *Leucaena*. Sunning extracted seed, and treatment with persistent grain-storage insecticides or CO_2, provide methods to control bruchids in seedlots

- Seeds of all species of *Leucaena*, except *L. salvadorensis* and *L. esculenta* have hard impermeable seed coats and require treatment to break the seed coat before sowing in order to obtain rapid, uniform and high final germination. Standard hot water treatments used for *L. leucocephala* cannot be applied indiscriminately to other species, but need to be calibrated and carefully applied. Mechanical scarification methods (manual scarification for small valuable seedlots, or machines such as the 'seed gun') provide good alternatives to hot water methods

- Inoculation with known compatible strains of *Rhizobium* is recommended when planting *Leucaena* in a new area to ensure effective nodulation

8 Conservation

8.1 Genetic conservation methods

Conservation of biodiversity in general, and forest genetic resources in particular, has, to date, concentrated on: (i) ***in situ*** protection of natural forest or other vegetation in protected areas such as biological reserves or sustainably managed forest reserves and/or (ii) ***ex situ*** conservation - in long term seed storage or living collections such as arboreta, botanic gardens, conservation stands and seed production areas - for a handful of species of high economic importance (National Research Council, 1991; Kemp, 1993; Kanowski and Boshier, 1997). A combination of complementary *in* and *ex situ* conservation is generally deemed to be more effective than a strategy that relies on one or the other alone (Maxted *et al*., 1997) and there is a strong case for coordinated conservation strategies in which technical options are integrated within a broader framework of action (NRC, 1991; Kemp, 1993; Kanowski and Boshier, 1997). However, there are few data to indicate how effective this combination of traditional *in* and *ex situ* measures is for conservation of either species or infraspecific diversity in areas of forest fragmentation. The handful of studies of individual plant groups and countries that have been carried out indicate that significant proportions of species (and intraspecific diversity) lie beyond the scope of strict *in* or *ex situ* conservation. For example, in Germany only 35-40% of the total of 30,000 species (all groups) are found in protected areas and the remaining species are almost confined to human-managed ecosystems (Pimbert, 1993). Effective *ex situ* conservation of the genetic resources of forestry species is limited to a trivial number of species (perhaps 100 worldwide; NRC, 1991). Furthermore, there are inherent deficiencies associated with *ex situ* populations as conservation genepools (Brown *et al*., 1989; Marshall, 1990; Young and Yeh, 1992).

The limitations of traditional *in* and *ex situ* conservation methods are one reason why those concerned with plant genetic resource conservation have turned to options that incorporate conservation criteria into forest and farm management practices as an alternative strategy for achieving conservation goals. Such an approach to conservation relying on managed agricultural and agroforestry production systems or small forest hyper-fragments is here termed ***circa situm*** conservation (termed '*circa situ* conservation' by Cooper *et al*., 1992; 'farmer-based conservation' by *e.g*. Brush, 1991; 'conservation *in hortus*' by Witmeyer, 1994; 'locally-based conservation' by Qualset *et al*., 1997; or subsumed within *in situ e.g*. by Lamola and Bertram, 1994; Brush, 1995; Bellon, 1996; Bellon *et al*., 1997; Maxted *et al*., 1997; Ortega, 1997). The potential and scope of *circa situm* conservation were discussed and promoted initially for agricultural crop varieties (Brush, 1991; Altieri and Merrick, 1987; Cooper *et al*., 1992; del Amo, 1992; Pimental *et al*., 1992; Lamola and Bertram, 1994) and farmer-based conservation is now widely recognized as a central component of agricultural crop genetic resource conservation strategies (Brush, 1995; Bellon, 1996; Bellon *et al*., 1997; Maxted *et al*., 1997; Ortega, 1997; Qualset *et al*., 1997) This approach has also been suggested for a number of tree species including *Leucaena* (Hellin and Hughes, 1993; Ponce, 1995 for *L. salvadorensis*, Hughes *et al*., 1995 for *Leucaena* more generally). The wider potential of *circa situm* conservation of trees has been pointed out by Gajasenei and Jordan (1992), Gibson (1992), Hughes (1994; 1995), Kanowski and Boshier (1997) and Barrance, (1997). The '*use it or lose it*' motto, now being adopted for example by some reserve managers to promote *in situ* biodiversity conservation is even more pertinent in highly fragmented forest and agricultural landscapes where a large fraction of biodiversity lies outside the scope of strict *in situ* reserves or expensive *ex situ* measures.

There is considerable confusion over definitions of *in situ* conservation. Farmer-based conservation is widely considered and defined to be a form of *in situ* conservation by those concerned with agricultural crop plants (Brush, 1995; Bellon, 1996; Bellon *et al*., 1997; Maxted *et al*., 1997; Ortega, 1997; Qualset *et al*., 1997). While the term *in situ* may indeed be appropriate for domesticated crops and their weedy close relatives, which thrive in open areas, and which may be unable to survive under natural habitat or forest conditions, it is less appropriate for on-farm conservation of trees. For forest trees, on-farm conservation bears little relation to classical *in situ* conservation which seeks to maintain populations in the 'natural' forest state. Thus at least for trees the distinction between strict *in situ* conservation through protection of natural forest, and farmer-based conservation in the very different habitats of the surrounding agricultural landscape, is very marked and potentially important for the outcome of conservation efforts. Thus in this discussion conservation outside natural forest habitats, but within the native geographical range, is distinguished as ***circa situm*** (see below).

In this chapter, the conservation status of *Leucaena* species is assessed, preliminary conservation categories are assigned to species, current conservation measures are documented and the relative actual and potential contributions of *in* and *ex situ*, and *circa situm* conservation of *Leucaena* assessed as a basis for discussion of conservation priorities and strategies. It is widely accepted that the conservation of genetic resources of economically important plant species and their close relatives provides security for future utilization

Box 7 Forest genetic resource conservation methods

- ***In situ*** conservation refers to maintenance of populations of species in the 'natural' state in the communities, ecosystems and habitats to which they naturally belong
- ***Ex situ*** genetic conservation refers to conservation of species outside the natural range in which they originally evolved. *Ex situ* methods include long-term seed storage and different types of living collections such as living gene banks, arboreta, botanic gardens, conservation stands and seed production stands
- ***Circa situm*** conservation refers to conservation in managed agricultural landscapes, in agroforestry systems, fence-rows, home-gardens and around settlements within the native geographic range of a species. *Circa situm* methods are distinguished from *in situ* because trees are removed from their natural *in situ* forest habitats and are subject to a quite different set of environmental influences, densities, ecological relationships and hence biotic and abiotic selection pressures. *Circa situm* conservation has also been described as *circa situ*, 'farmer-based conservation', 'conservation *in hortus*' or 'locally-based conservation'

and breeding. In a genus such as *Leucaena* with its multiple uses and high interspecific crossability, the whole genus is generally considered to comprise the potential genepool available for use and genetic improvement (Brewbaker and Sorensson, 1994; Sorensson and Brewbaker, 1994). It is also recognized by some that loss of intraspecific genetic diversity may be as important as species loss (*e.g.* Kanowski and Boshier, 1997). However, for *Leucaena* the effects of forest loss and fragmentation in terms of possible destruction of allelic complexes associated with locally adapted populations, as for many species, are unknown due to lack of data on patterns and levels of variation and gene flow (Section 6.4). New research investigating intraspecific diversity within one species, *L. salvadorensis*, under conditions of hyper-fragmentation of forest and *circa situm* conservation is in progress. The discussion here therefore focuses on conservation of species diversity.

8.2 Conservation status of *Leucaena* species

The overall 'natural' range occupied by *Leucaena* species is shown in Fig 10A. This map is based on 2393 data points derived from herbarium specimens with adequately known collection localities (88% of the total examined). The distribution shows the predominant occurrence of *Leucaena* species in seasonally dry tropical habitats with extension into some mid-elevation dry oak forest or dry mattoral (and pine forest). *Leucaena* species are virtually absent from the cold arid deserts of north central Mexico (although two species do extend into the more temperate, cold winter climates of the mountains of NE Mexico and Texas) and are only very sparsely distributed in the non seasonal wet lowland forests of the southern Gulf of Mexico (Tabasco and northern Chiapas); the Petén region of Guatemala and Belize; the Atlantic zone of Belize, Honduras, Nicaragua, Costa Rica and Panama; and the perhumid forests of the Darién/Chocó coastal zone of Colombia and north west Ecuador. Only two species, *L. diversifolia* and *L. multicapitula* occur on the fringes of the lowland wet forest zone. Within this overall distribution, species diversity is concentrated in Mexico (17 species, 10 endemics) and northern Central America (9 species, 4 endemics), with the highest number of species occurring in southern Mexico (Fig 10A).

The majority of *Leucaena* species are not in any way endangered, being widely distributed and locally abundant. Indeed, the genus is dominated by opportunistic species which thrive on disturbance sometimes becoming common in secondary vegetation including bush fallow (*e.g. L. collinsii* subsp. *zacapana, L. lanceolata, L. leucocephala* subsp. *leucocephala, L. pulverulenta, L. shannonii* and *L. trichodes*). A few of these are ruderal weeds of roadsides or waste ground (*e.g. L. leucocephala* subsp. *leucocephala* throughout the Yucatán Peninsula, Mexico; *L. shannonii* in Yoro, Honduras and Chiapas, Mexico; and *L. trichodes* in parts of Manabí, Ecuador). A few (*e.g. L. esculenta, L. pallida* and *L. leucocephala* subsp. *glabrata*) are also extremely widely cultivated within their native ranges as minor food plants (Chapter 4). Nevertheless, there are a number of important exceptions to this general rule and a few species of *Leucaena* are of significant conservation concern.

Although there is no universally accepted measure of conservation status or threat, it is widely agreed that a number of factors need to be taken into account in such assessments (Hawthorne, 1996b). Firstly, global rarity, or extent of occurrence, is generally accepted as a useful starting point in any assessment. Narrowly restricted endemics have much higher rarity value, and hence are likely to be of greater conservation concern than widely distributed species. The number of degree-square occurrences in a species distribution (Table 10) provides a crude measure of global rarity that may be used as a starting point for assessing conservation status. Detailed distribution maps (Chapter 11), again derived from botanical specimen localities, for each taxon provide these data for *Leucaena* (Table 10). However, global rarity is not in itself an adequate measure of conservation threat since some species with restricted distributions are locally very abundant. Conversely some widely distributed species are never locally abundant, always occurring as forest species which are likely to be at risk if forest is converted completely to secondary vegetation. Thus, crude measures of global rarity need to be modified on the basis of other considerations including local abundance, ecology (forest or non-forest species), taxonomy (*e.g.* existence of closely related subspecies) and economic importance in order to arrive at even a moderately adequate measure of conservation value. Several systems have been devised to categorize species in this way. The Star Rating method developed by Hawthorne (1996b) to assign species conservation categories for plants of Ghana provides one such method. Star ratings are defined and assigned initially on global distribution (number of degree-square occurrences in a species distribution), strongly modified subsequently by ecology, local abundance and taxonomy. The *IUCN Red List Categories* of conservation threat (International Union for the Conservation of Nature, 1994) are more widely known and have been used for over 30 years. The IUCN system adopts a slightly different approach based on species range, population size and actual or potential decline of species. A category of threat is assigned based on any one of four criteria relating to species range, population size and rate of decline. Both IUCN categories and Star Ratings here are tentatively assigned to each *Leucaena* taxon (Table 10). These are first approximations, based on available data and may be subject to progressive modification and updating as new data become available.

Eight species of *Leucaena* are endemic to areas encompassing fewer than five degree-squares; four of these are narrowly restricted endemics occurring in only one or two degree-squares. Several of the eight narrowly restricted taxa are locally abundant and thus of little or no conservation priority (Green/Blue Star species). For example, both subspecies of *L. collinsii*, are restricted to single, albeit extensive valley systems in Guatemala and southern Mexico (Fig 25), but both are locally abundant, and in the case of subsp. *zacapana*, extremely abundant, in secondary bush fallow. Conversely, one species, *L. cuspidata*, although not as restricted in distribution, does not thrive on disturbance and has a preference for forest areas, although it is occasionally found outside the forest. Such species are likely to be at risk if forest is converted completely to secondary vegetation and *L. cuspidata* is therefore categorized as of moderate conservation concern (Gold Star). Four species (*L. confertiflora, L. cuspidata, L. greggii* and *L. pueblana*) are both geographically restricted and susceptible to grazing pressure and are now generally restricted to ungrazed sites such as steep rocky bluffs and gullies and also qualify as Blue/Gold Star species. Three taxa, *L. lempirana, L. leucocephala* subsp. *ixtahuacana* and *L. salvadorensis*, occupy highly restricted distributions in areas of severe forest degradation and are assigned Gold Star rating. However, active retention and protection of trees in traditional agroforestry systems by local communities and farmers within their areas of distribution mitigates the current threat and downgrades their IUCN category.

Three species, *L. matudae, L. magnifica*, and the poorly known *L. involucrata*, are both globally (1-2 degree-square occurrences) and locally rare and are thus of critical conservation concern (Black Star species). For example, the known distribution of *L. magnifica* is restricted to less than 400 km^2 in the south eastern department of Chiquimula in Guatemala. With fewer than 400 known individuals (Hughes, 1986; 1991), this species is probably the most threatened in the genus. In addition to very restricted range and total population size, the stands of *L. magnifica* are hyper-fragmented and reduced to scattered remnants often comprising only a few individuals and urgent attention to conservation of populations of this species is required. Although these species clearly qualify as Black Star under the Star Rating system, the criteria used in the IUCN system mean that they are categorized as Endangered rather than Critically Endangered in that system, despite their very restricted distributions. However, any further decline would trigger upgrading to critically endangered IUCN status as well.

Some species which span several countries may be widespread and abundant in one country, but highly restricted and rare in a neighbouring territory. For example, *L. salvadorensis*, although reasonably common across southern Honduras and northern Nicaragua, is apparently highly restricted in eastern El Salvador (Boshier, pers. comm). Similarly, *L. multicapitula* and *L. trichandra* are widely distributed and reasonably abundant through most of their ranges but apparently restricted and uncommon in Nicaragua. Such species may therefore be of greater conservation concern nationally than internationally (Table 10).

8.3 *In situ* conservation

In situ conservation here refers to maintenance of populations of species in the 'natural' state in communities, ecosystems and habitats to which they naturally belong (Frankel, 1970; Soulé, 1991; Kanowski and Boshier, 1997).

Within Mesoamerica, the dry tropical forest ecosystem, where the majority of *Leucaena* species grow (Fig 10A), is under particular threat (Janzen, 1986; 1988; Murray *et al.*, 1995, Murphy and Lugo, 1995, Maass, 1995). Historically this forest type has been more readily converted for agriculture than wet forest. Of the seasonally dry forest formation, which originally extended in an almost continuous belt along the Pacific coast from NW Mexico in Sonora to Costa Rica with numerous inland valley extensions, only 0.09% has official reserve status and less than 2% remains *"sufficiently intact to attract the attention of the traditional conservationist"* (Janzen, 1988). Under the rather different definition of ecofloristic zones, Murray *et al.* (1995) estimated there to be 3% of the seasonally dry forest zone under any form of protection. Whatever figures are used, this is one of the world's most endangered tropical ecosystems.

The current system of protected areas in the tropical dry forest formation in Mexico and Central America is extremely limited. Protected areas have been established opportunistically and were not planned based on areas of high diversity or endemism. This scanty network is clearly inadequate to conserve the biodiversity of this ecosystem, although the fractions of species diversity within and outside protected areas remain to be quantified. Furthermore there is now only limited scope for the establishment of new protected areas in the dry tropical forest zone due to the extent of forest loss and fragmentation and many reserves, especially smaller ones, remain permanently susceptible to threats such as fire from outside (Janzen, 1983; 1987). Nevertheless, at least two of the Black/Gold star species, *L. pueblana* and *L. matudae*, occur in areas of high endemism, the Balsas Depression and the Tehuacan Valley where patches of more or less intact dry thorn scrub forest remain. Such dry forest hot spots of high bioquality could and should be afforded protection before they disappear.

While a network of protected areas that has 'arisen' in this way will, on grounds of probability alone, include many, if not most, of the widely distributed species, few of the rarer, narrowly restricted species are likely to be included. This is precisely the outcome for *Leucaena*. Approximately half the species of *Leucaena* are known to be present somewhere within a protected area of some sort (Biosphere Reserve, National Park or other biological reserve). However, these species correspond almost exactly to the set of widely distributed, common, Green Star species of little or no conservation concern. None of the rarer Blue, Gold or Black Star species are known to occur within any protected area. The current contribution of strict *in situ* methods to the conservation of *Leucaena* genetic resources is thus minimal and insignificant.

8.4 *Ex situ* conservation

Ex situ genetic conservation refers to conservation of species outside the natural range in which they originally evolved. *Ex situ* methods include long term seed storage, and different types of living collections such as living gene banks, arboreta, botanic gardens, conservation stands and seed production stands (Maxted *et al.*, 1997). At present there are few programmes specifically directed towards *ex situ* genetic conservation of *Leucaena* species and the genetic variation in the genus is currently not well conserved in any form of *ex situ* conservation.

Long term seed storage. Seed collections of *Leucaena*, including the three large CSIRO, Hawaii and OFI collections (Section 6.3) are, with limited exceptions, aimed at short- or medium-term storage. These 'working collections' are stored under normal seed storage conditions of low humidity and temperature (+4°C). Seeds of most species of *Leucaena* have hard seed coats and are orthodox in their storage requirements (Chapter 7). Under conventional seed storage conditions there is no reason to expect seed viability to drop significantly over periods of 30 or more years. Two species, *L. salvadorensis* and *L. esculenta*, apparently have softer seeds, manifested in their germination without pretreatment, but the implications of this for long term storage have not been investigated so far. Only two substantial collections - one held at the U.S.D.A. National Seed Storage Laboratory, Fort Collins, U.S.A. and the other at the Kew Seed Bank, Wakehurst Place, U.K. - are in long term storage conditions, at the lower temperatures (-20°C) necessary to store seed for up to 100 years.

- The USDA National Seed Storage Laboratory, NSSL, Fort Collins, USA collection includes 140 *Leucaena* accessions, of which 125 are of *L. leucocephala*. This collection includes only a small fraction of the genetic diversity in the genus; most species are not included at all. All accessions are held jointly by the University of Hawaii and U.S.D.A. regional working collections (Hughes *et al.*, 1995; Section 6.3).

- The Royal Botanic Gardens, Kew Seed Bank, Wakehurst Place, U.K. includes a small number (36) accessions representing 16 of the 22 species of *Leucaena* from the OFI seed collections deposited under long term storage conditions in 1996. Unfortunately the eight species not represented include several of the species (*e.g. L. confertiflora, L. cuspidata, L. greggii, L. involucrata, L. matudae* and *L. pueblana*) of greatest conservation concern, although two bulk seedlots of the endangered *L. magnifica* are included. It is again axiomatic that rarer species, some of which have only been discovered in the last five years and often occur in degraded and sometimes remote populations where it is more difficult to make large seed collections, are less well known and collected. Although all these species are included in the wider OFI 'working' seed *Leucaena* collections (Section 6.3), seed quantities were insufficient to meet the minimum requirements for long term seed storage. The Kew seedlots comprise between 1000 and

Table 10 Conservation status of *Leucaena* taxa

Species/subspecies	No. degree square occurrences in species distribution	Star Rating[1]	IUCN Threat Category[2]	Notes: Threats, cultivated status, occurrence in *in situ* protected areas
L. collinsii	7	Blue	LR:lc	Although restricted, often locally very abundant, ruderal, sometimes weedy and dominant in bush fallow, and cultivated for pods (subsp. *collinsii*) or firewood (subsp. *zacapana*). Subsp. *collinsii* probably present in the El Triunfo Biosphere Reserve, Chiapas, Mexico
subsp. *collinsii*	4	Blue	LR:lc	
subsp. *zacapana*	3	Blue	LR:lc	
L. confertiflora	4	Gold	VU-A1 & B1&2	Restricted, sometimes locally cultivated for pod production, susceptible to grazing pressure and harvesting of pods from wild populations; few wild populations known
var. *confertiflora*	4	Blue	VU-A1 & B1&2	
var. *adenotheloidea*	1	Blue	EN-B1&2	
L. cuspidata	4	Gold	VU-A1 & B1&2	Restricted distribution, forest understorey, susceptible to grazing pressure
L. diversifolia	12	Green	LR:lc	Widely distributed, sometimes locally abundant, sometimes cultivated as coffee shade
L. esculenta	22	Green	LR:lc	Widely distributed and extremely abundant in cultivation for pod production. Often the commonest tree in towns and villages in parts of Oaxaca, Puebla and Guerrero in Mexico. Some narrowing of genetic base in cultivated material possible in some areas
L. greggii	5	Blue	VU-A1 B1&2	Restricted; susceptible to grazing pressure, rarely abundant
L. involucrata	2	Gold ?Black	EN-B1&2	Poorly known; apparently very restricted; only collected in the last 50 years from one site in central Sonora, Mexico
L. lanceolata	29	Green	LR:lc	Locally very abundant in secondary vegetation, sometimes a ruderal weed; present in Chamela-Cuixmala Biosphere Reserve, Jalisco, Mexico
var. *lanceolata*	25	Green	LR:lc	
var. *sousae*	7	Green	LR:lc	
L. lempirana	2	Gold	VU-B1&2	Highly localized distribution in northern Honduras; threat mitigated by protection in traditional agroforestry systems
L. leucocephala	87	Green	LR:lc	see subspecies below
subsp. *leucocephala*	24	Green	LR:lc	Common ruderal weed throughout Yucatán and pantropically; common in several protected areas *e.g.* Sian Ka'an and Calakmul Biosphere Reserves
subsp. *glabrata*	71	Green	LR:lc	Very widely cultivated throughout Mexico, many parts of C. America and now pantropically. Origin unknown; not known in the wild; possible anthropogenic origin
subsp. *ixtahuacana*	2	Blue	LR:cd	Very restricted and locally not abundant; threat mitigated by local cultivation for pod production in Huehuetenango, Guatemala

Species/subspecies	No. degree square occurrences in species distribution	Star Rating[1]	IUCN Threat Category[2]	Notes: Threats, cultivated status, occurrence in *in situ* protected areas
L. macrophylla	32	Green	LR:lc	Widespread and often locally abundant; present in several protected areas including the Sierra de Manantlán, Jalisco and Volcan de San Martin Biosphere Reserves
subsp. *macrophylla*	22	Green	LR:lc	
subsp. *istmensis*	11	Green	LR:lc	
L. magnifica	1	Black	EN-B1&2 & C1&2a	Highly restricted to less than 400 km² (Fig 48); reduced to fewer than 400 known individuals (Hughes, 1986, 1991)
L. matudae	1	Black	EN-B1&2	Highly restricted (Fig 50) in dry forest
L. multicapitula	13	Blue Gold (Nic)	LR:lc	Widespread and locally abundant; present in Barro Colorado Island biological reserve, Panama; apparently infrequent and rare in Nicaragua
L. pallida	12	Green	LR:lc	Widely distributed and cultivated in south central Mexico for pod production; very abundant in parts of Oaxaca, Mexico
L. pueblana	3	Gold	VU-B1&2	Endemic to the Tehuacan Valley, Mexico and there never abundant; apparently susceptible to grazing pressure
L. pulverulenta	19	Green	LR:lc	Widespread and often locally abundant in secondary vegetation such as bush fallow; sometimes a ruderal weed of roadsides and waste ground; protected in Cerro de la Silla (Monumento Natural) and El Cielo/Sierra Alta Tanchipa (Biosphere Reserves); cultivated ornamental in Texas
L. retusa	24	Green	LR:lc	Widespread, occasionally locally common; present in protected areas in N. Coahuila and S. Texas (*e.g.* Big Bend National Park)
L. salvadorensis	3	Gold Black (El Sal)	LR:cd	Conservation threat mitigated by deliberate retention and protection of trees in traditional agroforestry systems. Good prospects for continued and expanded conservation through use; apparently rare in El Salvador
L. shannonii	20	Green	LR:lc	Widespread; ruderal, sometimes weedy
L. trichandra	27	Green Blue (Nic)	LR:lc	Widespread; extremely variable and some populations may be under threat; present in several protected areas (*e.g.* El Imposible, El Salvador, Lagunas de Montebello, Mexico, Cerro Uyuca, Honduras
L. trichodes	36	Green	LR:lc	Widespread, sometimes a ruderal weed of roadsides and bush fallow

[1] Star Rating: based on Hawthorne (1996b): Black = high conservation concern; Gold = moderate conservation concern; Blue = minor conservation concern; Green = no conservation concern
[2] IUCN 1994 Threat Categories, assigned based on WCMC (1996) *Conservation and Sustainable Management of Trees* project guidelines: EN = Endangered; VU = Vulnerable; LR = Lower Risk. LR:lc = Lower Risk least concern; LR:cd = Lower Risk, conservation dependent is here used to indicate dependent on continued conservation in traditional agroforestry systems (*circa situm*) (see below). A,B,C categories which follow the threat category refer to criteria used to define that category (see IUCN, 1994).
Nic = Nicaragua; El Sal = El Salvador

5000 viable seeds from bulk provenance collections each derived from 20-50 trees from wild populations. The aim is conserve this material for a period of up to 200 years.

▸ Smaller collections of *Leucaena* are represented in other long term stores such as the National Bureau of Plant Genetic Resources, New Delhi, India and the CATIE long term seed store in Costa Rica.

Thus it can be seen that the material currently held in long term seed storage does not address the conservation priorities (Table 10). Seed of the Blue/Gold/Black star species needs to be collected and added to *ex situ* long term seed storage collections to address this. However, it remains to be seen exactly what the utility of seed in long term storage may be. Seed from these collections is not available for general distribution and use. It is there to underwrite other seed distribution activities and realistically would only be used either for regeneration if viability were to drop or for re-introduction should a species become extinct in the wild.

Living collections. As with the majority of seed collections, the *ex situ* living collections of *Leucaena* species are not specifically directed at long term genetic conservation. A number of arboretum style collections have been established (Australia, Brazil, Colombia, Ethiopia, Hawaii, Honduras, India, Indonesia, Taiwan and others) including 3 'foundation' collections (Australia, Philippines and Brazil) comprising more than 70 accessions. In every case these are working collections or unreplicated evaluation trials, and therefore short term in duration. All are relatively insecure due to lack of long term support for maintenance and susceptibility to sporadic disasters such as fire, hurricane or urban development. Furthermore, the genepool that can be conserved in such collections is severely limited by lack of resources such as land; in general, species are represented by few trees per plot and few accessions or provenances. Finally, the genetic integrity of seed collected from mixed species living collections cannot be guaranteed without expensive controlled crossing due to high interspecific compatibility and hybridization (Bray, 1986; *e.g.* Howcroft, 1994 in Papua New Guinea) (Sections 5.5 and 5.6).

There are very few examples of *ex situ* plantings in the form of conservation stands, seed production areas or seed orchards where larger amounts of genetic variation can be included in isolated blocks guaranteeing production of pure seed. One example of this type of approach is the *ex situ* seed orchard programme being undertaken in Honduras for *L. salvadorensis* and *L. collinsii* (Ponce, 1995).

One might imagine that the large routine plantings of *Leucaena* as an exotic across the tropics could be making a significant contribution to *ex situ* conservation. However, planting of *Leucaena* has been dominated by essentially one species and has relied on an extremely narrow genetic base (Sections 6.3 and 9.3).

8.5 *Circa situm* conservation

Circa situm conservation refers to conservation in managed agricultural landscapes, in agroforestry systems, fence rows, home-gardens and around settlements within the native geographic range of a species. *Circa situm* is distinguished from *in situ* because trees are removed from their natural *in situ* forest habitats and are subject to a quite different set of biotic and abiotic selection pressures, ecological conditions and interactions.

Throughout most of the range of *Leucaena*, intact forest is now extremely reduced in area and hyper-fragmented. Here the traditional forest-agriculture frontier has long since gone and been replaced by an intimate and highly localized mosaic of small and vulnerable forest patches amidst a diffuse matrix of trees outside the forest in even smaller patches of remnant woodland, in traditional agroforestry systems on farms, in fencerows, home-gardens and around settlements (Barrance, 1997). This is the matrix of woodland and trees used by local communities and farmers which are conserved *circa situm*.

The fact that local communities and farmers have been actively using, retaining, protecting, cultivating and managing trees of a range of *Leucaena* species in traditional indigenous agroforestry systems (Chapter 4) over several centuries or even millennia, has ensured however that these species remain relatively abundant today despite the wholesale loss of forest cover in most areas. The geographical, historical and taxonomic scope of indigenous use and domestication is described in detail in Chapter 4. In south central Mexico at least 13 species of *Leucaena* are used for food while in Central America at least seven species are utilized and managed for poles and firewood. As a result, three species, *L. pallida*, *L. esculenta* and *L. leucocephala* subsp. *glabrata* are amongst the most common trees in many communities and settlements in south central Mexico. Several species with much more restricted distributions (*e.g. L. confertiflora*, *L. cuspidata*, *L. lempirana*, *L. leucocephala* subsp. *ixtahuacana*, *L. magnifica* and *L. salvadorensis*) although not actively transported and introduced into cultivation in new areas, are used, protected and occasionally cultivated locally within their native ranges. For the majority of species of *Leucaena*, local communities and farmers have thus been conserving a wide range of species through use over wide areas for several centuries. There is now somewhat belated acknowledgement and recognition of the role which generations of communities and farmers have had in conserving genetic resources of *Leucaena* amongst the scientific community (Hellin and Hughes, 1993; Hughes *et al.*, 1995).

The main **advantages** of farmer-based *circa situm* conservation through use over *ex situ* methods are that it:

(i) operates over large areas and thereby has the potential to conserve large amounts of genetic variation

(ii) decentralizes conservation and thereby minimizes risks of sporadic disasters such as fires

(iii) requires only limited investment of resources as the process becomes self sustaining

(iv) means that species are conserved within a range of habitats and conditions and continue to be exposed to biotic and abiotic stresses (albeit greatly altered from their natural state - see below) thereby maintaining potential for continued evolution in response to new selection pressures. *Circa situm* conservation is thus dynamic compared to static *ex situ* seed storage and has been (perhaps misleadingly) termed 'evolutionary conservation' (Worede, 1997).

(v) permits wider participation in conservation and recognizes the political, social and economic importance of retaining useful plant genetic resources in countries where these resources occur, thereby providing channels for benefit sharing (Section 9.6).

(vi) recognizes that *circa situm* actions are an important and integral element of wider production and survival strategies for resource poor farmers essential to sustaining rural livelihoods and environmental services.

Nevertheless, there may also be **limitations** associated with sole reliance on a *circa situm* approach:

(i) *circa situm* conservation is probably limited to species which are adaptable to open disturbed farm 'habitats' and/or which are of significant benefit to and genuinely preferred by farmers and local communities. In this sense *circa situm* conservation is inherently susceptible to fluctuations in farm economics and practices and therefore provides no guarantee of secure conservation in perpetuity. Most species of *Leucaena* are indeed well known, recognized and preferred by farmers and local communities (Chapter 4) and able to grow well in open on-farm conditions. *Leucaena* may thus be unusually amenable to conservation through use compared to other tree species, particularly in its wide use as a minor food plant in Mexico, which confers high potential for *circa situm* success. In these respects *Leucaena* is more akin to an agricultural crop plant than many forest trees.

(ii) introduced species, sometimes promoted by local, national or international development agencies, may displace local species from traditional agroforestry systems in similar fashion to the widely documented demise of traditional crop varieties following promotion of high yielding improved varieties (Bellon, 1996; Tripp and van der Heide, 1996). In the case of *Leucaena* this has not so far proved problematic despite widespread incorporation and planting of species such as *L. leucocephala* throughout Mexico and Central America. Many communities and farmers prefer to maintain and plant several species of *Leucaena* together, possibly including *L. leucocephala* alongside local species, recognizing the benefits of added diversity (Sections 4.3 and 4.6). However, there are likely to be limits to the resilience of local diversity in the face of concerted promotion of exotic species (even *Leucaena* species) by government agencies and NGOs, who adopt a blinkered approach to species selection that fails to take account of local diversity and opinion.

(iii) *Circa situm* conservation may entail some narrowing of the genetic base in cultivated, or semi-domesticated populations. Casas and Caballero (1996) provide some, albeit inconclusive, evidence for selection by farmers for pod and seed size in managed and cultivated populations of *L. esculenta* (Section 4.3). Research using molecular markers to quantify levels of diversity in semi-domesticated populations is needed to verify this. Such reductions in levels of diversity may be important and need to be compared with losses of genetic variation associated with *ex situ* methods which generally have limited scope to include more than a fraction of infraspecific diversity (Brown *et al.*, 1989; Marshall, 1990; Young and Yeh, 1992). In this respect *circa situm* methods may provide an acceptable compromise. There is also evidence to suggest that indigenous domestication in Mexico has resulted in a number of spontaneous hybrids (Hughes and Harris, 1994; in press; Section 5.5). Although it is true that spontaneous hybridization has increased overall genetic and useful diversity (Sections 5.5 and 5.6), hybridization may also pose threats to conservation through backcrossing and introgression. From a conservation standpoint, introgression can result in genetic contamination of native populations and consequent loss of adaptive gene complexes, or in extreme cases swamping or even extinction of rare species (Levin *et al.*, 1996). Isolation from cross compatible species should thus be considered in conservation efforts, especially for rare species. For example *circa situm* efforts to conserve particularly rare species such as *L. magnifica* could be compromised or displaced by hybridization with other cross compatible species cultivated in or near the few small populations which remain of that species.

(iv) At some level *circa situm* methods will always be 'second best' to *in situ* conservation. As mentioned above, environmental factors, tree densities, ecological relationships and hence selection pressures in human-managed agricultural landscapes are greatly altered from the natural state. Thus while *circa situm* conservation may allow some species, such as *Leucaena*, to survive and even thrive, it cannot conserve all the complexity of natural interactions associated with pristine forests (Janzen, 1983), nor natural patterns and levels of diversity within species. Genes that are successful in the farm/field habitat will be favoured and the original evolutionary equilibrium will be altered.

The potential to support, sustain and expand *circa situm* conservation through use has been explored recently for one species, *L. salvadorensis* in Honduras (Hellin and Hughes, 1993; Ponce, 1995; CONSEFORH, 1998). A number of basic measures required to promote or catalyze continued and expanded conservation through use and mitigate some of the possible limitations listed above are apparent from this work. Very often staff in organisations supporting community tree planting projects are unaware of, and/or unable to identify, the full range of local tree species and fall back on better known exotics. Identification tools, training and appropriate awareness raising extension material may be sufficient to rectify this (*e.g.* Hellin and Hughes, 1993; CONSEFORH, 1998). One of the aims of this *Handbook* is to provide such a tool and raise awareness of lesser known species. Lack of available seed supplies from national tree seed banks can also hinder use of lesser known species of *Leucaena*. Transfer of seed collection activities to farmers and local communities themselves is one immediate way to overcome this problem. Indeed seed demand in itself can provide an added benefit and hence incentive to maintain trees on farms, when farmers are collecting and exchanging or selling seed themselves. Encouraging use of **local** seed sources, collected from as many parent trees as possible also goes some way to ensuring maintenance of genetic variation in cultivated material. Indeed, 'locally-based conservation', a term coined by Qualset *et al* (1997), has great utility in guiding the practice of *circa situm* conservation action. It is use of local diversity and local issues of pride, ownership, cultural practices and economic value which will dictate the success of *circa situm* measures. Decentralization of seed collection and supply are thus likely to have multiple benefits.

However, defining what scale is 'local' is not straightforward; there may be a danger of over-localization. Scale needs to be determined by the distances over which the genetics of a species varies. This will depend on its distribution, breeding system (out crossing vs. self fertile), patterns and levels of geneflow and degree of population fragmentation. These are the same factors which inform about seed collection sampling strategies (Section 6.4) but for most *Leucaena* species there is a great dearth of data on these parameters. Hellin and Hughes (1993) attempted to draw a map as the basis for 'locally-based' conservation of *L. salvadorensis*, but this was based on pragmatic guesses rather than genetic data.

There is currently much discussion about giving practical recognition to the concept of Farmers' Rights arising from their past, present and future contribution to the conservation and development of genetic resources (Section 9.6). Sharing of benefits, however modest, arising from use and commercialization of *Leucaena* genetic resources might provide one way to provide additional support for *circa situm* conservation. Such benefits might be used to support community seed collection activities or establishment of tree nurseries in communities with important *Leucaena* species in their care.

8.6 Conclusions and recommendations

The current contribution of either strict *in* or *ex situ* measures for the conservation of *Leucaena* genetic resources is extremely limited because they have focused primarily on the widespread species of little or no conservation concern. They do not adequately address the conservation priorities as determined here (Table 8). It seems that for *Leucaena* what has happened outside protected areas has contributed more to effective conservation of diversity than protection of *in situ* reserves or *ex situ* collections. In the absence of sufficient investment in *ex* or *in situ* measures, *circa situm* conservation has been the only effective conservation option to date. It may be time to acknowledge the impracticality (costs and technical) of conserving all potentially useful species and genetic diversity *in* or *ex situ* and to recognize the important role of *circa situm* conservation. Concerted *in* and *ex situ*, and *circa situm* action is needed to improve the conservation of *Leucaena* genetic resources. As for other plant groups complementary conservation action is likely to be more successful than sole reliance on any one method (Maxted *et al.*, 1997).

Specific recommendations for genetic conservation of *Leucaena* are:

(i) *In situ* - there is still scope to establish new protected areas in remaining dry forest hot spots in the Balsas Depression, the Tehuacan Valley and coastal Oaxaca in Mexico. Protection of intact forest patches in these areas before they disappear could contribute to *in situ* conservation of some of the rarer *Leucaena* species of greatest conservation concern. Documentation of the occurrence of rare species of *Leucaena*, such as *L. matudae* and *L. pueblana*, in these areas adds ammunition to those fighting to establish new protected areas.

Box 8 Genetic Conservation of *Leucaena*

- The majority of *Leucaena* species (14 out of 22) are of minor or no conservation concern being widespread species which thrive on disturbance.
- Five species are of moderate conservation concern, while three are of high concern.
- Only 2-3% of the original Mesoamerican dry tropical forest, where most *Leucaena* species occur, remains, making this one of the world's most threatened ecosystems; only 0.09% has official reserve status.
- Only half of the species of *Leucaena* are known to be present in protected areas and these are the widespread species of little or no conservation concern. None of the species of greatest conservation concern are known to be present in protected areas. There is scope to incorporate some of the rarer species in new protected areas located in known dry forest bioquality hot-spots such as in the Balsas Depression and Tehuacan Valley in Mexico.
- 16 out of 22 species are represented in long-term seed storage, but the remaining eight species include a number of species of significant conservation concern.
- The majority of *Leucaena* species are protected and conserved *circa situm* through use by farmers and local communities in managed agricultural landscapes in many parts of Mexico and Central America. Farming communities have been and continue to be the primary custodians of *Leucaena* genetic resources. *Circa situm* methods provide the only viable conservation option, in the absence of more substantive investment in *in* or *ex situ* measures.

(ii) *Ex situ* - seed of the rarer, endangered Blue/Gold/Black star species needs to be added to the *ex situ* conservation seed collections in long term storage. However, such measures will, at best, provide a rescue option should a species become extinct in the wild.

(iii) *Circa situm* - the contribution of farmers and local communities throughout Mexico and Central America who have been and continue to be the primary custodians of *Leucaena* genetic resources needs to be given more substantive recognition. Farmer-based *circa situm* conservation of the majority of species of *Leucaena* has been operating more or less successfully for many centuries. Farmers and communities living in or near to populations of *Leucaena* species can be key contributors to their conservation and can decide the fate of *Leucaena* diversity. There appears to be good scope to extend and consolidate *circa situm* conservation for a wider range of species including some of those which are of significant conservation concern, such as *L. magnifica* and *L. lempirana*. Given appropriate support and encouragement, and stronger links between formal (exotic) and indigenous domestication (Tripp and van der Heide, 1996; Chapter 9), farmers and local communities may continue to be key contributors to the conservation of *Leucaena* in the future.

9 Domestication

9.1 Introduction

Any *Genetic Resources Handbook* could reasonably be expected to include discussion of how to use and domesticate the species and genetic diversity documented within it. After all, what is the point of documenting and understanding diversity if we don't know how to use it effectively? However, this chapter on domestication presents no detailed selection and breeding strategies. It is not a simple prescription of how to proceed with domestication. This is partly because no single strategy for genetic improvement of *Leucaena* will suffice. The diverse biophysical conditions, end products, species and hybrids, farming systems, clients and wider socio-economic and environmental contexts of *Leucaena* use -- with *"as many manifestations as there are situations"* (Kanowski, 1996: 298) -- will demand species- and location-specific approaches to domestication. Figs 7B-E, 8A-B, 9A-G, 10B and G illustrate a diverse set of farming systems and socio-economic contexts of *Leucaena* use. It is also because it has become abundantly clear in recent years that adapting conventional crop or tree improvement methods to the domestication of agroforestry trees used by smallholder farmers may not be straightforward. It has been widely stated that agroforestry tree domestication is as much a socio-economic, political and environmental challenge as a biological or technical one; that it is more complex than crop breeding or genetic improvement of plantation species; that the beneficiaries (clients) comprise a much more heterogenous community of tree growers than plantation enterprises; that delivery pathways for improved material are generally lacking and that, if delivered, improved material may be diluted by existing inferior landrace material; that much can be learned and gained from greater and more whole hearted participation of farmers in the domestication process; that domestication can have negative as well as positive environmental impacts *e.g.* on biodiversity conservation; that more substantive recognition of genetic resource property rights needs to be considered and better integrated into overall domestication efforts; and, perhaps most significantly, that conventional tree improvement strategies may not be appropriate or optimal (Hughes, 1994; 1995; Sinclair *et al.*, 1994; Kanowski, 1995; 1996; Simons, 1992; 1996a; 1996b; Simons and Kindt, 1996; Sinclair, 1996; Newton, 1996; Boshier and Beer, 1997; Edwards and Schreckenberg, 1997). However, detailed solutions to these numerous dilemmas remain elusive. Some have suggested that new strategies, or ways to adapt old strategies, will emerge from more detailed knowledge and better understanding of farmer decision making and germplasm delivery pathways (Simons, 1996a). In other words, once we know enough about these more complex circumstances, objectives and opportunities we will be in a position to design breeding strategies -- perhaps comprising enhanced domestication with fine tuning of 'associative traits' and more proactive advance seed multiplication -- that truly meet detailed farmer concern profiles and benefit sustainable agroforestry (Simons, 1996a). Others have suggested that a more radical shift towards locally-based (possibly restricted to native species and 'semi-domestication') participatory breeding by farmers (or at least facilitating local domestication by farmers), needs to be considered (Newton, 1996; Sinclair, 1996). Others again have been asking the more fundamental question 'to domesticate or not to domesticate?' (Simons and Kindt, 1996), and if we domesticate, what are the full environmental and socio-economic implications? For example, does domestication lead inevitably to full commercialization and incorporation into large scale plantations or commercial agriculture? The whole topic of domestication of agroforestry trees is in a state of flux and rethink, and the domestication of *Leucaena* is no exception.

In place of straightforward prescriptions, this chapter aims to reflect on possible future domestication in the light of: what has been achieved (or not) to date in the (formal) domestication of *Leucaena* as an exotic; how indigenous domestication has proceeded; and the recent insights that reveal the hitherto largely unacknowledged complexities of domestication of agroforestry trees. As a framework, contrasting and complementary aspects of indigenous and exotic domestication of *Leucaena* are presented in Table 11. Detailed discussion of the indigenous domestication of *Leucaena* as a minor food crop (Chapter 4), spontaneous and artificial hybrids (Chapter 5), and genetic conservation (Chapter 8) also provide important background. I hope that some guidelines, albeit general, for the future domestication of *Leucaena* may emerge from this discussion, but overall it raises more questions than it provides answers for.

9.2 Breeding objectives

Although there is a long history of introduction, cultivation, naturalization and incipient domestication (*e.g.* Dijkman, 1950) of *Leucaena* species outside their native ranges stretching back several centuries (Section 6.2), more intensive formal genetic improvement is in its infancy, restricted essentially to the last three decades. This has been carried out by a small number of organisations, most notably the University of Hawaii and CSIRO in Australia, often with very limited resources. These programmes were directed, at least initially, and to a significant extent even now, towards improving livestock fodder production. High yield, improved forage

Table 11 Contrasting and complementary aspects of indigenous and exotic domestication of *Leucaena*[1]

Domestication component	Indigenous domestication[2]	Exotic domestication
Taxonomic knowledge	Several folk taxonomies - finely differentiated local cognitive systems	One scientific taxonomy - very variable, but generally crude local cognitive systems
Primary product	Food (unripe pods and seeds), some wood	Livestock fodder (leaves), some wood
Time span	Several millennia	<100 years; mainly last three decades
Genetic conservation	Strong *circa situm*[3], some *in situ*	No *in situ* and weak *ex situ*, reliant on *circa situm*
Acquisition of new germplasm	Local neighbour exchange and other informal seedflow	Worldwide, from scientific institutions, seed companies, government and other agencies
Hybridization	Spontaneous hybrids common but limited to few species growing in any one area	Artificial hybridization expanded to whole genus; spontaneous hybrids common
Selection and breeding	Adoption and adaptation of spontaneous hybrids plus some 'incipient domestication'	Artificial hybridization, some selection and breeding; spontaneous hybrids rarely domesticated
Levels of genetic diversity in production systems	High - usually several species and high levels of infraspecific diversity	Low - usually one species utilizing one or a handful of narrowly based varieties or hybrids
Screening/ adaptation/ adoption of improved germplasm or hybrids	For local, not widespread adaptation	For widespread, not local adaptation
Gene technology	No	Yes - but hardly applied as yet to *Leucaena*
Farmer participation	Yes - domestication done by farmers	No (or very limited) - domestication undertaken for them
Beneficiaries	Smallholder farmers	Diverse - smallholder farmers, commercial agriculture and forestry enterprises
Weediness	Unproblematic	Problematic, fostered by domestication through on-going species introductions
Genetic resource access and property rights	Farmers' rights rarely acknowledged and largely unrecognized	Breeders' rights - first commercial Plant Breeders Right for *Leucaena* granted in 1997 (Uniquest, 1997)

[1] Based on, but much modified from, Berg *et al.* (1991)
[2] Indigenous domestication is described and discussed in detail in Chapter 4
[3] *Circa situm* conservation refers to conservation in managed agricultural landscapes, *i.e.* outside natural *in situ* habitats, but within the native geographic range of a species (Chapter 8)

quality (including low mimosine), acid soil tolerance and more recently psyllid resistance have been the main breeding objectives, but these have not been static. For example, the early work on breeding low mimosine varieties or hybrids was largely abandoned following solution of the mimosine problem, at least for ruminants, from a quite unexpected quarter through alteration of rumen microfloras (Section 3.7). The overwhelming shift in emphasis to breeding for psyllid resistance in the mid 1980s was also unexpected (Section 3.4). This could be abandoned should effective biocontrol of the psyllid be achieved. It has also been suggested that the solution to the poor acid soil tolerance of *Leucaena* is not likely to be found through breeding, but rather through use and domestication of other genera (Section 3.3). Thus, even over the last three decades, breeding objectives have changed dramatically in response to new and unforeseen challenges or novel and unexpected solutions. Breeding objectives for *Leucaena* have been, and are likely to continue to present, a moving target.

Breeding objectives may also vary from place to place dependent on the numerous factors (products, biophysical, socio-economic, economic) which characterize different farming systems. For example, indigenous domestication has focused mainly on pod traits related to food production (Chapter 4) while international domestication as an exotic has been directed towards leaf quality traits related to livestock fodder production. In some situations breeding objectives may be sharply defined. For example the traits to be selected to improve *Leucaena* for use in Australian pasture systems have been defined by detailed agronomic research over several decades. In other cases breeding targets are less well understood and remain blurry. Characterization of many tropical farming systems, and particularly the desirable traits of trees in agroforestry systems, has only just begun (Raintree and Tailor, 1992; Cromwell *et al.*, 1996). Only in the last few years have scientists, including tree breeders, made a start towards understanding the more complex 'associative traits' (*sensu* Sinclair, 1996) of tree-crop interactions to define suitable ideotypes for breeding. Furthermore, it is only recently that scientists have started to understand farmer 'concern profiles' and involve farmers in defining species priorities and breeding objectives in more detail (Franzel *et al.*, 1996; Simons, 1996a). If, as some have asserted, such studies are the staring point for tree improvement (Sinclair *et al.*, 1994; Sinclair, 1996), further modifications to, and great variation in, breeding objectives may be expected.

At the same time, it is increasingly clear that it will not be enough to breed high yielding, psyllid-resistant varieties or hybrids which produce high quality livestock fodder even if they are adaptable to a wide range of farming systems. Effective mechanisms for their multiplication, dissemination, maintenance, development, or control may not be in place to deliver improved material to growers. The fate of improved material once delivered must be considered to examine whether genetic gains are likely to be sustainable in the face of changing circumstances and objectives or possible genetic contamination from existing landraces or closely related species, and whether new material is likely to become weedy. Any new germplasm which is released must be shown to be environmentally benign (Section 3.9). Maintenance of high levels of genetic diversity in improved material which is deployed may be required to provide farmer security and scope for continued farmer based domestication. Risks of weediness and the need for security in relation to pests and diseases are key considerations. Finally, it is also becoming clear that genetic conservation needs to be considered as an integral part of genetic improvement programmes and that this is inextricably linked with recent trends to establish genetic resource property rights (Section 9.6).

The extent to which previous genetic improvement programmes for *Leucaena*, or more sophisticated breeding strategies now being implemented, are likely to address these wider challenges of diversity in relation to risks, participation by farmers, genetic resource property rights and environmental hazards associated with weediness, and how easily material released from these programmes has been or can be delivered to growers, are assessed below.

9.3 Diversity, risks and farmer security

The genetic vulnerability of the narrowly based varieties of *L. leucocephala* and the risks associated with their wide deployment of a single species were pointed out by Benge (1983) and Brewbaker (1980; 1983; 1985). These risks have since been starkly demonstrated by the susceptibility of *L. leucocephala* to the psyllid defoliator (Geiger *et al.*, 1995; Section 3.4) as well as other limitations (Chapter 3) with disastrous consequences for livestock production. Furthermore, narrowly based material has clearly not been amenable to any subsequent farmer-based domestication. There have been many calls for use of more diverse *Leucaena* material (*e.g.* Brewbaker, 1980; 1985; Hughes, 1988b; Bray, 1994; Geiger *et al.*, 1995).

Although some have emphasized diversity within species or hybrids, in the form of multi-parent composites to reduce risks (Simons, 1992), use of a larger number of species (even if they all comprise narrowly-based varieties) may provide a more robust alternative (Hughes, 1988b; 1994; 1995). The narrow genetic base of the handful of widely used lines of *L. leucocephala* was exacerbated by often virtually sole reliance on a single species in planting programmes. The disastrous consequences of failure for communities reliant on *L. leucocephala* would have been far less serious had *L. leucocephala* formed a smaller proportion of total planting programmes thereby spreading risks (Geiger *et al.*, 1995).

There are no firm guidelines to indicate what levels of diversity in tree populations are needed to provide

Box 9 Domestication

- Given the diverse biophysical conditions, end products, species and hybrids, farming systems, clients, and wider socio-economic and environmental contexts of *Leucaena* use, no single genetic improvement strategy will suffice. Species- and location-specific approaches to exotic domestication will be needed.

- Domestication of Leucaena as an exotic has been directed largely towards improved livestock fodder production. High yield, improved forage quality (including mimosine reduction), acid-soil tolerance and psyllid resistance have been the main breeding objectives. However, even in the space of three decades, breeding objectives have changed dramatically presenting breeders with a moving and sometimes blurry target.

- The main outcome of formal domestication has been the deployment of a series of self-fertile, low-diversity, high-yielding varieties and hybrids (*e.g. L. leucocephala* - K8, K636 ('*Tarramba*'), '*Cunningham*', LxL; *L. diversifolia* - K156 and *L. leucocephala* × *L. diversifolia* KX3 hybrid). For these domestication has comprised straightforward collection, evaluation and release with no complex selection and breeding beyond first generation hybrids.

- Exploiting artificial hybridization promises almost unlimited scope for *Leucaena* improvement in agroforestry systems. The potential to create adaptable, highly vigorous, high product quality, psyllid-resistant, and if desired, seedless hybrids has been amply demonstrated. Interest in artificial hybrids has focused so far mainly on three of the four tetraploid species. There is also growing interest in the development of sterile triploid hybrids which may be highly productive, psyllid-resistant and, being seedless, present no risk of weediness.

- Domestication has so far largely failed to address the wider challenges of farmer security and participation - which demand maintenance of higher levels of species and intraspecific diversity in material which is released - nor the delivery and maintenance of improved material, the hazards of weediness associated with self-fertile improved varieties and hybrids, or genetic conservation.

- Very little of the genetic diversity assembled in the three major *Leucaena* seed collections is currently available for routine use by *Leucaena* growers. An approach to deployment of self-fertile tetraploid seed that employs multi-line varieties as genetically diverse composite seedlots is long overdue. A much more proactive approach to and increased investment in seed production is required.

- Future success in maintaining unrestricted exchange of *Leucaena* genetic resources is likely to depend on the formation of partnerships between providers (farmers, rural communities, conservation organisations, rural development agencies and governments in the countries of origin), intermediaries (such as OFI) and users (growers, seed producers and breeders) of *Leucaena* genetic material, which clearly recognize the principle of fair and equitable sharing of benefits. Innovative approaches to sharing benefits from such partnerships are needed.

- The indigenous (informal) and exotic (formal) domestication of *Leucaena* have followed very different, and in some ways complementary paths. Much can be learned and gained from integration of these disparate activities.

adequate security under differing socio-economic conditions and different plantation, agro-forest and farm systems. The wider relationships between biodiversity, human welfare and farmer security are also complex (Blaikie and Jeanrenaud, 1996). In industrial plantation forestry, bio-energy plantations or commercial agriculture, cogent arguments in terms of yield gains, economics, marginal returns and uniformity of product can be made to support use of often highly bred, narrowly based seed sources or clones of a handful of well known exotic species. It is largely in this arena that crop breeding and tree improvement have operated successfully in the past (Kanowski, 1996). Under these circumstances genetically improved material may make the difference between economic viability, or not. Thus it may be that large scale commercial *Leucaena* pasture systems, such as those in northern Australia, depend on use of highly uniform, narrowly based, genetically improved cultivars which meet the very tight specifications of uniformity, leaf quality and high yield required to ensure the sort of animal live weight gains which make extensive beef production economically viable.

For smallholder subsistence agroforestry, the arguments in favour of relying on this type of genetic material appear to be less compelling. In subsistence farming, in addition to yield, site adaptability, and product quality, there are wider considerations of stability, security and risk reduction, micro-site matching, timing of production in relation to seasons, diversity of products, compatibility with crops and livestock, integration with farm/family labour profiles, and self sufficiency and autonomy. Most such subsistence agroforestry systems are more complex and varied than agricultural or plantation systems (Kanowski, 1996). Smallholder farmers have larger and often more complex 'concern profiles' (*sensu* Bellon, 1996) compared to commercial growers. These concerns demand use of highly diverse material that matches the diversity of products that has been traditionally harvested, in some areas, from natural forest. In general, the more diverse the forest or agro-forest in terms of species, the more secure the services and the wider the range of available products (Sargent, 1992). Furthermore, maintenance of diversity in subsistence farming is often part of an adaptive strategy that allows resource poor farmers to cope with the heterogeneous and uncertain ecological and socio-economic environments in which they work (Bellon, 1996; Edwards and Schreckenberg, 1997). Tree planting is often one part of that strategy (Chambers and Leach, 1989). For tree planting that adaptive strategy must incorporate genetically diverse material and probably include a variety of species (or hybrids) in any one area (Marten, 1988; Sinclair *et al.*, 1994). The "multipurpose" tree concept in itself has mitigated against use of a wider range of species (Barnes, 1990) as a way of obtaining multiple products and reducing risks.

The indigenous domestication of *Leucaena* in Mexico (Chapter 4) provides one example of maintenance and use of high levels of diversity in subsistence farming systems (Table 6). It is not uncommon to find two, three, or even four species of *Leucaena*, along with one or more spontaneous hybrids, growing sometimes in a single field (Fig 9F), but frequently within a single community in parts of south central Mexico. High diversity is favoured and fostered by farmers in their quest for products of differing qualities and species with different production seasons and site adaptabilities. It is axiomatic that deployment of diverse material is a prerequisite to facilitating on-going domestication by farmers after material is released. If farmer breeding is to be an active and effective component of domestication (see below), as many have suggested recently, diverse material will need to be released. For *Leucaena*, recognition, adoption and cultivation of spontaneous hybrids arising in cultivation has been the main process facilitating indigenous domestication. Such hybrids may be an equally important source of new variation in the future where *Leucaena* species are grown as exotics (see below; Chapter 5). In order to incorporate the concerns of subsistence farmers (who make up the vast majority of *Leucaena* users) for security, and promote their greater participation in domestication, maintaining high levels of species and intraspecific genetic diversity may be as important as other breeding objectives.

However, the formal domestication of *Leucaena* as an exotic has to date followed a very different approach. The main outcome of both the UH and CSIRO *Leucaena* genetic improvement programmes so far has been the deployment of a series of self fertile, low diversity, high yielding varieties and hybrids (*e.g. L. leucocephala* - K8, K636 ('*Tarramba*'), '*Cunningham*', L×L (a multiline intervariety hybrid of *L. leucocephala*); *L. diversifolia* - K156 and *L. leucocephala* × *L. diversifolia* KX3 hybrid) (Table 12). For these 'domestication' has been simple, in that it has involved no complex selection or breeding beyond first generation hybrids, but rather the straightforward collection, evaluation and release of superior varieties, several of which are essentially unaltered genetically from 'wild' or incipiently domesticated (Chapter 4) material. Domestication has always involved an extreme narrowing of the genetic base. Within three decades, following the release and promotion of the '*Giant*' or '*Salvador*' varieties of *L. leucocephala*, one or a few self pollinated varieties were being cultivated across the tropics. Most cultivated material of *L. leucocephala* can be traced back to a small number of cultivated trees in Mexico and El Salvador, subsequently replicated by self pollination and abundant seed production. The most widely cultivated variety, K8, represents largely selfed progeny of material originally collected from one or a few cultivated trees in the central Mexican State of Zacatecas. The K636, cv. '*Tarramba*' is similar. Deployment of the other self fertile species, *L. diversifolia* has proceeded along similar lines with promotion of, and reliance on, essentially one variety, K156, again derived from one or a few parent trees growing (and likely cultivated for their edible pods) in a backyard near Fortín, Veracruz, Mexico. Only a handful of parent lines, *e.g.* K636 × K156, have been used in the production of the self fertile *L. leucocephala* × *L. diversifolia*, KX3 hybrid.

It requires only a small step to incorporate at least somewhat greater diversity into the self fertile varieties of *Leucaena*. Deployment of self fertile species (or hybrid) in the form of multi-line varieties as genetically diverse composite seedlots could be one such step. The recent release of a more diverse composite multi-line intraspecific hybrid (L×L) of five *L. leucocephala* subsp. *glabrata*, '*Giant*' accessions (Austin *et al.*, 1997) is a significant step in this direction. However, the comparative lack of genetic and useful variation, particularly in psyllid resistance, within *L. leucocephala* (Sections 3.1 and 6.3), may limit the scope to develop diverse multi-line or multi-intervarietal hybrid composites for that species. However, for the other self fertile tetraploids and hybrids this is not the case. *L. diversifolia* is known to be more variable. Furthermore the natural distribution of this species is now known to be much more widespread than was previously acknowledged (Fig

Table 12 Identities and origins of widely deployed cultivars and hybrids of *Leucaena* species

Ident. No./ cultivar	Source	Origin
	L. leucocephala* subsp. *glabrata	
K8	One of the first (distributed from 1970 onwards), and perhaps the most widely cultivated of the '*Giant*' or '*Salvador*' type lines, originally selected for exceptional forage and wood yields (Brewbaker *et al.*, 1972). Formally registered as a cultivar by the University of Hawaii (Brewbaker, 1975).	Moyahua, Zacatecas, Mexico Collected 1959 by H.S. Gentry
K28	University of Hawaii - '*Giant*' or '*Salvador*' type	Collected at the Santa Tecla Experimental Station, El Salvador, 1963; origin unknown
K67	University of Hawaii - '*Giant*' or '*Salvador*' type	Collected at the Santa Cruz Portillo Experimental Station, El Salvador, 1963; unknown origin
'*Cunningham*'	Bred line created by crossing '*Peru*' and '*Salvador*' type lines between 1956 and 1958 by Gray at the CSIRO, Division of Agronomy, Cunningham Laboratory; formally registered by Hutton and Beattie (1976). Combines the vigour and erect habit of '*Salvador*' type and branchiness of the '*Peru*' type.	Cultivar *Peru* obtained from Argentina, but of supposed Peruvian origin x CPI 18228 *Salvador* accession obtained via Hawaii from Guatemala in 1953
K636 ('*Tarramba*')	'*Giant*' type accession: moderately psyllid-tolerant *cf.* other '*Giant*' lines (Wheeler *et al.*, 1987; Bray, 1987; Glover, 1988; Wheeler, 1988; Uniquest, 1997). Registered under Australian Plant Breeders Rights Scheme as cv. '*Tarramba*' (Uniquest, 1997); seed production licensed in Australia to LEUCSEEDS (1997).	Saltillo, Coahuila, Mexico Collected by A.J. Oakes, 1978
	L. diversifolia	
K156	University of Hawaii. Perhaps the most widely distributed accession of *L. diversifolia*	Backyard 3km N of Fortín de Flores, Veracruz, Mexico Collected by J.L. Brewbaker, 1967
	Hybrids	
KX2	Advanced generation artificial hybrid: *L. leucocephala* x *L. pallida* created at the University of Hawaii. Widely distributed and known to be psyllid-resistant, high forage yielding, and cool tolerant (Austin *et al.*, 1995; 1997). Advanced generation F_6 hybrids, as variety '*Ohana*', with seed available from HARC (Austin and Osgood, 1997).	Several combinations of accessions used but most promising are: K636 and K548 (*L. leucocephala*) x K748 (*L. pallida*) (Austin *et al.*, 1997).
KX3	Advanced generation artificial hybrid: *L. leucocephala* x *L. diversifolia* created at the University of Hawaii. Widely distributed and known to be cool tolerant, moderately psyllid-resistant and high yielding (Brewbaker *et al.*, 1988). Self fertile. Selfing and recurrent selection used to create more stable advanced generation hybrids (Brewbaker and Sun, 1996)	Several combinations of accessions used but most promising are: K636 (*L. leucocephala*) x K156 (*L. diversifolia*).

31; Hughes, in press); new provenances from five States in southern Mexico and one location in northern Guatemala, collected by OFI provide a broad genetic base for evaluation of diversity within *L. diversifolia* and for the establishment of genetically diverse seed production stands. These could be based on bulk seedlots which sampled 20-50 parent trees per provenance, or comprise more sophisticated seed orchards based on individual tree collections, of which there are 94 in the OFI collection. Thus for *L. diversifolia*, there is good immediate scope to design and propagate diverse and genetically robust composites in simple multi-line seed orchards.

Exploiting hybridization promises almost unlimited scope for *Leucaena* improvement (Chapter 5; see below). The potential to create adaptable, high yielding, high product quality, psyllid resistant, and if desired seedless hybrids has been amply demonstrated (Brewbaker and Sorensson, 1990; Brewbaker *et al.*, 1989; Sorensson, 1995). However, research is also needed to examine levels of genetic diversity within bred hybrid lines. Hybrids, simply because they combine the genomes of two species, do not necessarily overcome the problem of a narrow genetic base unless carefully managed. It has been suggested that significant enzyme diversity within hybrids can lead to stability across environments, and that the enormous range of phenotypes exhibited by segregating hybrids is indicative of high diversity (Sorensson, 1995). However, segregation may be a function of recombination and does not necessarily indicate high genetic diversity, particularly after several generations of selection. Thus, as for conventional selection and breeding, there appear to be strong arguments in favour of development of multi-line hybrids, based on a set of parent accessions (Chapter 5).

Very little of the diversity in *Leucaena* which has been assembled in the three major seed collections (Section 6.3), is currently available for routine use by *Leucaena* growers. This is partly because research to evaluate this diversity is incomplete and superior species and seed sources have yet to be identified and fully tested across sites, but it may also be because deployment of out crossing species is more difficult without more substantive investment in seed production. Seed of species or provenances of any out crossing species which have performed well in trials is unlikely to be immediately available.

9.4 Seed multiplication and delivery of improved material

There has been growing interest in understanding the fate of new genetic material after it is released (or introduced). This concern has come from several quarters. Agroforestry tree breeders have been concerned about how to inject improved material rapidly and effectively into widespread use (Simons, 1996a; 1996b) and about its possible subsequent contamination, and hence dilution by existing local inferior landrace material, or in the case of *Leucaena*, other cross compatible species (Chapter 5). Conversely, those concerned with farmer-based *circa situm* conservation have been concerned about the possible displacement, or contamination of traditional varieties (or native trees) conserved *circa situm*, by improved varieties (or exotic tree species) (Hughes, 1995; Bellon, 1996; Section 8.5). Those concerned with conservation more widely have also been interested in, and greatly concerned about, understanding why some introduced species invade and others do not. All these factors need to be considered in domestication of *Leucaena*. At one extreme, seedy self fertile species are extremely straightforward to distribute and often spread naturally, sometimes becoming weedy and invasive (Section 3.9), while at the other extreme, sterile triploid hybrids (Section 5.7) are extremely difficult to disseminate and establish in widespread cultivation with present technology but are environmentally benign.

Delivery pathways. There are sharply contrasting views about how best to deliver genetically improved trees to farmers and about tree seed supply pathways more generally in farmer and community based agroforestry. Some have emphasized the importance of local seed self sufficiency through neighbour exchange and other informal local (or possibly regional) seed flows for the success and sustainability of farmer and community-based tree planting projects. This is at least based partly on recent studies which show that neighbour exchange and other local 'informal' seed sources provide the main channels by which farmers currently obtain seed or seedlings for planting (*e.g.* Cromwell *et al.*, 1996; Brodie *et al.*, 1997). Abundant local availability of seed was certainly an important factor contributing to the spread and blanket adoption of *L. leucocephala*. Early and abundant seed production through self pollination, giving true bred material, meant that seed of *L. leucocephala* was spread extremely easily from country-to-country, region-to-region, organisation-to-organisation, and from farmer-to-farmer. Ease of delivery also contributed to very wide use of, and reliance on, an extremely narrow genetic base (see above). Others have placed greater emphasis on the effectiveness and importance of external seed supply through a variety of more formal hierarchical extension and dissemination pathways. Simons (1996a) describes these pathways in terms of **distribution** (to NARs, NGOs and communities), **dissemination** (to farmers) and **diffusion** (farmer-to-farmer exchange). Recently emphasis has been placed on speeding up the production and release of improved material by bringing forward seed multiplication concurrently with evaluation to ensure that it is delivered before inferior material is widely established (Simons, 1996a; 1996b). At the other extreme, some apparently envisage on-going reliance on external seed supply as a normal and sustainable component of all routine tree planting activities. Approaches to producing seed of more advanced and stable *Leucaena* hybrids generally rely either on more sophisticated technology such as hybrid seed orchards or vegetative propagation. Some have pointed out the potential increased profits from hybrid seed produced from sophisticated seed orchards relative to heavy, early seeding species such as *L. leucocephala*, for the development and growth of a successful *Leucaena* seed industry (Brewbaker and Sorensson, 1990; Sorensson, 1995). Reliance on continued external seed supplies to deliver improved material may be attractive to breeders and seed merchants, but most seem to accept that such dependence is neither acceptable, realistic, nor sustainable for resource poor farming communities (Cromwell *et al.*, 1996). Informal local seed flow among farmers is an inevitable, essential and potentially beneficial component of seed supply. Once farmers have the necessary germplasm on-farm, outside sources are likely to be more expensive than locally collected seed and will tend to become redundant (Edwards and Schreckenberg, 1997). Thus what is really important in any release of new material is to design such material with subsequent on-going diffusion, and domestication in mind.

Once again, seed distribution pathways vary greatly from country to country according to circumstances. In some situations, promotion, advertising and effective marketing of new material (*e.g.* LEUCSEEDS, 1997 in Australia) may be sufficient to prompt farmers to purchase improved seed. Provision of cultivar names such as '*Maya type*' for *Gliricidia sepium* (Simons, 1996b) or '*Tarramba*' for K636 *L. leucocephala* (Uniquest, 1997), is seen as an important factor in marketing and adoption of improved material. Even when outside seed is used, subsequent neighbour exchange seems likely. In other situations, farmers obtain all material locally either as seeds, or often as seedlings, from neighbouring natural vegetation, farms or villages. Tree seed purchased from the formal sector will almost always be more expensive than locally collected seed (Cromwell *et al.*, 1996). Informal local seed exchange has been the sole mechanism for indigenous domestication in Mexico. In other areas a mixture of seed sources, both local and external are used, often with seed or plants supplied by local or national development projects and NGOs. Such situations offer good scope for the development of community-based seed supply initiatives which may be able to incorporate some improved material (*e.g.* Barrance, 1997 in southern Honduras; Cromwell *et al.*, 1996).

For *Leucaena*, differences between self fertile and out crossing species, and variation in seed productivity dictate how easy or otherwise it is to distribute and deliver new material to farmers.

Self fertile species. The deployment of improved genetic material of *Leucaena* has, to date, comprised a small number of self fertile species or hybrids (*e.g. L. leucocephala* - K8, K636 ('*Tarramba*'), '*Cunningham*', LxL; *L. diversifolia* - K156 and *L. leucocephala* × *L. diversifolia* KX3 hybrid) (Table 12). Delivery of this improved material to all, whether commercial or smallholder farmers, has been relatively straightforward, facilitated by self fertility and abundant seed production. Seed increase of other self fertile tetraploid species, such as *L. diversifolia*, or the self fertile hybrid KX3 between *L. leucocephala* and *L. diversifolia*, is as easy as for *L. leucocephala*. Any new tetraploids produced via unreduced gametes (Sorensson, 1997) are also likely to be self fertile and therefore easily multiplied and exploited.

Out crossing species. Although the majority of *Leucaena* species are out crossing, there have been only limited attempts to domesticate any of the out crossing species of *Leucaena* so far. Seed of most of the self incompatible species of *Leucaena* is not available in bulk or semi-bulk quantities at present. The natural populations in Mexico and Central America provide the only source of bulk seed supplies for most species that is immediately available. Forest tree seed banks in Nicaragua, Honduras and Guatemala regularly supply bulk seed of a range of native *Leucaena* species.

Production of pure seed of out crossing species demands use of more diverse material than a single tree or variety. For example, a small seed orchard of 12 trees of each of 15 accessions of *L. pallida* was established to produce composite seed in Australia with some success (Bray, 1995b), but difficulties were encountered in seed production of the single superior *L. trichandra* line CPI46568 due to scant seed production. Two seed orchards of *L. salvadorensis* have been established in Honduras (Ponce, 1995) following the Breeding Seedling Orchard design, BSO, (Gibson, 1992). The BSO combines progeny testing, limited phenotypic selection within and between families and seed production within a single planting. The two BSOs in Honduras included 30 and 44 open pollinated half-sib families of *L. salvadorensis*, thereby maintaining a broad genetic base (Ponce, 1995). These were planted at close spacing in a replicated design with early assessment and progressive selective thinning to wide spacing for seed production. Even for this shy seeding species significant seed production has been obtained.

The problem of seed increase was clearly acknowledged within the *Leucaena* psyllid trial (LPT) programme coordinated by NFTA. The follow up *Leucaena* seed production (LSP) programme established seed production stands of a range of psyllid-tolerant species and hybrids in five countries, namely: India, Indonesia, Philippines, Taiwan and Thailand in 1989. However, once again, seed production from the LSP programme has been limited mainly to the self fertile tetraploids such as the K636 variety of *L. leucocephala*. In the LSP, two orchards were established at each site, usually with cross sterile taxa. Seed for 500+ trees, including a minimum of 10 accessions was supplied and it was recommended that orchards be established at some distance from the LPT trials. Success of the LSP was mixed and seed beetle infestations (Section 7.3) limited production of viable seed at some sites.

In the absence of alternatives, it is tempting to collect seed directly from research trials or arboreta. Research in Hawaii has shown that there are few genetic barriers to interspecific hybridization in *Leucaena* (Sorensson and Brewbaker, 1994; Section 5.2). This means that when species are brought into close proximity in cultivation, as happens in trials and arboretum collections, there will be many opportunities for spontaneous hybridization (Sections 5.5 and 5.6). The genetic integrity of seed, of all but the self fertile species and hybrids, collected from such areas cannot therefore be guaranteed, as demonstrated by Hutton (1981) and Hutton and Tabares (1982) for seed collected in trial plots at CIAT, Colombia. Further than this, the small plots in trials or arboreta contain too few parent trees to provide an adequate genetic base for routine seed production activities. Seed collections for routine planting, at least of self incompatible species, should thus not be made from trials or arboreta.

Hybrids. There are two main approaches to breeding interspecific hybrids to overcome variability resulting from segregation in advanced generation progeny and to create more stable hybrid lines (reviewed by Sorensson, 1995). The first relies on clonal propagation to capture hybrid vigour and vegetatively propagate clones of outstanding elite hybrid segregants. This approach has not been used so far for *Leucaena* because no routine technology for rooting cuttings has been developed, although there are several promising options under investigation (see below). The second approach is based on development of advanced generation progenies of fertile tetraploid hybrids through either mass selection or inbreeding and recurrent selection of self compatible segregants (Sorensson, 1995). These more complex strategies involving back-crossing and recurrent selection have been implemented to produce high yielding, stable, high forage quality, psyllid-resistant *L. leucocephala* × *L. pallida*, KX2 hybrids (Austin *et al.*, 1995; 1997). Problems posed by production of hybrid seed, and development of efficient vegetative propagation techniques are priorities for research in *Leucaena* hybrid breeding (Sorensson, 1995).

Hybrids vary greatly in their seed productivity. A few of the tetraploid hybrids, such as the *L. diversifolia* × *L. leucocephala* are self fertile and produce abundant seed. The remaining tetraploid hybrids also produce seed readily. Most diploid hybrids are at least partially fertile, although a few appear to be sterile (Brewbaker *et al.*, 1989) while triploids are generally sterile or nearly sterile and produce little or no seed (Brewbaker *et al.*, 1989; Sorensson, 1995). In Indonesia a programme of vegetative propagation using stem cuttings and bud grafting was used to establish grafted seed orchards of the *L. leucocephala* × *L. trichandra* triploid hybrid (Toruan-Mathius *et al.*, 1995). Although seed set is sparse, some hybrid seed has been produced. However, in most cases, routine planting and possible commercialization of triploid hybrids will require development of simple, effective and cheap methods of seed production and/or vegetative propagation.

Despite investigation into a wide range of techniques including rooted stem cuttings (Hu and Chi-Cheng, 1981; Bristow, 1983; Duguma, 1988; Litzow and Shelton, 1991; Brewbaker and Sun, 1995), tissue culture (Peasley and Collins, 1980; Glovak and Greatbatch, 1982; Nagami and Venketswaran, 1983; Ravishankar *et al.*, 1983; Datta and Datta, 1984; Toruan-Mathius, 1992), grafting (Versace, 1982; Brewbaker, 1988; Singh, 1989) and air-layering with hydro-foam (Osman, 1995) successful vegetative propagation in *Leucaena* has been limited to experimental rather than routine scale operations. There are indications that rooting ability is species-specific (Sorensson, 1995) although most research to date has been carried out on *L. leucocephala*.

Sorensson and Brewbaker (1987b) and Sorensson (1997) suggested use of unreduced gametes (eggs or pollen with twice the number of chromosomes *i.e.* which failed to undergo reduction division during mitosis) to overcome the difficulties of propagation and breeding of triploid hybrids. Tetraploid versions of 'triploid' hybrids would be expected to be cytologically stable and largely self fertile and could thus be directly exploited, propagated and delivered. The main problems are clearly the operational difficulty of managing unreduced gametes and the likelihood that such hybrids could be weedy.

Whether it is via vegetative propagation, unreduced gametes, or other methods, it is likely that diploid species will be more widely used as parents in artificial hybridization in the future. There are three times as many diploids as tetraploids with which to modify *L. leucocephala* which remains the primary species of interest for breeding.

Bray (1984) proposed a system for large scale production of hybrid seed using natural cross pollination. This system works by exploiting self incompatibility whereby single clones of the self incompatible species, acting as the female parent, are established by grafting and interplanted at an appropriate ratio and density with trees of the self compatible species, acting as the male parent. For example Bray and Fulloon (1987) describe one such seed orchard with five alternating rows of *L. leucocephala* and *L. pulverulenta* 2.5 m apart. This system has subsequently been advocated and attempted by others (*e.g.* Elevitch, 1996). The expectation is that open pollinated seed collected from the self incompatible cloned trees will be hybrid seed. For example seed produced from a single *L. trichandra* tree planted amongst *L. leucocephala* in Queensland, Australia, *"apparently produced nearly 100% hybrid seed"* (Gutteridge and Sorensson, 1992: 4). However, in other cases the purity of seed produced from the few pilot hybrid seed orchards established using this technique has been disappointing resulting in variable, and sometimes very low proportions of hybrid seed (*e.g.* 7-29% reported by Bray and Fulloon, 1987). It appears that a significant proportion of non-hybrid seed arises as selfs in some predominantly self incompatible species (Sorensson, 1989a; 1990). Separation of hybrid seed or seedlings at the nursery stage has been proposed as a solution to this difficulty (Sorensson and Sun, 1990). Bray and Fulloon (1987) ruled out seed size alone as a way of distinguishing hybrid from non-hybrid seed, but Sorensson (1990; 1993) and Sorensson and Shelton (1992) showed that simple counts of leaflets per pinna can be used in conjunction with other traits such as leaflet shape to reliably and easily identify and separate unwanted non-hybrid seedlings in nurseries prior to outplanting.

9.5 Farmer-based domestication

Most recent authors have emphasized that much can be learned and gained from greater participation by farmers in domestication efforts (Sinclair *et al.*, 1994; Sinclair, 1996; Simons, 1996a; Boshier and Beer, 1997). The history of *Leucaena* domestication is variable in this respect. On the one hand, indigenous domestication has been done by farmers while on the other, domestication as an exotic has been carried out largely without their input. Much has been achieved in recent years to enhance farmer participation in setting species priorities and defining breeding objectives with progressive development of participatory assessment methods (Simons, 1996a). The question remains are farmers likely to play any more active or central role in domestication? The short answer is undoubtedly yes, in that some degree of farmer-based domestication, which may mirror the indigenous domestication in Mexico is inevitable, but again the extent and outcomes of farmer domestication are likely to be extremely variable.

Detailed local knowledge systems and perceptions of diversity by farmers provide the basis for farmer-based domestication (Section 4.4) and for adoption, or not, of new improved material by farmers. For *Leucaena*, local knowledge systems are variably developed. In Mexico the indigenous domestication has been based on a series of finely differentiated cognitive systems which clearly recognize and name species and within-species variants. This acute perception of diversity provides the basis for selection and means that novel variants, such as new spontaneous hybrids, are noticed and, if desired, propagated and adopted. Elsewhere, local knowledge of *Leucaena* diversity, and associated naming systems are extremely variable. In many areas *Leucaena* is simply equated by local people (including field staff, technicians and administrators of rural development projects) with the one well known species, *L. leucocephala*, even though other species may be present in the area. In Kenya, *L. leucocephala* and *L. diversifolia* were considered one and the same until the arrival of the psyllid provided a more obvious (to local farmers) way of distinguishing them (Simons, 1996a). In Indonesia, more sophisticated local naming systems have developed for *Leucaena*; farmers recognize and name several species and noticed and domesticated one spontaneous hybrid (Section 5.5; Dijkman, 1950). Development of local knowledge is likely to depend on the history of introductions, the time elapsed since species were introduced, the degree to which species naturalize, the socio-economic importance and cultural significance in local farming systems and how much diversity (species/ hybrids/ within-species) has been introduced. Farmers who grow *Leucaena*, but who may be only familiar with *L. leucocephala*, are often astonished by and very interested in the diversity available in *Leucaena* when they visit species trials.

Local naming systems and farmer perceptions of diversity are usually based on readily perceived traits related to end use. The derivations of Mexican names from pod traits related to food use are one example (Fig 23; Section 4.4). Some traits, such as yield, which are noticed and measured by researchers may not be of primary interest to or be perceived by farmers and are unlikely to be the focus of farmer domestication. Furthermore, farmer thresholds may be very different from biological thresholds in domestication (Simons, 1996b). Other traits such as fodder quality may be the focus of farmer experimentation (de Boef *et al.*, 1993). However, whatever traits are of interest, it is likely that farmers will perceive diversity most readily among species and hybrids, rather than within species. As for the indigenous domestication, species level diversity and spontaneous hybrids probably provide the most fertile territory for the wider development of farmer-based domestication. However, compared to indigenous domestication, farmer based domestication elsewhere will be limited by poorly developed local knowledge systems and the lower priority often placed on non-food crops.

9.6 Farmers' rights, breeders' rights and access to genetic resources

No country is self sufficient in genetic resources; all are dependent on continued international exchange. This is very much the case for the genetic development of *Leucaena*, as new material is sought by *Leucaena* growers and breeders to meet new and unforseen challenges such as psyllid resistance. The three major *Leucaena* seed collections (Section 6.3) were assembled prior to the Convention on Biological Diversity (see below). Seed from these collections has up to now been readily available to all without the necessity to share benefits with the countries of origin, without the recipients having to concern themselves with the political, financial and administrative inconvenience of seeking access to genetic resources *in situ*, and with no constraints about what the material is used for. However, even the substantial *ex situ* seed collections of *Leucaena* will not remove the need for access to *in situ* genetic resources. For example, as promising new species and provenances are identified from trials it may be desirable to return to natural populations of these species and provenances to make new and more intensive collections that sample additional genetic diversity. The University of Hawaii seed collection expedition to Mexico in 1997 focusing particularly on *L. pallida* is one example. New collections of *L. trichandra* from south east Guatemala might be another (Section 6.5). Conservation of, and continued access to, material from wild (or incipiently domesticated) populations provides security for future breeding and utilization of *Leucaena*.

The history of transfer of genetic resources, and particularly forest genetic resources, around the globe has, until recently, been characterised by largely unrestricted access to material based on the principles of 'common heritage' and mutual benefits from international exchange. In recent years, a number of developments have meant that this situation is changing, with a trend towards withdrawal of both wild and improved genetic material from public ownership and greater control over access, supported by new legislation in a growing number of countries. This trend has been bolstered by the Convention on Biological Diversity, CBD, (United Nations Environment Program, 1994; subsequent Conferences of the Parties). The CBD emphasizes the sovereign rights of States to exploit their own genetic resources with access to them only through prior informed consent based on terms mutually agreed as a result of bilateral negotiations between provider and prospective user. The CBD also emphasizes 'fair and equitable sharing of benefits' resulting from the utilization and commercialization of genetic resources. Future success in maintaining unrestricted exchange of *Leucaena* genetic resources is thus likely to depend on the formation of partnerships between providers (farmers, rural communities, conservation organisations, rural development agencies and governments in the countries of origin), intermediaries (such as OFI) and users (growers, seed producers and breeders) of *Leucaena* genetic material, which clearly recognize the principle of fair and equitable sharing of benefits. Innovative approaches to maximising benefits from such partnerships are needed (ten Kate, 1995; Bell, 1997). The anomalous position of *ex situ* seed collections assembled prior to the CBD points to the need for retrospective international agreements covering their ownership, access and benefit sharing. Agreements will only come about and contribute to sustainable development through the initiative of prospective partners. The value of such partnerships will depend heavily on the commitment, knowledge and understanding of the implications of what is being undertaken by the various parties involved (Bell, 1997). One objective of this *Handbook* is to raise awareness of the role that farmers and local communities have played in conservation (Chapter 8) and indigenous domestication (Chapter 4) of *Leucaena* genetic resources amongst growers and breeders, as well as the scale and importance of their use (Chapter 3) and hybridization (Chapter 5) as exotics amongst those in Central America and Mexico.

The market value of genetic resources may be difficult to assess. However, it is clear that, compared to other sectors, such as agricultural crop genetic resources or pharmaceuticals, the genetic resources of *Leucaena* have only modest commercial value. Many of the users and beneficiaries are smallholder farmers of the tropics who use *Leucaena* to meet basic subsistence needs. Nevertheless, there are also commercial benefits associated with use of *Leucaena* genetic resources in the production of seed, the generation of improved genetic material and in commercial agriculture. For example *Leucaena* is planted on a large scale for the improvement of cattle pasture: 20,000 ha between 1984 and 1994 (Gutteridge and Shelton, 1994) and at least 35,000 ha total (Middleton *et al.*, 1995) in central Queensland, Australia. The volume and value of the global *Leucaena* seed trade, although unquantified, is clearly of commercial significance; there are many national and international seed companies which market seed of *Leucaena*. In Queensland more than 5,000kg of seed of *L. leucocephala* was produced for commercial sale in 1986-87 (Gutteridge and Stur, 1994) and in 1997, 7,000kg of seed of cultivar '*Tarramba*' alone, were produced and sold (Larsen[1] pers. comm.). Seed of the cultivar '*Tarramba*' (see below) sells at Austr.$40/kg (Bray, pers comm.) and of improved advanced generation KX2 (*L. leucocephala* x *L. pallida*) and L×L, *L. leucocephala* hybrids at U.S.$330/kg (Austin and Osgood, 1996; Austin *et al.*, 1997). Although several varieties of *Leucaena* have been registered in the past (*e.g.* '*Cunningham*' (Hutton and Beattie, 1976) and K8 (Brewbaker, 1975)), these have remained in the public domain as public varieties. However, the first case of commercialisation of a *Leucaena* variety has recently been granted under the Australian Plant Breeders Rights Scheme for the variety '*Tarramba*' (the K636 variety of *L. leucocephala* collected in 1978 near Saltillo, Coahuila, Mexico) (Uniquest, 1997). PBR certificates, formerly referred to as Plant Variety Rights, protect exclusive commercial rights to produce and sell seed of a registered variety and are a form of intellectual property right like a patent or copyright. The holder of a PBR certificate can license seed producers, with seed sales attracting a small royalty. PBR certificates conform with the 1991 revision of the International Convention for the Protection of New Varieties of Plants (the UPOV Convention). Sole seed production rights for '*Tarramba*' have been granted under license to LEUCSEEDS (1997).

As for other genetic resources, there are growing tensions over moves towards withdrawal of *Leucaena* genetic resources from public ownership, through declarations of property rights over both what were hitherto 'wild' (or incipiently domesticated) genetic resources and 'improved' varieties. Closer integration of indigenous and exotic domestication will be needed to avoid tensions inherent in the commercialisation of *Leucaena* genetic resources which are derived from and conserved elsewhere. These tensions are implicit in the third objective of the CBD, the fair and equitable sharing of benefits out of the utilization of genetic resources between different stakeholder groups. Issues underlying these tensions remain hotly contested and debated and the extent to which the *Leucaena* community will agree to discuss them, much less act upon the concerns and principles they represent, remains unclear.

In the case of *Leucaena* high priority needs to be given to sharing of benefits with farmers and communities in Mexico and Central America. This is because, for *Leucaena*, it is these farmers and local communities who have been and continue to be important architects of *Leucaena* diversity through indigenous domestication (Chapter 4). It is quite likely that *L. leucocephala* itself

[1] Peter Larsen, LEUCSEEDS, Banana, Queensland, Australia

was a direct product of that indigenous domestication process (Section 4.6). These same farmers and communities have also been and continue to be the primary custodians of the genetic resource providing the only viable conservation option for the majority OF species (Chapter 8). Although crop breeding and tree improvement might be expected to encompass the conservation of the genetic resources on which they depend, most breeding programmes fail to do this. Formal domestication of *Leucaena*, although utilizing an increasing range of species has continued to rely on *circa situm* methods (Table 11). As discussed in Chapter 8, local communities can decide the fate of the genetic resources around them and can be key contributors to their conservation and sustainable use. However, more substantive recognition of their role and rights as stewards of biodiversity is a prerequisite to maintaining that diversity (Bell, 1997). Kanowski (1996) characterizes such dependencies in tree breeding as 'backward links' and encourages tree breeders to 'look backwards' from the tree improvement cycle and acknowledge the value of *circa situm* (and *in situ*) conservation more explicitly. For *Leucaena* breeders and growers, as for other breeders, 'looking backwards' may be as crucial as 'looking forwards' if continued improvements in yield and quality of products are to be made.

Benefit sharing. While employment of farmers and local residents during seed collection expeditions contributes modest short term benefits to communities local to *Leucaena* genetic resources, more substantial support to sustain conservation and use is needed. One such mechanism is involvement of local communities and farmers in on-going supply of bulk seed for planting programmes. For most species of *Leucaena*, wild populations are still an important source of bulk seed supplies available for larger scale planting. Seed collection from trees on farms and sale to NGOs concerned with tree planting or national tree seed banks can provide an additional source of income for local communities (Barrance, 1997). For example, local community-based seed collections of *Gliricidia sepium* and *L. salvadorensis* in southern Honduras have been organised by a number of NGOs concerned with tree planting (Barrance, 1997). For a few species with known seed demand, establishment of community seed production stands may further assist this process. However, when seed is destined for onward sale or export, fair pricing mechanisms may be elusive in the face of profit seeking seed merchants.

More substantive recognition of the principles of the CBD will demand 'fair and equitable sharing of benefits' arising from the exotic domestication of *Leucaena* with the providers and custodians of *Leucaena* genetic resources in Mexico and Central America. It is extremely doubtful whether registration of PBRs for *Leucaena* varieties will enhance access to *Leucaena* genetic resources or contribute to the development of mutually beneficial partnerships between providers and users of genetic material. However, if such PBRs are enacted it is of paramount importance that benefits arising, however modest, are shared 'fairly and equitably' with donor countries, and farmers and local communities in the countries of origin. Establishment of property rights regimes which recognize the respective roles of different participants in conserving and developing *Leucaena* genetic resources may require monetary as well as rhetorical contributions by breeders, even though the means of delivery are still poorly developed and there is currently only limited experience on how to decide what constitutes 'fair and equitable sharing of benefits'. Directing a percentage of income derived from international seed sales or royalties (albeit modest) derived from licensing of PBRs could contribute to 'fair and equitable sharing of benefits'. Such income could be channelled through NGOs working to support rural development in communities with important *Leucaena* genetic resources in their care. *Circa situm* conservation is already operating successfully for many species of *Leucaena* to the benefit of both local communities in Mexico and Central America and *Leucaena* breeders and growers elsewhere (Chapter 8). However, in some areas, outside support is needed to promote, secure and expand *circa situm* use of species of *Leucaena*. Provision of detailed extension material on species identification, propagation, silviculture and management may be all that is needed to catalyze *circa situm* action (*e.g.* documentation of *L. salvadorensis* in Honduras by Hellin and Hughes (1993) and CONSEFORH (1998)). Similar support is needed for other species, for example, to support tree planting activities in villages such as El Rincón, Yerbabuena and Quetzaltepeque in the south eastern Guatemalan Department of Chiquimula which include the critically endangered *L. magnifica* (Section 8.2). For *Leucaena* scope to provide such support based on benefit sharing is limited by the generally low commercial value of *Leucaena* genetic resources and by the lack of well-developed understanding, communication and exchange between providers and users. However, even projects of modest national economic significance can create important opportunities for farmers, local communities and NGOs to enhance conservation. There is a strong case for international donor support for benefit sharing initiatives.

The OFI *Leucaena* seed collections were collected with the prior informed consent of the governments of 11 countries under a variety of research agreements and plant collecting permits. The OFI has also recognized the need to formalize agreements with seed recipients in the form of a Material Transfer Agreement, MTA (Appendix 4). This is designed to promote scientific exchange while at the same time recognizing the responsibilities of seed recipients towards the countries that provided the seed. The MTA also aims to encourage the development of beneficial partnerships between recipients and donor countries and communities. The OFI has been an important conduit for supply of *Leucaena* genetic resources, it maintains full details of seed providers and recipients on its database, and may also be able to assist as an intermediary to establish benefit sharing.

9.7 Conclusions

Formal domestication of *Leucaena* as an exotic has promised more than it has so far delivered. It has resulted, to date, in effective deployment of only a handful of high yielding, self fertile varieties and hybrids (*e.g. L. leucocephala* - K8, K636 ('*Tarramba*'), '*Cunningham*', LxL; *L. diversifolia* - K156, and *L. leucocephala* x *L. diversifolia* KX3 hybrid) (Table 12). For whatever end user or production system this has proved to be an unacceptably narrow and risky genetic base, although the disastrous consequences of this approach have no doubt had greatest relative economic impact on subsistence, as opposed to large scale commercial farmers. Such approaches have proved overly simplistic to match the diversity and complexity of circumstances, objectives and opportunities and have provided only risky and short lived solutions. Given that the risks of reliance on single self pollinated varieties have been so amply and starkly demonstrated in the last decade for *L. leucocephala*, it is surprising that some researchers continue to work with, promote and distribute seed of single line self pollinated varieties. The registration, promotion and seed production of another self pollinated variety (K636), as variety '*Tarramba*' (Uniquest, 1997; LEUCSEEDS, 1997), albeit with its superior psyllid tolerance and proven vigour over K8 and other varieties, although at some level adding to the genetic diversity in widespread use, perpetuates this flawed and genetically risky approach.

Only a small fraction of the diversity available within *Leucaena* has been tapped by formal domestication efforts and made available to growers. There is good immediate scope to develop and release more diverse material in the form of additional species and multi-line composites of self fertile species or hybrids. Deployment of greater diversity will reduce risks of failure due to pests and diseases and provide opportunities for subsequent farmer-based domestication, but could increase the risks of weediness. Further research is needed to perfect technologies to design and produce new *Leucaena* hybrids. Nevertheless, the potential to do so is within our grasp given modest investment in research. High interspecific crossability, diversity of useful characteristics amongst species and relative ease of artificial hybridization, mean that new hybrids can be designed and created virtually at will to meet specified criteria. However, deployment of hybrids, unless they are self fertile will depend on increasingly sophisticated technology in the form of hybrid seed orchards or vegetative propagation and may therefore be inappropriate for smallholder uptake. Self fertile varieties and hybrids are easy to deliver to growers but are also likely to be weedy (Section 3.9). Conversely, out crossing species or sterile hybrids are hard to deliver but are environmentally benign. There will always be trade-offs in domestication.

There will also be trade-offs in seed multiplication and delivery of improved material between those seeking to control and promote the delivery (or sale) of improved material, those trying to conserve land races and those advocating a more whole heartedly participatory approach with farmers pursuing their own domestication agendas. It seems likely that however well we understand farmer decision making and map out germplasm delivery pathways, the future of *Leucaena* domestication will by definition be participatory. It will no doubt harbour surprises such as novel spontaneous hybrids, some of which will be adopted and adapted and some of which will not thrive. The likely proliferation of spontaneous hybrids in coming years (Sections 5.5 and 5.6) could, as it has been for indigenous domestication, be the main mechanism for farmer-based domestication elsewhere.

The indigenous (informal) and exotic (formal) domestication of *Leucaena* have followed very different paths (Table 11). Furthermore, awareness of these parallel activities has remained low, with limited communication between different actors. Nevertheless, there may be features of both which can contribute and be incorporated into the other; much may be learned in both directions. There are also parallels which may indicate the likely course and outcomes of future domestication efforts. Furthermore, there are important interdependencies between indigenous and exotic domestication, particularly for genetic conservation, which demand recognition, but which have yet to be widely recognized or acknowledged for *Leucaena*. There have been calls for closer integration of indigenous and formal crop domestication (*e.g.* Tripp and van der Heide, 1996) and tree improvement and *in situ* or *circa situm* conservation (Kanowski, 1996); such links are overdue for *Leucaena*.

Leucaena breeders need to 'look backwards' to conserve genetic resources and support those already doing so, and 'look forward' to secure opportunities for continued improvement and predict future demands and risks. In short, they perhaps need to stop from time to time and 'look around' as far towards the horizons as they can in all directions to better assess the wider implications, likely outcomes, and limitations of their work.

10 Identification

10.1 The importance of accurate identification

This chapter aims to assist foresters, agronomists, breeders, other *Leucaena* growers, ecologists and ethnobotanists to identify species of *Leucaena*. Accurate identification underpins efficient use and conservation of genetic resources both in the natural populations in Latin America and where cultivated elsewhere. Conversely, misidentification can cause confusion which may persist for years. Seed collections (Chapter 6), *circa situm* planting (Chapter 8), breeding and tree improvement (Chapter 9) and wider ethnobotanical (Chapter 4) and ecological research depend crucially on the ability of a wide spectrum of people, not necessarily botanically trained, to accurately identify trees. As a wider range of species is brought into cultivation and domestication, accurate identification becomes a more critical, difficult and increasingly widespread problem. Confusion over identification of *Leucaena* material has already arisen on a number of occasions leading to misinterpretation of trial results, misidentification of seedlots and use of misidentified and poorly adapted material in planting programmes.

Formal taxonomic publications, such as the revision of Mexican species (Zárate, 1994) or the forthcoming taxonomic monograph of the genus (Hughes, in press) are of limited use to anyone interested in identifying trees in the field. Firstly, such publications are not widely distributed and available to all. Secondly, they tend to use a lot of technical jargon. Thirdly, they rely on details of flowers and fruits which are generally present on herbarium specimens - and even microscopic characters, such as pollen morphology - but which are not always observable in the field. Ideally it would be possible to identify trees using just the readily observed features of bark, shoots and leaves. However, in many cases, bark and leaf characters are not constant, but show continuous patterns of variation which overlap among species such that it is extremely difficult to reliably identify all species of *Leucaena* without recourse to some flower and fruit characters at times. Fortunately unlike for many larger forest trees, pods and flowers of *Leucaena* species are often present and reasonably accessible as they are small trees which flower and fruit from an early age often over long periods of the year. The aim here is to rely on and give first consideration to leaf characters where possible. Fruit and flower characters are used only where necessary and reliance on microscopic characters is avoided.

In *Leucaena*, an ever growing abundance of spontaneous and artificial hybrids (Chapter 5) greatly complicates, and heightens the need for, accurate identification. For example, Howcroft (1994) points out the difficulties of identifying putative hybrids in Papua New Guinea. Conversely, provision of good tools for identification is important for the detection of new spontaneous hybrids. Given the range of possible hybrid combinations in *Leucaena* that produce viable seed (Section 5.2) it is quite impossible to include all hybrids in routine identification tools. Two spontaneous hybrids which are common in parts of Mexico are included in the key. In addition, general guidelines for identification of putative hybrids are presented in Section 10.6.

10.2 How to use this chapter

Many people who come to identify *Leucaena* trees will not be trained botanists. For this reason botanical jargon has been kept to a minimum. However, species delimitation (Section 2.3), and hence recognition, is based on comparative morphology and anatomy (of all plant parts) and a basic understanding of the morphology of the different parts of *Leucaena* plants is needed to be able to identify them. Basic morphology is illustrated in Figure 16 and essential botanical terms explained in the glossary (Appendix 4). Identification characters are described and illustrated as far as possible in Section 10.3 (Figs 17-23). **It is well worth familiarizing oneself with these characters and illustrations before embarking on any identification using the keys.**

Identifying closely related species (or hybrids) is not always easy; there are no fullproof shortcuts that can make this task totally 'user-friendly'; some effort and work on the part of the user cannot be avoided! Five tools that can assist with identification are provided in this *Handbook*:

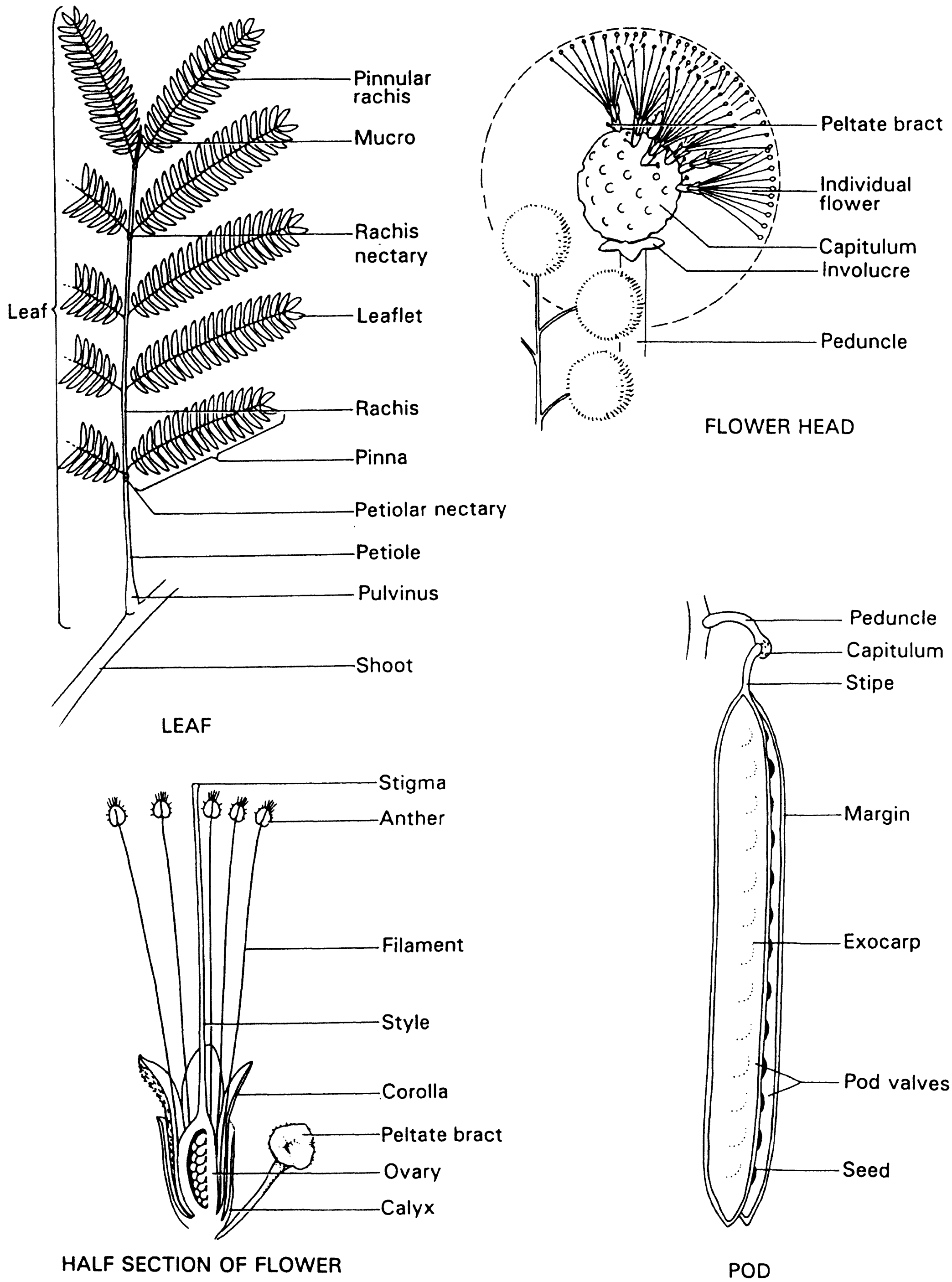
▸ Detailed tables listing species by morphological categories for leaf, bark, flower and fruit characters are provided (Tables 13-17) along with drawings or photographs (Figs 17-23) in Section 10.3. These provide spot character checks to assist with identification and explain the characters used in the keys.

▸ A character matrix (Table 18), or tabular key, provides a quick method to narrow down the identification to one of a small subset (maximum three) species (Section 10.5).

▸ The central tool for identification is a dichotomous diagnostic key (Section 10.5).

▸ Botanical drawings of all species, brief descriptions, and discussion of diagnostic botanical features which may assist identification, are provided in the species

Figure 16 Morphology of *Leucaena*



accounts (Chapter 11) which should be used in conjunction with the keys; the two are complementary. For example, once the key has been followed through until an identification has been obtained it is well worth cross checking the identification with the species description and drawing provided in Chapter 11.

▸ Section 10.6 describing methods used to identify hybrids.

If a specimen clearly falls outside the species included in the key and species accounts, it may well belong in another Mimosoid legume genus or alternatively it may be a hybrid (see below). It is not infrequent that material thought to be of a species of *Leucaena*, in fact belongs in another genus. Many Mimosoid legume genera look very similar to *Leucaena* in overall appearance and generic identification can be a bewildering task for non-botanists faced with an unknown Mimosoid legume specimen. A comprehensive key for identification of genera is beyond the scope of this Chapter. Such keys are generally available in regional or national Floras. However, in Section 10.4, features which characterize all *Leucaena* species are listed and spot characters to distinguish the closely related genera provided. It is always worth keeping the question - 'is it a Leucaena?' - in the back of one's mind when identifying species.

Where a specimen has been verified as a Leucaena, but still does not match any of the species included in the key and species accounts, it may be a hybrid. In such cases, reference should be made to Sections 10.6 and 5.3. However, as discussed in Section 5.3, identification and characterisation of putative hybrids is not straightforward. In some cases, certain identification using morphology alone may not be possible and there may be no alternative but to resort to advice from botanical experts who themselves would need to undertake further investigation to resolve hybrid identities. This will usually involve collection of botanical specimens and associated dried leaf material for detailed scientific analysis particularly using molecular markers (Section 5.3).

10.3 Identification characters

The characters used in the keys are those which should enable the field worker to identify a Leucaena. These are described and discussed in detail in this section. Full details of other morphological characters (*e.g.* pollen and anther glands) are provided in Hughes (1997b; in press).

LEAVES. All species of *Leucaena* have bipinnate leaves and the pinnae and leaflets are opposite (Fig 16). Because the leaves are divided into pinnae and leaflets, confusion about what comprises a leaf may arise. If there is doubt about the difference between leaves and leaflets, this should be resolved using Figure 16. The leaves of *Leucaena* species are very variable and provide some of the most conspicuous and useful characters for field identification. Both quantitative variation - in leaflet length and width, numbers of leaflets per pinna and numbers of pairs of pinnae per leaf - and qualitative variation in leaflet shape (including symmetry), and shape of the petiole gland are useful for identification.

Identification of trees which have been recently lopped (*e.g.* in forage hedgerows) is much more difficult as leaf traits on young resprout shoots are often very different from normal leaves on mature shoots and may be extremely variable. It may be better to postpone identification of such trees until more mature shoots are available.

Quantitative leaf variation. Four basic quantitative leaf traits can be measured or counted to describe a bipinnate leaf: number of pairs of pinnae per leaf, number of pairs of leaflets per pinna, leaflet length and leaflet width. These measures are not independent. Species with large leaflets have fewer pairs of pinnae and pairs of leaflets per pinna than species with small leaflets. Within *Leucaena* there is wide variation in these four leaf traits. For example the number of pairs of pinnae per leaf varies from 1-3 to more than 60, number of pairs of leaflets per pinna from 2-6 to 85, and leaflet length from 3-5 mm to 80-120 mm across species (Figs 17-18). The total number of leaflets per leaf ranges from 12 for large leaflet species such as *L. macrophylla* (Fig 45) to 12,000 for small leaflet species such as *L. esculenta* (Fig 32). Thus at the extremes, species are immediately distinguishable simply by looking at leaves. The basic question - 'does the species have small or large leaflets?' - is the most useful starting point for identification. However, while the extremes are poles apart and distinguished at a glance, variation within and between species is often overlapping, making it impossible to identify all species based on leaf traits alone. There is also considerable variation in leaflet shape with the genus (Figs 17-18). Again this is correlated with leaflet size. Large leaflets are generally elliptic, ovate or lanceolate and only weakly asymmetric at the base, whereas small leaflets are linear or narrow-oblong and usually strongly asymmetric at the base (Figs 17-18). Species are listed in Table 13 according to categories of leaflet size and shape.

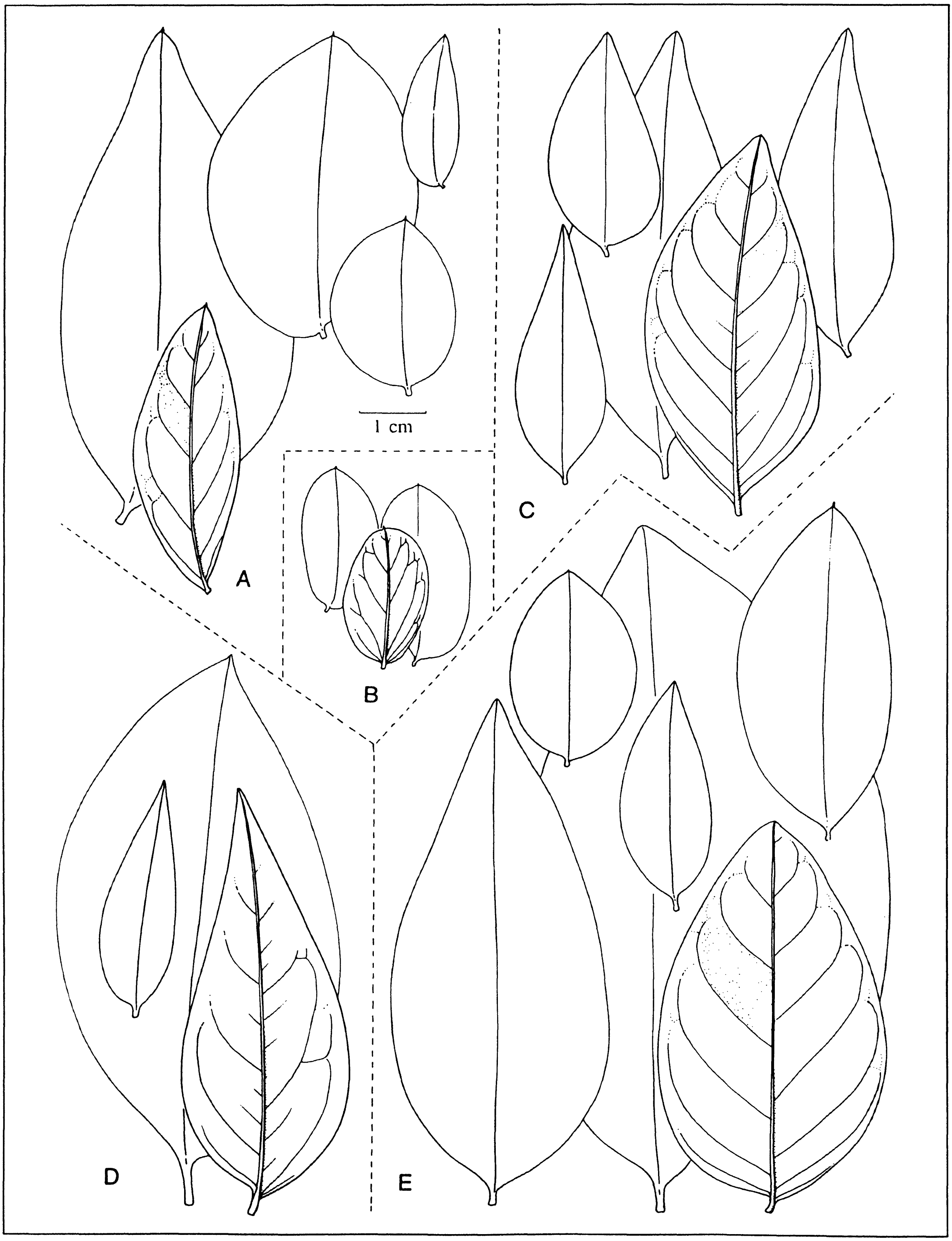


Figure 17 Leaflet size and shape: species with ovate or elliptic leaflets and weakly asymmetric bases. **A.** *L. lanceolata*; **B.** *L. retusa*: **C.** *L. multicapitula*; **D.** *L. macrophylla*; **E.** *L. trichodes*. Leaflets sampled to represent range of leaflet size and shape variation within species, including variation across intraspecific taxa where they exist

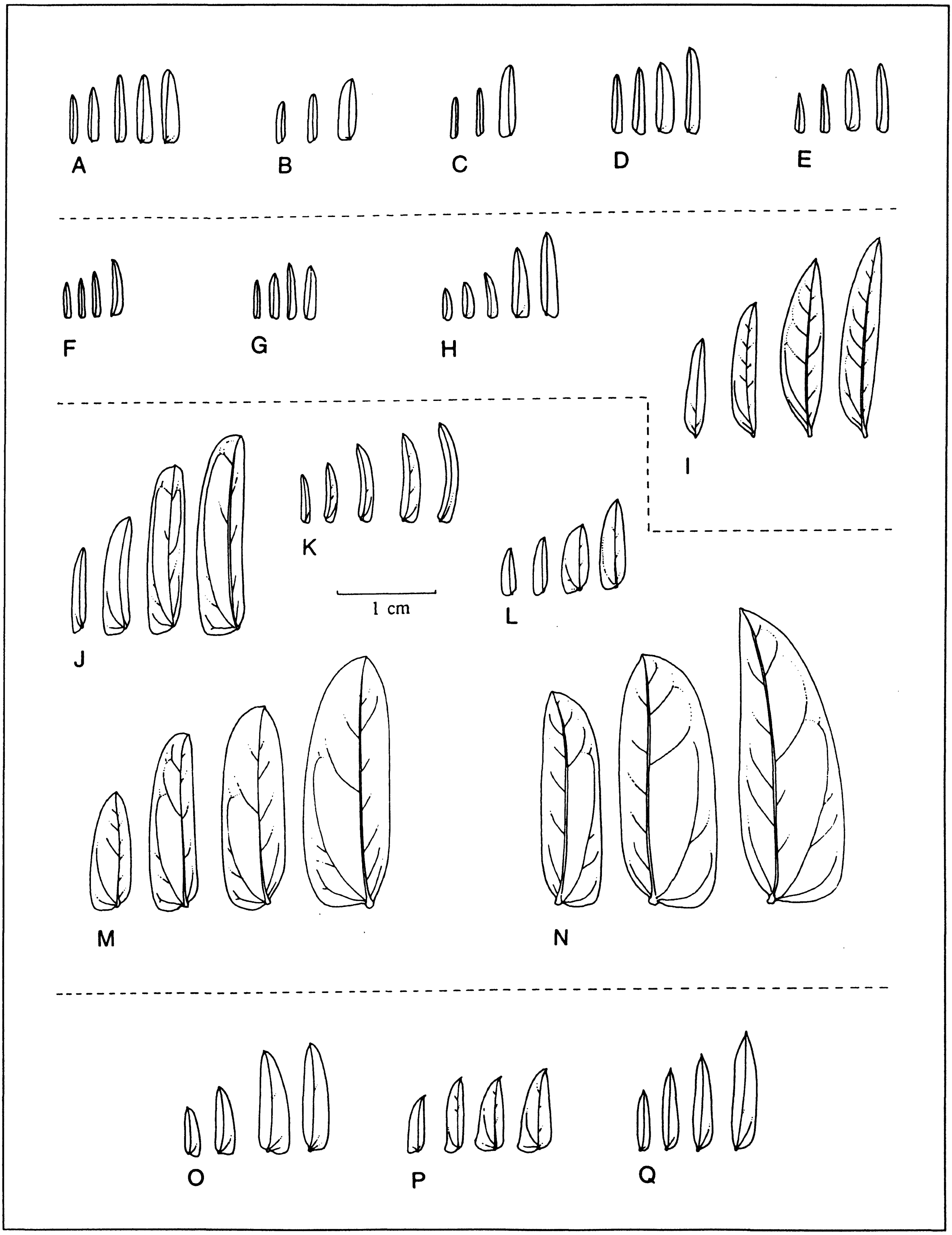


Figure 18 Leaflet size and shape: species with linear or linear-oblong leaflets with strongly asymmetric bases. **A.** *L. esculenta*; **B.** *L. involucrata*; **C.** *L. pueblana*; **D.** *L. pallida*; **E.** *L. matudae*; **F.** *L. trichandra*; **G.** *L. pulverulenta*; **H.** *L. diversifolia*; **I.** *L. leucocephala*; **J.** *L. salvadorensis*; **K.** *L. collinsii*; **L.** *L. lempirana*; **M.** *L. shannonii*; **N.** *L. magnifica*; **O.** *L. confertiflora*; **P.** *L. cuspidata*; **Q.** *L. greggii*. Leaflets sampled to represent range of leaflet size and shape variation within species, including variation across intraspecific taxa where they exist

Table 13 Categories of leaflet size and shape (leaf formula: number pairs pinnae per leaf; number pairs leaflets per pinna; leaflet length (mm); leaflet width (mm); normal range in **bold**, extreme range in brackets)

1. Leaflets elliptic, ovate or lanceolate, weakly asymmetric at base, large (>1 cm wide), 2-6 (-8) pairs of leaflets per pinna (Fig. 17)

	no. pairs pinnae	no. pairs leaflets	leaflet length (mm)	leaflet width (mm)
L. lanceolata	**2-5**	**2-5**(-7)	**16-70**	**8-35**
L. macrophylla	(1)**2-3**	**2-4**(-6)	(15-)**23-55**(-80)	(6-)**17-39**
L. multicapitula	(2-)**3-4**(-5)	**4-5**(-6)	(35-)**40-50**(-55)	(15-)**18-23**
L. retusa	(2-)**3-4**(-5)	(4-)**6-8**	(15-)**20-26**(-30)	(6-)**8-12**(-15)
L. trichodes	**2-3**(-4)	(1-)**2-4**(-6)	(22-)**28-60**(-118)	**10-50**(-71)

2. Leaflets linear, narrow-oblong, strongly asymmetric at base, small (<1cm wide), with 7-many pairs of leaflets per pinna (Fig. 18)

	no. pairs pinnae	no. pairs leaflets	leaflet length (mm)	leaflet width (mm)
L. collinsii	(5-)**6-16**	**25-56**	**3.7-7**	**1-1.9**
L. confertiflora	**5-7**	(18-)**22-26**	(5-)**7-10.5**	**2-3.4**
L. cuspidata	(9-)**11-16**(-18)	**38-45**(-50)	(5-)**5.2-6.6**	**1.5-2.3**
L. diversifolia	(14-)**16-24**(-28)	(43-)**48-62**	(2.9-)**4-5.5**(-7)	(0.6-)**0.8-1.2**
L. esculenta	(18-)**30-40**(-60)	(40-)**60-75**(-85)	**3.5-6.6**	**0.9-1**
L. greggii	(7-)**8-10**(-11)	(25-)**27-34**	(6-)**8-11**(-12)	(2-)**2.5-3**(-3.6)
L. involucrata	(13-)**16-22**	(32-)**40-51**	(3.9-)**5-6.6**	**0.9-1.7**
L. lempirana	**14-19**	(27-)**30-36**(-40)	**5-6**	**1.6-2**
L. leucocephala	(4-)**6-8**(-9)	**13-21**	**9-16**(-21)	**2-4.5**
L. magnifica	**4-7**	**11-16**	(20-)**22-26**	**9-12**
L. matudae	**15-18**(-21)	(39-)**60-75**(-84)	(4.7-)**5.5-6.8**	**1-1.4**
L. pallida	**15-27**	**39-50**(-58)	**6.1-8**(-9.8)	**1.2-1.6**(-1.9)
L. pueblana	(10-)**16-20**(-22)	(30-)**40-55**	**4.7-5.8**	**0.9-1.1**
L. pulverulenta	(12-)**14-16**(-18)	(55-)**61-69**(-75)	**4-5.2**	**0.8-1**
L. salvadorensis	**4-7**	**23-27**	**15-19**	**3-5**
L. shannonii	(2-)**4-6**(-7)	(5-)**7-13**(-20)	(13-)**16-20**	**5-7**
L. trichandra	(5-)**11-22**(-30)	(20-)**30-40**(-59)	**3-5.2**(-7)	**0.7-1.8**
L. leucocephala × *L. esculenta*	**9-14**	**24-31**	**9-14**	**1.9-2.7**
L. leucocephala × *L. diversifolia*	**10-16**(-18)	**22-36**(-48)	(6-)**8-10**(-11.9)	**1.2-2**(-2.3)

Table 14 Categories of petiole glands (dimensions are length x width x height, all in mm).

1. Petiole gland erect, stipitate (stalked), cylindrical, peg-shaped petiole gland (Figs. 19A-C)	
L. confertiflora var. *adenotheloidea*	0.5-1.5 x 0.5-1.5 x 1-1.5, cylindrical, peg-shaped, sometimes a double gland
L. cuspidata	1-1.5 x 1 x 1, cylindrical/peg-shaped
L. greggii	0.5 x 0.5 x 2-3, slender, erect, columnar
L. involucrata	1-1.5 x 1-1.5 x 1, short cylindrical peg-shaped
L. matudae	1.5 x 1 x 1, short stalked, peg-shaped
L. retusa	1 x 1 x 1-3 tall, slender, erect, cylindrical
2. Petiole gland flat, sessile (not stalked), cup-shaped, concave (with a broad pore) petiole gland (Figs. 19D-F)	
L. confertiflora var. *confertiflora*	0.5-1.5 x 0.5-1.5 x <1, round discoid or shallow crater-shaped
L. esculenta	5-8 x 3-4 x 1, flat, elliptic, large shallowly concave, cup-shaped
L. diversifolia	2.2-5.4 x 1.4-2.6 x 1, discoid, shallow cup-shaped, elliptic or rounded triangular
L. leucocephala	2-3 x 1.2-1.5 x <1, elliptic, concave
L. multicapitula	3-5 x 1-2 x 1, circular-elliptic, deep cup-shaped
L. pallida	3-4 x 1.8-3 x 0.5-0.8, shallow concave, elliptic
L. pueblana	2.5 x 1.5 x 1, elliptic, shallow cup-shaped, convex
L. trichandra	1.6-4.8 x 1-2.2 x 1 (-2), round or rounded triangular, cup-shaped, concave or deeply crater-shaped, sometimes double gland
L. leucocephala × *L. esculenta*	3.2-4 x 2.5-2.7 x <1, elliptic or circular crater-shaped
L. leucocephala × *L. diversifolia*	2.8-3.5 x 2-2.5 x <1, circular-elliptic, sessile, cup-shaped
3. Petiole gland flat, sessile (not stalked), convex, broadly conical or dome-shaped (pore narrow or sometimes invisible) (Figs. 19G-I)	
L. collinsii	2 x 1 x <1, elliptical, rounded conical or dome-shaped
L. lanceolata	2.5-3.5 x 1.5-2 x <1, rounded elliptic, dome-shaped
L. lempirana	3 x 1.5 x <1, elliptic, dome-shaped, rounded conical, often orange-yellow
L. macrophylla	2-3 x 1.4-2.3 x <1, elliptical, convex, rounded conical
L. magnifica	3-4 x 1.5 x <1, elliptical, dome-shaped, rounded conical
L. pulverulenta	3 x 1.5 x <1, oblong, irregularly lumpy, concave, pore usually invisible
L. salvadorensis	5 x 2.5 x <1, rounded-elliptic, dome-shaped, round conical
L. shannonii	2-3 x 1 x <1, elliptical, dome-shaped, rounded conical
L. trichodes	2-3.5 x 1.2-1.6 x <1, elliptical, rounded conical

Petiole gland. Glands, are found on the leaves of all species of *Leucaena* (Fig 16). These are often termed extrafloral nectaries because they occur on the leaves and secrete nectar. Exudation of nectar is apparently most active on younger leaves and is presumed to attract ants which protect developing leaves from other insects, although no such relationship has been demonstrated for *Leucaena*. Not all glands secrete nectar all the time; they often appear dry and inactive particularly on older leaves. The glands are small raised structures which occur on the upper surface of the petiole, sometimes scattered along the leaf rachis, often at the tip of the leaf rachis (Figs 19K-L) and sometimes at the tips of the pinnae. **The petiole gland is a very useful character for identification.** The number and arrangement of other leaf glands is extremely variable. Three types of petiole gland may be distinguished amongst species of *Leucaena*: (i) short, erect, stipitate (stalked), cylindrical or peg-shaped (Figs. 19A-C); (ii) flatter, sessile (not stalked), cup-shaped, concave with a broad pore (Figs 19D-F); (iii) flatter, sessile (not stalked) broadly conical or dome-shaped, convex, with a narrow pore (Figs. 19G-I). Gland type is generally constant within species, although variation occurs within *L. trichandra* and between varieties of *L. confertiflora*. Species are listed in Table 14 according to categories of petiole gland cross

Figure 19 Petiole glands of *Leucaena*. The shape of the petiole gland is a useful character for species identification; scale bar (A-I) = 2mm.

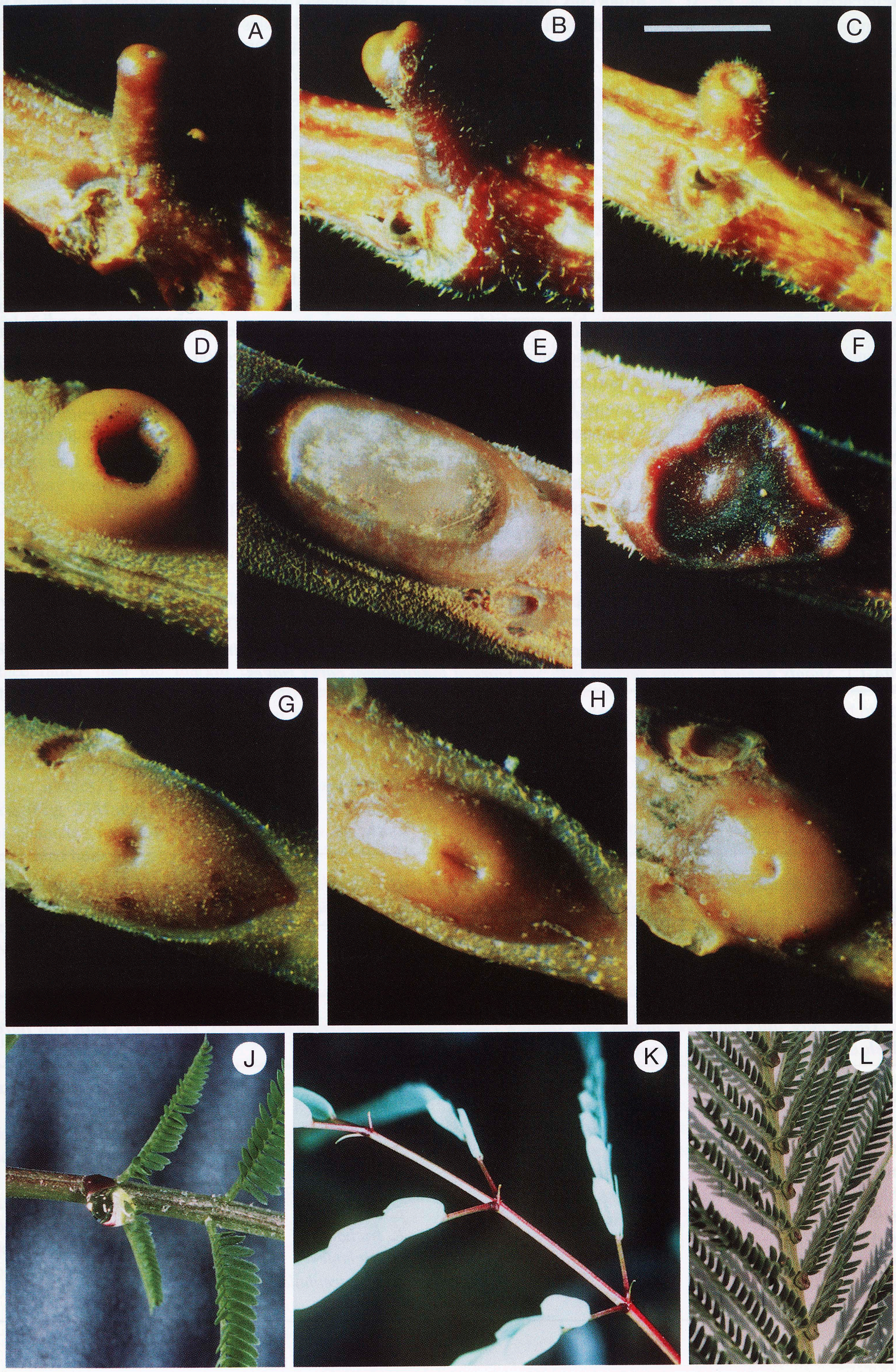
A-C. Short stipitate (stalked) peg-shaped, cylindrical glands (Type 1, Table 14). **A.** *L. matudae*; **B.** *L. greggii*; **C.** *L. retusa*.

D-F. Sessile (un-stalked), cup- or crater-shaped glands with a wide orifice (Type 2, Table, 14). **D.** *L. multicapitula*; **E.** *L. esculenta*; **F.** *L. trichandra*. The gland of *L. trichandra* is always cup-shaped, but can vary in shape from elliptic to round to triangular.

G-I. Sessile (un-stalked), rounded conical or dome-shaped glands with a narrow orifice (Type 3, Table 14). **G.** *L. collinsii* subsp. *collinsii*; **H.** *L. shannonii*; **I.** *L. salvadorensis*.

J. Droplet of nectar on the petiole gland of a young seedling leaf of *L. esculenta*. The nectar is presumed to attract ants which in return provide protection for young developing leaves, but no such association has been demonstrated for *Leucaena*. Nectar is produced mainly from young developing leaves; glands on older leaves are usually dry (as in **A-I**).

K-L. Multiple glands sometimes occur along the leaf rachis at the base of each pair of pinnae. **K.** Erect peg-shaped glands of *L. retusa*. **L.** multiple cup-shaped or discoid glands along the leaf rachis of *L. trichandra*.


A
B
C
D
E
F
G
H
I
J
K
L

-referenced to Fig 19. **It is important that these categories are clearly understood and familiar before using the keys.**

BARK AND SHOOTS. Two bark types with correlated surface patterns and internal structures occur in different species of *Leucaena*. The first type of bark is mid grey brown, with shallow rusty orange brown vertical fissures which become deeper and more pronounced with age with a thick outer bark; the inner bark or slash is thin, pale cream or cream streaked pinkish and fibrous (Figs. 20D-F). The majority of species of *Leucaena* have this type of bark (Table 15). The surface pattern of the second bark type is lustrous, pale metallic grey, like galvanised zinc, smooth when young, sometimes with an irregular 'semaphore' pattern of horizontally aligned pale brown lenticels (Fig. 20A), becoming horizontally or irregularly gnarled on larger trees; the inner bark is thick, the slash orange red or deep blood red and corky in texture (Figs 20A-C). This type of bark occurs in *L. esculenta* and closely related species (Table 15). Within this group there is a specialized scalloped surface pattern with sinuous ridges dividing depressions formed when scollop-shaped scales are detached; this is found only in *L. matudae* (Fig 20C). One species, *L. pallida* and one hybrid, *L. leucocephala* × *L. esculenta*, are somewhat intermediate between these two types but resemble the *L. esculenta* type in terms of surface pattern. This intermediacy has been attributed to the hybrid origins of these two species (Sections 5.3 and 10.6) between two parent species with different bark types.

Younger branches and shoots of *Leucaena* species may be either round in cross section (most species) or angled with conspicuous corky ridges running longitudinally along the outside of the shoot, in a few species of the *L. esculenta* alliance (Section 2.5). If a tree has angled shoots this is diagnostic of a small group of four species: *L. esculenta, L. involucrata, L. pallida, L. pueblana* and weakly in the *L. leucocephala* × *L. esculenta* hybrid (Table 15).

Table 15 Categories of bark and shoot types

1. Outer bark thin, smooth or gnarled, pale metallic grey surface, inner bark thick and corky, slash orange red (Figs. 20A-C). Shoots angled in cross section with 5-6 marked longitudinal corky ridges

L. esculenta
L. involucrata
L. pallida
L. pueblana
L. leucocephala × *L. esculenta*

2. Outer bark thin, pale metallic grey, distinctive scalloped surface pattern with sinuous ridges dividing depressions formed when scollop-shaped scales (Fig. 20C). Shoots round in cross section

L. matudae

3. Outer bark thick mid grey brown with shallow rusty orange brown vertical fissures, inner bark thin and fibrous, slash cream (Figs. 20D-F). Shoots round in cross section

L. collinsii	*L. magnifica*
L. confertiflora	*L. pueblana*
L. cuspidata	*L. pulverulenta*
L. diversifolia	*L. retusa*
L. greggii	*L. salvadorensis*
L. lanceolata	*L. shannonii*
L. lempirana	*L. trichandra*
L. leucocephala	*L. trichodes*
L. macrophylla	*L. leucocephala* × *L. diversifolia*

FLOWERS. The individual flowers of *Leucaena* are small, 5-15 mm in length, and arranged in compact capitate or globose heads (Fig 16) each with between 35 and 450 flowers. It is the flower head that is the visible unit of pollinator attraction and the numerous exposed stamen filaments and anthers which determine the size, colour and overall appearance of the flower head. Often the casual observer - in the same way as the pollinator - may observe and refer to 'flowers' when what is actually observed are flower heads. Although many features of the flowers are too small to be used for field identification (*e.g.* petal fusion, anther glands or pollen morphology) other traits such as colour, flower bracts and the arrangement of flower heads on shoots can be useful if the tree is flowering.

Flower colour. When flower heads are observed it is the anthers, stamen filaments and style which are seen and which determine the colour of the head rather than the corolla and calyx which are concealed. Colour of the filaments and anthers, and hence the flower head as a whole, may be white (most species of *Leucaena*) (Figs 21G-L), pink, reddish or pale purple (*L. confertiflora, L. diversifolia, L. pallida* and *L. trichandra*) (Figs 21C-F), or yellow (*L. retusa* and *L. greggii* only) (Figs. 21A-B).

Flower bracts. The individual flowers within the head are subtended by small bracts (Fig 16). In *Leucaena* these bracts are always peltate *i.e.* attached to the basal surface rather than the margin of the bract like an umbrella (Fig 16). These bracts are only visible when the flowers are in bud when they cover the developing flower head later becoming hidden within the head as the flowers open. The bracts of most species are round, but two species, *L. greggii* and *L. retusa*, have pointed bracts (Figs 21M and 59). This provides an immediate spot character for these two species when unopened flower head buds are present. The unopened heads of *L. retusa* and *L. greggii* with their protruding pointed scale-like bracts (Fig 21M) resemble small pine cones, while those of the remaining species are round (Fig 21N).

Flowering shoots. Flower heads are arranged in groups of 2-5 or occasionally up to 7 at nodes on shoots in the axils of leaves, young developing leaves or bracts. Flowering shoots in some species continue to grow and form leaves after flowering, with the pods formed below the apex of the shoot. Such shoots therefore have indeterminate growth and are termed auxotelic. In this case pods ripen within, rather than on the periphery of the tree crown. In other species the flowering shoot ceases to grow after flowering, the pods forming at the shoot tips on the periphery of the tree crown. This shoot type is determinate and termed anauxotelic. These shoots die back after pod ripening and new shoots for subsequent growth form below the shoot apex. In addition, flowering shoots may be unbranched (in most species) singly branched (*L. esculenta, L. macrophylla* and *L. magnifica*) or twice branched (*L. multicapitula* only). For mature trees, which are in flower these features of the flowering shoot may be useful additional characters for identification (Table 16). Species are listed by categories of flower colour and flower bract morphology in Table 16.

FRUITS AND SEEDS. Pods of most *Leucaena* species occur in groups of 1-4 per flower head, but in some species there can be 6-15 and occasionally up to 45. Pods vary in length, width (and hence shape), pod wall thickness and texture (papery to slightly woody), thickness of the pod margins, pubescence and mode of dehiscence (Figs 22 and 23). Although variation in pod shape is clear cut at the extremes, it is largely a function of the continuous variable pod width. Variation in pod width is overlapping among species and often extremely variable within species such as *L. lanceolata* (Fig 38) or *L. trichandra* (Fig 65) and thus of limited use for identification. Variation in pod pubescence, texture and margins, and seed size and shape, is similarly continuous and overlapping. Three pod/seed traits: partitioning of pods between seeds, mode of dehiscence, and seed alignment within pods provide reliable characters for identification of particular species.

Pods of a subset of six species of *Leucaena* are weakly partitioned between the seeds. In these species the seed chambers are clearly visible being slightly raised on the outside of the ripe pod wall (Figs 23 A-B, E-H). These pods also tend to be thicker, slightly woody, and are generally narrow-linear rather than linear-oblong in shape. In these species the seeds tend to be slightly rhomboidal in shape and are aligned obliquely (*L. involucrata, L. matudae, L. pallida* and *L. pueblana*) or longitudinally (*L. retusa* and *L. greggii*) within the pods. In the remaining species the seed chambers are not partitioned within the pod and are not raised on the outside of the pod walls, the pods are flat and tend to be broader, and linear-oblong, with papery or leathery pod walls, and circular or ovate seeds which are transversely aligned in the pod (Figs. 23 C-D and I-P).

Pods of all species are dehiscent (open when ripe). In the majority of species the pods open simultaneously along both margins, the pod walls reflexing transversely or barely twisting at all. In two species, *L. confertiflora* and *L. cuspidata*, pods open initially along only one pod margin with the pod walls, particularly of *L. cuspidata*, twisting into tight spirals after dehiscence, rather like pods of *Gliricidia* (Fig 23 C-D). Species are listed according to categories of pod characteristics in Table 17.

Figure 20 Bark

A-C and G. Bark surface pattern smooth or gnarled, pale metallic-grey with thin outer bark and thick corky inner bark, the slash bright orange or blood red (Types 1 and 2, Table 15). **A.** *L. pueblana*; **B.** *L. esculenta*; **C.** *L. matudae*: the bark of *L. matudae* although possessing all the characteristics of Type 1, has a specialized scalloped surface pattern with scollop-shaped depressions and is unique within *Leucaena*. **G.** cross section of bark of *L. pueblana* showing very thin outer bark with an intact outer epidermis and thick corky inner bark; scale bar = 0.25cm. Radial expansion is accommodated by internal growth of corky phloem tissue within the inner bark, rather than fissuring of the outer bark.

D-F and H. Bark surface pattern with shallow rusty orange brown vertical fissures (Type 3, Table 15). The outer bark is thick and fibrous and becomes progressive more fissured as the tree bole expands, the inner bark is thinner, lacks corky phloem development and is fibrous, the slash usually cream white or streaked pale pink. **D.** *L. pulverulenta*; **E.** *L. collinsii*; **F.** *L. diversifolia*. **H.** cross section of bark of *L. collinsii* showing the fissuring of the outer bark to accommodate radial expansion, the formation of a series of periderms within the outer bark and the thin, fibrous inner bark; scale bar = 0.25cm.

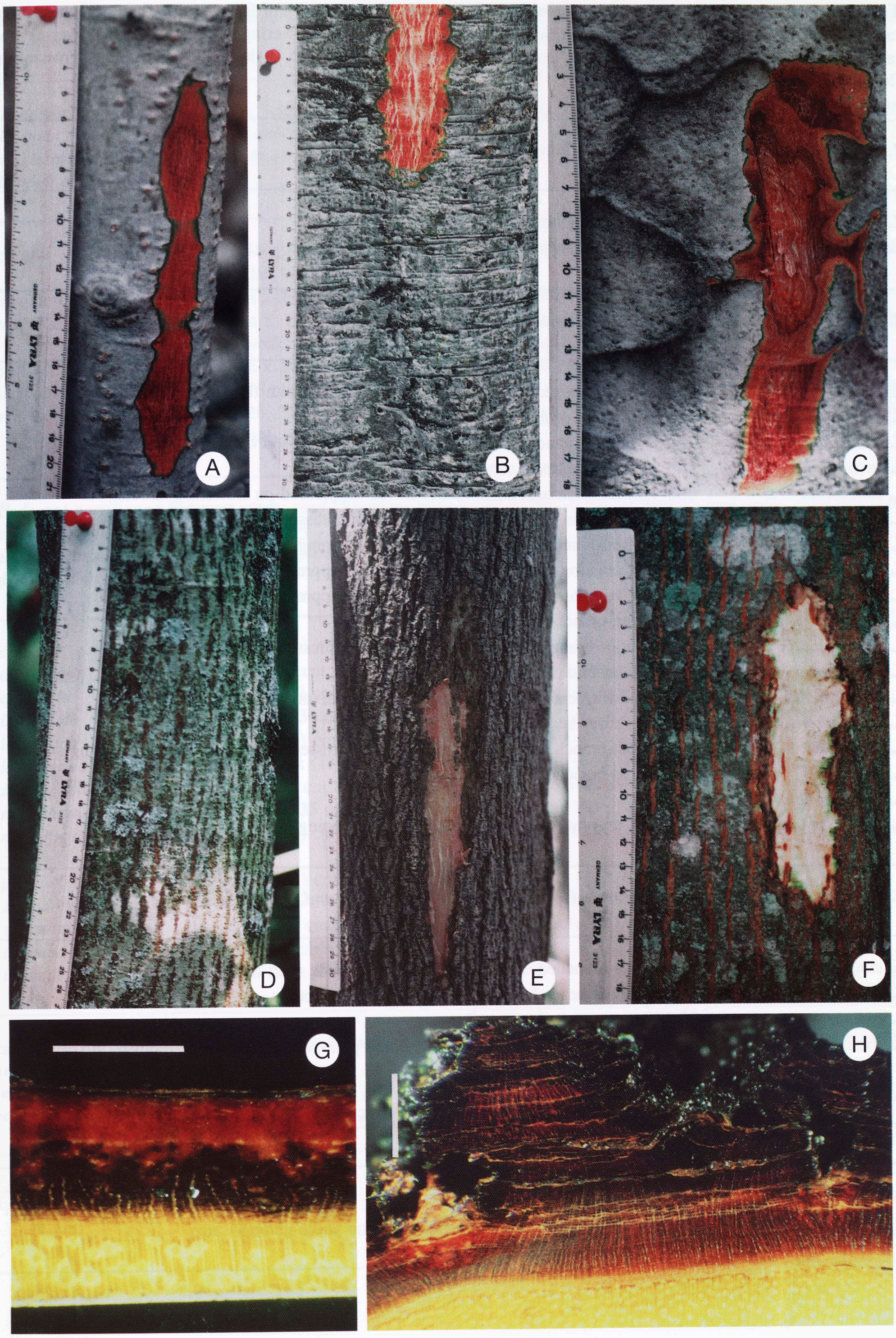

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Table 16 Categories of flowers and flowering shoots. Arranged by categories of flower colour/bracts; figures indicate range in numbers of flowers per flower head; branched or unbranched flowering shoots; type of flowering shoot: (auxotelic = flowering shoot continues to grow after flowering; anauxotelic = flowering shoot stops growing after flowering) (Fig 21).

1. Flowers bright yellow (Figs 21A-B), flower bracts pointed (Fig 21M)	
L. greggii	120-200, un-branched, auxotelic, long peduncles
L. retusa	150-190, un-branched, auxotelic, long peduncles
2. Flowers white (Figs 21G-L), flower bracts round (Fig 21N)	
L. collinsii	55-170, un-branched, auxotelic, leaves developing with flowers
L. cuspidata	135-150, cream-white, un-branched, auxotelic
L. esculenta	150-170, once-branched, anauxotelic, leaves suppressed on flowering shoots
L. involucrata	140-180, un-branched, auxotelic
L. lanceolata	300-450, un-branched, anauxotelic, leaves suppressed on flowering shoots
L. lempirana	100-130, un-branched, anauxotelic, leaves suppressed on erect terminal flowering shoots
L. leucocephala	100-180, un-branched, auxotelic, leaves developing with flowers
L. macrophylla	140-190, once-branched, anauxotelic, leaves suppressed on flowering shoots
L. magnifica	200-220, once-branched, anauxotelic, leaves suppressed on flowering shoots
L. matudae	90-120, un-branched, auxotelic
L. multicapitula	35-60, twice branched, anauxotelic, leaves suppressed on flowering shoots
L. pueblana	100-140, un-branched, anauxotelic
L. pulverulenta	45-65, flower heads lax in bud, un-branched, auxotelic
L. salvadorensis	90-140, flower heads on older wood, auxotelic
L. shannonii	80-140, un-branched, anauxotelic, leaves suppressed on erect terminal flowering shoots
L. trichodes	90-170, un-branched, anauxotelic
L. leucocephala × *L. esculenta*	130-160, un-branched, auxotelic, leaves developing with flowers
3. Flowers pink, reddish or pale purple (Figs 21C-F), flower bracts round (Fig 21N)	
L. confertiflora	55-170, un-branched, auxotelic, leaves developing with flowers
L. diversifolia	45-90, flower heads lax in bud, un-branched, auxotelic
L. pallida	95-110, un-branched, auxotelic
L. trichandra	60-165, un-branched, colour variable, pale pink-pale violet-mauve-reddish, auxotelic, leaves developing with flowers
L. leucocephala × *L. diversifolia*	sometimes pale pink, 130-160, un-branched, auxotelic, leaves developing with flowers

Table 17 Categories of pod morphology and dehiscence. Including pod length and width - extreme range in brackets, normal range in **bold**.

1. Pods partitioned between seeds, seed chambers clearly visible and slightly raised on ripe pod wall (Figs 23 A,B, E-H), pods thicker, slightly woody and generally narrow linear
Seeds rhomboidal, aligned obliquely or longitudinally
Pods open along both margins

L. greggii	(12-)**15-18**(-21) cm x **9-15** mm; narrow linear, slightly woody, thickened margins, seeds rhomboidal, longitudinal in pods
L. involucrata	**11-18** cm x **9-13** mm; narrow-linear, seed chambers visible, open slowly
L. matudae	**14-19** cm x **12-15**(-17) mm; slightly constricted between the seeds, seed chambers clearly visible, weakly partitioned, seeds obliquely aligned
L. pallida	**12-18** cm x **14-18** mm; valves thickened and leathery; seeds oblique
L. pueblana	(10-)**13-15** cm x **13-15** mm; valves thickened and leathery or slightly woody, seeds oblique
L. retusa	(12-)**16-20**(-25) cm x **11-13** mm; narrow linear, slightly woody, thickened margins, seeds rhomboidal, longitudinal in pods

2. Pods not partitioned between seeds, seed chambers not clearly visible or raised on ripe pod walls, pods broader, linear oblong, flat and papery or leathery
Seeds circular to ovate, transversely aligned in pod (Figs. 23 I-P)
Pods open along both margins

L. collinsii	**11-18**(-20) cm x (7-)**10-19** mm; glabrous, linear-oblong
L. diversifolia	(7-)**10-13**(-15) cm x (11-)**13-16**(-17) mm; papery, lustrous or pubescent
L. esculenta	(10-)**15-25**(-30) cm x **23-26** mm; flat, deep maroon unripe, orange-brown ripe
L. lanceolata	**10-38** cm x **8-36** mm; flat, glossy or pubescent; var. *sousae* largest pods of any species
L. lempirana	(10-)**12-20**(-25) cm x (18-)**20-26**(-32) mm; glabrous or densely pubescent
L. leucocephala	(9-)**11-19** cm x (13-)**15-21** mm; often 5-20(-45) per flower head
L. macrophylla	(9-)**12-21**(-24) cm x (9-)**14-23**(-26) mm; flat, papery, glossy or pubescent
L. multicapitula	**8-16** cm x **23-35** mm; flat, papery, oblong apex obtuse with a short beak
L. magnifica	(13-)**17-21**(-23) cm x **19-26** mm; dense velvety pubescence, deep maroon unripe, orange-brown ripe
L. pulverulenta	(12-)**14-18**(-21) cm x (14-)**16-23**(-24) mm; linear oblong, thin papery
L. salvadorensis	**14-18** cm x **26-29** mm; linear-oblong, leathery pod walls, thick margins
L. shannonii	(9-)**12-16**(-18) cm x (11-)**14-16** mm; narrow-oblong, often pubescent
L. trichandra	(5-)**7-11**(-17) cm x **13-23**(-29) mm; very variable in size
L. trichodes	(7-)**11-18** cm x **18-24** mm; linear oblong

3. Pods not partitioned between seeds, seed chambers not clearly visible nor raised on pod walls, pods flat, broader, linear oblong, papery or leathery
Seeds circular to ovate, transversely aligned in pod
Pods open initially along only one margin (Figs 23 C-D)

L. confertiflora	**9-15** cm x **16-26** mm; deep maroon unripe, dark brown ripe; open on one side
L. cuspidata	(10-)**14-22**(-28) cm x **20-30** mm; linear oblong, thick green and fleshy unripe, leathery when ripe, opening along one side only, the pod valves twisting into tight spirals after opening

Figure 21 Flower heads and flowers of *Leucaena* showing variation in flower colour, number of flowers per head, bract shape, ovary hairs and flower parts.

A-B and M. Species with bright yellow flowers and pointed flower bracts which are strongly exserted in bud. **A.** *L. greggii*; **B.** *L. retusa*; **M.** *L. retusa* flower head bud showing the cone-like appearance due to the exserted pointed flower bracts (Type 1, Table 16).

C-F. Species with flower parts tinged pink or reddish. **C.** *L. diversifolia*: anthers, stamens and style of *L. diversifolia* vary from whitish tinged very pale pink, strong shocking pink to bright scarlet; **D.** *L. trichandra*; **E.** *L. pallida*; **F.** *L. confertiflora*: flowers of *L. confertiflora* have pinkish anthers when they first open but which turn pale dirty grey or mauve when flowers fade (Type 2, Table 16).

G-L and N. Species with white flowers and round flower bracts which are not exserted in bud. **G.** *L. lanceolata*: the flower heads are densely packed with 300-450 flowers per head; **H.** *L. lempirana*; **I.** *L. matudae*; **J.** *L. esculenta*; **K.** *L. collinsii*: showing green bud, cream white open flowers fading dull tangerine two days after opening; **L.** *L. pulverulenta*: with few (45-65) flowers per head the buds appear lax; **N.** *L. shannonii* showing the 'berry-like' flower head buds with round flower bracts appressed to the bud (Type 3, Table 16).

O-P. Ovary; scale bar = 0.5mm. **O.** hairy ovary of *L. pulverulenta*; **P.** glabrous ovary of *L. esculenta*.

Q. Dissected flower of *L. pulverulenta* showing (left to right) the five-lobed calyx, corolla (with 5 fused petals), ten stamens and anthers, and hairy ovary, style and tubular, porate stigma; scale bar = 2mm. The flowers of *L. pulverulenta* are unusual within *Leucaena* in having basally fused petals; in most species the petals are free from each other to the base.

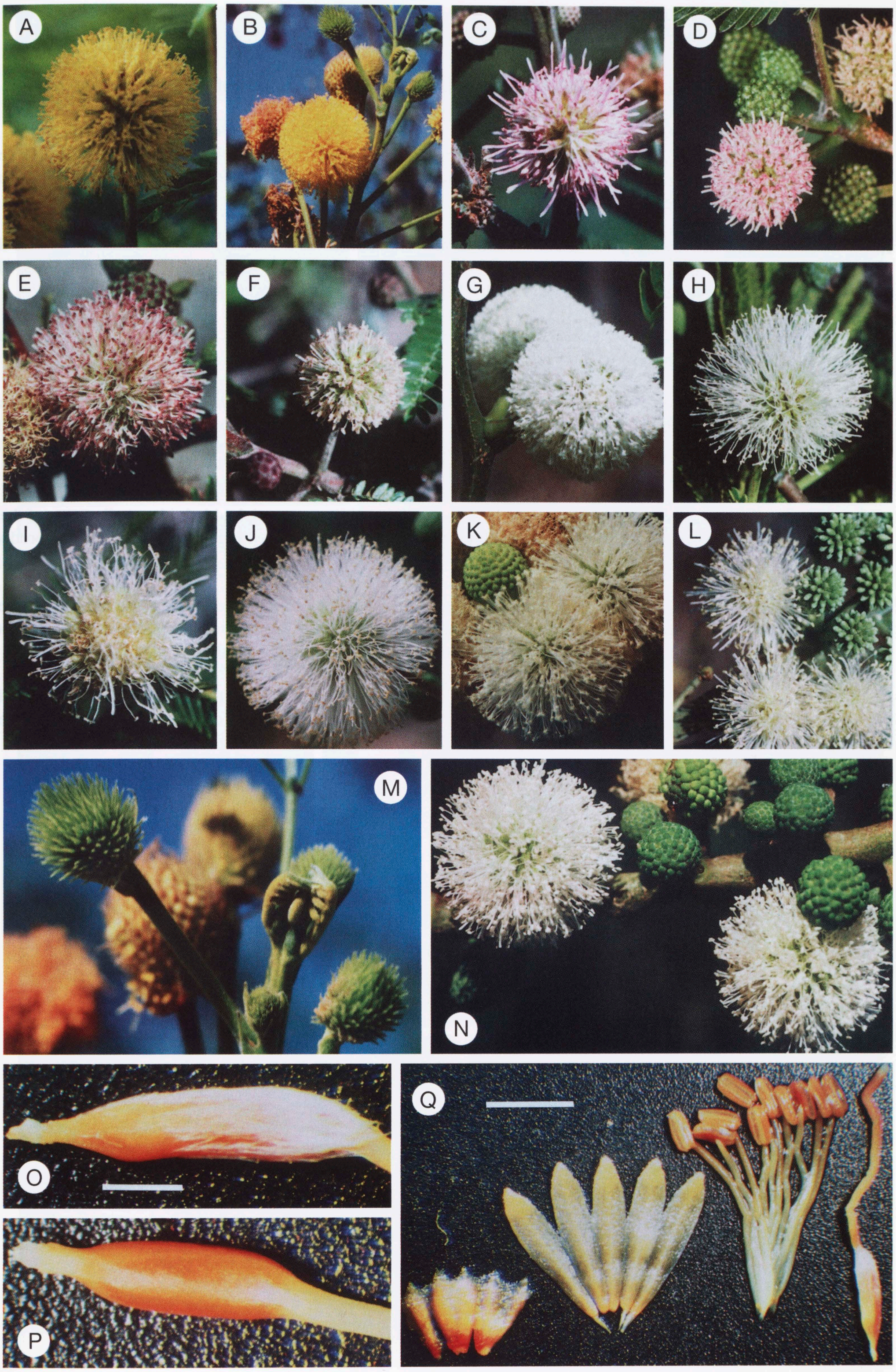
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Figure 22 Unripe pods of *Leucaena* and *Desmanthus* species and the derivations of their vernacular names.

A. *Guaje verde, guaje blanco, guaje de castilla* ('green or white podded *Leucaena*' or 'Castilian *Leucaena*') = *L. leucocephala* subsp. *glabrata*. The combined characteristics of high pod and seed set, self fertility, large seeds, 'sweet' flavour and year round pod production (assuming moisture permits) make *L. leucocephala* an outstanding and widely preferred species for food use.

B. *Efé de cerro, guaje de cerro, guache de cerro* ('hill or mountain *Leucaena*') = *L. cuspidata*. This name refers to the fact that *L. cuspidata* is only very rarely cultivated. Pods are generally collected from wild ('hill') populations. The unripe pods of *L. cuspidata* are thick, green and fleshy when unripe and leathery when ripe.

C. *Guaje rojo, guaje colorado* ('red-podded *Leucaena*') = *L. esculenta*. Along with *L. leucocephala* this is the most widely used and cultivated species for food use.

D. *Guaje delgado, guaje colorado* ('narrow- or coloured-podded *Leucaena*') = *L. pallida*. The pods of *L. pallida* closely resemble those of *L. esculenta* being reddish maroon unripe (*colorado*), but are narrower (*delgado*). *L. pallida* also complements *L. esculenta* in season of production (July-September) and greater cold tolerance and is often grown for these reasons, often at slightly higher elevations.

E. *Guaje macho* ('male *Leucaena*') = *L. leucocephala* x *L. esculenta* spontaneous triploid hybrids: seedlessness of these hybrids is widely recognized by local residents who refer to it in this way and often rogue trees which do not produce pods.

F. *Guaje de cerro* ('hill *Leucaena*') = *L. confertiflora*: like *L. cuspidata* (**B** above) *L. confertiflora* is rarely cultivated, the pods being harvested from wild populations. The vernacular name contrasts this species, with cultivated species such as *L. leucocephala* and *L. esculenta* (sometimes referred to as *guaje de huerta*: 'orchard *Leucaena*').

G and H. *Guaje de ratón* ('mouse *Leucaena*') = *Desmanthus pumilus* var. *pumilus* and *D. bicornutus* respectively. Unripe seeds of these species are consumed in similar ways to *Leucaena* but are referred to by this name in clear reference to the diminutive size of *Desmanthus* pods and seeds.


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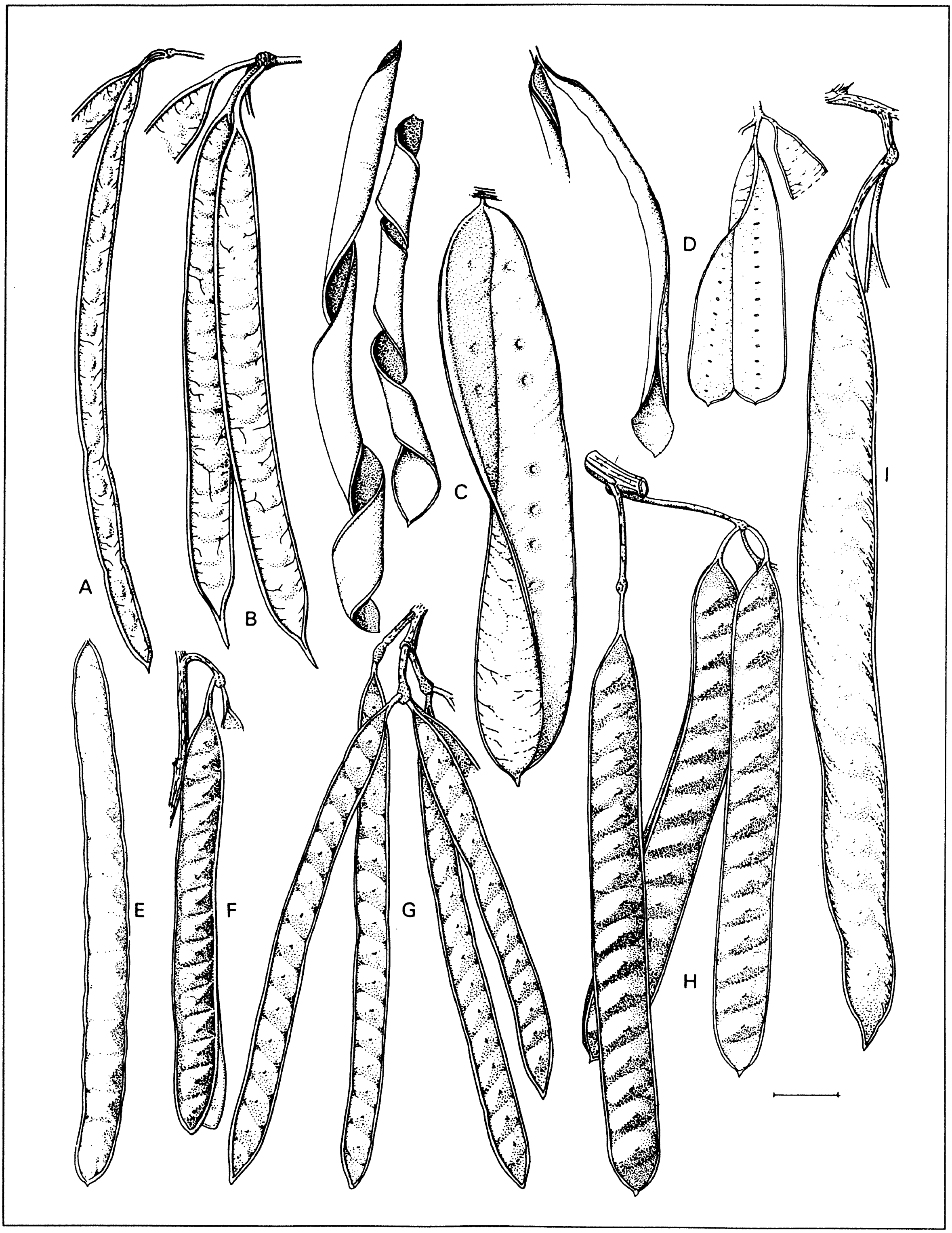

Figure 23 Variation in pod size and shape. **A.** *L. retusa*; **B.** *L. greggii*; **C.** *L. cuspidata*; **D.** *L. confertiflora*; **E.** *L. matudae*; **F.** *L. pueblana*; **G.** *L. involucrata*; **H.** *L. pallida*; **I.** *L. esculenta*; scale bar = 2cm.

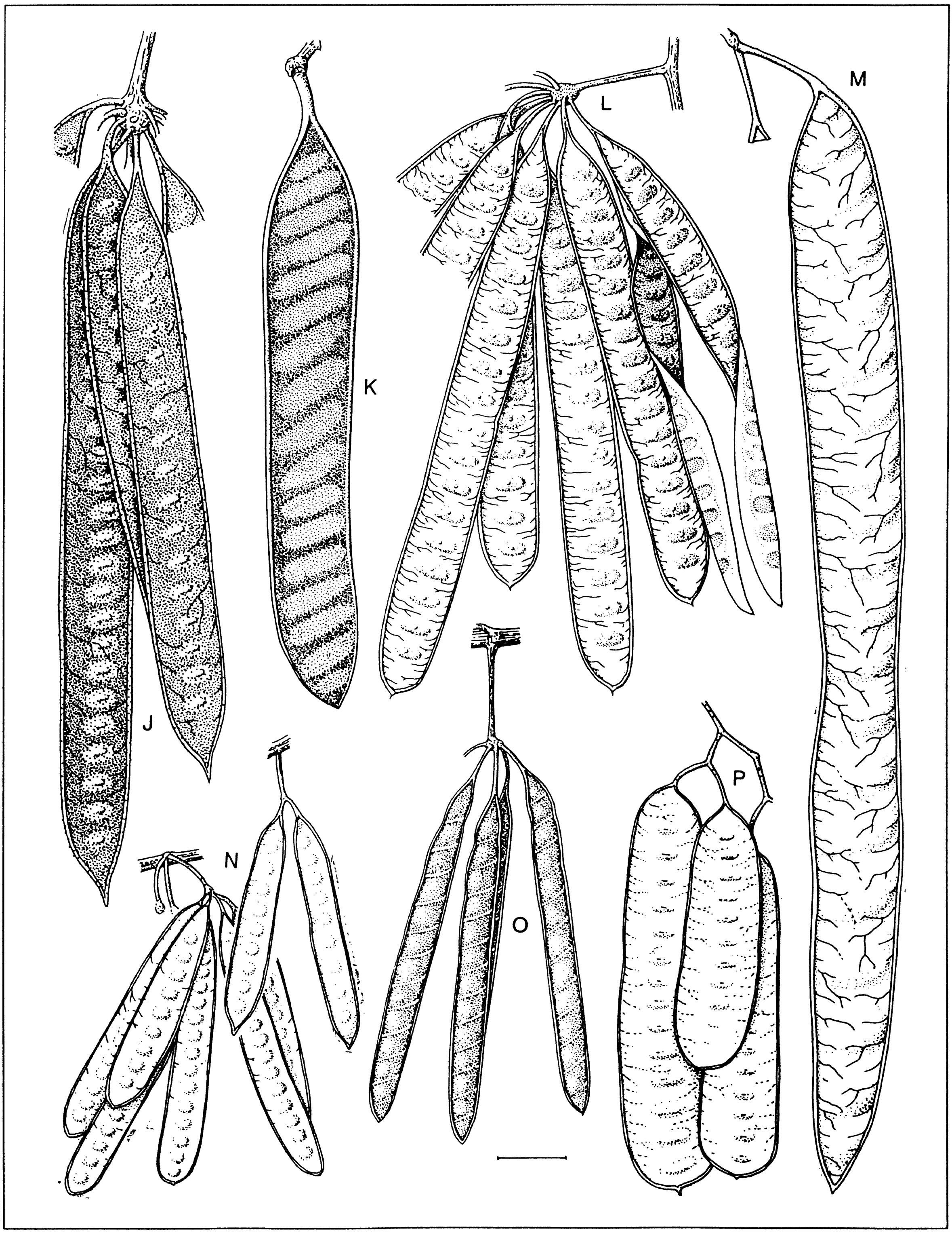

Figure 23 Variation in pod size and shape. **J.** *L. magnifica*; **K.** *L. salvadorensis*; **L.** *L. leucocephala* subsp. *glabrata*; **M.** *L. lanceolata* subsp. *sousae*; **N.** *L. trichandra*; **O.** *L. shannonii*; **P.** *L. multicapitula*; scale bar = 2cm.

10.4 Is it a *Leucaena*?

It is not infrequent that material thought to be of a species of *Leucaena*, in fact belongs in another genus. Many Mimosoid legume genera look similar to *Leucaena* in overall leaf morphology and appearance. It is always worth keeping the question - 'is it a Leucaena?' - in the back of one's mind when identifying species. With 50-60 genera and more than 3000 species in the legume subfamily Mimosoideae, many of them common trees in genera such as *Acacia*, *Albizia* or *Prosopis*, the task of identifying genera can be bewildering for non-botanists faced with an uncertain Mimosoid plant. A comprehensive key for identification of genera is beyond the scope of this Chapter but such keys are generally available in regional or national Floras. Features which either characterize only *Leucaena*, or which are found in all species, or none, are listed below. This means that if a specimen is not a *Leucaena* it can in most cases be quickly eliminated from consideration although this may cast no further light on its identity. For a small number of closely related genera (Section 2.2) this may be more difficult and characters to distinguish the closely related genera are discussed individually. The formal taxonomic classification of the Mimosoid legumes into tribes and genera is based on characters of the flowers such as number of stamens and fusion of stamens into a tube. Thus where there is doubt whether a specimen belongs within *Leucaena*, it may be necessary to look at flowering material.

One feature which is **unique** to *Leucaena* in all the Mimosoid legumes is that almost all species have **hairy anthers**. Although not always visible to the naked eye, the hairs on the exposed anthers of *Leucaena* flowers are easily observed with a simple x10 hand magnifying lens. If a specimen has hairy anthers, and it is a Mimosoid legume, then it is a *Leucaena*. However, three species of *Leucaena*, *L. greggii*, *L. retusa* and *L. pulverulenta* lack hairs on the anthers, so this character, while extremely useful, is not diagnostic for all species. Hairy anthers are particularly useful for identification outside the native range, given that of the three species lacking hairs, only *L. pulverulenta* has so far been widely cultivated.

A number of other features, although not diagnostic are **present in all** species of *Leucaena*:
- shoots lacking thorns or spines
- leaves always with a petiole gland
- flowers in capitate (globose) heads always with more than 30 flowers per head
- presence of a ring of fused bracts called an involucel at the base of, or just below, the flower head
- peltate flower bracts
- flowers with ten stamens, the stamens free to the base
- pendulous linear, more or less flattened, never truly woody, dehiscent pods
- seeds with a U-shaped pleurogram and a glossy rich reddish chestnut brown seed coat

If a specimen has any of the following features it is **not** a *Leucaena*:
- any type of thorns or spines (as for species of *Acacia, Prosopis, Dichrostachys, Mimosa* etc.)
- short shoots clothed in persistent stipule bases (brachyblasts)
- leaves lacking petiole glands
- flowers arranged in spikes rather than capitate (globose) heads
- fewer than, or more than, 10 stamens, as in *Acacia* and the *Ingeae*
- stamen filaments fused into a tube at the base as in *Calliandra, Inga, Albizia*
- flower heads with neuter flowers, often with showy staminodia of a different colour to the remaining fertile flowers, at the base of the flower head (*Dichrostachys*, most species of *Desmanthus*)
- thickened, woody indehiscent pods

Closely related genera. Genera which are considered to be closely related to *Leucaena* and their relationships and geographical distributions are discussed in Section 2.2 and illustrated in Fig 1. Only two species, *Desmanthus virgatus* and *Dichrostachys cinerea*, amongst all these genera are widely cultivated thereby narrowing confusion over identification to specific geographic areas. Species of only two of these genera, *Desmanthus* and *Schleinitzia*, are likely in practice to be confused with species of *Leucaena*.

***Desmanthus*.** Of the closely related genera which overlap with *Leucaena* in its native range, *Desmanthus* species are the most likely to cause confusion. *Desmanthus* may be distinguished from *Leucaena* by the following characters:
- *Desmanthus* species are generally small shrubs or herbs, and only occasionally form small, slender trees, while all species of *Leucaena* form small to medium sized trees.
- *Desmanthus* species have narrow linear, as opposed to the broad, basally winged, ovate stipules of *Leucaena* species.
- almost all species of *Desmanthus* have flower heads with two different types of flowers: fertile flowers at the apex and sterile flowers, often with showy staminodia, at the base of the flower head. Sterile flowers with showy staminodia are never found in *Leucaena*.
- the stigma in *Desmanthus* is broad funnel-shaped compared to the narrow tubular stigma of *Leucaena* species.

***Schleinitzia*.** Species of *Schleinitzia* have been variously placed in the genera *Leucaena, Piptadenia* and *Prosopis* in the past but have always been considered to have close affinities to *Leucaena* (Section 2.2). *Schleinitzia* species are restricted to the islands of the western Pacific and may be readily confused with *Leucaena* which is widely cultivated in that region. Species of *Schleinitzia* closely resemble *L. diversifolia* and *L. trichandra* in overall habit, leaf morphology and flower head size and colour. However, *Schleinitzia* species may

be distinguished from *Leucaena* by:
- the occurrence of small stalked anther glands on the tip of the anthers of freshly opened flowers; no species of *Leucaena* has stalked anther glands
- indehiscent, often slightly winged pods which only open partially along the margins
- broad funnel-shaped as opposed to narrow tubular stigma

***Leucaena multicapitula* and *Albizia adinocephala*.** In the seasonally dry tropical forests of Nicaragua, Costa Rica and Panama, *L. multicapitula* is often confused with, and misidentified as *Albizia adinocephala* due to their close similarity in leaf and pod morphology. In terms of leaf morphology the two species are extremely similar indeed although *L. multicapitula* tends to have more pairs of pinnae per leaf (3-4) and pairs of leaflets per pinna (4-5) than *Albizia adinocephala* (1-3 and 3-4 respectively). The only notable leaf difference is in the position of the petiole gland which in *L. multicapitula* is at the tip of the petiole immediately below the first pair of pinnae, while in *A. adinocephala* it is always below mid petiole sometimes close to the base. However, to be certain of distinguishing these two species either flowers or pods are required. *Albizia* is immediately distinguished by its numerous stamens per flower and larger flower heads. The seeds of *A. adinocephala* are also distinctive being pale tan or yellow brown and remain firmly attached to the pod valves after the pods have opened. In contrast, seeds of *Leucaena* are rich glossy reddish chestnut brown and are shed when the pods open.

10.5 Keys for identification of *Leucaena* species

In this section two keys are presented for identification of *Leucaena* species. Keys for the identification of subspecies are presented within the species accounts (Chapter 11). **It is important to understand and be familiar with the characters discussed and illustrated in Section 10.3 before embarking on using the keys.**

The first key (Table 18) is in the form of a table or two-way character matrix. In this table each box represents a unique combination of the character states specified down the left side and along the top. Species which show a particular combination of character states appear in the appropriate box. This key does not necessarily permit a unique identification as some boxes still have up to three species listed, but it can provide a quick way to identify distinctive species, or narrow down the choice to three species or fewer.

The main diagnostic key is dichotomous, *i.e.* it comprises a series of numbered mutually exclusive paired options (couplets) or questions. Deciding which of the two options fits your specimen or tree leads to the next, or a later, couplet in the key indicated by the number after each option. In this way it is possible to proceed sequentially through the key from number 1 until a name is reached and an identification is made. Leaf characteristics have been used in preference to flower and fruit characters as far as possible, and appear first in each couplet. However, in some cases closely related species cannot be separated using leaves alone. For example, it is extremely difficult to separate *L. lanceolata* from *L. macrophylla* and *L. trichodes*, using leaves alone because they have very similar and broadly overlapping leaf morphology, even though *L. lanceolata* is undoubtedly a distinct species distinguished by a suite of discrete flower and pollen characters. *L. macrophylla* and *L. trichodes* are closely related and doubtfully distinct species (Hughes, in press); there are few reliable characters that separate them. They are maintained as distinct species in the interim pending more detailed study of patterns of morphological variation across their very extensive combined distribution in Latin America. Such studies may indicate that they are more appropriately demoted to subspecies.

Leaflets vary in number and size within a single leaf. Measurements used in the key follow the conventions: leaflets per pinna counted on the mid-pinna; leaflet length and width measured on the mid leaflet of the mid pinna. Pod width always refers to the width at the widest part of the pod. Flower head diameters refer to fully open flower heads. Geographical distribution is included in the key where it could be a useful additional check on identification of trees in natural populations in Latin America.

Table 18 Tabular Key in the form of a two-way character matrix for *Leucaena*

	Leaflets large (>1cm wide), elliptic or ovate slightly asymmetric	Leaflets small (<1cm wide) linear oblong strongly asymmetric at base					
		Bark pale metallic grey, smooth or gnarled, inner bark thick, corky, slash deep orange-red		Bark mid grey-brown with shallow rusty orange-brown vertical fissures, inner bark fibrous, slash cream-coloured			
		Flowers white	Flowers pink	Leaflets >1cm long	Leaflets <1cm long		
					Flowers yellow	Flowers white	Flowers pink
Petiole gland stipitate, erect, peg-shaped	*retusa*	*matudae* *involucrata*			*greggii*		*confertiflora* var. *adenotheloidea*
Petiole gland sessile, flat, concave, crater-shaped, wide orifice	*multicapitula*	*esculenta* *pueblana*	*pallida*	*leucocephala*		*pulverulenta* *collinsii* *lempirana*	*confertiflora* var. *confertiflora*
Petiole gland sessile, flat, convex, rounded conical, dome-shaped, narrow pore	*lanceolata* *macrophylla* *trichodes*			*salvadorensis* *shannonii* *magnifica*		*cuspidata*	*trichandra* *diversifolia*

KEY TO THE SPECIES OF LEUCAENA

1 Leaflets large (>1 cm wide), elliptic, ovate or lanceolate, only weakly asymmetric at base, (1) 2-6 (-8) pairs per pinna **2**

Leaflets small (<1 cm wide), linear or narrow-oblong, strongly asymmetric at base, with (5-) 7-many pairs per pinna **6**

2 Petiole gland stalked (stipitate), columnar, peg-shaped, 1-3 mm tall; flower head stalks long (25-90 mm); flower bracts long pointed, strongly exserted in bud; flowers (stamen filaments, style and anthers) bright yellow; pods narrow, linear, thick, leathery or slightly woody; seeds rhomboidal, strongly oblique or longitudinal alignment in pods; NE Mexico (Coahuila and Chihuahua) and Texas, USA ***L. retusa***

Petiole gland not stalked (sessile), cup-shaped or rounded conical or dome-shaped, <1 mm tall; flower head stalks short (<20 mm); flower bracts round and only slightly exserted in bud; flowers (stamen filaments, style and anthers) white; pods broad linear-oblong, flat and papery; seeds ovate or elliptic, transversely aligned in pods **3**

3 Petiole gland concave, cup-shaped, flowering shoots twice-branched, open flower heads <8mm in diameter, < 60 flowers per head, S. Nicaragua, Costa Rica and Panama ***L. multicapitula***

Petiole gland convex, conical or dome-shaped, flowering shoots un-branched or once-branched, open flower heads >7mm in diameter, >90 flowers per head **4**

4 Open flower heads large, 20-40 mm in diameter, with >250 flowers per head; anthers lacking any gland or protrusion at the tip ***L. lanceolata***

Open flower heads small, 7-12 (-15) mm in diameter, with 90-190 flowers per head; anthers with a small dorsi-ventrally flattened, hooded gland or protrusion at tip **5**

5 Flowering shoots generally once-branched; Mexico ***L. macrophylla***

Flowering shoots generally un-branched; South America ***L. trichodes***

NOTE: these two species are closely related, doubtfully distinct and therefore difficult to distinguish

6 Young shoots angled in cross-section with longitudinal corky ridges **7**

Young shoots smooth and round in cross-section **9**

7 Leaves large with >25 pairs of pinnae and >60 leaflets per pinna; pods oblong or broadly linear-oblong >20 mm wide, not partitioned between seeds, the seed chambers not or barely visible on pod walls; seeds ovate >9 mm long ***L. esculenta***

Leaves with <25 pairs of pinnae and <55 pairs of leaflets per pinna; pods linear or narrowly linear-oblong <18 mm wide, partitioned between seeds, the seed chambers clearly visible on pod walls; seeds <8 mm long **8**

8 Leaflets <6 mm long; anthers white or cream-white; shoots strongly geniculate ***L. pueblana***

Leaflets >6 mm long; anthers pink or pale purple; shoots scarcely geniculate ***L. pallida***

9 Petiole gland not stalked (sessile), convex, low rounded conical or dome-shaped, the orifice a narrow pore, or sometimes invisible **10**

Petiole gland stalked (stipitate) peg-shaped **or** not stalked (sessile) but then concave, cup-shaped or discoid with a broad orifice **15**

10 Young developing leaves covered in short dense whitish-grey hairs; anthers lacking hairs with a small rounded protrusion or gland on tip; petals united at base; ovary with long whitish hairs; flower heads with <65 flowers and open in bud; NE Mexico (Veracruz - Tamaulipas) and USA in Texas ***L. pulverulenta***

Young developing leaves without whitish-grey pubescence; anthers hairy, lacking a gland; petals separate at the base; ovary without hairs or with very short velvety hairs; flower heads with (55-) 90-220 flowers and densely packed in bud; S. Mexico (Chiapas and Yucatán) and Central America **11**

11 Leaflet length 3-8(-10) mm; leaflet width <2 mm; pairs of pinnae per leaf (6-)10-20; pairs of leaflets per pinna 25-60 **12**

Leaflet length 13-26 mm; leaflet width >3 mm; pairs of pinnae per leaf 2-7; pairs of leaflets per pinna 5-27 **13**

12 Leaflets glabrous, or sparsely hairy only at base and on margins; flowering shoots indeterminate, *i.e.* continue to grow beyond the flowering region (auxotelic), leaves develop with flowers and pods are borne on older wood away from shoot tips; ovary glabrous; pods 7-19 mm wide, always glabrous; Mexico (Chiapas) and Guatemala ***L. collinsii***

Leaflets hairy on both surfaces; flowering shoots determinate, ending in an abortive vegetative apex (anauxotelic), leaf development suppressed on flowering shoots, pods and flowers borne on naked terminal shoots; ovary densely covered in short velvety hairs; pods 18-32 mm wide, often densely covered with velvety hairs; restricted to the Department of Yoro, Honduras ***L. lempirana***

13 Pairs of leaflets per pinna >20; leaflets <5 mm wide; pods leathery in texture, always glabrous ***L. salvadorensis***

Pairs of leaflets per pinna <20; leaflets >5 mm wide; pods flat and papery in texture, often but not always densely covered with velvety hairs **14**

14 Leaves <15 cm long; rachis <9 cm long; 2-5 pairs of pinnae; <11 pairs of leaflets per pinna; leaflets <19 mm long, <7 mm wide, upper surfaces not glossy; flowering shoots un-branched; flower heads <12 mm in diameter with <140 flowers per head; pods <13 mm wide ***L. shannonii***

Leaves >25 cm long; rachis >13 cm long; 4-7 pairs of pinnae; >12 pairs of leaflets per pinna; leaflets >20 mm long, >9 mm wide; upper surfaces glossy; flowering shoots once-branched; flower heads >20 mm in diameter with >200 flowers per head; pods >19 mm wide; restricted to Chiquimula, Guatemala ***L. magnifica***

15 Petiole gland concave, broadly cup-shaped, elliptic or circular **16**

Petiole gland small cylindrical, short stalked (stipitate), peg-shaped, circular **20**

16 4-9 pairs of pinnae per leaf with 13-21 pairs of leaflets per pinna ***L. leucocephala***

10-30 pairs of pinnae per leaf with (20-) 30-60 pairs of leaflets per pinna **17**

17 Leaflets >8 mm long, 1.2-4.5 mm wide; anthers, filaments and style white or tinged very pale pink **18**

Leaflets <7 mm long, 0.6-1.8 mm wide; anthers (and sometimes filaments and style) strongly tinged pink or reddish **19**

18 Bark pale metallic grey smooth (not fissured); flowering abundantly throughout the year but sterile and never sets seed ***L. leucocephala* × *L. esculenta***

Bark dark grey-brown with shallow rusty orange-brown vertical fissures; pod and seed set abundant ***L. leucocephala* × *L. diversifolia***

19 Leaflets >40 pairs per pinna; anthers sparsely hairy at tip only; ovary hairy on distal half ***L. diversifolia***

Leaflets generally <40 pairs per pinna; anthers densely hairy throughout; ovary glabrous ***L. trichandra***

20 Leaves with >9 pairs of pinnae and pinnae with >32 pairs of leaflets **21**

Leaves with <10 pairs of pinnae and pinnae with <32 pairs of leaflets **23**

21 Leaflets >1.5 mm wide, oblong, strongly asymmetric at base, often with a sharp point or small 'cusp' at tip, secondary venation clearly visible; pods 20-30 mm wide, oblong or linear oblong, flat, not partitioned between seeds, seed chambers not visible on outside, opening initially along one suture only, seeds round or elliptic and transversely aligned in pods, restricted to Hidalgo, Querétaro and San Luis Potosí States, Mexico ***L. cuspidata***

Leaflets <1.7 mm wide, linear, weakly asymmetric at base, acute at apex, only midrib visible; pods 9-15 mm wide, linear, sometimes slightly constricted, slightly thickened, endocarp partitioned between seeds, the seed chambers clearly visible on outside of pod, pods slowly opening along both margins, seeds weakly rhomboidal, obliquely aligned in pods **22**

22 Pods 9-13 mm wide not constricted; bark smooth, inner bark thin; Sonora and Sinaloa, Mexico ***L. involucrata***

Pods 12-15 mm wide, weakly constricted between the seeds, bark scalloped on surface with thick corky deep blood-red inner bark; Balsas Depression, Guerrero, Mexico ***L. matudae***

23 Leaves with <7 pairs of pinnae and <26 pairs of leaflets per pinna; flower head stalks <10 mm long; floral bracts round, scarcely exserted in bud, anthers hairy, dull pinkish-purple, filaments cream-white; pods papery in texture lacking a thickened woody pointed apex, opening initially along one margin; seeds aligned transversely in pods; central Mexico (Puebla and Oaxaca) ***L. confertiflora***

Leaves with >7 pairs of pinnae and >25 pairs of leaflets per pinna; flower head stalks 60-90 mm long; floral bracts pointed and exserted in bud; anthers glabrous; flowers (anthers, filaments and style) bright yellow; pods woody, with thickened margins and terminating in a thickened persistent point; seeds aligned longitudinally in pods; NE Mexico (Nuevo León and Coahuila) ***L. greggii***

10.6 Identification of hybrids

The ever growing abundance of spontaneous and artificial hybrids (Chapter 5) greatly complicates, and heightens the need for, accurate identification. Hybrids can be a major source of taxonomic confusion. Given the range of possible hybrid combinations in *Leucaena* that produce viable seed (Section 5.2) it is impossible to include all hybrids in identification keys. In this section general guidelines that may be used to assist with identification of hybrids are presented. However, it should be noted that in many cases it can be difficult to distinguish hybrids from 'normal' species. This can involve considerable research using diverse evidence from morphology, molecules and geography (Section 5.3). Full details of the criteria used to detect hybrids are presented in Section 5.3.

In practice, when trees or specimens of *Leucaena* are being identified, the possibility that they may be of a hybrid only arises when material cannot be matched with any known species of *Leucaena*. This is the first stage in suggesting a hybrid hypothesis and moving towards its identification. The second step should always be to survey what species of *Leucaena* are growing in the immediate vicinity. If there are two or more species growing in close proximity then hybridization is possible, and indeed likely (Section 5.2). Thus unusual morphology and geographic overlap of two or more species taken together provide initial signals that a specimen or tree may be a hybrid. If there are only two species growing together then further investigation of the identity of a putative hybrid may be relatively straightforward as these two species are the only possible parents. In general hybrids are morphologically intermediate between the two parent species, at least for the majority of characters. In *Leucaena*, morphological intermediacy in the four basic quantitative leaf traits listed in Table 13, has been investigated in detail by Sorensson (1993) using artificial hybrids. He demonstrated that hybrids show mid-parent values on a log scale with a dosage effect due to ploidy (Section 5.3). This means that if there are only two species in the area, the quantitative leaf morphology of the putative hybrid can be compared with that of the two parents to see if the hybrid is intermediate using one of the two equations shown in Section 5.3. If there are more than two species present in the immediate vicinity of the putative hybrid, then investigation of its identity is likely to be more difficult. However, hybrid leaf morphology may still be compared to the possible combinations of pairs of parents present in the area. Many hybrids show reduced fertility compared to the two parents manifest by their reduced pod and seed set. For example triploid hybrids are usually nearly or completely sterile. In addition, spontaneous hybrids are often infrequent or rare compared to the two parents. Lack of seed set and rarity may provide further, albeit not conclusive, indications that a tree may be a hybrid.

Sorensson (1990; 1993) and Sorensson and Shelton (1992) showed that some hybrids may be reliably separated at the seedling stage using juvenile leaves, which like adult leaves are also intermediate. This can be particularly useful where two-parent open-pollinated hybrid seed orchards (Section 9.4) tend to produce a mixture of parent and hybrid seed which can then be identified and separated at the nursery stage.

11 Species Accounts

The accounts presented in Chapter 11 provide summaries of information about the taxonomy, ecogeography, phenology, conservation and utilization of each species of *Leucaena* along with botanical drawings and distribution maps. Species are ordered alphabetically.

In the species accounts, bibliographic citations are provided for all accepted names, and synonyms are listed with their authorities. A complete checklist of all *Leucaena* names (accepted names, synonyms, doubtful and excluded names), along with full bibliographic citations of their original place of publication (protologue), and complete details of TYPE specimens, along with an index of synonyms, is presented in Appendix 1.

Brief botanical descriptions are provided. The convention for plant part (leaflet, pod, seed, tree size) dimensions is to list the normal range with absolute extremes as assessed from all botanical material viewed listed in brackets. Complete descriptions may be found in Hughes (in press). Keys to subspecies are included.

Botanical drawings of all species are included. Botanical vouchers for all material represented in the drawings is cited in Hughes (in press).

Altitude range is based on herbarium specimen records and presented as a range with extremes in brackets (outliers, based on examination of the frequency distribution of botanical specimen records.Phenology refers primarily (except where indicated) to native range.

Conservation status: two measures of conservation status the Star Rating (Hawthorne, 1996b) and the IUCN threat category (IUCN, 1994). These are fully explained in Chapter 8. Lists of common names are not exhaustive, but are derived from literature, herbarium specimen labels and field work.

Species distributions maps are of those herbarium specimens (2393 or 88% of the total examined) with verified Lat/Long and were prepared directly from the BRAHMS (Filer, 1996) *Leucaena* database using the mapping software MUSICA (Hawthorne, 1996a).

Data on psyllid resistance are from Mullen *et al.* (1996, 1997), on wood specific gravity data from Gourlay *et al.* (in press) and Stewart *et al.* (1993), and on fodder quality (largely from Stewart and Dunsdon, in press).

11.1 Leucaena collinsii

Leucaena collinsii Britton & Rose, N. America Flora 23: 126. 1928.

Subspecies

L. collinsii subsp. collinsii

L. collinsii subsp. zacapana C.E. Hughes, Kew Bulletin 46: 553. 1991.

Main attributes

L. collinsii is an important tree of the seasonally dry tropical inland valleys of southern Mexico and Guatemala. It is notable for its superior wood quality producing denser wood with a higher proportion of heartwood and higher durability than most other species of *Leucaena*; as a result it is highly prized by people in its native range for house construction and firewood (Figs 8C and 10B). *L. collinsii* is notably drought-tolerant: subsp. *zacapana*, grows in dry or semi-arid areas with 500-750mm rainfall and a long dry season of up to 7 months. *L. collinsii* (especially subsp. *collinsii*) is one of the most psyllid-resistant *Leucaena* species.

Botanical features (Fig 24)

Bark: mid grey brown with shallow rusty orange brown vertical fissures; slash cream white (Fig 20E).

Leaves: pinnae (5)6-16 pairs; pinnular rachis (3.7-)4-8.7 cm long; leaflets 3.7-7 mm long, 1-1.9 mm wide, 25-56 pairs per pinna, asymmetric about mid vein, broadly linear

Petiole gland: yellow green or green, sessile, round or elliptic, dome-shaped or rounded-conic with a narrow central pore, 2 x 1 mm

Flower heads: 9-24 mm in diameter, 55-170 pale cream-white flowers, in groups of 2-3 (-6) in leaf axils on actively growing shoots, the leaves developing with the flower heads, the flowering shoot indeterminate in growth with pods borne on older wood within crown

Pollen: tricolporate monads

Pods: 11-18(-20) cm long, (7-)10-19 mm wide, 1 or 2(-4) per flower head, linear-oblong or oblong, acuminate, or sometimes obtuse apically, sometimes with a short beak, flat, 9-20 seeded, mid-brown, glabrous, opening along both sutures.

Seeds: 6.5-8.8 mm long, 4-6.2 mm wide, 22,000-23,000 seeds/kg (subsp. *collinsii*) and 30,000-36,000 seeds/kg (subsp. *zacapana*)

Taxonomy and subspecies
Until recently *L. collinsii* was thought to be restricted to the central depression of Chiapas in southern Mexico forming a localised, discrete, uniform and readily distinguished species. Its inclusion as a subspecies of *L. esculenta* by Zárate (1984a) has now been abandoned. More recently it has become apparent that material from the Motagua Valley in Guatemala also belongs with *L. collinsii*. This realisation clarifies long standing confusion over the identity of the Motagua Valley *Leucaena* material which had been considered a variant of *L. diversifolia* (Hughes and Styles, 1984) or *L. trichandra* (Standley and Steyermark, 1946). Seed of this material was distributed from OFI in 1984 for trials misidentified as *L. diversifolia* (seedlots 15/83 and 18/84). Confusion arose due to the broad similarity in leaf and pod traits, but with collection of flowering material its affinities to *L. collinsii* became clear. The material from the Motagua Valley in Guatemala is now assigned to a separate subspecies *zacapana* described by Hughes (1991). The two subspecies are distinguished by a set of quantitative leaf and pod characters which show discontinuous variation correlated with geography.

KEY TO SUBSPECIES

Leaves >14 cm long, >7 pairs of pinnae, >45 pairs of leaflets per pinna, open flower heads >15 mm in diameter, >140 flowers per flower head, pods >16 cm long, >17 mm wide
subsp. *collinsii*

Leaves <12 cm long, <8 pairs of pinnae, <40 pairs of leaflets per pinna, open flower heads <16 mm in diameter, <55 flowers per flower head, pods <11 cm long, <12 mm wide
subsp. *zacapana*

Closely related species and identification
Although Zárate (1982; 1984a) originally treated *L. collinsii* as a subspecies of *L. esculenta* and later as a distinct species closely related to *L. esculenta* (Zárate, 1994), more recent molecular and morphological analysis suggests that the most closely related species is *L. trichandra* (Harris *et al.*, 1994a; Hughes, in press). *L. collinsii* is easily distinguished from *L. trichandra* by its convex, dome-shaped petiole gland with a narrow pore compared to the cup-shaped concave broad petiole gland of *L. trichandra* and by its white as opposed to pink flowers.

Chromosome number
Diploid, 2n=52, self incompatible (Pan and Brewbaker, 1988; Sorensson, 1989a).

Tree size and form (Fig 10B)
Small to medium sized tree, 10-15(-20) m tall, 20-40 cm bole diameter. Subsp. *collinsii* generally has a bole to 3-5 m ht. and a wide, open crown and heavy branching. Subsp. *zacapana* is very branchy when young with numerous small branches and a spreading crown. Trees frequently grow with a pronounced lean and branches are sometimes planar. Coppice resprouts are very numerous.

Distribution (Fig 25)
The two subspecies of *L. collinsii* occur in separate valley systems, isolated by high mountains, in southern Mexico and south east Guatemala. Subspecies *collinsii* is restricted to the central depression of Chiapas in the middle reaches of the Rio Grijalva watershed in southern Mexico and immediate border fringes of Guatemala in the Dept. of Huehuetenango. Subspecies *zacapana* is restricted to the middle and lower Rio Motagua Valley system in south east Guatemala mainly in Depts. Chiquimula, Progreso and Zacapa with outlying occurrences in Jalapa and Guatemala.
Degree-squares: 7; subsp. *collinsii*: 4; subsp. *zacapana*: 3
Altitude range: (100-) 400-900m

Ecogeography
Both subspecies occur in interior valleys with marked rain shadows and seasonally dry or semi-arid tropical, frost free,
climates. Rainfall ranges from 500mm in Zacapa, Guatemala to 1000mm in Chiapas with a long and severe dry season of 6-7 months. Both subspecies occur in remnant seasonally dry tropical forest and subsp. *zacapana* extends into semi-arid thorn scrub forest in the drier parts of the Motagua Valley often forming dense thickets in secondary vegetation.

Phenology
Flowering (July-) August-November (-December); fruiting February-April; deciduous during the prolonged dry season, December to April.

Conservation status
Although highly restricted in distribution, and hence globally rare, both subspecies are often locally very abundant, ruderal and sometimes weedy; subsp. *zacapana* is often dominant in bush fallow and subsp. *collinsii* protected or cultivated for its edible pods. Subsp. *collinsii* is probably present in the El Triunfo Biosphere Reserve, Chiapas, Mexico.
Star rating: Blue Star (both subspecies)
IUCN threat category: LR:lc (both subspecies)

Common names
Subspecies *collinsii*: *chalip (chilip)*, Huehuetenango, Guatemala, *chijlip* La Trinitaria, Chiapas, Mexico (*"chij"* = sweet; Tojolabal), *guash (huash)* Huehuetenango and Chiapas, *guash de monte* (as opposed to *guash de castilla* = *L. leucocephala*), *guaxin* La Chacona and Tuxtla Gutierrez, Chiapas, *guaje, guaje colorado*, *pǎka sasib* (Tzeltal) Municipio of Tenejapa (Berlin *et al.*,

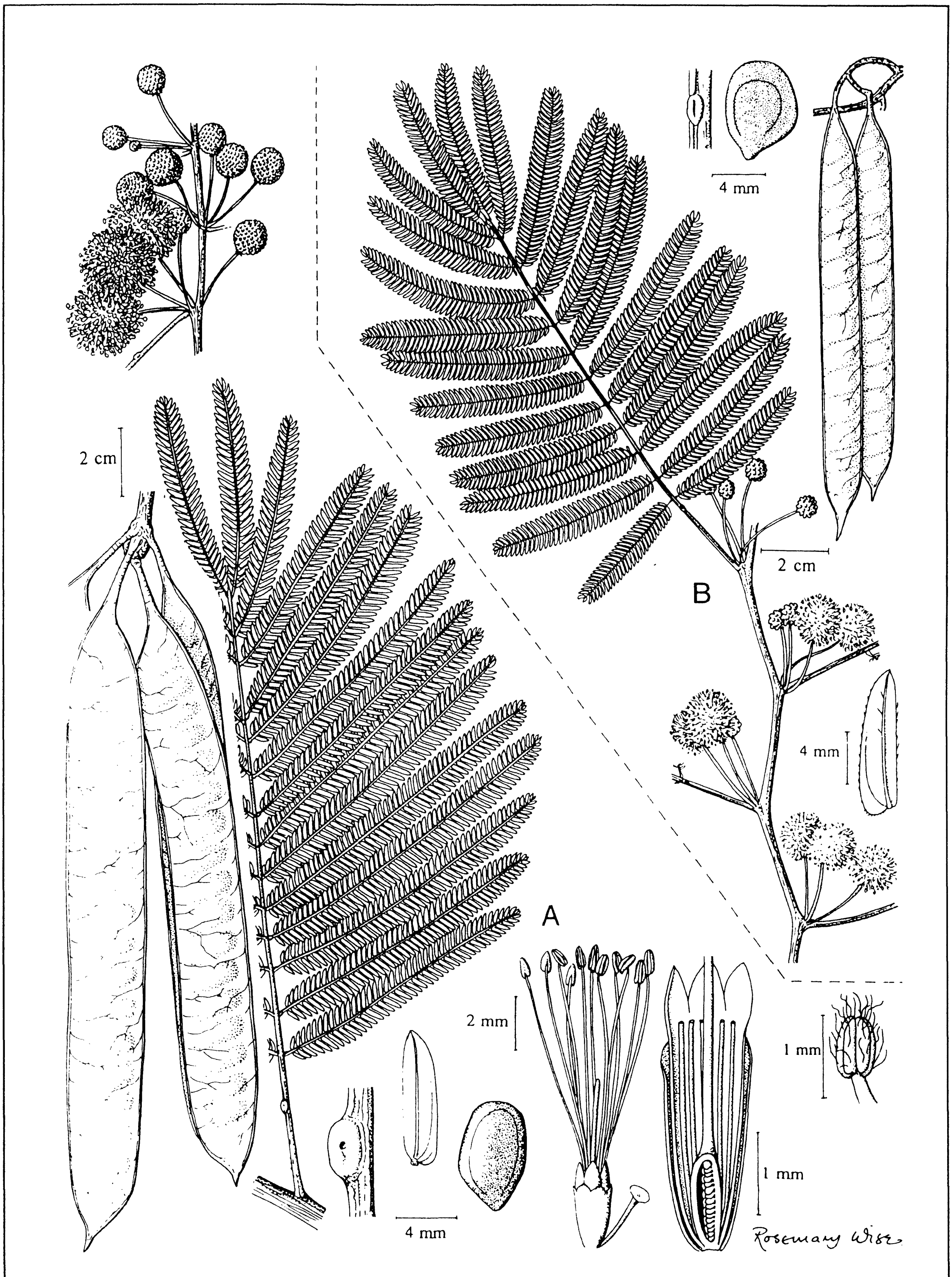

Figure 24 *Leucaena collinsii* **A.** subsp. *collinsii* **B.** subsp. *zacapana*

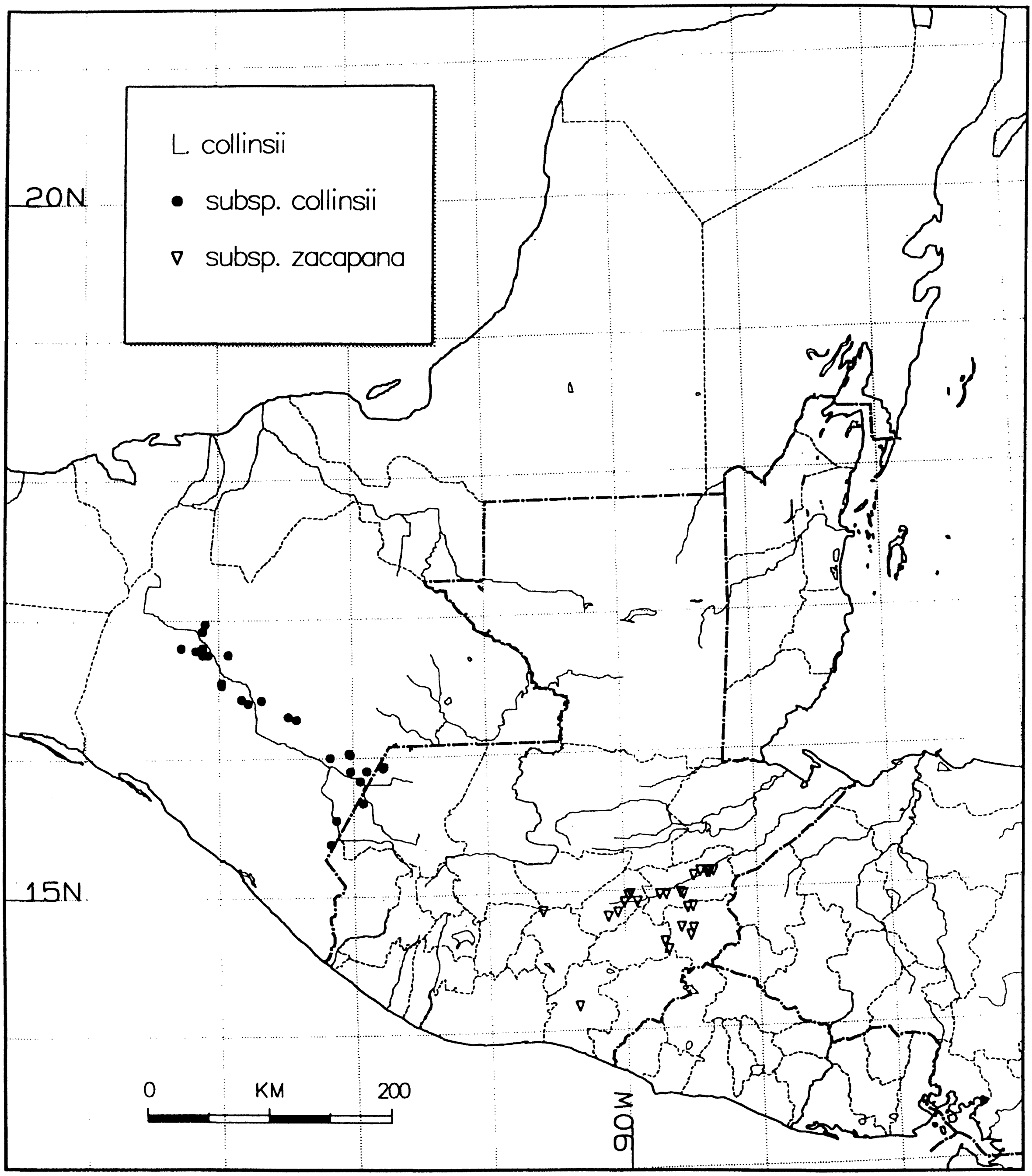

Figure 25 Map of southern Mexico and Guatemala showing the distribution of *L. collinsii*

1974). Subspecies *zacapana*: *guaje* (*yaje*).

Indigenous use and domestication

Trees of subsp. *collinsii* are particularly abundant in certain villages, *e.g.* Chacaj in Guatemala, where they are protected and cultivated for pod production. The unripe seeds are consumed locally and pods are marketed in nearby towns and also further afield in regional markets in the northern highlands of Guatemala (*e.g.* Todos Santos los Cuchumatanes) and the central highlands of Chiapas (*e.g.* San Cristobal de las Casas). Unlike subsp. *collinsii* there is no record of use of pods or seeds of subsp. *zacapana* as food. Trees of subsp. *zacapana* are however highly valued for their extremely dense wood with abundant heartwood which is ideal for fence posts and house construction, as well as one of the highest quality firewoods available (Fig 8C). Because of these qualities secondary stands are managed in parts of the Motagua Valley on a four year coppice rotation specifically for fuelwood production and individual trees are often protected in fields for pole production (Fig 10B).

Exotic use
Psyllid resistance: The high psyllid resistance of *L. collinsii* has been noted since the psyllid first appeared in Hawaii. It is now clear that subsp. *collinsii* shows higher resistance (highly resistant, 1-2 damage category) than subsp. *zacapana* (moderately resistant moderately susceptible, 2-4).
Wood quality: *L. collinsii* produces wood of higher density and a higher proportion of heartwood than most *Leucaena* species. Mean wood density of subsp. *zacapana* is higher (0.91) than for any other species and somewhat higher than subsp. *collinsii* (0.75) (Gourlay *et al.*, in press). Both subspecies are thus highly valued for wood production for high quality firewood and durable poles for local construction and fence posts. *L. collinsii* is always considered to be superior to *L. leucocephala* in wood quality (Figs 8C and 10B).
Fodder quality: Initial data on leaf quality indicate high digestibility and very low or zero condensed tannin content of leaves (Stewart and Dunsdon, in press).
Growth: *L. collinsii* has only been widely introduced into trials in the last decade. Trial results show that both subspecies can grow well on a range of sites. Subsp. *zacapana* which has been grown in Central America, promoted by the regional MADELENA project, (often misidentified as *L. diversifolia*) and was included in the OFI international trial of Central American dry zone species (initially also misidentified as *L. diversifolia*) outperforms *L. leucocephala* on some sites (Stewart and Dunsdon, 1994). With its higher wood density, it is one of the highest wood biomass producers of all *Leucaena* species (Stewart *et.al.*, 1991; 1993).
Weediness risk: *L. collinsii* and particularly subsp. *zacapana* produce abundant seed from an early age and, as demonstrated by its dominance of bush fallows in its native range in Guatemala, poses significant risks of becoming a ruderal weed of open disturbed habitats where introduced, but is likely to be less weedy than *L. leucocephala*.

11.2 Leucaena confertiflora

Leucaena confertiflora S. Zárate, Anales Instituto de Biología Univ. Nacional Autónoma de México. Serie Botánica 65: 148. 1994.

Varieties
L. confertiflora var. confertiflora
L. confertiflora var. adenotheloidea (S. Zárate) C.E. Hughes, Contr. Univ. Michigan Herb. 21: 287. 1997.
Synonym
L. confertiflora subsp. *adenotheloidea* S. Zárate

Main attributes
The characteristics of *L. confertiflora* remain poorly known. It was only discovered in 1976, and named in 1994. by Sergio Zárate in indigenous cultivation in informal orchards in the village of San Pedro Chapulco in Puebla, Mexico where it is grown as a source of edible pods and seeds. It forms a small multiple stemmed tree and apparently has little direct potential for wood or fodder production. It is however the highest elevation (to 2500m) species of *Leucaena* and is highly psyllid-resistant. As a tetraploid it could prove useful as a parent in artificial hybridization with other tetraploid species.

Botanical features (Fig 26)
Bark: smooth, mid grey brown with horizontally aligned pale orange brown lenticels and shallow rusty orange brown vertical fissures, slash green then cream
Leaves: pinnae 5-7 pairs; pinnular rachis 4-8 cm long; leaflets (5-)7-10.5 mm long, 2-3.4 mm wide, (18-)22-26 pairs per pinna, asymmetric at base, linear-oblong, acuminate, sometimes with a small curved point or 'cusp' at tip, glabrous except on margins, thick, almost leathery, dark glossy bottle green on upper surface.
Petiole gland: small and variable: either cylindrical, columnar, peg-shaped (var. *adenotheloidea*) or discoid, shallow cup-shaped (var. *confertiflora*), 0.5-1.5 mm long x 0.5-1.5 mm wide x 1-1.5 mm tall, sometimes with a gland at base of all pinnae pairs along leaf rachis. Occasional double glands occur in var. *adenotheloidea* (Fig 26).
Flower heads: 13-20 mm in diameter, 55-70 flowers, in groups of (1)2-5 in leaf axils on older shoots and on actively growing shoots developing with leaves; stamens pale creamy white, anthers densely hairy, dull pinkish grey or dull greenish brown fading dull mauve
Pollen: tricolporate monads
Pods: 9-15 cm long, 16-26 mm wide, 1-4(-7) per flower head, linear-oblong or oblong, the base acute, the apex rounded, often with a short pointed beak, flat, 10-15-seeded, deep maroon and slightly glossy unripe (Fig 22F) turning dark reddish-brown when ripe, glabrous or occasionally sparsely hairy, opening initially along one side only, the pod walls reflexing transversely, sometimes forming tight rolls after opening
Seeds: 6.5-8.3 mm long, 5-6.8 mm wide, aligned transversely in pods

Taxonomy and varieties
Leucaena confertiflora was discovered by Sergio Zárate and Bob Reid in cultivation in the small village of San Pedro Chapulco, Puebla, Mexico in 1976. At that time, Zárate (1984a; 1984b) considered it to be a subspecies of *L. cuspidata* and tentatively named it *L. cuspidata* subsp. *compactiflora* in recognition of the compact flower heads. It was later recognized as a distinct

species (Zárate, 1994) but it is only in the last decade that its identity, distribution, ecology and characteristics have been investigated in detail.

The material from Chapulco, and the surrounding area near Azumbilla and in the northern Sierra Zongolíca differs in the shape of the petiole gland from material from other areas further south in Puebla and Oaxaca. This difference was used by Zárate (1994) to divide *L. confertiflora* into two subspecies: *confertiflora* with sessile, discoid or shallow cup-shaped, concave glands and subspecies *adenotheloidea* with stipitate (stalked), erect peg-shaped, cylindrical glands, usually at the base of each pair of pinnae (Fig 26). Zárate (1994) discussed the lack of other distinguishing features between these two subspecies. Gland shape is clearly distinct at the extremes, and constant in most areas. However, variation within populations and even within individuals has been observed in some populations in Puebla. This inconstancy of the gland shape and the lack of other distinguishing features justify treatment at varietal rather than subspecific rank (Hughes, 1997a).

KEY TO VARIETIES

Petiole and leaf rachis glands not stalked (sessile), discoid, round, weakly concave or cup-shaped; usually only petiole and 1-2 rachis glands
var. *confertiflora*

Petiole and leaf rachis glands stalked (stipitate), erect, peg-shaped, cylindrical or pointed, occasionally double; usually petiole and 2-5 nectaries along rachis, sometimes at base of each pair of pinnae
var. *adenotheloidea*

Putative spontaneous hybrids between *L. confertiflora* and *L. pallida* have been found where the two parents are cultivated in informal orchards in the village of Santa Catalina Oxolotepec

Closely related species and identification

L. confertiflora is similar to *L. cuspidata* in leaf morphology, leaflet shape (with a 'cusp'), pod dehiscence initially along one side of pod only and flower colour. Zárate (1984a; 1994) considered the two to be closely related. In addition, these two species occupy similar distributions and habitats, at higher elevations in dry upland thorn scrub, inland and west of the Sierra Madre Oriental, separated by the central Mexican volcanic axis, *L. cuspidata* to the north and *L. confertiflora* to the south, suggesting isolation following recent volcanic activity. *L. confertiflora* may be distinguished from *L. cuspidata* by its papery as opposed to leathery or woody pods which reflex transversely rather than twist spirally after dehiscence.

Chromosome number

L. confertiflora (designated as *L. "glossy"*) was listed as tetraploid, 2n = 112 and self compatible by Sorensson and
Brewbaker (1994), a count confirmed for var. *adenotheloidea* by Palomino *et al.* (1995); the chromosome number of var. *confertiflora* is unknown. The origin of this tetraploid remains unknown. However, molecular and morphological data suggest *L. trichandra* as the most likely maternal parent species assuming a hybrid origin.

Tree size and form

Small, often multiple stemmed, branchy shrub or small tree 2-4(-6) m tall, 10-15 cm bole diameter with an open irregular, often spreading umbrella crown.

Distribution (Fig 27)

L. confertiflora var. *confertiflora* is restricted to the high, dry, inland hills and plateaux of Oaxaca and southern Puebla, between the coastal Sierra Madre Oriental and the Sierra Madre Sur. It occurs mainly in a belt extending from Cerro Nueve Puntas about 50km east of Oaxaca to western Oaxaca around Tamazulapan, and north into southern Puebla in the mountains south of the Tehuacan Valley around Caltepec. Var. *adenotheloidea* is restricted to a small area of central Puebla at the northern end of the Sierra Zongolíca, to the north east of the northern end of the Tehuacan Valley.

Degree-squares: 4; var. *confertiflora*: 4; var. *adenotheloidea*: 1

Altitude range: (1500-) 1750-2500 m. Growing to 2500m, var. *adenotheloidea* is the highest elevation taxon in the genus.

Ecogeography

L. confertiflora occurs as an understorey shrub or small tree in dry oak or pine-oak forest and dry mattoral, always on shallow black soils over calcareous rock. Trees are often very scattered and are susceptible to grazing pressure; extensive natural populations are infrequent and the species is threatened by grazing. It occurs at higher elevations than any other species of *Leucaena* and survives occasional moderate frosts. Conditions at Chapulco where it is cultivated, are cold and dry with 500-700mm rainfall and a 7-month dry season and regular moderate frost from December to February.

Phenology

Flowering November-February (-March), unripe pods July-December, ripe pods November-February, leafless during the cold/dry season from November to March.

Conservation status

L. confertiflora has a restricted distribution and is never locally abundant being susceptible to grazing pressure and harvesting of pods from wild populations. Few natural populations are known and these are severely degraded. In a few villages trees are cultivated and protected *circa situm* on a small scale but the species is

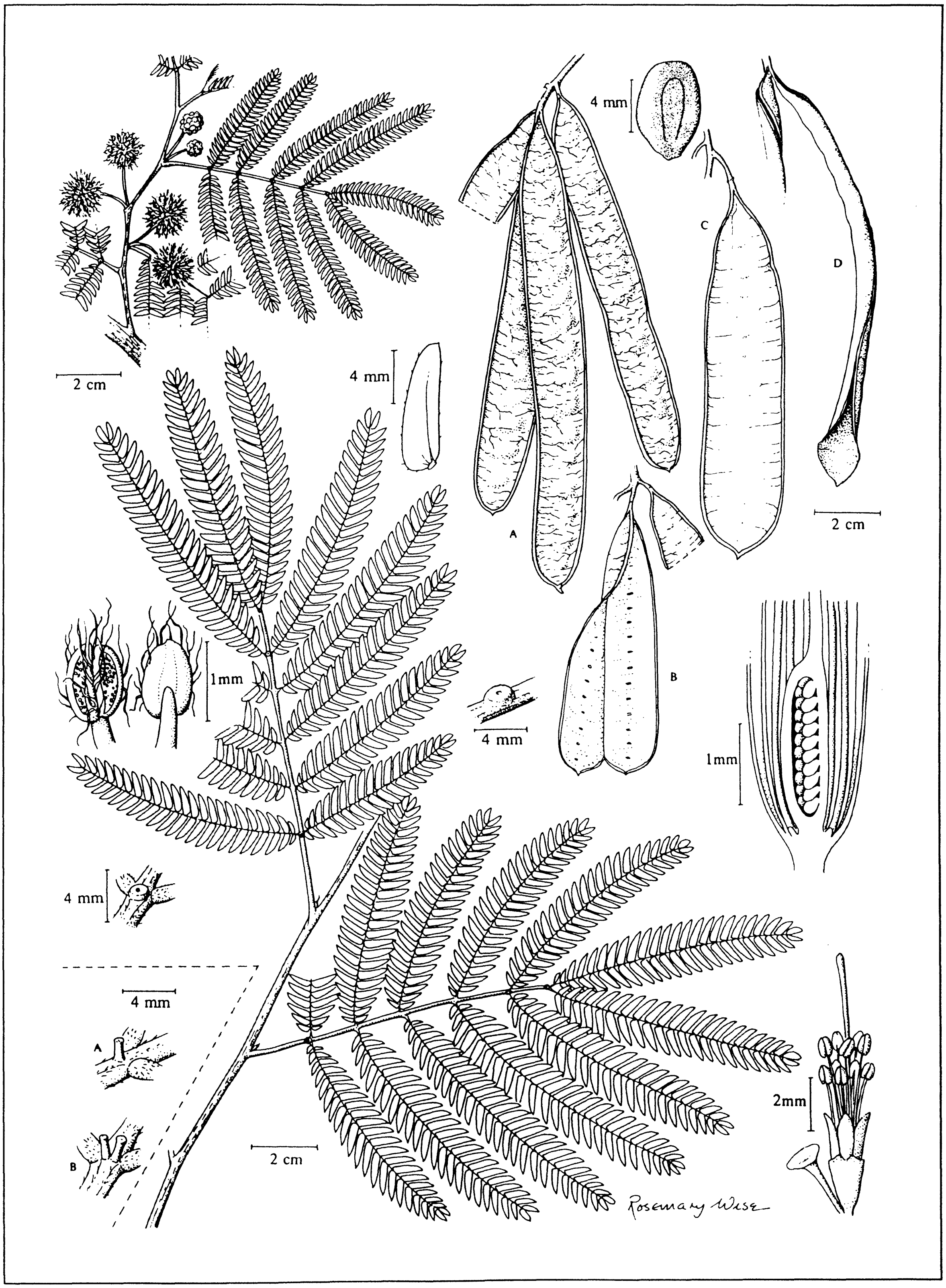

Figure 26 *Leucaena confertiflora* showing variation in pod shape and size. Inset shows petiole glands of var. *adenotheloidea*.

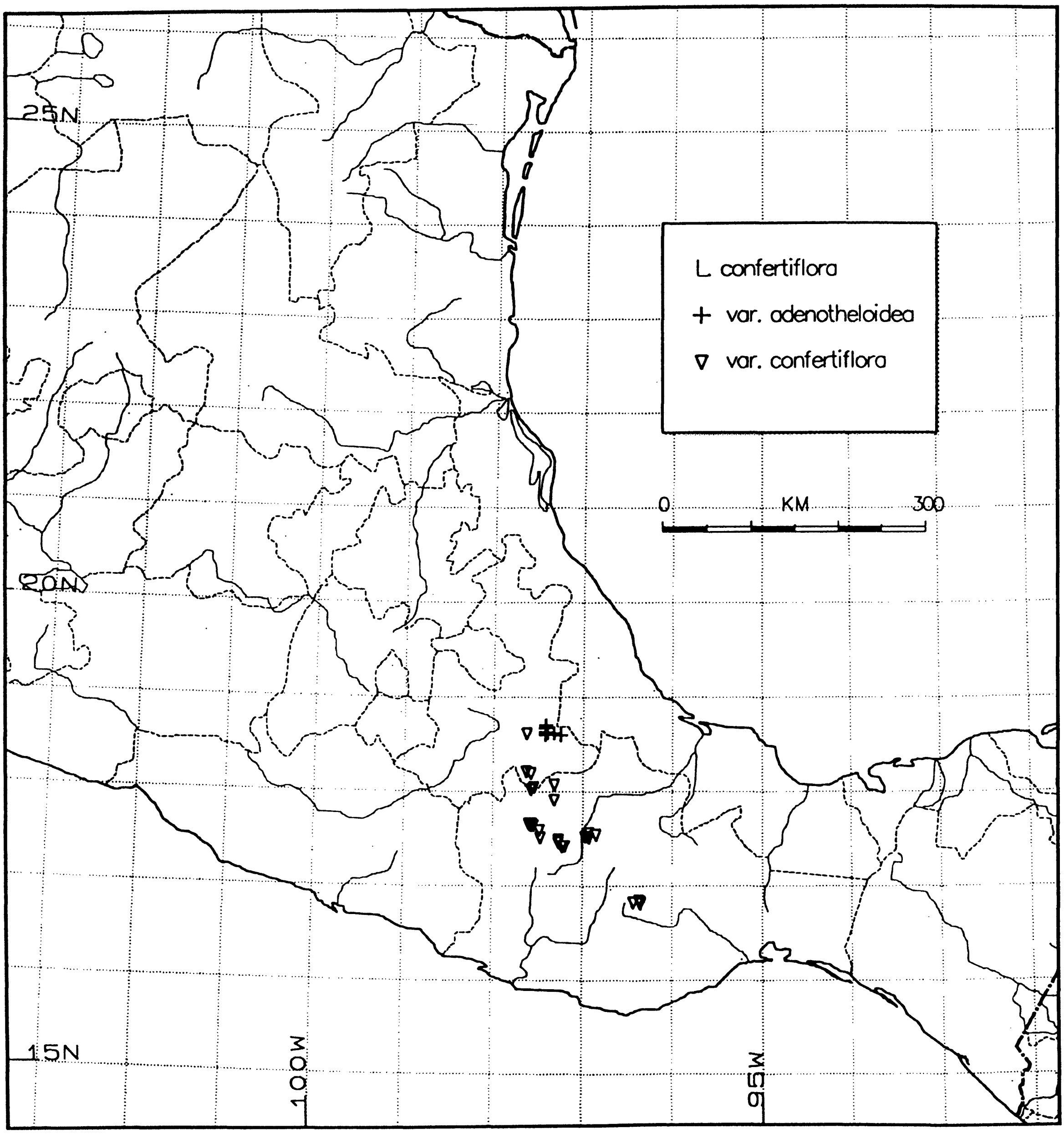

Figure 27 Map of central Mexico showing the distributions of *L. confertiflora*

nevertheless vulnerable and var. *adenotheloidea* endangered and of significant conservation concern.
Star rating: species: Gold star; vars: Blue star
IUCN threat category: species and var. *confertiflora*: VU-A1 & B1&2; var. *adenotheloidea*: EN-B1&2

Common names

Var. *confertiflora*: *huaje, guaje, guaje del cerro, guaje de venado*; var. *adenotheloidea*: *guaje zacatzín* (San Pedro Chapulco and Azumbilla), *guaje de huerta* (in cultivation) and *guaje de monte* (in natural populations) (in and around Santa Catalina Oxolotepec, Puebla).

Indigenous use and domestication

L. confertiflora var. *confertiflora* is used as a minor food, the unripe pods and seeds being collected and consumed locally. Pods are harvested from natural populations, often several kilometres distant from villages. There are no reports of widespread marketing of pods or cultivation of var. *confertiflora*, but harvesting from natural populations is still intensive. Var. *adenotheloidea* is also used and is locally cultivated in informal orchards in villages including San Pedro Chapulco, Azumbilla and Santa Catalina Oxolotepec, Puebla, Mexico, again as a source of food. Zárate (1984b) described a process of 'incipient domestication' for var *adenotheloidea* whereby cultivated material has been derived directly from adjacent natural populations, probably only in the last century. The unripe pods from San Pedro Chapulco and Santa Catalina Oxolotepec are consumed locally and sold in nearby markets as far away as Tehuacan. With pod production from June to August, *L. confertiflora* complements the more widely used *L. esculenta* (January-March) and *L. pallida* (November-December) giving virtually year-round pod production.

Exotic use and potential
The characteristics of *L. confertiflora* are poorly known. Limited knowledge is based on observations of trees in natural populations and in cultivation in Chapulco. Trees are small (<4 m ht.), bushy and always multiple-stemmed. Trees with as many as 20 stems are not uncommon and trees are normally spreading with flat-topped crowns. Preliminary evaluation data indicate that *L. confertiflora* is slow growing with low fodder digestibility and high condensed tannin content suggesting low potential for direct use. However, as a tetraploid, there is scope to incorporate *L. confertiflora* into artificial hybridization programmes, possibly to enhance cold tolerance or psyllid resistance of other tetraploid species.
Psyllid resistance: Limited data indicate that *L. confertiflora* is highly resistant (damage score ?1-3)

11.3 Leucaena cuspidata

Leucaena cuspidata Standley. Contributions from the U.S. National Herbarium 20: 189. 1919.

Synonyms: *Leucaena cuspidata* Standley subsp. *jacalensis* S. Zárate

Main attributes
L. cuspidata is one of the least well known species of *Leucaena*, its characteristics known largely from herbarium specimens and field observations in natural populations. It is a very distinctive species with thick pods which are fleshy unripe and leathery when ripe and which open initially along one side and later twist into tight spirals more reminiscent of pods of *Gliricidia* than other species of *Leucaena*. With only limited seed collections *L. cuspidata* has been cultivated so far in only a handful of trials, but preliminary data suggest that it has little direct potential for planting.

Botanical features (Fig 28)
Bark: on young branches smooth, mid grey-brown with pale brown lenticels, darker blackish-brown and rougher with shallow orange-brown vertical fissures on bole
Leaves: pinnae (9-)11-16(-18) pairs; pinnular rachis 7-10 cm long; leaflets (5-)5.2-6.6 mm long, 1.5-2.3 mm wide, (38-)40-45(-50) pairs per pinna; asymmetric at base, linear-oblong, acuminate, with a short curved point or 'cusp' at apex, almost leathery, dark glossy green above, paler mid- or grey-green below
Petiole gland: 1-2 small usually cylindrical, columnar, peg-shaped nectaries, 1-1.5 mm long x 1 mm wide x 1 mm tall
Flower heads 13-16 mm in diameter, with 135-150 flowers, in groups of (1-)2-4 in leaf axils on actively growing shoots; stamen filaments pale creamy white, anthers sparsely hairy, pale lemon-yellow
Pollen: tricolporate monads
Pods (10-)14-22(-28) cm long, 20-30 mm wide, 1 or 2 (3) per flower head, linear-oblong, slightly curved, acute at base and apex, flat, 13-15-seeded, pod walls thick, green and fleshy unripe turning mid reddish-brown, glabrous or pubescent, notably leathery or almost woody, opening initially along one side only, the pod walls later twisting, sometimes forming tight spirals
Seeds 8.1-10.6 mm wide, 9.4-11.8 mm long, aligned transversely in pods

Taxonomy and identification
Leucaena cuspidata was distinguished by Standley because of its unusual 'cuspidate' (with a curved point or *cusp* at the tip) leathery leaflets, which are quite unlike those of other species in the genus apart from *L. confertiflora*. The unusual broad, slightly curved pods with their initially fleshy and later thick leathery pod walls which open initially along one margin only and later twist and form tight spirals, confirm the distinction of *L. cuspidata* as an unusual species. Finally, seedling morphology of *L. cuspidata* is also unusual with the cotyledons held at, or slightly below, ground level, while all other species have the cotyledons held above ground level. Thus although Brewbaker (1987a) treated *L. cuspidata* as a doubtful species, it possesses a set of unusual characters and shows clear morphological, geographic and ecological identity as a distinct species.

The affinities of *L. cuspidata*, with so many unusual characters, remain uncertain. Zárate (1984a; 1994) indicated a close relationship between *L. cuspidata* and *L. confertiflora* indeed he first considered *L. confertiflora* to be a subspecies of *L. cuspidata*. A close relationship between these two species is supported by their unusual pod dehiscence, initially along one suture, and they occupy similar habitats immediately north (*L. cuspidata*) and south (*L. confertiflora*) of the main volcanic axis which lies across central Mexico (Figs 27 and 29).

Variation in the shape of the petiole gland and leaf and pod pubescence has been observed within *L. cuspidata* prompting Zárate (1984a; 1994) to distinguish subsp. *jacalensis* which he described as a strongly pubescent variant occurring as a restricted endemic around the town of Jacala, an area falling within the geographic range of *L. cuspidata* as a whole. Hughes (in press) observed that leaf, and particularly pod pubescence are very variable both between and within populations suggesting that these are sporadic variants rather than a distinct taxon and treated subspecies *jacalensis* as a synonym of *L. cuspidata*.

Chromosome number
Unknown

Tree size and form
Small, often multiple-stemmed tree 2-4(-6) m tall, 10-15 cm bole diameter and an open irregular spreading crown.

Distribution (Fig 29)
L. cuspidata is restricted to the drier mid-elevation west-facing slopes of the Sierra Madre Oriental in Mexico in the states of Hidalgo, Querétaro and San Luis Potosí. It is common only in Hidalgo, where the majority of botanical collections have been made, although, even here, most are from a restricted set of localities around the Barranca of Tolantongo; it is apparently rare in Querétaro and San Luis Potosí.
Degree-squares: 4
Altitude range: (1400-) 1600-2200 (-2400) m

Ecogeography
L. cuspidata occurs as an understorey shrub or small tree in mixed pine-oak-juniper forest and scattered in mixed dry and low mattoral. Associated canopy species include *Pinus cembroides, P. pinceana, Juniperus deppeana, J. flaccida* and *Quercus mexicana*. It occurs principally on steep rocky calcareous slopes, and at one locality in San Luis Potosí, sulphur deposits are common. Conditions in the native range are cold and dry. *L. cuspidata* grows from 1400m to 2400m elevation and withstands light to moderate frost. Rainfall ranges from about 500mm to 1200mm. It is grazed by goats and in many areas is now rare and restricted to steep cliffs and gullies that are inaccessible to browsing animals.

Phenology
Flowering February-May; fruiting (October-) November-December (-February)

Conservation status
L. cuspidata occupies a restricted distribution and is rarely locally abundant and if so only in forest. It is apparently susceptible to grazing pressure, and, unlike most species of *Leucaena*, does not appear to thrive on disturbance. For these reasons it is considered to be of significant conservation concern.
Star rating: Gold star
IUCN threat category: VU-A1 & B1&2

Common names
efe (= *guaje* in Otomi), *efe de cerro, gauche (guaje) de cerro, guachito, huaxi (guaje), guaje de cerro* (Hidalgo).

Indigenous use and domestication
Unripe pods are harvested and the seeds consumed locally and marketed in nearby towns such as Ixmiquilapan (Hidalgo). The seeds of *L. cuspidata* are large and are considered superior in quality to those of *L. leucocephala*. It is occasionally cultivated on a small scale for pod production (*e.g.* around Cardonal and above Jacala in Hidalgo).

Exotic use and potential
L. cuspidata generally forms only a small tree to 3-4m and occasionally 8m height. It is often multiple-stemmed and shrubby. It is therefore unlikely to have much direct potential for tree planting.
Psyllid resistance: limited data suggest *L. cuspidata* is moderately or highly psyllid-resistant (damage score ?2)
Wood quality: unknown
Fodder quality: preliminary data suggest low digestibility and high condensed tannin content
Growth: unknown, but likely to be slow growing
Weediness risk: *L. cuspidata* is one of only five species of *Leucaena* judged to have low risk of weediness due to its sparse and delayed seed production. Unlike the majority of species of *Leucaena*, *L. cuspidata* does not appear to thrive on disturbance.

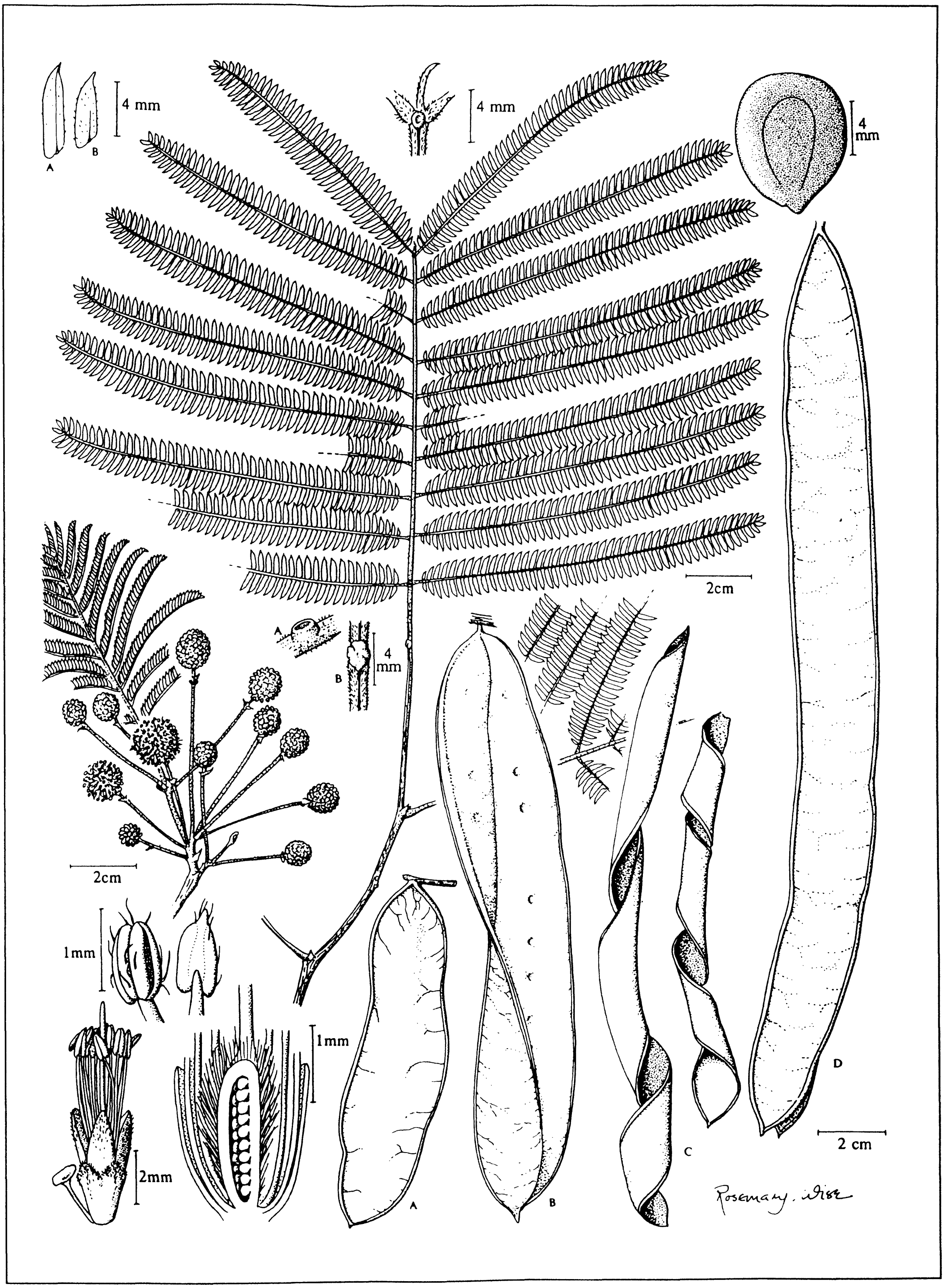

Figure 28 *Leucaena cuspidata* showing variation in pod shape and size.

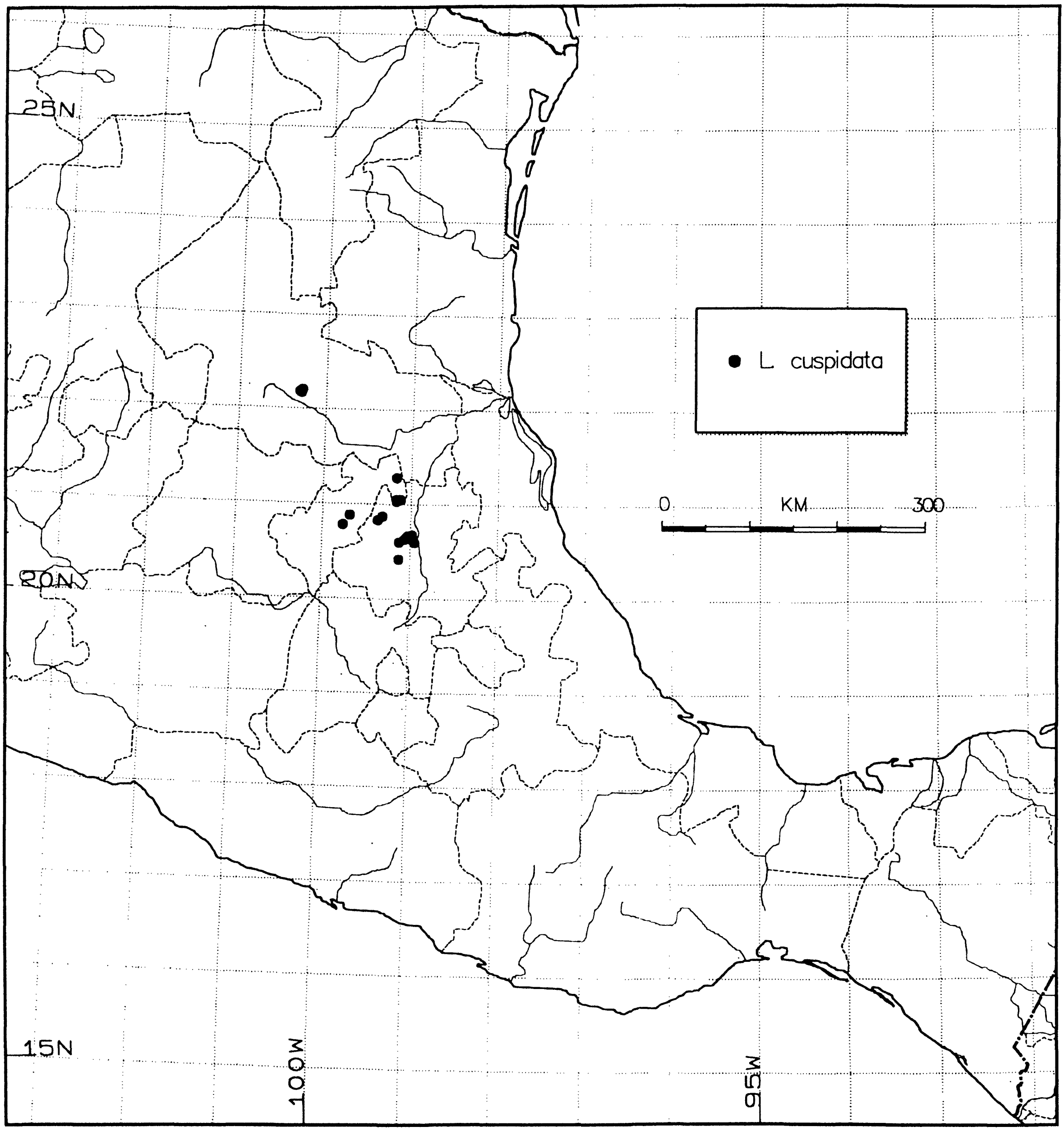

Figure 29 Map of central Mexico showing the distribution of *L. cuspidata*

11.4 Leucaena diversifolia

Leucaena diversifolia (Schltdl.) Benth. Hooker Journal of Botany 4: 417. 1842.

Synonyms
Acacia diversifolia Schltdl.
Leucaena diversifolia subsp. *diversifolia sensu* Pan
Leucaena laxifolia Urban
Leucaena brachycarpa Urban

Main attributes
After *L. leucocephala*, *L. diversifolia* is the most widely cultivated species of *Leucaena*. As a self compatible tetraploid, it is also one of the most important parent species in artificial hybridization. It is fast growing, shows moderate cool tolerance and psyllid resistance, and out yields *L. leucocephala* in cooler mid-elevation tropical highland areas. *L. diversifolia* sets prodigious quantities of seed from an early age and is potentially

weedy.

Botanical features (Fig 30)
Bark: on young branches smooth, rougher on bole, mid grey-brown with shallow rusty orange-brown vertical fissures, slash green then cream (Fig 20F)
Leaves: pinnae (14-)16-24(-28) pairs; pinnular rachis (3.5-)5-7(-8) cm long, densely covered with white hairs; leaflets (2.9-)4-5.5(-7) mm long, (0.6-) 0.8-1(-1.2) mm wide, (43-)48-58(-62) pairs per pinna, linear-oblong, acute at apex, strongly asymmetric at base, glabrous except hairy margins
Petiole gland: single flat sessile, discoid or shallow cup-shaped, elliptic, or sometimes rounded-triangular nectary, (2.2-)3-4.5(-5.4) mm long x 1.4-2.6 mm wide x 1 mm tall
Flower heads: 11-15 mm in diameter, the buds loosely packed, 45-90 flowers per head, in groups of 1-5(-7) in leaf axils, on actively growing indeterminate shoots, the leaves developing with flowers; stamen filaments, anthers and style white, pale pink, sometimes bright shocking pink, and occasionally bright scarlet, anthers sparsely hairy at tip
Pollen: tricolporate monads
Pods 1-6(-7) per flower head, (7-)10-13(-15.5) cm long, (11-)13-16(-17) mm wide, narrowly linear-oblong, flat, 6-20-seeded, pod walls thin, papery, dark brown or reddish-brown, sometimes lustrous, glabrous or covered in dense velvety hairs, opening along both sides.
Seeds 4.3-5.5 mm wide, 2.7-3.4 mm long, 60,000-80,000 seeds/kg - the smallest seeds of any species of *Leucaena*

Taxonomy and identification
In the past *L. diversifolia* has been taken to include two subspecies corresponding to known tetraploid and diploid cytotypes (Brewbaker, 1987a; Pan and Brewbaker, 1988; Zárate, 1994), commonly referred to as 'DIV4N' and 'DIV2N'. Pan (1985; 1988) postulated the tetraploid, referred to as subsp. *diversifolia*, to be an autotetraploid derived from the diploid taxon, referred to as subsp. *trichandra* (or sometimes subsp. *stenocarpa* by Zárate (1994) and Hughes (1993)). These two subspecies are more correctly treated as separate species (Hughes, in press). This is based on molecular evidence (Harris *et al.*, 1994a) which casts doubt on Pan's (1985) hypothesis. The narrower concept of *L. diversifolia* adopted by Hughes (in press) corresponds to the tetraploid species *i.e. L. diversifolia* subsp. *diversifolia sensu* Pan (1988) and Zárate (1994), with the diploid taxon restored to species rank, as *L. trichandra*.

Despite the clear molecular separation of *L. diversifolia* from *L. trichandra*, the morphological differences between them are limited largely to quantitative characters: *L. diversifolia* has larger leaves with more pairs of pinnae per leaf, longer pinnae and more pairs of leaflets per pinna, larger flowers and pollen, than in *L. trichandra*. In addition, the two species differ in a set of miscroscopic flower characters (Hughes, in press).

Molecular data show that *L. pulverulenta* is closely related to *L. diversifolia* and indicate that it was probably involved in the parentage of *L. diversifolia* (Harris *et al.*, 1994a). Morphological data also show a number of similarities between *L. diversifolia* and *L. pulverulenta* which support this: the leaves are very similar in terms of size, number of pinnae pairs, and number of leaflets, the pods are almost identical, the flower heads are similarly lax in bud with few flowers per flower head and both species have minute anther glands. The occurrence of *L. diversifolia* and *L. pulverulenta* growing together in north central Veracruz is consistent with a possible origin of tetraploid *L. diversifolia* that involved *L. pulverulenta*. *L. pulverulenta* is distinguished from *L. diversifolia* by its characteristic whitish-grey hairs on the young developing leaves and shoots, its irregular, lumpy verruca-like, as opposed to discoid or shallow cup-shaped petiole gland, its pale cream-white as opposed to pink flowers, and a number of petal and anther characters (Hughes, in press).

L. diversifolia has also been confused with *L. brachycarpa* described from Jamaica and Martinique, but Hughes (in press) and Hughes and Harris (in press) show them to be the same thing. Zárate (1994) applied the name *L. ×brachycarpa* to what he believed to be putative hybrids between *L. diversifolia* and *L. leucocephala*, but this was mistaken. Although spontaneous hybrids between *L. diversifolia* and *L. leucocephala* do occur in Mexico, Jamaica and elsewhere (Hughes and Harris, in press; Chapter 5), the original material of *L. brachycarpa* does not correspond to this hybrid, and the name *L. brachycarpa* is now known to be a synonym of *L. diversifolia*.

Chromosome number
Tetraploid, 2n=104 and self compatible (Pan and Brewbaker, 1988).

Tree size and form (back cover A)
Small to medium-sized tree 5-18(-20) m tall, 20-50 cm bole diameter, usually slender with a clear bole up to 10 m ht. and a light but spreading crown.
Distribution (Fig 31)
L. diversifolia is distributed along a narrow belt at mid elevations on the moist Gulf-facing slopes of the Sierra Madre Oriental of central and southern Mexico from Hidalgo south through Veracruz, northern Oaxaca and Tabasco to northern Chiapas and the northern fringes of the Guatemalan Dept. of Huehuetenango on the wet north-facing slopes of the Sierra de los Cuchumatanes. Taxonomic confusion and mis-identification have meant that most previous authors have considered *L. diversifolia* to be much more restricted than this, occurring only in central Veracruz, around Jalapa (Brewbaker, 1987a; Zárate, 1994). *L. diversifolia* has been introduced outside its native range in historical times (pre-1900) into Jamaica, Martinique (Urban, 1900;

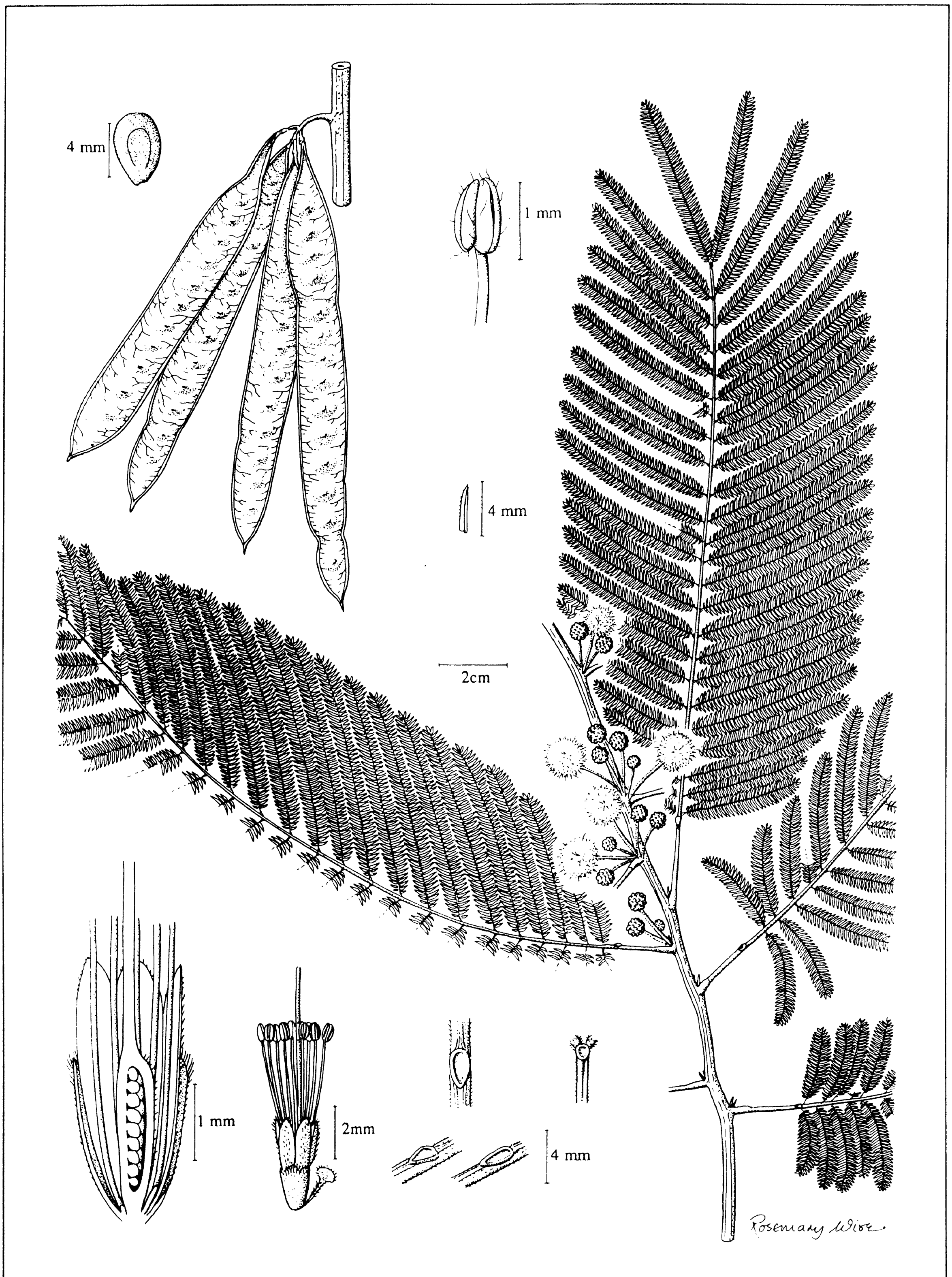

Figure 30 *Leucaena diversifolia*

Adams, 1972: 338) and Indonesia, usually for use as a shade tree for coffee. More recently, it has been more widely introduced as a reforestation species for wood and leaf fodder in tropical highland regions to complement the more tropical *L. leucocephala* (Brewbaker and Sorensson, 1994). After *L. leucocephala*, it is probably now the most widely cultivated species of *Leucaena* with a virtually pantropical, albeit somewhat scattered distribution.
Degree-squares: 12
Altitude range: 30-1500 (-1740) m

Ecogeography
The natural distribution of *L. diversifolia* corresponds to a narrow zone of moist or very moist submontane evergreen forest, subject to frequent mist and cloud cover. *L. diversifolia* also grows, sometimes abundantly, in secondary vegetation. As a mid-elevation species it shows tolerance of cool climates but not frost. In Hawaii on cool mid-elevation sites it out yields *L. leucocephala* (Brewbaker *et al.*, 1988), but it did not survive moderate frost in Florida (Williams, 1987). It thus grows well in cool stable frost-free climates that closely resemble conditions in the natural populations in Veracruz. Rainfall and cloud cover are high in the natural range with 1500-3500mm rainfall, a short dry season of 0-3(-4) months and frequent mist.

Phenology
Flowering (February-) May-June (-December), fruiting (June-) August-February (-April)

Conservation status
L. diversifolia is widely distributed, sometimes locally abundant, sometimes cultivated as coffee shade and apparently thrives on disturbance and is thus of little or no conservation concern. A growing abundance of spontaneous hybrids between *L. diversifolia* and *L. leucocephala* in parts of Mexico and Guatemala (Hughes and Harris, in press) could pose a threat of genetic contamination of native *L. diversifolia* populations in the future.
Star rating: Green star
IUCN threat category: LR:lc

Common names
Chalíp, guash (Huehuetenango, Guatemala), *shashíb, shashíbte* (Tzeltal, Chiapas, Mexico), *guache, guashí* (Hidalgo, Mexico), *guaje* (Oaxaca, Veracruz), *guaje blanco, guajillo, guaje del rio* (Veracruz, Mexico), *wild tamarind* (Jamaica: not distinguished from *L. leucocephala*).

Indigenous use and domestication
L. diversifolia is cultivated, usually as a shade tree over coffee plantations in Veracruz and Guatemala. The unripe pods and seeds are occasionally harvested and consumed, but not on the same scale as some other species of *Leucaena*.

Exotic use and potential
L. diversifolia has been used in ways similar to *L. leucocephala* for both fodder and wood. Its light crown makes it an ideal species for shade over perennial crops such as coffee and this has been one of the main uses in Jamaica, Papua New Guinea and, where cultivated within the native range, in Mexico and Guatemala. *L. diversifolia* has been introduced to a number of countries and has shown considerable potential; *e.g.* in Sri Lanka (Gunasena *et al.*, 1990), particularly under mid elevation cool, but frost-free, tropical highland conditions where it out yields *L. leucocephala* (Brewbaker *et al.*, 1988; Khajuria and Singh, 1991; Maasdorp, 1992). The most widely used seed source has been the University of Hawaii accession K156 from Veracruz, Mexico. *L. diversifolia* occupies a much wider distribution than was previously realised and new provenance seed collections across the range are now available from OFI for testing. *L. diversifolia* is also a promising parent in artificial hybridization and its hybrid with *L. leucocephala*, designated KX3 by the University of Hawaii, has proved to fast growing with impressive tree form.
Psyllid resistance: moderately resistant (damage score 2-5)
Wood quality: Mean wood density is moderate (0.68) with limited heartwood formation (Gourlay *et al.*, in press).
Fodder quality: several studies indicate that *L. diversifolia* has lower palatability, digestibility and higher condensed tannin levels than *L. leucocephala* (Bray, 1987; Austin *et al.*, 1991; Stewart and Dunsdon, in press), indicating lower fodder quality. However, digestibility and tannin levels are intermediate compared to all other *Leucaena* species.
Weediness risk: *L. diversifolia* is self fertile, flowers and fruits over an extended season, and sets prodigious quantities of seed from an early age. In other words it has all the invasive traits of *L. leucocephala* subsp. *leucocephala* and matches its weed risk assessment score (Section 3.9). This suggests that, given sufficient time following introduction, *L. diversifolia* has the potential to be as weedy as *L. leucocephala* subsp. *leucocephala*. It also forms spontaneous hybrids with *L. leucocephala* extremely easily wherever the two species are brought together in cultivation. These hybrids are also self fertile and extremely seedy, again suggesting weediness risks (Sections 3.9 and 5.6).

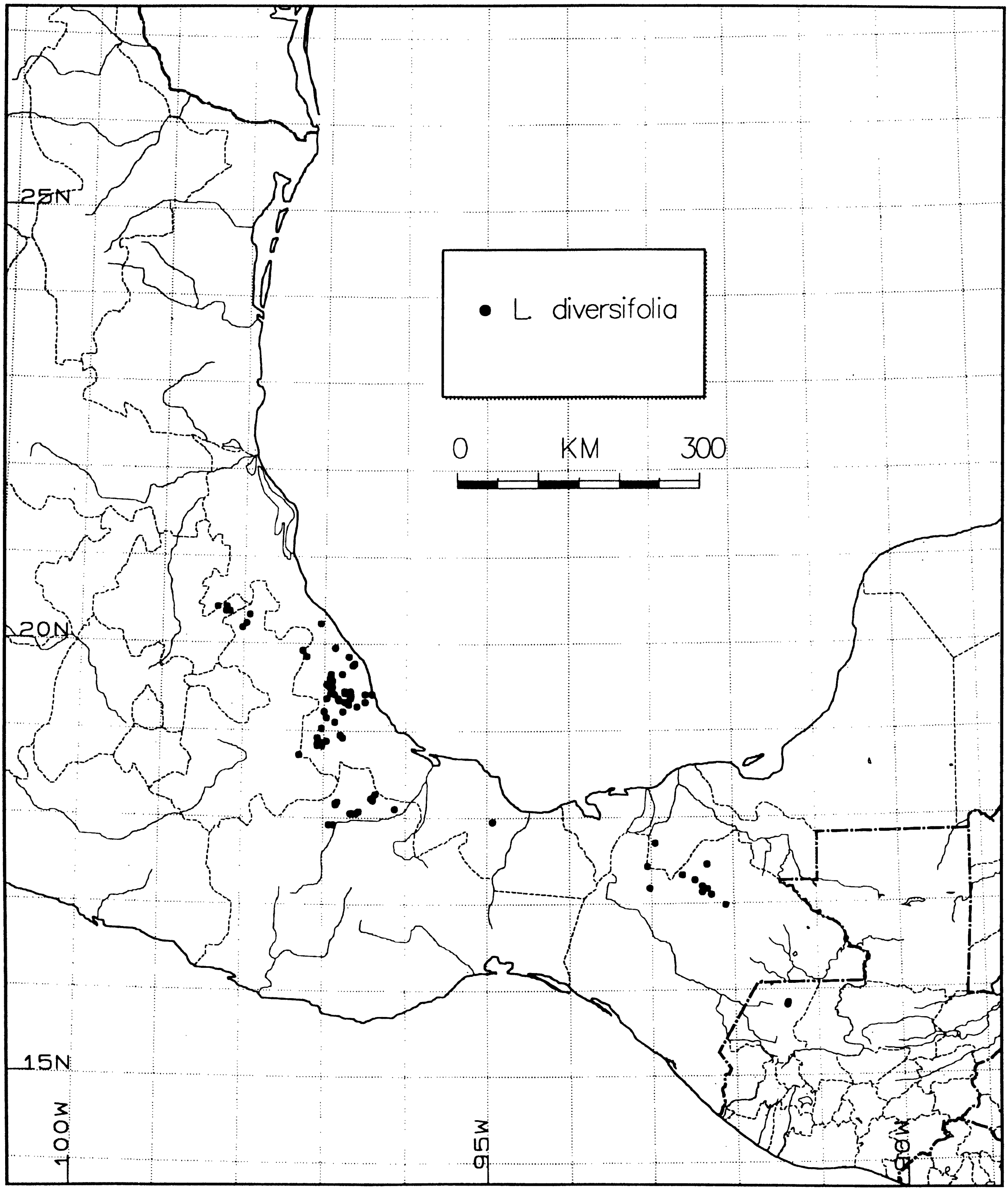

Figure 31 Map of south eastern Mexico and Guatemala showing the range of *L. diversifolia*

11.5 Leucaena esculenta

Leucaena esculenta (Sessé & Moc. ex DC.) Benth. Transactions of the Linnean Society 30: 442. 1875.

Synonyms
Acacia esculenta DC.
Mimosa esculenta Sessé & Moc.
Leucaena confusa Britton & Rose
Leucaena doylei Britton & Rose

Main attributes
L. esculenta is one of the best known species of *Leucaena* in its native range in Mexico. It is widely cultivated throughout the highlands of central Mexico for its edible pods which are harvested, marketed and eaten. The common name *guaje* is derived from the Nahuatl *huaxin*, from which the State and city of Oaxaca (meaning place where *huaxin* grows) are named. This species thus has a long and diverse history of human use, cultivation and incipient indigenous domestication stretching back over several millennia. In addition, *L. esculenta* has other attributes which suggest great potential for tree planting. It forms a large tree, is tolerant of annual lopping and adaptable to a range of management regimes in agroforestry, shows moderate cold tolerance and high psyllid resistance, and in Mexico is a prime agroforestry tree.

Botanical features (Fig 32)
Bark: thick, corky, pale silvery grey, with a metallic sheen like galvanized zinc, smooth becoming horizontally gnarled, slash bright green then deep orange-red (Fig 20B), shoots angular with 5-6 longitudinal corky ridges
Leaves: pinnae (18-)30-40(-60) pairs; pinnular rachis 9.5-12 cm long; leaflets 3.5-6.6 mm long, 0.9-1 mm wide, (40-)60-75(-85) pairs per pinna, asymmetric, linear, acute or subacute, glabrous
Petiole gland: large maroon-red, sessile, elliptic, shallowly concave, bath-shaped (Fig 19E), 5.5-8.0 x 3.1-3.9 mm
Flower heads: 25-28 mm in diameter, 150-170 flowers per head, in groups of 2-7 at nodes on often once-branched terminal determinate shoots with complete or partial suppression of leaf development, flowers white
Pollen: tricolporate monads
Pods: (10-)15-25(-30) cm long, 23-26 mm wide, 1-2 per flower head, oblong to linear-oblong, flat, (few-) 15-20 seeded, glossy reddish maroon unripe turning mid orange-brown when ripe, glabrous, opening along both sides
Seeds: 9.1-10.9 mm long, 7-9 mm wide, circular to ovoid, aligned transversely in pods; 8,700 seeds/kg

Taxonomy, closely related species and identification
L. esculenta is readily distinguished by its gnarled thick corky pale metallic-grey bark, strongly angled shoots, long elliptic sessile petiolar nectary, very large leaves with many pinnae pairs and numerous pairs of very small leaflets per pinna, large flower heads and large pods and seeds. Its close relatives are *L. pallida, L. pueblana, L. matudae* and *L. involucrata*, which together form a group of species (Fig 2, Section 2.5) all of which share the same silvery corky bark type (Figs 20A-C). Although Zárate (1984a; 1994) treated *L. esculenta* as a variable species and included *L. matudae* and *L. pallida* (treated by him as *paniculata*) as subspecies within it, they are in fact readily separated by several discrete characters and merit recognition as distinct species (Hughes, 1997a; in press). *L. matudae* is distinguished from *L. esculenta* by its unique scolloped bark surface pattern (Fig 20C), its small, erect peg-shaped petiole gland, weakly constricted pods, oblique seed alignment in pods and fewer pinnae pairs per leaf and leaflets per pinna. *L. pallida* is distinguished from *L. esculenta* by its leaves with fewer pairs of pinnae and fewer leaflets per pinna, pink flowers and thicker pods which are partitioned between the seeds, with the seed chambers clearly visible on ripe pods.

L. esculenta is known to hybridize readily with *L. leucocephala* subsp. *glabrata* (Hughes and Harris, 1994, Hughes, in press) where the two are brought together in cultivation in Mexico and Sénégal (Section 5.5).

Chromosome number
Diploid, 2n=52, self-incompatible (Hutton, 1981; Pan and Brewbaker, 1988)

Tree size and form (back cover D)
Small to medium-sized tree, (3-)10-15(-20) m tall, 20-70 cm bole diameter. Typically multiple-stemmed and branchy when young, older trees with a short clear bole to 5 m, heavy spreading branches and an open spreading rounded crown.

Distribution (Fig 33)
Unripe pods and seeds of *L. esculenta* are widely used for food and the species is extensively cultivated within Mexico and is now very abundant in gardens and backyards in and around towns and villages in many parts of central Mexico. This means that its present day distribution is more extensive than its true natural distribution which is difficult to define precisely. Zárate (1984a; 1994), Casas and Caballero (1996), Hughes and Harris (1994) and Hughes (in press) all postulated that it may be native only in central Mexico, in the upper Balsas depression in Guerrero, Morelos and possibly parts of Puebla and Michoacán where it is abundant and apparently natural in mid-elevation tropical dry deciduous forest.It is also abundant in other areas such

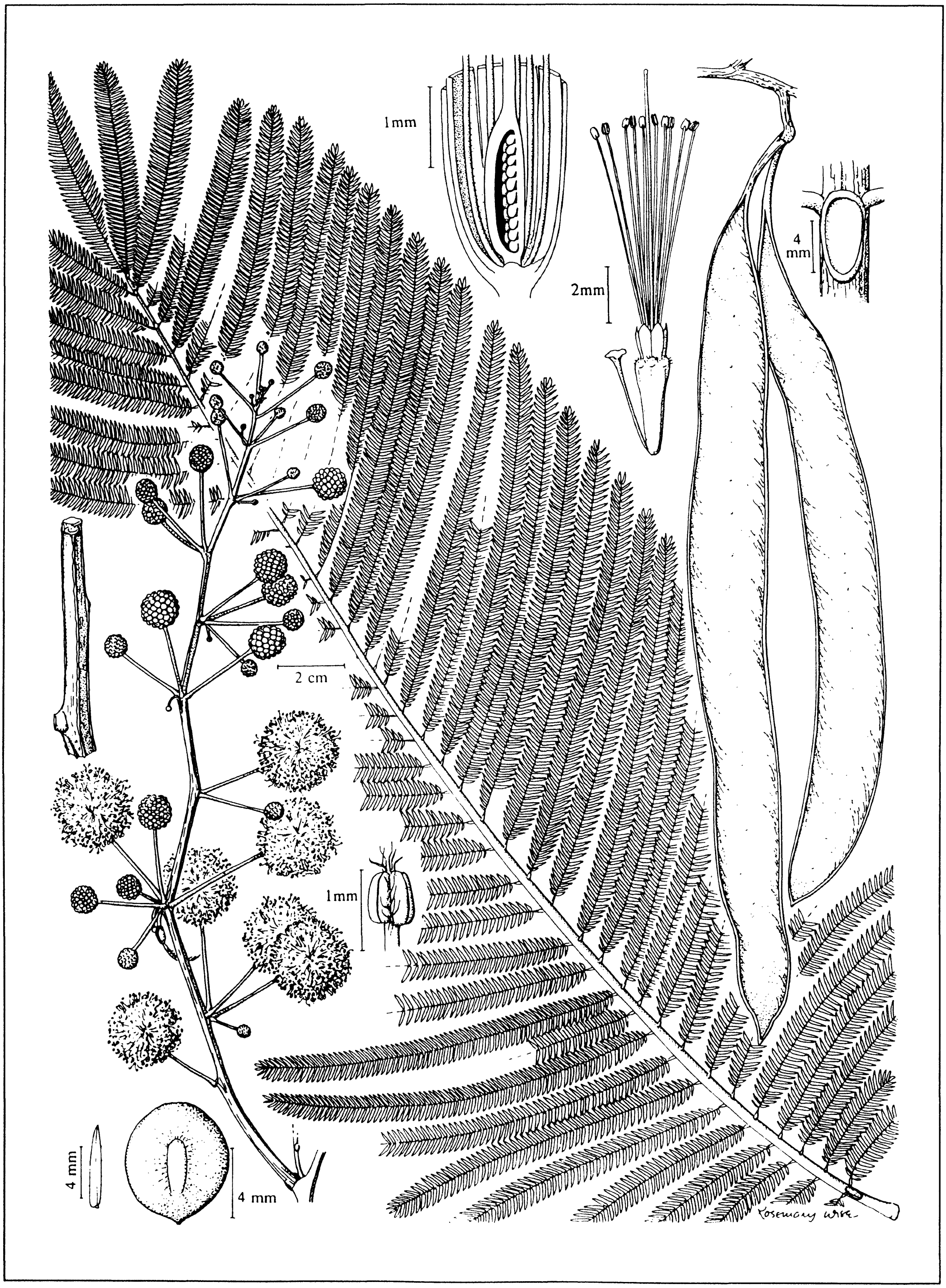

Figure 32 *Leucaena esculenta*

as the Tehuacan and Oaxaca Valleys, around Tuxtla Gutierrez, Chiapas and in parts of Jalisco, but in these areas is likely to be introduced, possibly in pre-Columbian times. *L. esculenta* is reported from Sénégal (Berhaut, 1956; Lock, 1989) and has been introduced more widely in trials in the last five years.
Degree-squares: 22
Altitude range: (400-) 600-1800 (-2080) m

Ecogeography
L. esculenta forms a canopy tree in mid-elevation seasonally dry deciduous tropical forest and, at higher elevations, in mixed oak-juniper forest. In parts of the native range *L. esculenta* experiences infrequent light frosts but it does not thrive above 2000m and its frost tolerance is thought to be limited. Rainfall in the native range is highly seasonal with between 800 and 1300mm rainfall and a dry season of around 7 months. Like most species of *Leucaena*, it occurs mainly on calcareous soils.

Phenology
Flowering (August-) October-November (-January); fruiting (January-) February-March (-April); trees are highly deciduous, losing most or all of the leaves during the dry season from January - April

Conservation status
L. esculenta is widely distributed and extremely abundant both in natural populations and in indigenous cultivation. It is often the commonest tree in towns and villages in parts of Oaxaca, Puebla and Guerrero in Mexico. The species is thus well conserved *circa situm* (Sections 4.3 and 8.5), although some narrowing of the genetic base in cultivated material is possible in some areas (Casas and Caballero, 1996).
Star rating: Green star
IUCN threat category: LR:lc

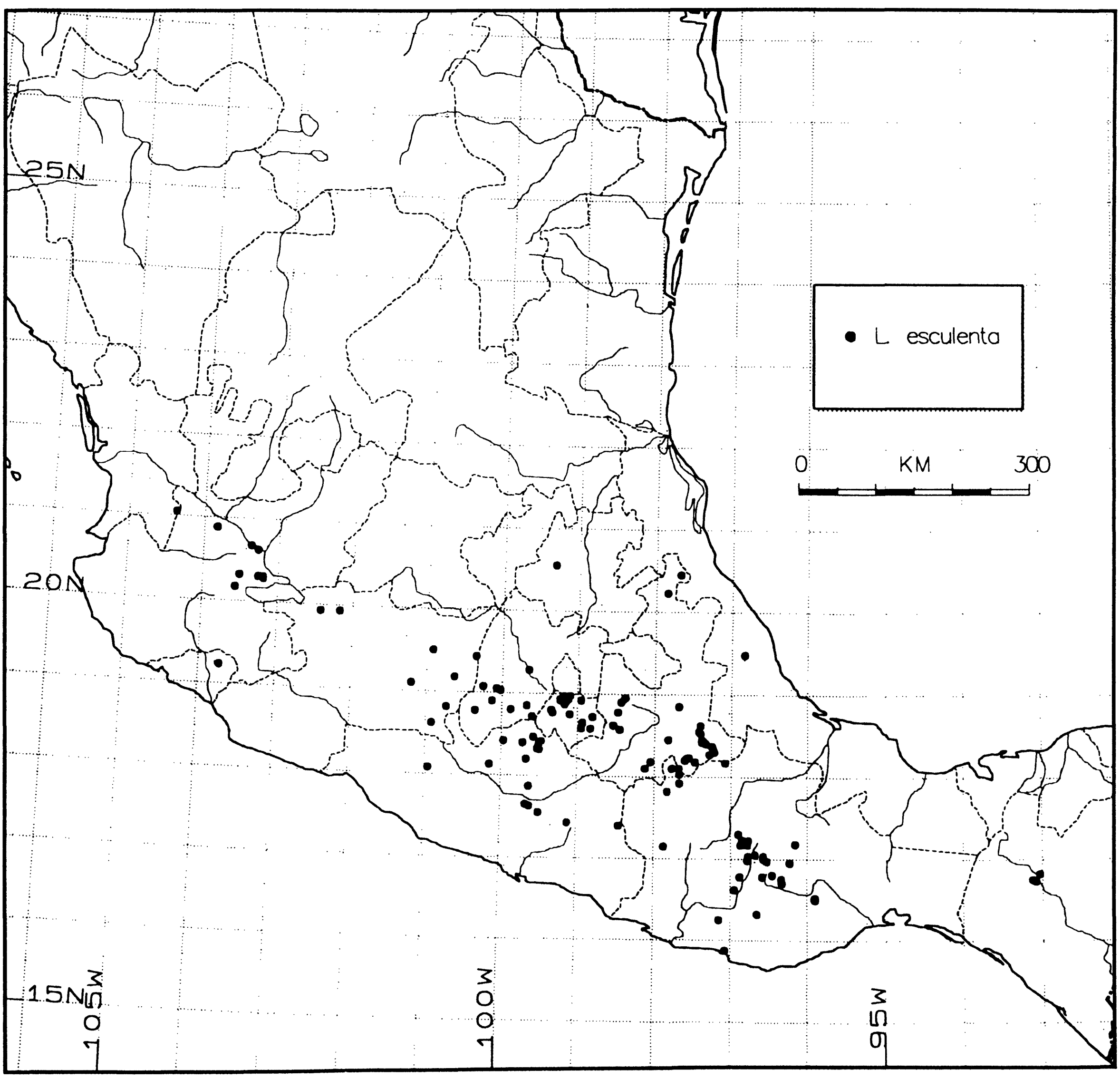

Figure 33 Map of south central Mexico showing the present day distribution of *L. esculenta*

Common names
The long history of use and widespread cultivation of *L. esculenta* in Mexico has given rise to numerous common names; these are fully documented by Zárate (1994) and Casas and Caballero (1996). The most widely used names are *guaje (huaje, uaxin, oaxin), guaje rojo (oaxin chichiltic), guaje colorado, guashe, guashi, guaje grande (hueyoaxin)* and *guaje mihuateco*, all names that derive from the Nahuatl *huaxin* (Standley, 1922; Casas and Caballero, 1996). The names *colorado* and *rojo* refer to the reddish-maroon unripe pods. Other names include: *diiwa, tondua cuuha* (Mixteco), *libad-lo* (Mixteco de la costa), *lya kures* (*guaje de sequia*, Zapoteco de Mitla), *yaga-la* (Zapoteco) *al-pa-la* and *pa-la* (probably Chontal names for *guaje*) (Zárate, 1994), *uachi* (*guaje*, Chiapas).

Indigenous use and domestication
L. esculenta is, along with *L. leucocephala*, by far the best known and most common species of *Leucaena* in the highlands of south central Mexico where it is very extensively cultivated for its edible unripe pods and seeds (Casas and Caballero, 1996; Zárate, 1984a; 1994). Indeed, in some areas, it is so popular and extensively cultivated that it is now one of the commonest tree species dominating many settlements in Oaxaca, Puebla and parts of Guerrero. Its use, cultivation and incipient indigenous domestication are discussed in detail in Sections 4.3 and 4.4 and by Casas and Caballero (1996) and Zárate (1984a; 1994). A complete spectrum of use from casual harvesting from natural populations, through protection and cultivation in informal orchards is evident for *L. esculenta*. This is accompanied by both local and large scale commercial harvesting and marketing of pods in all local and regional towns in south central Mexico and in Mexico City. Large quantities are collected, stored, transported and sold. The intensive food use of this species has given rise to a set of sophisticated indigenous classification and naming systems, and diverse cooking methods. The continuum of increasing human intervention, possibly accompanied by selection, has been described as incipient domestication (Chapter 4).

Exotic use and potential
The sophisticated traditional agroforestry systems which incorporate *L. esculenta* in Mexico provide evidence of the important agroforestry potential of this species. Trees are heavily lopped each year during the dry season when pods are produced and resprout vigorously with the onset of the rains and trees are maintained over a variety of crops. Seed production, although abundant in the native range, can be very sparse under some climatic conditions, such as in Hawaii and this may have limited its wider spread. However its rapid growth, moderate drought and cold tolerance, and high psyllid resistance indicate that *L. esculenta* has considerable untapped potential for wider planting. *L. esculenta* also has potential to be used in artificial hybridization. The sterile triploid hybrid between *L. esculenta* and *L. leucocephala* shows a set of desirable traits including seedlessness, high psyllid resistance, moderate drought tolerance and high yield making it one of the most attractive sterile hybrids (Section 5.7).
Psyllid resistance: highly resistant (damage score 1-2)
Wood quality: the wood of *L. esculenta* is average in density compared to other *Leucaena* species (mean 0.7), with slow early formation of heartwood (Gourlay *et al.*, in press) and provides high quality firewood. The wood is rarely used in Mexico simply because trees are protected for pod production in most areas.
Fodder quality: in Mexico, trees are also lopped in a few areas for livestock fodder and animals eat both leaves and unripe pods. However, low edible fraction, *in vitro* dry matter digestibility and high condensed tannin levels (Stewart and Dunsdon, in press) suggest that fodder quality of *L. esculenta* is likely to be significantly poorer than *L. leucocephala*.
Weediness risk: *L. esculenta* produces large quantities of seed on some sites, but is not particularly precocious, is self-incompatible and shows no significant weedy tendencies in its native range. Weediness risk although a possibility is thus lower than for *L. leucocephala*.
Propagation: the seeds are large, relatively soft and can germinate without pretreatment although germination is still slightly enhanced by manual scarification (Section 7.4). The large seeds mean that initial seedling growth is rapid.

11.6 Leucaena greggii

Leucaena greggii S. Watson, Proceedings of the American Academy of Arts and Sciences, Boston 23: 272. 1888.

Synonyms
Ryncholeucaena greggii (S. Watson) Britton & Rose

Main attributes
L. greggii, and the closely related *L. retusa* share a number of unique features which suggest that they are outliers in the genus. Their distinctiveness is further emphasized by their outlying northern distribution and their ability to withstand low winter temperatures. They are the two most northerly and cold tolerant species in the genus. The potential of *L. greggii* for planting is strictly limited by its small size, usually a large shrub or

small tree, and slow growth rates.

Botanical features (Fig 34)
Bark: on young branches smooth, mid-brown with pale orange-brown lenticels, darker blackish-brown and rougher with shallow orange-brown vertical fissures on bole
Leaves: pinnae (7-)8-10(-11) pairs; pinnular rachis 8-11 (-13) cm long, leaflets (6.5-)8-11.5(-12.1) mm long, (2-) 2.5-3.0(-3.6) mm wide, (25-)27-34 pairs per pinna, slightly asymmetric, linear-oblong, waxy blue-green
Petiole gland: slender cylindrical, columnar, peg-shaped, 0.5 mm diameter x 2-2.5 (-3.2) mm tall (Fig 19B), usually with a series of glands along the leaf rachis at the base of each pair of pinnae
Flower heads: 24-26 mm in diameter, (120-)150-200 flowers per head, in groups of 1-3 in leaf axils on actively growing shoots, flower head stalks 61-90 mm long, flower bracts peltate, acutely pointed and slightly exserted in bud; flowers bright yellow
Pollen: tricolporate monads
Pods: (12-)15-18(-21) cm long, 9-15 mm wide, 1-3(-5) per flower head, narrow linear, sometimes slightly curved, with a thick woody point at tip, 11-15 seeded, green and fleshy unripe turning mid- to orange-brown, glabrous, leathery or slightly woody when ripe, opening slowly along both margins.
Seeds 4.9-6.9 mm wide, 7.5-9.0 mm long, rhomboidal, longitudinally aligned in pods, 15,000-17,000 per kg

Taxonomy, closely related species and identification
L. greggii is most closely related to *L. retusa* and shares a set of diagnostic characters with that species, including yellow flowers held on long flower head stalks, pointed floral bracts that are slightly or conspicuously exserted in bud, thick, narrow, linear, woody pods with thickened margins, oblique or longitudinal seed alignment and erect columnar, peg-shaped leaf glands (Fig 19B) that are distributed along the length of the leaf rachis. These characters provided the basis for their previous placement in separate genera, *Ryncholeucaena* and *Caudoleucaena* each with one species, outside *Leucaena*. Although they do clearly belong within *Leucaena* they are unusual species (Hughes, in press). Molecular analysis also showed these two species to be very closely related (Harris *et al.*, 1994a). *L. greggii* and *L. retusa* also occupy similar geographic distributions and habitats; both are restricted to the mountains of NE Mexico and Texas, with cold winter climates, in dry mattoral or mixed dry oak-pine forest, usually on calcareous soils.

Although *L. greggii* and *L. retusa* are closely related, they are immediately distinguishable using leaves alone. *L. greggii* has small linear-oblong leaflets <12 mm long and <3.6 mm wide, with >7 pairs of pinnae per leaf and >25 leaflets per pinna while *L. retusa* has large ovate or elliptic leaflets >15 mm long and >6 mm wide, with <5 pairs of pinnae and <8 pairs of leaflets per pinna.

L. greggii has, in the past, sometimes been confused with *L. leucocephala*, presumably due to the broad similarity in quantitative leaf characters (Brewbaker, 1987a), although it is immediately distinguished by its unusual pods and flowers.

Chromosome number
Diploid, 2n=56, self-incompatible (Sorensson, 1989a)

Tree size and form (back cover C)
Shrub or small tree, 2-5 (-8) m tall, 10-15 cm bole diameter. Typically with brittle branches and a small round crown.

Distribution (Fig 35)
L. greggii is restricted to the mountains of NE Mexico in the northern part of the State of Nuevo León and the south of Coahuila. The distribution has been mapped by Bendeck and Foroughbakch (1988), who found it to be widespread but scattered along the Sierra Madre Oriental and the Sierra de Monterrey. Although it was reported from S. Texas, U.S.A.
by Sargent (1921), Britton and Rose (1928) and Cory and Parks (1937), this was questioned by Isely (1970) and Turner (1959) and is now clearly a mistake.
Degree-squares: 5
Altitude range: (700-) 1500-2000 (-2200) m

Ecogeography
L. greggii occurs mainly on steep mountain slopes, in canyons, ravines and on cliffs, mainly on N and NE facing slopes, often on shallow, skeletal, rocky, freely-drained soils derived from calcareous parent material such as limestone or gypsum. It is usually found in submontane mattoral or thorn scrub as a small canopy tree with diverse woody legumes, but also grows as an understorey tree or shrub in dry oak-pine forest. The foliage of *L. greggii* is apparently highly palatable and, in some areas, grazing pressure has reduced populations to scattered remnants in inaccessible gullies. In the native range *L. greggii* occurs in areas of low temperature and prolonged drought. After *L. retusa*, this is the most frost-tolerant species of *Leucaena* and can withstand regular frosts for several months of the year and temperature minima as low as -10°C. Rainfall ranges from 350 to 500mm with a long dry season from October to May.

Phenology
Flowering April - June (-August); fruiting (September-) October - November, the pods sometimes persistent on trees for several months after ripening; detailed phenological study reported in Bendeck and Foroughbakch (1988).

Conservation status
L. greggii is geographically restricted, susceptible to grazing pressure and rarely abundant. Heavy grazing pressure from goats in many of the natural populations

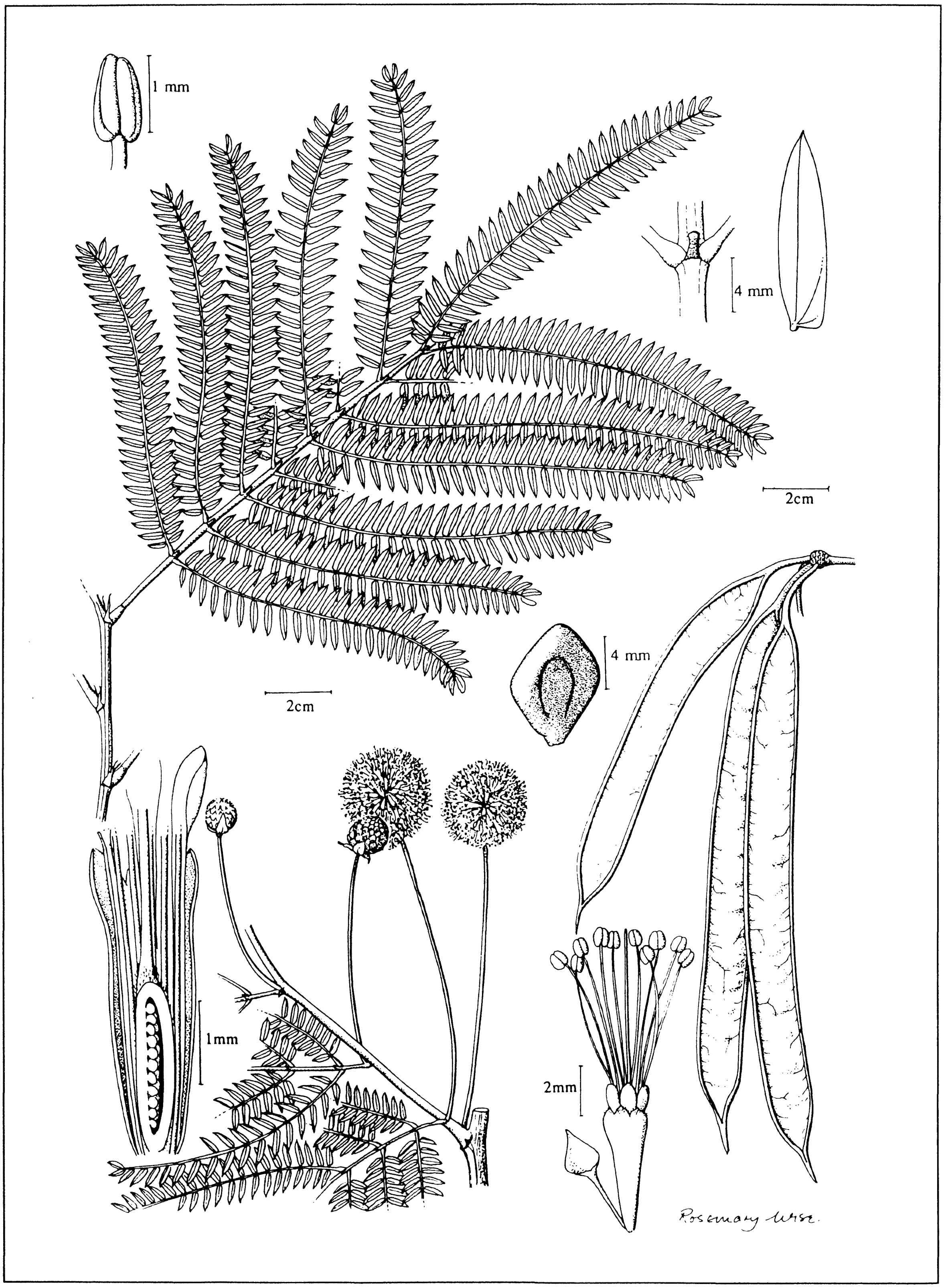

Figure 34 *Leucaena greggii*

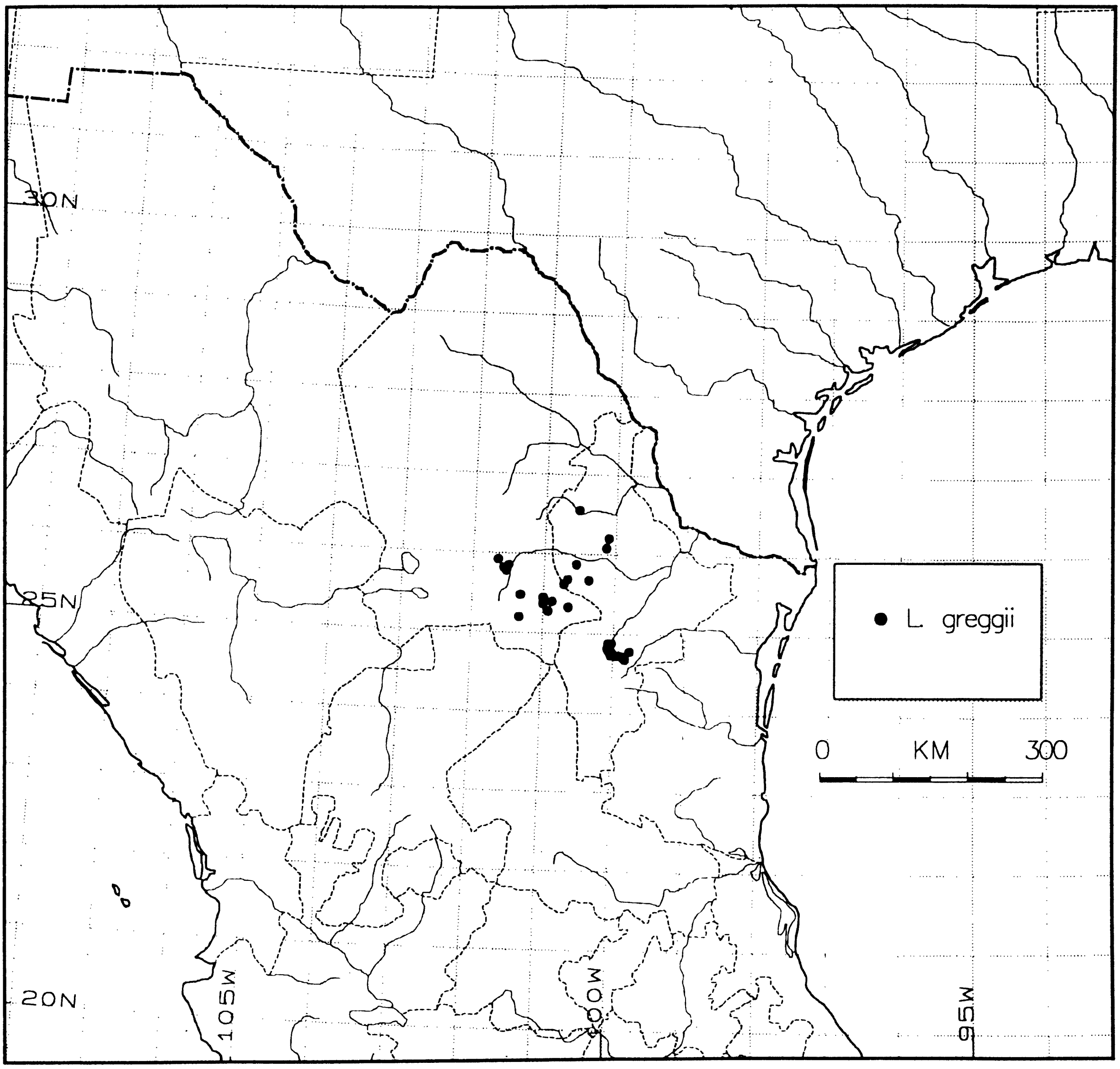

Figure 35 Map of northern Mexico and Texas, U.S.A. showing the distribution of *L. greggii*

means that natural regeneration is severely limited and further degradation is likely without protection. For these reasons it is categorized as vulnerable and of some conservation concern.
Star rating: Blue star
IUCN threat category: VU-A1 B1&2

Common names
guajillo, Gregg lead tree.

Indigenous use and domestication
L. greggii is apparently little used in its native range except locally as a source of firewood

Exotic use and potential
Although *L. greggii* is well liked locally for its dense wood which makes excellent firewood, it has little direct potential for planting being very slow growing in all plantings to date.
Psyllid resistance: highly resistant (damage score 1-2)
Wood quality: although the wood is of average density (mean wood density 0.71 reported by Gourlay *et al.*, in press), it makes high quality firewood, but is slow growing and produces small twisted branchy trees with little or no potential for wood production.
Fodder quality: leaves are known within the native range to be highly palatable and a preferred browse for goats in the dry thorn scrub where it is found in north east Mexico. However, when analyzed for fodder quality the leaves were found to have low digestibility and moderately high condensed tannin contents (Stewart and Dunsdon, in press). Fodder production would anyway be severely limited by slow growth rates.
Weediness risk: *L. greggii* is one of only five species of *Leucaena* with a low weed risk score (Section 3.9), being less precocious and seedy than most other species.

11.7 Leucaena involucrata

Leucaena involucrata S. Zárate, Anales del Instituto de Biología (Mexico) Serie Botánica 65: 138. 1994.

Main attributes

This poorly known species was discovered in remote mountains in the northern part of Sonora, Mexico only in 1991, and was formally named and described as recently as 1994. It appears to have affinities to *L. pallida* and members of the *L. esculenta* alliance but is geographically isolated from other species of that group. It forms a small tree, in sparsely populated mountains and appears to be little used. Its potential and characteristics are as yet largely unknown, but it is likely to show moderate frost tolerance. It is restricted to two known localities and is thus extremely rare and considered endangered.

Botanical features (Fig 36)

Bark: smooth, mid metallic-grey, blotched lighter grey with horizontally-aligned pale brown lenticels, inner bark greenish, then dark red

Leaves: pinnae (13-)16-22 pairs; pinnular rachis 5.5-8.3 cm long; leaflets (3.9-)5-6.6 mm long, 0.9-1.7 mm wide, (32-)40-51 pairs per pinna, asymmetric at base, linear or linear-oblong, acute at tip, hairy only on margins

Petiole gland: cylindrical, short peg-shaped, 1-1.5 x 1.2-1.5 mm and raised 1 mm above petiole with 1-4 (5) additional, small cylindrical glands at base of terminal pinnae pairs on leaf rachis

Flower heads: 16-20 mm in diameter, 140-180 flowers per head, in groups of 4-6 in leaf axils on actively growing shoots, stamen filaments pale creamy white, the anthers pale yellow turning dull orange

Pollen: tricolporate monads

Pods: 11-18 cm long, 9-13 mm wide, 1-4(-6) per flower head, linear, pointed at base and apex, often with a short beak at tip, flattened, 12-19-seeded, pod walls leathery, glossy reddish-brown unripe turning lustrous, rich orange-brown, glabrous when ripe, the margins slightly raised, weakly partitioned between seeds, the seed chambers visible on outside of pods, opening slowly along both sides

Seeds: 4.9-5.9 mm wide, 7-8 mm long, rhombic, strongly oblique seed alignment in pods

Closely related species and identification

My attention was first drawn to *L. involucrata* by the field notes on a botanical specimen collected in Sonora which describe the flowers as yellow, a flower colour known elsewhere in *Leucaena* only in *L. greggii* and *L. retusa,* two other northerly species. Given that the specimen was clearly not *L. greggii* nor *L. retusa* and was collected from northern Sonora, I suspected that this material belonged to an as yet un-named taxon with affinities to these two species. Field exploration in 1991 and 1992, allowed complete material to be collected for the first time and revealed that the flowers are cream-white not yellow (the anthers are dull yellow-orange). Although several other characters, including the narrow leathery pods, strongly oblique seed alignment and cylindrical petiole glands also suggest affinities with *L. greggii* and *L. retusa*, the Sonoran trees also show some affinities with the *L. esculenta* alliance and *L. pallida* and *L. matudae* in particular in terms of bark, leaves and flowering shoots. The true affinities of *L. involucrata*, as yet, remain uncertain.

Zárate (1994) named *L. involucrata* in reference to what he described as an unusually large ring of basally-united bracts or *involucel*, at the base of the flower head which envelopes the whole flower head bud in early development. Hughes (in press) can see no basis for this, as the ring of bracts is not unusually large. Despite this, *L. involucrata* does represent a species, distinct from *L. pallida,* recognized by its unusual narrow pods, white or cream flowers and small peg-shaped petiole glands. In an analysis of morphological data (Hughes, in press) (Section 2.5), *L. involucrata* was placed as the sister species to *L. matudae* within the '*L. esculenta* alliance' comprising *L. esculenta, L. pueblana, L. pallida* and *L. matudae*.

L. involucrata remains one of the least understood species in the genus. It is known from only five botanical collections, four of which are from the same locality in northern Sonora. The collection from the Sierra Surotato, Sinaloa, was attributed to *L. involucrata* by Hughes (in press) based solely on leaf characters, given the lack of flowers and immaturity of the fruits on that specimen. This material differs from the Sonoran collections in being more hairy. Complete exploration of the mountains between the northern outliers of *L. pallida* in the States of Jalisco and Zacatecas and the occurrence of *L. involucrata* in Sonora will be needed to delimit properly these species based on more complete material.

Chromosome number

Unknown

Tree size and form

Small, often multiple-stemmed tree 2-5(-8) m tall, 10-15 (-25) cm bole diameter with an open irregular spreading crown, the branches often slightly pendulous.

Distribution (Fig 37)

L. involucrata is restricted to the mountains of the north west Mexican states of Sonora and northern Sinaloa. Even within these states it occurs rarely and very

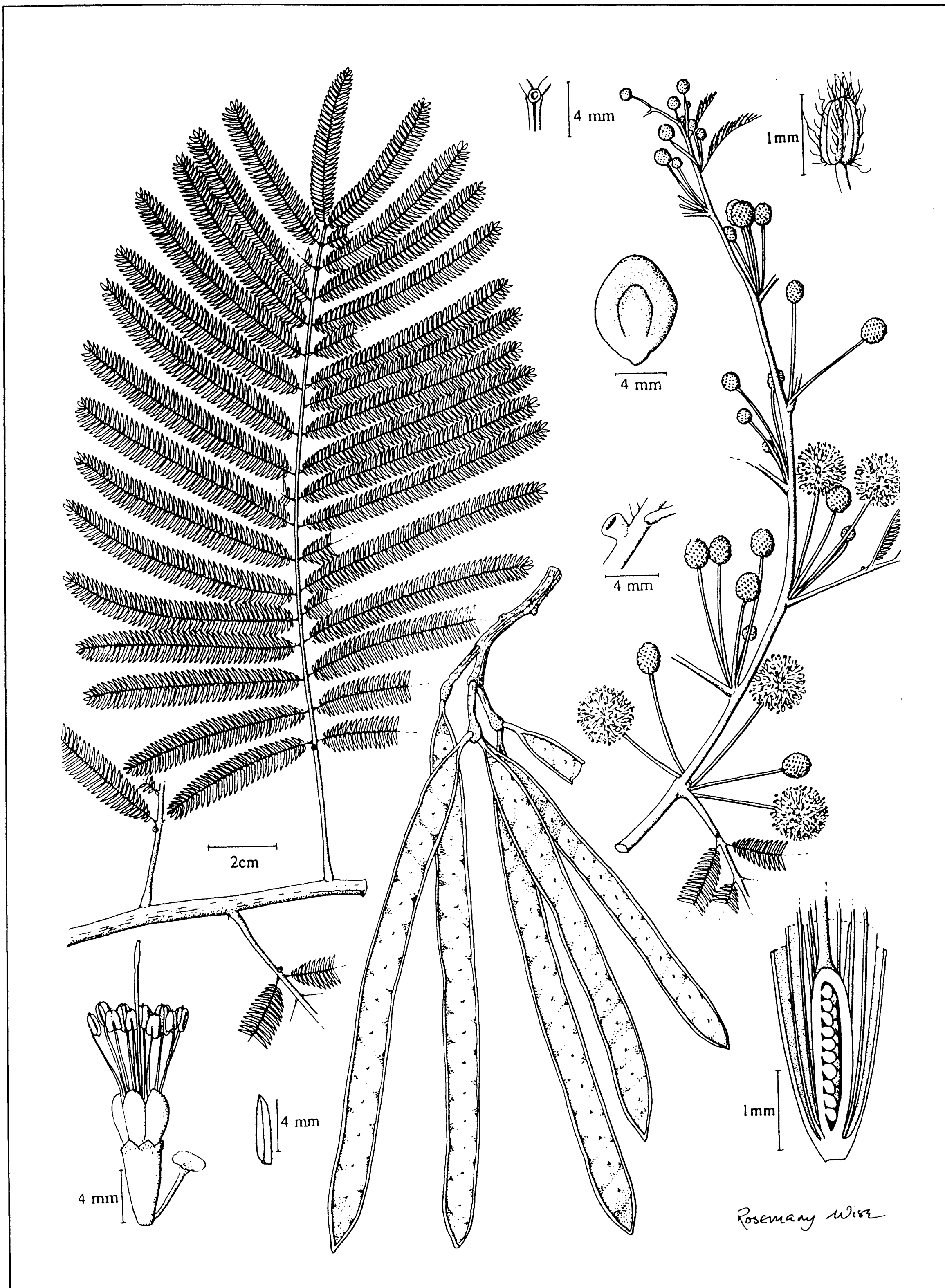

Figure 36 *Leucaena involucrata*

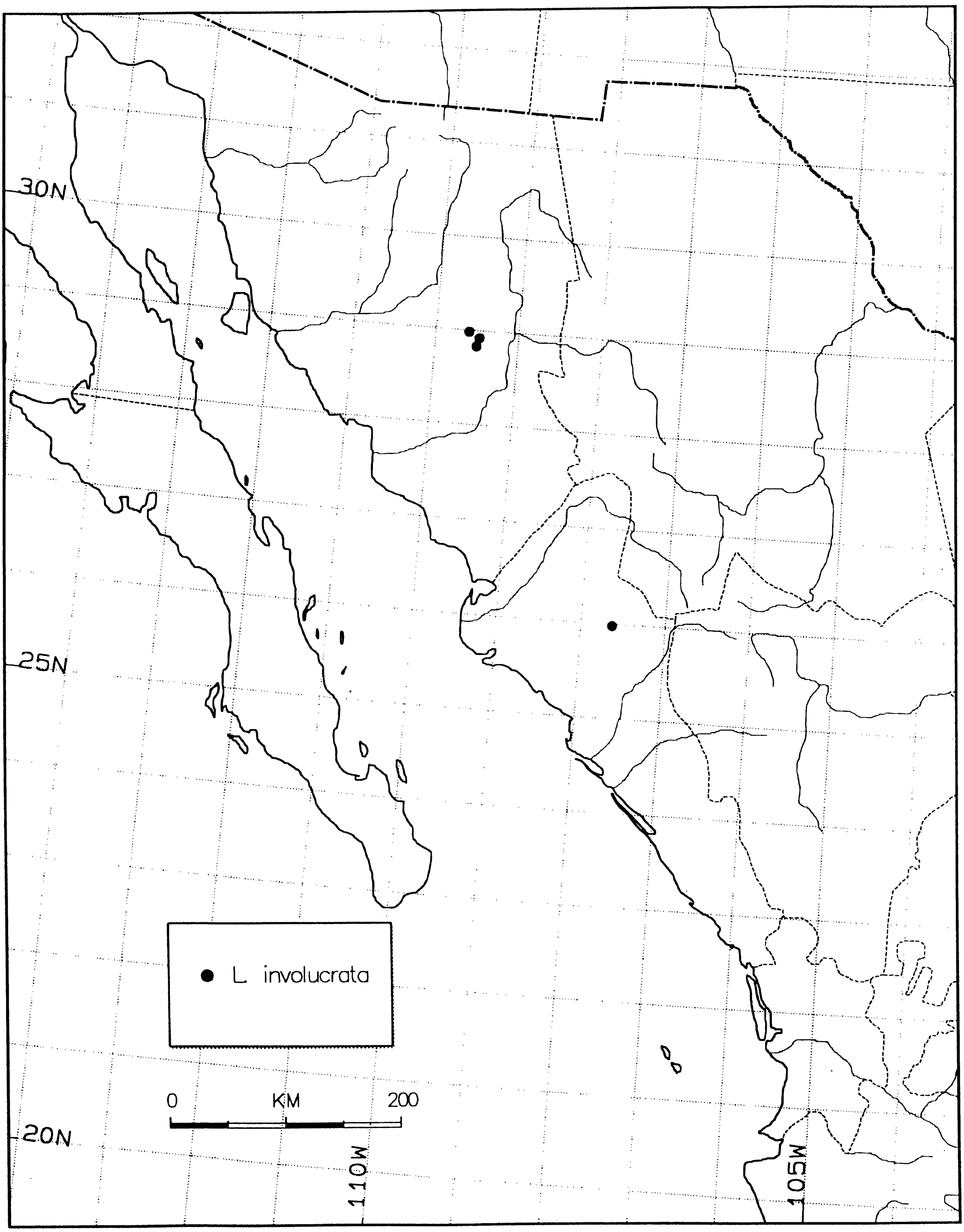

Figure 37 Map of north west Mexico showing the distribution of *L. involucrata*

sporadically, although, given that these areas are probably very under-explored and collected botanically, it may be more widespread and common than current botanical collections suggest. At present, *L. involucrata* is known from only two areas, in the hills east of Hermosillo south east of the dam at El Novillo and in the northern fringes of the Sierra de Surotato. Field exploration in 1991 in the Sierra Surotato, where it was collected in 1941, failed to relocate *L. involucrata*. Further field exploration will be needed to establish the

true extent of the natural distribution.
Degree-squares: 2
Altitude range: 400-1500 m.

Ecogeography
In the area of El Novillo in Sonora, it occurs in dry thorn scrub forest, rich in shrubby woody legumes, where it appears to be restricted to rocky calcareous outcrops. In this area it ranges from 500 to 700m elevation and occurring to almost 29°N latitude, grows in areas that experience moderate winter frost. The rainfall is low with around 500-700mm annual rainfall and a 6-8 month dry season. In the Sierra de Surotato it was described as an understorey tree in mixed pine-oak forest.

Phenology
Limited data indicate flowering (June-) July - September (-?), fruiting (August-) September - January.

Conservation status
Poorly known, but apparently very restricted and rare with only two known localities, and only collected in the last 50 years from one site in central Sonora, Mexico where stands of a few hectares are found on exposed calcareous outcrops.
Star rating: Gold/?Black star
IUCN threat category: EN-B1&2

Common names
barra blanca (Sonora).

Exotic use and potential
The characteristics of this species are poorly known. In the natural populations it generally forms a small tree to 2-5m height; occasional trees to 10m have been found. The trees are often multi-stemmed with spreading branches and open crowns. The first seed collections of this species were made in 1992 and little is so far known about its propagation or potential for planting.
Psyllid resistance: moderately susceptible (damage score ?4-5)
Wood quality: The species provides good quality firewood in the native range.
Fodder quality: unknown
Weediness risk: unknown, but probably not a high weed risk

11.8 Leucaena lanceolata

Leucaena lanceolata S. Watson, Proceedings American Academy of Arts & Sciences 21: 427. 1886.

Varieties
L. lanceolata var. lanceolata
Synonyms
Leucaena microcarpa Rose
Leucaena brandegeei Britton & Rose
Leucaena cruziana Britton & Rose
Leucaena palmeri Britton & Rose
Leucaena pubescens Britton & Rose
Leucaena purpusii Britton & Rose
Leucaena sinaloensis Britton & Rose
Leucaena sonorensis Britton & Rose
Leucaena nitens M.E. Jones

L. lanceolata var. sousae (S. Zárate) C.E. Hughes, Contr. Univ. Michigan Herb. 21: 288. 1997.
Synonyms
Leucaena rekoi Britton & Rose

Main attributes
Leucaena lanceolata is a truly tropical species and occurs, often abundantly across a wide distribution throughout the seasonally dry deciduous forest formation in Mexico. It is morphologically variable, with two recognized varieties, and ranges from a small shrubby tree in the north to a medium-sized upright tree to 20m height in the south. Some of the southerly provenances have produced high wood biomass yields in trials, but the species has been little used and is psyllid-susceptible. Recent research indicates that *L. lanceolata* may have been the paternal parent of *L. leucocephala* (Section 2.6).

Botanical features (Fig 38)
Bark: on young branches smooth, mid-grey or grey-brown, darker grey-brown and rougher with shallow rusty orange-brown vertical fissures on bole, often exuding gum, slash pale cream or pale salmon-pink
Leaves: pinnae 2-5 pairs; pinnular rachis 4.5-9 cm long, leaflets 16-70 mm long, 8-35 mm wide, 2-5(-7) pairs per pinna, slightly asymmetrical, broadly elliptic or elliptic-ovate, apex obtuse, acute or occasionally rounded, base obtuse, variably glabrous to densely hairy
Petiole gland: yellow-green or green, un-stalked, rounded, elliptic, dome-shaped or conical, convex, 2.5-3.5 x 1.5-2 mm
Flower heads: (15-)20-40 mm in diameter, (250-) 300-450 flowers per head, in groups of 1-3 in leaf axils on un-branched terminal determinate shoots on which leaf development is variably suppressed; flowers sweetly scented, often reported as smelling of papaya, melon or plantain, white or cream-white
Pollen: tricolporate monads
Pods: 10-38 cm long, 8-36 mm wide, borne on shoot tips, 1-6 per flower head, oblong to linear-oblong, flattened, 13-18-seeded, pale to dark orange-brown,

glabrous or with dense velvety hairs, papery, opening along both margins; the 40 cm long pods of var. *sousae* from parts of coastal Oaxaca are extremely large, exceeding the dimensions of any other *Leucaena* species
Seeds: 6.3-11.1 mm long, 3.8-8.7 mm wide, aligned transversely in pods, 17,000-39,000 seeds/kg

Taxonomy and varieties

Leucaena lanceolata is morphologically variable across its extensive and largely continuous distribution along the Pacific coast of Mexico from Sonora to Chiapas, with outlying occurrences in Baja California and Veracruz (Fig 39). Variation in quantitative leaf and pod traits and leaf and pod pubescence has been treated by different authors in different ways. Britton and Rose (1928) recognized nine separate species based on leaflet and pod size, shape and pubescence. In contrast, McVaugh (1987: 185) described *L. lanceolata* as a single wide ranging species, *"not convincingly divisible on the basis of pubescence, nor the width of the pod"*. Later Zárate (1994), followed McVaugh (1987) treating it as one variable species, but he also described a new subspecies *sousae* to account for an unusual variant from Michoacán and Oaxaca. Hughes (1997a; in press) examined the basis for subdivision of *L. lanceolata* and showed that there are no clear discontinuities in quantitative leaf or pod traits across the range that might be used to divide the species unambiguously. However, he also showed that there is still some evidence to support the recognition of subspecies *sousae* albeit as a variety rather than a subspecies due to blurring of discontinuities in morphological trends. The two varieties are distinguished by quantitative leaf and pod traits and pod pubescence.

KEY TO VARIETIES

Pods covered with dense velvety hairs, generally <18 cm long and <22 mm wide, leaflets generally <20 mm wide
var. *lanceolata*

Pods glabrous, usually lustrous or glossy, generally >20 cm long and >20 mm wide, leaflets generally >20 mm wide, restricted to Michoacán, Guerrero and Oaxaca
var. *sousae*

The division between the two varieties is arbitrary and not entirely satisfactory. Given these difficulties, identification of material from the particular areas (coastal Michoacán and Bahias de Santa Cruz, coastal Oaxaca) may be difficult.

Closely related species and identification

L. lanceolata is one of five species of *Leucaena* with large leaflets (Fig 17) which have sometimes been considered to be closely related (Zárate, 1984a; 1994) and which may be confused due to their broad similarity in leaf and pod traits. In practice *L. lanceolata* can be readily distinguished from *L. macrophylla, L. trichodes* and *L. multicapitula* by its much larger flower heads (2-4 cm in diameter) with numerous (>250) flowers per head. In addition, *L. lanceolata* is separated by its pollen which occurs as monads as opposed to the polyads of the other species (Hughes, 1997b). The true affinities of *L. lanceolata* are uncertain but apparently lie with the *L. shannonii* alliance and *L. collinsii* although it is immediately separated from those species by its large leaflets and few pairs of pinnae and leaflets.

Chromosome number

Diploid, 2n=52, self-incompatible (Gonzalez *et al.*, 1967; Pan and Brewbaker, 1988; Sorensson, 1989a)

Tree size and form

Small to medium-sized tree, 5-15(-20) m tall, 20-50 cm bole diameter. Typically branchy when young, older trees with a short clear bole to 5 m, upright angular branching and a narrow, open crown.

Distribution (Fig 39)

Var. *lanceolata* is distributed from Sonora and Chihuahua south east along the Pacific coast through Sinaloa, Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca and into the extreme south western corner of Chiapas with outlying occurrences near the southern tip of Baja California and in central Veracruz. Var. *sousae* is restricted to the Pacific coastal zones of south east Michoacán, with sporadic occurrences in Guerrero and the coast of Oaxaca as far east as Bahias de Santa Cruz. This is a more restricted distribution than that depicted by Zárate (1994).
Degree-squares: *L. lanceolata*: 29; var. *lanceolata*: 25; var. *sousae*: 7
Altitude range: 0-700 (-1100)m, mainly below 400m

Ecogeography

L. lanceolata occurs as a canopy or sub-canopy tree in the seasonally dry deciduous tropical forest which forms a more or less continuous belt along the Pacific coast of Mexico. It also occurs in secondary dry forest, dry thorn scrub forest and in some areas as a dominant element in secondary regrowth after cultivation of milpas. *L. lanceolata* is a truly tropical species and although it is distributed as far north as Chihuahua, well north of the Tropic of Cancer, it does not tolerate frost. Throughout the wide distribution of *L. lanceolata* rainfall is highly seasonal, between 900 and 1500mm, with a 3-6 month dry season.

Phenology

Flowering (August-) September-October (-December); fruiting (November-) December-March; deciduous during the dry season from December to April.

Conservation status: *L. lanceolata* is widely distributed and thrives on disturbance. Despite extensive clearance of the forest from throughout its natural range, it remains abundant in many areas and is of little or no conservation concern

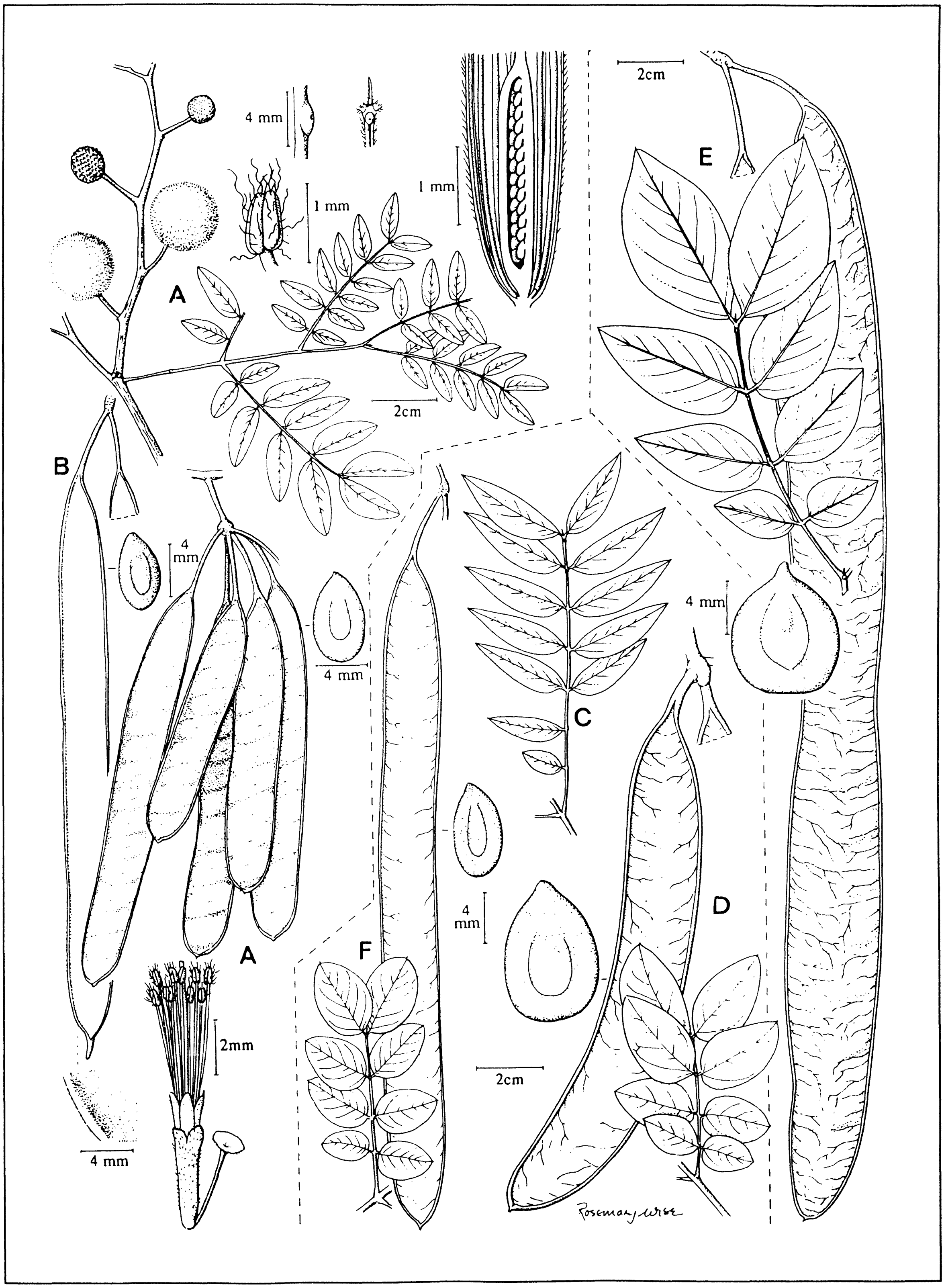

Figure 38 *Leucaena lanceolata* **A-D** var. *lanceolata*; **E-F** var. *sousae* showing variation in leaflet and pod size and shape

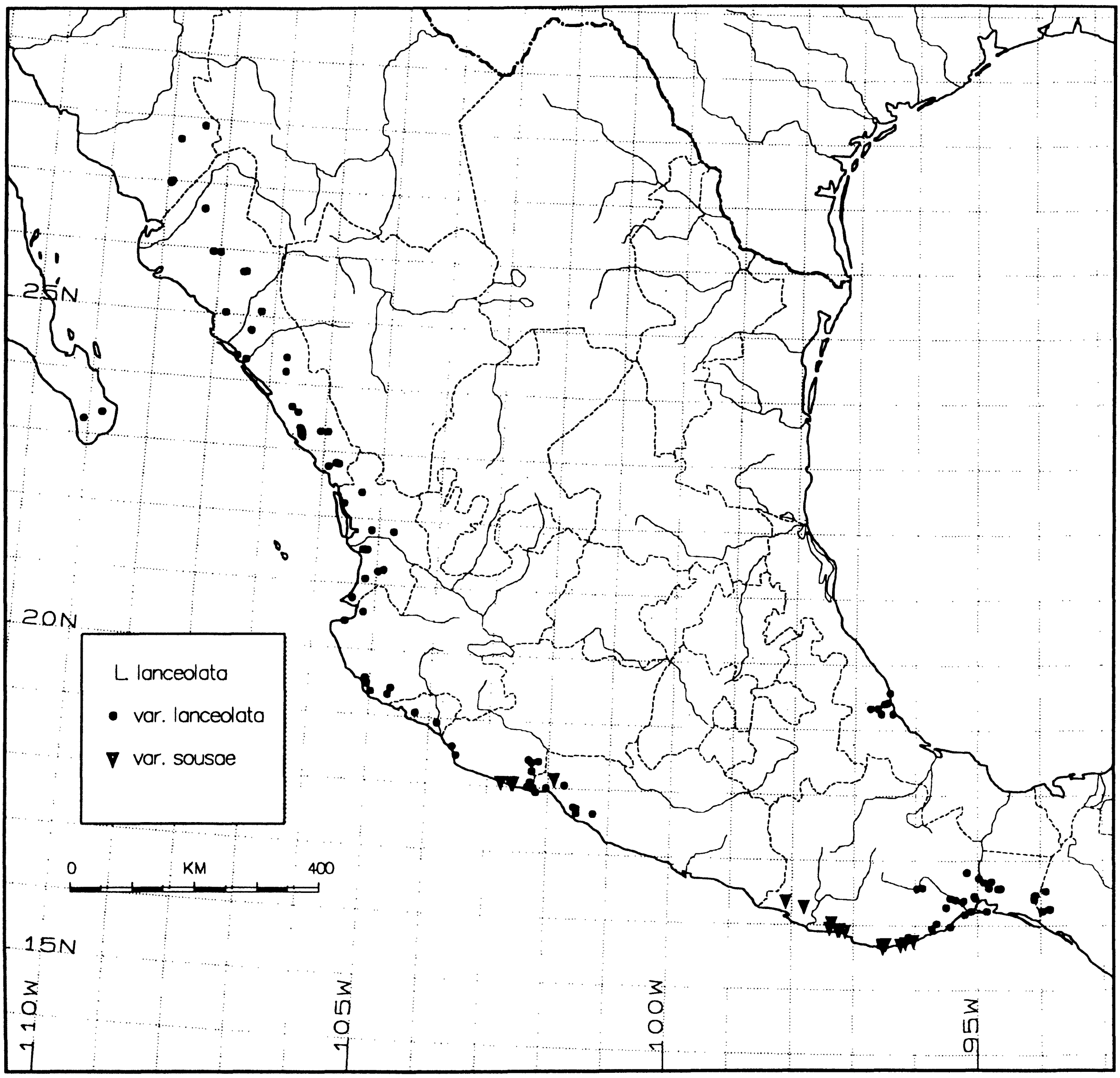

Figure 39 Map of Mexico showing the distribution of two varieties of *L. lanceolata*

Star rating: Green star (both subspecies)
IUCN threat category: LR:lc (both subspecies)

Common names

Var. *lanceolata*: *balillo* (Sonora), *guaje (palo de guaje, palo de huaje)* (all areas), *guaje blanco, guaje indio* (Veracruz), *guaje de monte, guaje de zopilote* (Oaxaca), *guajillo* (Sinaloa, Guerrero, Michoacán, Oaxaca), *palo blanco* (Oaxaca), *flor de canela* (Chiapas), *ejote, da-yuh* (Chatino, Oaxaca), *naj-py-team, yaga-la-sha-xi* (Oaxaca); var. *sousae*: *ejote, guaje, guaje de monte, guaje de zopilote* (Oaxaca), *guajillo* (Michoacán, Guerrero, Oaxaca), *da-yuh* (Chatino, Oaxaca)

Indigenous use and domestication

Limited to casual use for firewood and poles; pods are apparently little used. However, *L. lanceolata* is often a prominent element in bush fallows and is sometimes managed on a regular coppice rotation in cycle with crops.

Exotic use and potential

L. lanceolata has not been widely cultivated to date. It appears to have some potential for wood production being fast growing on some sites, with moderate wood density and good wood properties for poles or firewood. Although fodder quality appears to be good, use as fodder is limited by moderate susceptibility to the psyllid and low to moderate leaf yields. There is substantial provenance variation. Provenances from the southern part of the range around the isthmus of Tehuantepec, in Oaxaca and Chiapas, are generally faster growing and form larger trees to 20m height although these differences do not appear to coincide precisely with the two recognized botanical varieties.
Psyllid resistance: var. *lanceolata*: moderately

susceptible (damage score 4-5); var. *sousae*: moderately resistant (damage score 3-4)
Wood quality: the wood makes excellent firewood which is generally preferred over *L. leucocephala* in Mexico and occasionally wood is used for poles; mean wood density is moderately high: 0.7-0.75 (Gourlay *et al.*, in press).
Fodder quality: *in vitro* dry matter digestibility is high and condensed tannin content fairly low compared to other species (Stewart and Dunsdon, in press) and the fodder quality appears to be similar to *L. leucocephala* although this remains to be verified. In a few areas, such as southern Oaxaca, Mexico, the leaves are used for fodder, particularly for pigs.
Weediness risk: *L. lanceolata* as a whole, and var. *lanceolata* in particular, evidently thrives on disturbance and can be very common and weedy along roadsides in parts of the native range (*e.g.* in parts of the Tehuantepec Isthmus around Juchitán, Oaxaca), or in coastal vegetation and on dunes (*e.g.* around Huazantlán del Rio, east of Salina Cruz, Oaxaca). Given these tendencies it poses significant risks of becoming a ruderal weed of open disturbed habitats where introduced.

11.9 Leucaena lempirana

Leucaena lempirana C.E. Hughes, Contr. Univ. Michigan Herb. 21: 279. 1997.

Main attributes

Leucaena lempirana, the only species of *Leucaena* endemic to Honduras, is closely related to *L. salvadorensis* and, like that species, forms a medium-sized, well formed tree in its natural range. The wood is also similar to *L. salvadorensis* being hard and dense, with a high proportion of heartwood, and trees in parts of the native range are highly valued as a source of wood for firewood, fence posts and poles for local construction. *L. lempirana* was discovered only in 1990 and named in 1997, its characteristics and wider potential remain largely unknown.

Botanical features (Fig 40)

Bark: light grey-brown with powdery orange-brown lenticels and shallow rusty orange-brown vertical fissures, inner bark green
Leaves: pinnae 14-19 pairs; pinnular rachis 7-10 cm long, densely covered in short white hairs; leaflets 5-6 mm long, 1.6-2 mm wide, (27-)30-36(-40) pairs per pinna, asymmetric, oblong, obtuse to rounded at tip, round at base, densely covered in short white hairs
Petiole gland: one or occasionally two pale yellow to orange-yellow, un-stalked (sessile), elliptic dome-shaped or conical, 3 x 1.5 mm
Flower heads: 16-18 mm in diameter, 100-130 pale cream-white flowers per head, in groups of 3-5 at nodes or in leaf axils on long erect terminal determinate shoots on which leaf development is suppressed, the flower heads on the periphery of the tree crown; flowers white or pale cream-white
Pollen: tricolporate monads
Pods; (10-)12-20(-25) cm long, (18-)20-26(-32) mm wide, 1-3 per flower head, oblong to linear-oblong, tip with a beak 5-15 mm long, base cuneate, narrowly plano-compressed, 14-20 seeded, thin, flat and papery, mid orange-brown, nearly glabrous or with dense velvety hairs, opening along both margins.
Seeds: 6.6-8.8 mm long, 3.8-5.2 mm wide, aligned transversely in pods, 25,000-30,000 per kg

Closely related species and identification

The first herbarium specimen of *L. lempirana* was collected in 1990 by Gaspar Alvarado and Jon Hellin, foresters from the National Forestry School in Honduras. It was named in honour of the Indian chief Lempira, a Cacique from the Celaque region of Honduras, who was killed while attending a peace conference, the victim of a breach of truce imposed by the Spaniards and after whom the Honduran currency is named (Hughes, 1997a). *L. lempirana* shows closest affinities to *L. salvadorensis* and, to a lesser extent, *L. shannonii*. *L. lempirana* is distinguished from *L. salvadorensis* by its long terminal determinate flowering shoots, on which the flower heads and pods are borne on the periphery of the tree crown. These flowering shoots are strongly reminiscent of those of *L. shannonii*. It is distinguished from both *L. salvadorensis* and *L. shannonii* by its smaller and more numerous leaflets and pairs of pinnae per leaf. The pods are also similar to those of *L. shannonii* and are variably glabrous or hairy as for that species. *L. lempirana, L. salvadorensis* and *L. shannonii* form a group of closely related species (Section 2.5, Fig 2) and all occur in Honduras but occupy distinct and virtually separate (allopatric) distributions in different, isolated valley systems at low to mid elevations.

Chromosome number

Unknown

Tree size and form

Small slender tree 4-15(-20) m tall, 10-40 cm bole diameter. Typically with upright branching and a rounded crown above a short clear bole to 4m.

Distribution (Fig 41)

L. lempirana occupies a highly restricted distribution in

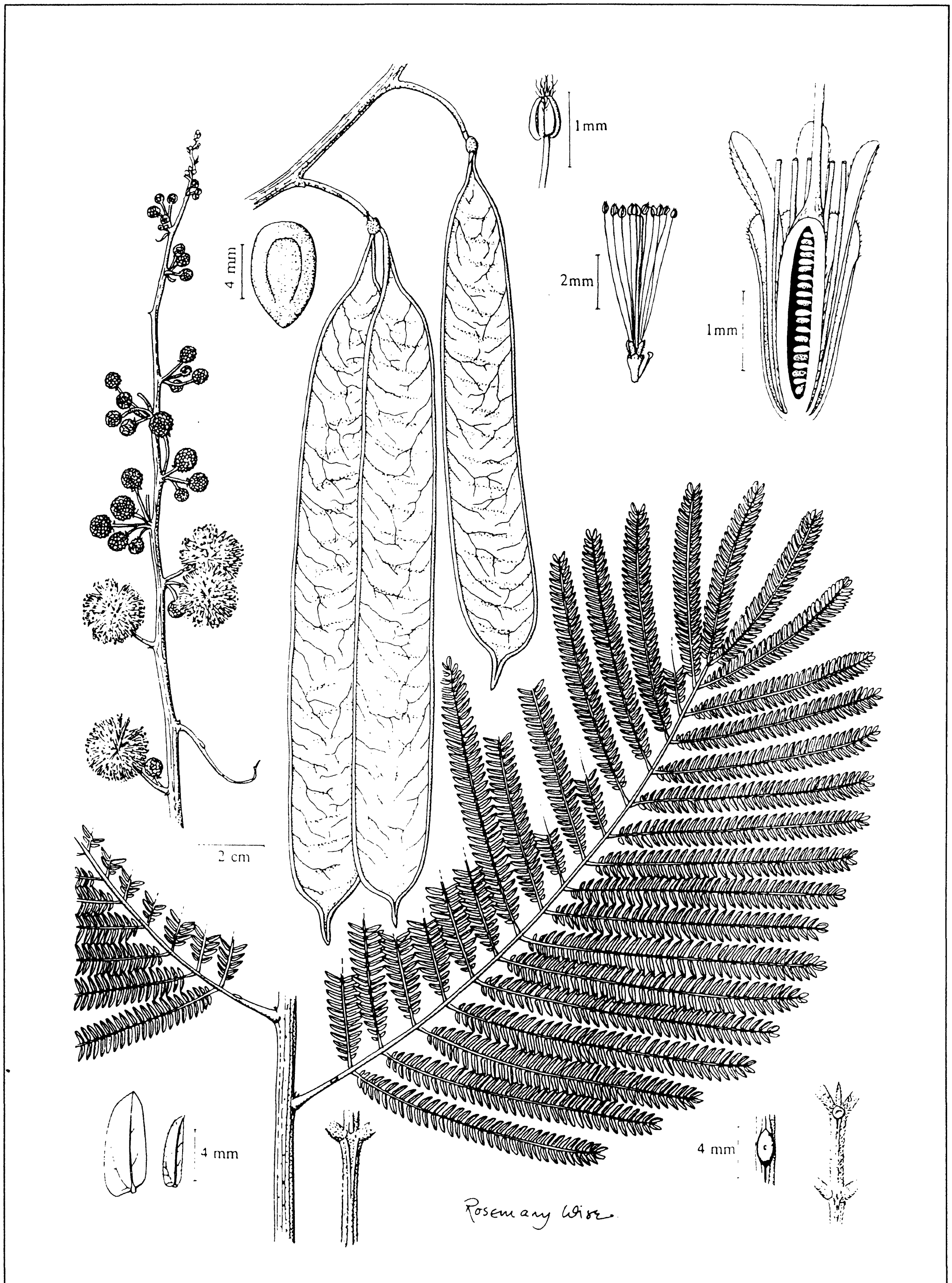

Figure 40 *Leucaena lempirana*

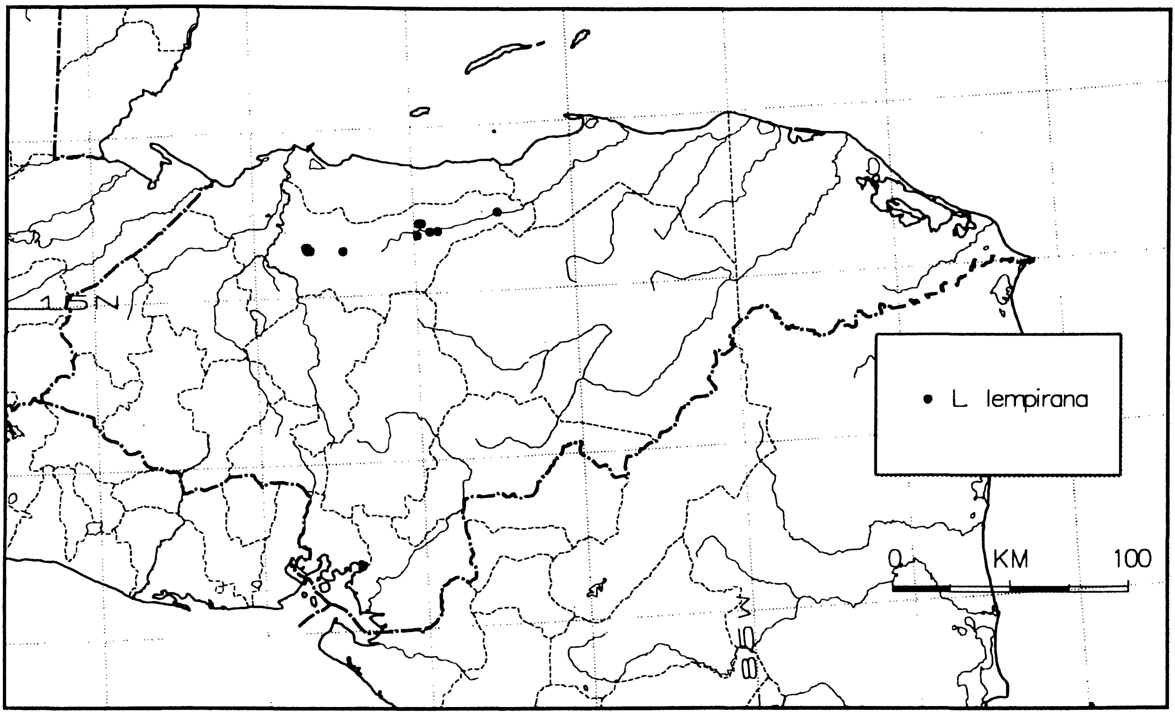

Figure 41 Map of Honduras, showing the distribution of *L. lempirana*

two valley systems, the Aguán and the valleys of Olomán and Cataguana in the Dept. of Yoro in northern Honduras. It occurs extensively throughout the upper Aguán Valley from Olanchito westwards towards Jocón. A second population was discovered in 1991 in low hills between the valleys Olomán and Cataguana west of the departmental town of Yoro.
Degree-squares: 2
Altitude range: 150-500m

Ecogeography
L. lempirana occurs in remnant semi-deciduous, sub-humid tropical forest, dry thorn scrub forest and scattered in secondary vegetation and pastures where trees are actively protected for production of fence posts. It is a truly tropical species restricted to low elevation valleys. Rainfall across the native range varies from 1000 to 1500mm with a 2-4 month dry season.

Phenology
Flowering August-November and sporadically till February, fruiting March-April; semi-deciduous February-April

Conservation status
L. lempirana occupies a highly localized distribution in northern Honduras and is known from only two valley systems. Although trees are protected *circa situm* in some areas in pastures, it is nonetheless vulnerable and of some conservation concern.
Star rating: Gold star
IUCN threat category: VU-B1&2

Common names
guaje (occasionally *frijolillo*) around Cuyamapa (Olomán Valley), *hoja menuda* (occasionally *barba de jelote*) in the Aguán Valley

Indigenous use and domestication
In some areas trees are actively protected in pastures and in secondary vegetation as a source of fence posts and poles.

Exotic use and potential
The characteristics of *L. lempirana* are poorly known and it has only been grown in a handful of trials to date. Its greatest potential is likely to be for wood production, but it remains to be seen if it is as productive as its close relative *L. salvadorensis*. Wider use is likely to be limited by high susceptibility to the psyllid
Psyllid resistance: highly susceptible (damage score 5-6)
Wood quality: The wood of *L. lempirana* is well known and valued being dense and durable and is used for firewood, fence posts and poles for local construction material in Honduras. Trees are sometimes protected by local ranchers as a source of fence posts in pastures and are occasionally abundant in small open stands
Fodder quality: limited data indicate that the leaves have high *in vitro* digestibility and low levels of condensed tannins, but the true fodder potential is unknown
Weediness risk: unknown

11.10 Leucaena leucocephala

Leucaena leucocephala (Lam.) de Wit. Taxon. 10: 53. 1961.
Synonyms
Mimosa leucocephala Lamarck

Subspecies
L. leucocephala subsp. **leucocephala**

L. leucocephala subsp. **glabrata** (Rose) S. Zárate. Phytologia 63: 305. 1987.
Synonyms
Leucaena glabrata Rose

L. leucocephala subsp. **ixtahuacana** C.E.Hughes, Contr. Univ. Michigan Herb. 21: 285. 1997.

Main attributes (Fig 7)
Leucaena leucocephala has been, and still is, the most important species of *Leucaena* in both the indigenous domestication, for pods for food production, and exotic domestication, as a tropical tree for fodder, wood and soil conservation. It is now grown throughout the tropics. The value of *L. leucocephala* lies in its combination of multiple products, fast growth, ease of propagation and management by farmers, and high quality products. It is one of the foremost tropical fodder trees, often being described as the 'alfalfa of the tropics' and was one of the first species to be used for the production of green manure in alley cropping systems. Its wider uses include small wood products such as firewood and poles as well as shade and soil conservation. These benefits, combined with abundantly available seed led to promotion of *L. leucocephala*, often heralded as a 'miracle tree' by national and international development agencies and its widespread use in tropical reforestation. With wider cultivation, a number of important limitations of *L. leucocephala* have become apparent including lack of cold and drought tolerance, poor growth on acid soils, heavy pod production - and resultant weediness, low wood durability and susceptibility to the psyllid.

Botanical features (Figs 42 and 43)
Bark: on young branches smooth, mid grey-brown, slash salmon-pink, darker grey-brown and rougher with shallow rusty orange-brown vertical fissures and deep red inner bark on older branches and bole
Leaves: pinnae (4-)6-9 pairs; pinnular rachis 5-10.2 cm long, leaflets 9-16 (-21) mm long, 2-4.5 mm wide, 13-21 pairs per pinna, slightly asymmetric, linear-oblong to weakly elliptic, acute at tip, rounded to obtuse at base, glabrous except on margins
Petiole gland: a single gland, 2-3 x 1.2-1.5 mm, green or yellow-green, not stalked (sessile), elliptic, concave, cup-shaped **Flower heads**: 12-21 mm in diameter, 100-180 flowers per head, in groups of 2-6 in leaf axils arising on actively growing young shoots, the leaves developing simultaneously with the flowers; flowers white or pale cream-white
Pollen: tricolporate monads
Pods: (9-)11-19 cm long, (13-)15-21 mm wide, (3-)5-20(-45) per flower head, linear-oblong, acute or rounded at apex, flat, 8-18-seeded, mid- to orange-brown, glabrous and slightly lustrous or densely covered in white velvety hairs, papery, opening along both margins
Seeds: 6.7-9.6 mm long, 4-6.3 mm wide, aligned transversely in pods; 15,000-20,000 seeds/kg

Taxonomy and subspecies
Resolution of the correct botanical name for *L. leucocephala* has been the result of intensive nomenclatural detective work by de Wit (1961) and colleagues. Prior to de Wit's study, the species was called *L. glauca*, a name de Wit showed to belong to a species of *Acacia* (Appendix 1). Full details of this rather awesome Linnean nomenclatural exercise are provided by Isely (1986) and Hughes (1997c).

Variation within *L. leucocephala* was first noted by agronomists evaluating different accessions for fodder production (*e.g.* Hutton and Gray, 1959; Brewbaker *et al.*, 1972). Two main variants, based primarily on habit, branchiness and vigour were recognized: firstly, a shrubby, low growing, highly branched, seedy, and often weedy, variant designated the '*Common*' type; secondly an erect, arborescent, lightly branched, less seedy variant designated the '*Giant*' or '*Salvador*' type (Hutton and Gray, 1959; Gray, 1967; Brewbaker *et al.*, 1972; Brewbaker, 1980; Brewbaker, 1987b). These variants were formally recognised as distinct subspecies by Zárate (1987a). These two subspecies correspond directly to the agronomic 'types' *viz*: subsp. *leucocephala* = '*Common*' type; subsp. *glabrata* = '*Giant*' type. Zárate (1987a) listed the characters, in addition to habit, branchiness and vigour, that distinguish subspecies *leucocephala* and *glabrata*. These included leaf size, leaflet size, pod and seed size, habit, and most notably shoot, leaf rachis, leaflet and pod pubescence. Subsp. *glabrata* has larger leaves, leaflets and pods and is almost entirely glabrous, compared to the smaller leaves, leaflets, pods and densely hairy shoot, leaf rachis and pods of subsp. *leucocephala* (Figs 42 and 43). The distributions of the two subspecies are largely allopatric, albeit with limited overlap in northern Veracruz, Mexico and the Isthmus of Tehuantepec (Fig 44), where some intermediates are encountered suggesting geneflow between the two subspecies (Zárate, 1987a). During recent exploration by Hughes and collaborators in northern Guatemala, an additional variant, which differed from both subsp. *leucocephala* and *glabrata*, was encountered in a localized area around the town of Ixtahuacan in the highlands of

Huehuetenango. This variant has the small leaves, leaflets and pods of subsp. *leucocephala*, but is glabrous like subsp. *glabrata*. This material was described by Hughes (1997a) as a third subspecies named *ixtahuacana*.

KEY TO SUBSPECIES

Leaves >19 cm long and >12 cm wide, pinnular rachis >8cm long, leaflets (11-)16-21 mm long, flower heads >18 mm in diameter with >120 flowers per flower head, pods 12-19 cm long and 18-21 mm wide
subsp. *glabrata*

Leaves <20 cm long and <12 cm wide, pinnular rachis <8cm long, leaflets 9-13 mm long, flower heads 13-17 mm in diameter with <125 flowers per flower head, pods 9-13 cm long, 13-18 mm wide

Shoots, leaves and pods covered with dense whitish velvety hairs
subsp. *leucocephala*

Shoots, leaves and pods glabrous
subsp. *ixtahuacana*

A third agronomic variant, the so called '*Peru*' type was recognized (Gray, 1968; Brewbaker and Hutton, 1979; Brewbaker, 1980) based on material introduced to Australia from Argentina, but of supposed Peruvian origin, and characterized by the erect habit of the '*Giant*' type but the greater branchiness of the '*Common*' type. The '*Peru*' type also belongs within subspecies *glabrata*. The bred line '*Cunningham*', released and widely planted in Australia (Gray, 1967; Hutton and Beattie, 1976), is a cross between the '*Salvador*' and '*Peru*' types and is therefore also attributable to subsp. *glabrata*.

Closely related species and identification

Leucaena leucocephala is known to be a self-compatible tetraploid (Section 2.6). However, despite its economic importance and considerable speculation, the origin of *L. leucocephala* remains unknown. Patterns of natural variation within *L. leucocephala* have been greatly disrupted by the widespread indigenous domestication as a minor food plant in Mexico (Whitaker and Cutler, 1966; Smith, 1967; Zárate, 1984a; 1984b; 1994; Casas and Caballero, 1996) such that it is now impossible to identify a 'centre' of morphological diversity, nor any unequivocally natural populations, although the widespread and abundant occurrence of subsp. *leucocephala* throughout the Yucatán Peninsula has led many to conclude that it is native there (*e.g.* Brewbaker, 1987b). *L. leucocephala* is widely suspected to be an hybrid between two overlapping diploid species. Harris *et al.* (1994a) showed that the most likely maternal parent species is *L. pulverulenta* suggesting a putative origin in eastern Mexico, possibly in northern Veracruz. Geographical and morphological evidence suggest that *L. lanceolata* is the most likely paternal parent species (Section 2.6). The lack of natural populations of *L. leucocephala*, along with increasing realization of the extent and importance of its indigenous domestication of *Leucaena* in Mexico, led Harris *et al.* (1994a) to speculate that *L. leucocephala* might have arisen in cultivation in pre-Columbian times following cultivation bringing the parent species into contact. Additional ethnobotanical evidence supports a possible anthropogenic origin (Section 4.6).

Material of subsp. *glabrata* was introduced from near Jocóro, Morazán Prov., El Salvador to Hawaii in 1945 (Brewbaker *et al.*, 1972; Brewbaker, 1980). The designation '*Salvador* type', which refers to this original collecting locality, led to subsequent confusion with *L. salvadorensis*, which was treated, until recently, as a synonym of *L. leucocephala* by Brewbaker who had visited El Jocóro in 1967 but failed to locate any trace of *L. salvadorensis* (Brewbaker, 1980; Hellin and Hughes, 1993; species account for *L. salvadorensis*).

Chromosome number

Tetraploid, 2n=104, self-compatible (Tjio, 1948; Table 3)

Tree size and form (Figs 7A-E)

Small, variably shrubby and highly branched (subsp. *leucocephala*), to medium-sized with a short clear bole to 5 m, upright angular branching and a narrow, open crown (subsp. *glabrata*), 3-15(-20) m tall, 10-50 cm bole diameter

Distribution and history of introduction (Fig 44)

Within Mexico, subsp. *leucocephala* is distributed mainly in the Yucatán Peninsula, in the States of Tabasco, Campeche, Quintana Roo and Yucatán, including the Island of Cozumel and extending south into northern Belize around Corozal and Orange Walk. Outlying occurrences include an area of central north Veracruz, between Tampico and Papántla, and infrequently across the Isthmus of Tehuantepec into Oaxaca. Despite the great abundance and widespread occurrence of subsp. *leucocephala* throughout the Yucatán, McClay (1990) doubted that it is native there because of the poverty of its phytophagous insect fauna and particularly the absence of the psyllid which was not found in that area despite exhaustive sampling (Waage, 1990). McClay (1990) went on to speculate that subsp. *leucocephala* might have been introduced to the Yucatán from elsewhere in Mexico, and possibly from Veracruz, in pre-Columbian times for the production of edible seeds and pods, although Brewbaker (1979) speculates that its main use in Yucatán might have been as a green manure for soil nitrogen. The capacity of subsp. *leucocephala* to naturalize, spread rapidly and dominate secondary vegetation on limestone soils has been amply demonstrated on many Pacific islands and parts of S.E. Asia, and may provide a possible explanation for its abundance in the Yucatán today.

There is broad consensus that subsp. *leucocephala* was introduced outside Mexico much earlier than subsp. *glabrata* which was spread across the tropics only in the last few decades. Subsp. *leucocephala* is reported to have been introduced to the Philippines during the Spanish occupation aboard one of the annual Spanish government galleons that sailed between Acapulco and Manila between 1521 and 1815 (Merrill, 1912). Communications between Spain and the Philippines during this period (almost 300 years) were via Mexico and led to the introduction of nearly 200 tropical American species including other well known legume trees (Merrill, 1912). Some speculate that it may have been introduced before 1600 (Brewbaker *et al.*, 1972; Brewbaker and Hutton, 1979; Pound and Martínez-Cairo, 1983). By the late 19th Century subsp. *leucocephala* had spread or been introduced through Asia and Africa and it is now pantropical, recorded from the majority of tropical and subtropical countries (*e.g.* Lock, 1989 for Africa; Nielsen, 1992b for Malesia). That spread of subsp. *leucocephala* preceded subsp. *glabrata* was confirmed during testing of accessions from around the world for forage during the 1950s, which revealed all non-Mesoamerican accessions to be of subsp. *leucocephala* (Hutton and Gray, 1959; Brewbaker *et al.*, 1972; Batson *et al.*, 1984). Thus, all early agronomic investigation and most Flora treatments and references to naturalization and weediness (Section 3.9) refer to subsp. *leucocephala* which is pantropically distributed and more widely naturalized than subsp. *glabrata*.

The natural distribution of subsp. *glabrata* remains unknown. Within Mexico and Central America it is extremely widespread (Fig 44) as a cultivated tree. Although it is sometimes locally naturalized, as around Acapulco, no clearly natural populations have been found to date. It is a very common backyard, street and orchard tree. Indeed, it is found in the majority of villages and towns in Mexico, in all tropical and subtropical areas (wet, seasonally dry and semi-arid), except above 2000 m elevation and in the northern States where regular frost limits its cultivation. There is some evidence to suggest that its distribution within Mexico has expanded over the last few millennia and is still growing (Hughes, in press; Section 4.3). The recent prominence given to subsp. *glabrata* as an agroforestry or fodder tree has prompted wider cultivation within Mexico and Central America and throughout the tropics. Although it has been widely introduced outside Mexico and Central America only in the last few decades, its active promotion in tropical reforestation means that it is now in cultivation pantropically.

Subsp. *ixtahuacana* is restricted to a small area of northern Guatemala and the immediate border zone in Mexico around Motozintla, largely in the valleys of the Rio Cuilco and Rio Selegua, in Huehuetenango and Chiapas. As far as is known, subsp. *ixtahuacana* has not been introduced outside its very restricted distribution in Guatemala and Mexico.

Degree-squares: *L. leucocephala*: 87; subsp. *leucocephala*: 24; subsp. *glabrata*: 71; subsp. *ixtahuacana*: 2

Altitude range: subsp. *leucocephala*: 0-250(-500) m; subsp. *glabrata*: 0-500 (-2100) m; subsp. *ixtahuacana*: 1350-2000m

Ecogeography

In the Yucatán Peninsula, subsp. *leucocephala* occurs primarily as a ruderal weed of disturbed sites including roadsides, waste ground, particularly around towns and cities, in abandoned milpas and neglected sisal plantations, along the coastal fringe, including the mangrove edge and frequently on and around Mayan ruins (Brewbaker, 1979). It grows on shallow limestone soils and coastal sand, often forming shrubby and sometimes dense thickets. Subsp. *leucocephala* is an aggressive colonizer of ruderal sites and secondary or disturbed vegetation in many parts of Asia and the Pacific (Fig 8D) (Section 3.9).

L. leucocephala is essentially a tropical species requiring warm temperatures of 25-30°C for optimum growth and with poor cold tolerance and significantly reduced growth during cool winter months in subtropical areas (Brewbaker and Sorensson, 1987a; Williams, 1987). For optimal growth it is therefore limited to areas below about 1500m altitude and 15-25° north or south of the equator. *L. leucocephala* sheds its leaves even with light frosts and heavy frost kills all above ground growth, although trees often resprout the following summer. It grows well only in sub-humid or humid climates (650-3000mm) with moderate dry seasons of up to 6-7months (Lascano *et al.*, 1995). *L. leucocephala* is known to be intolerant of soils with low pH, low P, low Ca, high salinity, high aluminium saturation and waterlogging (Brewbaker, 1987b) and has often failed under such conditions (Hutton, 1981; 1982; Oakes and Foy, 1984; Brewbaker, 1987b; Shelton, 1994; Blamey and Hutton, 1995).

Phenology

Flowering and fruiting throughout the year as long as moisture permits.

Conservation status

Subsp. *leucocephala*: widespread and locally abundant as a common ruderal weed throughout the Yucatán and pantropically; common in several protected areas such as the Biosphere Reserved of Sián Ka'an and Calakmul. Subsp. *glabrata*: Very widespread and abundant in cultivation throughout Mexico and many parts of Central America and now pantropically. Origin and natural populations unknown. Subsp. *ixtahuacana*: very restricted and not locally abundant but threat mitigated by local *circa situm* cultivation for pod production in

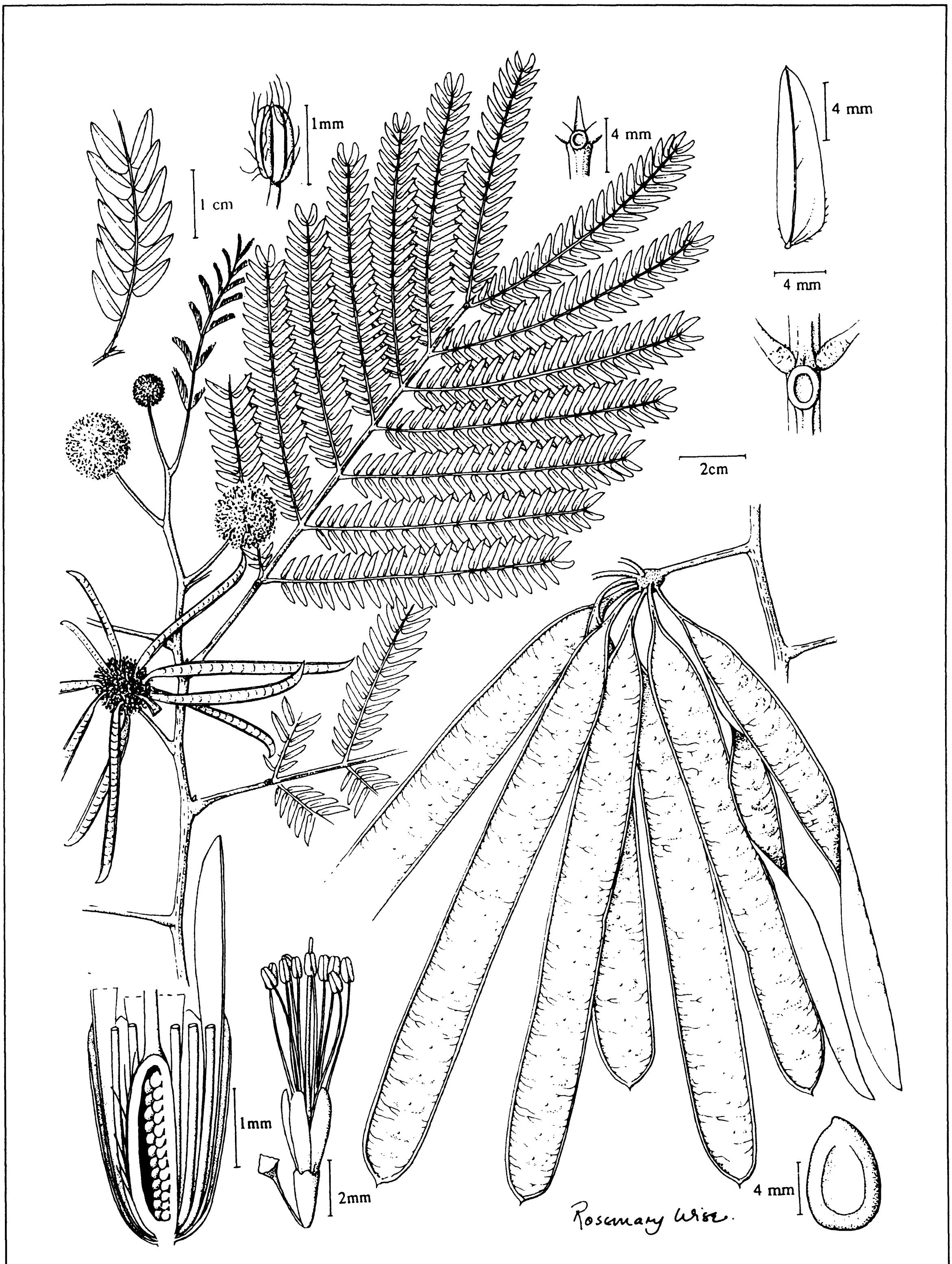

Figure 42 *Leucaena leucocephala* subsp. *glabrata*

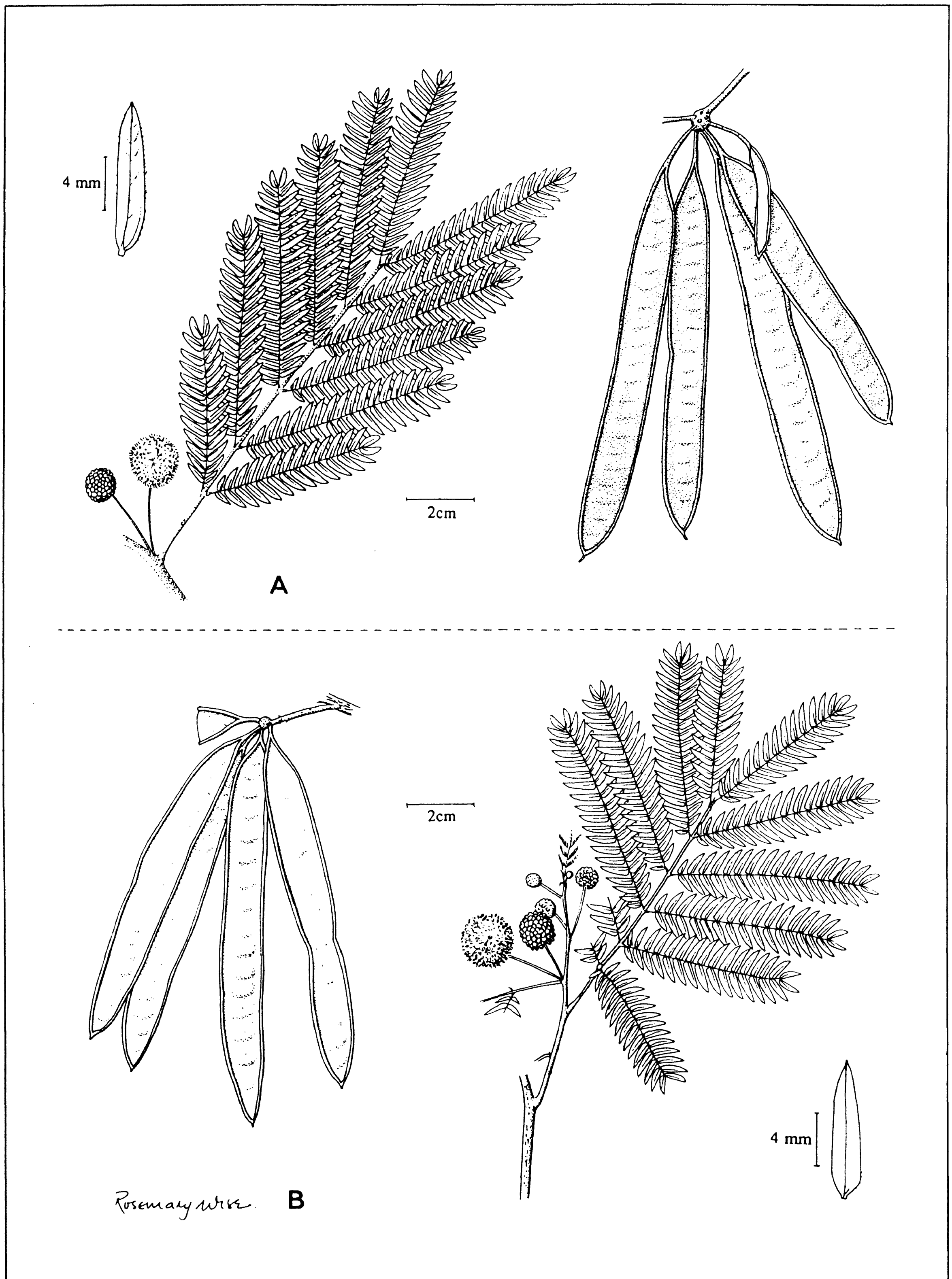

Figure 43 *Leucaena leucocephala*: **A** subsp. *leucocephala* and **B** subsp. *ixtahuacana*

Huehuetenango, Guatemala.
Star rating: subsp. *leucocephala* and *glabrata*: Green star; subsp. *ixtahuacana*: Blue star
IUCN threat category: subspp. *leucocephala* and *glabrata*: LR:Lc; subsp. *ixtahuacana*: LR:cd

Common names
Subsp. *leucocephala*: *guaje* (Mexico); *guaslim, tumbapelo* (Campeche, Mexico); *guaxin, huaxe, huaxin, huaxim, uaxi, uaxim, uaxin, waxim, xaxim* (Maya - Yucatán, Campeche, Quintana Roo, Mexico); *liliak* (Totonaco - Veracruz, Mexico); *lead tree* (Florida, Texas, USA); *koa-haole, false koa* (Hawaii); *wild tamarind* (Corozal, Belize); *jumby bean* (Bahamas); *aroma blanca* (Cuba); *lamtoro* (Indonesia, Malaysia); *ipil-ipil* (Philippines); *tangan-tangan* (Guam); *kanthum thect, kratin* (Cambodia); *kan thin* (Laos); *kra thin* (Thailand); *bo chet, schemu* (Vietnam); *subabul* (India); **subsp. *glabrata***: *guaje, guaje blanco, guaje verde, calguaje* (Mexico); *dormilón* (Tamaulipas, Mexico); *efe, guache, guache de tierra caliente* (Hidalgo, Mexico); *guas, guash, guashe* (Chiapas, Mexico); *guash de castilla* (Chiapas, Mexico), indicative of cultivation/introduction of material; *chalip* (Guatemala); *barba de leon* (El Salvador); *frijol guaje* (Honduras); **subsp. *ixtahuacana***: *guash criollo* (Ixtahuacan, Huehuetenango); the local name *criollo* indicates the distinction made by local people between it and either of the two introduced species *L. leucocephala* subsp. *glabrata* (*guaje*) and *L. collinsii* (*guash*) which are cultivated nearby

Indigenous use and domestication
Subsp. *glabrata* is a very common backyard, street and orchard tree cultivated for the production of unripe pods and seeds which are consumed and widely marketed throughout Mexico. Its unripe pods and seeds are highly preferred for food use, due to its very abundant and virtually year-round production of large pods, the large seed size and its "sweeter"flavour (Fig 9D). It has become - alongside *L. esculenta* - the most widely cultivated and marketed *Leucaena* within Mexico.

Subsp. *ixtahuacana* apparently occurs only in cultivation in fields and around houses. Trees are cultivated for the production of unripe pods and seeds which are locally consumed and marketed in the nearby villages of San Miguel, Colotenango and Ixtahuacan. The primary use appears to be medicinal, as a cure for stomach parasites; the unripe seeds are eaten with lemon and salt.

Exotic use and potential
Following agronomic trials in Australia cv '*Peru*' was released and widely used there. After further trials in Hawaii (Brewbaker *et al.*, 1972) and in Australia (Gray, 1967), another variety of *L. leucocephala*, designated K8 was formally released by the University of Hawaii (Brewbaker, 1975), and a handful of others (K28, K72, K636) followed. These accessions have subsequently been widely promoted and used throughout the tropics for reforestation (Pound and Martínez-Cairo, 1983; National Academy of Sciences, 1984), despite concerns over the genetic vulnerability of a handful of highly self-fertile lines, several of which originate from cultivated material from El Salvador, in single 'variety' plantations (Brewbaker, 1980; 1985). Considerable effort has been devoted to field testing of new accessions of *L. leucocephala*. This has revealed very limited useful variation. Although one accession of subsp. *glabrata* (K636 from Coahuila, Mexico) was found to be significantly more psyllid-tolerant and less seedy than the widely used K8, K28, K67 and K72 varieties, most accessions were found to be identical (Brewbaker *et al.*, 1972; Wheeler *et al.*, 1987; Arora, 1981). An initial report of isozyme variation in 12 individuals of *L. leucocephala* concluded that very little variation existed in this species (Schifino-Wittmann and Schlegel, 1990). Brewbaker and Sun (1996) found that more than 100 accessions of the '*Common*' type subsp. *leucocephala* material of the Pacific and indeed of the world outside Mexico, were of a single genotype. It is also well known that only a small number of accessions of the '*Giant*' or '*Salvador*' type subsp. *glabrata* (K8, K28, K72, K636) have been distributed, and that this subspecies also has a very narrow genetic base outside Mexico (Brewbaker, 1980; 1985).

Artificial hybridization has been the main thrust of breeding efforts to overcome some of the limitations of the species and its inherent lack of genetic and useful diversity (Brewbaker and Sorensson, 1990). *L. leucocephala* has been the most important parent in these programmes. Useful hybrids between *L. leucocephala* and other tetraploid species *L. diversifolia* (KX3) and *L. pallida* (KX2) have been produced. *L. leucocephala* has also been used to produce a series of impressive seedless triploid hybrids with different diploid species such as *L. esculenta, L. pulverulenta* and *L. trichandra*.

Psyllid resistance: highly susceptible (damage scores 5-9); subsp. *ixtahuacana*: moderately susceptible (damage score ?4-5) (Figs 7F-G)
Wood quality: The wood properties of *L. leucocephala* have been thoroughly investigated and documented (Bawagan and Semana, 1978; Guevara, 1978; Relwani, 1981; Bawagan, 1983; Pound and Martínez-Cairo, 1983; Van Den Beldt and Brewbaker, 1985). This work shows wood of *L. leucocephala* to be of medium density (0.5-0.7), with pale yellow sapwood and light reddish-brown heartwood, to machine easily, dry without splitting or checking and to have generally acceptable pulping characteristics (*e.g.* Tang, 1981). Most authors have emphasized the potential to use wood of *L. leucocephala* for a wide range of products including domestic and industrial fuel - including dendrothermal energy generation (Denton, 1983) - poles, posts, sawn timber, furniture, parquet flooring, particle board, and pulp. However, the potential to use *L. leucocephala* for saw timber is greatly limited by its generally small dimensions - usually not greater than 30cm diameter - its branchiness, which limits lengths of clear bole

available and means wood is often knotty, and its high proportion of juvenile wood. Nevertheless, there is growing use of small dimension sawn wood in a number of industries, such as flooring, which might include *L. leucocephala* in the future (*e.g.* Brewbaker and Sun, 1996). In practice, *Leucaena* wood is primarily used for fuelwood and charcoal for domestic household or local industrial (*e.g.* lime or pottery kilns) use, and for small dimension poles. Use of short rotation *L. leucocephala* for poles is limited by lack of durability and susceptibility to attack by termites and wood borers (Timyan, 1996). *L. leucocephala* provides fuelwood and charcoal of acceptable, although not highest, quality and it is a popular fuel, often competing with alternative local species, at least in areas where fuelwood is in short supply (National Academy of Sciences, 1980; 1984). The promised potential for large scale use of *Leucaena* in pulp production or dendrothermal energy plantations (Denton, 1983) has not come to fruition. Indeed, despite much discussion about its wood production potential, *L. leucocephala* has not been become an established or widely cultivated plantation species that is able to compete with the species of *Pinus, Eucalyptus* or *Acacia* which dominate tropical plantation forestry.

Fodder quality: *L. leucocephala* has been one of the foremost tropical fodder trees, often being described as the 'alfalfa of the tropics' (Bray, 1986; Pound and Martínez-Cairo, 1983; National Academy of Sciences, 1984; Brewbaker, 1987b, Shelton and Brewbaker, 1994). *L. leucocephala* is, in most respects, one of the highest quality and most palatable fodders trees of the tropics (Jones, 1979; 1994b; Pound and Martínez-Cairo, 1983; Brewbaker, 1987b; Shelton and Brewbaker, 1994; Norton *et al.*, 1995). Leaf quality of *L. leucocephala* compares favourably with alfalfa or lucerne (*Medicago sativa*) in feed value except for its higher tannin content (Jones, 1979) and mimosine toxicity to non ruminants (Bray, 1995a). Leaves of *L. leucocephala* have high nutritive value (high palatability, digestibility, intake and crude protein content), resulting in extremely impressive animal production with 70-100% increases in animal live weight gains compared to pure grass pastures (Figs 7B-C) (Shelton and Brewbaker, 1994; Jones, 1994b). In addition, *L. leucocephala* is very persistent over several decades of cutting or grazing, is highly productive, recovers quickly from defoliation, combines well with companion grasses and can be grazed with minimal losses due to trampling or grazing (Jones, 1994b).

Green manure: *L. leucocephala* was also one of the first species to be used for the production of green manure in alley cropping systems (Kang *et al.* 1981; 1985). Leaves of *L. leucocephala*, with even moderate yields, contain more than enough nitrogen to sustain a maize crop (Buddelman, 1989). The finely divided leaves with small leaflets decompose quickly providing a very rapid short term influx of nutrients. It has been suggested that leaves of *L. leucocephala* decompose too rapidly, resulting in leaching of nutrients away from the crop rooting zone, before being taken up by the crop (Robinson, 1986). This also means that they have little value as mulch for weed control.

Bio-engineering: the beneficial characteristics of *L. leucocephala* for use in bio-engineering to protect hill slopes and embankments from erosion were reviewed by Clark and Hellin (1996).

Growth: High yield has been a major factor prompting the promotion and adoption of *L. leucocephala* following the discovery and distribution of the '*Giant*' arborescent varieties, now assigned to subsp. *glabrata* (National Academy of Sciences 1984; Brewbaker, 1987b). The '*Giant*' varieties have universally out yielded the pantropically naturalized '*Common*' shrubby varieties belonging to subsp. *leucocephala* by 20-100% in leaf production and up to 2.5 times in wood production (*e.g.* Bray *et al.*, 1988; Brewbaker *et al.*, 1972; Brewbaker, 1980; Chadrasekaran, 1982; Gray, 1967; Hu *et al.*, 1980; Hutton and Bonner, 1960; Hutton and Gray, 1959; Ramirez, 1987; Relwani *et al.*, 1972). Despite field testing of large numbers of accessions of *L. leucocephala* subsp. *glabrata*, very little variation in yield has been detected, beyond the higher psyllid tolerance, and hence higher yield, shown by K636 (*e.g.* Wheeler *et al.*, 1987). On favourable sites (see above) *L. leucocephala* subsp. *glabrata* can indeed produce exceptionally high fresh leaf yields in the range 40-80 tonnes ha^{-1} yr^{-1} when moisture is not limiting, and 20-50 tonnes in seasonally dry or subtropical climates (Brewbaker, 1987b) comparable to other high yielding shrubby tropical legumes and the best herbaceous legumes. Wood yields from *L. leucocephala* over short (3-5yr) rotations also compare favourably with other species ranging from 3-4m height yr^{-1} and 10-60m^3 ha^{-1} yr^{-1} (Brewbaker, 1987b; Dutt, 1981; Van Den Beldt and Brewbaker, 1983; 1985). On less favourable sites, as in cooler tropical highland areas, on acid soils, or under high psyllid pressure, yields have often been disappointing and, under such conditions *L. leucocephala* is generally outperformed by other species of *Leucaena* or other genera.

Propagation: The propagation, growth and management of *L. leucocephala* have been investigated in great detail with numerous experiments on nursery methods and management regimes and many assessments of yield. This is reported in detail by Pound and Martínez-Cairo (1983), National Academy of Sciences (1984), Brewbaker (1987b) and Van Den Beldt and Brewbaker (1985).

Weediness risk: Subsp. *leucocephala* is an aggressive colonizer of ruderal sites and secondary or disturbed vegetation in many places both in Mexico, in the Yucatán Peninsula and in many parts of Asia, such as the Philippines where Merrill (1912) observed that it *"is now so thoroughly naturalized, common and widely distributed that the casual observer would consider it a native species"*. This has been attributed to its precocious year-round flowering and fruiting, abundant seed production, self fertility, hard seed coat, and ability to resprout after fire or cutting. It is now naturalized and weedy in many areas (Section 3.9). It is a weed of open

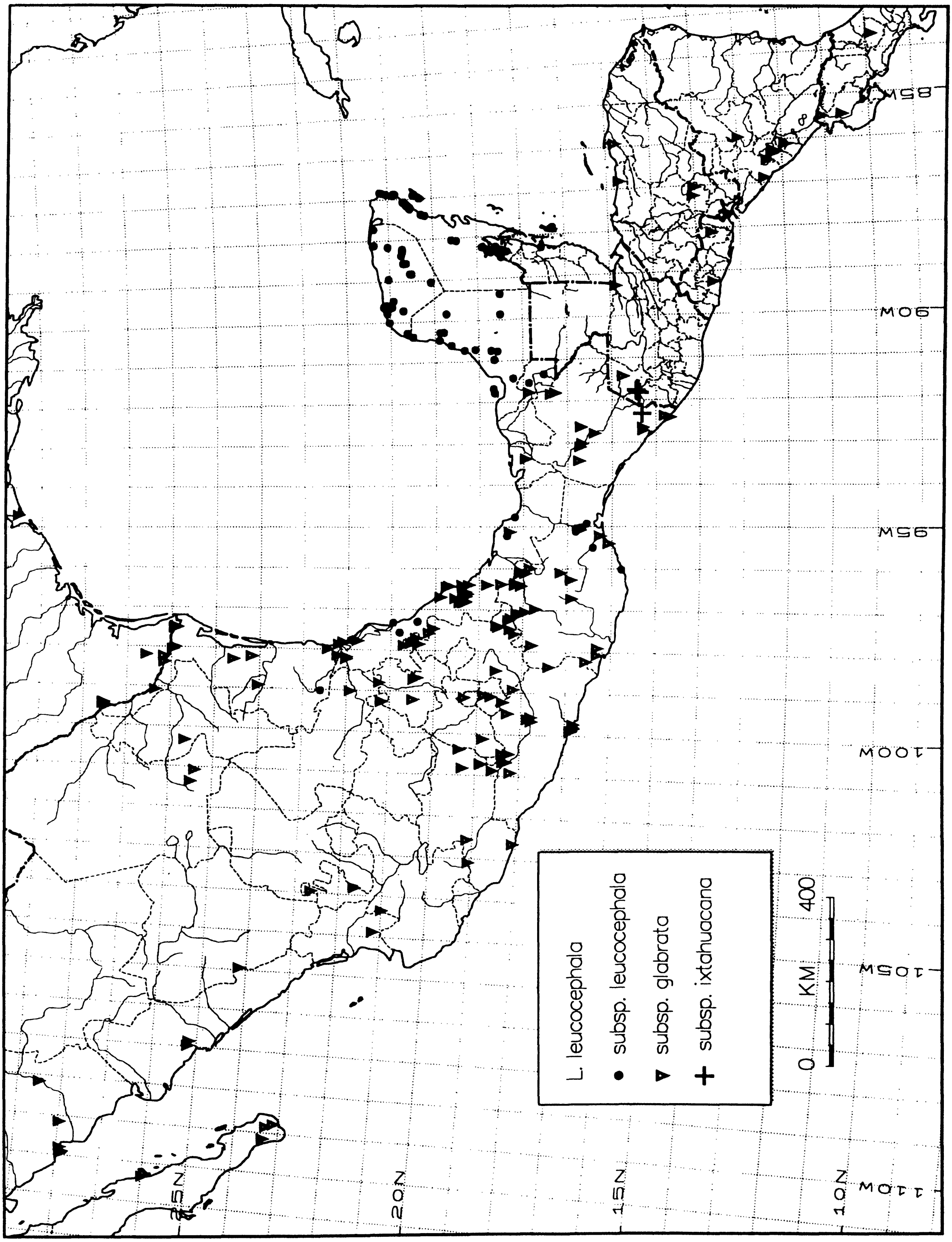

Figure 44 Map of Mexico and Central America showing the distribution of three subspecies of *L. leucocephala*

(often coastal) habitats, semi-natural, disturbed, degraded habitats, other ruderal sites (*e.g.* roadsides, abandoned fields and waste ground) and occasionally agricultural land where it has been planted as a shade tree over cacao. In this sense it is not one of the world's worst weeds and it is not known to invade undisturbed closed forest. However, in many areas it has formed dense monospecific thickets, as in Hawaii where it is reported to be replacing native *Metrosideros-Diospyros* forest and possibly threatening *Erythrina sanwichensis* in parts of its range (Fig 8D) (Cronk and Fuller, 1995). In Hawaii it is classified amongst the 12 worst pests out of 86 serious alien invaders. Such stands even if not of immediate conservation concern, can render extensive areas of disturbed ground unusable and inaccessible. On some Pacific islands, spread was accelerated by aerial seeding for rehabilitation of eroded lands (*e.g.* on Guam: Debell and Whitesell, 1993). Biological control has been contemplated in Hawaii (Smith, 1985) and South Africa (Neser, 1994), but is frustrated by its economic importance although proposals to release the seed eating bruchid *Acanthoscelides macrophthalmus* in South Africa are still being pursued (Neser, 1994) (Section 3.9). It has been suggested that subsp. *glabrata* will be less weedy than subsp. *leucocephala* (Shelton, 1996). However, this may be more a function of time since introduction (Section 3.9). Given its abundant, year-round seed production and self-compatibility, it seems likely that, given time, subsp. *glabrata* may also naturalize and become weedy.

11.11 Leucaena macrophylla

Leucaena macrophylla Benth. Botany of the Voyage of H.M.S. Sulphur 90. 1844.

Subspecies
L. macrophylla subsp. **macrophylla**
Synonyms
Leucaena macrocarpa Rose
Leucaena houghii Britton & Rose
Leucaena nelsonii Britton & Rose

L. macrophylla subsp. **istmensis** C.E. Hughes, Contr. Univ. Michigan Herb. 21: 283. 1997.

Main attributes
As indicated by the name '*macrophylla*', this species has the largest leaflets (3-7cm long) of any *Leucaena*. *L. macrophylla* is best known as a tree of the mid elevations of south central Mexico, but also occurs, as subsp. *istmensis*, at sea level along the Pacific and Gulf coasts. *L. macrophylla* has been little used. Recent trials indicate that subsp. *istmensis* is fast growing and outperforms subsp. *macrophylla*, but the potential of both subspecies is limited by psyllid susceptibility.

Botanical features (Fig 45)
Bark: pale to mid grey-brown, smooth with pale brown horizontally aligned lenticels on younger wood and shallow vertical rusty orange-brown fissures on older boles, inner bark cream
Leaves: pinnae (1-)2-3 pairs; pinnular rachis (6-)7-8.8 cm long, leaflets (15-)23-55(-80) mm long, (6-)17-39 mm wide, 2-4(-6) pairs per pinna, very slightly asymmetric, acute at base, ovate-elliptic, apex acute, sometimes densely hairy or glabrous
Petiole gland: sessile, convex, rounded conical, elliptical, 2.2-3 mm long x 1.4-2.3 mm wide, on ventral side of petiole at base of the basal pair of pinnae
Flower heads: small, 7-11(-15) mm in diameter, 140-180(-190) flowers per head, in groups of 3-5 on long, naked, once-branched shoots arising in leaf axils, the leaves strongly suppressed on the flowering shoots; flowers white; anthers very hairy
Pollen: polyads, of up to 28 loosely-attached pantoporate monads
Pods: (9-)12-24 cm long, (9-)14-26 mm wide, (1-) 2-4(-8) per flower head, linear-oblong, flat and papery, opening along both sides, variably glabrous and slightly lustrous or with dense velvety hairs
Seeds: 3.5-5.7 mm wide, 4.9-8.1 mm long, seeds/kg: 26,000 (subsp. *macrophylla*), 44,000-48,000 (subsp. *istmensis*)

Taxonomy and subspecies
Material from coastal Oaxaca and Veracruz differs from typical *L. macrophylla* in leaf and pod dimensions, habit and cpDNA (Harris *et al.*, 1994a), meriting recognition as a distinct subspecies. Although this material was attributed to subsp. *nelsonii* by Zárate (1994), Hughes (1993) and Harris *et al.* (1994a), and seed (OFI seedlot 47/85) distributed under that name, Hughes (1997a) showed that this name is incorrect thereby necessitating a new name '*istmensis*' to account for this material. The name *istmensis* refers to the occurrence of this subspecies across the Isthmus (*istmo*) of Tehuantepec.

KEY TO SUBSPECIES

Petioles >30 mm long, leaflets >27 mm wide, 2-3(-4) pairs per pinna, pods generally >23 mm wide
subsp. *macrophylla*

Petioles <22 mm long, leaflets <28 mm wide, 3-4(-6) pairs per pinna, pods <23 mm wide
subsp. *istmensis*

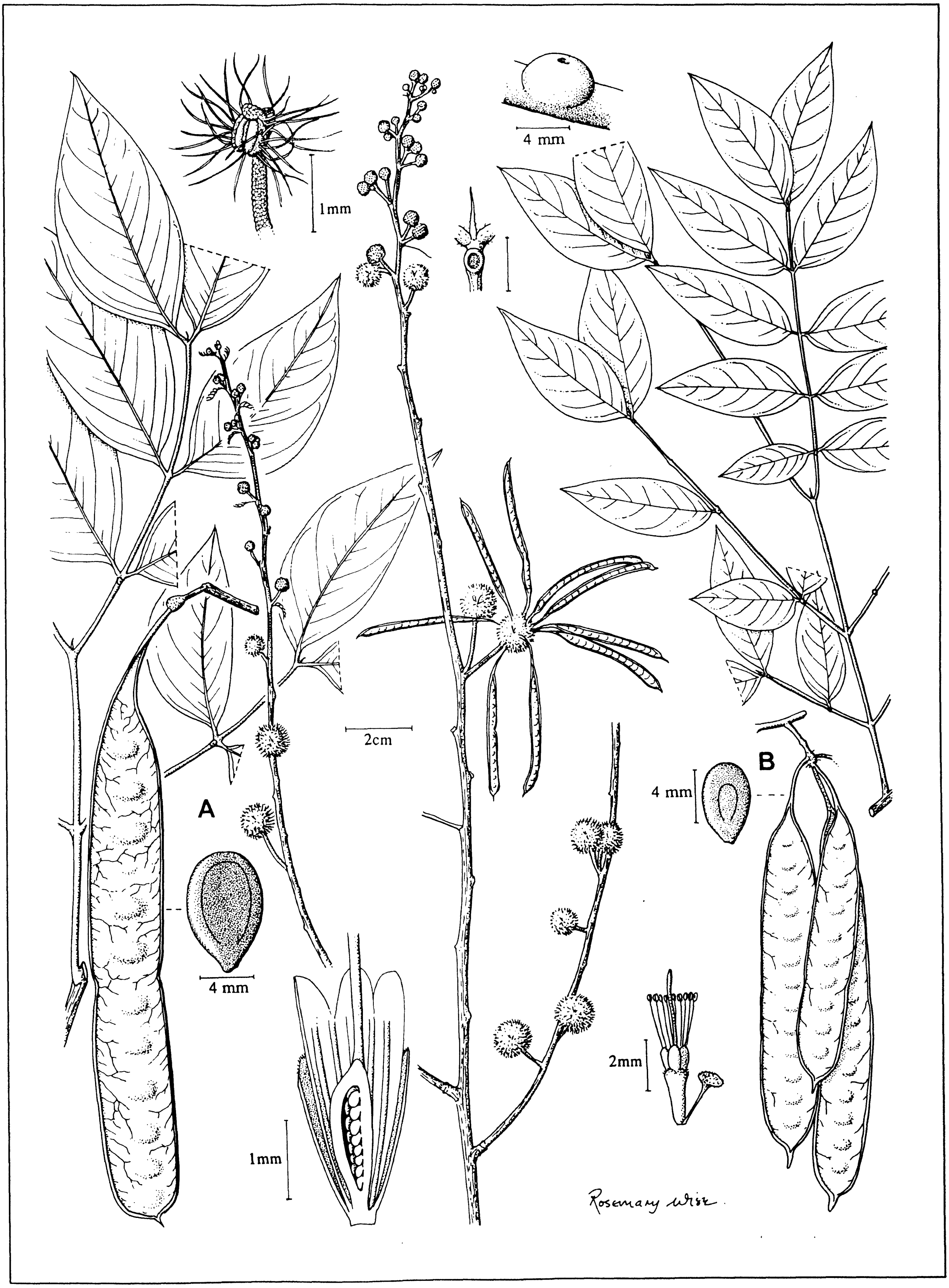

Figure 45 *Leucaena macrophylla*: **A** subsp. *macrophylla* and **B** subsp. *istmensis*

Closely related species and identification

Previous authors have considered the species of *Leucaena* with large leaflets - *L. lanceolata, L. macrophylla, L. multicapitula* and *L. trichodes* - to form a closely related group based on the strong overall similarity in leaf and pod morphology (Brewbaker, 1987a; Zárate, 1994). Detailed survey of pollen and anther morphology by Hughes (1997b) showed that *L. lanceolata* and *L. multicapitula* are clearly distinguished from *L. macrophylla* and *L. trichodes* by a set of pollen and anther characters. In addition, *L. lanceolata* is reliably distinguished from *L. macrophylla* by its large, many-flowered flower heads (20-40 mm in diameter with 250-450 flowers) compared to the very small flower heads of *L. macrophylla* (7-15 mm in diameter with 140-190 flowers).

The two subspecies of *L. macrophylla* and *L. trichodes* are closely related in that they both possess a set of discrete pollen and anther characters unique within *Leucaena*. The relationship between these two species has been neglected in most previous studies which have focused either on the North American (Standley, 1922; Britton and Rose, 1928; Zárate, 1994) or South American (Britton and Killip, 1936) species alone. There are no reliable discrete qualitative characters that distinguish *L. macrophylla* from *L. trichodes*. They were maintained as distinct species based on differences in the arrangement of flowering shoots, number of flowers per capitulum, molecular data and their geographical isolation (Hughes, 1997a). The flowering shoots of *L. macrophylla* are consistently once-branched, arising in leaf axils and forming long terminal, naked shoots with strong leaf suppression, while those of *L. trichodes* are usually more compact with fascicles of axillary capitula on unbranched shoots in leaf axils or occasionally on short once-branched shoots.

Chromosome number

Diploid, 2n=52, self-incompatible (Sorensson, 1989a)

Tree size and form

Subsp. *macrophylla* generally forms a small, slender, and unimpressive tree to 4-7m height and 10-15cm dbh. Tree form is generally upright with light branching. In contrast, subsp. *istmensis* forms a larger, consistently single-stemmed tree to 10-12m height with a compact narrow crown.

Distribution (Fig 46)

Subsp. *macrophylla* is distributed throughout the highlands and coastal foothills of west central Mexico in the States of Colima, Guerrero, Jalisco, Mexico, Michoacán, Morelos, Nayarit, the extreme NW of Oaxaca and the extreme SW of Puebla. Subsp. *istmensis* is restricted to south central Mexico along the coast, Isthmus of Tehuantepec and Pacific foothills in Oaxaca and in a restricted area around San Andrés Tuxtla in southern Veracruz.

Degree-squares: *L. macrophylla*: 32; subsp. *macrophylla*: 22; subsp. *istmensis*: 11

Altitude range: subsp. *macrophylla*: (20-)500-1900m; subsp. *istmensis*: 0-400(-1500)m

Ecogeography

Subsp. *macrophylla* forms a small understorey tree in a variety of forest types including seasonally-dry deciduous tropical forest, dry mattoral (mainly along streambanks), oak forest and oak/pine/juniper forest, and is particularly abundant in the dry tropical forest - oak forest transition zone. It may occur abundantly following disturbance in secondary vegetation or on roadsides. Subsp. *istmensis* is essentially a lowland species of the dry deciduous tropical forest, although it does extend infrequently to mid elevations in foothills in moister oak forest. It is most abundant in disturbed areas and in secondary vegetation where it is fast growing and can dominate early succession, later forming a sub-canopy or understorey tree. Although subsp. *macrophylla* grows at higher elevations, it is only moderately cold tolerant and does not withstand frost, while subsp. *istmensis* is truly tropical. The rainfall throughout the natural distribution of both subspecies ranges from 700-1500mm with a 4-6 month dry season. In Veracruz, *L. macrophylla* is found in much moister forest near Los Tuxtlas.

Phenology

Subsp. *macrophylla*: flowering (July-) September - December (-March); fruiting (January-) March - May (-June); subsp. *istmensis*: flowering October - February; fruiting (February-) March - April

Conservation status

L. macrophylla is of little conservation concern. It is widespread and often locally abundant and is present in several protected areas including the Sierra de Manantlán, Jalisco and Volcán de San Martín Biosphere Reserves.

Star rating: species and both subspecies: Green Star

IUCN threat category: LR:lc

Common names

Subsp. *macrophylla*: *frijolito* (Michoacán), *guaje* (Mexico, Guerrero, Puebla), *guaje amarillo* (Guerrero), *guaje blanco* (Guerrero and Michoacan), *guaje de venado* (Oaxaca), *guaje del cerro, guaje verde, calguaje, zarza guaje* (Guerrero), *guajillo* (Guerrero, Michoacan) and *guaje (huaje) brujo* (Morelos).

Subsp. *istmensis*: *duva de cerro, ndwa de monte* (= *guaje de cerro*, Mixteco, Oaxaca), *guaje, guajito, punta de guaje, tepeguaje rojo, yuanda-tu-cu-u* (Mixteco de la costa), *chicaoaxin* (= *guaje de hormiga*, Zárate, 1994) (all Oaxaca), *marinero, guaje de indio* (Veracruz).

Indigenous use and domestication

Although not as widely used as some other species of *Leucaena*, pods, seeds and young leafy shoots of subsp.

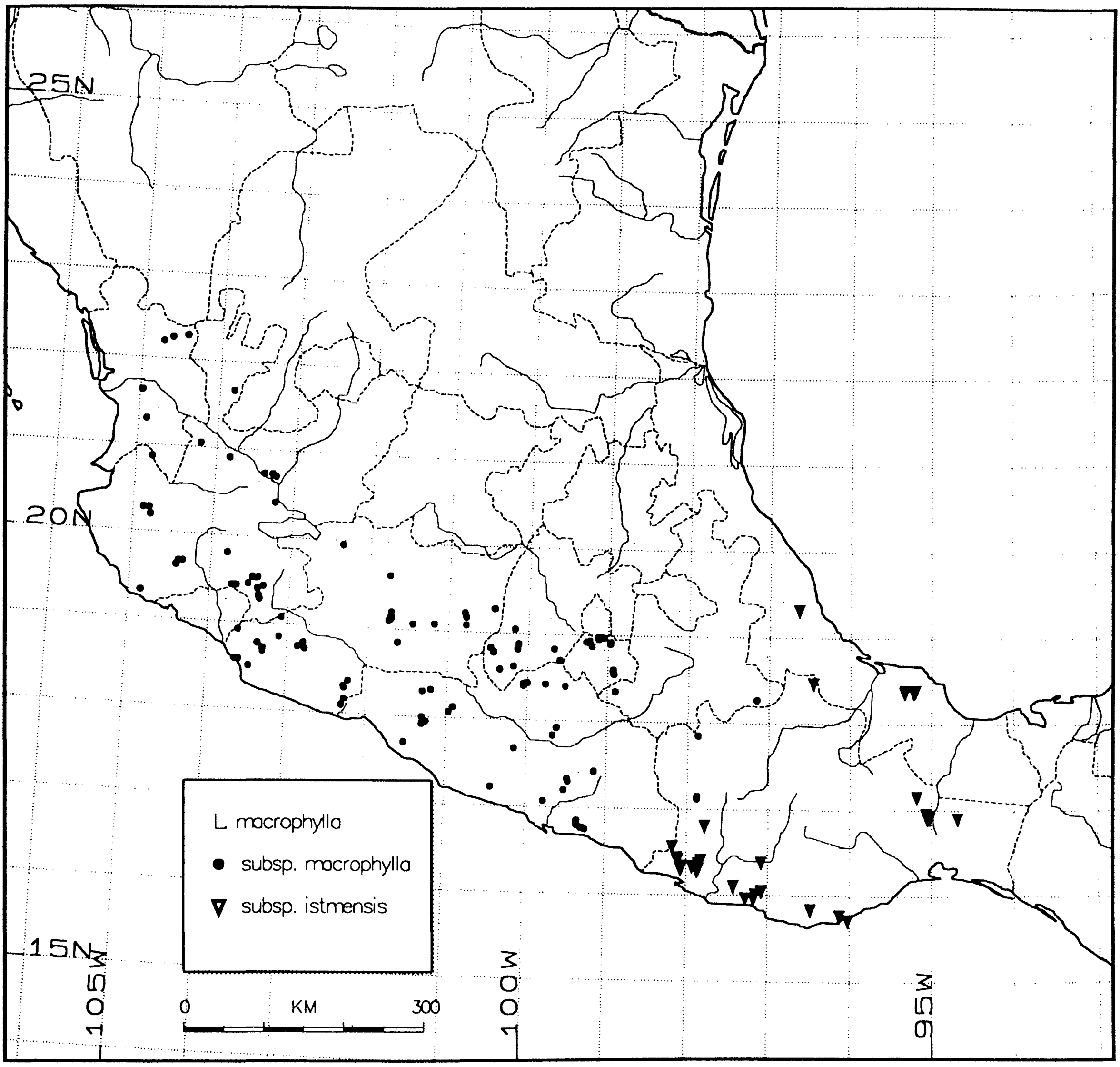

Figure 46 Map of southern Mexico showing the distributions of both subspecies of *L. macrophylla*

macrophylla are eaten either raw or cooked in some areas (Zárate, 1994) and pods are sold in local markets. Zárate (1994) also reports sporadic food use of unripe seeds of subsp. *istmensis*, but pods do not appear to be marketed or widely used. In coastal Oaxaca the wood of subsp. *istmensis* is locally prized for firewood and local construction material. The leaves are eaten by goats and cattle but little use is made of the trees for fodder in the native range.

Exotic use and potential

L. macrophylla has been little used outside its native range. Early trials evaluated subsp. *macrophylla* which showed little potential. However wider testing and inclusion of subsp. *istmensis* suggest that this subspecies may have some potential, at least for wood production, although this is limited by susceptibility to the psyllid. In a replicated trial in Honduras, subsp. *istmensis* was found to grow more than twice as fast as subsp. *macrophylla* and was one of the most productive taxa of all (Stewart *et.al.*, 1991; 1993) forming a tall, single-stemmed tree with good diameter growth and high wood biomass production.

Psyllid resistance: moderately susceptible (damage score 3-5)

Wood quality: mean wood density ranges from below average for *Leucaena* species for subsp. *istmensis* (0.64) to average for subsp. *macrophylla* (0.67) with moderate formation of heartwood (Gourlay *et al.*, in press).

Fodder quality: leaves of both subspecies have very high *in vitro* dry matter digestibility and low condensed tannin content (Stewart and Dunsdon, in press).

Weediness risk: both subspecies are common elements of secondary vegetation and have the potential to spread under open ruderal conditions.

11.12 Leucaena magnifica

Leucaena magnifica (C.E. Hughes) C.E. Hughes Contributions from the University of Michigan Herbarium 21: 286. 1997.

Main attributes
L. magnifica is notable for its late discovery (only in 1984) and its endangered status, both attributable to its extremely restricted natural distribution (to <400km^2). It is one of the most endangered species of *Leucaena* and is of significant conservation concern. It forms a '*magnificent*' medium-sized tree which appears to have good potential for use in agroforestry. It is highly appreciated in its native range for its high quality wood and soil fertility benefits and is maintained in traditional indigenous agroforestry systems. It has proved fast growing in a number of trials, but appears to be moderately susceptible to the psyllid which will limit its wide use as an exotic.

Botanical features (Fig 47)
Bark: on young branches smooth, mid-grey or grey-brown, inner bark salmon-pink, darker grey-brown and rougher with shallow rusty orange-brown vertical fissures and deep red inner bark on older branches and bole
Leaves: pinnae 4-7 pairs; pinnular rachis 10-16 cm long; leaflets (20-)22-26 mm long, 9-12 mm wide, 11-16 pairs per pinna, distinctly asymmetric about the mid vein, oblong, obtuse to rounded apically, rounded to truncate basally, glabrous and strongly glossy above, sparsely hairy below
Petiole gland: pale yellow-green, sessile rounded elliptic dome-shaped or rounded-conical, 3-4 x 1.5 mm
Flower heads: 21-26 mm in diameter, 200-220 pale cream-white flowers per head, in groups of 2-6 at nodes on terminal erect once-branched determinate shoots on which leaf development is strongly suppressed leaving the flower heads, and later the pods, exposed on the periphery of the tree crown
Pollen: tricolporate monads
Pods: (13-)17-23 cm long, (19-)22-26 mm wide, linear-oblong, obtuse or rounded apically, sometimes with a short beak, 3-10 mm long, flattened, deep maroon unripe turning mid orange-brown when ripe, densely covered in velvety hairs, occurring in conspicuous clusters of (5-)11-16 per flower head on branched terminal shoots on the periphery of the tree crown
Seeds: 7.7-8.8 mm long, 4.5-5.2 mm wide, 23,000-30,000 seeds/kg

Closely related species and identification
L. magnifica was first discovered in 1984 (Hughes, 1986) and originally described as a subspecies of *L. shannonii* (Hughes, 1991). Seed of *L. magnifica* was distributed (as OFI seedlots 91/84 and 58/88) under the name *L. shannonii* subsp. *magnifica*. It was raised to species rank based on more detailed character analysis and application of a standard species concept across the genus as a whole by Hughes (1997a).

L. magnifica is closely related to *L. shannonii* but also shows affinities to *L. lempirana* and *L. salvadorensis*. It is recognized as a species distinct from *L. shannonii* based on its once-branched flowering shoot. *L. shannonii* and *L. lempirana* have un-branched flowering shoots, while the flower heads of *L. salvadorensis* occur on older wood. Evidence from chloroplast DNA and isozymes also supports recognition of *L. magnifica* as a species distinct from *L. shannonii* (Harris *et al.*, 1994a; Chamberlain *et al.*, 1996). In addition, *L. magnifica* differs from *L. shannonii* in a suite of quantitative leaf and pod traits (Hughes, 1991): *L. magnifica* has larger leaves with more pairs of pinnae, more pairs of leaflets, larger leaflets, larger flowers, more flowers per flower head, larger pods and seeds, pods with dense velutinous pubescence, that are often deep maroon when unripe, and more pods per flower head than *L. shannonii*.

Chromosome number
Diploid, 2n=52, self-incompatible (Sorensson, 1989a). *L. magnifica* is characterized by extremely low levels of diversity as measured using isozyme markers (Chamberlain *et al.*, 1996).

Tree size and form
L. magnifica forms a small to medium-sized tree, 10-15(-20) m tall, 20-30(-70) cm bole diameter. It is typically branchy when young while older trees tend to have a short clear bole to 6 m and spreading angular branching and an open rounded crown.

Distribution (Fig 48)
L. magnifica is restricted to the Department of Chiquimula in south east Guatemala in a 400km^2 triangle bounded by the towns of Chiquimula, Quetzaltepeque and Ipala. Alongside *L. matudae* it is the most restricted species of *Leucaena*.
Degree-squares: 1
Altitude range: 600-950m

Ecogeography
L. magnifica occurs in degraded and highly disturbed mixed seasonally-dry deciduous tropical forest. It is a tropical species and occurs in areas with 800-1200mm rainfall and a 5-6 month dry season.

Phenology
Flowering (September-) October-November (-December), fruiting February-March, partly deciduous January-March

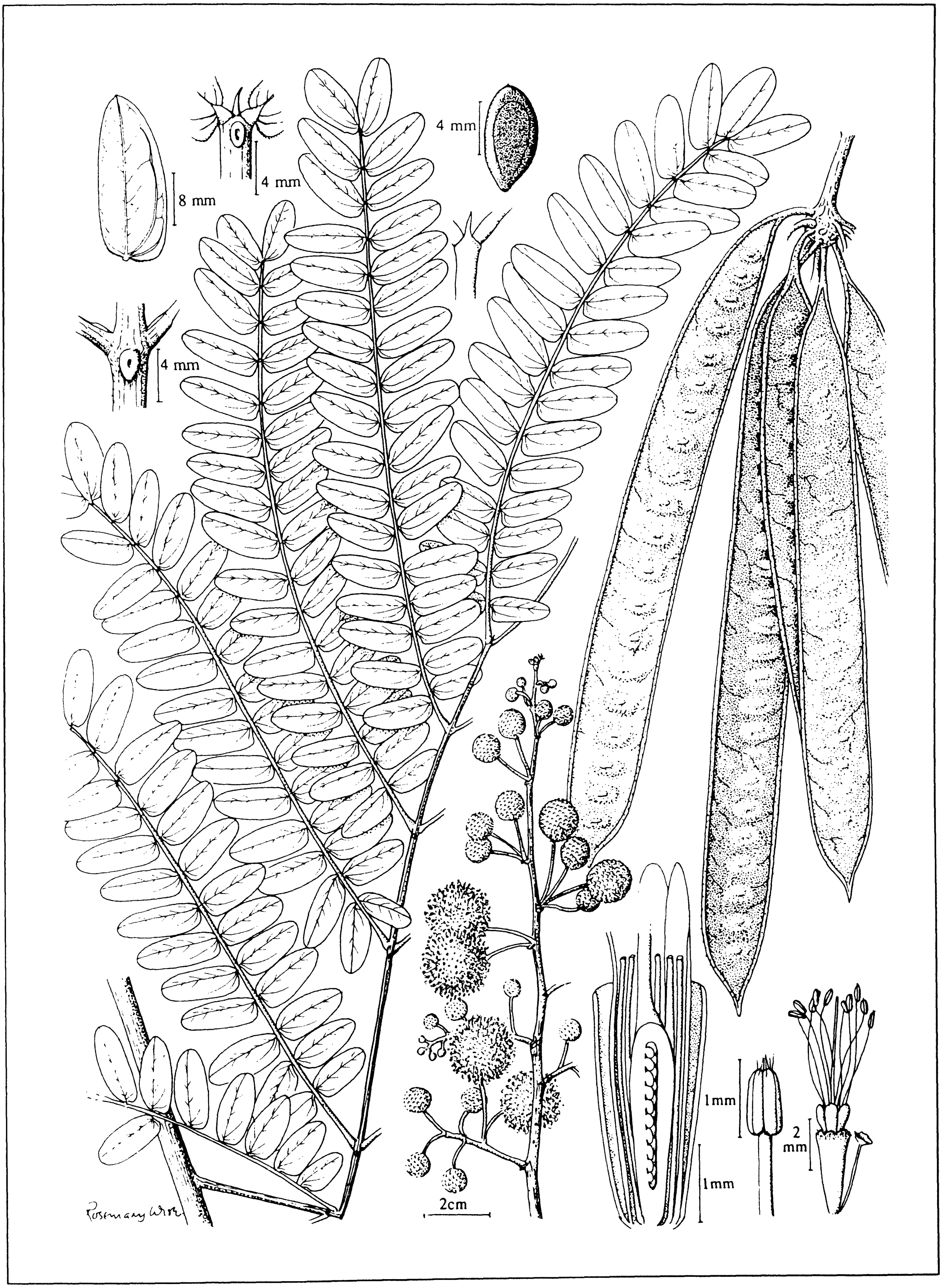

Figure 47 *Leucaena magnifica*

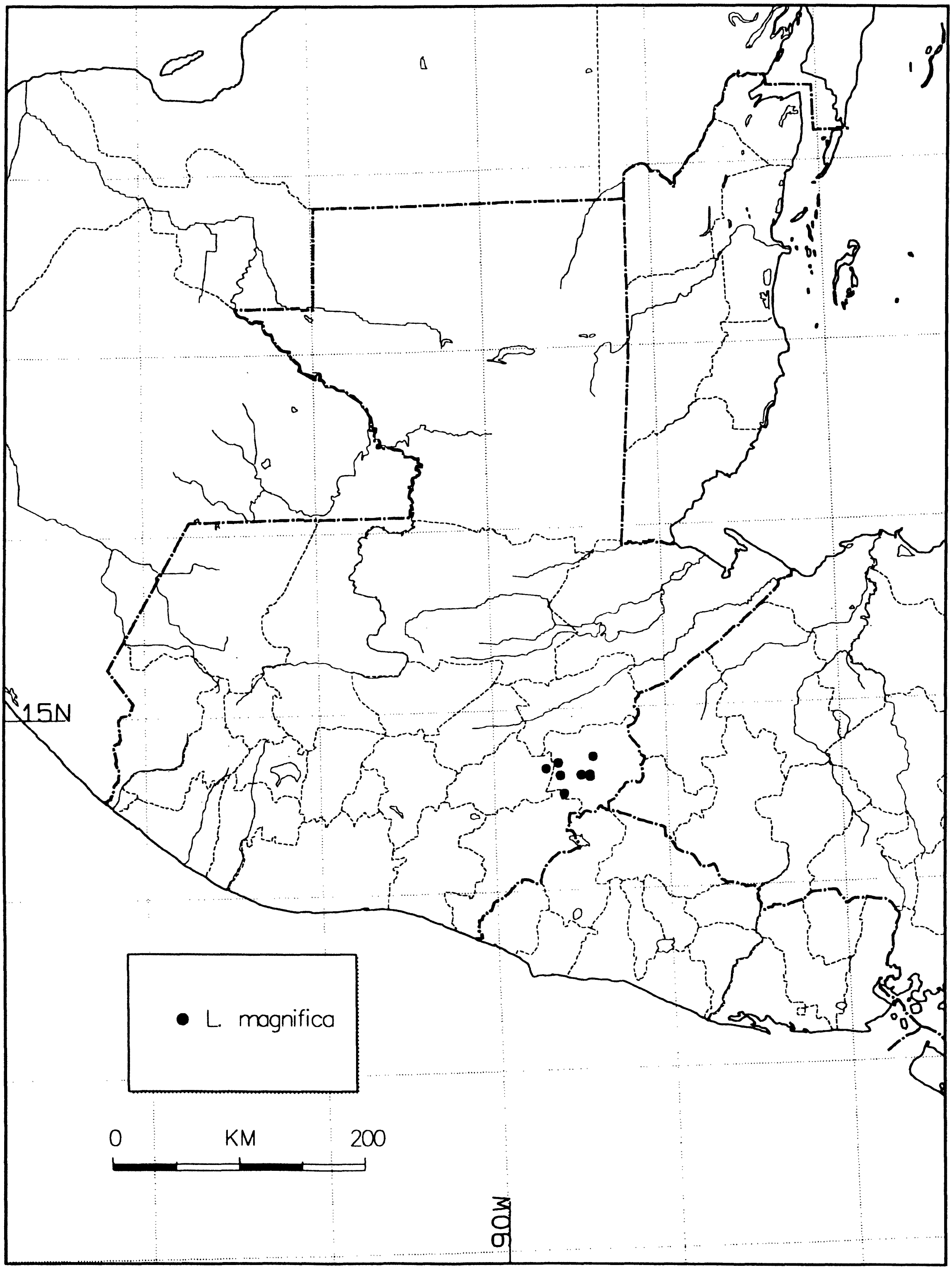

Figure 48 Map of Guatemala showing the distribution of *L. magnifica*

Conservation status

L. magnifica occupies a highly restricted distribution covering a total area of less than 400km². Within that area, it occurs in small, highly fragmented, scattered and degraded populations and is now reduced to fewer than 400 known individuals in its native range (Hughes, 1986; 1991). It is considered endangered and of significant conservation concern. Its active protection and use by farmers in traditional indigenous agroforestry systems offers scope for increased *circa situm*

conservation through use, although sole reliance on *circa situm* measures which are susceptible to future changes in farming systems could be risky (Chapter 8).
Star rating: Black Star
IUCN threat category: EN-B1&2 & C1&2a

Common names
guaje, palo de guaje, vainillo.

Indigenous use and domestication
Within its very localized distribution in Guatemala, trees of *L. magnifica* are well known by local farmers and highly appreciated for a wide range of purposes including firewood, posts and poles. Some farmers encourage and protect seedlings of *L. magnifica* on their fields recognizing the value of litter fall in the maintenance of soil fertility. Trees over crops are sometimes managed by lopping to reduce shade.

Exotic use and potential
L. magnifica has the potential to be a well formed medium-sized tree and to produce high quality wood, as demonstrated in its native range. It has only been cultivated on a few sites in small trial plots or as arboretum entries. In these plantings it has always out performed *L. shannonii* and in Hawaii it is one of the fastest growing species of *Leucaena*. It is however, too early to judge the potential of this species and further testing on a wider range of sites is needed.
Psyllid resistance: moderately susceptible (damage score 4-5)
Wood quality: The mean wood density is high (0.83) compared to other *Leucaena* species with moderate formation of heartwood (Gourlay *et al.*, in press) and, in its native range the wood is considered to be of high quality and dries readily
Fodder quality: *in vitro* dry matter digestibility of leaves is high and condensed tannin contents very low or zero (Stewart and Dunsdon, in press).
Weediness risk: although *L. magnifica* does not generally seed until year 2-3, it can produce prodigious quantities of seed and poses some risk of weediness in open habitats and on ruderal sites.
Propagation: *L. magnifica*, although not fruiting in the first two years, thereafter is often a prolific seed producer with large clusters of pods reminiscent of *L. leucocephala*.

11.13 Leucaena matudae

Leucaena matudae (S. Zárate) C.E. Hughes, Contr. Univ. Michigan Herb. 21: 286. 1997.

Synonyms
Leucaena esculenta (Sessé & Moc. ex DC.) Benth. subsp. *matudae* S. Zárate

Main attributes
Having been discovered only in 1984 and formally described only in 1994, and being restricted to a small area of the dry inland thorn scrub forest of the Balsas Depression of south central Mexico, the status and characteristics of *L. matudae* remain very poorly known. It has been included in field evaluation trials on only a handful of sites, but in all trials has proved to be slow growing and consistently multiple stemmed and branchy. It appears thus to have limited potential for planting but is highly psyllid-resistant and drought-tolerant possibly providing useful genes for inclusion in hybrids.

Botanical features (Fig 49)
Bark: pale whitish metallic grey, gnarled, thick, corky, shedding in thick circular plates to leave a very distinctive scalloped surface, inner bark green then deep blood-red, corky (Fig 20C)
Leaves: pinnae 15-18(-21) pairs; pinnular rachis 8.5-13 cm long; leaflets (4.7-)5.5-6.8 mm long, 1-1.4 mm wide, (39-)60-75(-84) pairs per pinna, asymmetric, linear, acute at apex, asymmetrically truncate at base, glabrous, margins ciliate, only asymmetric midrib visible
Petiole gland: maroon-tinged, short stalked, peg-shaped, cylindrical, 1.5 x 1 mm, at the distal end on adaxial side of petiole (Fig 19A).
Flower head: 18-22 mm in diameter, 90-120 pale cream-white flowers per head, in groups of 1-3 in leaf axils of actively growing shoots with synchronous leaf development
Pollen: tricolporate monads
Pods: 14.8-19 cm long, 12-15(-17) mm wide, 1 or 2 per flower head, linear to linear-oblong, slightly constricted between seeds, flat, dark maroon or maroon-brown, glabrous, leathery, the seed chambers prominent on outside of pods and weakly partitioned between the seeds
Seeds: 7.8-9.4 mm long, 6.1-9 mm wide; approx. 13,000 seeds/kg

Closely related species and identification
Leucaena matudae was originally described as a subspecies of *L. esculenta* (Zárate, 1994), but was raised to species rank by Hughes (1997a) in recognition of its clear morphological and molecular distinction from *L. esculenta*. The species was named in honour of the Japanese botanist, Eizi Matuda, who worked and lived in Mexico. Although morphological and molecular data support the placement of *L. matudae* in the *L. esculenta*

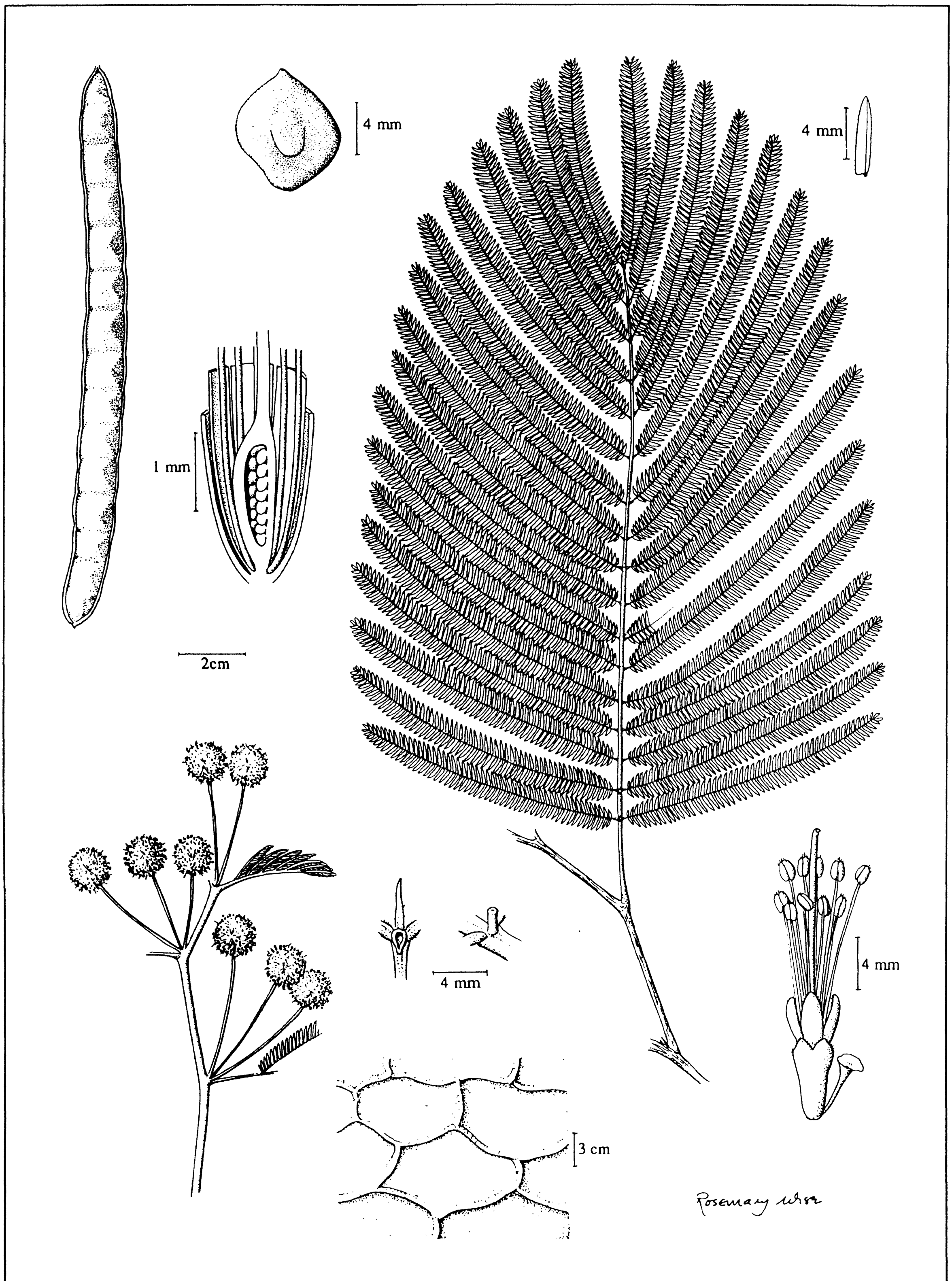

Figure 49 *Leucaena matudae*; scalloped bark surface pattern shown at bottom

alliance, it is distinguished by a set of discrete character states. The petiole gland of *L. matudae* is stalked, erect, cylindrical and quite unlike the large un-stalked, elongate, concave, bath-tub-shaped gland of *L. esculenta*. In addition, *L. matudae* may be distinguished by its round, as opposed to angular shoots, fewer pinnae pairs and leaflets per pinna, fewer flowers per flower head, smaller, weakly constricted pods which are partitioned between the seeds, and oblique alignment of seeds in the pods. Although *L. matudae* shares the same basic bark type as the remaining species in the *L. esculenta* alliance (thick corky bark, a pale metallic-grey surface and deep blood-red inner bark) (Fig 20C), the bark surface pattern in *L. matudae* is quite distinct and unique within the genus in having a scalloped surface resulting from shedding of small circular plates. In fact *L. matudae* shares most character states not with *L. esculenta*, but with *L. involucrata* and *L. pueblana*, but is still readily distinguished by its distinctive bark and unusual slightly constricted pods, but there is little doubt that these three species are closely related.

In addition to these morphological distinctions, *L. matudae* occupies a distinct and highly restricted distribution, endemic to a small area of dry canyons in the central Balsas Depression, in an area of known high endemism with a number of other woody legume species with similar restricted distributions such as *Desmanthus balsensis* and *Acacia velvae*.

Chromosome number
Diploid, 2n=52, self-incompatible (Sorensson, 1989a)

Tree size and form (back cover E)
L. matudae forms a small tree, (5-)8-10 m tall and up to 20-30 cm in diameter. Trees are typically multiple-stemmed and very branchy when young tending to form spreading crowns from an early age. Older trees have a short clear bole to 2-3 m, upright angular branching and a narrow, open crown.

Distribution (Fig 50)
L. matudae is restricted to a small area of the central part of the Rio Balsas Depression in Guerrero, Mexico, around Mezcala, the Canon de Zopilote and Xochipala. All the known botanical collections are from a very restricted area, but it is likely that it also occurs further east along the Rio Balsas.
Degree-squares: 1
Altitude range: 500-860m

Ecogeography
L. matudae occurs as a canopy tree in the dry deciduous tropical forest and dry thorn scrub forest, sometimes in small pure stands, usually on freely drained, dry, rocky calcareous slopes. It is a truly tropical species and shows no cold tolerance. Rainfall in the natural distribution is low, between 500 and 800mm, and highly seasonal with a dry season of up to 7 months.

Phenology
Flowering July - August (-October); fruiting (November-) December - February (-March). Strongly deciduous during the long dry season in native range (November - April).

Conservation status
The known distribution of *L. matudae* is highly restricted within an area of less than one degree-square making this species globally rare. Although locally common in a few areas, it is considered endangered and of significant conservation concern. *L. matudae* grows in a dry forest biodiversity hot spot with many known endemic species justifying establishment of a new dry thorn scrub protected area in this zone.
Star rating: Black Star
IUCN threat category: EN-B1&2

Common names
guaje, guaje brujo, guaje chismoso, guaje jilguero, guaje retinto, guaje risueno (Canon de Zopilote, Guerrero); the *tlapaloaxin* (*guaje escarlata, mexicano*) (information largely from Zárate, 1994)

Indigenous use and domestication
The main value of *L. matudae*, like *L. esculenta* is for its edible pods which are harvested for local consumption in November and December.

Exotic use and potential
L. matudae has only been planted to date in a few small trials and unreplicated plots and its characteristics remain poorly known. Although it is highly psyllid-resistant and has moderate wood density, in the few trials to date, it has proved slow growing (*e.g.* Stewart *et al.*, 1991; 1993). Furthermore, it is consistently multiple-stemmed with a branchy spreading crown from an early age.
Psyllid resistance: Highly resistant (damage score 1-2)
Wood quality: The wood is little used in the native range and mean wood density is moderately low (0.58) compared to other species of *Leucaena*; no heartwood is formed during the first five years (Gourlay *et al.*, in press)
Fodder quality: Stewart and Dunsdon (in press) showed the leaves of *L. matudae* to be low in crude protein, with high condensed tannin levels and moderate *in vitro* dry matter digestibility compared to other species of *Leucaena*
Growth: slow or very slow
Weediness risk: *L. matudae* is one of only five species of *Leucaena* judged to be of lower weediness hazard than *L. leucocephala* due to its less precocious and prolific seeding.

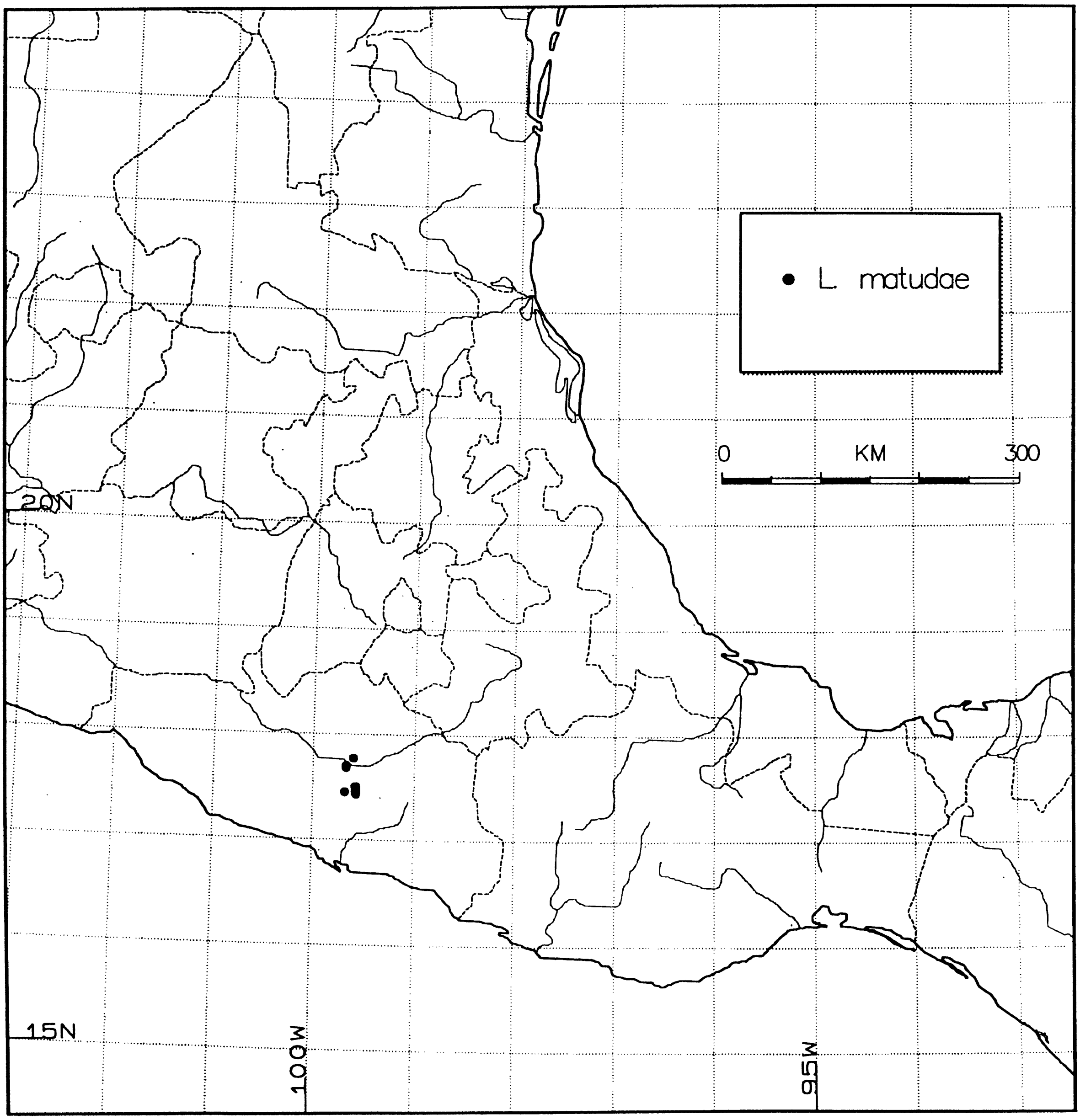

Figure 50 Map of southern Mexico showing the distribution of *L. matudae*

11.14 Leucaena multicapitula

Leucaena multicapitula Schery, Annals Missouri Botanical Garden 37: 302. 1950.

Main attributes

L. multicapitula is one of the less well known species of *Leucaena*. It is restricted to Nicaragua, Costa Rica and Panama. It is one of five species of *Leucaena* with large leaflets and has, in the past been confused with *L. trichodes* and *L. macrophylla*. Recent research has shown without doubt that it is a distinct species. It is distinguished by its pollen, which occurs in 16-grained polyads, and its twice-branched flowering shoots which are both unique within the genus. Apart from *L. diversifolia*, it is the only species of *Leucaena* found growing in wet tropical lowland forest, leading to speculation that it might be tolerant of acid soils. However in Panama, low soil pH is compensated for by high levels of Ca and Mg in the rooting zone. *L. multicapitula* forms a large tree to 25m ht and 50cm dbh, is fast growing in trials, but has low wood density and is highly susceptible to the psyllid.

Botanical features (Fig 51)
Bark: on young branches smooth, mid grey or grey-brown, inner bark salmon-pink; bark on bole mid grey-brown with shallow rusty orange-brown vertical fissures and pale cream-pink inner bark
Leaves: pinnae (2-)3-4(-5) pairs; pinnular rachis 7-10 cm long; leaflets 4-5(-6) pairs per pinna, (35-)40-50(-55) mm long, (15-)18-20(-23) mm wide, ovate, slightly asymmetric, rounded to obtuse at base, apically lanceolate, primary and secondary venation visible
Petiole gland: mid-green, un-stalked, elliptic, cup-shaped, 3-5 x 1-2 mm.
Flower heads: small, 5-8 mm in diameter, 35-50(-60) pale cream-white flowers per head, in groups of 2-5 on exposed twice-branched terminal shoots with leaf development suppressed. Twice-branched flowering shoots are unique within the genus
Pollen: occurring as 16-grained polyads composed of tightly-bound tetrads of tricolporate monads, a pollen type unique within *Leucaena*
Pods: 8-16 cm long, 23-35 mm wide, 1-2(-3) per flower head, oblong or linear-oblong, apically obtuse, or acuminate, sometimes with a short beak, flat, papery, mid orange-brown, glabrous, opening along both margins
Seeds: 7-9 mm long, 3.5-5.4 mm wide, approx 34,000 seeds/kg

Closely related species and identification
The distinction of *L. multicapitula* from *L. trichodes* and *L. macrophylla* has been doubted by several authors due to their close similarity in leaf and pod characters (Schery, 1950; Zamora, 1991); it was considered the same as *L. trichodes* by Janzen and Leisner (1980) and Brewbaker (1987a), and Zárate (1994) suggested treating it as a subspecies of *L. trichodes*. Zamora (1991) followed Schery (1950) and maintained it as distinct from *L. trichodes* distinguishing it by its flowering shoots which are consistently twice-branched and unique within the genus. However, *L. multicapitula* is also readily distinguished from *L. macrophylla* and *L. trichodes* by a number of other characters. Firstly, the petiole gland is concave, cup-shaped with a wide orifice compared to the convex, conical narrow-pored glands of the other species. Hughes (1997b) also discovered and documented a set of pollen and anther characters which clearly distinguish *L. multicapitula* from the remaining species with large leaflets. Taken together, these differences leave no doubt about distinction of *L. multicapitula*
as a separate species. Given these differences there is even some doubt that *L. multicapitula* is closely related to *L. trichodes/L. macrophylla* and its affinities remain uncertain.

Material of *L. multicapitula* from Costa Rica and Nicaragua shows some differences from the Panamanian material; the pods are consistently pointed at the apex compared to the characteristic rounded (sometimes beaked) pod apices of the Panamanian material.

In the absence of flowers, *L. multicapitula* has frequently been confused with *Albizia adinocephala* due to the broad similarity in leaf and pod morphology (Zamora, 1991). Correct identification of these two species is discussed in detail in Section 10.4.

Chromosome number
Diploid, 2n=52, self-incompatible (Sorensson, 1989a)

Tree size and form
L. multicapitula forms some of the largest trees of any species of *Leucaena* reaching, (10-)15-25 (-30) m ht. and 20-60(-80) cm in bole diameter. Trees typically have a short clear bole to 5-7 m, upright angular branching and a spreading, open crown

Distribution (Fig 52)
L. multicapitula occurs sporadically in southern Nicaragua, northern Costa Rica and central and eastern Panama. In Nicaragua it is restricted mainly to southern parts of the Department of Rivas around the SW corner of Lago de Nicaragua where it is abundant; elsewhere in Chontales and Zelaya it appears to be rare and very scattered. It is also restricted in Costa Rica, occurring abundantly only in northern Guanacaste, in a moist area 5-10 km S of the Nicaraguan border at Peñas Blancas (Janzen and Leisner, 1987). It occurs only rarely in Alajuela (Holdridge and Poveda, 1975). *L. multicapitula* is most widespread in Panama occurring from the Azuero Peninsula across central Panama into the eastern province of Darién. It is common in parts of the Azuero, in the provinces of Los Santos and Herrera, and in Cocle and the Canal Zone. On Barro Colorado Island it is rare, occurring only at the N end of the island (Croat, 1978).
Degree-squares: 13
Altitude range: 100-200 (-400)m

Ecogeography
L. multicapitula is a lowland species, and unlike other species of *Leucaena*, apart from *L. diversifolia* grows in wet lowland tropical forest in areas such as the Darién region and Barro Colorado Island in the Panama Canal which receive up to 2500mm rainfall with only a short dry season of 2-5 months. Because of its occurrence in lowland wet forest it was suspected that it might be tolerant of acid soil conditions. Investigations by Alvarez *et.al.* (1987) however, have shown that low soil pH is compensated for by high levels of Ca and Mg in the rooting zone in natural stands of *L. multicapitula* in Panama. It occurs particularly along river banks, streams and gullies, the shoreline on Barro Colorado Island and other gap sites or secondary forest.

Phenology
Flowering (May-) June-August (-October); fruiting (July-) August-October

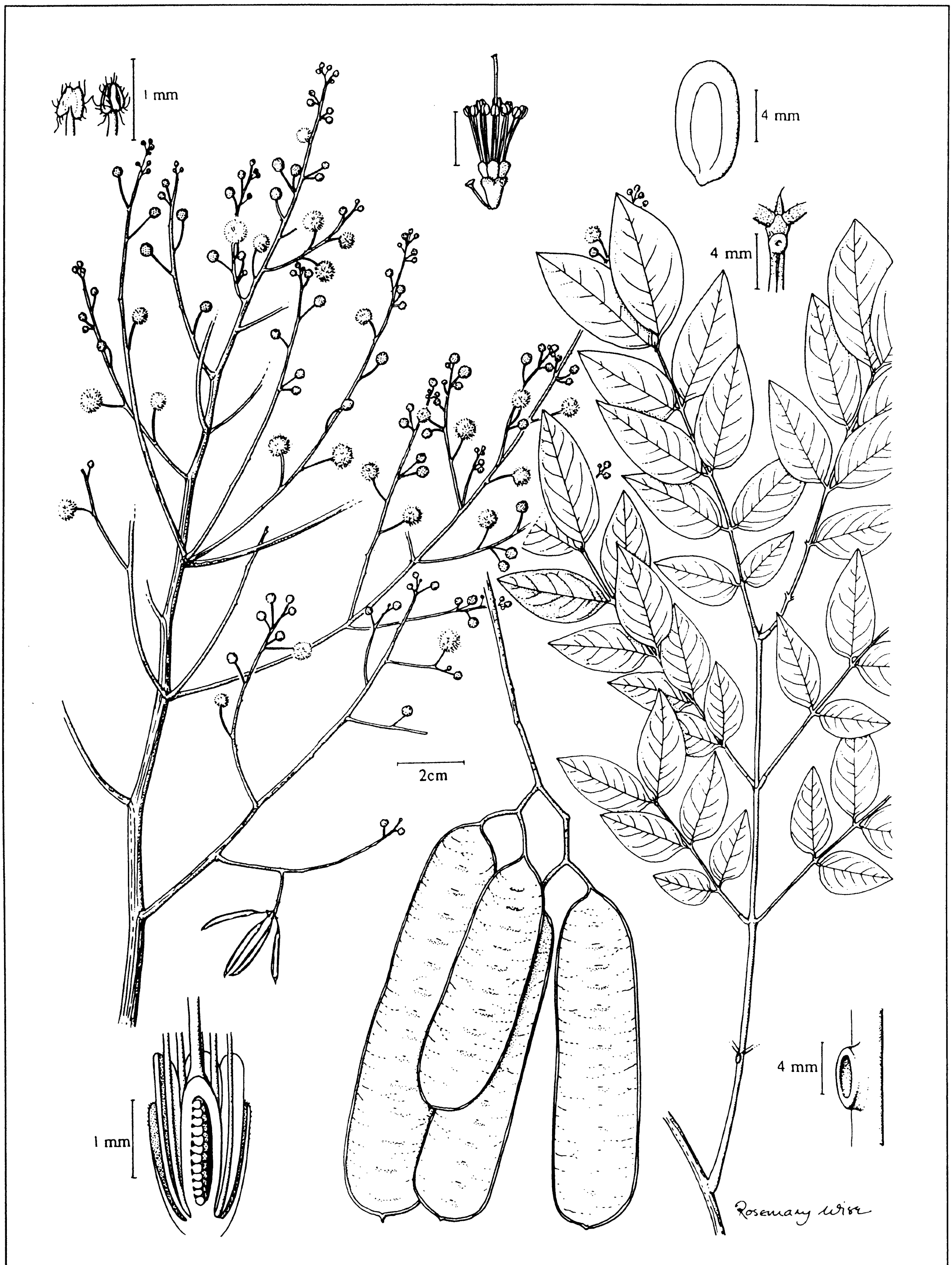

Figure 51 *Leucaena multicapitula*

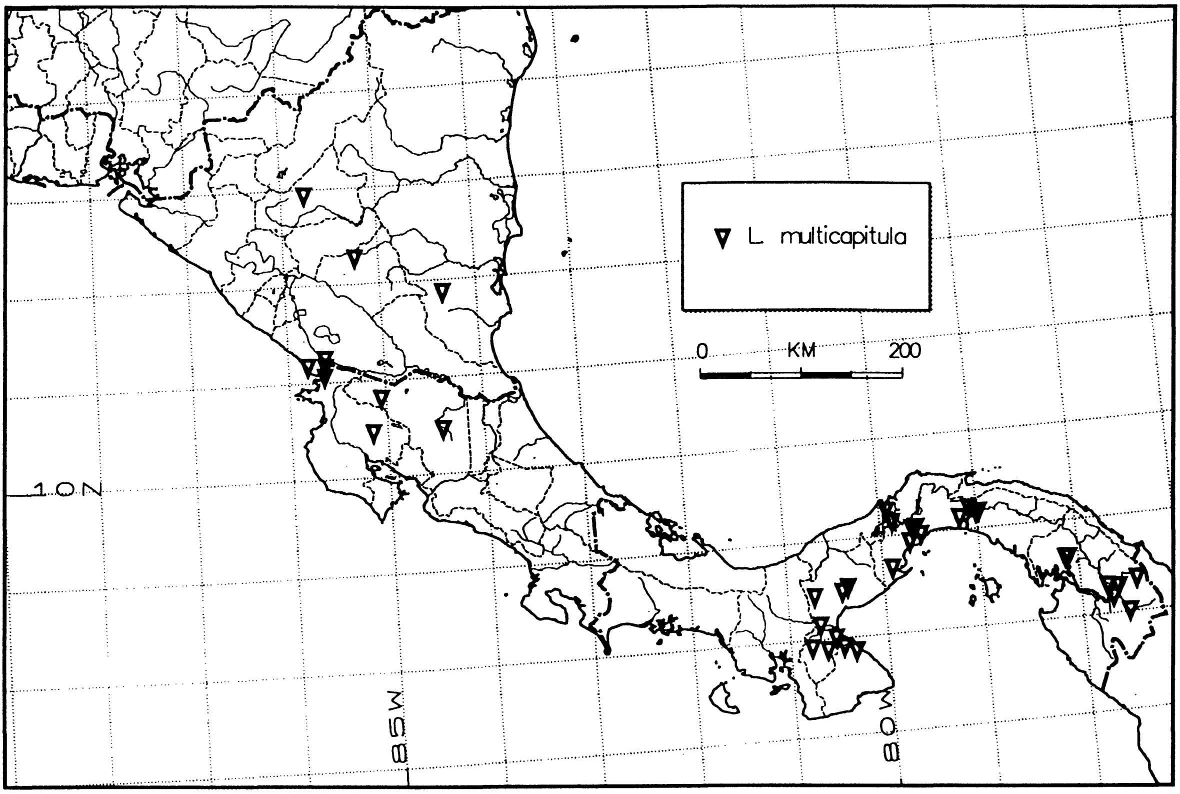

Figure 52 Map of Nicaragua, Costa Rica and Panama showing the distribution of *L. multicapitula*

Conservation status
L. multicapitula is widespread and locally abundant at least in parts its range, although it is apparently infrequent or rare in Nicaragua. It also occurs within the Barro Colorado Island Biological Reserve and is not considered of significant conservation concern except nationally in Nicaragua
Star rating: Blue Star (Gold Star in Nicaragua)
IUCN threat category: LR:lc

Common names
frijolillo (Panamá and Nicaragua); *guajillo* (Nicaragua)

Indigenous use and domestication
Limited to local harvesting of wood for poles and firewood from natural populations.

Exotic use and potential
L. multicapitula forms one of the largest trees of any species of *Leucaena*. Trees are often well formed with a clear bole to 5-7m height and trees are valued for production of construction poles in its native range. It has been reported to be fast growing (Stewart *et al.*, 1991; 1993), but has low wood density and is highly susceptible to attack by the psyllid.

Psyllid resistance: highly susceptible (damage score 5-7)
Wood quality: The large dimensions and reasonable tree form of *L. multicapitula* in the natural populations, particularly mean that it is highly valued by local residents in Panama for poles for house construction. The wood also makes good quality firewood and is easily split. The wood is favoured over the introduced *L. leucocephala* in Panama even though the mean density is among the lowest for all species of *Leucaena* at 0.56; heartwood forms abundantly from an early age (Gourlay *et al.*, in press)
Fodder quality: Leaves are eaten by cattle but it is not widely used for livestock fodder in its native range. In common with the other large leaflet species, *L. multicapitula* leaves have high *in vitro* digestibility and very low condensed tannin contents (Stewart and Dunsdon, in press). Combined with its high crude protein content compared to other species of *Leucaena*, Stewart and Dunsdon (in press) judged *L. multicapitula* to have high leaf quality
Growth: reported to be fast growing in some trials managed for wood production
Weediness risk: significant, but unknown

11.15 Leucaena pallida

Leucaena pallida Britton & Rose, Mimosaceae. North American Flora 2: 126. 1928.

Synonyms
Leucaena esculenta (Sessé & Moc. ex DC.) Benth. subsp. *paniculata* (Britton & Rose) S. Zárate
Leucaena dugesiana Britton & Rose
Leucaena oaxacana Britton & Rose
Leucaena paniculata Britton & Rose

Main attributes
L. pallida has emerged as an increasingly important species in recent years either for use in its own right, or as a parent in artificial hybrids. It has been promoted as a substitute for *L. leucocephala* for forage production in areas where high psyllid pressure limits yields from *L. leucocephala*. *L. pallida* and its hybrid with *L. leucocephala* (KX2) show excellent psyllid resistance, high forage yields, cool tolerance, high seedling vigour and shy seeding, and have spreading branchy habit, a set of traits which are ideal for forage production. However, doubts remain over the nutritive value of *L. pallida* leaves which have a lower edible fraction, higher condensed tannin content and lower digestibility than *L. leucocephala*. *L. pallida* and particularly the KX2 hybrid with *L. leucocephala* have been the focus of intensive selection and breeding efforts in recent years in Hawaii and seed of advanced generation F_6 hybrids is now available. In its native range, *L. pallida* is widely used and cultivated for its edible pods and seeds which complement other species in terms of season of production.

Botanical features (Fig 53)
Bark: smooth, mid metallic-grey, blotched lighter grey with horizontally-aligned pale brown lenticels, inner bark greenish
Leaves: pinnae 15-27 pairs; pinnular rachis 7.5-10.5(-13.5) cm long, sparsely hairy, leaflets 6.1-8 (-9.8) mm long, 1.2-1.9 mm wide, 39-50(-58) pairs per pinna, asymmetric truncate at base, linear or linear-oblong, acuminate at apex
Petiole gland: un-stalked, shallow crater-shaped, elliptical, 3.2-4 mm long x 1.8-3.2 mm wide
Flower head: 14-16 mm in diameter, 95-110 flowers per head, in groups of 3-5 in leaf axils on actively growing shoots, sometimes with suppression of the leaves on the flowering shoot; flowers appear pale pink or dull purplish mauve (exposed anthers and style are pink, pale pink or dull purple)
Pollen: tricolporate monads
Pods: 12-18.5 cm long, 14-18 mm wide, (1-)3-5 per flower head, linear, slightly thickened and leathery, glossy maroon unripe turning mid reddish- or orange-brown, glabrous or occasionally hairy, weakly partitioned between seeds, the seed chambers visible on outside of pod
Seeds: 5.1-6.5 mm wide, 6.2-7.7 mm long, slightly rhombic, aligned transversely or oblique-transversely in pods, 20,000-25,000 seeds/kg

Closely related species and identification
Britton and Rose (1928) distinguished four species (*L. pallida, L. dugesiana, L. oaxacana, L. paniculata*), now considered to be the same thing (Brewbaker, 1985; Hughes, 1993; Zárate, 1994). There has been some disagreement over which is the correct name for this species, and about whether it should be considered a distinct species or a subspecies of *L. esculenta*. The name *L. esculenta* subsp. *paniculata* was used by Zárate (1984a; 1994) and this was followed by Hughes (1993). Some seedlots (notably OFI seedlots 52/87 and 79/92) were distributed using this name. *L. pallida* is now accepted as the correct name following Brewbaker (1985), and in line with the wide use of this name in the agronomic literature (Hughes, in press).

L. pallida belongs in the *L. esculenta* alliance along with *L. esculenta, L. matudae, L. involucrata* and *L. pueblana*, and it shows particular affinities with *L. pueblana* and *L. matudae*. It is distinguished from *L. pueblana* by its pink or purple anthers, larger leaves and leaflets and from *L. matudae* by its unstalked, shallow cup-shaped petiole gland.

Pan (1985) and Pan and Brewbaker (1988) showed *L. pallida* to be a tetraploid (2n = 104) and suggested it had originated as a hybrid between *L. esculenta* and *L. trichandra* based on evidence from cytology, morphology and distributions. Molecular data of Harris *et al.* (1994a) supported a hybrid origin for *L. pallida* with *L. esculenta* as the maternal parent. However, the recent recognition of *L. pueblana* as a distinct species (Hughes, in press) suggests that may be the maternal parent rather than *L. esculenta*.

Seed and botanical material collected from in and immediately around the village of San Pedro Chapulco in Puebla, Mexico was originally referred to *L. pallida*. However, Harris *et al.* (1994a) showed that the chloroplast DNA of this material (OFI seedlot 52/87) did not group with other *L. pallida* accessions, and concluded that the material from San Pedro Chapulco is likely to be a hybrid. The exact identity of this hybrid remains unknown. The unusual performance, psyllid resistance and leaf chemical composition of accession 52/87 and other seed accessions from San Pedro Chapulco (UH accessions K804-806 and K953) (Austin *et al.*, 1995; 1997; Sorensson *et al.*, 1994; Shelton *et al.* pers comm) support the distinction of this material from

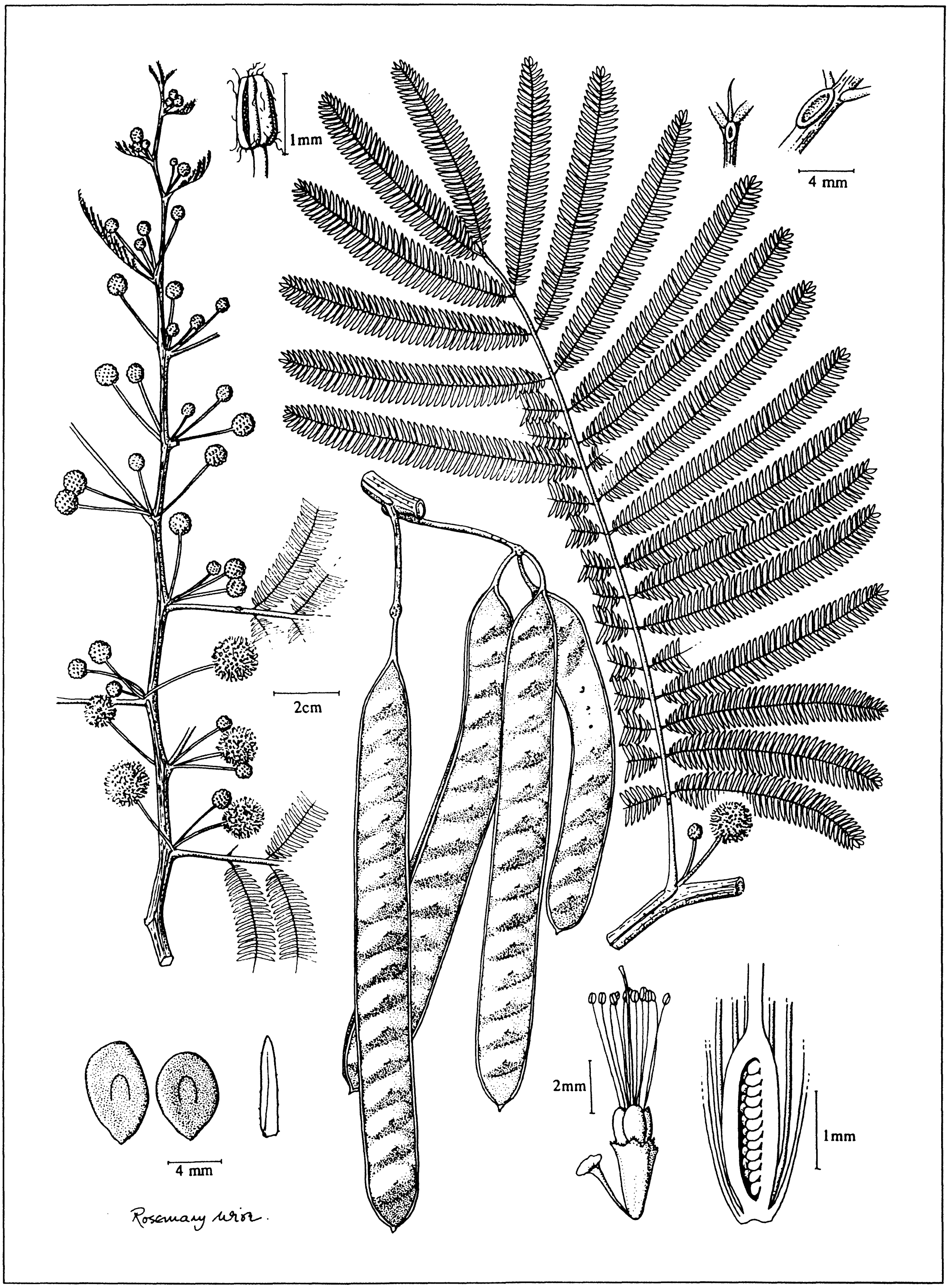

Figure 53 *Leucaena pallida* typical *L. pallida*.

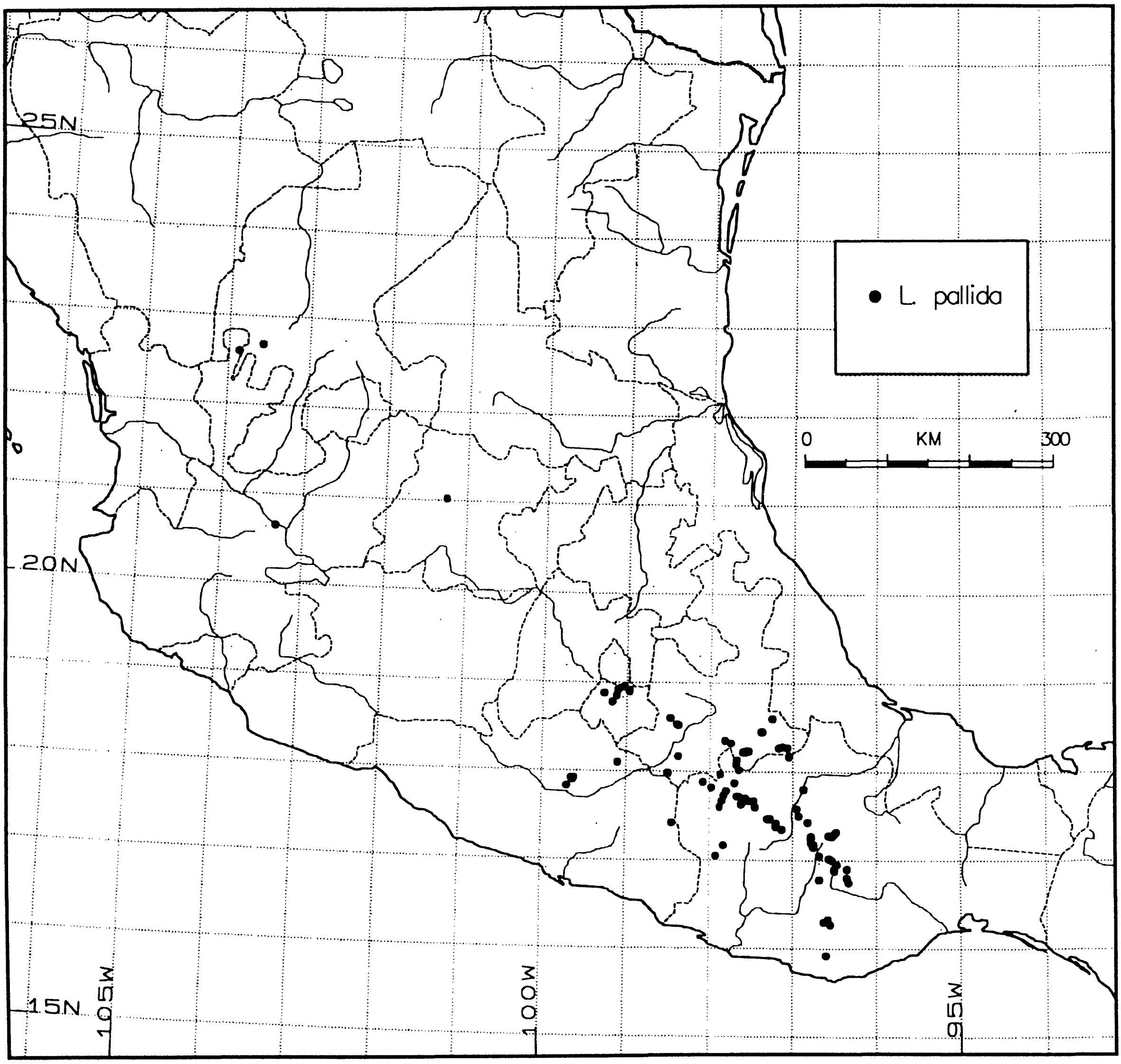

Figure 54 Map of south central Mexico showing the distribution of *L. pallida*

Variants of *L. pallida* with hairy pods have been collected on hills around Mezcala in central Guerrero.

Chromosome number
Tetraploid, 2n=104, self-incompatible (Pan and Brewbaker, 1988; Sorensson, 1989a)

Tree size and form
L. pallida forms a small, often multiple-stemmed tree to 3-7(-10) m tall and 10-15(-30) cm bole diameter with an open irregular spreading crown. Trees are often multiple-stemmed with 2-4 stems per tree but can be upright and narrow
crowned or spreading.

Distribution (Fig 54)
L. pallida is distributed mainly in the mid interior highlands of south central Mexico in the States of Oaxaca, Puebla, Morelos and eastern Guerrero, with sporadic outlying occurrences in Jalisco, Zacatecas and Guanajuato, each represented by only one or two botanical collections, mostly from the last century. *L. pallida* is extensively cultivated for its edible pods and seeds, and these outliers almost certainly represent locations where it has been introduced in cultivation. As for other widely cultivated species such as *L. esculenta* and *L. leucocephala*, the natural distribution of *L. pallida* is now difficult to ascertain. In parts of Oaxaca it is extremely abundant in cultivation in these areas and sometimes locally naturalized.
Degree-squares: 12
Altitude range: (850-)1300-2200(-2480) m

Ecogeography *L. pallida* grows on shallow calcareous soils, in disturbed dry thorn forest, dry mattoral, oak forest, oak-pine forest and particularly in the oak-dry thorn forest transition zone. *L. pallida* occurs at higher elevations often in the same areas as *L. esculenta* and is moderately frost tolerant unlike *L. esculenta*. However, occasional severe frosts (below -8°C) can damage severely all above ground parts although trees can resprout following frost damage. Rainfall in the native range is generally low and highly seasonal with 500-1000mm annual rainfall and a 5-7 month dry season.

Phenology

Flowering (April-) May - October (-December), fruiting (October-) December - March (-April), leafless during part of the dry season from December - March

Conservation status

Few clearly natural populations of *L. pallida* have been found and these are scattered and degraded. However, it is widespread in cultivation in parts of the highlands of south central Mexico and in some areas is extremely abundant in cultivation. At present, *L. pallida* is thus effectively conserved *circa situm* in traditional orchards and agroforestry systems (Fig 19F). Conservation is however dependent on continuation of such conservation through use (Chapter 8).
Star rating: Green Star
IUCN threat category: LR:cd

Common names

Most commonly *guaje, guaje colorado* or *guaje rojo*, names that are applied equally frequently to *L. esculenta* which is perceived to be closely related; *guaja, guajal, guajal de castilla, guaje barbero, guaje delgado* (in reference to its pods narrower than those of *L. esculenta*), *guaje de risa* (Guerrero), *ndwan duchi* (Mixteco, zona La Montana, Guerrero; Casas and Caballero, 1996), *lobada le-eg* (Zapoteco, Guelatao, Oaxaca; Zárate, 1994), *lya gusgih* (Zapoteco de Mitla = *guaje de lluvias*; Zárate, 1994), *guajentudi, huaje, texcalera* and *timbre*.

Indigenous use and domestication

L. pallida is extensively cultivated for its edible pods and seeds. In parts of Oaxaca, in and around many towns and villages, *L. pallida* is extremely abundant, cultivated in "guajales", often along terrace boundaries, often with *L. esculenta, L. confertiflora* and species of *Schinus, Agave* and *Opuntia*. In these areas, it is valued particularly because it produces unripe pods earlier than *L. esculenta*, thereby extending the overall productionperiod. Unripe pods, seeds and flower head buds are harvested and consumed locally as well as being transported and sold in local and regional market towns.

Exotic use and potential

L. pallida shows moderate to high psyllid resistance, good cool and moderate frost tolerance and high growth rates. As a tetraploid it is part of the 'primary genepool' referred to by Sorensson and Brewbaker (1994) and is fully cross-compatible with the other tetraploid species including *L. leucocephala* and *L. diversifolia*. Its greatest promise has been as the *L. pallida* × *L. leucocephala*, KX2 hybrid which has generated considerable interest in recent years for use to replace *L. leucocephala* in forage production in areas where the psyllid has reduced forage yields from *L. leucocephala* (Austin *et al.*, 1995; 1997; Brewbaker and Sun, 1996; Shelton and Brewbaker, 1994; Sorensson, 1995; Sorensson and Brewbaker, 1986; Sorensson *et al.*, 1994). The KX2 hybrid shows excellent psyllid resistance, exceptional forage yields, good cool tolerance and excellent seedling vigour, and is a shy seeder with a spreading branchy habit, a suite of traits which are ideal for forage production. However, doubts remain over the nutritive value of *L. pallida* and the KX2 hybrid compared to the excellent forage quality of *L. leucocephala*. Leaves of *L. pallida* and the KX2 hybrid have a lower edible fraction, higher condensed tannin levels and lower digestibility than *L. leucocephala* (Wheeler *et al.*, 1994). Neither *L. pallida* nor KX2 have shown good potential for wood production although the species is used for firewood in its native range.
Psyllid resistance: moderately to highly resistant (damage score 1-5)
Wood quality: there are few data which indicate wood quality or density of *L. pallida* wood.
Fodder quality: doubts remain over the nutritive value of *L. pallida* and the KX2 hybrid with *L. leucocephala* due to their lower edible fraction, higher condensed tannin content and lower digestibility than *L. leucocephala* (Austin *et al.*, 1995; Shelton, 1995; Norton *et al.* 1995; Wheeler *et al.*, 1994).
Growth: *L. pallida* and particularly the KX2 *L. pallida* × *L. leucocephala* hybrid show exceptional forage yields. Early generation hybrids segregate wildly and are self-incompatible and thus highly variable in growth, form and leaf nutritive value and therefore amenable to recurrent selection (Brewbaker and Sun, 1996). Advanced generation F_6 hybrids have been produced in Hawaii to overcome this variability and seed, marketed as the 'Ohana' variety, is available (Austin and Osgood, 1996).
Weediness risk: *L. pallida* and the KX2 hybrid are self-incompatible and seed less prolifically and precociously than the high weed risk species *L. leucocephala* and *L. diversifolia*. Beyond that, little is known of the weediness risks associated with *L. pallida*.

11.16 Leucaena pueblana

Leucaena pueblana Britton & Rose. North American Flora 23: 126. 1928

Main attributes
The characteristics of *L. pueblana* remain poorly known. Although described as a distinct species in 1928, it was subsequently considered to be the same thing as *L. trichandra* and largely ignored until new field work confirmed that it does in fact represent a distinct species (Hughes, in press). It is notable for its restricted natural distribution in the semi-arid Tehuacan Valley in Mexico and its presumed drought tolerance. In common with other members of the *L. esculenta* alliance, it appears to be highly resistant to the psyllid but have poor fodder quality. Further evaluation will be needed to test the potential of this little known species.

Botanical features (Fig 55)
Bark: whitish, pale to mid metallic-grey, smooth with horizontally aligned, raised, orange-brown pustular lenticels, inner bark thick, corky, bright green then deep orange- to blood-red
Leaves: pinnae (10-)16-22 pairs; pinnular rachis 4-8 cm long; leaflets 4.7-5.8 mm long, 0.9-1.1 mm wide, (30-)40-55 pairs per pinna, slightly asymmetric, linear, rounded at apex, rounded to truncate at base
Petiole gland: reddish-green or brown, un-stalked elliptic shallow crater-shaped, or discoid, 2.4 x 1.6 mm
Flower head: 18-25 mm in diameter, 100-140 flowers per flower head, in groups of 2-6 at nodes on un-branched terminal determinate shoots, the leaves suppressed on flowering shoots; flowers cream-white
Pollen: tricolporate monads
Pods: (10-)13-15 cm long, 13-15 mm wide, 1-2 per flower head, linear, the seed chambers raised and clearly visible, valves green, strongly tinged scarlet unripe, rich orange-brown, glabrous, slightly lustrous when ripe, leathery or slightly woody, opening slowly along both sides
Seeds: 7.5-8 mm long, 5.8-6.1 mm wide, aligned obliquely in pods

Closely related species and identification
Leucaena pueblana was treated as conspecific with *L. trichandra* (*L. diversifolia* subsp. *stenocarpa*) by both Brewbaker (1987a) and Zárate (1994). Detailed examination of the original botanical material of *L. pueblana* reveals a set of characters that distinguish it from *L. trichandra. L. pueblana* is distinguished by its angular shoots with corky ridges, the arrangement of the flower heads on exposed terminal shoots on which leaf development is suppressed, the longer flower head stalks, larger flowers, glabrous ovary and rounded leaflet tips none of which are characters of *L. trichandra*.

The true affinities of *L. pueblana* lie with the *L. esculenta* alliance, and with *L. pallida* and *L. matudae* in particular. It shares the characteristic thick corky, pale metallic grey bark of the *L. esculenta* group. It groups closely with these species in the morphological and chloroplast DNA analyses (Harris *et al.*, 1994a; Hughes, in press; Sections 2.6 and 2.6). *L. pueblana* is distinguished from *L. pallida* by its white or cream-white flowers, its smaller leaves with more pinnae pairs, and smaller leaflets.

Chromosome number
Unknown

Tree size and form
L. pueblana forms a small tree, 5-10 m tall and 5-20(-30) cm in bole diameter. Trees are sometimes multiple-stemmed and typically branchy when young, with an open rounded crown when older.

Distribution (Fig 56)
L. pueblana occupies a clearly defined distribution, restricted to below 2000m in the Tehuacan and Cuicatlán Valley system of southern Puebla and northern Oaxaca in Mexico. That there is an endemic *Leucaena* in the Tehuacan Valley comes as little surprise given that it is an area well known for its high endemism (Smith, 1965). Several other species of *Leucaena*, including *L. confertiflora, L. esculenta, L. leucocephala* and *L. pallida* also occur in or around the fringes of the Tehuacan Valley. Of these, *L. confertiflora* and *L. pallida* occur at higher elevations, sometimes in cultivation, generally above *L. pueblana. L. esculenta* is very widely cultivated but doubtfully native (Zárate, 1994), especially in the mid elevation zone (1000 - 2000 m) and *L. leucocephala* is very abundant, but almost certainly introduced (Zárate, 1994) and only in cultivation in the lower valley (500 - 1500 (-2000)m). By contrast *L. pueblana* appears to be native throughout the lower to middle zone (500 - 1500m), occurring scattered in undisturbed dry thorn scrub.
Degree-squares: 3
Altitude range: 580-2000 m

Ecogeography
L. pueblana forms a canopy tree in the prevalent dry thorn scrub forest of the mid and lower Tehuacan Valley. It is a mid-elevation species, but the limits of its distribution, below 2000m suggest that it is intolerant of frost. It grows under semi-arid conditions with between 500 and 700mm annual rainfall and a prolonged dry season of 6-8 months and is, with *L. collinsii* subsp. *zacapana* and *L. matudae*, likely to be amongst the most drought-tolerant species in the genus.

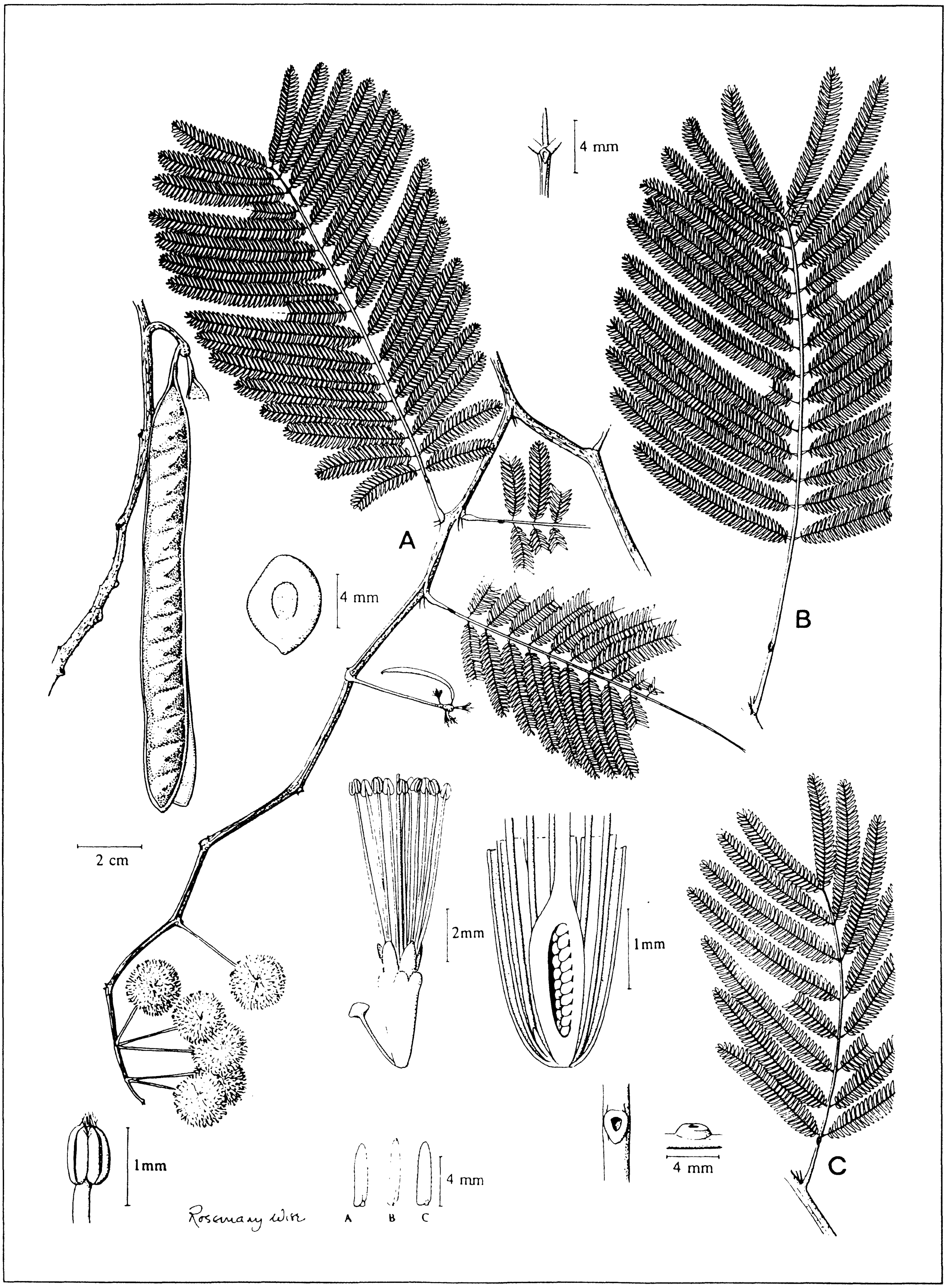

Figure 55 *Leucaena pueblana*; **A-C** showing variation in leaf morphology

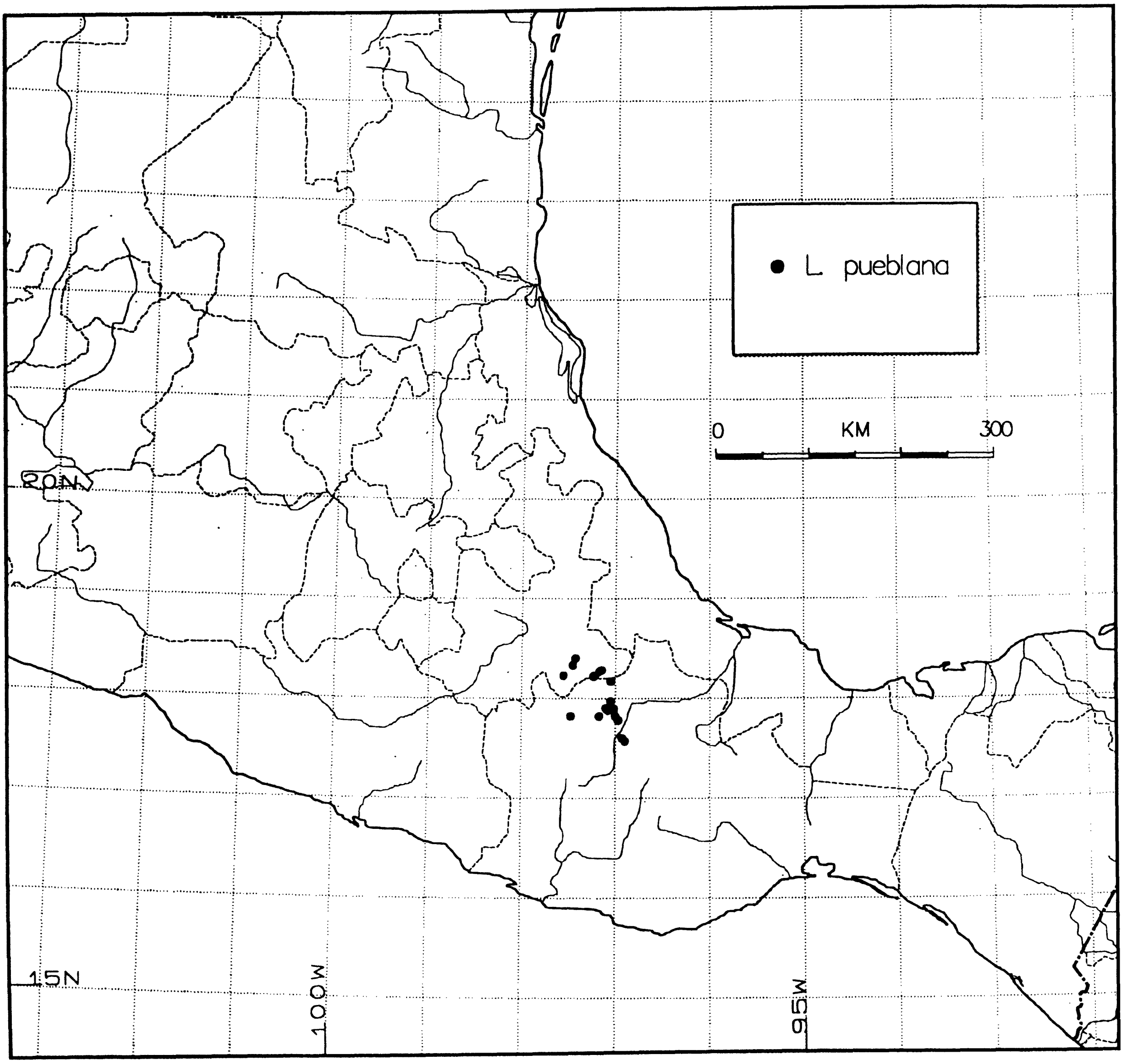

Figure 56 Map of south central Mexico showing the distribution of *L. pueblana*

Phenology
Flowering November-December, fruiting (December-) January-February (-March); deciduous December-May

Conservation status
L. pueblana occupies a restricted distribution, endemic to the Tehuacan Valley. It is never abundant and regeneration is apparently susceptible to grazing pressure. It is therefore considered vulnerable to further degradation and of some conservation concern
Star rating: Gold Star
IUCN threat category: VU-B1&2

Common names
Guaje

Indigenous use and domestication
L. pueblana has not been recorded in cultivation in Mexico, and it is likely that it is the only species of *Leucaena* native in these lower reaches of the Tehuacan valley. Perhaps because it is not widely cultivated, or because it has remained poorly known, the ethnobotany of *L. pueblana* has not been widely investigated. Nevertheless Smith (1967) mentions the occurrence of *L. pueblana* seed and pod fragments in some of the pre-Columbian cave settlement deposits of the valley indicating that seeds and unripe pods may have been harvested for food from the dry thorn scrub, possibly as early as 5,000-3,500 BC, and more definitely from 200 BC onwards.

Exotic use and potential
L. pueblana is one of the least well known species of *Leucaena*. It has been included in trials on a handful of sites, notably in Australia, only in the last few years, following the recent realization that it does in fact represent a species distinct from *L. pallida*.
Psyllid resistance: highly resistant (damage score 1-2)

Wood quality: unknown
Fodder quality: initial data indicate that *L. pueblana* may have low nutritive value, due to the low edible fraction, low *in vitro* digestibility and moderate condensed tannin content of its leaves.
Growth: unknown
Weediness risk: unknown

11.17 Leucaena pulverulenta

Leucaena pulverulenta (Schltdl.) Benth., Hooker Journal of Botany 4: 417. 1842.

Synonyms
Acacia pulverulenta Schltdl.

Main attributes
L. pulverulenta is one of the better known species of *Leucaena* having been introduced into cultivation, and artificial hybridization programmes, earlier than the majority of species. It is known to show moderate cold and limited frost tolerance, produces hard, heavy, close-grained wood, is fast growing and its leaves provide acceptable fodder. Early interest in *L. pulverulenta* arose due to the low mimosine content of the leaves and its potential to be used in breeding low mimosine hybrids. The *L. pulverulenta* × *L. leucocephala* hybrid, which is extremely vigourous and has low mimosine content was both the first spontaneous hybrid documented in *Leucaena* and the first hybrid in the genus to be used commercially. However, the potential of *L. pulverulenta* and its hybrid with *L. leucocephala* has been short lived due to their overwhelming susceptibility to the psyllid and they have been little used in recent years except in areas where the psyllid does not present a significant limitation.

Botanical features (Fig 57)
Bark: on young branches smooth, pale orange-brown, pale yellow or grey-brown on bole with shallow rusty orange-brown vertical fissures, the inner bark green
Leaves: young foliage whitish-grey (densely covered in short white hairs); pinnae (12-)14-18 pairs; pinnular rachis 5-6.5 cm long, densely covered with short white hairs; leaflets (4-)4.4-5.2 mm long, 0.8-1 mm wide, (55-) 61-69(-75) pairs per pinna, oblong, acute at base
Petiole gland: large, oblong, slightly asymmetric, irregularly lumpy or wart-like, dark reddish-brown, 3 mm long x 1.5 mm wide and 1 mm tall
Flower head: 15-20 mm in diameter, the buds lax, with few (45-65) flowers per flower head, in groups of 3-7 in leaf axils, often densely packed on actively growing shoots; flowers cream-white
Pollen: tricolporate monads
Pods: 12-18(-21) cm long, (14-)16-24 mm wide, 1 or 2(-3) per flower head, narrowly linear-oblong, acute at base, round at tip usually with a short straight or recurved point, flat, papery, dark brown, slightly lustrous, glabrous, opening along both sides
Seeds: 3.2-4.2 mm wide, 6.5-7.9 mm long, aligned transversely in pods, 32,000-52,000 seeds/kg

Closely related species and identification
L. pulverulenta is unique within the genus in possessing basally-united petals, a character state associated with other genera, glabrous anthers, chromosome no. 2n = 56 (shared with *L. retusa* and *L. greggii*) and presence of a protrusion on the anther (shared with *L. retusa* and *L. cuspidata)* (Hughes, 1997b). In addition, Zárate (1994) pointed out the unusual spiral phyllotaxy found in *L. pulverulenta* (shared with *L. diversifolia* and *L. leucocephala*). Finally, the young shoots and developing leaves of *L. pulverulenta* are densely covered in a short white or whitish-grey hairs, which are also unique within the genus. Thus *L. pulverulenta* is an unusual species within *Leucaena*. Its affinities lie firstly with *L. retusa* and *L. greggii*, but also with the two tetraploid species *L. leucocephala* and *L. diversifolia*.

Evidence from the analysis of chloroplast DNA data suggests a close relationship between *L. pulverulenta, L. leucocephala* and *L. diversifolia* (Harris *et al.*, 1994a; Hughes and Harris, in press). This suggests *L. pulverulenta* as the most likely maternal parent for these two tetraploids. The occurrence of all three species growing together in central Veracruz, Mexico is consistent with possible origins that involved *L. pulverulenta* as one parent.

A close relationship between *L. pulverulenta* and *L. diversifolia* is also suggested by morphological similarities and *L. diversifolia* is the species most likely to be confused with *L. pulverulenta* particularly in areas where the two occur together. The two species have very similar leaves in terms of numbers of pairs of pinnae, number of pairs of leaflets and size of leaflets, the pods are almost identical and the inflorescence is similarly lax as seen in bud with few flowers per flower head. *L. pulverulenta* is distinguished from *L. diversifolia* by its characteristic whitish-grey hairs, its lumpy wart-like, as opposed to cup-shaped elliptic, petiole gland, its glabrous anthers and cream-white, as opposed to pinkish flowers.

A number of putative spontaneous hybrids between *L. pulverulenta* and *L. leucocephala* have been reported from genera such as *Alantsilodendron, Dichrostachys* and *Calliandropsis* (Section 2.2). Other unusual

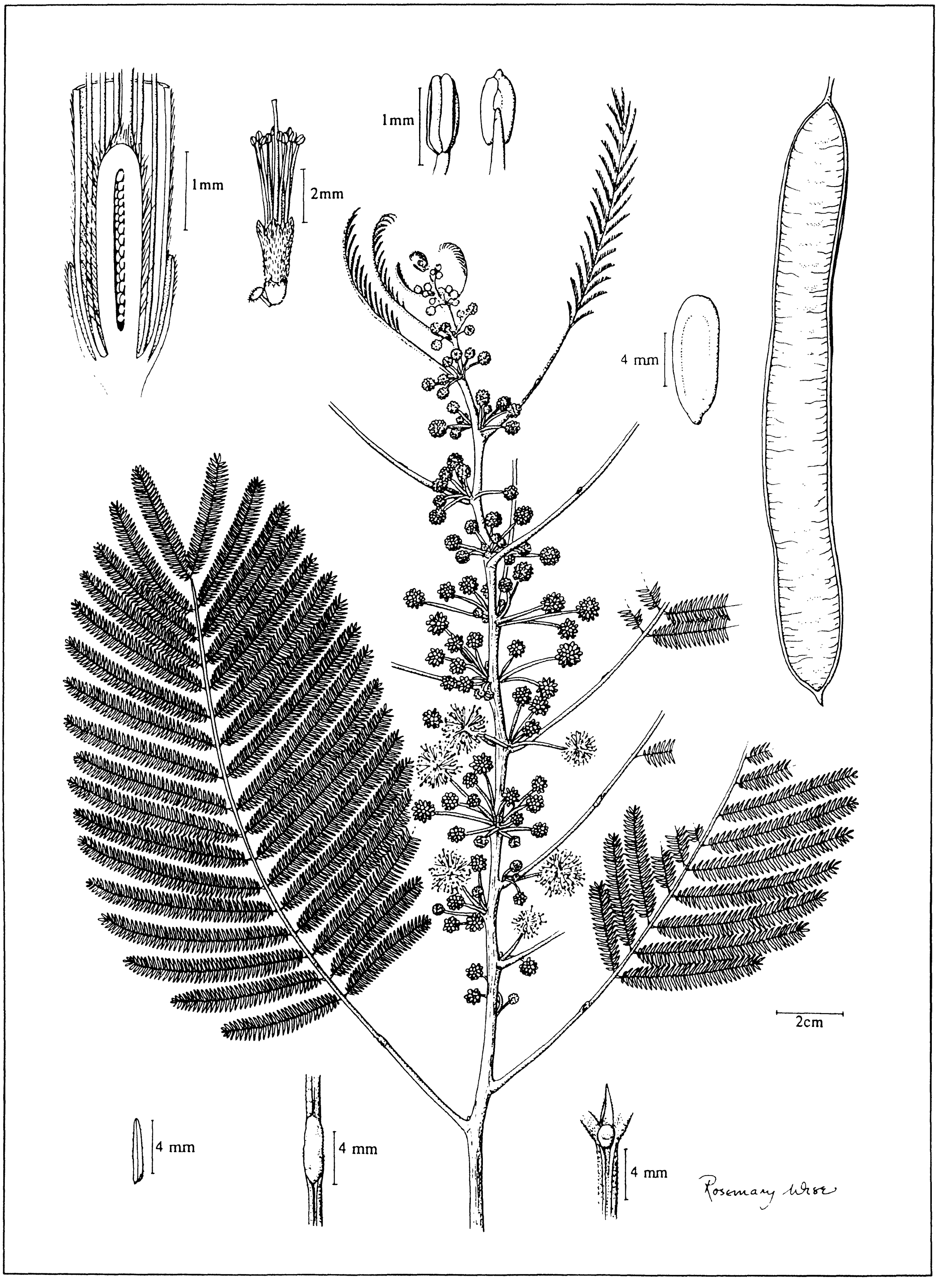

Figure 57 *Leucaena pulverulenta*

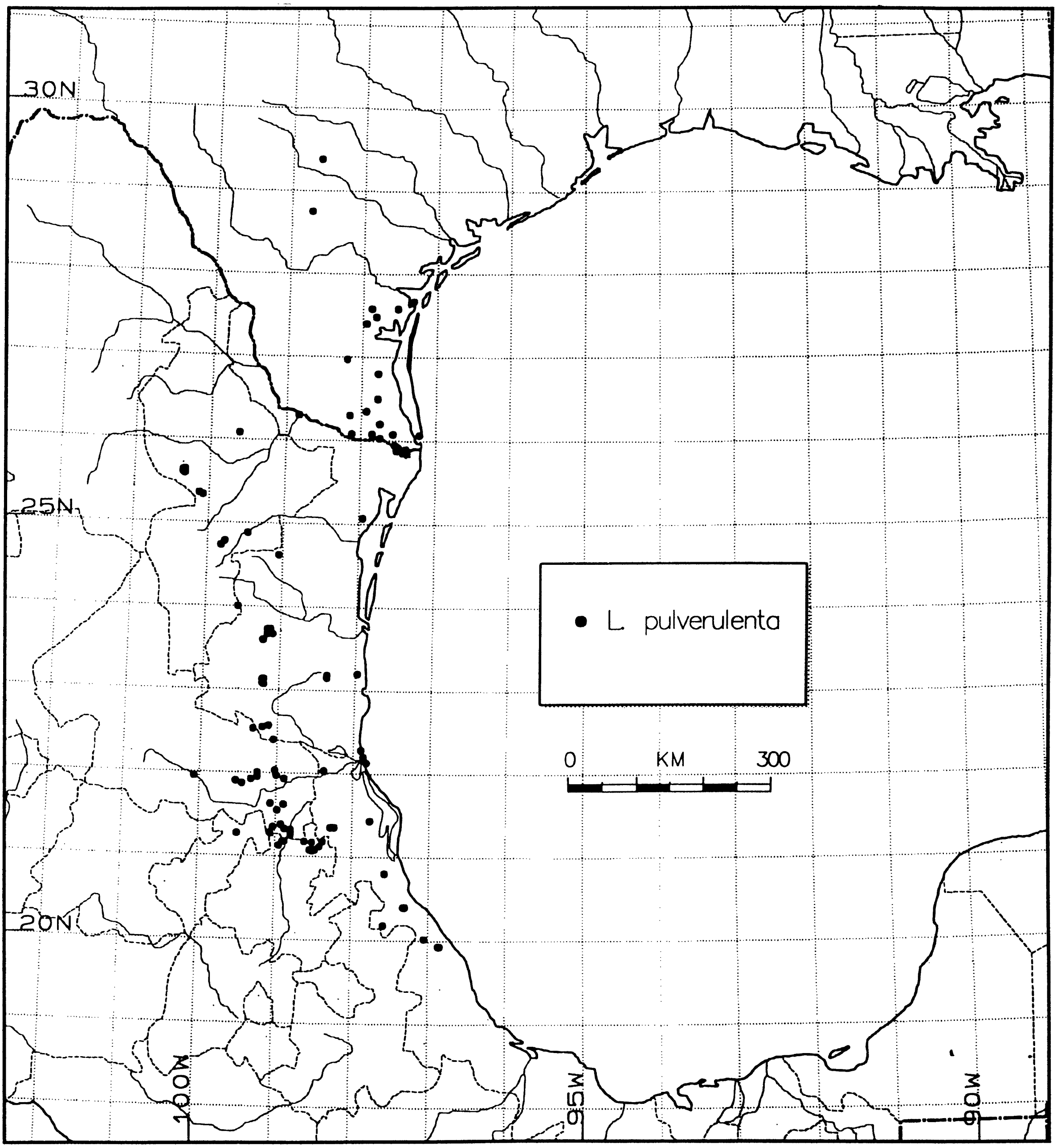

Figure 58 Map of north eastern Mexico showing the distribution of *L. pulverulenta*

character states include Indonesia (Dijkman, 1950; Lowry *et al.*, 1984) and Texas, U.S.A. (Correll and Johnston, 1970). These hybrids are most likely to be the result of artificial sympatry following cultivation of one or both parents (Sections 4.6 and 5.5).

Chromosome number

Diploid, 2n=56, self-incompatible (Turner and Fearing, 1960; Gonzalez *et al.*, 1967)

Tree size and form

In the natural stands, *L. pulverulenta* is generally a small tree or shrub often in secondary regrowth. However Isley (1973) states that *"it is almost a shock to realise that massive trees in a few preserves of native vegetation along the lower Rio Grande belong to this same species"* and Sargent (1889) reports trees as large as 20m height, again in the Rio Grande valley, indicating the potential of the species in terms of size. *L. pulverulenta* thus forms a small to medium-sized tree 20-50 cm in bole diameter, usually with a clear bole up to 10 m ht. and a light feathery crown.

Distribution

L. pulverulenta is distributed primarily along the wet, east facing slopes of the Sierra Madre Oriental in NE Mexico from around Misántla in central Veracruz, north

through Hidalgo, San Luis Potosí, Tamaulipas to around Monterrey in Nuevo León. It is also found in some areas on the lower coastal plains surrounding the Gulf of Mexico, extending north into Texas. In Texas, *L. pulverulenta* is commonly cultivated as an ornamental in towns especially in south Texas in Cameron and Hidalgo Counties, but also further north for example in Kingsville; it was also reported as an ornamental from New Orleans, Louisiana by Sargent (1921). In parts of south Texas it is abundant and weedy forming thickets along roadsides, canal banks and on waste ground. Being both cultivated and weedy has led to speculation that *L. pulverulenta* may be introduced to Texas, but Sargent (1889) and Isely (1973) report large trees to 20m ht. that are apparently indigenous in the lower Rio Grande Valley. *L. pulverulenta* also occurs spontaneously in parts of western Java, Indonesia, especially around Bandung (Nielsen, 1992b), where it is introduced in cultivation and where hybrids with *L. leucocephala* have apparently arisen spontaneously and been subsequently cultivated (Dijkman, 1950).
Degree-squares: 19
Altitude range: 0-1400 (-1850) m

Ecogeography
L. pulverulenta ranges in latitude from 19° to 29° N and in altitude from sea level to 1500m and has occasionally been recorded as high as 1800m elevation. Light frosts occur in parts of the natural range; occasional severe frosts apparently damage *L. pulverulenta*. The moderate frost tolerance is confirmed by the studies of Glumac *et al.* (1987) using cultivated material in Texas. More northerly occurrences in Texas may indeed be introductions, with trees killed back following occasional severe frosts (Glumac *et al.*, 1987; Correll and Johnston,. 1970). Rainfall in the native range varies from 700 to 1000mm with a 5-6 month dry season and *L. pulverulenta* thrives in seasonally dry conditions where tested in Honduras (Stewart *et al.*, 1991; 1993). *L. pulverulenta* typically grows on shallow soils over limestone. It occurs as an understorey tree in a variety of forest types from moist evergreen submontane *Liquidambar - Podocarpus* forest to drier oak or pine-oak forest and extending into dry mattoral in some areas; it also occurs abundantly in secondary vegetation, along roadsides and in bush fallows and can be a ruderal weed on roadsides and waste ground.

Phenology
Flowering (November-) February-July (-August), fruiting August-November

Conservation status
L. pulverulenta is of little or no conservation concern. It is widespread and often locally abundant in secondary vegetation such as bush fallows, sometimes a ruderal weed of roadsides or waste ground. *L. pulverulenta* is also present in several biological reserves including the Cerro de la Silla (Monumento Natural) and the El Cielo/Sierra Alta Tanchipa Biosphere Reserve. It is widely cultivated as an ornamental in south Texas.
Star rating: Green Star
IUCN threat category: LR:lc

Common names
barba de chivo (San Luis Potosí); more widely in Mexico: *guache, guache de monte, guaje, guaje de monte, guajillo, huash, huaxe*; *liliakiwi* (Totonaco, considered a wild form of *liliak*, *L. leucocephala*); *thuk* (Huastec) San Luis Potosí and Veracruz; *timbre, tzuqui, palo seco* (San Luis Potosí); *tze* (= *guaje* in Mazateco); *tepeguaje* in Texas

Indigenous use and domestication
L. pulverulenta is known for food and medicinal use (Alcorn, 1984) and is considered an important species in the bush fallow system of the Huastec region of NE Mexico. Zárate (1994) reports that the unripe seeds and flower buds are eaten raw with enchiladas.

Exotic use and potential
The early promise shown by *L. pulverulenta*, with its high wood quality, acceptable forage quality, notably low mimosine content, moderate cold tolerance and fast growth has been short lived due to its overriding susceptibility to the psyllid. The *L. pulverulenta* × *L. leucocephala* hybrid was both the first spontaneous hybrid documented in *Leucaena* (Dijkman, 1950; Lowry *et al.*, 1984; Brewbaker, 1988) and the first artificial hybrid to be used commercially. The hybrids, being triploid, are largely sterile and, in Indonesia have been propagated by grafting for use as shade trees over tea where seedless varieties are preferred to avoid regeneration and weed problems (Dijkman, 1950). It was the focus of breeding, prompted by its low mimosine content and excellent vigour. It was artificially created in Hawaii (Gonzalez *et al.*, 1967) Australia (Bray, 1984; 1986; Bray *et al.*, 1988; Bray and Fulloon, 1987), India (Gupta, 1990; Gupta *et al.*, 1986) and Colombia (Hutton, 1985) and shown to outperform *L. leucocephala* (Brewbaker, 1987b). However, As with *L. pulverulenta* itself, its promise has been short lived due to its overwhelming susceptibility to the psyllid. *L. pulverulenta* is frequently cultivated as an ornamental or shade tree in gardens in south Texas.
Psyllid resistance: moderately-highly susceptible (damage score 4-7)
Wood quality: The wood of *L. pulverulenta* is recognized to be of high quality, although wood density of juvenile wood can be rather low and variable. The wood is reported to be heavy, hard, close-grained with rich dark-brown heartwood, reflected in the common name *lead tree*. It was used in the past for lumber, including railway sleepers in south Texas (Sargent, 1921; Standley, 1922; Isely, 1970; 1973). Mean wood density of five year-old trees in Honduras was moderate (0.65) compared to other *Leucaena* species, but had a high proportion of heartwood (Gourlay *et al.*, in press)
Fodder quality: Interest in use of *L. pulverulenta* for forage arose because of its reported low mimosine

content compared to other species. Interest in low mimosine has however waned, at least for ruminants. In other respects it produces forage of acceptable, though not optimal quality with significantly lower *in vitro* digestibility, crude protein, and higher condensed tannin content than *L. leucocephala* (Stewart and Dunsdon, in press).

Growth: *L. pulverulenta* shows good growth on certain sites. However, it is its hybrid with *L. leucocephala* which is exceptionally high yielding, outperforming *L. leucocephala* by 70% in forage and 100% in wood yields.

Weediness risk: *L. pulverulenta* shows weedy tendencies in parts of the native range, spreading and colonizing ruderal sites such as roadsides, abandoned fields and canal banks sometimes forming dense thickets, particularly in south Texas (Isely, 1970). It is therefore considered to pose significant risks of becoming a ruderal weed where introduced.

11.18 Leucaena retusa

Leucaena retusa Benth. in Gray, Plantae Wrightianae 1: 64. 1852.

Synonyms

Caudoleucaena retusa (Benth.) Britton & Rose

Acacia sabeana Buckley

Main attributes

L. retusa is the most northerly species of *Leucaena* and grows in cold dry areas in the extreme north of Mexico and in the southern U.S.A. It is closely related to *L. greggii* and the two together are highly distinctive outlier species in the genus both geographically and morphologically. *L. retusa* appears to have little or no direct potential for tree planting programmes being a small, shrubby, slow growing tree with brittle wood. A few hybrids using *L. retusa* as a parent have been attempted with the aim of enhancing cold tolerance in other species of *Leucaena*.

Botanical features (Fig 59)

Bark: on young branches smooth, mid-brown with pale orange-brown lenticels, darker blackish-brown and rougher with shallow orange-brown vertical fissures on bole

Leaves: pinnae (2-)3-4(-5) pairs; pinnular rachis 9-11 cm long; leaflets large, (15-)20-26(-30) mm long, (6-)8-12 (-15) mm wide, (4-)6-8 pairs per pinna, asymmetric, obliquely ovate or elliptic-lanceolate

Petiole gland: a series of small cylindrical, columnar, peg-shaped glands, 1 mm long x 1 mm wide and 1-3 mm tall on upper side of petiole and rachis at base of each pair of pinnae

Flower head: 20-25 mm in diameter, 150-190 flowers per head, in groups of (1-)2-4 in leaf axils on actively growing shoots; flower head stalks very long (26-90 mm); flower bracts pointed and clearly visible in bud; flowers bright yellow

Pollen: tricolporate monads

Pods: (12-)16-20(-25) cm long, 11-13 mm wide, 1-2(-5) per flower head, narrow linear, terminating in the thickened persistent point, green and fleshy unripe turning mid- to reddish-brown, glabrous, strongly leathery or almost woody, the margins markedly thickened, opening slowly along both sides

Seeds: 7.3-8.5 mm long, 4.8-6.5 mm wide, circular to strongly rhombic, aligned strongly obliquely or longitudinally in pods, around 17,000 seeds/kg

Closely related species and identification

Placement of *L. retusa* on its own in the segregate genus, *Caudoleucaena* by Britton and Rose (1928) has not been followed by any subsequent authors, all of whom treated it as a species of *Leucaena*. Nevertheless, along with *L. greggii*, *L. retusa* does show a number of unusual features including glabrous anthers, chromosome number 2n = 56 (with *L. pulverulenta*), erect, peg-shaped petiole glands, one at the base of each pair of pinnae, yellow flowers, long pointed floral bracts that are exserted in bud, very long flower head stalks compared to all other species, thick woody pods and rhomboidal seeds which are longitudinally or obliquely aligned in the pods. A close relationship between *L. retusa* and *L. greggii* is also supported chloroplast DNA data (Harris *et al.*, 1994a). The separation of *L. retusa* and *L. greggii* from the remaining species in the genus is further emphasized by their outlying northerly distributions and their ability to withstand low winter temperatures (Glumac *et al.*, 1987), the unusual *Rhizobium* affinities of *L. retusa* which failed to nodulate when inoculated with strains that effectively nodulate other species of *Leucaena* (Halliday and Somasegaran, 1983), and their very slow growth in field trials compared to other species (Stewart *et al.*, 1991; 1993). These two species, and *L. retusa* in particular, are thus highly distinctive within the genus. *L. retusa* is readily distinguished from its close relative *L. greggii* on leaf characters alone. *L. retusa* has few pairs of large elliptic or ovate leaflets while *L. greggii* has many pairs of small linear-oblong leaflets.

Chromosome number

Diploid, 2n=56, self-incompatible (Pan and Brewbaker, 1988; Sorensson, 1989a)

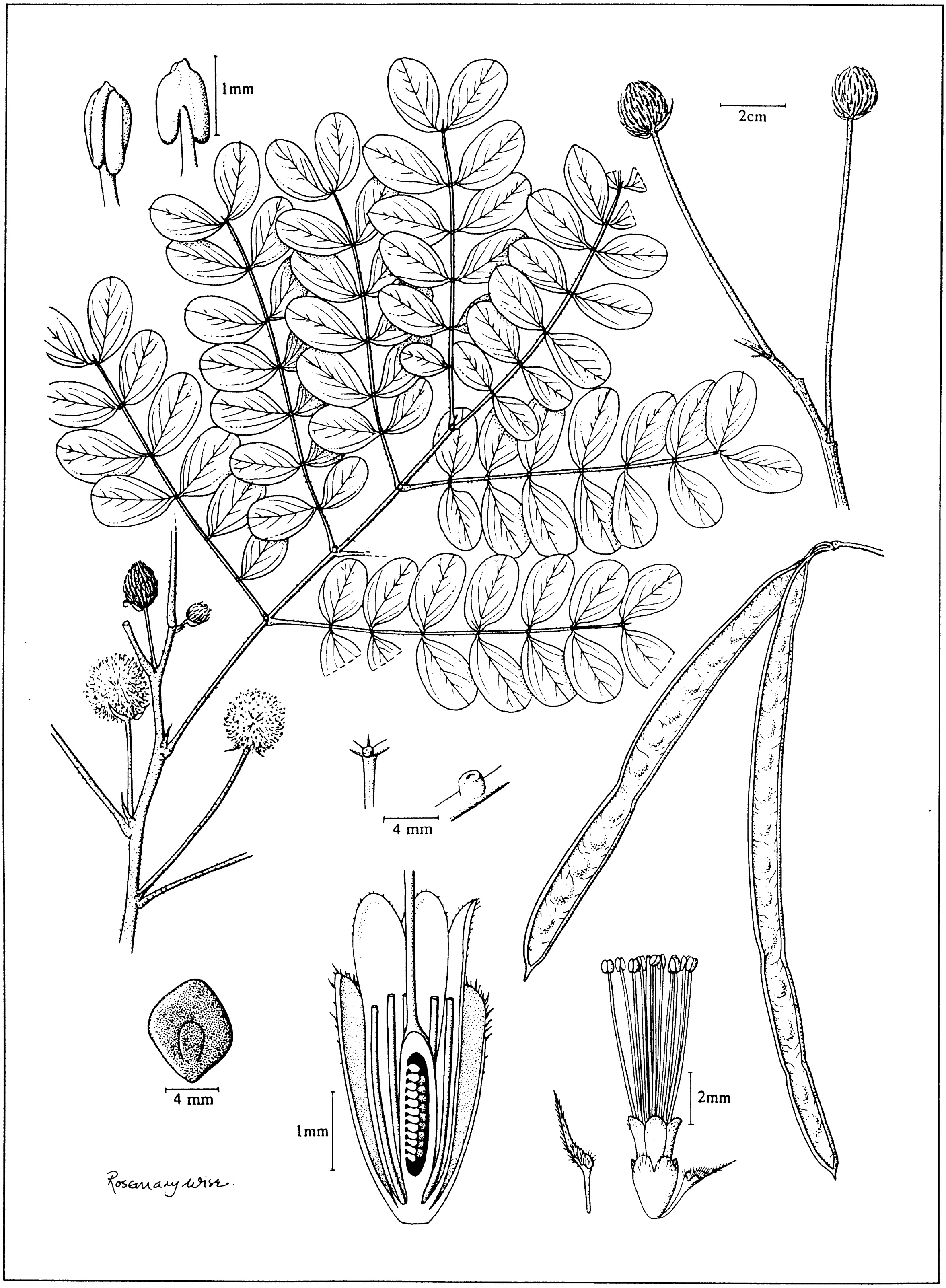

Figure 59 Leucaena retusa

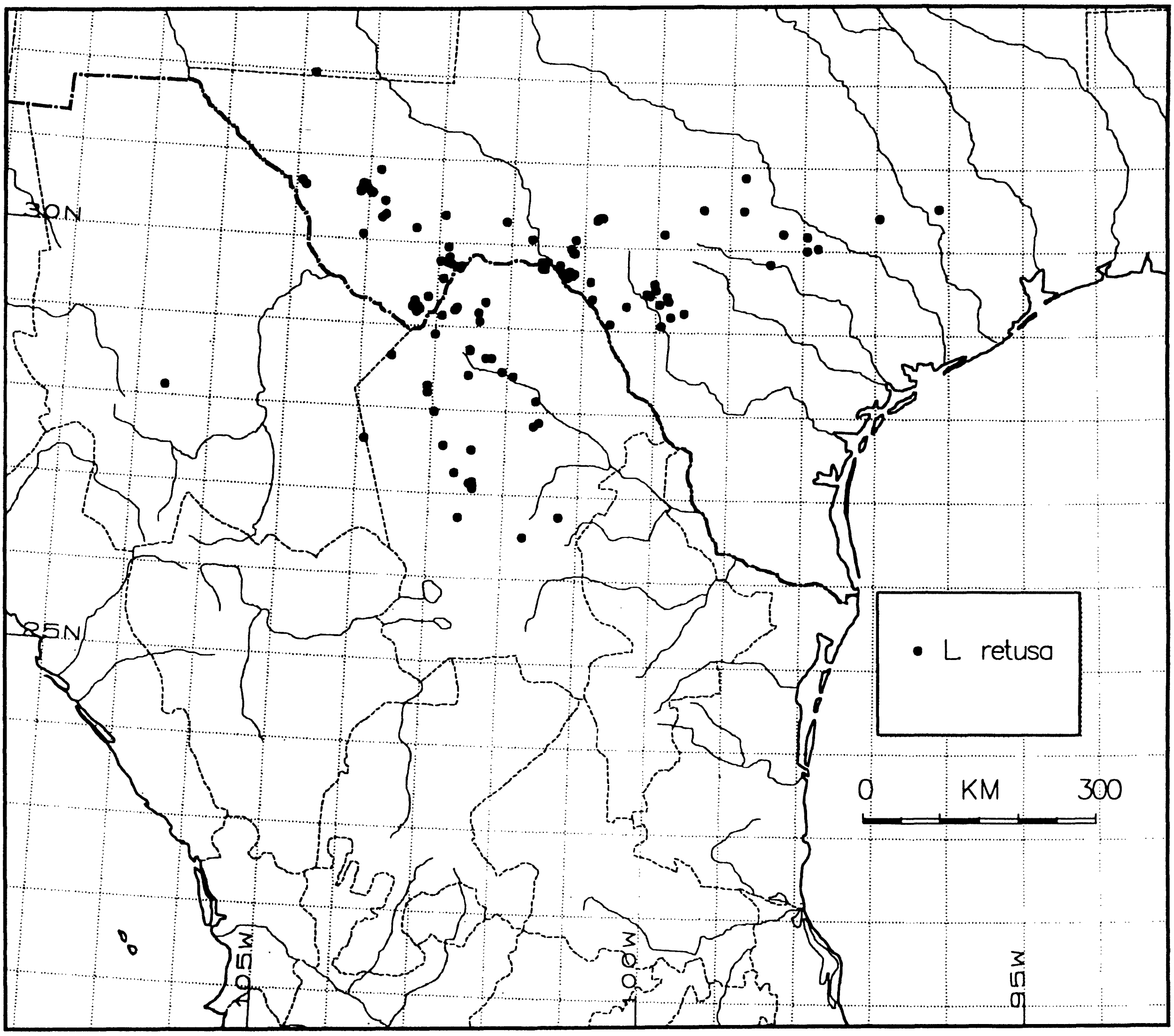

Figure 60 Map of northern Mexico and Texas, U.S.A. showing the distribution of *L. retusa*

Tree size and form
L. retusa forms a shrub or small tree to 2-5(-8) m tall and 10-15 cm stem diameter. It is typically slow growing with brittle branches and a small round crown.

Distribution (Fig 60)
L. retusa occurs in the extreme north of Mexico, mainly in the State of Coahuila and in the southern U.S.A., mainly in south central and western Texas; single collections from Chihuahua, Mexico and New Mexico, U.S.A. are clearly outliers and it is apparently rare in those States.
Degree-squares: 24
Altitude range: (120-) 400-1900 m

Ecogeography
L. retusa is the most northerly species in the genus occurring from 26°43'N to 31°52'N and extends into mountains as high as 1900m and is thus the most frost-tolerant species occupying a warm temperate climate with cold winters. It can withstand several months of regular frost with temperatures as low as -15°C and deep snow in the winter months from December to February. Trees cultivated in Texas showed good resistance to frost down to -12°C (Glumac *et al.*, 1987). Rainfall is low throughout the distribution with between 500 and 900mm of rain and a 6-7 month dry season. It occupies a wide range of habitats from moist to semi-arid and montane to deep canyon mainly on rocky sites and predominantly on limestone but in some areas also on igneous rocks. It occurs as an understorey shrub or small tree in a range of open vegetation types including mixed pine-oak forest with *Pinus ponderosa*, scrub oak-juniper forest, chaparral and semi-arid thorn-scrub forest.

Phenology
Flowering (March-) April-June (-August); fruiting (July-) August-October (-November); leafless during the cold winter season from December-February

Conservation status
L. retusa is of little or no immediate conservation concern. It is widespread and sometimes locally

abundant. It is present in a number of protected areas in N. Coahuila and Texas (*e.g.* Big Bend National Park).
Star rating: Green Star
IUCN threat category: LR:lc

Common names
cafecillo and *planta de patro* (Coahuila); *little-leaf lead tree, golden-ball lead tree* (Vines, 1960), *lead tree, woohoo* and *hiusache* (Texas)

Indigenous use and domestication
Unknown

Exotic use and potential
L. retusa is extremely slow growing, compared to almost all other species of *Leucaena* (*e.g.* Stewart *et al.*, 1991; 1993) and clearly has little direct potential for tree planting programmes. However, attempts have been made to incorporate the cold tolerance of *L. retusa* into other species through hybridization (Sorensson, 1995).
Psyllid resistance: highly resistant (damage score 1-2)
Wood quality: The wood is of average density (0.73) (Gourlay *et al.*, in press) and is known to be brittle. Although used to a limited extent for firewood, it has little importance
Fodder quality: *L. retusa* shows little potential for forage production being extremely slow growing. However, the few studies of leaf quality indicate that it has high *in vitro* dry matter digestibility but moderate or high condensed tannin levels (Stewart and Dunsdon, in press).
Growth: *L. retusa* has been found to be very slow growing in all trials to date. It has been found that the normal *Rhizobium* strains used for the majority of *Leucaena* species do not promote nodulation in *L. retusa* again indicating its distant relationship from other species in the genus.
Weediness risk: *L. retusa* is a shy seeder compared to the majority of species of *Leucaena* and it is one of only five species judged to have a low hazard of becoming a weed.

11.19 Leucaena salvadorensis

Leucaena salvadorensis Standley ex Britton & Rose, North American Flora 23(2): 125. 1928.

Synonyms
Leucaena shannonii J.D. Smith subsp. *salvadorensis* (Standley ex Britton & Rose) S. Zárate

Main attributes *L. salvadorensis* remained poorly known until recently; it had been largely overlooked as a distinct species until its status and potential were revealed by Hughes and collaborators (Hughes, 1988a; Hellin and Hughes, 1993). Within its restricted natural distribution in Central America it is highly esteemed, protected, managed and even cultivated by farmers who value its durable wood for house construction (Figs 8A-B). Despite its local value, *L. salvadorensis* has hardly been cultivated outside its native range except in a handful of trials. It combines high yield with high wood density and, on some sites, it has been the highest wood biomass producer of all *Leucaena* species. It appears to be one of the best species of *Leucaena* for wood production.

Botanical features (Fig 62)
Bark: on young branches smooth, mid grey or grey-brown, inner bark salmon-pink, darker grey-brown and rougher with shallow rusty orange-brown vertical fissures and deep red inner bark on older branches and bole
Leaves: pinnae 4-7 pairs; pinnular rachis 13-16 cm long; leaflets 15-19 mm long, 3-5 mm wide, 23-27 pairs per pinna, asymmetric, linear-oblong, obtuse or rounded apically, rounded or truncate basally
Petiole gland: yellow-green or orange, un-stalked rounded, elliptic dome-shaped or conical, 5 x 2.5 mm
Flower head: 23-25 mm in diameter, 90-140 pale cream-white flowers per head, in groups of 2-6 in leaf axils arising on older woody shoots, the leaves developing after the flower heads
Pollen: tricolporate monads
Pods: 14-18 cm long, 26-29 mm wide, 1-2 per flower head, oblong to linear-oblong, acuminate, or sometimes obtuse apically, flat, mid- to reddish-brown, glabrous, leathery, the margins thickened, opening along both sutures; pods take up to 10 months to ripen
Seeds: 8.5-11.8 mm long, 5.2-6.7 mm wide, aligned transversely in pods, 12,000-15,000 seeds/kg

Closely related species and identification
L. salvadorensis was first described in 1925 by Standley based on material collected near Jocóro in eastern El Salvador. Since that time the status of *L. salvadorensis* as a distinct species has been questioned by several authors (Standley and Steyermark, 1946; Zárate, 1984a; 1987b; Brewbaker *et al.*, 1972; Brewbaker and Ito, 1980; Brewbaker and Sorensson, 1994) with most treating it either as the same thing as, or a subspecies of, *L. shannonii* or *L. leucocephala*. Excluding the original botanical specimen, collected in 1924, only three further specimens of *L. salvadorensis* were collected prior to 1980 and the taxonomic confusion was thus, at least in part, due to lack of botanical material.

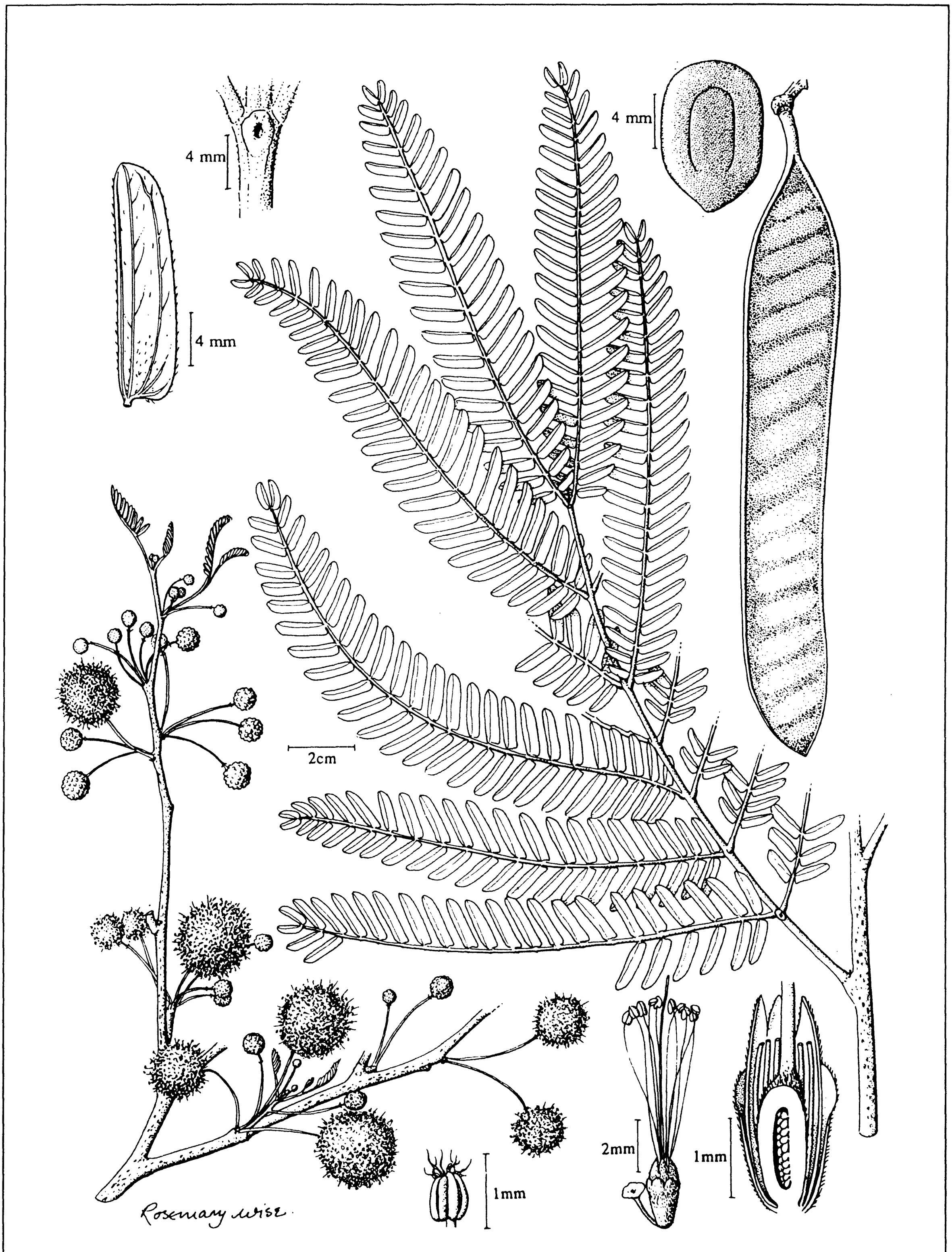

Figure 61 *Leucaena salvadorensis*

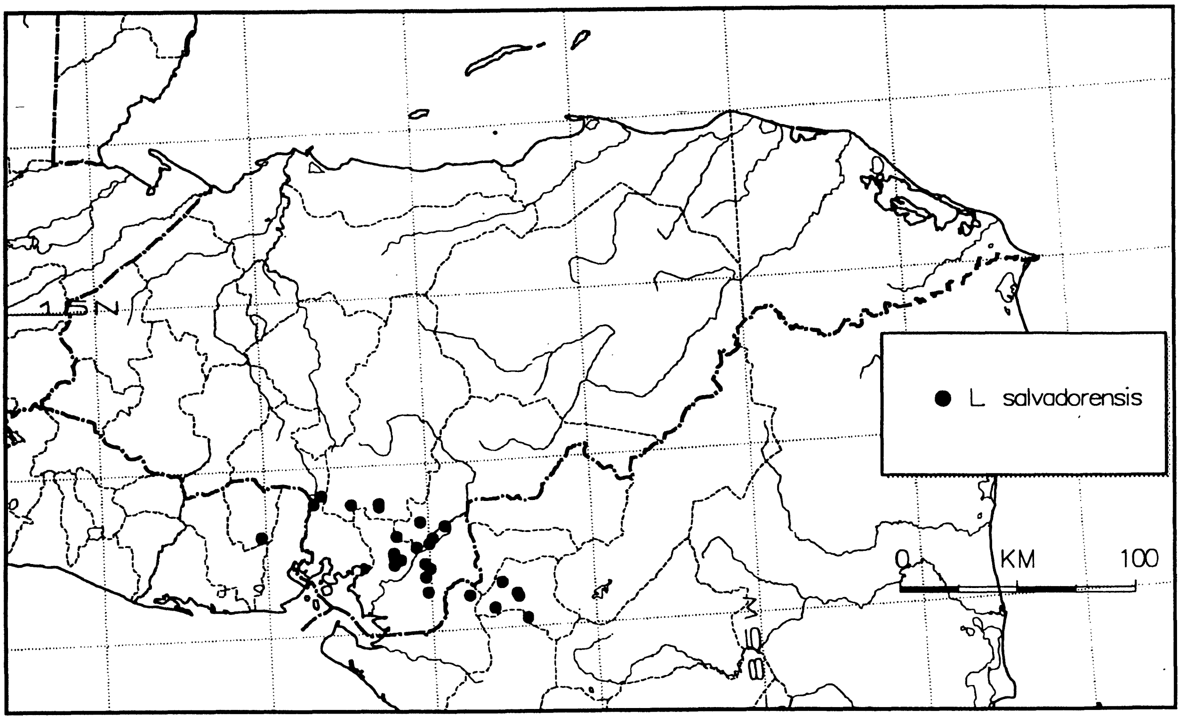

Figure 62 Map of Honduras showing the distribution of *L. salvadorensis*

The use of the '*Salvador*' designation for the '*Giant*' type of *L. leucocephala* subsp. *glabrata*, a different species, has added further confusion. In the last 15 years more detailed taxonomic studies have been carried out which support recognition of *L. salvadorensis* as a distinct species (Hughes, 1988a; Hellin and Hughes 1993; Chamberlain *et al.*, 1996).

L. salvadorensis is most closely related to *L. lempirana*, a relationship supported by morphological (Hughes, in press), cpDNA (Harris *et al.*, 1994a), seed protein (Chamberlain, 1993) and isozyme data (Chamberlain *et al.*, 1996). *L. salvadorensis* belongs within the *L. shannonii* alliance with *L. lempirana*, *L. magnifica* and *L. shannonii* itself but is distinguished from *L. lempirana*, *L. magnifica* and *L. shannonii* by the arrangement flower heads on older wood with the pods borne away from the ends of the shoots and by its leathery as opposed to papery pods. In addition, leaflets of *L. salvadorensis* are longer than those of *L. lempirana*. *L. salvadorensis* and *L. shannonii* occupy non-overlapping but contiguous distributions. *L. leucocephala* is now frequently cultivated in areas of remnant *L. salvadorensis* stands, but no hybrids between the two have so far been encountered.

Chromosome number
Diploid, 2n=56, self-incompatible (Sorensson, 1989a)

Tree size and form (Figs 8A and back cover B)
L. salvadorensis forms a small to medium-sized tree, 10-15 (-20) m tall and 20-70 cm bole diameter. It is typically very branchy when young, older trees often have a short clear bole to 5 m, upright angular branching and a narrow, open crown.

Distribution (Fig 62)
L. salvadorensis is restricted to the south facing, seasonally dry Pacific slopes of eastern El Salvador, southern Honduras and northern Nicaragua. Recent field exploration in eastern El Salvador suggests that it is restricted there to areas close to the Honduran border.
Degree squares: 3
Altitude range: (150-) 300-800 (-1080)m

Ecogeography
L. salvadorensis occurs in remnant seasonally dry deciduous tropical forest and is often locally protected around settlements, in fencelines and farmers' fields in traditional agroforestry systems outside remnant forest patches (Hellin and Hughes, 1993). It is a truly tropical lowland species and is restricted to the seasonally dry Pacific watershed where rainfall ranges from 800 to 1500mm with a 5-7 month dry season. It generally grows on young, skeletal, shallow soils which are of volcanic origin are freely drained and have suffered severe abuse through slash and burn agriculture, desiccation and erosion.

Phenology
Flowering March-April and sporadically May-October, fruiting February-March; deciduous December-March

Conservation status

L. salvadorensis occupies a limited distribution and is never locally abundant. Forest cover has been reduced to scattered small remnants throughout the distribution of *L. salvadorensis*. As a result it is now rare in many parts of its range. However, the obvious conservation threat to this species is mitigated by deliberate retention, protection and management of trees in traditional agroforestry systems by farmers who use the wood of *L. salvadorensis* for house construction (Fig 8A) (Hellin and Hughes, 1993; Ponce, 1995). There are good prospects for continued and expanded *circa situm* conservation. However, this will depend on *L. salvadorensis* continuing to be of value and benefit to farmers and compatible with current farming systems. It is apparently rare, and probably endangered in El Salvador.

Star rating: Gold Star (Black Star in El Salvador)

IUCN threat category: LR:cd

Common names

In Honduras, *sepia (sepria)*, occasionally *frijolillo*, *aserillo* (Dept. Valle and El Salvador); in Nicaragua, *frijolillo*, occasionally *vaina*, *sepia* (Dept. Chinandega only)

Indigenous use and domestication

The value of *L. salvadorensis* is recognised by farmers in southern Honduras and trees are regularly protected and maintained over crops and planted along terrace boundaries in traditional agroforestry systems. Young trees are highly branched and tend to have spreading crowns. Trees are sometimes managed by regular pruning to produce straight poles and reduce shade over crops.

Exotic use and potential

Psyllid resistance: moderately susceptible (damage score 3-5)

Wood quality: *L. salvadorensis* forms one of the larger Leucaenas commonly reaching 15m in height and 30cm dbh and sometimes up to 20m height and 70cm dbh. The tree, with pruning, produces straight medium dimension poles which are durable in contact with the ground, making it ideal for house construction. The wood is of high mean density (0.81), with abundant heartwood from an early age (*e.g.* 56% at 5 years) (Gourlay *et al.*, in press). It is also easily split and dried and all in all makes excellent firewood (Figs 8A-B).

Fodder quality: The fodder value is little known with no tradition of tree fodder use in Honduras. However the intensive grazing of natural regeneration by livestock gives some indication of palatability. Initial investigation of nutritive value indicates that it has as high *in vitro* digestibility, low condensed tannin levels, but lower palatability than *L. leucocephala* (Stewart and Dunsdon, in press).

Propagation and growth: Unlike all other *Leucaena* species, seed of *L. salvadorensis* does not need pretreatment (Hawkins and Ochoa, 1991). Seeds germinate rapidly after sowing in 3 to 7 days. There are few extensive plantings of *L. salvadorensis* to date and little is known about growth rates. However, preliminary trials indicate that the species can grow as well as *L. leucocephala* and can outperform all other species of *Leucaena* in wood biomass production on some sites (Stewart *et al.*, 1991; 1993). Seed orchards of *L. salvadorensis* have been established in Honduras (Ponce, 1995). Species characteristics are reviewed by Hellin and Hughes (1993).

Weediness risk: *L. salvadorensis* flowers and fruits much more shyly than most *Leucaena* species and trees rarely fruit in the first year. Thereafter flowering and seed production are relatively sparse, pods being produced singly on flower heads. This means that it is one of only five species of *Leucaena* judged to be of low weediness risk.

11.20 Leucaena shannonii

Leucaena shannonii Donn. Smith., Botanical Gazette 57: 419. 1914.

Main attributes

The potential of *L. shannonii* for direct use in tropical tree planting is extremely limited. It is generally slow growing and usually forms a spreading, branchy tree of poor form. Furthermore, it shows weedy tendencies in its natural range and is considered to pose some risk of becoming a ruderal weed in areas where introduced. It is moderately susceptible to the psyllid and shows few unique beneficial characteristics for inclusion in artificial hybrids.

Botanical features (Fig 63)

Bark: on young branches smooth, mid grey or grey-brown, inner bark salmon-pink, darker grey-brown and rougher with shallow rusty orange-brown vertical fissures on bole, inner bark cream

Leaves: pinnae (2-)4-7 pairs; pinnular rachis 3-8 cm long; leaflets (13-)16-18(-20) mm long, 5-7 mm wide, (5-)7-13(-20) pairs per pinna, the basal leaflets shorter, the apical pair shorter and wider, distinctly inequilaterally asymmetric about the mid vein, linear-oblong, rounded at tip and base

Petiole gland: yellow-green, un-stalked, rounded elliptic dome-shaped or rounded conical, 2-3 x 1 mm

Flower head: 11-12 mm in diameter, 80-140 pale cream-white flowers per head, in groups of 2-6 at nodes on long erect terminal shoots, often with leaves suppressed and the flower heads and pods exposed on ends of otherwise naked shoots
Pollen: tricolporate monads
Pods: (9-)12-16(-18) cm long, (11-)14-17 mm wide, 1-2 (-3) per flower head, linear-oblong, flat, papery, mid- to reddish-brown, glabrous or densely covered in velvety hairs, opening along both sutures
Seeds: 6.2-7.5(-8.5) mm long, 4.5-5.6(-6.3) mm wide, aligned transversely in pods; 30,000-36,000 seeds/kg

Closely related species and identification
L. shannonii belongs to a group of closely related species, referred to in Section 2.5 as the '*L. shannonii* alliance' comprising *L. lempirana*, *L. magnifica*, *L. salvadorensis* and *L. shannonii* itself. Although the distinction of these four species was doubted by Zárate (1987b; 1994), who preferred to view *L. shannonii* as a widespread variable species with a number of subspecies within it, Hughes (1997a; in press) presented discrete character evidence to suggest that they are distinct species. The four species are distinguished by type and branching of flowering shoots, hairiness of the ovary, fixed differences between aggregations of population allele frequencies for some species pairs (Chamberlain *et al*., 1996), chloroplast DNA data (Harris *et al*., 1994a), and a set of quantitative leaf and pod traits which are congruent with their virtually non-overlapping distributions in Central America. Within the *L. shannonii* alliance, *L. shannonii* is probably most closely related to *L. magnifica*, with the latter originally described as a subspecies of *L. shannonii* (Hughes, 1991; 1997a). Detailed distinctions between all four species are presented in Sections 11.9, 11.12 and 11.19.

Chromosome number
Diploid, 2n=56, self-incompatible (Hutton, 1981; Pan and Brewbaker, 1988)

Tree size and form
L. shannonii forms a small to medium-sized tree, 10-12 (-15) m tall and 20-30 (-50) cm bole diameter. Trees are typically branchy when young, and older trees have a short clear bole to 5 m, spreading angular branching and an open rounded crown.

Distribution (Fig 64)
L. shannonii occurs widely from southern Mexico (Campeche and Chiapas only) south through Guatemala (only in Jutiapa and Jalapa), El Salvador and Honduras to south central Nicaragua as far south as Chontales. The distribution is highly disjunct with isolated occurrences in the southern Yucatán Peninsula and the central depression of Chiapas, and a scattered distribution through Central America, mainly in the seasonally dry inland valleys, and only rarely (in El Salvador) reaching the Pacific coast.
Degree squares: 20
Altitude range: (5-) 400-1000 (-1450) m

Ecogeography
L. shannonii is a truly tropical, lowland species, occurring from 12°-20°N, in seasonally dry deciduous tropical forest, secondary vegetation and fencelines. It occurs in seasonally dry climates with 800-1200mm rainfall and a 5-6 month dry season. It is occasionally invasive, occurring as a roadside weed or abundantly in secondary vegetation often in bush fallow after cultivation (*e.g.* in Yoro, central north Honduras).

Phenology
Flowering August-November (-February), fruiting February-March, partly or completely leafless February-March

Conservation status
L. shannonii is widely distributed, often locally abundant in secondary vegetation and sometimes a ruderal weed of roadsides. It thrives on disturbance and is of little or no conservation concern.
Star rating: Green Star
IUCN threat category: LR:lc

Common names
barba de jelote (Olancho, Honduras), *cascahuite* (San Miguel, El Salvador), *frijolillo* (Honduras and Nicaragua), *guacamayo* (Intibuca, Honduras), *guaje* (El Salvador, Guatemala, Honduras, Mexico, Nicaragua), *guash* (Chiapas, Mexico), *guashín* (Campeche, Mexico), *guajillo* (Jutiapa, Guatemala), *memblén* (Honduras, Francisco Morazán), *vainillo* (Jutiapa, Guatemala and Estelí, Nicaragua).

Indigenous use and domestication
L. shannonii is little used within its native range except for firewood.

Exotic use and potential
Trees of *L. shannonii* are generally of poor form, being branchy and spreading and generally slow growing compared to other *Leucaena* species and the species is judged to have limited potential although its wood is widely used for firewood in the native range and fodder quality is apparently high (Stewart and Dunsdon, in press). Brewbaker (1987b) cites *L. shannonii* as a species of particular value for bee forage.
Psyllid resistance: moderately susceptible (damage score 3-5)
Wood quality: The mean wood density of *L. shannonii* is high (0.86) with a high proportion of heartwood (Gourlay *et al*., in press), and provides firewood of high quality. However, being a slow growing tree of generally poor form, it has little potential for production of poles or posts.
Fodder quality: *L. shannonii* has been little used for

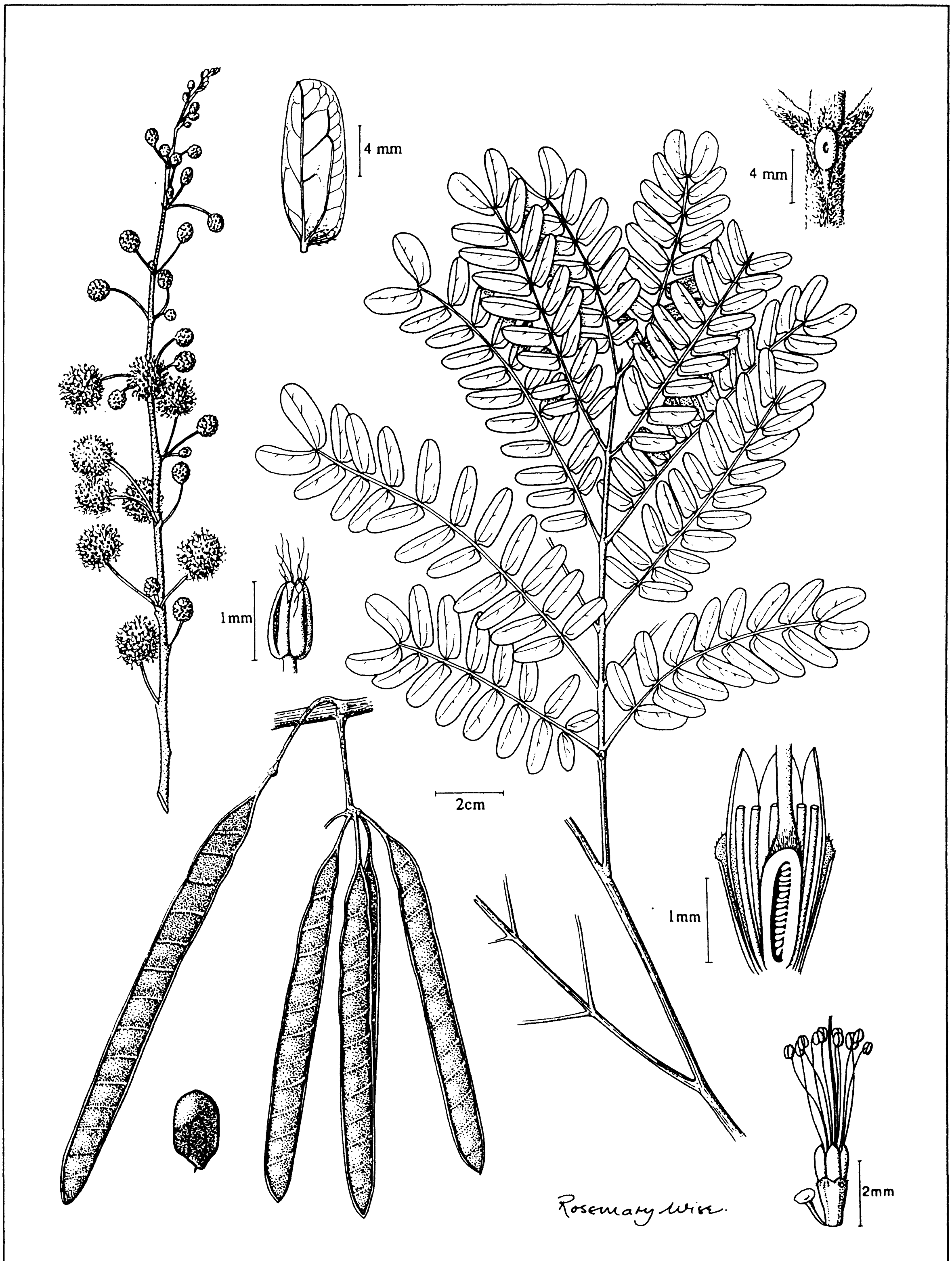

Figure 63 *Leucaena shannonii*

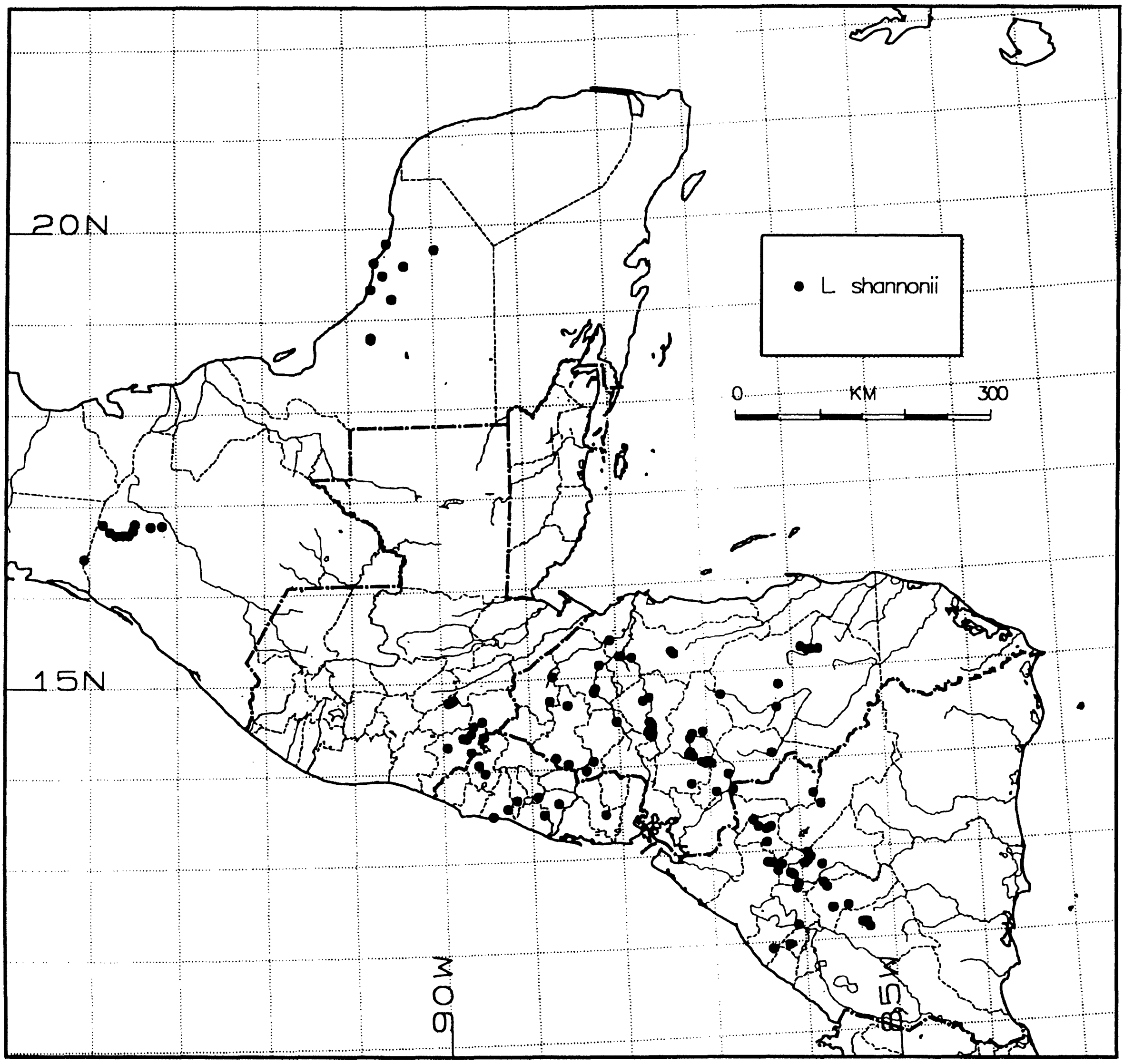

Figure 64 Map of southern Mexico and northern Central America (Belize, Guatemala, Honduras, El Salvador and Nicaragua) showing the distribution of *L. shannonii*

fodder. Preliminary analysis of nutritive value indicates that the leaves have very high crude protein content and *in vitro* dry matter digestibility and low condensed tannin content compared to other *Leucaena* species (Stewart and Dunsdon, in press).

Growth: *L. shannonii* has been widely tested throughout the dry tropics having been included in the OFI international trial of dry zone species from Central America, and has been found to perform less well than *L. leucocephala* on almost all sites (Stewart and Dunsdon, 1994). It also grows slowly in other trials (Brewbaker, 1987b; Stewart *et.al.*, 1991; 1993).

Weediness risk: *L. shannonii* is a prolific and precocious seeder and shows weedy tendencies within its natural range, often spreading and colonizing ruderal sites such as roadsides or abandoned fields and sometimes forming dense thickets. The species is considered to pose some risk of becoming a ruderal weed in areas where it is introduced, although, as a colonizing species which thrives on disturbance, it is unlikely to invade pristine closed forest communities.

11.21 Leucaena trichandra

Leucaena trichandra (Zucc.) Urban, Symbolae Antillanae 2: 267. 1900.

Synonyms

Acacia trichandra Zuccarini
Leucaena diversifolia (Schltdl.) Benth. subsp. *trichandra* (Urban) F.J. Pan
Leucaena stenocarpa Urban
Leucaena diversifolia (Schltdl.) Benth. subsp. *stenocarpa* (Urban) S. Zárate
Leucaena guatemalensis Britton and Rose
Leucaena revoluta Britton and Rose
Leucaena standleyi Britton and Rose
Senegalia albanensis Britton and Rose

Main attributes

The most striking feature of *L. trichandra* is its great within species variability. This is manifest in tremendous morphological variation in quantitative leaf and pod traits, high levels of genetic diversity and significant provenance variation in growth, psyllid resistance and fodder quality. Psyllid resistance varies from highly resistant to moderately susceptible and condensed tannin levels in leaves from very low (nearly zero) to high. Such variation is perhaps not surprising given the very wide and highly disjunct natural distribution of *L. trichandra* across the highlands of southern Mexico and northern Central America. It means that provenance (seed source) is of overwhelming importance for this species. Initial results indicate that seed sources from SE Guatemala are superior in growth and psyllid resistance but more intensive provenance investigation is needed. *L. trichandra* is also the most likely source of acid soil tolerance within *Leucaena*, given its occurrence as an understorey tree in pine forest on nutrient-poor, acid soils in many parts of Central America, but again, more seed sources need to be tested. It is clear that some seed sources of *L. trichandra* have good potential to contribute to *Leucaena* planting and to be used in artificial hybridization.

Botanical features (Fig 65)

Bark: on young branches smooth, rougher on bole, mid grey-brown to dark blackish-brown with shallow rusty orange-brown vertical fissures, the inner bark green and deeper bark cream, sometimes streaked pink or reddish
Leaves: pinnae (5-)11-22(-30) pairs; pinnular rachis (3-)4-6(-8.4) cm long; leaflets (3-)3.8-5.2(-7) mm long, (0.7-)1-1.4(-1.8) mm wide, (20-)30-40(-59) pairs per pinna, linear-oblong, acute at tip, strongly asymmetric at base
Petiole gland: one, or rarely a pair of adjacent glands, un-stalked, strongly and deeply cup- or crater-shaped, round, or sometimes rounded-triangular, occasionally elliptic, 1.6-3.4 (-4.8) mm long x 1-1.7 (-2.2) mm wide and 1-2 mm tall, with an additional 1 or 2 (-15) glands at base of terminal and sub-terminal pairs of pinnae and, where many, at the base of all pairs of pinnae
Flower head: 7-10(-12) mm in diameter, (60-)70-130(-165) flowers per head, heads in groups of (1-)3-5 in leaf axils, on actively growing indeterminate shoots; colour variable: stamen filaments white, sometimes tinged pink; anthers very hairy, pale cream-white, very pale pinkish-grey, pale, dull or bright rose pink or occasionally pale violet, style white, white tinged pink or occasionally deep pink or scarlet
Pollen: tricolporate monads
Pods: (5-)7-11(-16.5) cm long, 13-23(-29) mm wide, (1)2-4(-15) per flower head, narrowly or broadly linear-oblong, occasionally oblong, flat, papery, yellow-green or reddish-green often deep maroon and very glossy unripe, becoming pale yellow- or deep reddish-brown when ripe, sometimes lustrous, glabrous or sometimes covered in dense velvety hairs, opening along both sides
Seeds: 2.8-3.7(-4.2) mm wide, 4.5-6.5(-7.3) mm long, aligned transversely in pods, 40,000-70,000 seeds/kg

Taxonomy and identification

L. trichandra is better perhaps known either as *L. diversifolia* subsp. *trichandra* (Pan, 1985; Pan and Brewbaker, 1988) or *L. diversifolia* subsp. *stenocarpa* (Zárate, 1994), or simply as 'diploid *L. diversifolia*' (DIV2N), but is now accepted as a distinct species correctly named *L. trichandra* (Hughes, in press). Viewing *L. trichandra* as a subspecies of *L. diversifolia* was based partly on the hypothesis that tetraploid *L. diversifolia* is derived directly (*i.e.* as an autotetraploid) from diploid *L. trichandra* (Pan, 1985; 1988). Harris *et al.* (1994a) showed that this hypothesis is incorrect thereby removing any grounds for treating the two taxa as subspecies. The true affinities of *L. trichandra* remain uncertain but it appears to be closely related to *L. collinsii* (Hughes, in press).

L. trichandra is taken here to include *L. stenocarpa, L. guatemalensis, L. standleyi* and *L. revoluta*, species recognized, along with *L. trichandra*, as distinct by Britton and Rose (1928). Although *L. trichandra* is indeed a very variable species (see below), the characters used by Britton and Rose to distinguish these species are all highly variable and incongruent with other characters or geography, and often vary within populations. Such characters are of little use in species delimitation (Hughes, 1997a; in press).

L. trichandra is an extremely variable, indeed probably the most variable, species of *Leucaena*. There is great variation in quantitative traits such as leaf size, number of pairs of pinnae, number of pairs of leaflets, leaflet size, pod dimensions (Fig 65), chloroplast DNA, and isozymes (Harris, unpubl. data) across the natural range.

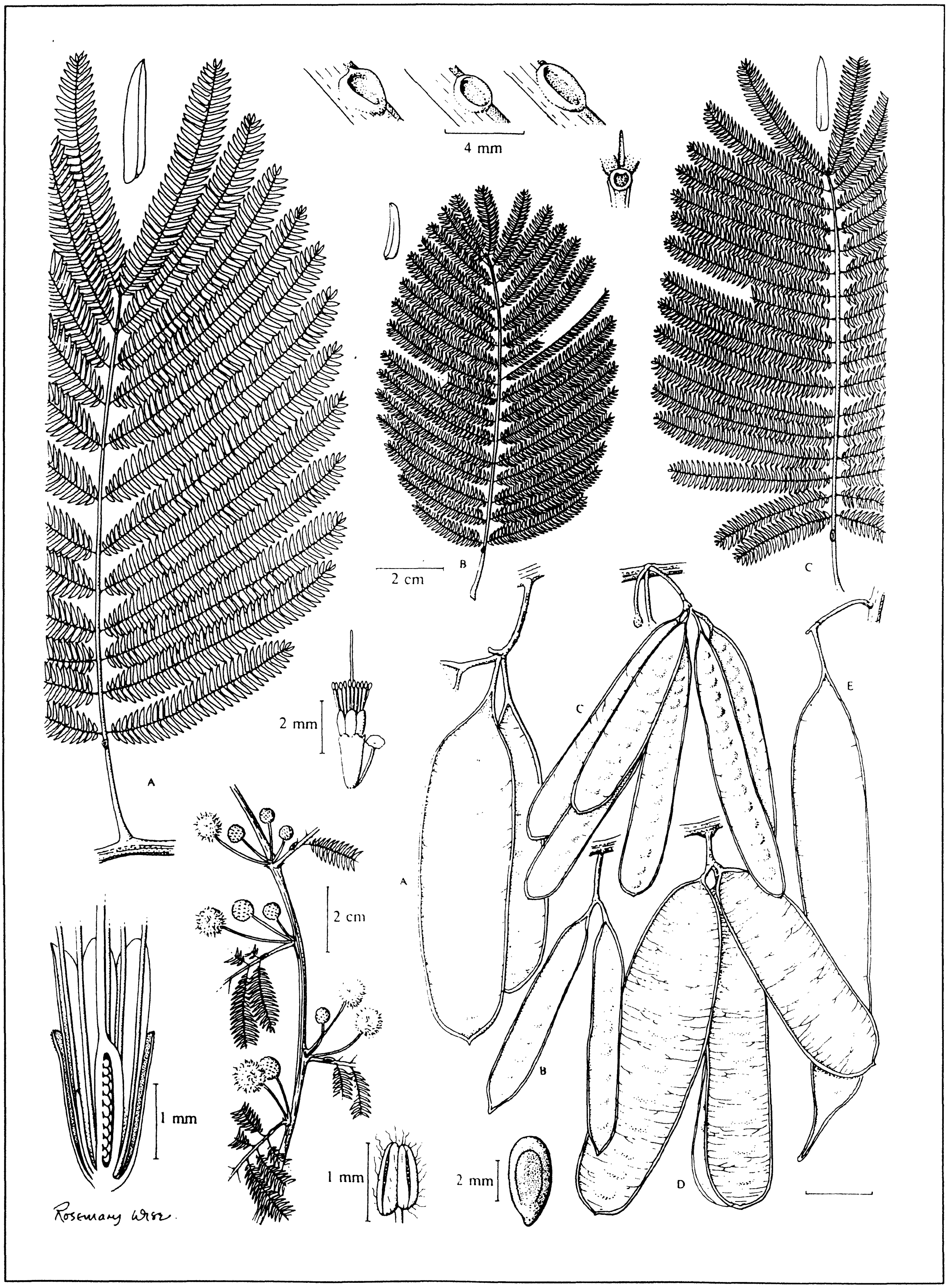

Figure 65 *Leucaena trichandra*, illustrating the tremendous variation in leaf and pod morphology and size across the very extensive geographic range of *L. trichandra*. Botanical voucher specimens are cited in Hughes (in press).

The most notable variant occurs in the mountains near the small town of Erandique, Honduras and has large leaves with fewer pairs of pinnae, fewer leaflets per pinna, large glossy leaflets and often, white flowers. Material from Huehuetenango and San Marcos in north west Guatemala is also very different from the rest of the *L. trichandra*. Although recognition of subspecies or varieties to describe this variation might be desirable, patterns of variation correlated with geography or other characters remain to be fully investigated; in the meantime *L. trichandra* is treated as a single variable species (Hughes, in press). Such variability is not unexpected given the very extensive distribution scattered across highly dissected mountainous territory in a series of highly disjunct and often isolated populations.

Chromosome number
Diploid, 2n=52, self-incompatible (Hutton, 1981; Pan and Brewbaker, 1988; Sorensson, 1989a)

Tree size and form
L. trichandra is extremely variable in size and habit ranging from a small slender shrub to 2m height to a medium-sized tree to 20m height and 50cm bole diameter in some parts of Guatemala and southern Honduras. Tree form is also very variable, usually slender with a clear bole up to 3 m ht. and a light feathery but spreading and irregular crown often modified by lopping.

Distribution (Fig 66)
L. trichandra is the most widely distributed species of *Leucaena* (after *L. leucocephala* which is extensively cultivated), occurring from northern Nicaragua at 13°06'N, through Honduras, El Salvador, Guatemala, Belize, southern Mexico in Chiapas and Oaxaca, and sporadically through south central and western Mexico as far north as Durango at 25°25'N.
Degree-squares: 27
Altitude range: (200-) 700-2000 (-2500) m

Ecogeography
L. trichandra occurs primarily as a small understorey tree or shrub in pine, mixed pine-oak and oak forest at mid elevations. It also extends at lower elevations into dry deciduous forest, dry mattoral and dry secondary forest and occurs on a wide range of soils from shallow calcareous over limestone to shallow infertile more acid soils over volcanic ignimbrites and tuffs. *L. trichandra* is known to possess some tolerance of acid soil conditions (Hutton 1981; 1983; 1990; 1995). This is perhaps not surprising given its occurrence as an understorey tree in pine forest in parts of Central America where trees grow on thin, heavily leached, nutrient-poor lithosols developed from volcanic tuffs. *L. trichandra*, with its known within species variability, is the most likely source of acid soil tolerance in the genus (Section 3.3). It occurs in mixture with other species of *Leucaena* including *L. esculenta* and *L. pallida*. Although *L. trichandra* shows tolerance of cooler conditions it does not tolerate frost.

Phenology
Flowering (May-) June - September, fruiting (February-) March-May

Conservation status
L. trichandra is a very widely distributed, but extremely variable species, and is often locally common. While the species as a whole is of little or no conservation concern, certain populations or provenances may be under threat. It is present in a number of protected areas (*e.g.* El Imposible, El Salvador; Lagunas de Montebello, Mexico; Cerro Uyuca, Honduras). It is apparently rare in Nicaragua where it has only been collected once from a single locality where it is rare.
Star rating: Green Star (Blue Star, Nicaragua)
IUCN threat category: LR:lc

Common names
barba león (Huehuetenango, Guatemala), *chalí* (Guatemala, Guatemala), *frijolillo* (Intibuca, Honduras), *guaje (huaje)* (widely in Guatemala, El Salvador, Honduras and Mexico), *guaje chiquito, guaje flojo* (Mexico, Mexico), *guaje rojo* (Ahuacahapan, El Salvador), *shashíb (shashíl, shaskíb, xaxíb, shashíbtez, k'ushabil shashíb* = edible *sasib*) (Tzeltal, Chiapas, Mexico), *quebracho (quebrachillo)* (names normally applied to *Lysiloma spp.*) (Paraíso and Lempira, Honduras, Guatemala, Guatemala), *tze* (Mazateco, Oaxaca, Mexico), *vainillo* (Chiquimula, Honduras). Berlin *et al.* (1974) provide the variant *bac'il sasib* (= genuine *sasib*) and point out that *sasib* is a polytypic generic tree name containing at least five species in four genera, all of which are Mimosoid legumes with finely divided leaves. Zárate (1994) lists two additional Zapotec names used in Oaxaca: *la-aye-ti* (= *guaje chiquito*) and *lobadaviyia* (= *guaje de pajaro*)

Indigenous use and domestication
L. trichandra is sporadically cultivated as a shade tree over coffee, often with species of *Inga* and *Erythrina*. The unripe pods, seeds and flower buds are consumed in parts of southern Mexico but, because the seeds of other species are larger, those are generally preferred. *L. trichandra* seeds are harvested and occasionally marketed in July-September. In Chiapas, trees are sometimes planted and frequently protected when land is cleared (Berlin *et al.*, 1974).

Exotic use and potential
The great morphological and genetic variability found within *L. trichandra* is matched by tremendous variation in species characteristics. It is extremely important to take account of this within species variation in the utilization of this species. Correct choice of provenance (seed source) will dictate the success of tree planting efforts. While systematic provenance studies are needed to investigate provenance variation in more detail, preliminary results show that material from SE Guatemala (*e.g.* seed sources OFI 53/88 and CPI46568)

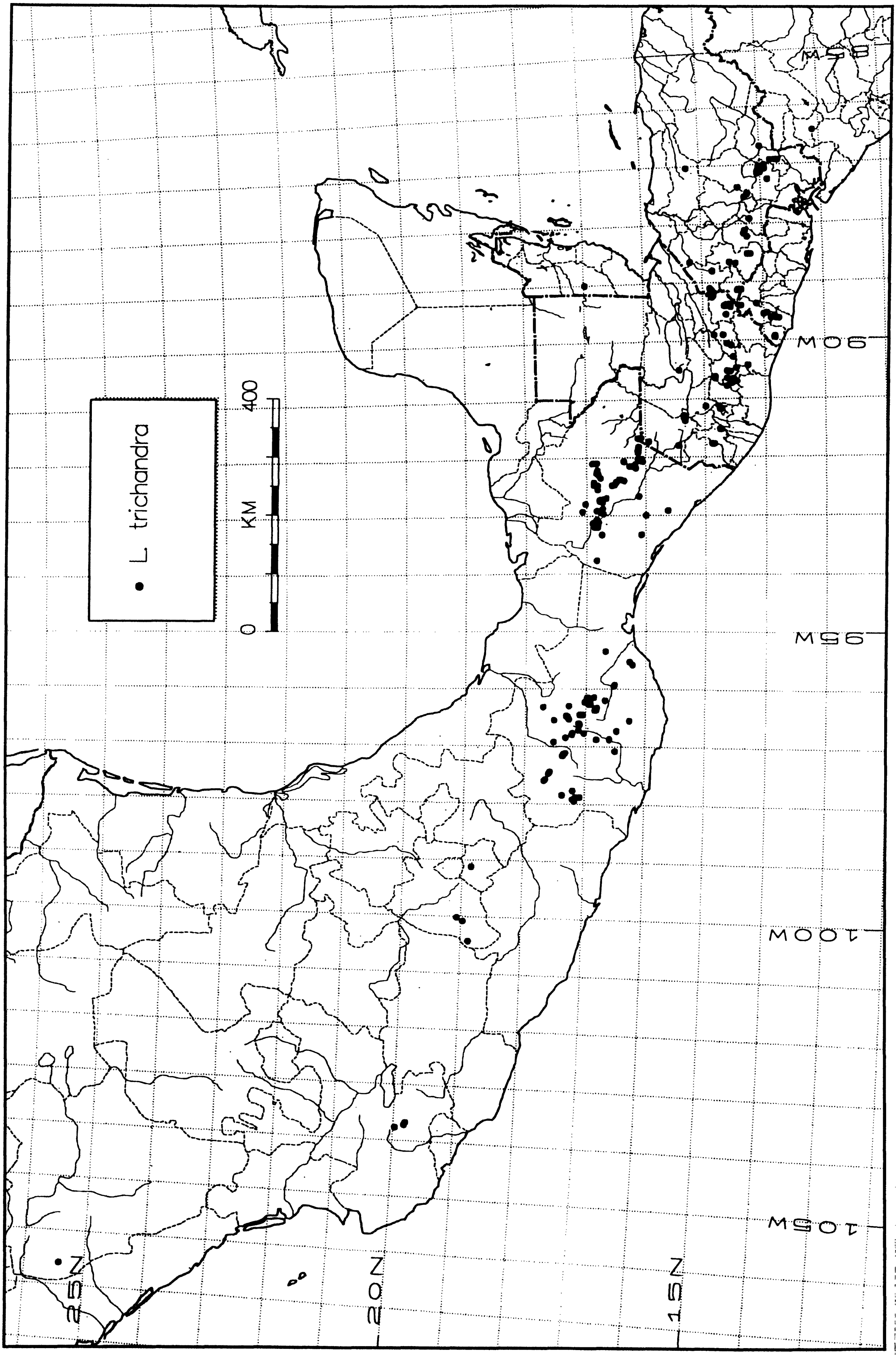

Figure 66 Map of Mexico and Central America showing the distribution of *L. trichandra*

are generally superior in growth and psyllid resistance to other sources which have been tested. Indeed seed sources 53/88 and/or CPI46568 have performed well in trials in Honduras (Stewart *et al.*, 1991; 1993), Australia (Bray, 1982; Mullen *et al.*, 1996) and Tanzania (Otsyina and Msangi, 1995). Intensive exploration, collection and testing of material from SE Guatemala would be worthwhile. Triploid hybrids between *L. trichandra* and *L. leucocephala* apparently arose spontaneously in Indonesia (Toruan-Mathius *et al.*, 1995) and have been recreated artificially in Hawaii (Sorensson, 1995). They set few seeds, have good dry leaf matter digestibility, are highly psyllid-resistant and moderately cold-tolerant (Sorensson, 1995; Toruan-Mathius *et al.*, 1995).
Psyllid resistance: variable for different provenances from highly resistant (*e.g.* seed sources OFI 53/88 and CPI46568) to moderately susceptible (damage score ranges from 1-6)
Wood quality: the wood density of *L. trichandra* varies with seed source. Superior seed sources have average mean wood density (0.7) and moderately high proportions of heartwood (Gourlay *et al.*, in press). The wood is valued for poles and firewood in parts of the natural range.
Fodder quality: as for other traits, fodder quality (*e.g. in vitro* digestibility and condensed tannin content) varies greatly with seed source; for example condensed tannin content varies from very low (zero) to very high across different seed sources of *L. trichandra* (Stewart and Dunsdon, in press)
Growth: wood and fodder yields vary greatly with seed source. For example in a wood production trial in Honduras, two seed sources of *L. trichandra* were ranked 3rd and 37th out of 39 *Leucaena* species and provenances (Stewart *et al.*, 1991; 1993). Seed sources OFI 53/88 and CPI46568 have been among the highest yielding accessions.
Weediness risk: seed production, like other traits varies with provenance. Some seed sources of *L. trichandra* produce prodigious quantities of seed from a very early age and for this reason *L. trichandra* should be considered to pose a significant risk of becoming a ruderal weed where introduced.

11.22 Leucaena trichodes

Leucaena trichodes (Jacq.) Benth., Hooker Journal of Botany 4: 417. 1842.

Synonyms
Mimosa trichodes Jacq.
Acacia trichodes (Jacq.) Willd.
Leucaena canescens Benth.
Acacia pseudotrichodes DC.
Acacia trichodella A.
Leucaena pseudotrichodes (DC.) Britton & Rose
Leucaena colombiana Britton & Killip
Leucaena bolivarensis Britton & Killip
Leucaena trichodes (Jacq.) Benth. var. *acutifolia* Macbr.

Main attributes
L. trichodes is the only species of *Leucaena* native to South America where it is widely distributed and extends as far south as 15°S in Peru. It is closely related to, and doubtfully distinct from *L. macrophylla*. The two species together are unusual in the genus with unique pollen and anthers and are reproductively more isolated in the genus than the majority of species. Although it is a well known species in its native range, it has not been planted elsewhere as yet. Its wider potential is likely to be limited by moderate susceptibility to the psyllid.

Botanical features (Fig 67)
Bark: pale to mid grey-brown, smooth with pale brown, slightly raised, horizontally aligned lenticels on younger wood and shallow vertical rusty orange-brown fissures on older boles, inner bark cream
Leaves: pinnae 2 or 3 (-4) pairs; pinnular rachis 4.6-8.2(-11) cm long; leaflets 22-60(-118) mm long, (10-)15-50(-71) mm wide, (1)2-4(-6) pairs per pinna, very slightly asymmetric, acute at base, ovate-elliptic, apex variable acute or obtuse, sometimes rounded
Petiole gland: un-stalked, convex, rounded conical, elliptical, 2-3.5 mm long x 1.2-1.6 mm wide
Flower head: 8-12 mm in diameter, 90-170 flowers per head, in groups of 3-5 in leaf axils on actively growing shoots, sometimes with suppression of the leaves on the flowering shoot and sometimes with once-branched flowering shoots; flowers cream white
Pollen: loosely aggregated polyads composed of 22-28 pantoporate monads
Pods (7-)11-18 cm long, 18-24 mm wide, 1-3(-4) per flower head, linear-oblong, flat, thin and papery, variably glabrous and slightly lustrous or with dense velvety hairs, green or dark maroon unripe turning mid reddish- or orange-brown, opening along both sides
Seeds: 4-5.8 mm wide, 6.1-8.2 mm long, aligned transversely in pods, 18,000-30,000 seeds/kg

Closely related species and identification
L. trichodes is one of a group of closely allied large-leaflet taxa that has been taken to include *L.*

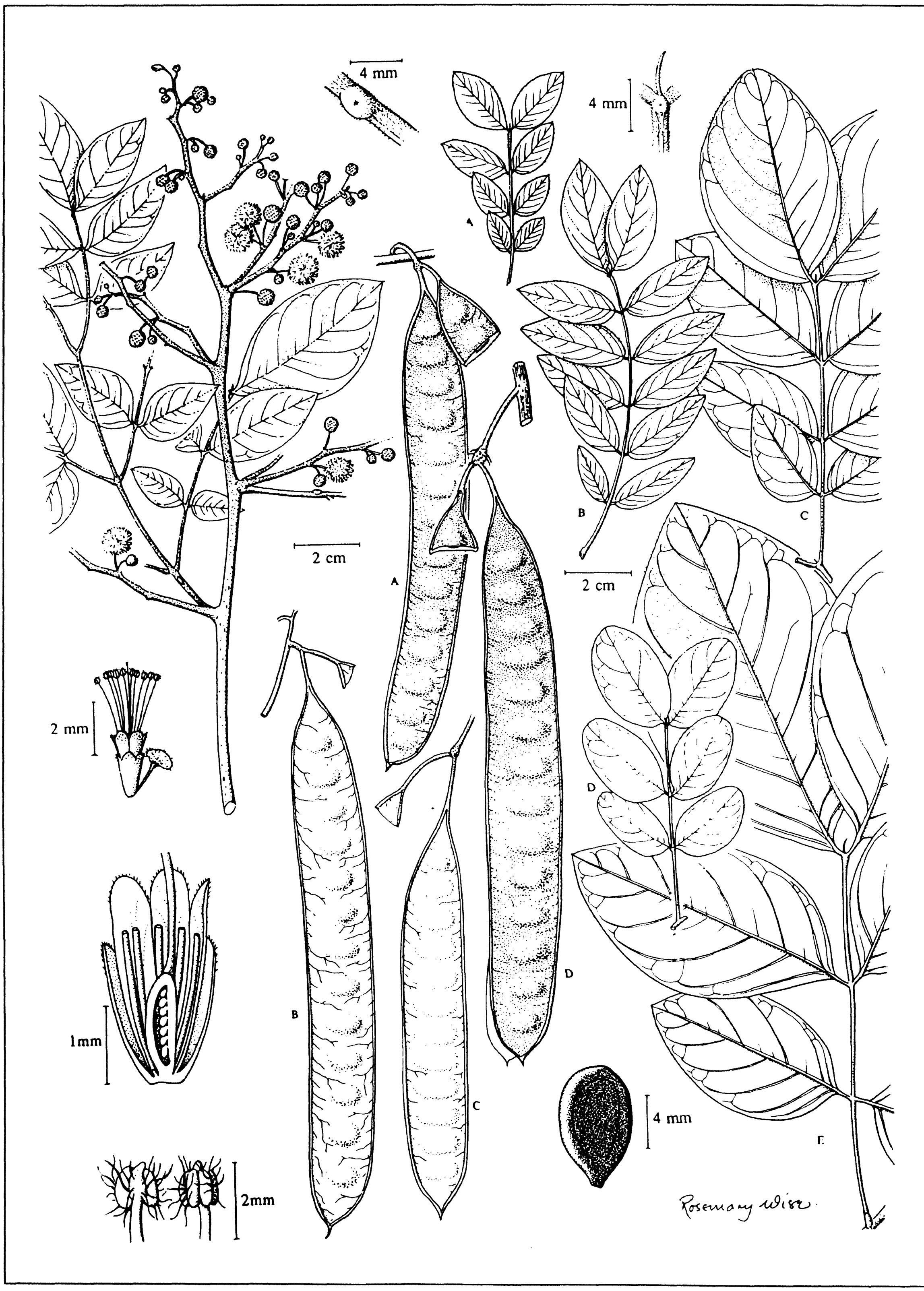

Figure 67 Leucaena trichodes, illustrating variation in pod and leaf morphology; botanical voucher specimens are cited in Hughes (in press).

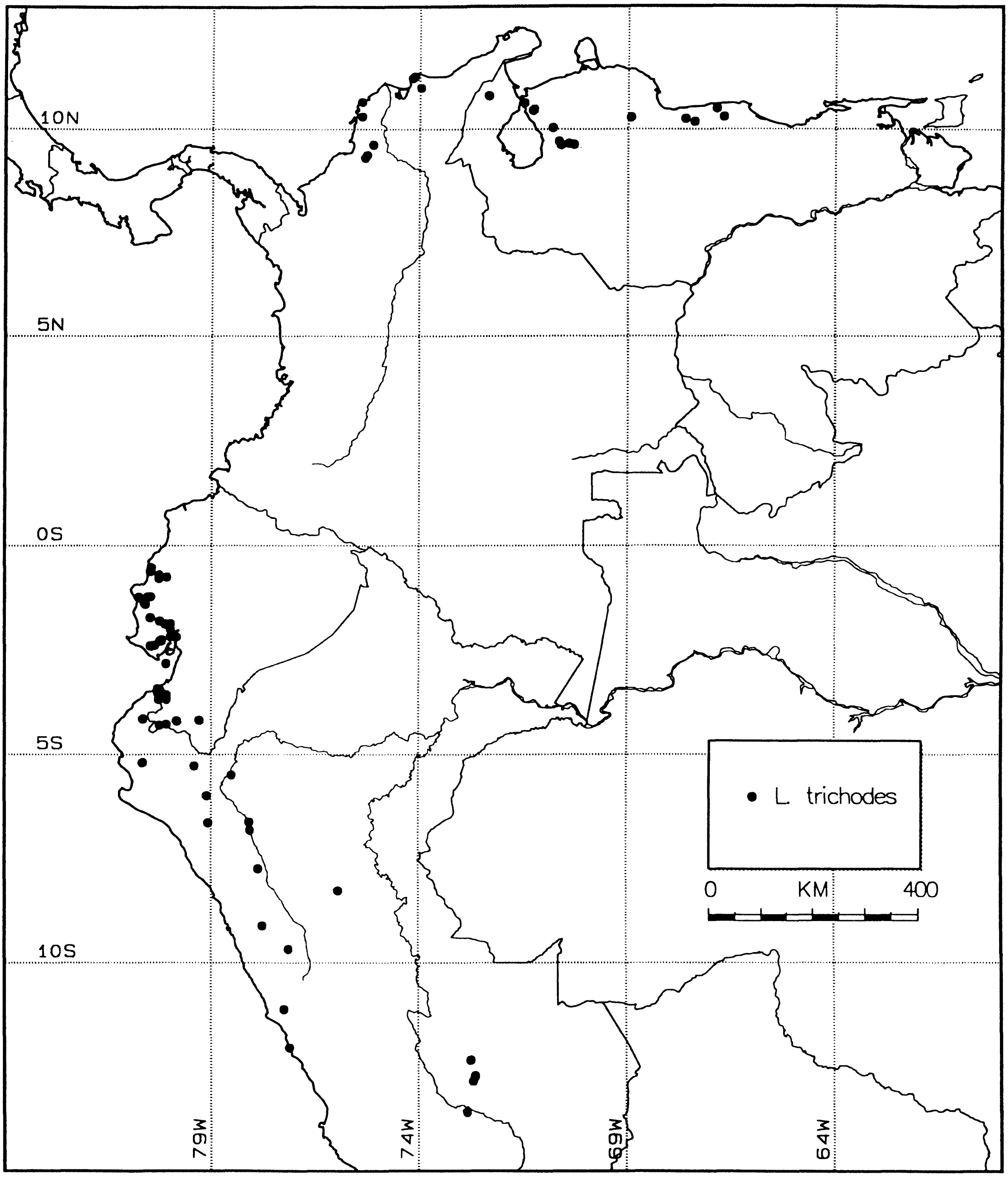

Figure 68 Map of north west South America showing the distribution of *L. trichodes*

macrophylla and *L. multicapitula*. The distinction of *L. multicapitula* as a separate species from *L. trichodes* was doubted by several authors (Janzen and Leisner, 1980; Brewbaker, 1987a; Zárate, 1994) due to their close similarity in leaf and pod morphology. Detailed survey of anther and pollen morphology (Hughes, 1997b) revealed a set of discrete characters that distinguish these two species fully justifying treatment of *L. multicapitula* as a separate species. The distinction of *L. trichodes* from *L. macrophylla* is more problematic given the lack of discrete morphological characters which distinguish these two species. They appear to form a widespread (northern Mexico to Peru), but highly disjunct and somewhat variable (in terms of leaf and pod dimensions) pair of closely related and doubtfully distinct species (Hughes, in press), which share a set of unique pollen and anther characters (Hughes, 1997b).

The origin, whether native or introduced, of *Leucaena* trees in Hispaniola described as *L. pseudotrichodes*, based on material from Santo Domingo, Dominican Republic, remains uncertain. What is clear, is that this species has been present on Hispaniola at least since 1821, and is now widespread in both the Dominican

Republic and Haiti. Most authors have treated *L. pseudotrichodes* as the same thing as *L. trichodes* (*e.g.* Bentham, 1875; Brewbaker, 1987a). Hughes (in press) discussed the possible affinities of *L. pseudotrichodes* and also concluded that it should be treated as a synonym of *L. trichodes*.

Segregation of the other species treated here as synonyms of *L. trichodes* (*L. canescens, L. bolivarensis* and *L. colombiana*) relied on shoot, leaflet and pod pubescence which are now seen to be highly variable locally, and unreliable characters. Similarly *L. trichodes* var. *acutifolia* was distinguished from typical *L. trichodes* solely by its acute or acuminate leaflets (Macbride, 1943). Leaflet shape is highly variable within *L. trichodes* (Fig 67) and use of this character alone does not constitute grounds for recognition of a distinct variety (Hughes, in press).

Chromosome number
Diploid, 2n=52, self-incompatible (Gonzalez *et al.*, 1967; Pan and Brewbaker, 1988)

Tree size and form
L. trichodes forms a small, sometimes multiple-stemmed tree or shrub (1-) 3-10 (-15) m tall and 10-15 (-30) cm in bole diameter with an open irregular narrow crown and upright angular branching.

Distribution (Fig 68)
L. trichodes is the only species in the genus that grows naturally south of the equator or indeed in South America, where it occurs across the northern coastal regions of Colombia (Bolivar and Magdalena) and Venezuela (Aragua, Distrito Federal, Miranda, Trujillo, Yaracuay and Zuila) and in coastal provinces of Ecuador and Peru as far south as 13°S in the departments of Cuzco and Apurimac. This distribution is discontinuous, broken by the Andes Mountains and outlying ranges that separate populations. Geographic isolation of populations may account for some of the morphological variation encountered. It is not clear whether the common and widespread occurrence of *L. trichodes* in Hispaniola (both Dominican Republic and Haiti) indicates that it is native there or is the result of an early (pre-1821) introduction and subsequent naturalization and spread.
Degree-squares: 36
Altitude range: 0-1500 (-2300) m

Ecogeography
L. trichodes occurs primarily in seasonally dry deciduous tropical forest and dry thorn scrub forest. It is particularly common following disturbance, in secondary vegetation and along roadsides and in some areas it forms the dominant woody cover in abandoned milpas, occasionally forming weedy thickets on open ground. *L. trichodes* is a truly tropical species. It grows principally in seasonally dry climates with 500-1000mm rainfall and a 5-7 month dry season. In parts of coastal Ecuador where *L. trichodes* is very common, rainfall is extremely variable from year to year and *L. trichodes* is able to withstand considerable drought.

Phenology
Flowering: Venezuela and Colombia: (August-) September-November, Ecuador and Peru: (February-) April-August (-October), fruiting: Venezuela and Colombia: (November-) January-May (-June), Ecuador and Peru: (March-) June-September (-November), partially deciduous

Conservation status
L. trichodes is very widely distributed and often locally abundant. It thrives on disturbance and is, in some parts of its native range, a ruderal weed of roadsides and bush fallow and is thus of little or no conservation concern.
Star rating: Green Star
IUCN threat category: LR:lc

Common names
arabisco (Peru: Huanuco), *beranero* (Colombia: Bolivar), *canafistula de monte* (Colombia: Santa Marta), *capra (chapra)* (Ecuador: El Oro, Loja, Guayas), *chalon* (Ecuador: Guayas), *chamba* (Peru: Cuzco, Macbride, 1943), *mihan (miham)* (Ecuador: Manabi), *pela caballo* (Ecuador: Manabi), *platanito* (Colombia: Bolivar), *ramon* (Venezuela: Aragua, Trujillo), *vainita* (Venezuela: Trujillo), *veranero* (Colombia: Bolivar, Britton and Killip, 1936), *yerba de la lancha* (Peru: Macbride, 1943).

Indigenous use and domestication
Within the native range, the wood of *L. trichodes* is widely used for posts, poles, firewood and occasionally sawtimber and the leaves as fish poison (Cajamarca, Peru) or livestock feed, although toxicity leading to hair loss in animals (hence vernacular *pela caballo*) is often reported. In some areas trees are protected and managed over crops in traditional agroforestry systems.

Exotic use and potential
L. trichodes has not been widely planted to date and its potential remains largely unknown but is likely to be limited by susceptibility to the psyllid. *L. trichodes* is one of the few species which has lower crossability with other species and this will limit use in hybridization.
Psyllid resistance: moderately susceptible (damage score 3-5)
Wood quality: like most species of *Leucaena*, the wood of *L. trichodes* provides good quality firewood and is widely used in the native range although its mean wood density (0.63) is low compared to other *Leucaena* species (Gourlay *et al.*, in press)
Fodder quality: the leaves of *L. trichodes* have high *in vitro* digestibility and very low (nearly zero) condensed tannin content (Stewart and Dunsdon, in press).
Weediness risk: *L. trichodes* thrives on disturbance and can be a ruderal weed colonizing open habitats (bush fallow and roadsides) within the native range, indicating its potential to become a ruderal weed where introduced.

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Appendix 1. Checklist of accepted names, synonyms, doubtful and excluded names, and their type specimens and protologues and index of synonyms

A full taxonomic monograph of *Leucaena* has recently been completed (Hughes, in press). That monograph provides a definitive account of the taxonomy of the genus for botanists and systematists. This Handbook includes summary information on the taxonomy of *Leucaena* for a wider audience and attempts to clarify the confusion which has arisen over the correct scientific names to be used for some taxa (Chapter 2). In this Appendix a complete checklist of all the scientific names ever applied to *Leucaena* is presented for reference. It is always important to use the accepted scientific name to facilitate communication. Most users and researchers do not need to concern themselves with the full intricacies of taxonomy and its associated nomenclatural procedures. However, when there is confusion, this checklist can be used to check accepted names or synonyms. There are 85 different scientific names, or name combinations, which have at some point been used for *Leucaena*. However, there are only 22 accepted species, 4 accepted subspecies and 2 accepted varieties. The remainder are treated by Hughes (in press) as either synonyms, or doubtful or excluded names.

Accepted names are shown in the list below in **bold** while *synonyms* are listed in *italics* and indented. Doubtful names are those which cannot be assigned with certainty to any known species and excluded names are those which are now assigned to species of genera other than *Leucaena*. These are listed separately at the end. In line with the International Code for Botanical Nomenclature, all scientific names have two pieces of basic information associated with them. Firstly, there is the authority (author) place (journal *etc*) and year of publication. This is simply the bibliographic citation of the original description, usually called the protologue, of a species. These are listed in abbreviated form following each name in the checklist. Secondly, there is the TYPE specimen which refers to the botanical specimen (or drawing/painting) used by, and usually cited by, the author with the original description of a species. Details of all TYPE specimens are listed after the publication details in the format: - TYPE: COUNTRY. Region: Locality, Locality notes, Latitude, Longitude, Altitude, Date of collection, *Collector name and number* (acronyms of herbaria where specimens are housed).

Leucaena Bentham in Hook. J. Bot. 4: 416. 1842. - TYPE: *Leucaena diversifolia* (Schltdl.) Benth.
  Ryncholeucaena Britton & Rose. N. Amer. Fl. 23: 130. 1928. - TYPE: *Leucaena greggii* S. Watson
  Caudoleucaena Britton & Rose. N. Amer. Fl. 23: 130. 1928. - TYPE: *Leucaena retusa* Benth.

Leucaena collinsii Britton & Rose, N. Amer. Fl. 23(2): 126. 1928.
  Leucaena collinsii subsp. **collinsii**
    L. esculenta (Sessé & Moc. ex DC.) Benth. subsp. *collinsii* (Britton & Rose) S. Zárate, Bull. Intern. Group. Study of Mimosoideae 12: 30. 1984. - TYPE: MEXICO. Chiapas: "Castla Gutierrez" (Tuxtla Gutierrez), 6 Jan 1907, *Collins GN & Doyle CB 157* (holotype: NY, isotype: US).
  Leucaena collinsii subsp. **zacapana** C.E.Hughes. Kew Bull. 46(3): 553. 1991. TYPE: GUATEMALA. Zacapa: Estanzuela in dry thorn forest, 1 Mar 1988, *Hughes CE 1102* (holotype FHO, isotypes K MEXU).
Leucaena confertiflora S. Zárate, Anal. Inst. Biol. Univ. Nac. Auton. Mexico. Ser. Bot. 65(2): 148. 1994. -TYPE: Mexico. Oaxaca. Matatlán, Cerro Nueve Puntas nr shortwave relay mast, 5km S of Matatlán, 16°49'N 96°21'W, 2050m, 11 January 1980, *Zárate S 428* (holotype MEXU).
  Leucaena confertiflora S. Zárate var. **confertiflora**
    Leucaena confertiflora S. Zárate subsp. *confertiflora* S. Zárate, Anal. Inst. Biol. (Mex.) Ser. Bot. 65(2): 148. 1994.
  Leucaena confertiflora S. Zárate var. **adenotheloidea** (S. Zárate) C.E.Hughes, Contr. Univ. Mich. Herb. 21: 287. 1997.
    Leucaena confertiflora S. Zárate subsp. *adenotheloidea* S. Zárate, Anales Inst. Biol. (Mex.) Ser. Bot. 65(2): 149. 1994. - TYPE: Mexico. Puebla. San Pedro Chapulco, 13km NE of Tehuacan on rd towards Orizaba, 18°36'N 97°25'W, 2100m, 7 December 1981, *Zárate S 610* (holotype MEXU).
Leucaena cuspidata Standley. Contr. U.S. Nat. Herb. 20: 189. 1919. - TYPE: MEXICO. San Luis Potosí: Minas de San Rafael, 22°12'N 100°16'W, May 1911, *Purpus CA 5183* (holotype US, isotypes GH,MO,NY,UC).
    Leucaena cuspidata Standley subsp. *jacalensis* S. Zárate. Anal. Inst. Biol. Ser. Botánica. Mexico. 65: 144. 1994. - TYPE: MEXICO. Hidalgo: 7km NE of Jacala, 21°03'N 99°10'W, 15 August 1964, *Quintero G 1292* (holotype MEXU).
Leucaena diversifolia (Schltdl.) Benth. Hook. J. Bot. 4: 417. 1842.
    Acacia diversifolia Schltdl. Linnaea 12: 570. 1838. - TYPE: MEXICO. Veracruz, "in sylvis prope Jalapam", Aug 1828, 19°26'N 96°55'W, *Schiede CJW 693* (holotype HAL; isotypes, GH NY).
    Leucaena diversifolia subsp. *diversifolia sensu* Pan. Quart. J. Chin. For. 21: 89. 1988 and Zárate, S. Anal. Inst. Biol. (Mex.) Ser. Bot. 65: 150. 1994.
    Leucaena brachycarpa Urban. Symb. Antil. 2: 265. 1900. TYPE: MEXICO. Veracruz: Tuspango nr Cordoba, 18°50'N 97°01'W,

2 June 1865, *Bourgeau, M 2401*, (lectotype designated by Zárate (1994) BR; isolectotypes F K US).

Leucaena laxifolia Urban. Symb. Antil. 2: 266. 1900. TYPE: MEXICO. No locality data, 1833, *Sommerschuh s.n.* (holotype B destroyed; isotypes US NY)

Leucaena esculenta (Sessé & Mociño ex DC.) Benth. Trans. Linn. Soc. 30: 442. 1875.

Acacia esculenta DC., Prodr. 2: 470. 1825.

Mimosa esculenta Sessé & Mociño Pl. Nov. Hisp. 178. 1890; ed. 2. 165. 1893. The TYPE is a plate of the painting made by the artists of the Sessé & Mociño Real Expedición, "in temperatis Novae Hispaniae locis", probably based on specimens from nr Mexico City; it is plate 6331.627 of the Torner Collection of Sessé & Mociño Biological Collections, no. 185 of the *Icones Florae Mexicanae*, represented at G-DC by plate 209 of de Candolle's collection (McVaugh, 1980; 1987); neg. 30593 F. A specimen at OXF (ex herb. Lambert.), labelled by Pavón "*Mimosa esculenta*" and by Bentham "*Leucaena esculenta*" was mistakenly taken as the lectotype of *M. esculenta* (McVaugh, 1987), and is perhaps a typotype.

Leucaena confusa Britton & Rose, N. Amer. Fl. 23: 128. 1928. - TYPE: Mexico, Jalisco: hills nr Tequila, 18 Oct 1893, *Pringle CG 4534* (holotype NY, isotypes BM GH MO UC US).

Leucaena doylei Britton & Rose, N. Amer. Fl. 23: 128. 1928. - TYPE: Mexico, Chiapas: nr "Castla" (Tuxtla) Gutierrez, 6 Jan 1907, *Collins GN & Doyle CB 161* (holotype NY, isotypes US, photo F).

Leucaena greggii S. Watson, Proc. Am. Acad. Arts and Sci., Boston. 23: 272. 1888.

Ryncholeucaena greggii (S. Watson) Britton & Rose N. Amer. Fl. 23: 130. 1928. - TYPE: MEXICO. Nuevo León, Dry ravine east of Rinconada, 25°41'N 100°40'W, 25th May 1847, *Gregg s.n.* (lectotype, NY; isolectotype GH).

Leucaena involucrata S. Zárate, Anal. Inst. Biol. (Mexico) Ser. Bot. 65: 138. 1994. - TYPE: MEXICO. Sonora: El Novillo, 28° 55'N 109° 28'W, 19 Aug 1991, *Hughes CE 1522,* (holotype, MEXU, isotypes FHO K NY MO).

Leucaena lanceolata S. Watson, Proc. Am. Acad. Arts & Sci. 21: 427. 1886. - TYPE: Mexico. Chihuahua: Batopilas, Hacienda San Miguel, SW Chihuahua, 27°53'N 108°26'W, Sep 1885, *Palmer EJ 6,* (holotype, GH, isotypes, NY UC US).

Leucaena lanceolata var. **lanceolata**

Leucaena microcarpa Rose, Contr. U.S. Natl. Herb. 5: 141. 1897. - TYPE: Mexico. Baja California Sur: nr Miraflores, 23° 21'N 109° 47'W, 13 Oct 1890, *Brandegee TS 186,* (holotype, US, isotype, UC).

Leucaena brandegeei Britton & Rose, N. Amer. Fl. 23: 128. 1928. - TYPE: Mexico. Baja California Sur: nr La Mesa, Cape region, 31 Oct 1902, *Brandegee TS s.n.* (holotype, NY, isotypes, US UC).

Leucaena cruziana Britton & Rose, N. Amer. Fl. 23: 123. 1928. - TYPE: Mexico. Veracruz: Barranca de Panoaya, 19° 18'N 96° 25'W, Dec 1919, *Purpus CA 8387* (holotype, NY, isotypes US UC GH).

Leucaena palmeri Britton & Rose, N. Amer. Fl. 23: 123. 1928. - TYPE: Mexico. Sonora: nr Alamos, 26° 59'N 108° 57'W, 20 Sep 1890, *Palmer EJ 718* (holotype, NY, isotype, US).

Leucaena pubescens Britton & Rose, N. Amer. Fl. 23: 122. 1928. - TYPE: Mexico. Sinaloa: nr Mazatlan, 23° 14'N 106°24'W, 1925, *Ortega JG 5988* (holotype, NY, isotypes, US GH).

Leucaena purpusii Britton & Rose, N. Amer. Fl. 23: 123. 1928. - TYPE: Mexico. Veracruz: rim of barranca nr Remudadero, 19° 15'N 96° 34'W, Jan 1926, *Purpus CA 10607* (holotype, NY, isotype, US).

Leucaena sinaloensis Britton & Rose, N. Amer. Fl. 23: 124. 1928. - TYPE: Mexico. Sinaloa: vicinity of Palmar, 22° 13'N 105° 36'W, 15 Apr 1910, *Rose JN et al. 14650* (holotype, NY, isotype, US).

Leucaena sonorensis Britton & Rose, N. Amer. Fl. 23: 122. 1928. - TYPE: Mexico. Sonora: Sierra de Alamos, nr Alamos, 26° 58'N 108° 57'W, 14 Mar 1910, *Rose JN et al. 12821* (holotype, NY, isotype, US).

Leucaena nitens M.E. Jones, Contr. West. Bot. 15: 136. 1929. - TYPE: Mexico. Sinaloa: nr Mazatlan, 23° 14'N 106°24'W, 20 Nov 1926, *Jones ME 22465* (holotype POM, isotypes, MO US).

Leucaena lanceolata var. **sousae** (S. Zárate) C.E. Hughes Contr. Univ. Michigan Herb. 21: 288. 1997.

L. lanceolata subsp. *sousae* S. Zárate, Anal. Bot. Inst. Biol. (Mexico) Serie Botánica. 65: 117. 1994. - TYPE: Mexico. Oaxaca. 17km WNW of Puerto Escondido, district of Juquila, 15°57'N 97°13'W. 21 Oct 1976, *Sousa M 6390* (holotype MEXU, isotype UC).

Leucaena rekoi Britton & Rose, N. Amer. Fl. 23: 122. 1928. - TYPE: Mexico. Oaxaca: nr Pochutla, close to the Pacific coast, 15° 44'N 96° 28'W, 28 Sep 1917, *Reko BP 3632* (lectotype, here designated, flowering shoot and leaves only, US).

Leucaena lempirana C.E. Hughes, Contr. Univ. Mich. Herb. 21: 279. 1997. - TYPE: Honduras. Yoro: 6km SE El Negrito, side rd to Nuevo Esperanza nr Rio Cuyamapa, Otomán Valley, 15°17'N 87°40'W. 25 Feb 1991, *Hughes CE 1412,* (holotype EAP; isotypes FHO, K, MEXU, NY).

Leucaena leucocephala (Lam.) de Wit. Taxon. 10: 53. 1961.

Leucaena leucocephala subsp. **leucocephala**

Mimosa leucocephala Lamarck. Encycl. Méth. Bot. 1: 12. 1783.

Acacia leucocephala (Lam.) Link. Enum. Hort. Berol. 2: 444. 1822. - TYPE: *Lamarckian Herb.* "Mimosa latisiliqua", "Mimosa leucocephala", (holotype: P-LA, microfiche K).

Leucaena leucocephala subsp. **glabrata** (Rose) S. Zárate. Phytologia 63(4): 305. 1987.

Leucaena glabrata Rose. Contr. U.S. Natl. Herb. 5(3): 140. 1897. - TYPE: MEXICO. Guerrero: vicinity of Acapulco, Oct. 1894 - Dec 1895, *Palmer EJ 368* (holotype: US; isotypes: GH F MO NY UC).

Leucaena leucocephala subsp. **ixtahuacana** C.E.Hughes, Contr. Univ. Mich. Herb. 21: 285. 1997. - TYPE: GUATEMALA. Huehuetenango: 1km ENE of San Miguel, track running WSW from Ixtahuacan into the valley of the Rio Cuilco, 15°23'N, 91°50'W, *Hughes et al. 1689* (holotype: FHO; isotypes: E,K,MEXU,MO.NY).

Leucaena macrophylla Benth. Bot. Voy. Sulphur. 90. 1844. - TYPE: MEXICO. Guerrero: Acapulco, 1841, *Hinds RB s.n.*, (holotype, K).

Leucaena macrophylla Benth. subsp. **macrophylla**

Leucaena macrocarpa Rose. Contr. US Nat. Herb. 1(9): 327. 1895. - TYPE: MEXICO. Jalisco: Rio Blanco, Aug 1886, *Palmer EJ 320 pro parte,* (mixed collection, flowering specimen lectotype (designated McVaugh, 1987) US, isolectotype, NY; fruiting specimen is *Albizia occidentalis* Brandegee).

Leucaena houghii Britton & Rose. Mimosaceae. N. Amer. Fl. 23(2): 123. 1928. - TYPE: MEXICO. Morelos: Cuernavaca, 18° 55'N 99° 16'W, 28 May 1899, *Rose JN 4362,* (holotype, NY, isotype, US).

Leucaena nelsonii Britton & Rose. Mimosaceae. N. Amer. Fl. 23(2): 124. 1928.

Leucaena macrophylla Benth. subsp. *nelsonii* (Britton & Rose) S. Zárate. Anales del Inst. Biol. Mexico. Ser. Bot. 65(2): 113. 1994. - TYPE: MEXICO: Guerrero: between San Marcos and Copala, 16°45'N 99°15'W, 8 Feb 1895, *Nelson EW 2286*, (holotype NY, isotype US).

Leucaena macrophylla Benth. subsp. **istmensis** C.E. Hughes, Contr. Univ. Michigan Herb. 21: 283. 1997. - TYPE: MEXICO, Oaxaca: 40km W of Puerto Escondido, coast rd to Pinotepa Nacional, nr San Isidro Llano Grande, 2km inland from Pacific coast, 15°58'N 97°10'W, 26 Mar 1989, *Hughes CE 1338* (holotype FHO, isotypes distributed to AAU, K, MEXU, NY).

Leucaena magnifica (C.E. Hughes) C.E. Hughes, Contr. Univ. Michigan Herb. 21: 286. 1997.

Leucaena shannonii Donn. Smith subsp. *magnifica* C.E. Hughes, Kew Bull. 46: 547. 1991. - TYPE: GUATEMALA. Chiquimula: Llano Grande, 1.5km SW of Quetzaltepeque, rd towards Esquipulas, 14°37'N 89°27'W, 26 Feb 1988, *Hughes 1093* (holotype FHO isotypes K MEXU).

Leucaena matudae (S. Zárate) C.E. Hughes, Contr. Univ. Michigan Herb. 21: 286. 1997.

Leucaena esculenta (Sessé & Mociño ex DC.) Benth. subsp. *matudae* S. Zárate, Anal. Inst. Biol. (Mex.) Ser. Bot. 65(2): 134. 1994. TYPE: Mexico. Guerrero. Casa Verde, nr Venta Viejo in the Canon de Zopilote, *"guaje chismoso"*, 17°50'N 99°34'W, 12 Dec 1978, *Halbinger 288* (holotype MEXU, isotypes ENCB MO NY).

Leucaena multicapitula Schery, Annals Missouri Bot. Gard. 37: 302. 1950. - TYPE: PANAMA. Canal Zone: Rio Cocoli, Miraflores, 9°05'N 79°38'W, 20 June 1938, *White P 135* (holotype GH; isotypes MO US).

Leucaena pallida Britton & Rose, N. Amer. Fl. 23: 126. 1928. - TYPE: MEXICO. Jalisco: nr Huejuqilla, 22° 36'N 103° 52'W, 25 Aug 1897, *Rose JN 2569*, (holotype, NY, isotypes, US (excluding flowering shoot which is *L. leucocephala*) GH).

Leucaena dugesiana Britton & Rose, N. Amer. Fl. 23: 127. 1928. - TYPE: MEXICO. Guanajuato: Guanajuato, 21° 01'N 101° 15'W, 11 Jul 1899, *Rose JN & Hough 4841*, (holotype, NY, isotype, US).

Leucaena oaxacana Britton & Rose, N. Amer. Fl. 23: 127. 1928. - TYPE: MEXICO. Oaxaca: nr the city of Oaxaca, 17°03'N 96° 41'W, 18 Jun 1899, *Rose JN & Hough 4648*, (holotype, NY, isotype, US).

Leucaena paniculata Britton & Rose, N. Amer. Fl. 23: 128. 1928.

Leucaena esculenta (Sessé & Mociño ex DC.) Benth. subsp. *paniculata* (Britton & Rose) S. Zárate, Anales Inst. Biol. Univ. Nac. Auton. Mexico. Ser. Bot. 65(2): 133. 1994. - TYPE: MEXICO. Morelos: nr Cuernavaca, 18° 53'N 99° 16'W, 15 Aug 1906, *Rose JN & Rose 11090*, (holotype, NY, isotype, US).

Leucaena pueblana Britton & Rose. N. Amer. Fl. 23: 126. 1928. - TYPE: MEXICO. Oaxaca: West side of the valley of Cuicatlán, 17° 47'N 96° 58'W, 9 Nov 1894, *Nelson EW 1886,* (holotype, NY; isotype, US).

Leucaena pulverulenta (Schltdl.) Benth., Hook. J. Bot. 4: 417. 1842.

Acacia pulverulenta Schltdl. Linnaea 12: 571. 1838. - TYPE: MEXICO. Veracruz: "ad ripam fluminis Misantlensis, pr. San Antonio, reg. calidae", February, *Schiede & Deppe s.n.* (holotype: HAL (*n.v.*); isotypes: OXF US NY photo ex B).

Leucaena retusa Benth. in Gray, Plantae Wrightianae 1: 64. 1852.

Caudoleucaena retusa (Benth.) Britton & Rose. N. Amer. Fl. 23: 131. 1928. - TYPE: USA. Texas: Bottom of the Rio Nueces, 29°26'N 100°05'W, June 1849, *Wright C 171* (lectotype, here designated, K, isolectotypes BM,GH,NY,OXF,US).

Acacia sabeana Buckley. Proc. Acad. Nat. Sci. Philadelphia 453. 1861. - TYPE: USA. Texas: banks of San Saba River, N of Fort Mason, rd to Camp Colorado, 13°52'N 98° 48'W, June 1861, *Buckley s.n.* (holotype PH).

Leucaena salvadorensis Standley ex Britton & Rose, N. Amer. Fl. 23: 125. 1928.

Leucaena shannonii J.D. Smith subsp. *salvadorensis* (Standley ex Britton & Rose) S. Zárate, Ann. Miss. Bot. Gdn. 74: 499, 1987. - TYPE: EL SALVADOR. Morazán: nr Jocóro, 1924, *Calderón S 2031* (holotype: NY; isotype fragment: US).

Leucaena shannonii Donn. Smith., Bot. Gazette 57: 419. 1914. - TYPE: EL SALVADOR. Cuscatlán: Cojutepeque, 13°42'N 88°56'W, 900 m, Dec 1892, *Shannon WC 5032* (lectotype, here designated, US).

Leucaena trichandra (Zucc.) Urban. Symbolae Antillanae 2: 267. 1900.

Acacia trichandra Zuccarini. Abh. Math. Phys Cl. K. Baer Akad. Wiss. 2: 349. 1837?.

Leucaena diversifolia (Schltdl.) Benth. subsp. *trichandra* (Urban) F.J. Pan. Quart. J. Chinese For. 21: 89. 1988. - TYPE: Cultivated "in horto Monacensi a. 1835, crescit in imperio mexicano, unde semina communicavit clar. de Karwinski", Herb. Regium Monacense, (holotype M, fragment and tracing ex M at US).

Leucaena stenocarpa Urban. Symbolae Antillanae 2: 266. 1900.

Leucaena diversifolia (Schltdl.) Benth. subsp. *stenocarpa* (Urban) S. Zárate. Anal. Inst. Biol. (Mexico) Ser. Bot. 65: 152. 1994. - TYPE: MEXICO. Oaxaca: foothills of Sierra San Felipe, N of Oaxaca, 1900m, 17°07'N 96°43'W, 26 May 1894, *Pringle CG 4656*, (holotype B probably destroyed; isotypes A F K MEXU MO NY UC US).

Leucaena guatemalensis Britton and Rose. N. Amer. Fl. 23: 126. 1928. - TYPE: GUATEMALA. Guatemala: on plains nr Guatemala City, 14°37'N 90°31'W, July 1860, *Hayes S 23*, (holotype GH; isotypes K NY MO US).

Leucaena revoluta Britton and Rose. N. Amer. Fl. 23: 127. 1928. - TYPE: MEXICO: Chiapas, mountain slopes nr Fenix, 17 May 1900, *Purpus CA 10158*, (holotype NY: isotype US).

Leucaena standleyi Britton and Rose. N. Amer. Fl. 23: 128. 1928. - TYPE: EL SALVADOR, Santa Ana: vicinity of Santa Ana, 750m, 13°59'N 59°32'W, *Standley PC 20409* (holotype NY; isotypes GH US).

Senegalia albanensis Britton and Rose. N. Amer. Fl. 23: 117 1928. - TYPE: MEXICO, Oaxaca: Monte Alban, 5 September 1894, *Smith CL 320* (holotype NY, photo ex NY at K)

Leucaena trichodes (Jacq.) Benth. Hook. J. Bot. 4: 417. 1842.

Mimosa trichodes Jacq. Hort. Schoenbr. 3: 76 (plate 394). 1798.

Acacia trichodes (Jacq.) Willd. Species Plantarum 4: 1063. 1805. - TYPE: VENEZUELA. Caracas, *Jacquin NJ*, (holotype W, ex herb. Jacq. photo FHO photo US).

Leucaena canescens Benth. Plant. Hartweg. 117. 1839. - TYPE: ECUADOR. Guayas: nr Guayaquil, *Hartweg CT 655,* (holotype, K photo MO; isotypes, NY OXF W).

Acacia pseudotrichodes DC. Prodromus 2: 466. 1825.

Leucaena pseudotrichodes (DC.) Britton & Rose. Mimosaceae. N. Amer. Fl. 23: 124. 1928. -TYPE: DOMINICAN REPUBLIC. Santo Domingo, 1821, *Bertero, CG s.n.* (holotype G-DC, photo FHO).

Leucaena colombiana Britton & Killip. Ann. N.Y. Acad. Sci. 35: 146. 1936. - TYPE: COLOMBIA. Magdalena: north of Bonda, Santa Marta: 4 Aug 1898, *Smith HH 37,* (holotype, NY; isotypes, K MO US CAS UC).

Leucaena bolivarensis Britton & Killip. Ann. N.Y. Acad. Sci. 35: 147. 1936. - TYPE: COLOMBIA. Bolivar: nr Turbaco, Torecilla, 10 Nov 1926, *Killip EP 14239,* (holotype, NY isotypes, K US GH).

? *Leucaena trichodes* (Jacq.) Benth. var. *acutifolia* Macbr. Fl. Peru. Leguminosae. Bot. Ser. Field Mus. Nat. Hist. 13(3): 99. 1943. - TYPE: PERU: Piura: Parinas valley, *Haught F119* (type not found).

DOUBTFUL AND EXCLUDED NAMES

Leucaena blancii Ramírez Goyena. Fl. Nicaraguense 1: 379. 1911. This name has previously been considered a synonym of *L. leucocephala* subsp. *glabrata* (Brewbaker, 1987a; Zárate, 1994), based on the complete description and comparison with *L. glauca* (= *L. leucocephala* subsp. *leucocephala*) in the protologue. Lacking a type, the name cannot be assigned with certainty.

Leucaena boliviana Rusby. Bull. N.Y. Bot. Gard. 8: 91. 1912. - TYPE: BOLIVIA, San Buena Ventura, *Williams RS 356* (NY) = *Acacia glomerosa* Benth. vel. sp. aff. det. L. Rico & G.P. Lewis (K), 20/5/93, matched with *Smith DN' et al. 13577* (K,LPB,MO).

Leucaena formosa Griseb. Cat. Pl. Cubens. 82 and 284 (addenda). 1866. - TYPE: CUBA. *Wright C 2392* (holotype ?MA isotypes GH NY) = *Lysiloma sabicu* Benth. Hook. J. Kew Gard. Misc. 6: 236. 1854. See also Shaw and Schubert (1976).

Leucaena forsteri Benth. Lond. J. Bot. 5: 94. 1846. - TYPE: TAHITI. *Bertero & Moerenhout s.n.* (lectotype P not seen). = *Schleinitzia insularum* (Guill.) Burkart. J. Arn. Arb. 57: 524. 1976. See also Verdcourt (1977) and Nevling and Niezgoda (1978).

Leucaena glauca (L.) Benth. Hook. J. Bot. 4: 416. 1842. *Mimosa glauca* L. Sp. Pl. Ed. 1. 1: 520. 1753. - TYPE Herb. A. van Royen (L, herb no. 908.132-54). = *Acacia glauca* (L.) Willd. Sp. Pl. Ed. 4 vol. 4,2: 1075. 1806. Linnaeus (1753) applied the name *M. glauca* to a specimen described by van Royen in Holland. De Wit (1961, 1975) clearly shows the van Royen specimen to be an acacia, now *A. glauca* (L.) Willd. (formerly *A. villosa*). In 1763 Linnaeus misapplied the name to material of *L. leucocephala* (Lam.) de Wit. Bentham established the genus *Leucaena* and applied it to this 1763 material (*L. glauca* (Willd.) Benth., basionym *M. glauca* L. 1763).

Leucaena insularum (Guill.) Däniker. Vierteljahrschr. Nat. Ges. Zurich Jahrg. 77 (Beibl. 19): 176. 1932. *Acacia insularum* Guill. Ann. Sci. Nat. ser. 2. 7: 360. 1837. - TYPE: TAHITI. *Bertero & Moerenhout s.n.*, (lectotype P not seen). = *Schleinitzia insularum* (Guill.) Burkart. J. Arn. Arb. 57: 524. 1976. See also Verdcourt (1977) and Nevling and Niezgoda (1978).

Leucaena insularum (Guill.) Däniker var. *guamensis* Fosberg & Stone. Micronesia 2: 67. 1965. - TYPE: MARIANA IS. Guam: Cocos Island, *Fosberg 43502*, (holotype US; isotypes BISH, F, L, NY). = *Schleinitzia fosbergii* Nevl. & Niezgoda. Adansonia Ser. 2. 18: 362. 1978.

Leucaena latisiliqua (L.) Gillis & Stearn. Taxon 23: 185-191. 1974. - TYPE: Plumier, Catalogus Plantarum Americanarum. 1703, 17, cum Plantarum Americanarum fasciculus primus 1755, tab 6; Burman, J. (Ed.) = *Lysiloma latisiliqua* (L.) Benth. Trans Linn. Soc. Lond. 30: 534. 1875. *Mimosa latisiliqua* L. Sp. Pl. ed 1, 1:519. 1753. De Wit (1975) showed that the basionym is clearly applicable to a species of *Lysiloma.*

Leucaena plurijuga Standley. Contr. U.S. Natl. Herb. 20: 189. 1919. - TYPE: MEXICO. Michoacán: Monte León, 12 November 1892, *Pringle CG 5352* (holotype US). = *Albizia plurijuga* (Standley) Britton & Rose.

Leucaena ulei Harms in Ule. Verhand Bot. Prov. Brand. 47: 162. 1907. - TYPE: BRAZIL. Amazónas: Cachoeira dos Marmellos, nr Rio Madero, March 1902, *Ule E 6085* (holotype B, destroyed, isotypes F, K, NY; photos ex B FHO US). = *Parkia ulei* (Harms) Kuhlm. Arch. Jard. Bot. Rio de Janeiro 4: 356. 1925. See also Hopkins (1986).

INDEX OF SYNONYMS

Leucaena blancii Goyena == ?
Leucaena bolivarensis Britton & Killip == **Leucaena trichodes** (Jacq.) Benth.
Leucaena boliviana Rusby == **Acacia glomerosa** Benth.
Leucaena brachycarpa Urb. == **Leucaena diversifolia** (Schltdl.) Benth.
Leucaena brandegeei Britton & Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena canescens Benth. == **Leucaena trichodes** (Jacq.) Benth.
Leucaena colombiana Britton & Killip == **Leucaena trichodes** (Jacq.) Benth.
Leucaena confertiflora S. Zárate subsp. *adenotheloidea* S. Zárate == **Leucaena confertiflora** S. Zárate var. **adenotheloidea** (S. Zárate) C.E.Hughes
Leucaena confertiflora S. Zárate subsp. *confertiflora* == **Leucaena confertiflora** S. Zárate var. **confertiflora** (S. Zárate) C.E.Hughes
Leucaena confusa Britton & Rose == **Leucaena esculenta** (Sessé & Moc. ex DC.) Benth.
Leucaena cruziana Britton & Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena cuspidata Standley subsp. *jacalensis* S. Zárate == **Leucaena cuspidata** Standley
Leucaena diversifolia (Schltdl.) Benth. subsp. *stenocarpa* (Urb.) S.Zárate == **Leucaena trichandra** (Zucc.) Urban
Leucaena doylei Britton & Rose == **Leucaena esculenta** (Sessé & Moc. ex DC.) Benth.
Leucaena dugesiana Britton & Rose == **Leucaena pallida** Britton & Rose
Leucaena esculenta (Sessé & Moc. ex DC.) Benth. subsp. *paniculata* (Britton & Rose) S.Zárate == **Leucaena pallida** Britton & Rose
Leucaena esculenta (Sessé & Moc. ex DC.) Benth. subsp. *matudae* S.Zárate == **Leucaena matudae** (S. Zárate) C.E. Hughes
Leucaena esculenta (Sessé & Moc. ex DC.) Benth. subsp. *collinsii* (Britton & Rose) S. Zárate == **Leucaena collinsii** Britton & Rose subsp. **collinsii**
Leucaena forsteri Benth. == **Schleinitzia insularum** (Guill) Burkart
Leucaena glabrata Rose == **Leucaena leucocephala** (Lam.) de Wit subsp. **glabrata** (Rose) S. Zárate
Leucaena glauca (Willd.) Benth. == **Acacia glauca** (L.) Willd.
Leucaena guatemalensis Britton & Rose == **Leucaena trichandra** (Zucc.) Urban
Leucaena houghii Britton & Rose == **Leucaena macrophylla** Benth. subsp. **macrophylla**
Leucaena insularum (Guillaumin) Daniker == **Schleinitzia insularum** (Guill) Burkart
Leucaena lanceolata S. Watson subsp. *sousae* S. Zárate == **Leucaena lanceolata** S. Watson var. **sousae** (S. Zárate) C.E.Hughes
Leucaena latisiliqua (L.) Gillis & Stearn == **Lysiloma latisiliqua** (L.) Benth.
Leucaena laxifolia Urb. == **Leucaena diversifolia** (Schltdl.) Benth.
Leucaena macrocarpa Rose == **Leucaena macrophylla** Benth. subsp. **macrophylla**
Leucaena macrophylla Benth. subsp. *nelsonii* (Britton & Rose) S. Zárate == **Leucaena macrophylla** Benth. subsp. **macrophylla**
Leucaena microcarpa Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena nelsonii Britton & Rose == **Leucaena macrophylla** Benth. subsp. **macrophylla**
Leucaena nitens M.E. Jones == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena oaxacana Britton & Rose == **Leucaena pallida** Britton & Rose
Leucaena palmeri Britton & Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena paniculata Britton & Rose == **Leucaena pallida** Britton & Rose
Leucaena plurijuga Standley == **Albizia plurijuga** (Standl.) B.& R.
Leucaena pseudotrichodes (DC.) Britton & Rose == **Leucaena trichodes** (Jacq.) Benth.
Leucaena pubescens Britton & Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena purpusii Britton & Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena rekoi Britton & Rose == **Leucaena lanceolata** S. Watson var. **sousae** (S. Zárate) C.E.Hughes
Leucaena revoluta Britton & Rose == **Leucaena trichandra** (Zucc.) Urban
Leucaena shannonii J.D.Smith subsp. *magnifica* C.E.Hughes == **Leucaena magnifica** (C.E. Hughes) C.E. Hughes
Leucaena shannonii J.D.Smith subsp. *salvadorensis* (Standl. ex B. & R.) S. Zárate == **Leucaena salvadorensis** Standley ex Britton & Rose
Leucaena sinaloensis Britton & Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena sonorensis Britton & Rose == **Leucaena lanceolata** S. Watson var. **lanceolata**
Leucaena standleyi Britton & Rose == **Leucaena trichandra** (Zucc.) Urban
Leucaena stenocarpa Urb. == **Leucaena trichandra** (Zucc.) Urban
Leucaena trichodes (Jacq.) Benth. var. *acutifolia* Macbr. == **Leucaena trichodes** (Jacq.) Benth.
Leucaena ulei Harms == **Parkia ulei** Kuhlmann

Appendix 2. The OFI *Leucaena* seed collections

Summary data associated with the OFI *Leucaena* seed collections are presented here as a reference for anyone who needs to look up the identity, or seed collection site data, of a particular seedlot. All seedlots are assigned a unique **identity number** in the form **17/86** which refers to the 17th seedlot collected during 1986. The data presented here are sorted by year of collection and seedlot number within year. To find a seedlot, first look for the year (the last two digits) then for the seedlot number for that year. The data are presented in the following format:

ID No. Species name
COUNTRY, Major area, Provenance (seed collection site); Latitude Longitude; Altitude; Stand type
Botanical voucher collector name and number, Herbaria where vouchers are housed; number of parent trees in bulk seedlot and individual 'family' seedlots; date of collection
Notes

Stand type is a field describing the type of population or 'stand' of trees where the seed was collected. Categories are as follows: natural population; seed orchard; plantation (exotic); plantation (in native range); cultivated indigenous (*guajal*) (Chapter 4); naturalized stand; unknown; controlled cross.

Botanical voucher: Almost all seedlots are vouchered with a botanical specimen. This allows the identity to be checked by anyone by viewing the specimen should doubt arise in the future about what species a seedlot belongs in. Usually several duplicates of each botanical specimen were collected and distributed to a number of herbaria. The herbaria where duplicate specimens are housed are indicated by a series of internationally accepted acronyms (as listed in Index Harbariorum: Holmgren *et al.*, 1990). The ones used here are as follows: E=Royal Botanic Gardens, Edinburgh, U.K.; EAP=Standley Herbarium, Escuela Agrícola Panamericana, El Zamorano, Honduras; FCME=Herbarium, Facultad de Ciencias, Universidad Nacional, Mexico; FHO=Forest Herbarium Oxford, U.K.; K=Royal Botanic Gardens, Kew, U.K.; MEXU=National Herbarium, Mexico; MO=Missouri Botanical Garden, U.S.A.; NY=New York Botanical Garden, U.S.A.; PMA=Herbarium, Universidad de Panamá, Panama; QAME= Herbarium Luciano Andrade Marín, Centro Forestal Conocoto, Ecuador; UANL=Herbarium, Universidad Autónoma de Nuevo León, Mexico.

Parent trees: The seed collections comprise both bulk (composite) seedlots collected from more than one parent tree and individual ('family') seedlots collected from a single parent tree; these fields indicate the number of parent trees included in a bulk collection and the number of individual family seedlots collected.

Notes: Additional information about the distribution of parent trees, the bulking of seed and cross referencing to seedlots collected from the same population in different years.

Databases: The seed data are stored and maintained on the OFI seed database which uses the SISTEM+ (Species Information Seed, Trials and Environment data Management) software (Filer, 1997). A subset of these data are also held on the *World Leucaena Catalogue* (Bray *et al.*, 1997).

Seed availability: The quantity of seed collected varies for different seedlots depending on the objective of the particular collection and not all seedlots are available for widespread distribution. Requests for seed should be addressed to: Trials Manager, Oxford Forestry Institute, Department of Plant Sciences, University of Oxford, South Parks Road, OXFORD, OX1 3RB, U.K. Fax: +44-(0)1865-275074; Email: Alan.Pottinger@plant-sciences.ox.ac.uk.

Material Transfer Agreement: The OFI *Leucaena* seed collections were collected with the prior informed consent of the governments of 11 countries under a variety of research agreements and plant collecting permits. The OFI has recognized the need also to formalize agreements with seed recipients in the form of a Material Transfer Agreement, MTA (Appendix 4). This is designed to promote scientific exchange while at the same time recognizing the responsibilities of seed recipients towards the countries that provided the seed. The MTA also aims to encourage the development of beneficial partnerships between recipients and donor countries and communities. The ability to provide reliable data about seed collections and to track their distribution is crucial not only for routine coordination of trials and across-site analysis of trial results, but also to map specific lines of communication between providers and users of genetic resources along which benefit-sharing mechanisms can develop. The local communities where and with whom seed collections were made form an essential component of seed source information, along with routine country/locality information. In the case of the OFI *Leucaena* seed database, both the local communities who provided the seed and the seed recipients who are establishing trials are recorded to facilitate targeting of shared benefits. The OFI has been the conduit for supply of genetic resources and may also be able to assist as an intermediary to establish benefit-sharing.

40/78 **L. leucocephala subsp. glabrata**
NICARAGUA, Matagalpa, Sebaco; 12.39N 86.07W; 450m; Plantation (native range)
Chaplin GE s.n., FHO; Parent trees: Bulk 10 / Individual 0; Collected on ?/ 3/78
Small bulk seed collection from cultivated woodlot nr Sebaco. *L. leucocephala* recently introduced to Nicaragua and widely planted for windbreaks.

19/81 **L. leucocephala subsp. glabrata**
HONDURAS, Choluteca, Duyure; 13.38N 86.55W; 1050m; Plantation (native range)
Stead JW & Styles BT 705, FHO,MEXU; Parent trees: Bulk 10 / Individual 18; Collected on 9/ 1/81
Seed colected from 10 trees in a planted woodlot close to Duyure, 25km from San Marcos de Colon. Identified as variety K8 by *Brewbaker*.

15/83 **L. collinsii subsp. zacapana**
GUATEMALA, El Progreso, Puerto de Golpe; 14.58N 89.58W; 350m; Natural population
Hughes CE 299, FHO,MEXU; Parent trees: Bulk 25 / Individual 25; Collected on 17/ 2/83
Seed collected from 25 separate trees in the local vicinity of Puerto de Golpe and partially bulked after extraction. Same site as seedlot 18/84.

22/83 **L. shannonii**
HONDURAS, Comayagua, Comayagua; 14.22N 87.39W; 650m; Natural population
Hughes CE 239, 282, 310, 311, FHO,MEXU; Parent trees: Bulk 30 / Individual 24; Collected on 10/ 2/83
Same site as 26/84. Seed collected from 24 trees scattered throughout the upper Comayagua Valley from Comayagua to La Paz, and kept separate by parent tree until after extraction then partially bulked with seed from a further 6 trees.

18/84 **L. collinsii subsp. zacapana**
GUATEMALA, El Progreso, Puerto de Golpe; 14.59N 89.57W; 325m; Natural population
Hughes CE 299, FHO,K,MEXU; Parent trees: Bulk 20 / Individual 0; Collected on 15/ 3/84
Seed bulked from 20 scattered trees. Same site as seedlot 15/83.

19/84 **L. magnifica**
GUATEMALA, Chiquimula, El Rincón; 14.40N 89.42W; 925m; Natural population
Hughes CE 412, 413; Hughes & Styles 135, FHO,K,MEXU; Parent trees: Bulk 25 / Individual 25; Collected on 29/ 2/84
Seed collected from 25 trees and kept separate until after extraction and then partially bulked.

26/84 **L. shannonii**
HONDURAS, Comayagua, Comayagua; 14.22N 87.39W; 650m; Natural population
Hughes CE 239, 282, 310, 311, FHO,MEXU; Parent trees: Bulk 18 / Individual 0; Collected on 15/ 2/84
Same site as 22/83. Seed collected from 18 trees widely scattered throughout the upper Comayagua Valley from Comayagua to La Paz and subsequently bulked.

43/85 **L. lanceolata var. lanceolata**
MEXICO, Oaxaca, San Jon; 16.02N 95.39W; 10m; Natural population
Hughes CE 559-570, FHO,K,MEXU; Parent trees: Bulk 120 / Individual 20; Collected on 24/ 2/85
Seed collected from 20 trees scattered between San Jon and Rincón Bamba, 40km W of Salina Cruz, and maintained separate by parent tree, with an additional bulk collection from 120 trees.

44/85 **L. lanceolata var. lanceolata**
MEXICO, Sinaloa, Escuinapa; 22.46N 105.54W; 60m; Natural population
Hughes CE 603-613, FHO,MEXU; Parent trees: Bulk 85 / Individual 20; Collected on 15/ 3/85
Seed collected from 20 trees immediately S of Escuinapa, and kept separate by parent tree until after extraction then partially bulked with seed from an additional 65 trees.

45/85 **L. collinsii subsp. collinsii**
MEXICO, Chiapas, Narcisco Mendoza; 16.36N 93.00W; 475m; Natural population
Hughes CE 527, 530-539, 662, FHO,K,MEXU; Parent trees: Bulk 25/ Individual 25; Collected on 1/ 4/85
Same site as 52/88. Seed collected from 25 trees scattered around Narcisco Mendoza, 20km S of Tuxtla Gutierrez in Central Depression of Chiapas, and kept separate by parent tree until after extraction then partially bulked.

46/85 **L. lanceolata var. lanceolata**
MEXICO, Michoacán, Playa Azul; 18.04N 102.34W; 15m; Natural population
Hughes CE 631, FHO,K,MEXU; Parent trees: Bulk 45 / Individual 23; Collected on 21/ 3/85
Seed collected from 25 trees scattered along the coast 10-35km W of Playa Azul rd towards Barra de Navidad and kept separate by parent tree until after extraction then partially bulked with seed from a further 20 trees.

47/85 **L. macrophylla subsp. istmensis**
MEXICO, Oaxaca, San Isidro Llano Grande; 15.59N 97.16W; 10m; Natural population
Hughes CE 580-585, 650-655, FHO,K,MEXU; Parent trees: Bulk 20/Individual 20; Collected on 28/ 3/85
Seed collected from 20 trees in a population close to rd 40km W of Puerto Escondido, 2km E of San Isidro Llano Grande, and kept separate by parent tree until after extraction then partially bulked.

2/86 **L. trichodes**
VENEZUELA, Trujillo, Cuicas; 9.38N 70.18W; 550m; Natural population
Hughes CE 775, 778, FHO,K,MEXU; Parent trees: Bulk 20 / Individual 20; Collected on 10/ 3/86
Seed collected from 20 trees 6km SW of Cuicas on rd to Monay, about 45km NE of Valera, and kept separate by parent tree until after extraction then partially bulked with seed from a further 30 trees.

17/86 **L. salvadorensis**
HONDURAS, Choluteca, La Garita; 13.26N 87.11W; 540m; Natural population
Hughes CE 742, 756 & 824, FHO,K,MEXU; Parent trees: Bulk 55 / Individual 25; Collected on 11/ 2/86
Same site as 36/88. Seed collected from 55 widely scattered trees in hills centred on the village of La Garita, 25km NW of Choluteca. Seed from 25 trees kept separate by parent tree until after extraction then partially bulked with seed from the remaining trees.

19/86 **L. greggii**
MEXICO, Nuevo León, El Barrial; 24.53N 100.01W; 1550m; Natural population
Hughes CE 695, FHO,K,MEXU; Parent trees: Bulk 30 / Individual 10; Collected on 19/ 9/86
Same site as 20/86, 21/86, 26/86 and 82/87. Seed collected from 30 trees scattered in mountains around El Barrial which lies 70km W of Linares and kept separate by parent tree until after extraction then partially bulked.

20/86 **L. greggii**
MEXICO, Nuevo León, Iturbide; 24.53N 100.01W; 1550m; Natural population
Hughes CE 695, FHO,K,MEXU; Parent trees: Bulk 30 / Individual 10; Collected on 0/ 9/86
Same site as 19/86, 21/86, 26/86 and 82/87. Seed collected from 30 trees scattered above Iturbide around 70km W of Linares and kept separate by parent tree until after extraction then partially bulked.

21/86 **L. greggii**
MEXICO, Nuevo León, Rayones; 24.53N 100.01W; 1550m; Natural population
Hughes CE 695, FHO,K,MEXU; Parent trees: Bulk 30 / Individual 10; Collected on 0/ 9/86
Same site as 19/86, 20/86, 26/86 and 82/87. Collected from 10 trees around Rayones, nr Iturbide, 70km W of Linares, kept separate by parent tree and partially bulked.

22/86 **L. pulverulenta**
MEXICO, Nuevo León, Ejido el Popote; 24.54N 99.29W; 320m; Natural population
Leila Bendeck Anastas s.n., UANL; Parent trees: Bulk 10 / Individual 3; Collected on 28/ 8/85
Small bulk seed collection from 10 trees around Ejido El Popote, 10km NE of Linares.

23/86 **L. retusa**
MEXICO, Coahuila, Sierra la Encantada; 28.44N 102.20W; 1000m; Natural population
Leila Bendeck Anastas s.n., UANL; Parent trees: Bulk 10 / Individual 10; Collected on 16/11/85
Seed collected from 10 trees scattered widely on slopes of the Sierra La Encantada, about 120km NW of Muzquíz and kept separate by parent tree until after extraction then partially bulked.

26/86 **L. greggii**
MEXICO, Nuevo León, El Barrial; 24.53N 100.01W; 1550m; Natural population
Hughes CE 695, FHO,K,MEXU; Parent trees: Bulk 30 / Individual 0; Collected 9/86
Same site as 19/86, 20/86, 21/86 and 82/87. Seed collected from 30 trees scattered around Iturbide, El Barrial and Rayones, in mountians approx. 70km W of Linares, kept separate by parent tree then partially bulked.

44/87 **L. pallida**
MEXICO, Guerrero, Mazapa; 17.55N 99.37W; 1300m; Natural population
Hughes CE 886, FHO,K,MEXU; Parent trees: Bulk 1 / Individual 1; Collected on 28/ 2/87
Single tree seed collection from hills 5km SW of Mezcala, S of Rio Balsas. Unusual pubescent podded variant of *L pallida*.

45/87 **L. diversifolia**
MEXICO, Veracruz, Corral Falso; 19.26N 96.45W; 800m; Natural population
Hughes CE 916-918, FHO,K,MEXU; Parent trees: Bulk 30 / Individual 20; Collected 15/3/87
Seed collected from 20 trees scattered over a wide area S and E of Corral Falso, 25km SE of Jalapa, kept separate by parent tree untial after extraction then bulked with seed from a further 10 trees.

46/87 **L. diversifolia**
MEXICO, Veracruz, Xalapa; 19.32N 95.55W; 1300m; Natural population
Hughes CE 921- 923, FHO,K,MEXU; Parent trees: Bulk 15 / Individual 15; Collected on 18/ 3/87
Seed from 15 trees scattered over a wide area S and SE of Jalapa, partially bulked after extraction.

47/87 **L. esculenta**
MEXICO, Guerrero, San Martin Pachívia; 18.18N 99.45W; 1550m; Natural population
Hughes CE 894, 895, 898, FHO,K,MEXU; Parent trees: Bulk 50 / Individual 24; Collected on 5/ 3/87
Seed collected from a total of 50 trees, 24 kept separate by parent tree, scattered in the hills N of San Martin Pachívia towards Ixcatoapan de Cuauhtemoc.

48/87 **L. esculenta**
MEXICO, Michoacán, Tiringucha; 18.38N 100.48W; 600m; Natural population
Hughes CE 903, FHO,K,MEXU; Parent trees: Bulk 15 / Individual 10; Collected on 9/ 3/87
Seed collected from 15 trees from a restricted area 2km NE of Tiringucha or 18km N of Huetamo de Nunez, kept separate by parent tree until after extraction then partially bulked.

49/87 **L. matudae**
MEXICO, Guerrero, Mezcala; 17.51N 99.40W; 600m; Natural population
Hughes CE 879, 883, FHO,K,MEXU; Parent trees: Bulk 14 / Individual 14; Collected on 27/ 2/87
Small collection from 14 trees scattered on slopes above the dry valley of the Rio Xochipala 5-15km SW of Mezcala. Seed kept separate by parent tree then partially bulked.

50/87 **L. lanceolata var. sousae**
MEXICO, Oaxaca, Cacalote; 16.02N 97.35W; 50m; Natural population
Hughes CE 866 & 872, FHO,K,MEXU; Parent trees: Bulk 25 / Individual 25; Collected on 19/ 2/87
Seed collected from 25 trees widely scattered 3-10km E of the village of Cacalote, 40-50km W of Puerto Escondido and kept separate by parent tree until after extraction then partially bulked.

51/87 **L. lanceolata var. sousae**
MEXICO, Oaxaca, Puerto Angel; 15.40N 96.30W; 50m; Natural population
Hughes CE 835-6, 841-2, 849-851, 857-8., FHO,K,MEXU; Parent trees: Bulk 35 / Individual 20; Collected on 10/ 2/87. Seed collected from 20 trees scattered over a 50km stretch of Pacific coastal plain between Bahias de Santa Cruz in the E and San Agustinillo in the W, and kept separate by parent tree until after extraction then partially bulked with seed from a further 15 trees.

52/87 **L. ? hybrid**
MEXICO, Puebla, San Pedro Chapulco; 18.38N 97.24W; 2100m; Cultivated indigenous (guajal)
Hughes CE 924, 929, 930, FHO,K,MEXU; Parent trees: Bulk 25 / Individual 20; Collected on 20/ 3/87
Seed collected from 25 trees scattered in and around the villages of San Pedro Chapulco and Azumbilla. Collected as *L. pallida*, (although distributed initially under the name *L. esculenta* subsp. *paniculata*), but shown by Harris et al (1994a) to be of hybrid origin. Parentage unknown. Seed kept separate by parent tree until after extraction then partially bulked.

53/87 **L. shannonii**
MEXICO, Campeche, Champotón; 19.20N 90.43W; 10m; Natural population
Hughes CE 507, 933-935, FHO,K,MEXU; Parent trees: Bulk 30 / Individual 20; Collected on 25/ 3/87
Seed collected from 20 trees scattered along coastal fringe S of Champotón and kept separate by parent tree then partially bulked with seed collected from an additional 10 trees.

81/87 **L. multicapitula**
PANAMA, Los Santos/Herrera, Los Santos; 7.55N 80.25W; 40m; Natural population
Hughes CE 1025, 1029, 1032-1035., FHO,K,MEXU,PMA; Parent trees: Bulk 30 / Individual 20; Collected on 3/10/87. Seed collected from 20 trees scattered in hills SE and W of Los Santos, and kept separate by parent tree until after extraction then partially bulked with seed from a further 10 trees.

82/87 **L. greggii**
MEXICO, Nuevo León, El Barrial; 24.53N 100.01W; 1550m; Natural population
Hughes CE 695, 1048, 1056, 1057, FHO,K,MEXU,UANL; Parent trees: Bulk 80 / Individual 20; Collected on 7/11/87. Same site as 19/86, 20/86, 21/86 and 26/86. Seed collected from 80 trees scattered over a wide area above and around Iturbide in mountains approx. 70km W of Linares, with seed of 20 trees kept separate by parent tree and the remainder bulked.

83/87 **L. pulverulenta**
MEXICO, Tamaulipas, Altas Cumbres; 23.36N 99.14W; 1250m; Natural population
Hughes CE 1051-1053, FHO,K,MEXU,UANL; Parent trees: Bulk 60 / Individual 20; Collected on 2/11/87. Seed collected from 60 trees scattered along rd SW from Ciudad Victoria towards Tula, 25-35km from Ciudad Victoria. Seed kept separate for 20 parent trees and partially bulked with seed from an additional 40 trees.

84/87 **L. pulverulenta**
USA, Texas, South Texas; 27.35N 97.50W; 20m; Natural population
Hughes CE 1058, 1059 & 1061, FHO,K,MEXU; Parent trees: Bulk 50 / Individual 10; Collected on 10/11/87. Seed collected from 50 trees scattered over a large area of south Texas from Kingsville to Raymondville with seed kept separate for 10 trees and the remainder bulked.

86/87 **L. multicapitula**
COSTA RICA, Guanacaste, Penas Blancas; 11.10N 85.37W; 160m; Natural population
Hughes CE 1024, 1041, 1042, FHO,K,MEXU,PMA; Parent trees: Bulk 3 / Individual 0; Collected on 17/10/87. Small bulk collection from 3 trees near the Rio Zonzapote, 5km S of Penas Blancas.

32/88 **L. leucocephala subsp. glabrata**
HAITI, Operation Double Harvest; Plantation (exotic)
Parent trees: Bulk ? / Individual 0;
Bulk seed collection from planted material in Haiti. Shown by Harris *et al.* (1994b) to be highly variable possibly due to hybridization.

34/88 **L. salvadorensis**
HONDURAS, Choluteca, Yusguare; 13.15N 87.06W; 450m; Natural population
Hughes CE 746, 1062, 1066, FHO,K,MEXU; Parent trees: Bulk 18 / Individual 18; Collected on 10/ 2/88
Seed collected from 18 trees in two widely scattered groups at Charco Verde and around Calaire in hills above Yusguare and kept separate by parent tree until after extraction, then partially bulked.

35/88 **L. trichandra**
HONDURAS, Comayagua, Zambrano; 14.14N 87.25W; 1150m; Natural population
Hughes CE, 1083 & 1085, FHO,K,MEXU; Parent trees: Bulk 25 / Individual 10; Collected on 22/ 2/88
Seed collected from 10 trees scattered in pine forest 10km N of Zambrano, and kept separate by parent tree then partially bulked with seed from a further 15 trees.

36/88 **L. salvadorensis**
HONDURAS, Choluteca, La Garita; 13.26N 87.11W; 500m; Natural population
Parent trees: Bulk 30 / Individual 30; Collected on 20/ 2/87
Same site as 17/86. Seed collected from 30 trees scattered in hills around La Garita, 25km NW of Choluteca, and kept separate by parent tree until after extraction then partially bulked.

44/88 **L. leucocephala subsp. glabrata**
GUATEMALA, Zacapa, Gualán; 15.07N 89.21W; 150m; Plantation (native range)
Parent trees: Bulk ? / Individual 0; Collected on 10/ 2/88
Bulk seed collection from woodlot plantation used by BANSEFOR as a seed production stand.

45/88 **L. leucocephala subsp. glabrata**
GUATEMALA, Escuintla, Masagua; 14.22N 90.47W; 150m; Plantation (native range)
Parent trees: Bulk ? / Individual 0; Collected on 10/ 2/88
Bulk seed collection from woodlot plantation used by BANSEFOR as a seed production stand.

51/88 **L. collinsii subsp. collinsii**
GUATEMALA, Huehuetenango, Chacaj; 16.36N 93.00W; 500m; Cultivated indigenous (guajal)
Hughes CE 1137-8, 1187, FHO,K,MEXU; Parent trees: Bulk 20 / Individual 0; Collected on 2/ 5/88
Seed bulked from 20 trees scattered in and around the village of Chacaj where it is widely cultivated as a source of edible pods.

52/88 **L. collinsii subsp. collinsii**
MEXICO, Chiapas, Narcisco Mendoza; 16.36N 93.00W; 475m; Natural population
Hughes CE 527, 530-539, 662, FHO,K,MEXU; Parent trees: Bulk 20 / Individual 0; Collected on 4/ 4/88
Same site as 45/85. Bulk seed collection from 20 trees scattered around Narcisco Mendoza which lies 20km S of Tuxtla Gutierrez in the central depression of Chiapas.

53/88 **L. trichandra**
GUATEMALA, Guatemala, Los Guates; 14.49N 90.37W; 1450m; Natural population
Hughes CE 1106, 1128, 1129, FHO,K,MEXU; Parent trees: Bulk 40/Individual 20; Collected on 26/3/88
Seed collected from 20 trees scattered between villages of Los Guates and Saucite, 13km ENE of San Juan Sacatepequez, kept separate by parent tree then partially bulked with seed from a further 20 trees.

54/88 **L. trichandra**
GUATEMALA, Huehuetenango, Aguacatán; 15.21N 91.17W; 1760m; Natural population
Hughes CE 1130, FHO,K,MEXU; Parent trees: Bulk 5 / Individual 0; Collected on 29/ 3/88
Seed bulked from 5 trees scattered on rd E of Aguacatán towards Huehuetenango.

55/88 **L. macrophylla subsp. macrophylla**
MEXICO, Guerrero, Vallecitos; 18.00N 101.18W; 1150m; Natural population
Hughes CE 1179, FHO,K,MEXU; Parent trees: Bulk 25 / Individual 10; Collected on 22/ 4/88
Seed collected from a total of 25 trees scattered in mountains 15km N of Vallecitos, close to rd Zihuatanejo to Ciudad Altamirano. Seed kept separate by parent tree for 10 trees then partially bulked with seed from an additional 15 trees.

56/88 **L. collinsii subsp. zacapana**
GUATEMALA, Zacapa, Gualán; 15.07N 89.21W; 150m; Natural population
Hughes CE 1120, 1122-3, 1125-6, FHO,K,MEXU; Parent trees: Bulk 70/Individual 20; Collected on 23/3/88. Seed collected from 20 well scattered trees in and around the town of Gualán, kept separate by parent tree until after extraction then partially bulked with seed from a further 50 trees.

57/88 **L. collinsii subsp. zacapana**
GUATEMALA, Chiquimula, El Carrizal; 14.40N 89.30W; 550m; Natural population
Hughes CE 1096-1097, FHO,K,MEXU; Parent trees: Bulk 18 / Individual 18; Collected on 21/ 3/88
Seed collected from 18 trees scattered over a small area and kept separate by parent tree until after extraction then partially bulked.

58/88 **L. magnifica**
GUATEMALA, Chiquimula, Quetzaltepeque; 14.37N 89.27W; 625m; Natural population
Hughes CE 1089, 1090, 1093, FHO,K,MEXU; Parent trees: Bulk 50/Individual 30; Collected on 26/ 2/88
Seed collected from 30 well scattered trees and kept separate by parent tree until after extraction then partially bulked with seed from a further 20 trees.

61/88 **L. trichodes**
ECUADOR, Manabí, Jipijapa; 1.21S 80.34W; 200m; Natural population
Hughes CE 992,997,1000,1195,1197,1200, FHO,K,MEXU,QAME; Parent trees: Bulk 50 / Individual 30; Collected on 20/ 7/88. Seed collected from 50 trees over a wide area from Julcuy to Chone, centred on town of Jipijapa.

31/89 **L. diversifolia**
MEXICO, Oaxaca, Temascal; 18.16N 96.22W; 30m; Natural population
Hughes CE 1310, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 13/ 3/89
Single tree collection, 10km NE of Temascal.

32/89 **L. ? hybrid**
MEXICO, Oaxaca, Huautla; 18.05N 96.47W; 1780m; Cultivated indigenous (guajal)
Hughes CE 1317, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 14/ 3/89
Single tree collection rd between San Juan Coatzospan and Santa Maria Asuncion, SW of Huautla, Sierra Mazateca. Putative hybrid between *L. pallida* and *L. diversifolia.*

33/89 **L. confertiflora var. adenotheloidea**
MEXICO, Puebla, San Pedro Chapulco; 18.37N 97.25W; 2030m; Cultivated indigenous (guajal)
Hughes CE 1321, FHO,K,MEXU,NY; Parent trees: Bulk 15 / Individual 0; Collected on 20/ 3/89
Same site as 119/92 and 87/94. Small bulk seed collection from 15 trees in household orchard cultivated for pod production in the village of San Pedro Chapulco.

34/89 **L. pueblana**
MEXICO, Puebla, Coxcatlán; 18.16N 97.10W; 1400m; Natural population
Hughes CE 1327, FHO,K,MEXU,NY; Parent trees: Bulk 4 / Individual 0; Collected on 23/ 3/89
Small bulk seed collection from 4 trees scattered on slopes above the town of Coxcatlan on the N side of the Tehuacan Valley.

39/89 **L. macrophylla subsp. istmensis**
MEXICO, Oaxaca, Coyula; 15.47N 96.07W; 10m; Natural population
Hughes CE 854, 855, 1340, FHO,K,MEXU,NY; Parent trees: Bulk 10/Individual 0; Collected on 26/ 3/89
Small bulk seed collection from 10 trees, 10km E of Coyula, 20km E of Puerto Angel, between Coyula and Bahia Santa Cruz. Unusual pubescent, small-podded variant of *L. macrophylla* subsp. *istmensis.*

1/90 **L. diversifolia**
PAPUA NEW GUINEA, Unknown, Bulolo; Plantation (exotic)
Parent trees: Bulk ? / Individual 0; Collected on 1989
Small bulk seed collection from the Department of Forests Forest Research Station at Bulolo, Papua New Guinea. Identity uncertain, no voucher seen.

98/90 **L. salvadorensis**
HONDURAS, Choluteca, La Galera; 13.20N 87.01W; 500m; Natural population
Parent trees: Bulk 21 / Individual 21; Collected on 21/ 3/89
Seed collected from 21 trees and kept separate by parent tree until after extraction then partially bulked.

99/90 **L. salvadorensis**
HONDURAS, Choluteca, Namalí; 13.34N 87.12W; 580m; Natural population
Hughes CE 1211, FHO,K,MEXU; Parent trees: Bulk 6 / Individual 4; Collected on 15/ 2/89
Seed collected from 6 scattered trees around Portillo Grande.

100/90 **L. salvadorensis**
HONDURAS, Choluteca, Choluteca; 13.23N 87.07W; 200m; Natural population
Parent trees: Bulk ? / Individual 2; Collected on 0/ 0/ 0
Locailty and parentage details unknown.

1/91 **L. shannonii**
GUATEMALA, Jutiapa, Jutiapa; 14.25N 89.41W; 700m; Natural population
Hughes CE 1417, EAP,FHO,K,MEXU,NY; Parent trees: Bulk - / Individual 20; Collected on 3/ 3/91
Seed collected from 20 trees scattered between Estanzuela and Santa Catarina Mita and kept separate by parent tree.

2/91 **L. shannonii**
NICARAGUA, Chontales, La Puerta; 12.11N 85.18W; 340m; Natural population
Hughes CE 1399, 1401, FHO,K,MEXU,NY; Parent trees: Bulk - / Individual 12; Collected on 7/ 2/91
Seed collected from 12 trees scattered around La Puerta which lies 16km N of Juigalpa and kept separate by parent tree.

3/91 **L. trichandra**
HONDURAS, Copan, Copan; 14.50N 89.10W; 800m; Natural population
Hughes CE 1418, EAP,FHO,K,MEXU,NY; Parent trees: Bulk 25 / Individual 25; Collected on 7/ 3/91
Seed collected from 25 trees scattered across an area of 100 square km centred on Copan and kept separate by parent tree until after extraction then partially bulked.

4/91 **L. trichandra**
HONDURAS, Lempira, Erandique; 14.12N 88.33W; 1900m; Natural population
Hughes CE 1421-1424, 1427, 1708-1710., FHO,EAP,K,MEXU,NY.; Parent trees: Bulk 55 / Individual 25; Collected on 8/ 3/91. Seed colected from 25 trees scattered 6-20km SW of Erandique in the Sierra La Laguna and kept separate by parent tree until after extraction then partially bulked with seed from a further 30 trees.

5/91 **L. lempirana**
HONDURAS, Yoro, Valle del Aguán; 15.25N 86.57W; 300m; Natural population
Hughes 1447, Hellin & Hughes 8,11,14, FHO,K,EAP,MEXU,NY; Parent trees: Bulk 35 / Individual 20; Collected on 25/ 3/91. Seed collected from 20 trees scattered throughout the mid Aguán Valley although concentrated in an area 10km W of Olanchito, kept separate by parent tree until after extraction then partially bulked with seed from an additional 15 trees.

6/91 **L. lempirana**
HONDURAS, Yoro, Cuyamapa; 15.17N 87.40W; 200m; Natural population
Hughes CE 1411,1412,1414 & 1712, E,FHO,K,MEXU,EAP,NY; Parent trees: Bulk 104 / Individual 62; Collected on 23/ 3/91. Seed collected from 54 separate trees scattered on both sides fo the Rio Cuyamapa in low hills between the vallies Olomán and Cataguana, and kept separate by parent tree until after extraction then partially bulked with seed from an additional 50 trees.

7/91 **L. salvadorensis**
NICARAGUA, Estelí, San Juan de Limay; 13.12N 86.29W; 700m; Natural population
Hughes CE 1407,1408,1431,1434,1444, FHO,EAP,K,MEXU,MO,NY; Parent trees: Bulk 60 / Individual 30; Collected on 14/ 3/91. Seed collected from 60 trees scattered over a wide areas of more than 100 square km on hills above San Juan de Limay. Seed was kept separate by parent tree for 30 trees and then partially bulked with seed from the remaining 30 trees.

24/91 **L. leucocephala subsp. ixtahuacana**
GUATEMALA, Huehuetenango, Ixtahuacan; 15.25N 91.48W; 1750m; Cultivated indigenous (guajal)
Hughes CE 1469, EAP,FHO,K,MEXU,NY; Parent trees: Bulk 3 / Individual 0; Collected on 9/ 4/91
Same site as 117/92. Seed bulked from 3 trees scattered along rd W from Ixtahuacan to Cuilco.

33/91 **L. confertiflora var. adenotheloidea**
USA, Hawaii, Waimanalo; Controlled cross; 1988
Weights refer to no. of seeds 9/14-5/88
K745-1:H SELF *L. confertiflora* self-pollination (4x)
Original K745 collected by Sergio Zárate from San Pedro Chapulco in 1982.

41/91 **L. diversifolia**
USA, Hawaii, Waimanalo; Controlled cross
Weights refer to no. of seeds ?? date
K156-1:H SELF *L. diversifolia* self-pollination (4x)

73/91 **L. leucocephala subsp. leucocephala**
USA, Hawaii, Waimanalo; Controlled cross; 1989
Weight refers to no. of seeds 8/22-37/89
K9-1:W SELF *L. leucocephala* subsp. *leucocephala* self pollination (4x)

74/91 **L. leucocephala subsp. glabrata**
USA, Hawaii, Waimanalo; 0m; Controlled cross; 1990
Weight refers to no. of seeds 5/2-10/90
K636-1:H SELF *L. leucocephala* subsp. *glabrata* self-pollination (4x)

145/91 **L. leucocephala subsp. glabrata**
MEXICO, Sinaloa, Caitime; 25.13N 107.59W; 110m; Cultivated indigenous (guajal)
Hughes CE 1519, E,FHO,K,MEXU,NY; Parent trees: Bulk 5 / Individual 0; Collected on 16/ 8/91
Small bulk seed collection from 5 trees 4km S of Caitime, 30km S of Guamuchil, 76km N of Culiacán.

146/91 **L. involucrata**
MEXICO, Sonora, El Novillo; 28.55N 109.28W; 700m; Natural population
Hughes CE 1522, 1533, FHO,K,MEXU,EAP,MO,NY; Parent trees: Bulk 5 / Individual 0; Collected on 19/ 8/91.
Same site as 87/92. Small bulk seed collection from 5 scattered trees on steep rocky slopes between El Novillo and Bacanora about 140km E of Hermosillo.

34/92 **L. leucocephala subsp. glabrata**
USA, Hawaii, Waimanalo; Plantation (exotic)
Dudley N, K636 ; Parent trees: Bulk 25 / Individual 0; Collected on 0/10/91

78/92 **L. pallida**
MEXICO, Oaxaca, Guelatao; 17.18N 96.30W; 2030m; Cultivated indigenous (guajal)
Hughes CE 1662, E,FHO,K,MEXU,NY; Parent trees: Bulk 10 / Individual 10; Collected on 23/ 2/92
Seed collected from 10 trees scattered between and around Guelatao de Juarez and Ixtlan de Juarez and kept separate by parent tree until after extraction then partially bulked.

79/92 **L. pallida**
MEXICO, Oaxaca, Tamazulapan; 17.41N 97.35W; 1900m; Cultivated indigenous (guajal)
Hughes CE 1629, 1630, FHO,E,K,MEXU,MO,NY; Parent trees: Bulk 50 / Individual 20; Collected on 17/ 2/92.
Seed collected from 20 scattered trees 3-10km W of Tamazulapan above and below the rd to Huajuapan de León, and kept separate by parent tree until after extraction then partially bulked with seed from a further 30 trees. Seed very heavily predated by bruchids.

80/92 **L. leucocephala subsp. leucocephala**
MEXICO, Campeche, Francisco Escárcega; 18.35N 90.46W; 150m; Natural population
Hughes CE 1734, E,FHO,K,MEXU,MO,NY; Parent trees: Bulk 10 / Individual 0; Collected on 1/ 4/92
Small bulk seed collection from 10 trees scattered along roadside near Francisco Escárcega.

81/92 **L. diversifolia**
MEXICO, Hidalgo, San Bartolo Tutotepec; 1500m; Natural population
Hughes CE 1613, E,FHO,K,MEXU,NY; Parent trees: Bulk - / Individual 13; Collected on 13/ 2/92
Small collection from 13 scattered trees 8km W of San Bartolo Tutotepec, rd to Tuto and San Jeronimo.

82/92 **L. diversifolia**
GUATEMALA, Huehuetenango, Barillas; 15.51N 91.22W; 1550m; Natural population
Hughes CE 1693, E,FHO,K,MEXU,MO,NY; Parent trees: Bulk 20 / Individual 20; Collected on 1/ 3/92
Seed collected from 20 separate trees and partially bulked after extraction. Trees scattered over a 10km radius from Barillas.

83/92 **L. diversifolia**
MEXICO, Oaxaca, Jalapa de Díaz; 18.04N 96.34W; 450m; Natural population
Hughes CE 1314, 1316, 1666 & 1669, FHO,K,MEXU,NY,MO,E; Parent trees: Bulk 50 / Individual 20; Collected on 24/ 2/92.
Seed collected from 20 trees scattered on slopes above the Rio Santo Domingo, 6km W of Jalapa de Díaz, or 70km W of Tuxtepec and kept separate by parent tree until after extraction then partially bulked with seed from a further 30 trees.

84/92 **L. leucocephala subsp. glabrata**
MEXICO, Oaxaca, Teotitlán del Camino; 18.10N 97.05W; 990m; Cultivated indigenous (guajal)
Hughes CE 1638, E,FHO,K,MEXU,MO,NY; Parent trees: Bulk 1 / Individual 1; Collected on 19/ 2/92
Single tree collection from 3km N of Teotitlán del Camino, Tehuacan Valley.

85/92 **L. leucocephala subsp. glabrata**
MEXICO, Hidalgo, Tamazunchale; 21.17N 98.48W; 170m; Cultivated indigenous (guajal)
Hughes CE 1591, E,FHO,K,MEXU,NY; Parent trees: Bulk - / Individual 10; Collected on 9/ 2/92
Seed collected from 10 trees scattered along the rd 10-50km N and NW of Tamazunchale, kept separate by parent tree.

86/92 **L. leucocephala subsp. glabrata**
MEXICO, Querétaro, Lagunita; 21.14N 99.15W; 1140m; Cultivated indigenous (guajal)
Hughes CE 1596, E,FHO,K,MEXU,NY; Parent trees: Bulk 10 / Individual 10; Collected on 10/ 2/92
Seed collected from 10 trees scattered in and around the settlement of Lagunita, 35km ESE of Jalpan de Sierra, kept separate by parent tree until after extraction then partially bulked.

87/92 **L. involucrata**
MEXICO, Sonora, El Novillo; 28.55N 109.28W; 700m; Natural population
Hughes CE 1572, FHO,K,MEXU,E,NY,MO; Parent trees: Bulk 20 / Individual 0; Collected on 29/ 1/92
Same site as 146/91. Small bulk seed collection from 20 scattered trees on steep rocky slopes between El Novillo and Bacanora about 140km E of Hermosillo.

88/92 **L. cuspidata**
MEXICO, Hidalgo, Jacála; 21.02N 99.10W; 1840m; Cultivated indigenous (guajal)
Hughes CE 1586, E,FHO,K,MEXU,NY; Parent trees: Bulk 10 / Individual 0; Collected on 8/ 2/92
Same site as 90/94. Small seed collection bulked from 10 trees 9km NE of Jacála nr Puerta de Zorra.

89/92 **L. cuspidata**
MEXICO, Hidalgo, Mina San Miguel; 20.50N 99.23W; 1930m; Natural population
Hughes CE 1583, E,FHO,K,MEXU,NY; Parent trees: Bulk 10 / Individual 0; Collected on 8/ 2/92
Small bulk seed collection from 10 trees 15km N of Zimipan rd to Mina San Miguel.

90/92 **L. lanceolata var. lanceolata**
MEXICO, Sonora, Sierra de Alamos; 26.59N 108.57W; 510m; Natural population
Hughes CE 1577, FCME,FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 31/ 1/92
Seed collected from a single tree, near TYPE localities of *L. palmeri* and *L. sonorensis*.

91/92 **L. leucocephala subsp. glabrata**
MEXICO, Baja California Sur, El Pescadero; 23.22N 110.09W; 20m; Cultivated indigenous (guajal)
Hughes CE 1547, FCME,FHO,K,MEXU,NY;
Parent trees: Bulk 4 / Individual 0; Collected on 21/ 1/92
Small bulk seed collection from 4 trees cultivated in gardens 9km S of Todos Santos in village of El Pescadero.

92/92 **L. leucocephala subsp. glabrata**
MEXICO, Sonora, Tecupa; 28.31N 109.10W; 630m; Cultivated indigenous (guajal)
Hughes CE 1574, FCME,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 31/ 1/92
Single tree collection from small roadside tree main rd ESE from Hermosillo to Chihuahua 51km ESE of Tonichí, 3km from Tecupa.

93/92 **L. leucocephala subsp. glabrata**
MEXICO, Hidalgo, Ixmiquilapan; 20.30N 99.12W; 1770m; Cultivated indigenous (guajal)
Hughes CE 1578, E,FHO,K,MEXU,NY;
Parent trees: Bulk 3 / Individual 3; Collected on 7/ 2/92
Small bulk seed collection from 3 trees cultivated for pod production on the outskirts of Ixmiquilapan.

94/92 **L. leucocephala subsp. glabrata**
MEXICO, Sonora, Empalme; 27.57N 110.48W; 10m; Cultivated indigenous (guajal)
Hughes CE 1568, FCME,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 28/ 1/92
Single tree collection from fenceline/garden tree cultivated for pod production in back streets of Empalme.

95/92 **L. leucocephala subsp. glabrata**
MEXICO, Baja California Sur, Loreto; 5m; Cultivated indigenous (guajal)
Hughes CE 1557, FCME,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 24/ 1/92
Single tree collection, main street of Loreto

117/92 **L. leucocephala subsp. ixtahuacana**
GUATEMALA, Huehuetenango, Ixtahuacan; 15.23N 91.50W; 1350m; Cultivated indigenous (guajal)
Hughes CE 1689, E,FHO,K,MEXU,MO,NY;
Parent trees: Bulk 10 / Individual 7; Collected on 28/ 2/92
Same site as 24/91. Seed bulked from 10 trees scattered around the village of San Miguel which lies 5km W of Ixtahuacan.

118/92 **L. diversifolia**
MEXICO, Hidalgo, San Bartolo Tutotepec; 1470m; Natural population
Hughes CE 1612, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 13/ 2/92
Seed from a single tree above the Rio Pantepec 6km NW of San Bartolo Tutotepec.

119/92 **L. confertiflora var. adenotheloidea**
MEXICO, Puebla, San Pedro Chapulco; 18.37N 97.24W; 2030m; Cultivated indigenous (guajal)
Hughes CE 1614, E,FHO,K,MEXU,NY;
Parent trees: Bulk 15 / Individual 0; Collected on 15/ 2/92
Same site as 33/89 and 87/94. Small bulk seed collection from 15 trees in household orchard in village of San Pedro Chapulco.

120/92 **L. confertiflora var. adenotheloidea**
MEXICO, Puebla, Santa Catalina Oxolotepec; 18.36N 97.15W; 2410m; Cultivated indigenous (guajal)
Hughes CE 1616, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 15/ 2/92
Single tree seed collection on track above village of Santa Catalina Oxolotepec. mountains 20km NE of Tehuacan.

121/92 **L. leucocephala subsp. glabrata**
MEXICO, Puebla, Zapotitlán Salinas; 18.19N 97.28W; 1500m; Cultivated indigenous (guajal)
Hughes CE 1618, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 16/ 2/92
Single tree seed collection in the village of Zapotitlán Salinas, 30km SW of Tehuacan.

122/92 **L. pallida**
MEXICO, Puebla, Santiago Acatepec; 18.14N 97.33W; 1950m; Cultivated indigenous (guajal)
Hughes CE 1620, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 16/ 2/92
Single tree seed collection 4km E of Santiago Acatepec, 45km SW of Tehuacan rd to Haujuapan de León.

123/92 **L. ? hybrid**
MEXICO, Puebla, Santiago Acatepec; 2080m; Cultivated indigenous (guajal)
Hughes CE 1625, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 16/ 2/92
Same tree as 93/94. Single tree seed collection in the village of Santiago Acatepec. Growing with *L. esculenta, L. pallida, L. leucocephala* and *L.* ×*mixtec*, and of spontaneous putative hybrid origin amongst cultivated species but unknown and probable 3-way parentage. See Hughes & Harris (1994) for information.

124/92 **L. confertiflora var. confertiflora**
MEXICO, Oaxaca, Tamazulapan; 17.40N 97.36W; 2350m; Natural population
Hughes CE 1631, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 18/ 2/92
Single tree collection 5km SW of Tamazulapan, rd to Chilapa de Díaz. 1 seed!

125/92 **L. pueblana**
MEXICO, Oaxaca, Tehuacan Valley; 17.53N 97.01W; 610m; Natural population
Hughes CE 1648, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 20/ 2/92
Single tree collection from the lower Tehuacan Valley 35km S of Teotitlán del Camino.

126/92 **L. diversifolia**
MEXICO, Oaxaca, San Juan Coyula; 17.55N 96.53W; 1740m; Natural population
Hughes CE 1651, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 20/ 2/92
Single tree collection from 2km NE of village of San Juan Coyula, track ENE from Santiago Quiotepec, slopes above lower Tehuacan Valley.

127/92 **L. confertiflora var. confertiflora**
MEXICO, Oaxaca, El Moral; 17.32N 96.58W; 2000m; Natural population
Hughes CE 1653, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 20/ 2/92
Same site as 85/94. Single tree collection from 10km N of El Moral, rd S from Tehuacan Valley to Oaxaca.

128/92 **L. trichandra**
MEXICO, Oaxaca, Oaxaca; 17.06N 96.37W; 1870m; Natural population
Hughes CE 1654, E,FHO,K,MEXU,NY;
Parent trees: Bulk 3 / Individual 0; Collected on 22/ 2/92
Small bulk collection from 3 trees along rd 10km NNE of Oaxaca towards Tuxtepec.

129/92 **L. trichandra**
MEXICO, Oaxaca, San Bartolo Albarradas; 16.57N 96.16W; 2060m; Natural population
Hughes CE 1657, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 22/ 2/92
Single tree collection 10km E of Mitla towards San Bartolo Albarradas.

130/92 **L. confertiflora var. confertiflora**
MEXICO, Oaxaca, Nueve Puntas; 16.50N 96.21W; 2100m; Natural population
Hughes CE 1660, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 22/ 2/92
Same site as 84/94. Single tree collection below Cerro Nueve Puntas, 10km SE of Matatlán.

131/92 **L. trichandra**
MEXICO, Oaxaca, Guelatao; 17.18N 96.30W; 2030m; Natural population
Hughes CE 1663, E,FHO,K,MEXU,NY;
Parent trees: Bulk 12 / Individual 0; Collected on 23/ 2/92
Small bulk seed collection from 12 trees scattered between Guelatao de Juarez and Ixtlan de Juarez.

132/92 **L. macrophylla subsp. istmensis**
MEXICO, Oaxaca, Matias Romero; 16.56N 95.02W; 140m; Natural population
Hughes CE 1670, E,FHO,K,MEXU,NY;
Parent trees: Bulk 3 / Individual 0; Collected on 25/ 2/92
Small bulk of 3 trees, 15km N of Matias Romero rd to Acayucan.

133/92 **L. leucocephala subsp. leucocephala**
MEXICO, Oaxaca, Matias Romero; 16.48N 95.03W; 220m; Natural population
Hughes CE 1671, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 25/ 2/92
Single tree collection 10km S of Matias Romero, rd to La Ventosa.

134/92 **L. lanceolata var. lanceolata**
MEXICO, Oaxaca, Matias Romero; 16.46N 95.03W; 220m; Natural population
Hughes CE 1672, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 25/ 2/92
Single tree collection, 12km S of Matias Romero, rd to La Ventosa.

135/92 **L. shannonii**
MEXICO, Chiapas, Cintalapa de Figueroa; 16.41N 93.37W; 475m; Natural population
Hughes CE 1676, E,FHO,K,MEXU,MO,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 26/ 2/92
Single tree collection rd 5km E of Cintalapa de Figueroa to Ocozocuautla.

136/92 **L. leucocephala subsp. glabrata**
MEXICO, Chiapas, Cintalapa de Figueroa; 16.46N 93.26W; 680m; Cultivated indigenous (guajal)
Hughes CE 1679, E,FHO,K,MEXU,NY;
Parent trees: Bulk 3 / Individual 0; Collected on 26/ 2/92
Small bulk collection from 3 roadside trees rd 39.5km E of Cintalapa de Figueroa to Tuxtla.

137/92 **L. trichandra**
MEXICO, Chiapas, La Trinitaria; 16.05N 92.03W; 1400m; Natural population
Hughes CE 1682, E,FHO,K,MEXU,NY;
Parent trees: Bulk 5 / Individual 0; Collected on 27/ 2/92
Small bulk seed collection from 5 trees scattered on rd 10-15km SE of La Trinitaria.

138/92 **L. trichandra**
GUATEMALA, Huehuetenango, Aguacatán; 1600m; Natural population
Hughes CE 1691, E,FHO,K,MEXU,MO,NY;
Parent trees: Bulk 5 / Individual 0; Collected on 28/ 2/92
Seed collected from 5 trees near the village of Rio Blanco, immediately NW of Aguacatán.

139/92 **L. leucocephala subsp. glabrata**
GUATEMALA, Huehuetenango, Barillas; 15.48N 91.48W; 1125m; Cultivated indigenous (guajal)
Hughes CE 1698, E,FHO,K,MEXU,MO,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 1/ 3/92
Seed from a single tree below Aldea Florida, 10km NE of Barillas.

140/92 **L. trichandra**
GUATEMALA, San Marcos, San Marcos; 14.51N 91.46W; 2030m; Natural population
Hughes CE 1701, E,FHO,K,MEXU,MO,NY;
Parent trees: Bulk 10 / Individual 0; Collected on 3/ 3/92
Small bulk seed collection from 10 trees scattered on rd between San Marcos and Coatepeque.

141/92 **L. shannonii**
HONDURAS, Yoro, Santa Rita; 15.12N 87.50W; 360m; Natural population
Hughes CE 1714, E,FHO,K,MEXU,MO,NY;
Parent trees: Bulk 5 / Individual 0; Collected on 7/ 3/92
Small bulk seed collection from 5 trees scattered by rd E from Santa Rita towards Yoro.

146/92 **L. diversifolia**
MEXICO, Chiapas, Ocosingo; 16.59N 92.06W; 1170m; Natural population
Hughes CE 1733, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 31/ 3/92
Seed collected from a single tree 4km ESE of the turnoff to Yajalón rd from Ocosingo to Palenque.

147/92 **L. leucocephala subsp. leucocephala**
MEXICO, Quintana Roo, Chetumal; 18.31N 88.24W; 20m; Natural population
Hughes CE 1735, E,FHO,K,MEXU,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 2/ 4/92
Single tree seed collection from outskirts of Chetumal, rd to Escarcega.

148/92 **L. xspontanea**
GUATEMALA, Huehuetenango, Barillas; 15.48N 91.48W; 1500m; Cultivated indigenous (guajal)
Hughes CE 1695, E,FHO,K,MEXU,MO,NY;
Parent trees: Bulk 1 / Individual 1; Collected on 1/ 3/92
Seed collected from a single tree in backyard in La Florida, 5km NNE of Barillas. *L. xspontanea* is a hybrid between *L. diversifolia* and *L. leucocephala.*

30/93 **L. leucocephala subsp. glabrata**
MADAGASCAR, Antisiranana, Montagne des francais; 0m; Plantation (exotic)
Lewis GP, K; Parent trees: Bulk 1 / Individual 1; Collected on 4/12/92

83/94 **L. cuspidata**
MEXICO, Hidalgo, Camarones; 20.41N 98.59W; 2040m; Natural population
Hughes CE 1851, FHO,K,MEXU,NY; Parent trees: Bulk 40 / Individual 20; Collected on 27/11/93
Seed collected from 20 trees scattered on slopes above the village of Camarones in mountains approx. 55km NE of Ixmiquilapan, kept separate by parent tree until after extraction then partially bulked with seed from a further 20 trees.

84/94 **L. confertiflora var. confertiflora**
MEXICO, Oaxaca, Nueve Puntas; 16.50N 96.21W; 2000m; Natural population
Hughes CE 1777, FHO,MEXU,NY,K; Parent trees: Bulk 2 / Individual 0; Collected on 8/11/93
Same site as 130/92. Small bulk seed collection from 2 trees on Cerro Nueve Puntas, 5km S of Matatlán.

85/94 **L. confertiflora var. confertiflora**
MEXICO, Oaxaca, El Moral; 17.34N 96.56W; 1900m; Natural population
Hughes CE 1780, FHO.MEXU,K,NY; Parent trees: Bulk 3 / Individual 0; Collected on 10/11/93
Same site as 127/92. Small bulk seed collection from 3 trees close to rd N from Oaxaca to Teotitlán 10km N of El Moral.

86/94 **L. confertiflora var. confertiflora**
MEXICO, Oaxaca, Santa Catarina Zapoquila; 18.03N 97.33W; 2260m; Cultivated indigenous (guajal)
Hughes CE 1812, FHO,K,MEXU,NY; Parent trees: Bulk 3 / Individual 0; Collected on 18/11/93
Small bulk seed collection from 3 trees SE of Santa Catarina Zapoquila towards Membrillo, 23km SE of San Francisco de Huapanapan.

87/94 **L. confertiflora var. adenotheloidea**
MEXICO, Puebla, San Pedro Chapulco; 18.37N 97.25W; 2030m; Cultivated indigenous (guajal)
Hughes CE 1796, FHO,MEXU,K,NY,MO; Parent trees: Bulk 30 / Individual 17; Collected on 13/11/93
Same site as 33/89 and 119/92. Seed collected from 17 trees in household orchard cultivated for pod production in the village of San Pedro Chapulco, kept separate then partially bulked with seed from a further 13 trees.

88/94 **L. confertiflora var. adenotheloidea**
MEXICO, Puebla, Santa Catalina Oxolotepec; 18.36N 97.15W; 2350m; Cultivated indigenous (guajal)
Hughes CE 1799, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 13/11/93
Single tree collection Santa Catalina Oxolotepec, Sierra Zongolica, 20km NE of Tehuacan.

89/94 **L. cuspidata**
MEXICO, Hidalgo, Tolantongo; 20.39N 99.03W; 1860m; Natural population
Hughes CE 1850, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 27/11/93
Single tree seed collection rd NE from Cardonal to Cieneguilla, upper reaches of Barranca de Tolantongo.

90/94 **L. cuspidata**
MEXICO, Hidalgo, Jacála; 21.03N 99.10W; 1770m; Cultivated indigenous (guajal)
Hughes CE 1856, FHO,K,MEXU,NY; Parent trees: Bulk 10 / Individual 0; Collected on 29/11/93
Same site as 88/92. Small bulk collection - 10 trees nr Puerta de Zorra, 9km NE of Jacála.

91/94 **L. pueblana**
MEXICO, Puebla, Zapotitlán Salinas; 18.14N 97.33W; 1850m; Natural population
Hughes CE 1787, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 11/11/93
Single tree collection 16km SW of Zapotitlán Salinas, rd Tehuacan to Huajuapan de León.

92/94 **L. pallida**
MEXICO, Puebla, Santiago Acatepec; 18.13N 97.35W; 2080m; Cultivated indigenous (guajal)
Hughes CE 1795, FHO,MEXU,NY,K; Parent trees: Bulk 1 / Individual 1; Collected on 12/11/93
Single tree collection from cultivated tree Santiago Acatepec.

93/94 **L. ? hybrid**
MEXICO, Puebla, Santiago Acatepec; 18.13N 97.35W; 2080m; Cultivated indigenous (guajal)
Hughes CE 1788, FHO,MEXU,K,NY; Parent trees: Bulk 1 / Individual 1; Collected on 12/11/93
Same tree as 123/92. Single tree collection in Santiago Acatepec. Resembles *L. ×mixtec* but fertile - putative hybrid ? more than two parent species.

94/94 **L. ? hybrid**
MEXICO, Puebla, San Pedro Chapulco; 18.36N 97.25W; 1970m; Cultivated indigenous (guajal)
Hughes CE 1882, FHO,MEXU,K,NY; Parent trees: Bulk 1 / Individual 1; Collected on 7/12/93
Single tree collection - unusual putative hybrid - large tree in San Pedro Chapulco where *L. confertiflora, L. pallida, L. esculenta, L. leucocephala* and a second hybrid cultivated. Origin unknown.

95/94 **L. ? hybrid**
MEXICO, Puebla, Santa Catalina Oxolotepec; 18.36N 97.15W; 2350m; Cultivated indigenous (guajal)
Hughes CE 1801, FHO,MEXU,NY,K; Parent trees: Bulk 1 / Individual 1; Collected on 13/11/93
Single tree seed collection from unusual putative hybrid with clusters of very narrow falcate pods in Santa Catalina Oxolotepec where *L. confertiflora, L. pallida* and *L. esculenta* are cultivated for pod production.

96/94 **L. ? hybrid**
INDONESIA, West Java, Ponduk Gedeh; Seed Orchard
Hughes CE 1898, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 1/2/94
Single tree seed collection from a putative hybrid between *L. leucocephala* and *L. trichandra* collected at Pondok Gedeh IBRIEC Research Station, 25km S of Bogor. Same as RSB01 which may be the same as PG79, possibly originating from N. Sumatra.

97/94 **L. xspontanea**
MEXICO, Veracruz, Jalcomulco; 19.25N 96.53W; 960m; Plantation (native range)
Hughes CE 1869, FHO,MEXU,NY,K; Parent trees: Bulk 1 / Individual 1; Collected on 5/12/93
Single tree collection 1km NW of Tuzunapan, 12km from Coatepec.

98/94 **L. xspontanea**
MEXICO, Veracruz, Plan del Rio; 19.24N 96.38W; 310m; Natural population
Hughes CE 1876, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 6/12/93
Single tree collection 1km N of Plan del Río main rd 40km SE from Jalapa to Veracruz.

99/94 **L. xspontanea**
MEXICO, Veracruz, Plan del Río; 19.24N 96.38W; 310m; Natural population
Hughes CE 1877, FHO,MEXU,K,NY; Parent trees: Bulk 1 / Individual 1; Collected on 6/12/93
Single tree collection 1km N of Plan del Río 40km SE Jalapa rd to Veracruz.

100/94 **L. leucocephala subsp. glabrata**
MEXICO, Veracruz, Plan del Río; 19.24N 96.38W; 310m; Cultivated indigenous (guajal)
Hughes CE 1878, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 6/12/93
Single tree collection. 1km N of Plan del Río, 40km SE of Jalapa, rd to Veracruz.

101/94 **L. leucocephala subsp. glabrata**
MEXICO, Veracruz, Plan del Río; 19.24N 96.38W; 310m; Cultivated indigenous (guajal)
Hughes CE 1879, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 6/12/93
Single tree collection 1km N of Plan del Río, 40km SE of Jalapa rd to Veracruz.

102/94 **L. leucocephala subsp. glabrata**
MEXICO, Puebla, Santiago Acatepec; 18.13N 97.35W; 2080m; Cultivated indigenous (guajal)
Hughes CE 1791, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 12/11/93
Single tree collection cultivated tree in Santiago Acatepec.

103/94 **L. leucocephala subsp. leucocephala**
MEXICO, Veracruz, Tihautlán; 20.48N 97.34W; 100m; Natural population
Hughes CE 1861, FHO,MEXU,NY,K; Parent trees: Bulk 10 / Individual 10; Collected on 1/12/93
Collected from 10 trees scattered 13km N of Tihuatlán, kept separate by parent tree.

104/94 **L. diversifolia**
MEXICO, Veracruz, Maria de la Torre; 20.14N 97.03W; 110m; Natural population
Hughes CE 1864, FHO,MEXU,NY,K; Parent trees: Bulk 1 / Individual 1; Collected on 1/12/93
Single tree collection 12km N of Maria de la Torre, rd to Poza Rica.

105/94 **L. diversifolia**
MEXICO, Tabasco, Teapa; 17.42N 92.57W; 30m; Natural population
Hughes CE 1885, FHO,K,MEXU,NY; Parent trees: Bulk 1 / Individual 1; Collected on 8/12/93.
Single tree seed collection rd 40km S of Villahermosa towards Teapa.

106/94 **L. diversifolia**
MEXICO, Veracruz, Huatusco; 19.09N 96.58W; 1375m; Natural population
Hughes CE 1881, FHO,MEXU,K,NY; Parent trees: Bulk 1 / Individual 1; Collected on 6/12/93
Single tree collection 5km SW of Huatusco, rd Huatusco to Fortín. Close to K156 locality.

107/94 **L. diversifolia**
MEXICO, Chiapas, Yajalón; 17.12N 92.23W; 725m; Natural population
Hughes CE 1887, FHO,MEXU,NY,K; Parent trees: Bulk 1 / Individual 1; Collected on 9/12/93
Single tree seed collection, 5km W of Yajalón.

137/94 **L. pallida**
AUSTRALIA, Queensland, Samford; Seed Orchard
Parent trees: Bulk 15 / Individual 0; Collected on 26/ 9/94
Same as 14/96. Corresponds to CSIRO composite of *L. pallida* (CQ3439), from a seed orchard established incorporating 15 accessions of *L. pallida* tested by CSIRO at Samford in Australia. Collected from site 041 in 1994. No selection involved and some parents may have been interspecific hybrids.

1/95 **L. hybrid**
USA, Hawaii, Waimanalo; Controlled cross
Parent trees: Bulk 10 / Individual 0; Collected 1995
KX2 (*L. leucocephala* x *L. pallida* hybrid) special composite F5 - made up of the 5 superior trees in set 92-3. From initial cross K376 x K8.

2/95 **L. hybrid**
USA, Hawaii, Waimanalo; Controlled cross
Parent trees: Bulk 10 / Individual 0; Collected 1995
KX2 (*L. leucocephala* x *L. pallida* hybrid) special composite F5 - F5 generation seed from superior parent trees in set 92-3. From initial cross K376 x K8.

3/95 **L. xspontanea**
USA, Hawaii, Waimanalo; Controlled cross
Parent trees: Bulk 10 / Individual 0; Collected 1995
KX3 (*L. diversifolia* x *L. leucocephala* hybrid) composite-F4 seed from selected parents in set 92-4. Initial cross K156 x K636.

4/95 **L. xspontanea**
USA, Hawaii, Waimanalo; Controlled cross
Parent trees: Bulk 10 / Individual 0; Collected 1995
KX3 (*L. diversifolia* x *L. leucocephala* hybrid) parent 91-6. Variety K156 x K636 F4 seed.

5/95 **L. xspontanea**
USA, Hawaii, Waimanalo; Controlled cross
Parent trees: Bulk ? / Individual 0; Collected 1995
KX3 (*L. diversifolia* x *L. leucocephala* hybrid) parent 91-13. Variety from K156 x K636 F4 parent.

6/95 **L. xspontanea**
USA, Hawaii, KX3 single UH F4 family;; Controlled cross
Parent trees: Bulk 1 / Individual 1; Collected 1995
KX3 (*L. diversifolia* x *L. leucocephala* hybrid) parent 91-6. Variety K156 x K636 F4 seed.

11/95 **L. diversifolia**
AUSTRALIA, Queensland, Mount Cotton; Seed Orchard
Parent trees: Bulk ? / Individual 0; Collected 1995
Collected by Univ. of Queensland from progeny derived from K156 via University of Hawaii. Origin from Fortín, Veracruz, Mexico. Same as K156.

12/95 **L. leucocephala subsp. glabrata**
AUSTRALIA, Queensland, Mount Cotton; Seed Orchard
Parent trees: Bulk ? / Individual 0; Collected 1995
Collected by Univ. of Queensland at Mount Cotton. Corresponds to Cunningham variety released and widely planted in Australia (Gray, 1967) and is a cross between the Salvador and Peru cultivars

14/96 **L. pallida**
AUSTRALIA, Queensland, Mount Cotton; Seed Orchard
Parent trees: Bulk 15 / Individual 0; Collected 1995
Corresponds the the CSIRO composite of *L. pallida* (CQ3439), a seed orchard established with 15 CSIRO accessions (with no selection) propagated by ATFGRC. This seedlot derived from progeny of the CSIRO composite grown by the University of Queensland at Mount Cotton. Same as 137/94.

8/97 **L. leucocephala subsp. glabrata**
USA, Hawaii, LxL (Kunia substation); 21.21N 155.02W; 85m; Seed Orchard
Parent trees: Bulk ? / Individual 0; Collected on 6/97
Composite F_2 intraspecific cross based on 6 *L. leucocephala* hybrids (K397 x K565 & K608 x K565 & K548 x K565 & K548 x K636 & K608 x K397 & K397 x K608)

Appendix 3. Seed distribution and trials

Background. The ability to provide reliable data about seed collections and to track their distribution is crucial, not only for routine coordination of trials and across-site analysis of trial results, but also to map specific lines of communication between providers and users of genetic resources along which benefit-sharing mechanisms can develop (Section 9.6). Furthermore, detailed recording of data on seed distribution will undoubtedly prove an invaluable tool documenting the history of introductions when dealing with any future problems of weediness and for investigation of spontaneous hybrids, should they arise. The OFI SISTEM+ (Species Information, Seed, Trials and Environment data Management) database has the capacity to be used in an integrated fashion to store all data on seed collections, seed distribution and trials.

The OFI *Leucaena* seed collections (Appendix 2) assembled over a 15-year period comprise more than 1000 seedlots. However, the majority of these were collected between 1985 and 1993. Early collections, before 1985 were opportunistic and formed part of wider efforts to explore and collect the genetic resources of Central American dry zone agroforestry trees more generally. From 1985 to 1989 the focus of collections narrowed to five woody legume genera (*Leucaena, Gliricidia, Parkinsonia, Albizia* and *Prosopis*) and more intensive collections of *Leucaena* were undertaken during that period. From 1990 to 1993 a project based at OFI concentrating solely on the genetic resources of *Leucaena* allowed seed collections to be intensified and completed.

Distribution of seed of *Leucaena* followed a similar pattern. From 1984 seed of three species, *L. shannonii, L. collinsii* subsp. *zacapana* (which was mis-identified at that time as *L. diversifolia*; seedlots 15/83 and 18/84), and *L. leucocephala* subsp. *glabrata* was distributed as part of a broader package of dry zone species for the establishment of a series of species elimination field trials (Hughes and Styles, 1984). Final results from these trials were synthesized and reported by Stewart and Dunsdon (1994). This showed the excellent growth of *L. collinsii* subsp. *zacapana*.

Distribution of the main OFI *Leucaena* seed collections started in 1988, for the establishment of a small number of prototype trials, even though additional seed collections were still being assembled. These initial trials provided the opportunity to test a wide range of species and provenances for the first time and yielded useful preliminary results (*e.g.* Stewart *et al.*, 1991; 1993) and material for research on leaf and wood quality. They also provided insights for planning of the subsequent LEUCNET trials. With completion of the seed collections in 1993, the main seed distribution programme started in earnest in 1994, under the umbrella of the LEUCNET research and development network. Seed for a total of 81 *Leucaena* species/provenance evaluation trials has been distributed from OFI so far. In addition 3 'foundation' collections (containing >70 accessions) and 5 provenance/progeny trials have been supplied. A large number of seedlots have also been distributed to researchers for *Rhizobium*, molecular and cytological investigations. In total, more than 3500 *Leucaena* seedlots have been distributed in the last 10 years. Preliminary results have been reported and published for many trials.

This Appendix provides an outline summary of the scope of the OFI *Leucaena* seed distribution programme to mid-1997. Seed distribution at OFI is coordinated by Alan Pottinger; much of the information presented here was compiled by him. Pointers to publications of trial results are provided where known. Alongside collaboration with all the individual agencies who have established trials, many have been established in collaboration with four regional projects which coordinate their own regional sub-networks. These are indicated as follows:

[1]Trial established under, ACIAR Project No. 9433 'New leucaenas for southeast Asian, Pacific and Australian agriculture' coordinated by the University of Queensland. Results presented at ACIAR Project No. 9433 Coordination Meeting April 1997

[2]Trial established under CIAT management as part of DFID FRP Project R6551

[3]Trial established under ICRAF management as part of DFID FRP Project R6551

[4]Trial established under FSP (CIAT-CSIRO) management as part of DFID FRP Project R6551

Summary of *Leucaena* seed distribution from OFI

COUNTRY Organisation	Seed order: Date & No.	Number of seedlots	Trials: objectives, establishment status & results
AUSTRALIA Univ. of Queensland	9/94 2288	81	[1]Foundation collection - evaluating wood+leaf quality, cold tolerance, psyllid reistance; est. 3/95 at Redland Bay, Queensland; results - 3 months (Mullen, 1995); 24 months in [1]No. 1; psyllid resistance (Mullen *et al.*, 1996); fodder quality (Mullen *et al.*, 1996)
AUSTRALIA Univ. of Queensland	9/94 2288	26	[1]Spp/prov evaluation trial; est 9/95 at Brian Pastures, Queensland; results - 18 months in [1] No. 3; fodder quality (Mullen *et al.*, 1996)
AUSTRALIA Queensland DPI, Trop. Beef Centre	9/94 2288	27	[1]Spp/prov evaluation trial - Cold tolerance, psyllid resistance, yield, nutritive value; est. 9/95 at Rockhampton, Queensland; results - 18 months in [1]No. 4
AUSTRALIA CSIRO	9/94 2288	25	[1]Spp evaluation trial - psyllid resistance, yield, nutritive value; est. 9/95 at Townsville, Queensland; results - 18 months in [1]No. 5
AUSTRALIA West Austr. Dept. Ag.	9/94 2288	25	[1]Spp/prov evaluation trial; est. 9/95 at Ord River, Western Australia; results - 18 months in [1]No. 6
BOLIVIA Misíon Británica	8/96 2421	19	Spp/prov evaluation trial; Seed received; no information
BOTSWANA Dept. of Agric. Res.	9/95 2363	21	Spp/prov evaluation trial; est. 1/96; results - 5 months (Karachi and Lefofe, 1997)
BRAZIL IBAMA	3/96 2419	5	Spp/prov evaluation trial; due to be est. early 1997
BRAZIL EMBRAPA-CNPG	6/96 2446	16	[2]Spp/prov evaluation trial; est. 12/96 in Colombo
BRAZIL Univ. Rio Grande do Sol	11/95 2390	97	Spp/prov evaluation trial and cytological studies; 91 accessions est. 11/96; report: Schifino-Wittmann (1997)
COLOMBIA CORPOICA	6/96 2446	16	[2]2 Spp/prov evaluation trials; to be est. in Cordoba and Cesar in early 97
COSTA RICA CATIE	9/90 1975	24	5 Spp/prov evluation trials; est. 4/91 (1 in Costa Rica, 4 in Nicaragua); results - (Costa Rica) 6 + 12 months in Viquez (1995)
COSTA RICA CIAT	5/96 2434	18	[2]Spp/prov evaluation trial; est. 8/96 at Atenas; results - 3.5 + 9.8 months (Argel and Perez, 1997)
ETHIOPIA Forage Legume Agr. Gp., ILCA	9/86 1376	12	Spp elimination trials; no information
ETHIOPIA ILRI	6/96 2441	42	Spp/prov evaluation trial plus seed for on-going ILRI research; planned for E African Highlands
FRANCE CIRAD	3/96 2417	23	*Rhizobium* experiments
GHANA Animal Res. Inst.	11/95 2387	19	Spp/prov eval trial; seed received 12/95; est planned 9/97
HONDURAS CONSEFORH	12/88 1812-6	33	Spp/prov evaluation trials (see Ponce, 1995): est. 8/89 La Soledad, Comayagua; results - nursery Hellin and Gomez (1991); 12 months Stewart *et al.* (1991); 24 months Stewart *et al.* (1993); wood quality Gourlay *et al.* (in press); fodder quality Stewart and Dunsdon (in press) est. 8/89 El Zamorano. Francisco Morazán subset of accessions included in 3rd trial est. 1993 Santa Rosa, Choluteca
HONDURAS EAP-El Zamorano	6/96 2446	16	[2]Spp/prov evaluation trial; est in 12/96
INDIA Central Arid Zone Res. Inst.	6/85 1219 2/87 1435	3 13	Spp elimination trials; no information
INDIA Indian Grassland & Fodder Res. Inst.	2/90 1946	33	Inclusion in wider evaluation and breeding programme on *Leucaena* (see Gupta, 1990); est. 8/91 at Jhansi; report in Gupta and Pathak (1995)

COUNTRY Organisation	Seed order: Date & No.	Number of seedlots	Trials: objectives, establishment status & results
INDIA Centre for Arid Zone Studies (Bangor)	4/95 2321 5/96 2437	10 3	2 spp/prov evaluation trials for drought tolerance, and cutting ht; est. 6/95 in Madhya Pradesh; report on wood calorific value (Bezkorowajnyj *et al.*, 1996)
INDIA BAIF	8/86 1365 9/95 1364-5	8 21	Spp elimination trial; no information Spp/prov evaluation trial (planned 1 on-station; 1 on-farm); seed received; discussions on-going re est. of trial
INDIA Indo-Swiss Project Orissa	2/97 2491	5	Spp/prov evaluation trials on-station and on farm; to be est. 6/97
INDIA Nimbkar Agric Res. Inst.	1/96 2359	21	Spp/prov evaluation trial; seed received; No information on trial est.
INDIA Nat. Res. Ctre Agro-Forestry	9/95 2358	18	On-going breeding and evaluation work in Uttar Pradesh; seed received
INDIA YS Parmar Univ. Hort. & Forestry	3/96 2418	19	Spp/prov evaluation trial; no information
INDIA Indira Ghandi Agric. Univ.	6/96 2448	16	Spp/prov evaluation trial; no information
INDONESIA Small Ruminant-CRSP	8/95 2361	21	[1]Spp/prov evaluation trial; est. in North Sumatra 12/95; results - 8 mths in [1]No. 10
KENYA ICRAF	11/94 2297	136	[3]Progeny trials: *L. diversifolia* (47 families), *L. trichandra* (21 families, *L. esceulenta* (25 families), *L. pallida* (42 families), *L. leucocephala* (1 family); est. Machakos 4/96
KENYA ICRAF	5/95 2329-2337	21	[3]Spp/prov evaluation trials on ICRAF sites; est. Machakos and Kibwezi 5/96; 2 to be est. Embu
KENYA Kenya Aagric Res. Inst.	8/95 2360	21	[1]Spp/prov evaluation trial est. at Katumani 4/96; results - 12 months in [1]No. 11
LAOS CIAT	9/94 2288	21	[4]Spp/prov evaluation trial; est. Res. Stn. nr Vientiane 7/96
LESOTHO Forestry Division	7/88 1750	16	Spp elimination trials; data on file at OFI; all species killed by frost; no publications
MADAGASCAR National Seed Bank	7/96 2451	16	Spp/prov evaluation trial; est. 5/97
MALAWI ICRAF	9/90 1979	24	[3]Spp/prov evaluation trial; est. at Chitedze 12/91; severe drought 91/92; results - 48 months ICRAF Ann Rep. 1995
MALAWI ICRAF	7/95 2347	20	[3]Spp/prov evaluation trial; seedlings at Makoka raised in 96; no information on trial est.
MALI ICRAF	5/95 2329-2337	21	[3]Spp/prov evaluation trial; no information on trial est.
MEXICO INIFAP	5/96 2433	16	[2]Spp/prov evaluation trial; to be est. in Veracruz 4/97
MEXICO Univ. Autónoma de Yucatán	6/96 2446	16	[2]Spp/prov evaluation trial; to be est. in Yucatán 4/97
MEXICO Univ. Nac. Autónoma de México	3/86 1285	6	Isozyme studies of the *L. shannonii* alliance
MEXICO Univ. Autónoma de Nuevo León	11/85 1252 7/86 1339 7/88 1665	6 2 7	Inclusion in on-going spp/prov evaluation trial programme; est. Linares; results - 48 months (Foroughbakhch and Hauad, 1990)
MEXICO Univ. Autónoma de Nuevo León	6/96 2446	16	[3]Spp/prov evaluation trial; to be est. in Nuevo León 4/97
MOZAMBIQUE Ministerio da Agricultura	11/95 2348 10/96 2477	21 18	Spp/prov evaluation trials; in nursery and planning to est. 2 trials 11/96

COUNTRY Organisation	Seed order: Date & No.	Number of seedlots	Trials: objectives, establishment status & results
MOZAMBIQUE DANIDA	6/96 2440	2	On-farm trials; seed received; no information
NEPAL Ctre Arid Zone Studies (Bangor)	10/96 2478-80 3/97 2494	5	Spp/prov evaluation trials and on-farm research; est. on bunds 7-8/97
NICARAGUA DANIDA-Nicaragua Tree Seed Ctre	5/96 2413	19	2 Spp/prov evaluation trials; est. 9/96; no information
NIGERIA Nat. Animal Production Res. Inst.	8/96 2465	16	Spp/prov evaluation trial; seed sent 2/97; no information
PANAMA Univ. de Panama	6/96 2446	16	[2]Spp/prov evaluation trial; to be est. 4/97
PAPUA NEW GUINEA Dept. of Agriculture	9/94 2288 2456, 2485	21	[1]Series of spp/prov evaluation trials: [1]est. at Erap 10/95; results - 16 mths in [1]No. 8 [1]est. at Aiyura 11/95; results - 16 mths in [1]No. 8 [1]est. at Lae 10/95; results - 16 mths in No. 8 [1]*L. collinsii* subsp. *collinsii* grazing trial est. at Munum 10/96 - 1/97; report in [1]No. 14
PHILIPPINES Forest Res. Inst.	7/86 1344	4	Spp. elimination trial; no information
PHILIPPINES Bureau of Animal Industries	9/94 2288	21	[1]Series of spp/prov eval trials: [1] est. at Lipa City 6/95; results - 20 mths in [1]No. 7 [1] est. at Tanay, Rizal 7/95; results - 20 mths in [1]No. 7 and in Castillo *et al.* (1997) [1] est. at Nueva Ecija 10/95; results - 18 mths in [1]No. 7 [1] grazing trial est. at Milagros Livestock Prod Ctre, Masbate 6/96; results at 7 mths in [1]No. 15 [1] palatability experiment at Bureau of Plant Industry Farm, Lipa City, 5 and 6/96; results in [1]No. 19
PHILIPPINES IRRI	9/94 2349	76	[1] Foundation collection: wood+leaf quality, cold tolerance, psyllid resistance; est. at Los Banos 9/95; results - 18 mths in [1]No. 2; psyllid resistance (Mullen *et al.*, 1996)
PHILIPPINES City Vet. Office, Cagayan de Oro City	7/96 2443-4	16	2 spp/prov evaluation trials; no information on est.
SOUTH AFRICA Univ. of Stellenbosch	3/96 2442	16	3 Spp/prov eval trials; est. planned for 5 or 6/98
SRI LANKA Univ. Peradeniya	6/92 2100 6/93 2179	9 16	Spp/prov evaluation trial; est. 11/92 Dodongolla; results - Gunasena and Wickramasinghe (1995) *L. diversifolia* prov trial; est. 12/93 Dodongolla; results - Gunasena (1995, 1996)
SRI LANKA GTZ	12/95 2393	19	Spp/prov evaluation trial; est. due early 96
TANZANIA ICRAF	8/92 2119	23	[3]Spp/prov evaluation trial; est. 2/93 at Tabora; results - ICRAF Ann Rep 1995 and Otsyina and Msangi (1995)
TANZANIA ICRAF	5/95 2329-2337	21	[3]Spp/prov evaluation trial; est. at Shinyanga 11/95
TANZANIA ICRAF	8/95 2369 7/96 2453	9	[3]More comprehensive look at best species from previous OFI trial, plus additional promising spp; est. at Tabora 11/95; poor establishment; results - ICRAF Ann Rep 1995 (LEUCNET News 3: 11-14) [3]establishment of fodder banks and on-farm trials; no information
TANZANIA Evergree Trust	8/95 2366-7	21	Spp/prov evalutaion trial; est. Pemba 2/96
TANZANIA Farm Africa	3/97 2495	4	On-farm tial follow-up to earlier trial est 1993 at Dareda; planned est 1997
THAILAND Dept. Livestock Development	6/96 2438	15	2 spp/prov evaluation trials; est late 96; prelim data at OFI

COUNTRY Organisation	Seed order: Date & No.	Number of seedlots	Trials: objectives, establishment status & results
THAILAND Univ. of Chiang Mai	3/96 2423	9	Spp/prov evaluation trial; est. ?; reported 8/97
U.K. Univ. St. Andrews	90-92 2016, 2037, 2038, 2079, 2113, 2250	approx 500	Miscellaneous molecular studies to examine species relationships, hybrid identities and origins of tetraploid species; results Harris *et al.* (1994 a, b); Harris *et al.* (1996); Harris (1995); Hughes and Harris (1994, in press)
U.K. Univ. Nottingham	1996-7 2457, 2466	11	Cytological studies
U.K. Univ. Cambridge	10/90 1988 10/91 2033	750 210	Isozyme and seed storage protein analyses; results - Chamberlain *et al.* (1996); Harris *et al.* (1996)
U.S.A. Source Ecosystems, Hawaii	8/95 2362	21	Spp/prov evaluation trial; est. delayed due to lack of suitable site
U.S.A. Univ. of Hawaii	1983-1993 Misc	435	Miscellaneous seedlots for testing and incorporation in hybridization/ breeding
U.S.A. Univ. of Hawaii	8/95 2357	74	Foundation collection for spp/prov evaluation trial
VENEZUELA Univ. del Zulia	6/96 2446	16	[2]Spp/prov evaluation trial; est. 12/96
VIETNAM College Ag. & Forestry, Bac Thai	9/94 2288	21	[1]Spp/prov evaluation trial to look at frost tolerance, acid soil tolerance and psyllid resistance; est. at Bac Thai in 6/96; results - 8 months in [1]No. 9 and Van Khoa *et al.* (1997)
VIETNAM Goat & Rabbit Research Centre	9/94 2288	21	[1]Spp/prov evaluation trial to look at frost tolerance, acid soil tolerance and psyllid resistance; est. at Ha Tay in 6/96; results - 8 months in [1]No. 9 and Van Khoa *et al.* (1997)
VIETNAM CIAT	9/94 2288	21	[4]Spp/prov evaluation trial; est. at Tay Nguyen Univ in Buon Ma Thuot 7/96
ZAMBIA ICRAF	5/90 1962	18	Spp/prov evluation trial; est. 5/92 at Chipata; results - ICRAF Ann Rep 1995 (LEUCNET News 3: 11-13)
ZIMBABWE Nat. Botanical Garden	4/88 1727	15	Arboretum collection
ZIMBABWE French Goat Programme	6/88 1742-3	19	Spp elimination trial
ZIMBABWE ICRAF	9/90 1974	21	[3]Spp/prov evaluation trial; est. 91/92 at Dombashawa; results - ICRAF Ann Rep 1995; Dzowela *et al.* (1995)
ZIMBABWE ICRAF	7/95 2331, 2350,	17	[3]More comprehensive look at most promising species from OFI trial, plus additional promising species; est. at Dombashawa 12/95
	9/96 2439	2	[3]On-farm trials; no information

Appendix 4. Material Transfer Agreement

Oxford Forestry Institute Material Transfer Agreement

Introduction

The Oxford Forestry Institute (OFI) has, for more than 30 years, been involved in collection of seed from wild populations of trees. This seed has been used for distribution to researchers in the tropics to evaluate performance of a variety of tree species over a range of sites and to investigate patterns of genetic variation. The approach of OFI is to support free exchange of seed and information between researchers in order to improve knowledge of the potential for various tree species to provide goods and services.

In response to current international interest in issues relating to transfer of germplasm, OFI has recognized the need to formalize agreements with seed recipients in the form of a Material Transfer Agreement (MTA). The MTA is designed to promote scientific exchange while at the same time recognizing the responsibilities of seed recipients towards the countries that donated seed for experimentation. Furthermore, as most of the seed distributed by OFI is not indigenous to the recipient country, the MTA also highlights the need for caution when considering the need to request seed. The following guidelines are designed to assist in this respect.
Please note that seed will only be issued by OFI upon receipt of a signed copy of the MTA.

Warning It is important that seed recipients consider the implications of introducing exotic species in relation to the potential threat of invasiveness. It is recommended that seed is requested only after consideration of these points.

- Introductions should only be considered if clear and well-defined benefits to man or natural communities can be foreseen and demonstrated.
- Introductions should only be considered if no native species is suitable for the purpose for which the introduction is being made.
- Introductions should not be made into pristine or semi-natural habitats, reserves of any kind or their buffer zones and, in most cases, oceanic islands.
- Introductions should not be made until risks of invasion have been assessed based on available data, including the autecology of the species, conditions in the area of introduction, reports of weediness from other areas, and the likelihood of interspecific hybridization with closely related species.
- Introductions should be made initially in small, closely monitored field trials under quarantine conditions. Monitoring should include assessment of seed production and dispersal and natural regeneration into surrounding areas. Collection of seed from trials by station workers or visitors needs to be controlled by harvesting all seed before it ripens, or removing flowers.

Material Transfer Agreement for seed order

The recipient organisation agrees:

- not to claim ownership over the seed received or its progeny, nor to seek intellectual property rights or plant variety rights over that genetic material or information produced from work in which it is involved;
- to ensure that any person or institution to whom it makes samples subsequently available is bound by the same provision;
- to manage the seed and any trees grown from it in such a way as to minimize as far as possible any potential threat from the species becoming an invasive weed;
- that the Oxford Forestry Institute does not accept liability for any consequences resulting from the use of the seed.

Name of person or institution requesting germplasm

Address

Signature

Date

Index to Scientific Names

Accepted names are in Roman type; the main entry for each species is in **bold**; synonyms are in *italics*

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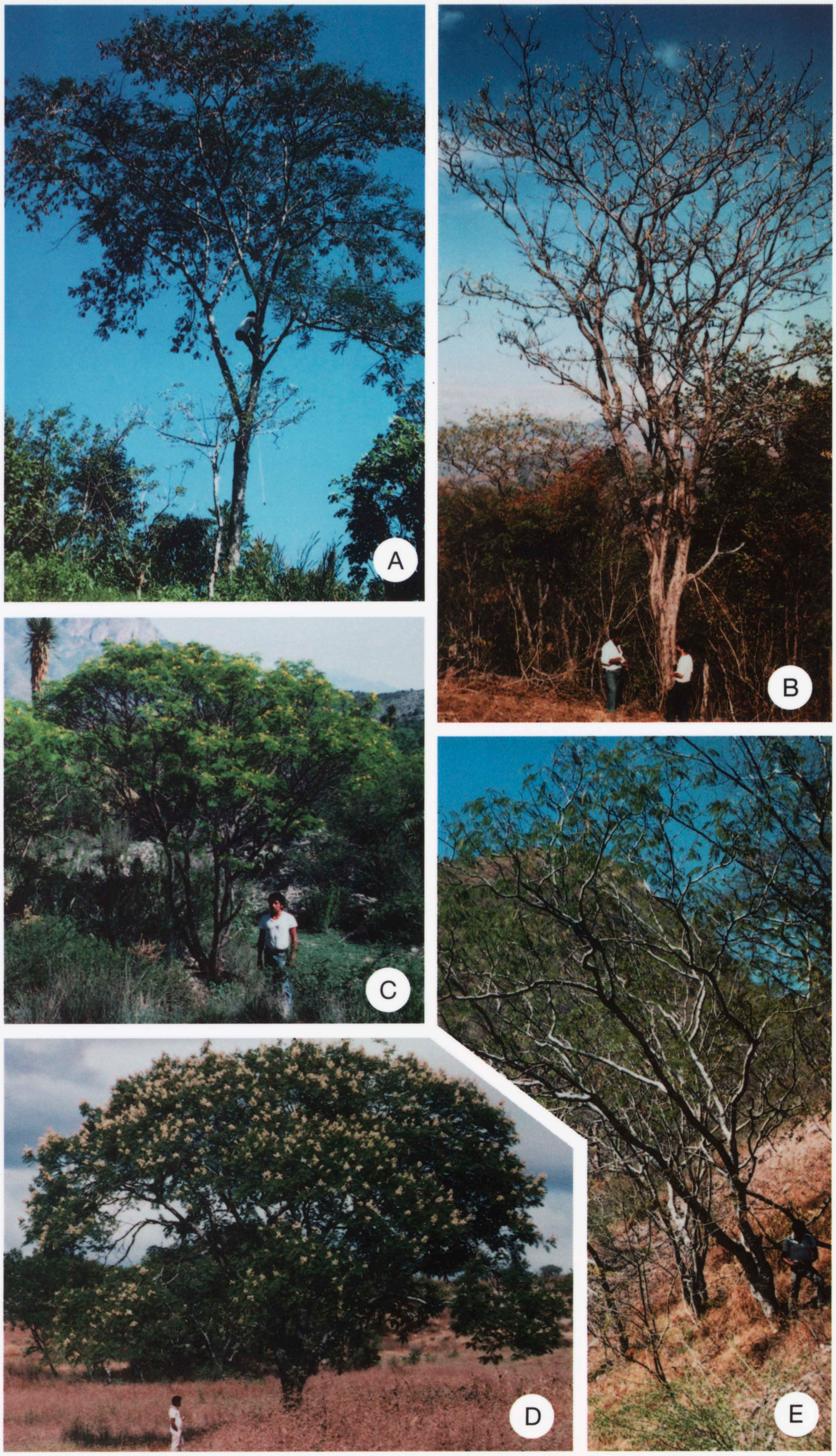
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