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TROPICAL FORESTRY PAPERS 33

Gliricidia sepium

Genetic resources for farmers

Edited by J.L. Stewart, G.E. Allison and A.J. Simons

OXFORD FORESTRY INSTITUTE
DEPARTMENT OF PLANT SCIENCES
UNIVERSITY OF OXFORD
1996

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FORESTRY RESEARCH PROGRAMME

TFP33 *Gliricidia sepium* Stewart, Allison & Simons OFI

Photographs

Front cover

Natural population of *Gliricidia sepium* at Gualán, Zacapa, Guatemala (C.E. Hughes)

Back cover

Top: *Gliricidia sepium* growing under dry conditions (less than 800 mm rainfall), Los Amates, Puebla, Mexico (C.E. Hughes)

Bottom: Provenance trial, Chipata, Zambia (A.J Simons)

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List of Acronyms

Institutions

ACIAR	Australian Centre for International Agricultural Research, Canberra, Australia
BAIF	Bharatiya Agro-Industries Foundation, Pune, Maharashtra, India
BALITNAK	Balai Penelitian Ternak, Ciawi, Bogor, Java, Indonesia
CABI	Commonwealth Agricultural Bureau International, Wallingford, Oxfordshire, UK
CATIE	Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba, Costa Rica
CIAT	Centro Internacional de Agricultura Tropical, Cali, Colombia
CIPAV	Centro para la Investigación en Sistemas Sostenibles de Producción Agropecuaria, Cali, Colombia
COHDEFOR	Corporación Hondureña de Desarrollo Forestal, Tegucigalpa, Honduras
CONSEFORH	Conservation and Silviculture of Dry Zone Forest Species Project, Siguatepeque, Honduras
CSIRO	Commonwealth Scientific and Industrial Research Organization, Canberra, Australia
FAO	Food and Agriculture Organization of the United Nations, Rome, Italy
GTZ	Deutsche Gesellschaft für Technische Zusammenarbeit, Eschborn, Germany
HMSO	Her Majesty's Stationery Office, London, UK
ICRAF	International Centre for Research in Agroforestry, Nairobi, Kenya
ICRISAT	International Centre for Research in the Semi-arid Tropics, Hyderabad, Andhra Pradesh, India
IDRC	International Development Research Centre, Ottawa, Canada
IITA	International Institute for Tropical Agriculture, Ibadan, Nigeria
ILCA	International Livestock Centre for Africa (Humid Zone Programme), Ibadan, Nigeria
ILRI	International Livestock Research Institute (Humid Zone Programme), Ibadan, Nigeria (formerly ILCA)
IMI	International Mycological Institute, Egham, Surrey, UK
IUFRO	International Union of Forestry Research Organizations, Vienna, Austria
NFTA	Nitrogen Fixing Tree Association, Hawaii, USA
ODA	Overseas Development Administration, London, UK
OFI	Oxford Forestry Institute, Oxford, UK
PRONAM	Programme National Manioc, Kinshasa, Zaire
SFRI	State Forest Research Institute, Jabalpur, Madhya Pradesh, India
TNAU	Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India
UNESCO	United Nations Educational, Scientific and Cultural Organization, Paris, France
UNAM	Universidad Autónoma de México, Mexico City, Mexico
UP	University of Peradeniya, Peradeniya, Sri Lanka
USDA	United States Department of Agriculture
VISCA	Visayas State College of Agriculture, Baybay, Leyte, Philippines

Terminology

CAP	Cleaved amplified product
DM	Dry matter
DNA	Deoxyribonucleic acid
dNTP	Deoxyribonucleotide triphosphates
HYB	High-yielding bulk
MPT	Multipurpose tree
NGO	Non-governmental organization
PCR	Polymerase chain reaction
RAPD	Random amplified polymorphic DNA
REML	Residual maximum likelihood
RFLP	Restriction fragment length polymorphism
SALT	Sloping agricultural land technology
SALT-2	Simple agro-livestock technology
SSCP	Single-strand conformation polymorphism
SSR	Simple sequence repeat
UK	United Kingdom
USA	United States of America

Acknowledgements

The inspiration for this Tropical Forestry Paper arose directly from the work of Tony Simons and Andrew Dunsdon on the genetic resources of *Gliricidia sepium* which they studied intensively for more than five years. Their research, and the production of this Tropical Forestry Paper, were entirely funded by the Forestry Research Programme of the Overseas Development Administration, under research schemes R4525 and R4856; this support is gratefully acknowledged

The successful operation of the OFI international trial network and feeding trials would not have been possible without the cooperation and logistical support offered by all collaborating institutions and organizations. Thanks are due to them and in particular to those many members of their staff, too numerous to mention individually, whose hard work and enthusiasm were driving forces in the success of the network.

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R. Jambulingam, TNAU:	8C

1 Introduction

Gliricidia sepium (Jacq.) Steud. is a typical example of a multipurpose tree species, providing essential products and services on farms in the tropics, yet with no industrial role and therefore largely ignored by researchers and foresters until quite recently. In the mid-1970s a shift in donor emphasis in forestry towards small-scale and community initiatives led to a sudden increase in research interest (and donor investment) in trees and shrubs which farmers had already, in many cases, been using for centuries. Professionals in the fields of forestry, agriculture and rural development had hitherto paid little attention to these species. The result has been a huge accumulation, since the early 1980s, of research findings on all aspects of the biology, use and management of *G. sepium.*

The species' appeal lies in its current almost pantropical distribution, its wide range of uses (including fodder, fuelwood and poles, live fencing, erosion control, shade and support for other crops, and soil improvement through biological nitrogen fixation), its ease of (propagation either from seed or from stakes), and its vigorous response to a wide range of management techniques. Native to the seasonally dry parts of Mexico and Central America, it is now cultivated throughout Meso-America as a result of domestication over many centuries. During colonial times, and then most recently through the activities of rural development agencies, it has been introduced, and subsequently become naturalized, in many parts of the semi-arid and sub-humid tropics.

Within much of its native range, *G. sepium* is one of many species commonly found growing on farms and used for a variety of purposes but rarely actively propagated. In parts of Central America and Mexico (generally the wetter eastern areas where the species is probably naturalized rather than truly native), a more intensive use has developed, involving active management of rows of planted trees in boundaries and fence lines. Elsewhere in the tropics, new uses for *G. sepium* have arisen in response to local priorities, such as management for fodder (still a rare use of the species in Meso-America) and in contour hedgerows for erosion control on hillsides.

This Tropical Forestry Paper aims to provide a synopsis of the current state of knowledge with regard to *G. sepium*, summarizing research findings and attempting also to synthesize these into practical recommendations for practitioners. Each chapter addresses a different subject area; some of these are necessarily of more immediate practical applicability than others which explore more fundamental scientific issues. Throughout the book there is an emphasis on *G. sepium* as a genetic resource; this theme is central to several of the chapters, and the same perspective also runs through chapters primarily concerned with other issues, such as utilization, propagation and husbandry. The widespread cultivation of *G. sepium* from the earliest times has had profound effects on present-day patterns of genetic variation. All existing populations have been disturbed to some extent by human activity, and there is a strong possibility that in many introduced populations genetic diversity may not be sufficient to ensure long-term stability.

The subtitle *genetic resources for farmers* is intended to reflect not only the genetic resource perspective of the book but also the importance of recognizing, when planning research and development for this species, the context in which it is used. There has been a tendency in research on multipurpose trees to apply the industrial species' paradigm of formal on-station field experimentation, sometimes without mechanisms in place (or sufficient information about socio-economic conditions) to allow effective dissemination and uptake of the results of the research. An attempt has therefore been made here to balance descriptions of the more formal research with discussion of related issues and implications. Thus the description of the provenance and progeny trial network (Chapter 8) is followed by a discussion of issues relating to the release of selected germplasm to smallholder farmers, and scenarios for its future maintenance and development (Chapter 9). The sections of utilization (Chapter 4) and on propagation, husbandry and management (Chapter 5) combine summaries of research findings with recommendations, often arising directly from the research, on practical aspects of *G. sepium* production and use.

Other chapters are, by nature, of less immediate applicability for field practitioners, but they are included here for completeness, to provide a point of reference, and to give insights into the ways in which 'purer' research provides an essential foundation for more applied studies. Examples are the sections on taxonomy (Chapter 2), distribution, ecology and reproductive biology (Chapter 3), pests and diseases (Chapter 6) and molecular approaches to the study of genetic variation (Chapter 7). In summary, this book can be referred to at different levels: by students and researchers, for information about the biology and genetics of *G. sepium*; and by practitioners, seeking advice on ways in which this important species can be used and managed.

2 Taxonomy

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2.1 Introduction

The small genus *Gliricidia*, comprising three species, belongs to the tribe Robinieae, subfamily Papilionoideae in the family Leguminosae. Other well-known members of this tribe are the genera *Sesbania* and *Robinia*. Recent taxonomic studies of the Robinieae by Lavin and Sousa (1995) have included a revision of the genus *Gliricidia.*

Gliricidia has two close relatives, the genera *Hybosema*, with two species from Mexico and Central America, and *Poitea,* with 12 species from the Caribbean. Together, these three genera form a well-supported taxonomic group, although the exact relationships between them remain unresolved (Lavin and Sousa, 1995). *Gliricidia* may thus be equally related to both *Hybosema* and *Poitea*. *Poitea* and *Gliricidia*, for example, share derived characters such as flowers with staminal tubes containing two bundles of stamens and seedlings with foliar epigeal cotyledons. In contrast, *Poitea* and *Hybosema* share flowers with narrowly cylindrical bilobed calyces. In essence, including the two species of *Hybosema* within *Gliricidia* (*i.e. H. ehrenbergii* and *H. robustum*) would result in *Gliricidia* no longer forming a legitimate taxonomic group. Lavin and Sousa (1995) classify *Gliricidia*, along with *Hybosema*, *Poitea*, and tentatively the genus *Lennea*, in the *Gliricidia*-group of the tribe Robinieae.

Though part of the *Gliricidia*-group, *G. sepium* can be confused with a species outside the group. Specimens of *G. sepium* occasionally display the subopposite branching pattern that is otherwise distinctive of the Cuban *Hebestigma*. Furthermore, some of these same trees also show *Hebestigma*-like inflorescence production: racemes clustered at the tip of a stem and in the axils of aborted or highly reduced leaves. It appears that in these specimens the arrested vegetative production during raceme production is released following flowering. Such specimens are superficially very similar to *Hebestigma cubense*, but they are readily distinguished by the hairless to sparsely bristly flower stalks and calyces. These structures in *Hebestigma* are covered in dense woolly hairs.

Gliricidia ehrenbergii, a shrubby upland species from Mexico and Central America, previously known variously by the synonyms *G. guatemalensis* and *G. meistophylla*, is no longer included within *Gliricidia* having been transferred to the genus *Hybosema* by Lavin and Sousa (1995). A new addition to *Gliricidia* however, is *G. brenningii*, formerly known as *Yucaratonia brenningii* (Lavin and Sousa, 1995). Harms (1923) originally placed *G. brenningii* in *Sesbania* as *S. brenningii*, although he did state that he was not completely certain of this placement. Later, Burkart (1969) recognized the proximity of *S. brenningii* to both *Sesbania* and *Gliricidia* but decided to place it in the monotypic genus *Yucaratonia*. Hughes (1990) further noted the proximity of the then *Y. brenningii* to *Gliricidia*. This has since been confirmed by Lavin and Sousa (1995) who included the species within *Gliricidia* as *G. brenningii*. This inclusion is justified in that it clearly has the calyx and standard petal that are considered diagnostic of the genus. In fact, the flowers of *G. brenningii* have whitish petals and are borne from long hanging axillary racemes, similar to, although longer and more pendulous than, those of *G. maculata*. The characteristics which support the newly circumscribed *Gliricidia* as a legitimate genus are described below.

2.2 Species of *Gliricidia*

The genus name *Gliricidia* is usually associated with *G. sepium* because it is the most widely known and cultivated species. Of the three species of *Gliricidia, G. maculata* and *G. brenningii* are less well-known than *G. sepium* and unknown outside their native ranges in tropical America.

Gliricidia brenningii is easily distinguished from the other two species but the differences between *G. sepium* and *G. maculata* are much more obscure, making identification difficult. *Gliricidia maculata*, despite its quite separate distribution in the Yucatan, has frequently been confused with *G. sepium*. Much of this confusion occurs in exotic locations and is partly a result of being confirmed only recently as a distinct species (Hughes, 1987, Lavin *et al.*, 1991). For this reason, descriptions of all three species are presented to demonstrate the main distinguishing features. A more detailed discussion of the differences between *G. sepium* and *G. maculata* is presented below.

Main distinguishing features

The characteristics which most readily distinguish the genus *Gliricidia* are the cup-shaped calyces which persist well into fruit maturation, and the five-petalled flowers with a standard petal that is reflexed to 180° when the flowers open. All three species share these diagnostic features.

At species level, *G. brenningii* is easily distinguished from the other two species by the size, shape and number of leaflets comprising the leaves, and the presence of small appendages found at the base of the leaflet stalks. In addition, *G. brenningii* is the only species that has a nectar-bearing disk at the base of the staminal tube which is the principal diagnostic feature of the species. Pods can also be used for identification of *G. brenningii*, being much longer and broader than the pods of the other two species and also of a much darker maroon-brown colour. A further aid to identification is *G. brenningii*'s limited distribution in Ecuador and Peru (Map 1 and the species description below). The characteristics that distinguish *G. maculata* from *G. sepium* are much less obvious although the limited distribution of *G. maculata* (Map 2), in climatic conditions that are humid, can be a useful indicator. The botanical differences between these two species are described in detail in Table 2.1, Section 2.3.

Species descriptions

Gliricidia brenningii (Harms) Lavin, comb. nov.

Synonyms: *Sesbania brenningii* Harms.
Yucaratonia brenningii (Harms) Burkart

Common names: Yuca de ratón, yucaratón, nacadero (Ecuador)

Main attributes: *Gliricidia brenningii* is cultivated widely within its native range, displaying the same qualities, such as ease of propagation from cuttings and vigorous resprouting, associated with the better-known *G. sepium*. It is used in live fencing, established by stakes and pollarded regularly. The wood is of a high quality and is valued locally for construction. Mature trees can reach 40 cm in diameter with a clean straight bole. The woody material obtained from pollarding is, apparently, little used (Hughes, 1990). Mature trees are left for shading coffee after forest clearance has taken place. Like *G. sepium*, and as its common name suggests, *G. brenningii* is also utilized in the production of rodent poison.

Botanical description: *Gliricidia brenningii* is a small to medium-sized, commonly single-stemmed tree ranging from 3 to 18 m tall. The bark is thornless, yellowish-brown to whitish in colour and in older trees is slightly fissured near the base. Leaves are alternate and pinnate with between 33 and 41 leaflets per leaf which are thin and oblong, with a rounded apex (Figure 2.1**A**). When mature, the upper surface of the leaflet is smooth and hairless to slightly hairy with no tanniniferous deposits. The lower surface can be covered with straight stiff or silky hairs and is usually marked by a few purplish tanniniferous spots deposited in small patches in the centre of the leaflet. Small appendages can be found at the base of the leaflet stalk: these are very small (0-1 mm in length), and therefore not readily noticed, but are not found in the other two species (Figure 2.1**B**). The white flowers are arranged in conspicuously long, pendulous inflorescences (Figure 2.1**C** and Plate 2A), remaining the same colour with age. The calyx is distinctly tapered at the base and is usually smooth and hairless (Figure 2.1**D**). At the base of the staminal tube there is a nectar-bearing disk which only occurs in *G. brenningii* (Figure 2.1**E**). The pods are explosively dehiscent and are longer and broader than in the other two species (Figure 2.1**F**). They are strongly laterally compressed, dark brown in colour, smooth and hairless, and contain 4-15 seeds per pod.

The main flowering season is from January to April, becoming sporadic later. Woody fruits persist from May to October, but probably ripen during only the latter two of these months (Hughes, pers. comm.)[1].

Natural distribution and habitat: The native distribution of *G. brenningii* is tentatively considered to be Ecuador and adjacent northern Peru, even though nearly all collections come from cultivated plants, mainly from living fences (Map 1). Specimens indicated to be from natural habitats are very few and are generally from secondary vegetation along streams. Habitats include lowland seasonally deciduous and evergreen forests and thorn scrub, and *G. brenningii* occurs commonly as part of living fence systems or is cultivated as shade over coffee crops. It tends to be concentrated along the Pacific slope of southern-central Ecuador and the immediately adjacent northern fringes of Peru. Elevation ranges from sea level to 820 m. Co-dominant plant genera often include *Guazuma*, *Inga*, and *Mutingia*.

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[1] *C.E.Hughes, Oxford Forestry Institute, Dept. of Plant Sciences, University of Oxford, Oxford, UK.*

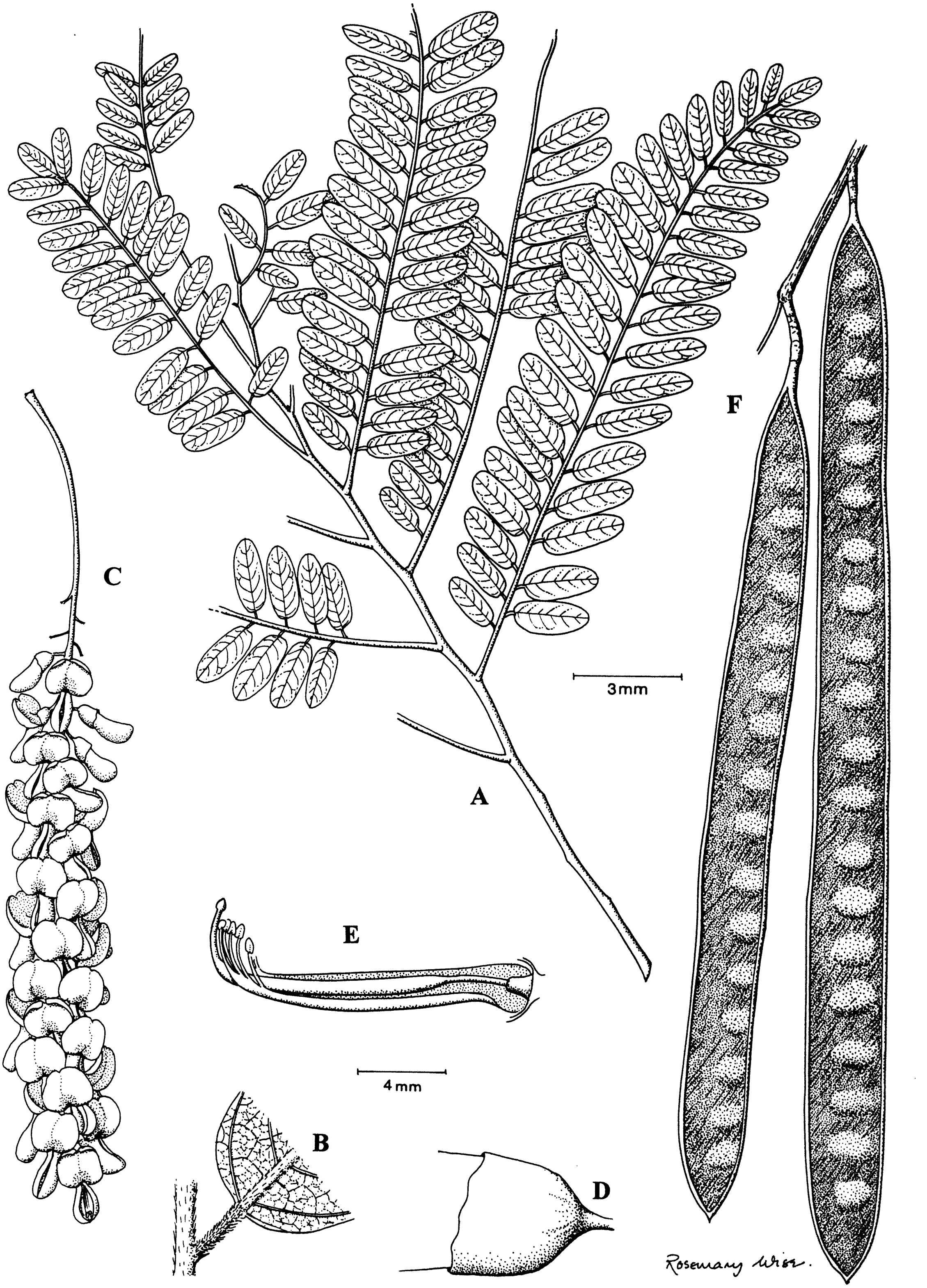
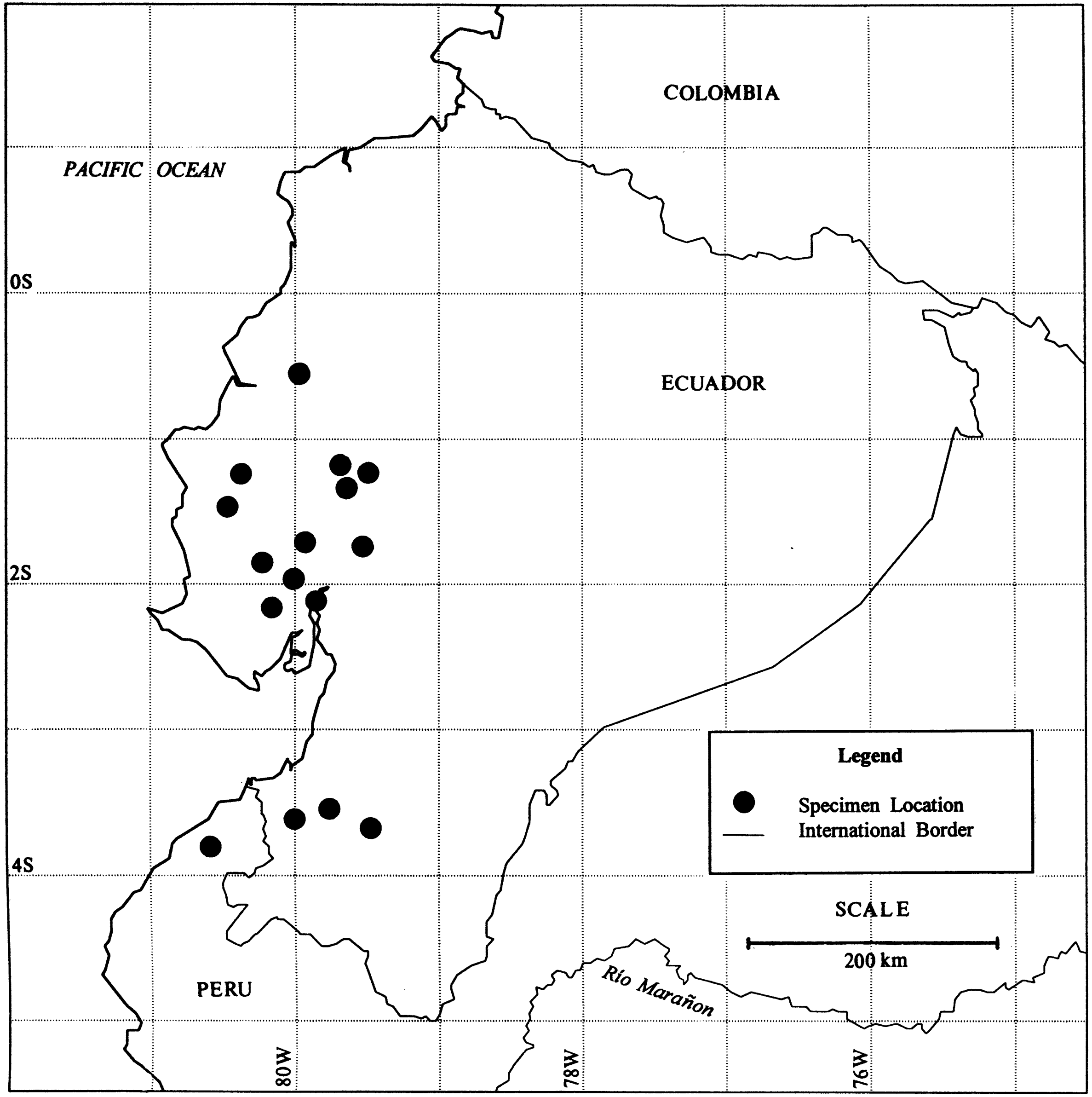


Figure 2.1 *Gliricidia brenningii.* **A**-alternate, pinnate leaves showing rounded apex and small size of leaflets; **B**-leaflet stalks showing small appendages at the stalk base, and stalk hairs; **C**-long, pendulous inflorescence; **D**-smooth hairless calyx; **E**-staminal tube showing nectar-bearing disk at the base; **F**-long, broad pods

Map 1 Specimen locations of *Gliricidia brenningii* (after Lavin and Sousa, 1995)



Gliricidia maculata (H. B. K.) Steudel, Nom. Bot., ed. 2, 1:688. 1840.

Synonyms: *Robinia maculata* H. B. K.
Lonchocarpus maculatus (H. B. K.) DC.
Gliricidia sepium (Jacquin) Steudel forma *maculata* (H. B. K.) Urban

Common names: Cocoite blanco (Campeche, Mexico), xakyaab (Quintana Roo and Yucatan, Mexico)

Main attributes: *Gliricidia maculata* appears to be very rarely cultivated within its native range. Where it is cultivated, it is as live fencing or in some instances as an ornamental. Evidence to date suggests that *G. maculata* cannot compete with *G. sepium* in terms of wood biomass production (Stewart and Simons, 1995) and no work has been carried out regarding its potential as fodder. As far as is known, *G. maculata* has not been cultivated as an exotic except where it has been introduced very recently.

Botanical description: *Gliricidia maculata* is a small to medium-sized tree which can have a shrubby appearance, ranging in height from 2 to 13 m. The bark is light brown to grey and occasionally, on older trees, it can be slightly fissured near the base. Leaves are alternate and pinnate with 7-15 (-19) leaflets per leaf which are leathery in texture, oblong to broadly oblong in shape and rounded at the apex, though sometimes ending in a point (Figure 2.2**A**). At maturity, the upper surfaces of the leaflets are smooth and hairless, usually with no tanniniferous patches, whilst the lower surfaces can have a covering of bristles with purplish tanniniferous patches evenly scattered over the leaflet lamina (Figure 2.2**B**). The flowers are arranged in loose pendulous inflorescences (Figure 2.3**C** and Plate 2C) and are usually white in colour although occasionally pinkish, changing to a mottled whitish-brown or faint purple colour with age. The stalks of the individual flowers have very bristly to silky hairs covering them and often have a grainy appearance and texture (not shown). The calyx has a distinct taper at the base and can be covered in bristly or silky hair with a grainy texture (Figure 2.2**D**). Pods are explosively dehiscent but are shorter and narrower than in *G. brenningii* or *G.sepium*, and strongly laterally compressed (Figure 2.2**F**). They are a light to dark reddish-brown colour becoming paler yellow-brown with age, and contain 3-8 seeds per pod.

Flowering occurs primarily from November to March and occasionally into April, which is similar to the closely-related *G. sepium.* Mature fruits may persist throughout much of the year, from February to November.

Natural distribution and habitat: *Gliricidia maculata* is native to Mexico, primarily in the Yucatan Peninsula, in Campeche, Yucatan and Quintana Roo, but extends sporadically south into Chiapas, and also into Belize and adjacent Guatemala (Petén) (Map 2). Elevation ranges from sea level to 400 m (950 m in Chiapas). Habitats include seasonally deciduous forests and thorn scrub and occasionally lowland rain forest (*e.g.*, Laguna Miramar, Chiapas). *Gliricidia maculata* occurs at a very low density, as isolated individuals. The co-dominant woody plants include species of *Bursera*, *Caesalpinia*, *Cedrela*, *Chloroleucon*, *Crescentia*, *Cordia*, *Ficus*, *Guazuma*, *Haematoxylum*, *Heliocarpus*, *Ipomoea*, *Karwinskia*, *Leucaena*, *Lysiloma*, *Manilkara*, *Mimosa*, *Pachira*, *Piscidia*, *Senna*, *Tabebuia*, and *Talisia*.

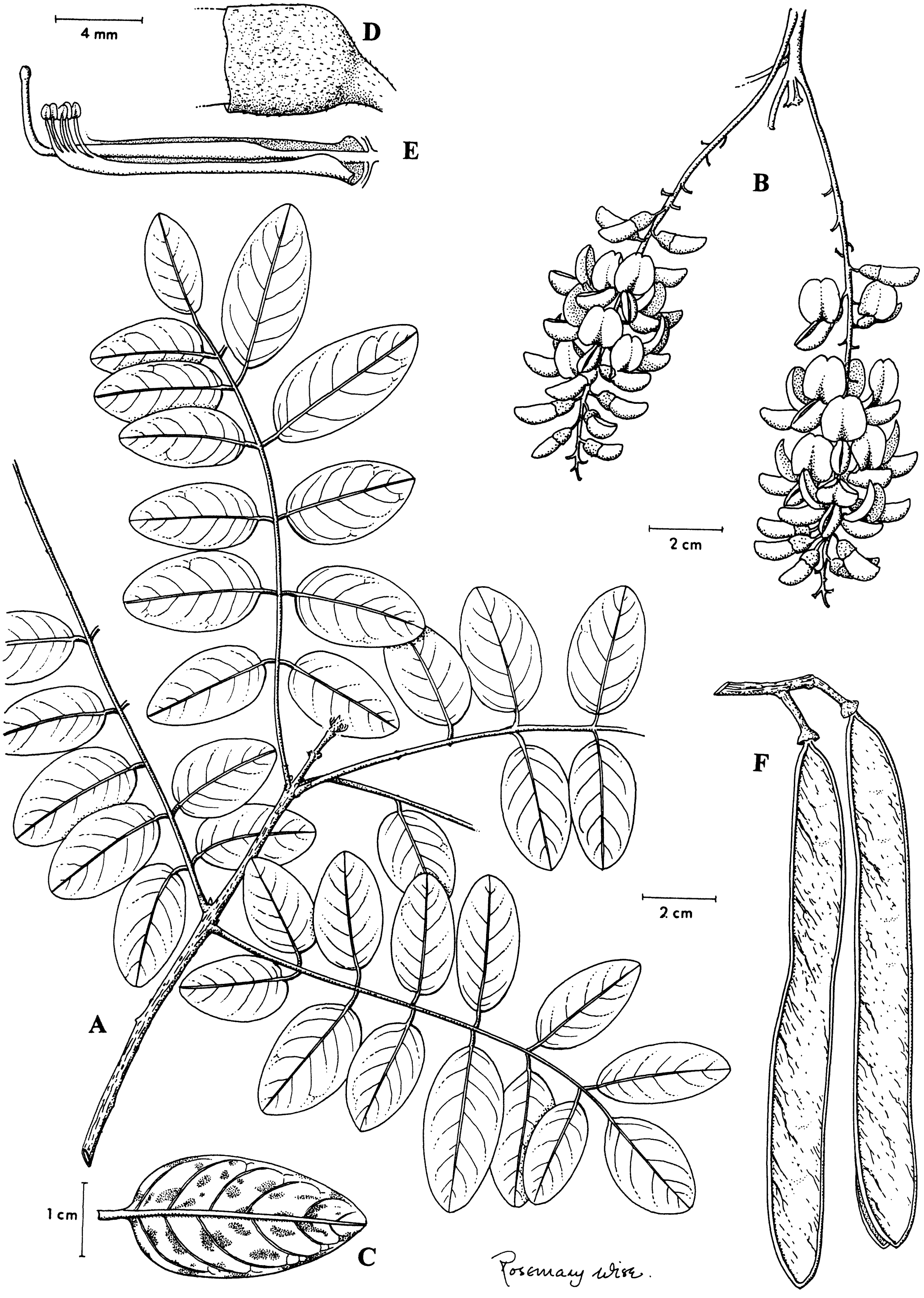
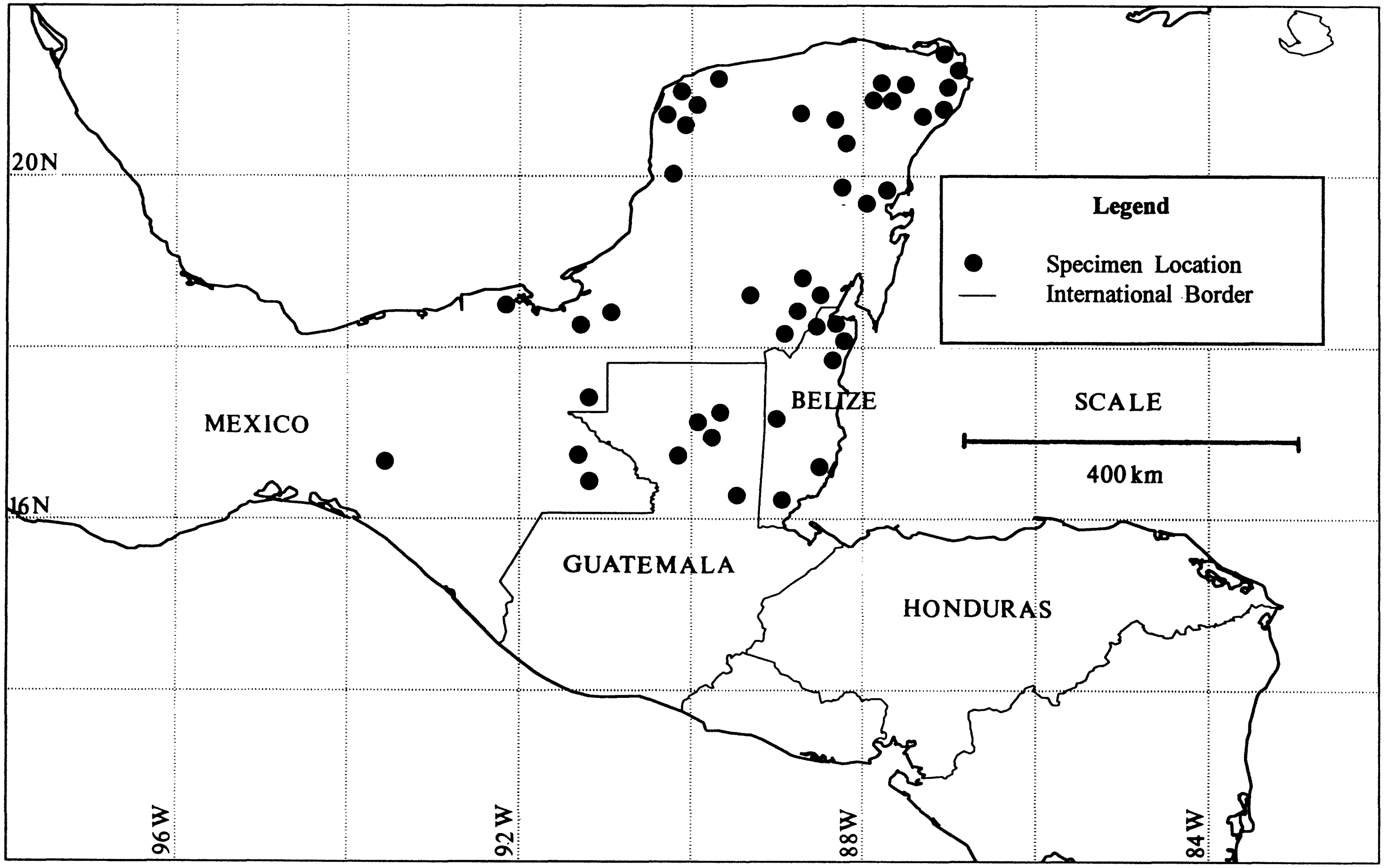


Figure 2.2 *Gliricidia maculata*. **A**-alternate pinnate leaves showing the broadly oblong shape of the leaflets and rounded apices; **B**-detail of the lower surface of the leaflet showing tanniniferous patches; **C**-loose, pendulous inflorescence; **D**-calyx showing distinctive hairs and grainy appearance; **E**-staminal tube; **F**-narrow pods

Map 2 Specimen locations of *Gliricidia maculata* (after Lavin and Sousa, 1995)



Gliricidia sepium (Jacquin) Steudel, Nom. Bot. ed. 2, 1: 688. 1841.

Main attributes are not presented here because they are discussed in Chapter 4. Distribution and habitat are described in Section 3.1.

Synonyms: *Robinia sepium* Jacquin, *Lonchocarpus sepium* (Jacquin) DC., *Robinia rosea* Mill., *Lonchocarpus roseus* (Mill.) DC., *Robinia variegata* Schlechtend., *Millettia luzonensis* A. Gray, *Gliricidia maculata* var. *multijuga* M. Micheli, *Gliricidia lambii* Fernald.

Common names: Madre de cacao, madrecacao, madreado, mata-ratón (Mexico, Guatemala), cacahuananche (Guatemala), madero negro (Nicaragua), cocoite (Mexico), balo (Panama), quick stick (Jamaica).

Botanical description: *Gliricidia sepium* is a small to medium-sized tree ranging in height from 2 to 12 m. The bark ranges from greyish-brown to whitish in colour and can be deeply fissured at the base of older stems. Leaves are alternate and pinnate with (7-) 13-21 (-25) leaflets per leaf which are papery in texture and oblong in shape with a distinctive pointed tip (Figure 2.3**A**). Leaflet size increases towards the distal end of the leaf. At maturity the upper surface of the leaflets ranges from smooth and hairless to bristly and usually has no tanniniferous patches. The lower surface can also be smooth and hairless or bristly, and commonly has purplish tanniniferous patches concentrated toward the centre of the leaflet lamina. The flowers are arranged on conspicuosly short upward-curving to erect inflorescences which are usually pink in colour, fading to a whitish-brown or faint purple with age (Figure 2.3**B** and Plate 2D). The individual flower stalks and calyces are usually hairless (Figure 2.3**C**). The pods are explosively dehiscent, strongly laterally compressed and pale green or reddish-green when unripe (Plate 2B), turning straw yellow-brown when fully ripe (Figure 2.3**E**). The pods contain 3 to 10 seeds.

In native populations (Pacific coastal Mexico and Central America: Map 3), the main flowering season is from late November to the end of March. In parts of the naturalized range, and where *G. sepium* is an exotic, if there is no pronounced dry season flowering can occur at any time of the year and does not always lead to pod set (see Section 3.1).

A formal botanical description for *G. sepium* is given in the box on page 13.

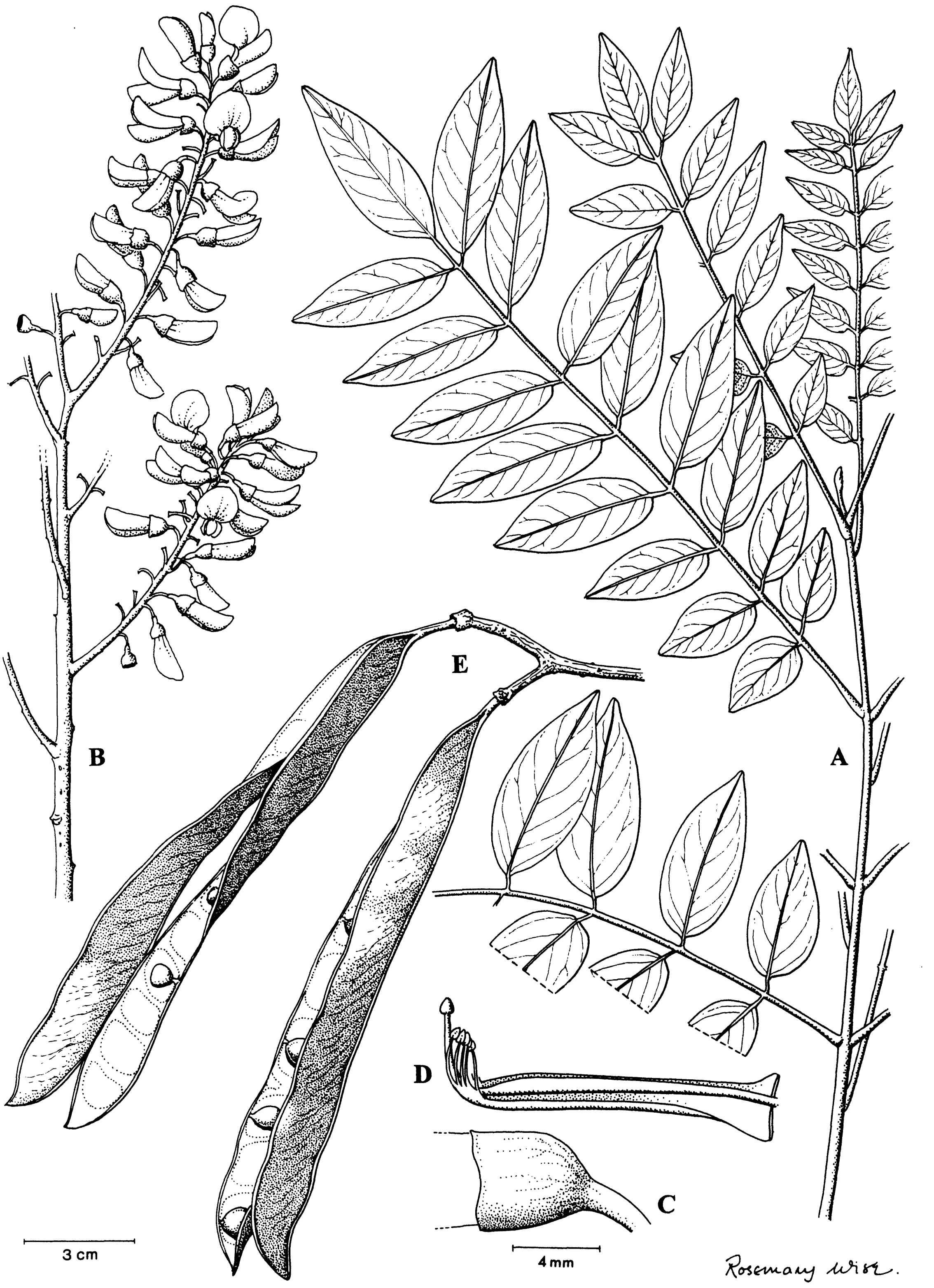
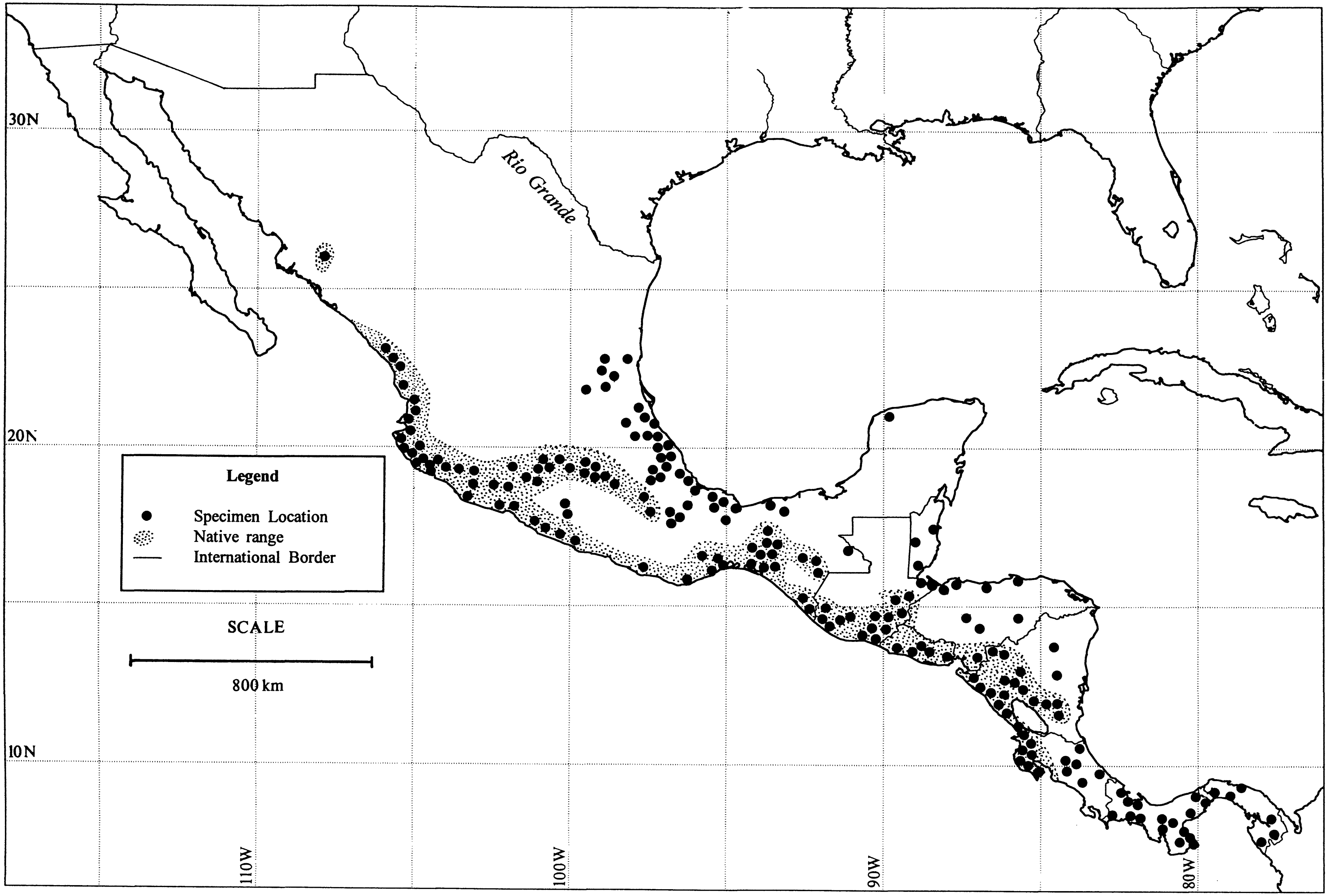


Figure 2.3. *Gliricidia sepium.* **A**-alternate, pinnate leaves showing distinctive pointed apices of the leaflets and the increase in leaflet size towards the distal end; **B**-conspicuously short and upright inflorescence; **C**-smooth and hairless calyx; **D**-staminal tube; **E**-pods

Map 3 Specimen locations of *Gliricidia sepium* and its tentative native range (after Hughes, 1987; Lavin and Sousa, 1995)



Formal botanical description of *Gliricidia sepium.*

Single- to multi-stemmed trees, rarely shrubby, 2-15 m tall. Stems erect, 5-30 cm diameter at base, with or without major branches from near base; bark greyish-brown to whitish, minutely to deeply furrowed toward the base on older stems; branches glabrate to sparsely or densely sericeous with mostly whitish, sometimes brownish, trichomes especially at the distal branch ends. Leaves alternate to occasionally subopposite, larger leaves (15-) 19-30 (-35) cm long; leaflets generally opposite, occasionally alternate, (7-) 13-21 (-25) per leaf, thin, slightly to conspicuously distally accrescent, narrowly elliptic to elliptic, rarely broadly elliptic, acuminate to sometimes cuspidate, rarely rounded, the larger 44-83 mm long, (17-) 21-42 (-48) mm wide, (at maturity) upper surface glabrous to strigose, usually without dark tanniniferous patches, the lower surface glabrate to strigose, usually with purplish tanniniferous patches concentrated toward the centre of the leaflet lamina or scattered evenly throughout; stipules triangular, 0.5-2.0 mm long, readily caducous; stipels absent. Inflorescence rachises 2.5-15.0 (-17) cm long, ascending to lax, subsessile, in the axis of coeval leaves or from leafless nodes of older stems, with mostly a synchronous maturation of flowers on a single rachis, the stipe 1-8 mm long, glabrate to sparsely strigose, rarely tomentose or granuliferous, with 30-100 nodes and 0.1-2.0 (-4) mm between nodes. Flowers ebracteolate, with a well-developed hypanthium; floral bracts 0.8-1.2 (-2.0) mm long, triangular, rarely ligulate, tomentose usually over the entire abaxial surface, or at least on the distal portion, generally persistent; pedicels 5-11 (-15) mm long at anthesis, glabrous to sometimes sparsely strigose, rarely granuliferous. Calyx campanulate, distinctly attenuate at base for (1-) 2-4 mm, glabrous to sparsely strigose, rarely granuliferous, tube (note that this should include the long-attenuate base) (5.5-) 6-9 mm long, with the inconspicuous five lobes 0.1-0.2 mm long, more-or-less evenly spaced. Standard light-pink to pinkish, rarely entirely whitish, ageing mostly a whitish discoloured brown or faint purple, nectar guide a broad light to deep yellowish patch, blade reflexed about 180° at anthesis, 15-23 mm long, 15-23 mm wide, orbicular, emarginate, subequal in length to keel petals, with two prominent callosities on either side of the midrib in the region of the nectar guide, claw abruptly contracted from the blade; wings 15-23 mm long, perpendicular to the plane of the keel, usually pinkish, rarely entirely whitish; keel petals valvately connate distally to nearly the tip, 15-22 mm long, adnate for much of the distal end, straight, with a blunt tip, usually pinkish, rarely entirely whitish. Staminal tube diadelphous, with basal fenestrae; anthers included in the keel tip, basally attached to the filaments, the broad connective reddish-brown; Pollen spheroidal, tricolate, mesocolpium rugulate-perforate, polar regions smooth. Ovary stipitate, the stipe nearly as long as the calyx tube, glabrous, eglandular with 7-12 ovules, not borne from a gynoecial disk. Style glabrous, the base thin and imperceptibly confluent with the distal portion of the ovary, not becoming displaced to the carinal side during fruit maturation, 4-5 mm long at anthesis; stigma ciliate, terminal on a distally tapered style. Legumes stipitate, glabrous, eglandular, inner epidermis of the endocarp of adjacent valves spongy and abutting between seeds, forming irregular seed compartments, the valves woody at maturity, elastically and explosively dehiscent, the dorsal and ventral margins generally parallel in fruit, 10-17 (-23) cm long, 14-22 mm wide, strongly laterally compressed, light to dark reddish-brown; seeds transversely oriented, lenticular, not constricted in the middle, accumulating canavanine, 3-10 per pod, lenticular, 8.5-11.5 mm diameter, uniformly light brown, aging dark brown, hilum apical and attached to a very short funiculus, testa firmly adherent. Seedlings with foliar epigeal cotyledons, 1- several eophylls alternate, 1 - foliolate, metaphylls and mature leaves 5 - many foliate, alternate. Base chromosome number $\underline{x}$ = 10, 11.

Source: Lavin and Sousa, 1995.

Plate 2

A - Long, pendulous inflorescence of *Gliricidia brenningii*

B - Unripe pods of *Gliricidia sepium* showing red-green colour

C - Loose, pendulous inflorescence of *Gliricidia maculata*

D - Short, upward-curving inflorescence of *Gliricidia sepium*

E - Flowers of *G. maculata* (L), *G. maculata* x *G. sepium* hybrid (C) and *G. sepium* (R)

2.3 Differences between *G. maculata* and *G. sepium*

During the 1980s, the name *G. maculata* was used often when referring to *G. sepium* (Whiteman *et al.*, 1986, Reynolds, 1988) because there was debate concerning the recognition of *G. maculata* as a separate species and because the two species often were considered to be conspecific. Hughes (1987) was the first to reinstate *G. maculata* as a species distinct from *G. sepium*. Subsequent work by Lavin *et al.* (1991) and Chamberlain and Galwey (1993) confirmed the distinction of *G. maculata* as a species cryptically distinct from *G. sepium*. Furthermore, this distinction is in agreement with molecular studies of population variation (Section 7.3) and chloroplast DNA restriction site analysis (Lavin *et al.*, 1991). Some confusion, however, has persisted, particularly in the forestry and agronomic literature where the two names are often used synonymously (Stewart and Simons, 1995). Given that *G. maculata* has not been cultivated outside its small native range, it is certain that the *G. maculata* discussed in most of this literature is in fact *G. sepium*.

The differences between *G. maculata* and *G. sepium* are many, though often subtle (Lavin and Sousa, 1995). The distribution of *G. maculata* is centred in the Yucatan Peninsula, including Belize and northern Guatemala; it also occurs occasionally southward into Chiapas, Mexico (Map 2). Unlike *G. sepium*, populations of *G. maculata* frequently comprise scattered individuals, often in undisturbed forests. Like *G. sepium*, *G. maculata* is brought into cultivation, but only in this region, where it is used for living fences, and in construction or occasionally as ornamentals. Notably, there is no evidence to suggest use of the leaves of this species for livestock fodder, and many label data on herbarium specimens state that the leaves are poisonous. No specimen assigned to *G. maculata* is known to have been brought into cultivation elsewhere in Central America or Mexico, let alone in the Caribbean, South America, Africa or Asia. In contrast, the native range of *G. sepium* is concentrated in Pacific coastal Mexico and Central America and populations usually comprise dense stands in disturbed areas, such as gulleys, roadsides, and steep hillsides; most commonly, *G. sepium* is found in, or escaped from, cultivation. *Gliricidia sepium*, unlike *G. maculata*, has been brought into cultivation in the Antilles, South America and, more recently, pantropically.

There are at least ten diagnostic characteristics which, when used in combination, can readily distinguish *G. sepium* from *G. maculata*. According to Lavin and Sousa (1995), a combination of any four of these characteristics is sufficient, as when determining the identity of a single flowering or fruiting herbarium specimen. These characteristics are listed in Table 2.1.

At the least, if a given specimen of *Gliricidia* consists only of flowering material (*i.e.* without leaves) and the flowers are pinkish, then *G. maculata* can be distinguished by its short calyx tube, usually less than 7 mm, that has a tapering calyx base covered with bristle-like or soft silky hairs. This tapering calyx base is usually less than 2 mm long, and all flowers are borne along a raceme rachis that is commonly more than 10 cm long.

G. sepium has been moved around so much by man that hybridization with *G. maculata* is likely (Plate 2E). This has been the subject of molecular studies, the results of which are presented and discussed further in Section 7.3.

Table 2.1 Diagnostic characteristics used to distinguish *G. sepium* from *G. maculata* (derived from Lavin and Sousa, 1995)

Diagnostic characteristic	***G. sepium***	***G. maculata***
1. Leaflet apices of mature leaves	When leaves are fully flushed and fruits are beginning to mature, mature leaflets have tapering, pointed apices (Figure 2.3**A**).	Nearly all mature leaflet specimens have rounded apices (Figure 2.2**A**).
2. Leaflet texture	Leaflets are uniformly thin. The upper surface of the leaflets is greenish and the finest veins here are very distinct. In dried herbarium specimens the upper surface of the leaflets is often cracked along these fine veins.	Leaflets are uniformly leathery. The upper surface of the leaflets is greyish-green and very rough. The fine veins are not distinct, nor do they show up as cracks on the upper surfaces of dried herbarium specimens.
3. Number of leaflets per leaf[1]	Leaflet number per leaf ranges from between 5 to 25.	Leaflet number per leaf ranges from 7 to 19.
4. Size of leaflets along the leaf rachis[2]	The leaflets nearly always get larger towards the distal end of the leaf (Figure 2.3**A**).	The leaflets rarely get larger towards the distal end of the leaf (Figure 2.2**A**).
5. Petal colour[3]	Nearly all specimens have flowers with pinkish petals. In dried herbarium specimens the back of the standard petals tends to be uniformly light to reddish-brown and mottling, if present, tends to be inconspicuous.	Nearly all specimens have flowers with whitish petals. In dried herbarium specimens the back of the standard petals tends to be distinctly finely mottled brownish-red on a brownish-white background.
6. Hairiness of the flower stalk and calyx	The flower stalks (not shown) and calyces are almost hairless (Figure 2.3**C**). The few bristle-like hairs that do occur are at a very low density (0-3 per 0.25mm^2). The appearance of the flower stalks is smooth.	The density of bristle-like hairs on the flower stalks (not shown) and calyces is much higher (9-48 per 0.25mm^2) (Figure 2.2**D**). The appearance of the flower stalks can be grainy.
7. Length of inflorescence rachis (stalk)[4]	Inflorescence rachises tend to be quite short (2.5-16.5 cm long). A more qualitative trait is the direction in which the inflorescence hangs. In *G. sepium* it grows in a fairly upright and erect, curving manner (Figure 2.3**B**).	Inflorescence rachises tend to be longer (5.0-23.0 cm long). In *G. maculata* the inflorescence grows almost vertically downwards (Figure 2.2**C**).
8. Length of the calyx tube[5]	The length of the calyx tube ranges from 5.5 to 9.0 mm. The calyx tube has a more pronouncedly tapered base (1-) 2-4 mm long.	The length of the calyx tube ranges from 5.0 to 7.5 mm. The calyx tube has a less tapered base, 0.5-2.0 mm long.
9. Mature pod	The mature pod is generally broader (14-22 mm wide) (Figure 2.3**E**).	The mature pod is generally narrower (13-16 (-21) mm wide) (Figure 2.2**F**).
10. Seeds	Mature seed is generally larger (8.5-11.5 mm in diameter).	Mature seed is generally smaller (5.5-9.0 mm in diameter).

[1] Leaflet number: though the difference between the means is significant (Lavin and Sousa, 1995), this characteristic, by itself, would be useful only in assigning a specimen with 21 - 25 leaflets per leaf to *G. sepium*.

[2] Size of leaflets along the leaf rachis: as a measure of this the terminal leaflet is nearly always longer than the most adjacent lateral leaflet in *G. sepium*, whereas in *G. maculata* it is shorter (Lavin and Sousa, 1995).

[3] Petal colour: flowers of *G. maculata* are generally white or very pale pink, while those of *G. sepium* are usually mid to strong pinkish (Plate 2E). This characteristic is not completely reliable, for example where the species co-occur, such as at Petén in Guatemala. Here, *G. maculata* is occasionally found to have pink flowers and *G. sepium* whitish flowers.

[4] Inflorescence length: though the difference between the means is statistically significant (Lavin and Sousa, 1995), overlap is often too great to be useful in species determination.

[5] Length of calyx tube: though the difference between the means is significant (Lavin and Sousa, 1995), only lengths greater than 7.5 mm can be used confidently to place a specimen into *G. sepium*.

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3 Ecology and Reproductive Biology

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3.1 Distribution and ecology

Distribution in tropical America

Much of the region of tropical America in which *G. sepium* is now distributed has undergone such a high degree of human disturbance that it is extremely difficult to do more than postulate its true native distribution. When the Spanish colonists arrived in Mexico and Central America they observed indigenous peoples using and cultivating *G. sepium* for a number of purposes, including shade for cocoa trees. Indeed, several of the vernacular names derive from these observations: *xakyaab* (Maya), *cacahuananche* (Nahuatl) and *madre de cacao* (Spanish), all meaning "mother of cacao" (Hughes, 1987). The plethora of indigenous names for the species testifies to its local importance before European colonization. This, combined with the widespread movement of peoples, the very widespread present-day cultivation of *G. sepium*, and its ability to invade and colonize secondary vegetation following disturbance, has probably caused substantial movement of germplasm throughout tropical America. It is therefore reasonable to assume that the original distribution of *G. sepium* was much smaller in area than its present distribution suggests (Map 3 in Section 2.2). On the other hand, the seismic upheavals which have characterized the geology of Meso-America would also have created favourable conditions for a pioneer tree such as *G. sepium*, thus making a fairly broad distribution possible. Given these potential influences, there are likely to be considerable differences between the present day distribution and the immediate pre-colonial distribution, and between the pre-colonial and pre-human distributions. Clearly, the delimitation of the native range of *G. sepium* is open to conjecture.

In present-day tropical America, *G. sepium* is distributed in Mexico, throughout Central America and many of the Caribbean Islands, and much of northern South America; recently it has also been introduced further south. Standley and Steyermark (1946) placed the native distribution from Mexico to the Guyanas. McVaugh (1987) extended this distribution to include the West Indies. There is, however, circumstantial evidence to suggest that *G. sepium*'s native range is limited to the seasonally dry deciduous forest of the Pacific coastal lowlands and some dry inland valleys of Central America and Mexico (Janzen, 1986; Hughes, 1987; and Map 3 in Section 2.2). Janzen (1986) suggests it occurs from middle to late succession throughout very dry deciduous forest on dry lowland hills in Guanacaste, Costa Rica; however, its intolerance of heavy shade suggests a species of early ecological succession, as does its ability to colonize disturbed open ground.

The ecology of *G. sepium*, which flowers in the dry season once it has shed its leaves, supports further the hypothesis that it is native to the seasonally dry Pacific coast. The paucity of seed production in more humid environments, such as Campeche in Mexico and Atlántida in northern Honduras, would suggest that it is not native there. In these more humid regions, *G. sepium* is usually cultivated by means of cuttings. In the dry regions of northern South America, where *G. sepium* is also found, disturbance has been such that it is impossible to determine whether these populations are native or naturalized although Hughes (pers. comm.)[1] suggests that it is not native, commenting that it is rarely to be found growing outside cultivation. If it is not native, the introduction must have taken place some time ago since Jacquin observed the tree being used for hedges around Cartagena, Colombia in the mid-eighteenth century (McVaugh, 1987), and gave the tree the epithet *sepium*: "of hedges".

Molecular studies using isozymes (Chamberlain, 1993) have identified some populations which are not in genetic equilibrium and therefore presumed to be derived from multiple introductions. These studies also suggest a uniformity within the Panama population of *G. sepium*, implying that this population is not part of the native range. This is discussed in greater detail in Chapter 7.

Those areas in tropical America where *G. sepium* is found commonly but presumed not to be native are usually described as forming part of the naturalized distribution. A naturalized population is taken to mean one which has been introduced but is able to reproduce itself. Given that some populations within tropical America, such as those in Tabasco and Campeche in Mexico, are unable to reproduce sexually, the regions which fall outside Hughes' tentative native range should be described as areas where *G. sepium* is cultivated and in some cases naturalized (Hughes, 1987).

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Exotic distribution

Gliricidia sepium now has a pantropical distribution, resulting from waves of introductions over several centuries. The areas where *G. sepium* is found outside tropical America define the exotic distribution of the species.

The first wave of introductions outside tropical America can be traced to the early period of Spanish colonization. Wiersum and Dirdjosoemarto (1987) cite the Spanish as taking it to the Philippines in the early 1600s. The Spaniards are also believed to have introduced *G. sepium* into the Caribbean for the purpose of shading cocoa and later, coffee (Ford, 1987). In a later wave of introductions, it was introduced to Sri Lanka in the 1880s as shade in tea plantations. This material is believed to have come from the island of Trinidad where it had also been introduced, again probably by the Spanish. The Sri Lanka introduction is believed to have been made with seed from only one tree (Hughes, 1987). From Sri Lanka, it spread to India, Indonesia, Malaysia and Thailand. A third wave of introductions to West Africa and Uganda occurred in the early part of the twentieth century, as shade for plantation crops (Tothill, 1940). Lavin *et al.* (1991) were able to trace the broad origin of exotic populations through chloroplast DNA analysis. Populations from Cuba, Dominican Republic, Puerto Rico, Colombia, Venezuela and Nigeria were all shown to originate from Central America (as distinct from Mexico), whereas land race material from Thailand contained chloroplast genomes from both Central America and Mexico.

Much of the material introduced into exotic locations during the colonial era is still of unknown origin, however, its spread around the world having taken place in an entirely unplanned and undocumented way. It is also likely that these introductions have been from a narrow genetic base which has probably led to inbreeding. This is supported by the findings of several performance trials which tested local land races from Indonesia, Sri Lanka, the Philippines and Nigeria against seed collected in tropical America; local land races were consistently outperformed (*e.g.* Sumberg, 1985b; Bumatay *et al.*, 1987).

The most recent introductions have taken place in the last 15 to 20 years as interest in the species as a multipurpose, nitrogen-fixing tree has developed. Initiatives in the 1980s resulted in the collection of *G. sepium* seed from tropical America and new introductions to 55 countries throughout the tropics have since been made, resulting in a very high demand for seed (Pottinger, 1992).[2]

In some parts of the exotic distribution *G. sepium* has become naturalized, reproducing itself without the need for further plantings. This is the case in parts of southern India and in the area around Durban in South Africa. In many areas, however, climatic and biological conditions are such that trees are not able to reproduce sexually and therefore have to be planted or cultivated from cuttings. Seibert (1987) reports from Kalimantan in Indonesia that there is a lack of flowering, which is probably due to the absence of a distinct dry season (Hughes, 1987). In other areas, such as parts of Nigeria, flowering occurs but there is little or no pod development (Sumberg, 1985a). Hughes (1987) suggested that this could be due to an absence of suitable pollinators. Flowering and pod set are discussed in more detail in Section 3.2.

Ecology

Being an aggressive pioneer species, *G. sepium* can be found in a wide range of habitats, with soil types ranging from pure sand (Plate 3B) to deep alluvial lake bed deposits, with rainfall from as little as 600 mm to as much as 3500 mm, and at elevations from sea level to 1200 m above sea level. The human destruction of much of the dry forest of tropical America (which now constitutes less than 2% of its original area) has resulted in the creation of substantial areas suitable for the colonization and natural regeneration of *G. sepium* (Plate 3A). Furthermore, the geological history of Meso-America, with volcanic eruptions and shifting land masses, provided new niches for *G. sepium* to colonize and flourish. This can be seen on Volcán Masaya in Nicaragua where various eruptions during this century, the most recent in the 1970s, have produced barren, ash-laden or laval habitats which have been quickly colonized by *G. sepium*.

Fire is a common feature of land preparation in many parts of the seasonally dry regions of Central America and Mexico. Although the ecology of *G. sepium* does not require fire, it is tolerant of it and trees resprout quickly with the onset of the rains in the natural distribution (late April/early May). Hughes (1987) observed that *G. sepium* readily colonizes fields that are left fallow after slash and burn agriculture. The high incidence of deliberate burning may be responsible for the frequent occurrence of *G. sepium* in secondary vegetation and agricultural fallows. Fire is not generally a feature of the Meso-American dry forest ecosystem, and many other species are damaged or killed by such frequent burning.

Although Holm *et al.* (1979) describe *G. sepium* as a severe weed in Jamaica, Hughes and Styles (1984) consider *G. sepium* to have only a slight weediness hazard. It has not been reported as a weed elsewhere, perhaps because it is coppiced regularly and not permitted to set seed. Reproductive constraints in some exotic environments, possibly due to a lack of pollinators (see

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[2] *Collections were made during the 1980s by CATIE, NFTA and OFI.*

above) will also tend to reduce the weediness hazard associated with introductions of *G. sepium*.

Habitat

Soil type

Gliricidia sepium is found on a great number of different soil types. In much of its putative native distribution, soils of volcanic origin predominate. These soils are usually superficial, often highly eroded or compacted as a result of slash and burn agriculture, and are generally sandy and stony making them freely drained. For the most part these soils are acidic (pH 4.5-6.2) although in some areas, where limestone is the parent material, they are slightly alkaline.

Stands of *G. sepium* are also found on deep black vertisols (of the black-cotton type), usually in valley bottoms or the sites of previous lakes, such as in the region of Laguna Tecomapa, Matagalpa, Nicaragua. These soils have a heavy clay content and are prone to shrinking and cracking in the dry season (Plate 3C). This does not however appear to impede the growth of *G. sepium*.

Numerous coastal populations of *G. sepium* exist along the Pacific coast of Meso-America including Playa Tamarindo, Guanacaste in Costa Rica, Monterrico in Guatemala and several sites in Mexico. These sites can be very sandy and saline, with trees growing within a metre of the high-tide mark (Plate 3B). The coastal populations typically are shorter and more multi-stemmed than inland populations, and also tolerate up to 2-3 m of stem being buried by shifting sand.

The ability of *G. sepium* to grow on such a wide variety of soil types has meant that outside its native range much attention has been focused upon its use on difficult sites. Numerous authors attest to its ability to grow on disturbed and denuded sites (Perino, 1979; Glover, 1986; Hughes, 1987) and on steep slopes. Perino (1979) established *G. sepium* successfully on 40% slopes with less than 4% organic matter content and virtually no nitrogen. A trial in Karnataka, India reported by Hebbara *et al.* (1992) demonstrated that *G. sepium* can perform well on marginally saline vertisols. Maiti *et al.* (1991) however, report poor performance on saline coastal wasteland. It is *G. sepium*'s apparent ability to grow on very difficult sites that has resulted in its use in the reclamation of badly disturbed and contaminated industrial sites. Singh *et al.* (1992) describe the reclamation of fly-ash slurry pits in Madhya Pradesh, India with a variety of tree species, of which *G. sepium* was the best performer. It is also used in the reclamation of open-cast mining sites (Plate 3F).

Although tolerant of a wide variety of soil types and low nutrient composition, *G. sepium* will not tolerate very acid soils combined with high aluminum saturation. Very poor performance of *G. sepium* has also been reported on highly compacted cattle lands in Central America (CATIE, 1986; 1991). Although many authors (*e.g.* Chadokhar, 1982; Glover, 1986; Szott *et al.*, 1991; Hairiah *et al.*, 1992; Escalante, 1995) have observed *G. sepium* growing well on acidic soils where *Leucaena leucocephala* cannot, further studies have shown that *G. sepium*'s tolerance of acidity is limited. Powell (1995) suggests that it can tolerate soils of pH as low as 4.2-4.5. In an experiment in Cameroon, Duguma (1995) found that the growth of both *L. leucocephala* and *G. sepium* was very poor on acidic soils with a pH of 3.75. Argel and Maass (1995) also observed poor performance on acidic soils, particularly where they contained high concentrations of aluminum. Similarly Dierolf and Yost (1989) report poor survival on Indonesian soils with a high aluminum saturation. MacDicken (1994) and Powell (1995), however, suggest that *G. sepium* can tolerate aluminum saturation levels of over 70%. Under strongly acid conditions (less than pH 4.2) *Rhizobium* cannot function and nitrogen fixation does not occur (Sanginga *et al.* 1995). Maclean *et al.*, (1992) found that biomass production could be improved on acid soils in the Philippines by adding lime. In an experiment on acid upland sites, 6 t ha^{-1} of lime was broadcast and this more than doubled biomass production.

Topography, altitude and climate

The topography of Meso-America varies greatly over relatively small distances. The ability of *G. sepium* to grow in the myriad of micro-habitats created by such topography has contributed to its evolution and population differentiation. *Gliricidia sepium* generally occurs from sea level to 1200 m in altitude although in favourable micro-climates it can also occur at higher elevations; herbarium records from UNAM suggest that it may be found up to 1600 m above sea level.

Gliricidia sepium does not usually occur above 1200 m because it is not tolerant of frost and growth can be hindered by cold temperatures. Whiteman *et al.* (1986) reported leaf fall and poor growth when temperatures dropped below 15°C in south-east Queensland, Australia, although temperatures as low as 5°C have been recorded within the species' putative native range at sites such as Volcán Suchitán in Guatemala. Low temperatures will check growth, but prolonged frost will kill trees (an occasional frost will cause leaf drop and dieback but the tree is usually able to resprout). Its distribution within Meso-America stops at the frost line. Outside areas prone to frost, *G. sepium* occurs under very varied climatic conditions, as shown by the wide variation in mean monthly temperature recorded during collections from sites throughout Meso-America (20.7-29.2°C).

Gliricidia sepium is native to sub-humid conditions with mean annual rainfall of 900 to 1500 mm, although it is also found at much drier sites, for example in eastern Guatemala where rainfall is as low as 600 mm, and at much wetter sites where rainfall can be as high as 3500 mm, such as Retalhuleu in Guatemala (Hughes, 1987). Within its putative native range, however, even where total rainfall is high, a clear dry season also exists. This is not always the case in exotic locations where total rainfall may not be any higher, but is more evenly distributed throughout the year. The length of dry season (defined here as including months with less than 50 mm of rainfall) within the putative native range varies from three to eight months.

Stands and associated vegetation

Gliricidia sepium is found growing in pure stands or at lower densities in association with a wide variety of dry forest species. Pure stands may be more or less even-aged (Plate 3E) or of mixed ages. Populations which have colonized a site after disturbance (natural or human) or a newly migrated population (*e.g.* from a newly established fence line) tend to be even-aged. Initial densities can be very high (more than 1 tree per m^2), although self-thinning of these stands will occur as competition increases. Typical densities for trees of 5 - 10 m in height would be 200 - 600 trees per hectare. Stands of mixed age show a random spatial pattern of age (size) class. Seedlings do not perform well under shady conditions and are therefore rarely found under large trees (Plate 3E).

The vegetation found in association with *G. sepium* will vary depending upon the degree of disturbance of the site, soil type, altitude and climatic conditions. Potentially, it can be associated with any of the species found in the deciduous dry forests of Meso-America. The most commonly co-occurring tree genera within its putative native distribution are: *Acacia, Bauhinia, Bursera, Brosimum, Caesalpinia, Calicophyllum, Combretum, Crescentia, Dalbergia, Enterolobium, Guazuma, Haematoxylum, Juliania, Lonchocarpus, Lysiloma, Pithecellobium, Senna, Simarouba, Swietenia* and *Tabebuia* (Lavin and Sousa, 1995; Hughes, unpublished).

Conservation status

As a result of the colonizing nature of *G. sepium*, it is under no threat at the species level, being found throughout Meso-America. At the provenance level, however, certain important populations, such as Retalhuleu in Guatemala, are under serious threat of degradation from human encroachment and, in the case of Retalhuleu, river erosion (Plate 3D). Additionally, the outcrossing nature of the species, and the high degree of gene flow that occurs as a result of human movement of germplasm, has implications for the genetic conservation of valuable provenances.

3.2 Reproductive biology

For any species, a sound knowledge of reproductive biology is an essential prerequisite for planning effective programmes of genetic improvement, seed multiplication or genetic conservation. The breeding system (whether the species is self-fertile or outcrossing) influences the partitioning of genetic variation within and between populations, and hence the choice of sampling strategies for seed collection. For outcrossing species, the mode of pollination (wind, insect, bat, bird *etc.*), and the behaviour of the pollinator also affects population structure and population differentiation through its influence on gene flow. Phenological differences (*e.g.* in timing of flowering) can create constraints to mating, either between populations or between individuals within a population, thus reducing the effective size of the breeding population. Finally, the mode of seed dispersal determines the pattern of distribution of seeds from the mother tree, again affecting gene flow both within and between populations.

Breeding system

Gliricidia sepium has hermaphrodite flowers. Controlled crossing studies in Honduras by the author (Plate 3K), using flowers protected in insect-proof bags (Plate 3L), have shown it to be an obligate outcrosser. Pollen applied with a brush to the receptive stigma resulted in fertilization and subsequent seed set when pollen from other trees was used, but fertilization never occurred with pollen from the same tree. The self-incompatibility in *G. sepium* appears to be very robust; this is supported by observations that isolated trees produce few, if any, pods. Palmer (pers. comm.)[3] observed profuse production of pods on a single, isolated *G. sepium* tree in Australia, and concluded that these must be from selfed flowers; but this is a highly unusual observation. According to Shivanna and Owens (1989) the self-incompatibility of *G. sepium* is contrary to that expected for papilionoid legumes, most of which are self-compatible. For tropical trees in general, however, Bawa (1974) reported that most were self-incompatible.

A study of outcrossing rates at Monterrico, Guatemala, using isozymes, confirmed that *G. sepium* is strongly outcrossing and suggested a robust incompatibility mechanism. This study is described in Chapter 7. There is also evidence from the isozyme data that some mating between related individuals (as distinct from selfing) does occur, resulting in low levels of inbreeding. Studies of seed:ovule ratios, however, suggest that *G. sepium* does not tolerate a high level of inbreeding. In *G. sepium*, as in other legumes, not all the ovules found in the flower develop into seeds.

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[3] *B. Palmer, CSIRO Davies Laboratory, Townsville, Queensland 4814, Australia.*

Plate 3

- A - *G. sepium* colonizing fallow land, Vado Hondo, Chiquimula, Guatemala
- B - *G. sepium* growing on shifting sand, San Mateo, Oaxaca, Mexico
- C - *G. sepium* growing on a vertisol, Belen Rivas, Nicaragua
- D - River erosion threatening natural populations at Retalhuleu, Guatemala
- E - Mature natural stand at El Roblar, Guanacaste, Costa Rica
- F - Reclamation of open-cast mining site, SFRI, Madhya Pradesh, India

Studies of seed:ovule ratio in *Gliricidia sepium*: summary of findings

Studies were carried out by the author in Central America, using the following material: (I) pods from controlled crosses in field trials in Honduras between related (half-sib) and unrelated individuals of one provenance, and between individuals from different provenances; (ii) open-pollinated pods from three provenances in the same trial; (iii) pods from three natural populations in Guatemala and one in Mexico. The controlled crosses indicated that relatedness of parents reduces seed:ovule ratio. This finding was then used to draw other conclusions about within- and between-population variation in *G. sepium*.

Controlled crosses

- Unrelated trees from the same population which were crossed displayed nearly double the seed:ovule ratios of trees from the same half-sib family which were crossed. This may imply that *G. sepium* carries a high genetic load, which is expressed by inbreeding and results in abortions.
- Crossing of trees from different populations, however, gave a much lower seed:ovule ratio than crosses within a population, suggesting reproductive constraints other than inbreeding in this case; the breakdown of locally adapted gene complexes could result in outbreeding depression.

Natural populations

- Differences in seed:ovule ratio were found between natural populations, which may imply that some are more genetically diverse than others. The lowest ratio was found in the population from Palmasola, Mexico, which may be introduced rather than native.

Trial populations

- Seed:ovule ratios in the trial populations were higher than in the natural populations. This could be due to the removal of population structure in the trial situation (whereas in natural stands close neighbours are more likely to be related); however, these pods were collected from three provenances in a single trial, so some inter-provenance crossing is also likely, suggesting an effect contrary to that found with controlled crosses between different populations.

The seed:ovule ratio can be used as an overall indicator of reproductive success. Studies by the author of this ratio in *G. sepium*, following controlled crossing of related and unrelated individuals, have shown that the ratio is much lower when close relatives (half-sibs) are crossed, suggesting intolerance of a high level of inbreeding. Other conclusions from the studies of seed:ovule ratio (Plate 3G) are summarized in the box above.

Mechanism of incompatibility

A gametophytic system of incompatibility is thought to operate in *G. sepium*, whereby self pollen can germinate but is prevented from fertilizing the ovule. Normally, once deposited on a stigma, pollen takes 2-4 hours to germinate and after by 8-12 hours may have reached the base of the style. Fertilization is usually complete within 12-16 hours. Any self pollen that germinates, and reaches the ovary, is prevented from entering the micropyle by the pollen tubes which become bifurcated.

Pollination mechanism

Although *G. sepium* is an insect-pollinated species, it attracts few insect visitors because of the difficulty in prising apart the standard and keel petals to gain access to the nectaries. The papilionoid flower has rigid keel petals which protect the stigma and keep it enclosed until they are splayed apart when entry to the nectaries is attempted (Plate 3H). Of the 250 species of bee found in the dry forest of Central America (Frankie *et al.*, 1976), fewer than 10 have been observed on the flowers of *G. sepium*. Some moths avoid this restricted access to the nectaries by inserting their proboscis down a small opening. They do not however, achieve pollination because they do not come into contact with the stigma or the anthers. Ants and thrips may also visit flowers to obtain nectar without coming into contact with the stigma.

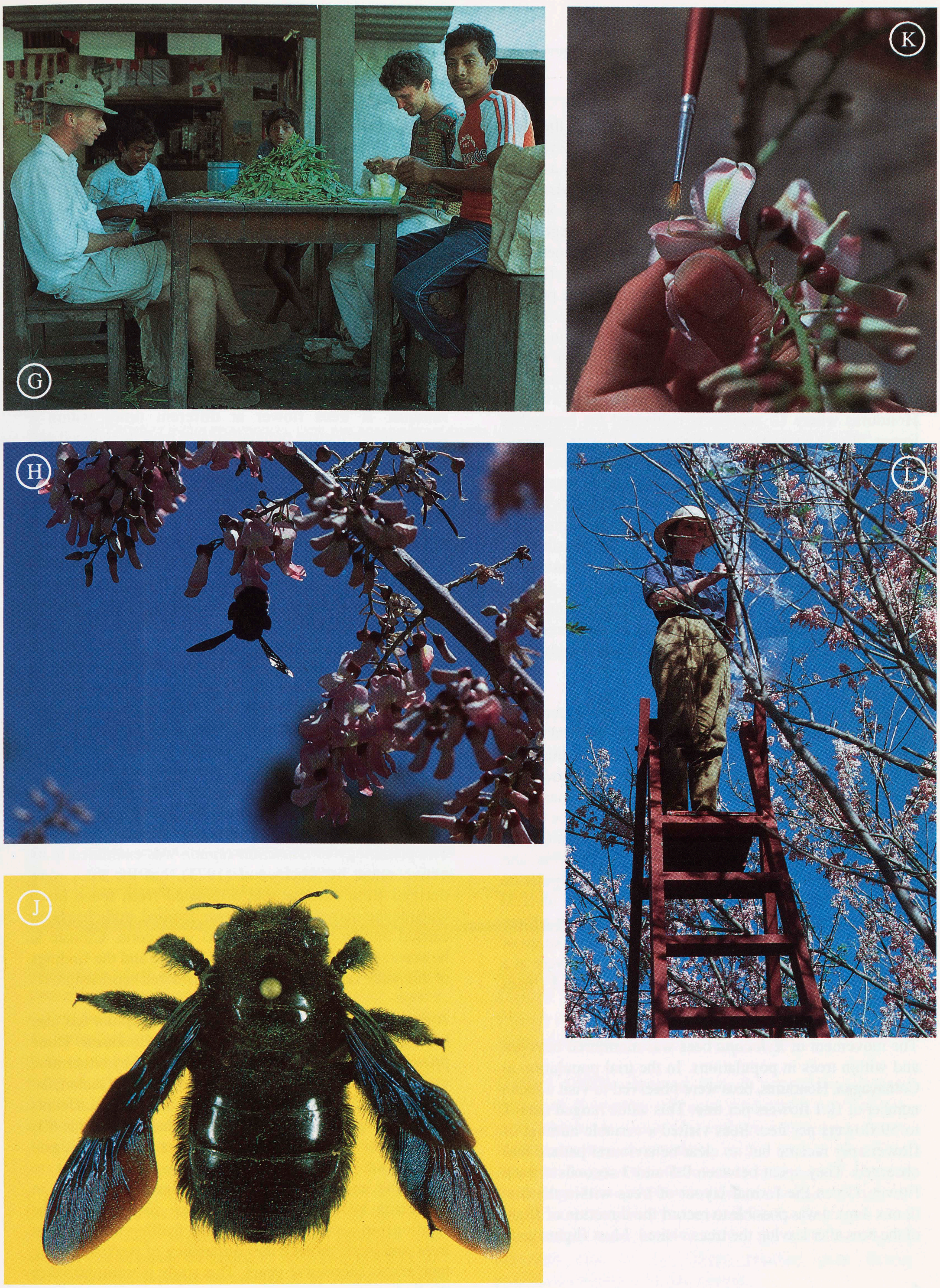

Plate 3 cont.

- G - Determining seed:ovule ratios, El Banco, Guatemala
- H - Pollinator visiting flowers
- J - Pollinator *Xylocopa fimbriata*
- K - Artificial pollination
- L - Insect-proof bags being used to carry out controlled crosses, Guatemala

Pollinators

Large bees are best suited to *G. sepium*, with the most conspicuous visitor being a large black bee, *Xylocopa fimbriata* (Plate 3J). Another species (or possibly a sexual dimorphism) of *Xylocopa* (brown bodied) has also been seen occasionally by the author on *G. sepium*. Slightly smaller *Centris* bees also visit *G. sepium*, although these are less frequently observed. Both these genera are attracted to the nectar of *G. sepium* and are effective pollinators although *X. fimbriata* appears to be the primary pollinator (Janzen, 1983). *Apis* sp. bees also visit *G. sepium* for nectar but usually after the keel petals have lost their rigidity (1-2 days after flower opening) when the stigma has probably already dried out. Their effectiveness as pollinators is therefore limited. In areas such as Pavana in Honduras where *G. sepium* is cultivated for honey-bee forage, there is no evidence of higher fruit:flower ratios (as might be expected if they were effective pollinators). One species of small stingless bee (*Trigona* sp.) is attracted to the pollen of *G. sepium*, chewing at the keel petals to gain access to the pollen and thereby damaging the stigma. It is therefore unlikely that *Trigona* sp. are responsible for much pollination. All species of bee seen by the author on *G. sepium* moved readily between trees. This finding differs from that of Frankie *et al.* (1976) in a study of *Andira inermis*, another Central American dry forest tree, where 70 species of bee were recorded of which only eight species moved between trees.

In pollination studies by the author, the frequency of sightings of *Xylocopa* varied considerably between sites. This is unlikely to be explained by differences in the times of day at which observations were made since *Xylocopa* bees were sighted from 0700 to 1800 at most sites. This between-population difference is more likely to be due to the density of *G. sepium* at a site, although the availability of alternate food sources, abundance of predators and parasite levels might also play a role. In a trial population at Comayagua, Honduras, trees planted at a density of 1250 per hectare were visited by more than 50 bees over a three day period.[4] In an equivalent area in a natural population of *G. sepium* at La Garita, Honduras, where trees were at a density of approximately 100 per hectare, only 11 bees were recorded in the same period of time.

The movement of *Xylocopa* bees was monitored between and within trees in populations. In the trial population in Comayagua, Honduras, bees were observed to visit a mean number of 10.1 flowers per tree. This value ranged from 1 to 59 flowers per tree. Bees visited a variable number of flowers per raceme but no clear behavioural pattern was observed. They spent between 0.5 and 3 seconds at each flower. Given the formal layout of trees within the trial (2 m x 4 m), it was possible to record the direction of flight of the bees after leaving the trees visited. Most flights were between trees in rows (*i.e.* over 2 m distances). This has implications for seed orchard design: line plots with more than one family member at final spacing are likely to result in a significant amount of crossing between related individuals. At final thinning, spacing that is as square as possible would be most desirable in promoting outcrossing.

Flowering and pod production

Phenology

Studies of phenology are important for conservation and improvement programmes for a number of reasons. The timing and quantity of flowering can influence population structure by affecting the extent to which mating is random. If trees flower at different times within a population, effective population size may be reduced and crossing may be more limited than assumed, for instance with increased crossing of related individuals if these flower at the same time. Relatedness within a population may therefore be higher than expected, and this will affect the degree of diversity that is sampled when seed is collected. The number of flowers and seeds borne by trees also affects their contribution towards the pollen and seed genetic pools. This has implications for sampling variation and also for the prospect of genetic improvement.

Some detailed studies in tropical trees have been undertaken since Bawa (1974) pointed out the paucity of knowledge of their reproductive biology. Studies in Central America have focused largely on Costa Rican forests in the work by Janzen (1983) and others (*e.g.* Frankie *et al.*, 1974; Bawa, 1979; Boshier, 1992). Boshier (1992), in his account of the reproductive biology of *Cordia alliodora*, drew together elements of floral and seed phenology in an explanation of mating system and gene flow in the species. The phenology of *Gliricidia sepium* was examined in its native range by Rockwood (1973), but the trees were derived from cuttings that originated from fence lines. Outside the native range the most detailed study has been carried out by Sumberg (1985a) in Nigeria. Climate is however, atypical for flowering in Nigeria and the findings of this study cannot therefore be considered representative.

A detailed study of the phenology of *G. sepium* has also been carried out by the author in a trial in Honduras. Three provenances were studied, each represented by either nine or eleven half-sib families: Monterrico, Guatemala; Masaguara, Honduras and Belen Rivas, Nicaragua. Details of these provenances can be found in Chapter 8, Table 8.1. The objectives of the investigation were: (I) to investigate provenance variation in *G. sepium* with respect to flowering and fruiting; (ii) to examine the variation in flowering between half-sib families; (iii) to study the relationship between flowering and fruiting in individual trees; and (iv) to monitor the consistency of peak flowering time across successive years. This study is summarized in the box.

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[4] *Number of bees that visited the trial was determined by capture and mark methods.*

Study of genetic variation in phenology of *Gliricidia sepium* in a trial in Honduras

In 1990 and 1991, detailed phenological observations were made by the author in a provenance/progeny trial in Honduras with three provenances (Monterrico, Guatemala; Belen Rivas, Nicaragua; and Masaguara, Honduras), each comprising 9-11 half-sib families. Only the key findings from these studies are presented here.

Timing and quantity of flower production

The overall flowering period was 48-70 days, with most flowering occurring within a peak period of 20-30 days.

- *Variation between provenances*: significant provenance effects were found for number of racemes per tree and number of pods per tree. There were also clear differences in the timing of peak flower production. Monterrico was the earliest to flower, and the most abundant; Belen Rivas was the latest and the least productive.

- *Variation within provenances*: there was no significant family effect on flower number. The timing of flower production appeared to be more synchronous for some provenances than for others, with Masaguara the most variable in this respect.

- *Variation between trees*: within one family of Masaguara provenance, peak flowering time was found to vary by up to 39 days, although most individuals reached peak flowering within a 14-day period.

Pod production

- *Variation between and within provenances*: there was significant variation between provenances at both the provenance and the family level, with Monterrico producing 2.5 times as many pods as Belen Rivas.

- *Variation between trees*: great variation was found between individual trees in total pod number (0 to 534).

Fruit:flower ratio

- The correlation between raceme number and pod number was found to high ($r=0.73$) and highly significant ($p<0.001$). Consistent with this was the lack of provenance or family variation found in fruit:flower ratio.

Consistency in phenology across years

- Trees were classified as 'early', 'medium' or 'late' flowering: in Monterrico and Masaguara provenances, 54% and 47% of trees, respectively, were in the same category in 1990 and 1991, with less than 2% changing by more than one category (late to early or vice versa). In Monterrico provenance only 26% were unchanged, with 8% changing more than one rank, suggesting that provenances may vary in predictability of flowering time.

The habitats which were sampled by Hughes (1987) for the assembly of range-wide seed collections of *G. sepium* varied greatly in rainfall, altitude and soil type, and this was reflected in variation in the timing of flowering and fruiting. At higher elevations flowering and seed production can take place up to two months later than at sea level. The study in Honduras also showed a significant difference between provenances in peak flowering time when grown in a common environment. Monterrico provenance flowered the earliest in both native and trial populations, whereas Masaguara provenance flowered before Belen Rivas in the trial and after it in the native population. This suggests that both genotype and environment influence the timing of flowering and pod set. The differences between provenances in flowering time supports the conclusion from molecular studies (see Chapter 7; and Chalmers *et al.*, 1992) and field trials (see Chapter 8) that substantial population differentiation exists within *G. sepium*.

Hughes (1987) observed that, in natural populations, timing of flowering and seed production was not only predictable but also generally uniform within a population. More intensive observations in the trial in Honduras, however, suggest that there is not strict synchronicity in flowering. Among fifteen individuals within one half-sib family of Masaguara provenance, individual trees were observed to reach peak flowering up to 39 days apart, although nine of the fifteen reached peak flower production within a 14-day period.

Floral development

A clear stimulus for flower initiation in *G. sepium* is the onset of the dry season. In the native range, trees begin losing their leaves in December and floral buds subsequently appear on woody stems. Floral buds first appear at proximal branch positions with the most distal portions of flowering branches acquiring raceme buds one to four weeks later. After emergence of the raceme bud, it takes approximately two weeks before the petals show beyond the calyx. At this stage the calyx is full size (6-9 mm long). Ten days after the petals first emerge, and when they are approximately 15 mm long, the flower has usually opened fully. The time interval between the opening of the first and last flowers in a raceme is approximately a week although it can vary from five to ten days. Individual racemes typically contain 20-40 floral buds although not all of these may develop fully (see box in Section 2.2 for a full botanical description).

Gliricidia sepium is distinctly protandrous: the anthers dehisce two to three days before the flowers open, when the petals protrude approximately 10 mm beyond the calyx. The pollen from the ten anthers is tightly packed in one aggregation between the two keel petals. The stigma generally becomes receptive before the flower opens. Indeed, in controlled pollinations it is possible to achieve fertilization if pollination is carried out before the flower opens. Successful fertilization has been seen on some flowers which would have been expected to open 2-3 days later. This was confirmed by florescence microscopy and monitoring pollen tube growth to the ovary. Flowers begin opening from 0700 to 0800 and, although this may continue up until 1700, most flowers have usually opened by 1200. The length of time an individual flower persists depends upon climatic conditions, although most flowers only last 24-48 hours.

Nectar is released from the nectaries at the base of the flower at or around flower opening. Newly-opened flowers may have a range in nectar quantity of 0.2-6.0 µl. Flowers surveyed in Honduras had a mean nectar content of 1.2 µl at opening. Nectar continues to be released during the next 24-48 hours and a mean total nectar content per flower of 7.0 µl can be expected, with a range of 0.3-11.1 µl. Presumably nectar is released over a long period to attract multiple visits from pollinators thus increasing chances of pollination and promoting outcrossing.

Pod development and production

The period from fertilization to pod dehiscence is to a certain extent dependent upon climatic conditions, which may explain the wide range in pod ripening times (35-60 days). Pods can reach full size within three weeks of fertilization although they will still be green and succulent at this stage. Pod length varies widely between 10 and 20 cm, although most of the variation is accounted for by the different numbers of developing seeds per pod. Combining the 3-4 weeks required for floral initiation and the 5-9 weeks required for pod development, an 8-13 week dry season is needed for successful seed set in *G. sepium.* Climatic conditions in some exotic locations are therefore a probable explanation for the inability of *G. sepium* to set pods, or even to flower.

Pod counts taken one week after pollination, when unfertilized flowers have abscissed, and at maturity, revealed that only 44% of putative fertilized pods developed to maturity. This indicates competition for resources rather than late-acting self-incompatibility. Most racemes have one or two mature pods.

Although in open-pollinated stands of *G. sepium* it is uncommon to find inflorescences producing more than two pods, when controlled pollinations are carried out it is possible to achieve more than ten pods per inflorescence. This could indicate inefficiency in the natural pollination process; for instance much of the pollen deposited could be from flowers on the same tree, which would not result in seed production owing to the self-incompatibility of *G. sepium*. Many other factors might also be involved, such as the effect of bagging in protecting newly-formed pods from damage or predation. It is also possible that some trees are more attractive to pollinators than others: the principal reward for the primary pollinator (*Xylocopa fimbriata*) is nectar and it is likely that this effects the number of foraging bees and hence the amount of fertilization achieved. Preliminary observations by the author suggest wide variation in timing of nectar release, duration of nectar production and the quantity of nectar produced; this would be an interesting area for further research.

Individual trees differ widely in the number of pods they produce. Trees in native populations can carry anything from none to 1500, although about 300 is typical. It is common to find small clumps of trees in natural populations that have large numbers of pods on them. It is not known whether this is a genetic influence (either in terms of attractiveness to pollinators or being good seed parents), a phenological effect, or due to the proximity of the trees to the nests of pollinators. Yearly variations in the number of pods per tree also occur. In the *G. sepium* trial in Honduras discussed above, containing three provenances, the number of pods per tree were counted for the periods 1990/1991 and 1991/1992. Little correlation was found between pod number per tree from one year to another. Given that these observations were made at a fairly uniform trial site, this indicates that it would be difficult to select trees for inclusion in a seed orchard, either from wild populations or from trials, on the basis of high pod production.

The tremendous variation in pod number for trees in the Honduras trial (*i.e.* 0-534) concurs with observations of trees in natural and naturalized populations. In Costa Rica, Rockwood (1973) found trees with a range of 0-1626 pods per tree in fence line trees, whilst in Nigeria Sumberg (1985a) recorded 16-760 pods per tree and Atta-Krah (1987) 5-706 pods per tree. In the Honduras study, most of the variation was observed in Belen Rivas population, which can be explained not only by the variation in flower number but also by the variation in timing of flowering, with the later flowering trees incurring higher levels of pod abortion and problems of pod immaturity. This trial was only 2.5 years when it was assessed and yet even at this age trees of Monterrico, Masaguara and Belen Rivas provenances could be expected to produce an average of 150 g, 106 g and 60 g of seed per tree, respectively (based on 7 seeds per pod and 8000 seeds per kg). These figures would equate to 187 kg, 132 kg and 75 kg per ha of seed orchard at 2 m x 4 m spacing.

In the absence of a replicated experiment at another site to complement the Honduras study, the existence of genotype x environment interactions for pod number can only be inferred from other experiments where pod number was counted. In Nigeria, Atta-Krah (1987) found that Monterrico and Masaguara provenances produced 290 and 41 pods per tree, respectively, concurring with the result of the present experiment. Conflicting results were obtained in Indonesia by Nitis *et al.* (1991), however, who recorded 162 and 225 pods per tree for Monterrico and Belen Rivas provenances respectively. Although the latter values are means for only three trees per provenance, these results support the hypothesis that genotype x environment interaction for pod production may exist. Rajaram (1990) reported the complete absence of flowering in some provenances in a field trial in southern India. The underlying cause of this possible genotype x environment interaction remains unclear, but it could have important implications for seed production in exotic locations.

Seed dispersal

Upon reaching maturity, pods dehisce in an explosive manner. Torsion builds up in the pod valves and seeds are ejected, their flight similar to that of a discus. A detailed study on seed dispersal was carried out by the author at Pavana, Honduras. Trees isolated by more than 100 m from neighbours, and trees at the edge of a population, were studied. The dispersal distances showed a bimodal distribution. The first mode comprises about 32% of the seeds, which fall within 8 m of the base of the tree owing to gravity or to hitting branches. The second mode has a skewed distribution with 42% falling between 14 m and 22 m from the base of the tree, although a considerable number (13%) travel 24-28 m from the tree. The maximum distance that any one seed was seen to travel was 37 m. Wind plays a part in the direction of seed dispersal. Some seeds, which are not ejected from the curled pod valve, may be dispersed by the wind after the valve falls to the ground. Secondary dispersal by rain is also possible, causing rivulets which may carry curled pods containing seeds.

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4 Utilization

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4.1 Introduction

The spread of *Gliricidia sepium* around the world from its fairly restricted native range in Central America, and its inclusion in a wide range of farming systems, is due in large part to its truly multipurpose nature. Its versatility in terms of products such as animal fodder, fuelwood and poles is matched by its provision of several important 'service' functions, notably live fencing, soil amelioration through nitrogen fixation (usually by application of leaf mulch or 'green manure'), and shade and support for crops. Several important physiological attributes make it ideally suited to these many functions. One of the most important is its ability to resprout vigorously and repeatedly after cutting (Plate 4D), allowing not only repeated harvesting of fodder, fuel and green manure but also manipulation of the canopy to vary the intensity of shading at different times of year. Another is the ease with which *G. sepium* can be established vegetatively, from cuttings.

As for most 'multipurpose' trees, different uses of *G. sepium* predominate in different farming systems, and a particular tree will generally be managed for only one or two products or services. In Central America for instance, *G. sepium* is used mainly as a live fence, particular in cattle pastures (Plate 4F); but there is little use of *G. sepium* (or other tree species) as fodder. In Sri Lanka, *G. sepium* is widely used as a shade for tea and as a dry season fodder by smallholders. Live fences are also an important use here, and indeed much of the fodder probably comes from live fences, but the form of the fences is very different from those in Central America (Plate 4G) (see Section 4.3).

In general, although *G. sepium* is very widely used in most parts of the semi-arid and sub-humid tropics, its intensive cultivation for a particular use is relatively uncommon in its native range, where it is more often seen by smallholder farmers as one of a series of useful woody species on the farm (Plate 4A). It is one of the most widely-researched non-industrial tree species worldwide, reflecting its greater perceived importance outside the native range; yet the number and variety of its uses in different farming systems mean that results of studies within particular areas or systems should be applied with caution elsewhere.

4.2 Fuelwood

Attributes

The ability of *Gliricidia sepium* to withstand repeated cutting, its fast growth and the good burning characteristics of its wood, make it an important fuelwood species for the sub-humid tropics. The wood is hard and relatively heavy, with specific gravity usually in the range 0.5-0.6, and occasionally as high as 0.8 (Glover, 1989). It also burns slowly, without sparking and with little smoke, and produces good embers (CATIE, 1986). Trees managed in a coppice system produce wood of small diameter which is easy to handle and to dry, although, as it contains little or no heartwood, the specific gravity will tend towards the lower end of the range (0.4). In very humid climates, however, drying *G. sepium* can be a problem, and it may even sprout during storage.

Domestic production

In many tropical countries, wood provides over 90% of domestic energy consumption (Eckholm *et al.*, 1984); so any tree species with desirable fuelwood characteristics has a potential role to play as a provider of wood energy, particularly to rural households where no alternative is available. During the 1980s it became increasingly apparent that tree planting by farmers and local communities is usually motivated by the desire for higher-value products than fuelwood (FAO, 1986) and that fuelwood is usually either gathered off-farm (Plate 4K) or is a by-product from trees grown primarily for some other purpose. This is true in general for *G. sepium*: it is usually planted on farms for other uses such as live fencing, shade/support for other crops, or fodder, and the use of lopped branches for fuelwood may be a secondary function. For instance in a survey of *G. sepium* use in Costa Rica (Sánchez and Payne, 1987), the primary uses on farms were identified as live fencing (95% of respondents) and shade for crops and pasture (16% of respondents); however, 73% cited fuelwood from *G. sepium* as an additional advantage of this species. In southern Honduras, *G. sepium* is not much used as fuel, being preferred for other uses such as production of poles and posts (Colindres *et al.*, 1995), for which trees are allowed to grow to large diameter without cutting. Fuelwood is more likely to be important where another use, such as live fencing or shade for perennial crops, involves periodic pruning which provides fuelwood as a by-product.

Commercial production

There are some instances of *G. sepium* fuelwood being harvested on a larger scale and entering the market economy. In the species' native range in Central America, natural or semi-natural stands (*e.g.* secondary growth on abandoned agricultural land) are harvested by fuelwood contractors for sale in urban markets. Extensive naturalized stands of *G. sepium* are rare elsewhere in the tropics, but there are specific instances of its cultivation for fuel, for example in the Ilocos region of the Philippines where farmers growing tobacco manage *G. sepium* woodlots to provide fuel for curing the tobacco (Wiersum and Dirdjosoemarto, 1987).

Yield

Wood biomass yields from *G. sepium* plantations have been studied in depth by CATIE (Hughell, 1990), and the results of this research are summarized in a silvicultural guide to the species (CATIE, 1991). According to these studies, optimal wood production is achieved by planting at a spacing of 2 m x 2 m (2500 trees ha^{-1}), and cutting on a three-year cycle by coppicing all stems to 10-20 cm above ground level. In the regrowth, only diseased or damaged stems are removed. This regime gives a mean annual increment of 2.0-5.3 t ha^{-1} yr^{-1} dry weight, depending on site quality (on very poor sites the cutting interval should be increased to five years or more). This management regime also produces stems of an ideal size for fuelwood (Glover, 1989). Woodlot and coppice management are discussed in more detail in Section 5.3.

These yield data are lower than some of the other values quoted in the literature. Kwesiga (1994), in a *G. sepium* provenance trial in Zambia planted at 2 m x 2 m spacing and grown without cutting for 39 months after establishment, found provenance means for total wood dry matter production (stems + branches) in the range 6.35-27.00 t ha^{-1} at 27 months and 7.35-28.72 t ha^{-1} at 39 months. These correspond to mean annual production of 2.82-12.00 t ha^{-1} yr^{-1} over 27 months and 2.26-8.84 t ha^{-1} yr^{-1} over 39 months, suggesting that on this site the maximum mean annual increment is reached earlier than the three years prescribed by CATIE as the optimum cutting cycle. In another provenance trial, in Malawi, Ngulube (1994) reported mean wood production over three years from establishment in the range 3.1-5.1 t ha^{-1} yr^{-1}, but this was in an alley cropping trial with six cuts over this period, which would be expected to give much lower wood production than a plantation grown without any cutting for three years.

Production from mature individual trees can of course be much higher, but represents a single rather than a sustained yield. Salazar (1984), for instance, reported a yield of 307 kg of dry wood per tree from 30 year old trees, 16 m in height, in Costa Rica.

4.3 Living fences

The most widespread use of *Gliricidia sepium* within Central America is for live fencing, typically around cattle pastures and to delineate boundaries. The fences usually consist of trees established from stakes at 0.75-2.0 m spacing, with barbed wire between them. The trees are pollarded at a height of 0.75-2.0 m, and are typically maintained for 30 years or more. The frequency of cutting is determined by the required end use: every two to three months for fodder (to give a high leaf : wood ratio) or every one to three years for fuelwood, stakes for further planting, or stakes to support crops or vegetables (CATIE, 1986). Generally, the longer the cutting interval, the higher the overall biomass production. The management of live fences is discussed further in Section 5.3. An experiment at CATIE at San Carlos, Costa Rica, gave a wood yield of 0.7 t km^{-1} (dry weight) with three-monthly cutting and 2.8 t km^{-1} with six-monthly cutting. In general, as might be expected, yields from prunings in live fences increase with the maturity of the trees: in another experiment by CATIE, a 13-year-old fence line in Honduras produced 17.6 t km^{-1} dry weight of firewood, as well as 1000 poles km^{-1}, after 15 months of regrowth (CATIE, 1986).

Studies have also been carried out on leaf production from mature trees in live fence lines. Although at present *G. sepium* live fences in Central America are managed mainly for wood products (fuelwood and stakes), their potential for leaf biomass production has also been investigated in a number of studies by CATIE. Ranges of yields of edible and total biomass from live fences at four sites, for three different cutting intervals, are given in Table 4.1.

Table 4.1 Annual biomass production from *Gliricidia sepium* live fences in the humid lowlands of Costa Rica (source: CATIE, 1987)

Pruning interval (months)	Edible dry matter (t km^{-1})	Total dry matter (t km^{-1})
2	0.14-1.24	0.14-1.24
4	1.00-5.58	1.58-7.77
6	0.35-3.55	0.59-7.48

The use of relatively widely-spaced trees with barbed wire between them is typical of the extensive ranching systems of Central America. By contrast, in smallholder systems where *G. sepium* is used as a live fence it is typically planted at very close spacing, using smaller cuttings, to form a livestock-proof barrier (stockade) without the need for barbed wire. In Sri Lanka, for example, fences around home gardens are constructed in this way, whilst in Bali the cuttings are interwoven to provide an even denser barrier.

Alternatively, wider-spaced *G. sepium* plants may be connected by bamboo poles instead of wire (Simons and Stewart, 1994).

The suitability of *G. sepium* for fencing is due largely to the ease with which it can be propagated from stakes or cuttings. Preparation of stakes and the establishment of live fences is discussed in Section 5.2.

4.4 Green manure

The benefits of incorporation of green leaf material into soil are well known: increase in soil organic matter and nitrogen; improvement of soil physical characteristics, aeration and drainage; and (where the leaves are initially applied as a surface mulch) weed control, reduction of surface soil erosion, reduction in soil temperature, and conservation of moisture. Each of these aspects has been studied in detail in *Gliricidia sepium*, owing to the great interest during the 1980s in alley cropping as a means of maintaining soil fertility without recourse to expensive inorganic fertilizers, and as a sustainable alternative to shifting cultivation (bush fallow) systems (*e.g.* Kang *et al.*, 1990).

Production systems

Mulching of annual and perennial crops

Alley cropping involves the establishment of woody hedgerows, usually of nitrogen-fixing leguminous species. The majority of the research on alley cropping has focused on *G. sepium* and *Leucaena leucocephala* as the hedgerow species (Kang *et al.*, 1989). The hedges are typically planted about 4 m apart, across arable fields. They are regularly lopped, and the prunings are laid on the surface (mulch) or incorporated into the soil between the alleys (green manure) to improve crop production. Similar systems, in which some or all of the prunings are removed for animal fodder, are known as alley farming rather than alley cropping.

Although most of the recent research on the use of *G. sepium* as green manure has been in the context of alley cropping, it has been used for several decades as a green manure on rice paddies in south India and Sri Lanka, grown on the bunds between the paddy fields (Plate 4C). It was also recommended as a green manure for perennial crops in Sri Lanka as early as the 1930s (Holland, 1931). The Coconut Research Institute in Sri Lanka has focused on the use of *G. sepium* green manure under coconut (Liyanage and Wijeratne, 1987). The principle of green manuring can thus be applied to any crop; alley cropping is just one of many possible applications.

Erosion control on hillsides

The application of the alley farming concept that seems to have been most widely taken up by farmers is as a combined production system and conservation measure on steep slopes (Plate 4B). The 'sloping agricultural land technology' (SALT) was initially developed by the Mindinao Baptist Rural Life Centre in the Philippines, but has been taken up in many areas of the humid/sub-humid tropics, including Java (Hawkins *et al.*, 1990) and Sri Lanka (Decurtins and Mohns, 1994). Contour hedgerows, and regular application of prunings in the alleys between them, provide physical erosion control, including passive terrace formation as soil and organic matter accumulates on the uphill side of each hedge. In a study in Kenya, Omoro and Nair (1993) found that application of *G. sepium* mulch to a 15% slope reduced soil loss by 43% and water loss by 52%, compared to unmulched controls. The use of contour planting to control erosion also has important economic implications. Siebert and Lassoie (1991), working in Sumatra, found that bench terraces, grass bunds, and grass plus *G. sepium* hedgerows with mulching all gave similar reductions in runoff and soil erosion relative to conventional cultivation methods; but the 'agronomic' techniques (bunds and hedgerows) are much cheaper to build and maintain than bench terraces. Sections 5.2 and 5.3 discuss further the establishment and management of erosion control hedges.

The original SALT concept involved the return of all the foliage to the alleys, but several variants have also been developed, including the 'simple agro-livestock technology' (SALT-2) in which goats are included in the system (Laquihon and Pagbilao, 1994). *Gliricidia sepium* is one of the main species used in SALT systems, along with *Leucaena leucocephala*), *L. diversifolia, Calliandra calothyrsus, Flemingia macrophylla, Acacia villosa* and *Desmodium rensonii.*

A participatory study with a group of 200 farmers in the Philippines has monitored farmers' adoption of SALT technology over a four year period (Fujisaka *et al.*, 1994). Eighty of the farmers took up some form of contour hedgerows on an average of 55% of their sloping land area. Of the hedgerows, a total of 47% included *G. sepium.* Whilst 96% of adopters of hedgerows recognized their value in reducing soil erosion, 45% also considered the production of dry season fodder by *G. sepium* to be important. In contrast, only 15% of the adopters used the prunings for green manure.

Attributes

Leaves

Gliricidia sepium has several characteristics that make it particularly suitable for use as a green manure. It is high in several major nutrients: 3.0-4.5% nitrogen, 0.2-0.3% phosphorus, 1.6-3.6% potassium, 1.4% calcium and 0.4-0.6% magnesium. Alley farming systems typically produce 500-3000 kg of leafy biomass ha^{-1} harvest^{-1} (dry weight), depending on site conditions, tree density and cutting frequency (Glover, 1989). The nutrient contribution to the crop, assuming all the prunings are used as green manure, is shown in Table 4.2. Trees, however, will compete with crops for nutrients so the actual benefit to the companion crop will be lower.

The extent to which green manuring meets the nutrient requirements of the crop depends on the nature of the crop and the characteristics of the soil. In a study at IITA, Ibadan (southern Nigeria), an alley cropping experiment producing *G. sepium* yields towards the top of the range shown in Table 4.2, on an Oxic Paleustalf (USDA) soil (Yamoah *et al.*, 1986b) met 71% of the nitrogen (N) requirements of maize on that site (Yamoah *et al.*, 1986a). However, this assumes that the entire nutrient content of the prunings is available to the crop, whereas in practice a number of other aspects reduce its actual availability. As well as competition for nutrients with the hedgerow trees, the inclusion of twigs with the green leaf material has been shown to reduce N availability in the short term. This is because the twigs absorb and thereby immobilize the nitrogen (Constantinides and Fownes, 1993), though the long-term availability of this immobilized nitrogen is uncertain.

Table 4.2 Nutrient contribution of *Gliricidia sepium* prunings (from Glover, 1989)

Nutrient ($kg\ ha^{-1}$)	**Amount of prunings ($kg\ ha^{-1}\ cutting^{-1}$)**			
	500	1000	2000	3000
Nitrogen	15-23	30-45	60-90	90-135
Phosphorus	1-1.5	2-3	4-6	6-9
Potassium	8-18	16-36	32-72	48-108
Calcium	7	14	28	42
Magnesium	2-3	4-6	8-12	12-18

The rate of nitrogen release is also critical. Mwiinga *et al.* (1994) have shown that *G. sepium* and *Leucaena leucocephala* leaves decompose in soil more rapidly, and have a higher N content, than other commonly-used hedgerow species (*Sesbania sesban, Senna siamea, Flemingia macrophylla* and *Pericopsis angolensis*). According to Budelman (1988), in a study in Ivory Coast the half-life of prunings (*i.e.* the time taken for half the dry matter to disappear) was only 22 days. The timing of nutrient release must coincide with that of the crop's requirements. In *G. sepium*, nitrogen release was shown to fall below the crop's requirements in the second half of the 120-day growing period, for maize in southern Nigeria (Yamoah *et al.*, 1986a). 50% of the available phosphorus was released in 20 days, at the same site (Kang and Mulongoy, 1987). Studies in Togo by Lehmann *et al.* (1995) found that peak nitrogen requirements for maize were from the fourth to the sixth week of development, by which time *G. sepium* prunings applied just before or at the time of sowing would have already released most of their nitrogen. Rapid decomposition also reduces the effectiveness of *G. sepium* mulch for soil moisture conservation, soil temperature regulation and weed control (Rippin *et al.*, 1994); however the same attribute makes it a suitable species for mulching in rice paddies.

Leaf age also affects the rate of nutrient release, with young leaves decomposing more rapidly than old ones (Glover, 1989). Warm, humid conditions accelerate nutrient release; in Costa Rica, faster decomposition of *G. sepium* prunings is obtained at 15-20% soil moisture content, and the best time for their incorporation into the soil is at the end of the rainy season, when soil moisture is not limiting for crop growth (CATIE, 1991).

Roots

A frequent criticism of alley cropping systems is the potential for competition, both above and below the ground, between the hedgerows and the inter-planted crop. Rao *et al.* (1993) investigated the rooting pattern of regularly pruned hedgerows of *G. sepium, Leucaena leucocephala* and *Senna siamea*. Pruning restricted rooting depth to 1.5 m in all three species, but lateral penetration into the alleys was sparser in *G. sepium* than in the other species, suggesting less below-ground competition with inter-planted crops.

Effect on crop yields

There have been many studies, both field trials and pot experiments, to measure the effect of green manuring with *G. sepium* on crop yields. Most studies have shown a positive response to leaf application, for a wide range of crops, including taro (Kidd and Taogaga, 1985), rice (Gonzal and Raros, 1988), yam (Budelman, 1989), sorghum (Reddy *et al.*, 1991; Ramamoorthy and Paliwal, 1993), and maize (Atta-Krah and Sumberg, 1987). For instance Budelman (1989) found that yields of water yam increased by 2 t ha^{-1} (fresh weight) for each additional 1 t ha^{-1} dry matter of *G. sepium* mulch applied, up to a maximum yield of 15 t ha^{-1}. Not all experiments have shown a positive effect from applying *G. sepium* leaf mulch, however. Kass and Jíminez (1986), in Costa Rica, found no significant effect on either maize or beans of applying leaf mulch, even at a very high rate (20 t ha^{-1}); however this result was only from a single harvest, and the authors suggest that the difference due to mulch application would be likely to increase in subsequent harvests. This is supported by another study in Costa Rica, in an alley cropping system with *G. sepium* and *Erythrina poeppigiana* (Haggar *et al.*, 1993), which concluded that the long-term build-up of mineralizable N in the soil organic matter was more important than direct release of N from newly-applied mulch. The effect of spacing and management on the yield of associated crops is discussed further in Sections 5.2 and 5.3.

Plate 4

- A - Typical smallholder farm with a variety of tree species (including *G. sepium*), Ixtapa, Guatemala
- B - SALT terracing with *G. sepium*, Davao, Philippines
- C - Prunings used as green manure in rice paddies, Dodangola, Sri Lanka
- D - *G. sepium* resprouting after cutting, San Mateo, Oaxaca, Mexico
- E - *G. sepium* stand (background) and coppice regrowth (foreground) in the dry season, San Mateo, Oaxaca, Mexico

Although *G. sepium* prunings have generally been found to have a beneficial effect when applied to crops, several studies have demonstrated an allelopathic effect of the leachate (aqueous extract) from *G. sepium* leaves. In laboratory tests, aqueous extracts in the range 2-4% (weight/volume) have been shown to depress germination of a wide range of crops (Patil, 1994). Ramamoorthy and Paliwal (1993) demonstrated inhibition by aqueous leaf extract of germination and root elongation in sorghum (*Sorghum vulgare*), and identified fifteen potentially toxic compounds in the extract. In a pot trial, Yobterik *et al.* (1994) found that ground *G. sepium* leaf and twig suppressed growth of maize (*Zea mays*), but the mulch was applied at a rate equivalent to 20 t DM ha^{-1}, much higher than would normally be used in the field. In this study the toxicity was attributed to high manganese levels in the *G. sepium* leaves.

The most thorough field study to date of phytotoxicity in *G. sepium* was carried out at IITA in southern Nigeria (Tian and Kang, 1994). In one experiment, prunings were applied to maize and cowpea, on the day of planting, at rates of 0, 0.5, 1, 2, 5, 10 and 20 t DM ha^{-1}. Significant leaf chlorosis occurred at application rates of 5 t ha^{-1} in cowpea and 1 t ha^{-1} in maize. Despite the chlorosis, however, maize biomass increased with application rate. The addition of *G. sepium* had no significant effect on cowpea biomass, even at 20 t ha^{-1}.

In a second experiment in the same study, 10 t ha^{-1} of prunings were applied as mulch at planting and one, two and three weeks before planting maize. By applying the mulch even one week before planting, the level of chlorosis was reduced from 47% to 2%. Biomass production at 20 days after planting was also significantly higher when the mulch was applied one to two weeks before planting, but not three weeks before planting. This suggests that the phytotoxic effect of *G. sepium* is transient under field conditions, and that application of mulch or green manure shortly before planting greatly reduces the problem, but that owing to the rapid decomposition of *G. sepium* leaves it is important to plant within one to two weeks of application.

Hedgerow management

A great deal of research has focused on the management of *G. sepium* hedgerows in alley farming systems. Planting density, cutting height and cutting frequency, and age at first cutting can all be manipulated to increase output from the system as a whole. In practical terms, management generally comprises a balance between maximizing leaf biomass production, companion crop production and weed suppression with minimizing shading and socio-economic costs (principally labour). Sections 5.2 and 5.3 discuss spacing and management in detail.

4.5 Fodder

Gliricidia sepium is among the best-known and most widely-researched forage tree legumes. Its prominence is derived from its high nutritive value for ruminants, in terms of both chemical composition and animal production; its high leaf biomass production, sustainable over many years of repeated pruning or coppicing; and its provision of dry season green fodder. Although normally deciduous in areas with highly seasonal rainfall, the leaves are retained well into the dry season on resprouts following pruning (Plate 4E), allowing it to be used as a source of dry season fodder if managed under a regular cutting regime.

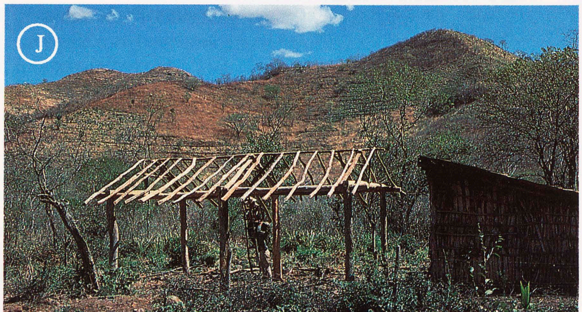
Toxicity problems have been encountered when *G. sepium* is fed to non-ruminants. There are no reports of toxicity to ruminants, although palatability seems to be a constraint in some parts of the tropics. Interest in *G. sepium* as a fodder has been further heightened in recent years in the search for alternatives to *Leucaena leucocephala*. This was the most widely used tropical tree fodder until its decimation by the defoliating psyllid *Heteropsylla cubana*, which spread throughout the tropics from the mid-1980s to the mid-1990s.

Leaf biomass production

There have been many studies of Gliricidia sepium leaf biomass production under a range of climatic and edaphic conditions, and under various management regimes differing with respect to variables such as establishment methods (seedlings versus stakes of various sizes), plant spacing, pruning height and pruning frequency. Values reported for annual leaf dry matter production generally range from about 2 t ha^{-1} (Wong and Sharudin, 1986) to 20^{-1} t ha (Sriskandarajah, 1987). There is a wealth of published data on leaf biomass yields, mainly from alley cropping experiments, but it is often difficult to make direct comparisons between these, or to predict yields on other sites, because genetic, environmental and management effects can, between them, result in the tenfold range of yields cited above.

Vegetative propagation from large cuttings (stakes) usually gives higher productivity initially, but once plants grown from seed are well established the difference in productivity tends to disappear. In an establishment trial in Nigeria, stakes gave higher leaf production for the first four harvests after establishment, but by the fifth (one year after the first) the differences were no longer significant (Atta-Krah and Sumberg, 1987). Propagation from stakes is discussed further in Section 5.2.

Gliricidia sepium managed for leaf production, whether in line or block plantings, is generally planted at very close spacing with frequent pruning at about 0.5-1.0 m above ground level. The optimum frequency of pruning for leaf production depends on the local climate; clearly trees can be



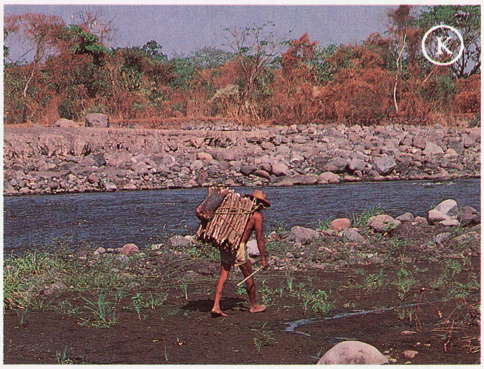


Plate 4 cont.
F - Live fence on cattle farm near La Entrada, northern Honduras
G - Closely spaced and interwoven live fence, Bali, Indonesia
H - Goats eating *G. sepium*, Nuevo León, Mexico
J - *G. sepium* posts used in house construction, Linaca, Choluteca, Honduras
K - *G. sepium* fuelwood collected off-farm, Retalhuleu, Guatemala
L - *G. sepium* shading tea in Sri Lanka

lopped more frequently in the wet than in the dry season. In general, total annual biomass yield increases with less frequent cutting, but as this also increases the wood:leaf ratio the effect of cutting interval on leaf yield is less pronounced (Ivory, 1990). For *G. sepium* grown in the humid tropics and used only for fodder, a cutting interval of six to twelve weeks is usually recommended. On a subtropical site in Australia, however, Gutteridge and MacArthur (1988) obtained higher leaf yields from one harvest per year than from three to six harvests. The effects of pruning height and frequency are discussed further in Section 5.3.

Where *G. sepium* is being grown in pure plots for leaf biomass production (protein banks), high planting densities give reduced yield per plant, owing to competition, but high total yield per unit area (Ella *et al.*, 1989). In a spacing experiment in Indonesia, with a herbaceous forage (*Panicum maximum*) grown under *G. sepium* planted at 5000, 10000, 20000 and 40000 trees ha^{-1}, the highest leaf biomass production per hectare was at the highest density, but the pattern of variation in grass production under the trees was more complex. In the wet season harvests, grass production tended to be lower at higher tree densities, while the opposite was true during the dry season (Ella *et al.*, 1991). This suggests that in this experiment, light was the limiting factor to grass growth during the wet season, and moisture during the dry season, when the shade provided by the denser plantings of *G. sepium* was actually beneficial to grass growth.

Nutritive value and effects on animal production

Leaf chemical composition

Evaluation of the feeding value of *Gliricidia sepium* leaves in terms of their chemical composition and *in vitro* digestibility reveals a highly nutritious fodder, high in protein, low in fibre and highly digestible. Nutritional data from a number of studies are summarized in Table 4.3.

Table 4.3 Summary of nutritive value estimates for *Gliricidia sepium* (source: Glover, 1989)

Component	Range
Gross energy (kcal kg^{-1})	4600-5000
In vitro digestibility (%)	48-77
Crude protein (%)	18-30
Acid detergent fibre (%)	18-34
Neutral detergent fibre (%)	27-50
Crude fibre (%)	13-30
Ether extract (%)	4-8
Ash (%)	6-10
Calcium (%)	1-2
Phosphorus(%)	0.2-0.3

Gliricidia sepium is also very low in extractable tannin, as measured by the acid-butanol assay for condensed tannins (Porter *et al.*, 1986) or the radial diffusion method for protein precipitation activity (Hagerman, 1987). There is some evidence that significant amounts of tannin may be bound to the cell wall fraction (Reed, pers. comm.)[1], but the high digestibility of *G. sepium* in the rumen suggests that this does not adversely affect the nutritive value.

Panjaitan (1988) found that in Indonesia *G. sepium* leaves had a higher crude protein content in the wet season than in the dry season. The dry matter digestibility is increased by the addition of energy sources such as cassava to the diet (Ademosun *et al.*, 1985); conversely, the digestibility of low quality feeds can be increased by the addition of legume leaves (Ivory, 1990).

Effect on production in ruminants

Gliricidia sepium is generally used as a high protein supplement to low quality feeds such as grass, straw and other crop residues, although it may also occasionally be fed alone; for instance Perera (1992) reported its use in Sri Lanka during the dry season as a sole feed for domestic goats. According to Kabaija and Smith (1989), *G. sepium* can provide all livestock mineral requirements if fed as a sole feed, except for copper and phosphorus which may need to be supplemented. The use of pure *G. sepium* is unusual, however, even during the dry season. Liyanage and Wijeratne (1987) found that with Sri Lankan heifers a *G. sepium*/*Brachiaria milliformis* (grass) mixture (50% of each in the diet) gave greater live weight gain than *G. sepium* alone. According to Preston and Leng (1987), the response curve for growth rate of steers in Colombia fed on King grass (*Pennisetum purpureum*), supplemented with increasing levels of *G. sepium*, reached a maximum at about 30% *G. sepium*. This result is in agreement with much of the research published to date, that about 30% is the level at which the *G. sepium* protein is most effectively used in mixture with low quality basal feeds. It is usually uneconomical to use higher levels of protein-rich feeds; if the nitrogen:energy ratio becomes too high, the extra protein may be used to provide metabolic energy through gluconeogenesis, rather than contributing amino acids for synthesis of new protein (in tissue, milk *etc.*). This is an energetically inefficient metabolic option, as reflected in the reduced gains observed at supplementation levels above about 30%.

There are many reports of improvements in animal production (both meat and milk) in both large and small ruminants when *G. sepium* forage is used as a supplement. For Tabasco sheep in Mexico, intake and dry matter digestibility both increased when *G. sepium* was used as a

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supplement, up to 30% of the diet, with grass hay (Nochebuena and O'Donovan, 1986). Chadhokar and Kantharaju (1980) found that *G. sepium* supplementation levels up to 80% increased survival and growth of Bannur ewes and lambs in Sri Lanka, and Van Eys *et al.*(1986), among others, have demonstrated an increase in live weight gain for goats fed Napier grass supplemented with *G. sepium.* For large ruminants, Chadhokar and Lecamwasam (1982) and Premaratne (1990) reported increases in live weight gain for milking cows and buffalo respectively on low protein diets supplemented with *G. sepium*, although supplementation levels over 50% are reported to cause tainting of milk.

Although most studies on the use of *G. sepium* as a supplement have compared basal diet offered alone and supplemented with *G. sepium*, there has also been some research on the potential for this and other leguminous forages to substitute for concentrates in mixed diets. Richards *et al.* (1994a, 1994b) investigated the effect of replacing concentrate with *G. sepium* as a supplement to King grass (*Pennisetum purpureum*). In an experiment with concentrate comprising 40% of the diet as the positive control, substitution of half of this with *G. sepium* gave a significant reduction in live weight gain in growing goats (Richards *et al.*, 1994a). This was thought to be due to lower available dietary energy in the diet containing *G. sepium.* In a second experiment with lactating goats, substitution of half the concentrate ration with *G. sepium* gave no reduction in milk yield, when dried banana (*Musa paradisiaca*) was added to the *G. sepium*-supplemented diet to equal the energy content of the control diet (Richards *et al.*, 1994b). The conclusion from these studies was that *G. sepium* can substitute for up to 50% of concentrate without loss of production, but only in isoenergetic diets.

Effect on production in non-ruminants

While reports of *G. sepium* as a feed for ruminants are almost universally positive in terms of its effects on animal production, the picture is very different for non-ruminants, which generally do not thrive on *G. sepium* and may indeed display clear signs of poisoning. The use of *G. sepium* leaves, seeds and bark as a rodenticide is discussed in Section 4.7. Ahn (1990) found that rats fed a diet containing 20% dried leaf showed reduced intake, weight loss and foetal deaths. Non-ruminants are generally more susceptible to toxic compounds than ruminants, which have the potential to metabolize them in the rumen (Norton, 1994).

Studies of the use of *G. sepium* leaves as a feed for chickens and rabbits (Cheeke and Raharjo, 1987) have given some disappointing results in terms of animal production. For rabbits fed dried leaves *ad libitum*, *G. sepium* gave much lower intake, live weight gain and *in vivo* digestibility, as well as appearing less palatable, than either *Leucaena leucocephala* or *Sesbania grandiflora*, despite appearing equally promising in terms of leaf chemical composition. This is, however, in contrast to the results obtained by Onwudike (1995) who found higher live weight gain and fewer signs of toxicity with *G. sepium* than with *L. leucocephala* fed to growing rabbits in mixture with concentrates.

Cheeke and Raharjo (1987) found that *Gliricidia sepium* leaf meal fed to chicks significantly depressed growth, even when comprising only 10% of a mixed diet. In this experiment no signs of toxicity were observed, although the authors mention eye cataracts, blindness and death in ducks and chickens fed *G. sepium* in an earlier, unpublished study. In a similar study in India, chicks were fed *G. sepium* as 5%, 10% or 15% of a mixed diet for 18 weeks (Mishra *et al.*, 1977). Depression in intake and live weight gain was only observed at the 15% level, which also resulted in 40% mortality associated with liver and kidney damage. Cheeke and Raharjo (1987) suggest that the anti-nutritive factor may be a non-protein amino acid; another possibility is coumarin, a low molecular weight phenolic compound that occurs in fresh leaves at levels up to 0.7% of the dry matter (Wina *et al.*, 1993), and is a precursor of phyto-oestrogens which can cause infertility and abortion in sheep (Cox and Braden, 1974).

Palatability

The high nutritive value of *G. sepium* and its positive effects on production should make it an ideal feed for ruminants. There is, however, a problem with its acceptability to livestock that has limited or even prevented its use as fodder in many parts of the tropics, despite the major contribution it could make to animal nutrition in these areas. There is no evidence that *G. sepium* is toxic to ruminants, but perceptions regarding its palatability vary greatly around the world, and there are many reports of limitations to its use because of animals' reluctance to eat it (*e.g.* Lowry *et al.*, 1992, for Indonesia; Dharia *et al.*, 1993, for India). However, palatability appears to be more of a problem in some parts of the world than in others. In some areas, such as Colombia and Sri Lanka, there seems to be no palatability constraint, and as a result *G. sepium* is an important dry season feed in both these countries.

The cause of the unpalatability is not known, but it is thought to be due to the odour of the leaves; animals seem to reject *G. sepium* on the basis of smell, without tasting the leaves. One secondary compound thought to contribute to the characteristic smell of the leaves is coumarin. It is widely believed that palatability is improved by wilting the leaves for several hours before feeding them. Merkel *et al.* (1994), however, carried out a preference test with sheep in Indonesia and found no significant difference in acceptability between wilted (for 6 or 24 hours) and unwilted leaves. If palatability is determined by coumarin or other volatile compounds released from the leaf surface, these may be lost on wilting; Merkel *et al.* suggest that low coumarin levels in the material they used may have been responsible for the lack of effect of wilting in their experiment.

In Queensland, where tropical forage tree legumes are being tested for use in systems where hedgerows are browsed by cattle, both *Leucaena leucocephala* and *Calliandra calothyrsus* are showing promise but research on *G. sepium* has been largely abandoned because of the animals' refusal to eat live material from the hedgerows (Palmer, pers.comm.)[2]. In villages around Ibadan in southern Nigeria, the ILCA Humid Zone Programme established feed gardens of *Leucaena leucocephala* and *G. sepium*. Goats browsing in these areas eat all the *L. leucocephala* but leave the *G. sepium* untouched. However in Sri Lanka, Perera (1992) reported that *G. sepium* cannot be used as a live fence in goat pastures because of browsing of stems and bark as well as leaves. The need to wilt *G. sepium* before feeding it is thus not universal. Conversely, in areas where there is a serious palatability problem, even wilting does not always improve the acceptability to a level where *G. sepium* is readily adopted as a feed.

A second aspect known to be important in getting animals to accept *G. sepium* is accustomization. Carew (1983), in an experiment in southern Nigeria in which *G. sepium* was fed as a sole feed to sheep and goats previously unexposed to it, found that the animals' intake decreased, with considerable weight loss, in the first three weeks of the experiment. After this both sheep and goats started to gain weight slowly, but it took up to 15 weeks for intake to rise back above initial levels. Thereafter, however, both intake and live weight gain continued to increase up to the end of the experiment at 21 weeks. There are many examples of animals eating *G. sepium* without any problem on research stations, because they are well accustomed to it, but farmers reporting palatability problems when attempts are made to disseminate the research results. Even where animals are initially reluctant to eat *G. sepium*, however, they will usually start to eat it willingly if they are given time to become accustomed to it (*e.g.* Madany, 1992, in Somalia).

Other possible determinants of palatability include the physiological and phenological state of the plant at the time of cutting; climatic or edaphic effects on leaf chemical composition; differences in behaviour or in rumen flora between animals of different breeds, or animals living under different conditions; and genetic variation in the *G. sepium* itself. The last of these has been investigated further by Larbi *et al.* (1993), and in provenance-based feeding trials coordinated by the Oxford Forestry Institute (see Section 8.3). These studies all showed clearly that sheep and goats could and did discriminate between provenances, but that the local land race, to which they were accustomed, was preferred over any other provenance.

The possibility that leaf age could affect palatability was raised by Rodríguez *et al.* (1987). In an experiment with three periods, mean daily dry matter intake of *G. sepium* dropped from 1.5 kg per animal in the first period to less than 0.5 kg in the third. *In vitro* digestibility and protein content both rose over the course of the experiment, but dry matter content dropped, suggesting that younger leaves were being used as the experiment progressed. The drop in intake without any apparent associated reduction in nutritive value suggests a loss of palatability. This could have been caused by the difference in leaf age, but other explanations might have been the effect of season, or the fact that the leaf material came from different sites in the different periods. The use of material from different sites could introduce genetic or environmental variation, or both.

Management of *G. sepium* feed to overcome palatability problems (Source: Lowry, 1990)

- Wilt foliage before feeding.
- Offer mature rather than young (newly-flushed) foliage.
- Offer for prolonged periods, without alternatives, until intake increases.
- Pen unaccustomed and adapted animals together.
- Temporarily add molasses or salt.

Although it has been suggested that coumarin might affect acceptability of *G. sepium* through metabolic effects, Wina *et al.* (1993), working in western Java, showed that coumarin is completely metabolized *in vitro* over 48 hours by rumen flora from sheep, and addition of extra coumarin *in vitro* has little effect on dry matter digestibility of *G. sepium*. Although the effect of coumarin in the rumen may be affected by the composition of the rumen microflora, this study suggests that if coumarin is indeed a determinant of palatability, it is more likely to affect the smell and taste of *G. sepium* than its degradability in the rumen.

Management for fodder

The main role for *Gliricidia sepium* as a fodder is in cut-and-carry systems (Plate 4H), providing a high-protein supplement to lower-quality feeds, particularly in the dry season when no green herbaceous vegetation is available. An advantage of *G. sepium* in this regard is that it responds to pruning by retaining its leaves for longer into the dry season. In its native range the dry season is pronounced, with five consecutive months (December to April) receiving less than 10 mm mean rainfall (Hughes, 1987). During this period the *G. sepium* trees become leafless, then flower and set seed. The same phenological pattern occurs throughout

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[2] *B. Palmer, CSIRO Davies Laboratory, Townsville, Queensland, Australia.*

the tropics wherever the dry season is pronounced, but the leaf fall can be prevented by pruning before the onset of the dry period. Since availability of dry season forage is a major constraint to animal production in many parts of the tropics, *G. sepium* can make an important contribution in this role (*e.g.* Liyanage *et al.*, 1990).

The increased palatability of *G. sepium* on wilting makes it generally more suitable for cut-and-carry than for browsing systems. Foliage may be obtained from live fences or from more intensive production systems including alley farming and protein banks. The latter two systems have been the subject of detailed research but the extent to which they have been adopted by farmers is very variable. Details of spacing and management of *G. sepium* to maximize fodder production are discussed in detail in Sections 5.2 and 5.3.

Silage

Conservation of *G. sepium* foliage as silage is one possible strategy to increase availability of protein-rich dry season feed. Research on this at CATIE (Kass and Rodríguez, 1987; Pezo *et al.*, 1990) has shown that in *G. sepium* silage a high proportion of the nitrogen fraction is in volatile form (ammonia) which would be lost during fermentation. This is associated with low levels of lactic acid. Preconditioning, by addition of readily fermentable carbohydrate sources such as molasses or chopped sugar cane, decreases ammonia and increases lactic acid concentration. Studies using different levels of sugar cane molasses suggest that 2% is sufficient as an additive before fermentation. Initial feeding experiments suggest that silage prepared in this way is readily eaten by goats (Pezo *et al.*, 1990).

4.6 Shade and support for crops

One of the common uses of *Gliricidia sepium* is as a shade for perennial crops (tea (Plate 4L), coffee, and cocoa). Its traditional use as a shade tree, and as a nurse tree for shade-loving species, is reflected by one of its common names in its native range, *madre de cacao* (mother of cacao): it is also used as a nurse tree for cacao in other parts of the world, including the Philippines (Perino, 1979) and Indonesia (Glover, 1989). Attributes contributing to its value as a shade tree include its fine, feathery foliage giving light shade, and the ability to withstand repeated pruning and to resprout vigorously. This allows the shade to be manipulated so as to vary in intensity in different seasons. Managed under a regime of 'low shade' (*i.e.* with repeated cutting), *G. sepium* trees need replacing every eight to twelve years. In very dry areas, where the shade trees might compete with the crop for moisture, the *G. sepium* is pruned at the onset of the dry season, both to reduce water loss through transpiration and so that the prunings can be applied as mulch for further conservation of moisture (CATIE, 1991). The nitrogen-fixing ability of *G. sepium* is an additional advantage on some sites; but on acid soils, for instance in the tea gardens of Sri Lanka, the pH is too low for effective nitrogen fixation. However the trees still contribute to soil amelioration through the provision of organic matter and 'minor' elements such as copper, molybdenum, zinc and boron (Kathiravetpillai, 1990). The establishment and management of shade trees is discussed further in Sections 5.2 and 5.3.

Gliricidia sepium is also widely used as a support for climbing crops such as black pepper, yam and vanilla; again, the shade from pollarded regrowth on the live supports can be manipulated to optimize conditions for the crop whilst providing useful secondary products and services such as green manure and nitrogen fixation. The management of crop supports is discussed in more detail in Section 5.3.

4.7 Other uses

Poles and posts

Although *G. sepium* does not produce large diameter logs, its wood is highly preferred in parts of Central America for poles, used as support struts in house construction (Plate 4J), and as 'mother posts' in live fence establishment (Colindres *et al.*, 1995). CATIE (1991) and Hughell (1990) have undertaken experiments in natural and planted stands to determine growth rates in Central America. Mature trees planted for high shade over coffee, which have never been pruned, can reach heights of 19 m and diameters of 26 cm at 30 years of age (Salazar, 1984). These trees have probably benefitted from the fertilizer applied to the coffee.

It is rare for *G. sepium* to be managed exclusively for pole production but this is discussed briefly in Section 5.3.

Crop protection

Some evidence exists to suggest that *G. sepium* can protect certain crops from fungal, insect and viral attack. *Gliricidia sepium* hedgerows have been found to reduce the incidence of disease in groundnut inter-crops. In an experiment in Ivory Coast, Schroth *et al.* (1995) found that the incidence of rust (*Puccinia arachidis*) and late leafspot (*Phaesariopsis personata*) was much reduced in plots where groundnuts were inter-cropped with *G. sepium* hedges, compared to sole cropping plots. It is possible that the *G. sepium* mulch acts as a physical hindrance to the dissemination of spores by wind and rain. These diseases commonly strike approximately 40 days after sowing; careful timing of the application of mulch can therefore help to minimize infection. It is also suggested that *G. sepium* mulch has a fungicidal effect, thus dispensing with the need to burn crop residues which is the recommended practice for reducing the incidence of leafspot.

Schroth *et al.* (1995) also reported that *G. sepium* hedges in Ivory Coast acted as a diversionary host of *Aphis craccivora*, the main vector of the rosette virus which is responsible for considerable damage in groundut. It is possible that the abundant foliage of *G. sepium*, when it resprouts during the cropping season, attracts the insect vector away from the leaves of the groundnut. In Sri Lanka, *G. sepium* planted in tea plantations has been observed to act similarly as a diversionary host to control the spread of the low-country live-wood tea termite (*Glyptotermes dilatatus*)(Liyanage, 1987). Swarms of the insects are attracted to the freshly-cut stumps of lopped *G. sepium* trees.

Medicinal and fungicidal properties

Gliricidia sepium has a number of traditional medicinal uses in its native range in Central America. Using data from ethnobotanical surveys in Guatemala, Caceres *et al.* (1993) evaluated the antifungal properties of 52 plant species. *Gliricidia sepium* was shown to have high activity against several common skin fungi (*Aspergillus flavus, Epidermophyton floccosum, Microsporum canis* and *Trichophytum rubrum*), which it is used to treat in traditional medicine. In another study, in Panama, a crude extract of *G. sepium* was again found to be among the most active of 28 species tested for antifungal activity, in this case against *Candida albicans* and *Cladosporium cucumerinum* (Rahalison *et al.*, 1993). As in Guatemala, *G. sepium* in Panama is used in traditional medicine to treat fungal complaints.

Rodenticide

The toxicity of *G. sepium* to rodents has led to its use as a poison in Central America. This is reflected both in one of its common Spanish names in Latin America, *mataratón* (rat killer), and in the word *Gliricidia* (from the Latin *glis*, a dormouse, and *caedere*, to kill). To use *G. sepium* as a rodenticide, the leaves, seeds or powdered bark are mixed with cooked rice or maize and allowed to ferment for several days (Glover, 1989). The mechanism of toxicity of *G. sepium* is not understood. Coumarin may be implicated: the related haemorrhagic compound dicoumarol (Warfarin) is a commercial rodenticide. Sotelo *et al.* (1986) found a heat-stable toxin in *G. sepium* seeds which killed mice within a week of feeding. This could be canavanine (2-amino-4-guanido-oxybutyric acid), a non-protein amino acid which they isolated from the seeds.

Bee forage

Gliricidia sepium flowers prolifically in areas with a pronounced dry season. Its attraction for honey-bees (*Apis* sp.) makes it a useful species for honey production. There are reports of its value from several parts of the world including Colombia (Domingo, 1993) and India (Gupta, 1993).

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5 Propagation and Husbandry

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5.1 Seed collection and storage

Good procedure for seed collection, handling and storage is important whether the seed is destined for research purposes or for dissemination by afforestation programmes. Careful selection of parent trees can reduce the likelihood of inbreeding and thus maintain a greater degree of genetic diversity. Appropriate handling and storage can prolong significantly the viability of the seed and maximize germination rates. In this section, guidelines are given for the collection, handling and storage of seed destined for planting programmes rather than specifically for research (selection strategies in seed collection for research purposes are discussed in more detail in Section 8.1).

Selection

Gliricidia sepium is an insect-pollinated outcrossing species and it is therefore desirable, when planning seed collections (see Section 3.2) to select a large number of trees within a given population with sufficient distance between them to minimize the likelihood of co-ancestry. Hughes (1987a) and Willan (1985) recommend the random selection of at least 25 trees per provenance collected and, given that during dehiscence seed may travel distances of 37 m, a distance of 50 m or more between trees is recommended.

Selection of seed trees

- Collect seed from at least 25 trees.
- Select trees that are at least 50 m apart.
- Avoid selecting trees for their appearance (phenotypic selection).
- If possible, avoid collecting seed from fence lines.

The selection of parent trees based purely on phenotypic characteristics should be avoided unless selection for a particular trait, such as stem straightness, is sought. This is because the appearance of the tree gives no indication of important attributes such as product quality or responses to management. The temptation to collect seed only from the most accessible trees, such as those found close to roads or with particularly heavy seed set, should be resisted. If seed is to be collected from fence lines or other vegetatively propagated material, only a few clones may be represented and inbreeding depression may be seen in future generations. Seed should therefore never be collected from a single fence line. In programmes where farmers are encouraged to collect seed from their own trees for personal use or for sale, an important message to convey is the need to collect seed from a large number of trees to minimize the risk of inbreeding.

In any seed collection programme, it is important to have a good understanding of the timing and intensity of flowering and fruiting. Within its putative native range, *G. sepium* normally flowers profusely and predictably. In a study of floral phenology in Honduras in 1990, it was observed that only 17 trees (4.1%) of two years of age failed to flower out of a total of 394 trees. This figure rose slightly for the same trees in 1991 to 26 trees (6.5%), but only nine trees out of the 394 failed to flower in either year (2.2%). *Gliricidia sepium* flowers and fruits in the dry season while leafless. Leaf fall usually occurs in January or February and flowering normally takes place between January and March. Hughes (1987a) observed that the timing of flowering and pod set was strongly related to altitude; at higher elevations (900 m and above), peak seed ripening can occur up to two months later than at sea level. Seed collection programmes within the native range, therefore, can be planned to take advantage of this staggered timing of seed production (see also Section 3.1).

Hughes (1987a) also observed that within the native range flowering and fruiting generally occur synchronously at a given site. It takes around 40 days from flowering to pod ripening and most individuals within a population will disperse their seed within a 20-day period. This has important implications for seed collection planning as peak seed production occurs within a relatively short period of time.

Outside the native range of *G. sepium*, particularly where it has been cultivated in more humid environments without a pronounced dry season, seed production can be very low. Low pod set has been observed in the humid regions of Central America and Mexico (Hughes 1987a), in Sri Lanka and Hawaii (Glover, 1986), and in Nigeria (Sumberg, 1985). This could be the result of a less pronounced dry season or, as Hughes (1987a) suggests, the result of other factors such as an absence of pollinators or the fact that much of the material cultivated in these areas is of limited clonal origin.

Seed collection

It is generally good practice to collect seeds when they are mature (Willan, 1985) as they have a higher germinative energy and are likely to remain viable for longer periods in storage. Collecting mature seed is not always possible, however; it has already been mentioned that the synchronous flowering and fruiting of *G. sepium* at a given site means that peak seed maturation can occur over a relatively short period of time. In order to extend the collection period, seed can be harvested either before it is completely mature or from the ground after it has been shed.

Seed collection

- Wherever possible collect seed from mature pods (when the pods are yellow/brown in colour).
- Green pods can be collected shortly before maturity so long as they are dried carefully in a well-ventilated place, first in the shade and then in the sun, to complete ripening.
- Seed can be collected from the ground so long as there has been no rain since it was shed, but this can be time-consuming and seed will be of unknown parentage.

By far the easiest way to make a seed collection is to collect mature pods from trees (Plate 5A). Mature pods are yellow or brown in colour and extremely brittle. Depending on the size of the tree, pods might be hand-picked or removed with a long-handled pruner. Pod ripening is usually quite synchronous within a tree obviating the need to make several collections from the same tree at periodic intervals (as is the case with *Calliandra calothyrsus*). Seeds of *G. sepium* are naturally shed through explosive dehiscence. Accordingly, some eye protection should be worn when collecting very mature pods to prevent injury.

Viable seed can be extracted successfully from green pods although the stage of ripeness has a large bearing on the germination rate and long-term viability. Iji *et al.* (1993) reported higher germination rates in seed harvested later and noted that the time between sowing and emergence was shortest with mature seed. Green pods should only be collected when there is no alternative. Hughes (pers. comm.)[1] has observed that there is a critical size to which the seed and pods grow after which they begin to shrink as they ripen. Dehiscence then takes place after 10-14 days. Seed can be collected successfully at the time of maximum seed and pod size. Salazar (1988) estimates a yield of 300 g to 400 g of clean seed per tree. Once collected, if the pods are still fleshy, they should be dried in a well-ventilated place, first in the shade and then in the sun (or artificially), as soon as possible (Plate 5C). Seed extraction and handling is discussed in more detail below.

Hughes (1987a) successfully collected seeds from the ground at several sites. As long as climatic conditions are favourable and it has not rained since the seed was shed, this is a very good method. The advantages of ground collection are that the seed is fully ripe, and dries whilst exposed on the ground, thus reducing its moisture content substantially. This is beneficial for storage. Seed collected from the ground is easily identifiable by its darker brown 'tanned' appearance (Plate 5B). The principal disadvantages of ground collection are the increased possibility of insect predation and the fact that collection needs to take place from all parts of the population, oweing to the mixing which occurs when the seed dehisces. It is also very labour-intensive with as little as 0.5 kg per day being collected per person (Hughes, pers. comm.). Germination rates for seed collected from the ground, however, are generally very good.

Seed production from individual trees can be enhanced by pollarding. It was observed that repeated pollarding of trees from which seed was collected at Retalhuleu, Guatemala, gave a dramatic increase in seed yield in subsequent years. Approximately 75% of the seed crop was collected from the 150 or so trees of this provenance in successive years from 1991 to 1995, although pollarding did not begin until 1992. The seed yield for the years 1991-1995 were 7 kg, 5 kg, 10 kg, 18 kg and 29 kg respectively. Aken'Ova and Sumberg (1986) however, found that cutting trees retarded pod set in Nigeria. If collections are made from natural stands it is important to leave sufficient seed for natural regeneration of the stand. No more than 75% of pods should be removed from any one tree.

Seed predation does not seem to be a major problem in *G. sepium*. It is not attacked by bruchids as is seed of many other Central American woody legume genera (*e.g. Acacia, Calliandra, Leucaena*). Infestation of pods by caterpillars may, however, destroy three or four seeds per pod.

Seed handling

The time between collection and extraction is critical and is often overlooked (Bonner *et al.*, 1994), resulting in damage and subsequent poor germination and low viability. This is

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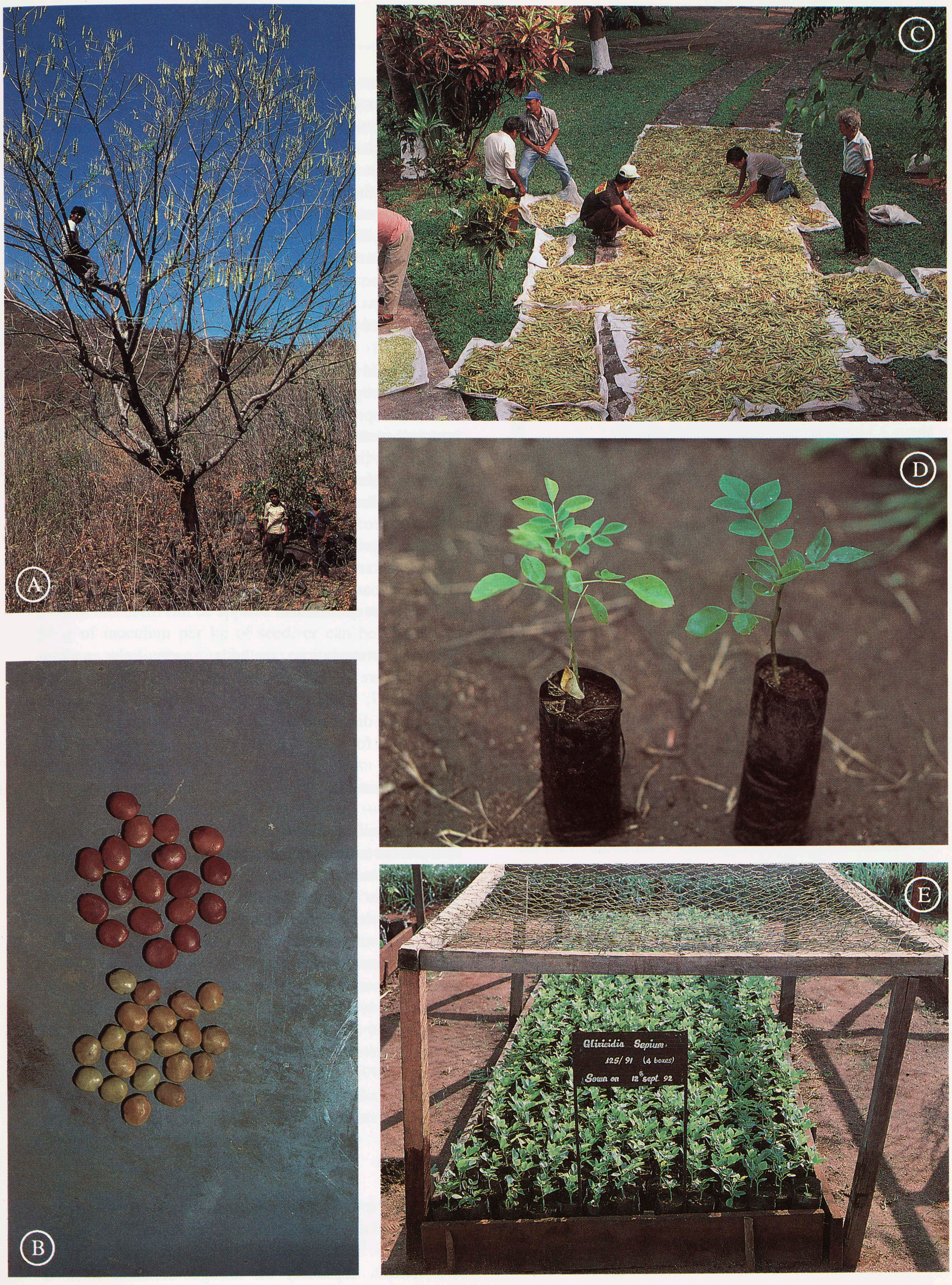

Plate 5

A - Collecting mature seed, La Garita, Honduras

B - Seed collected from ground (dark) and from pods (pale)

C - Spreading pods out evenly to dry, Retalhuleu, Guatemala

D - Unnodulated (L) and nodulated (R) seedlings, FRIM, Zomba, Malawi

E - Retalhuleu provenance seedlings in the nursery, ICRAF, Machakos, Kenya particularly true of seed which has been collected when not fully mature. It is important to avoid overheating in the drying process because the combination of moisture and heat will increase the chance of infection by saprophytic fungi. Pods should be dried in the sun but piled no deeper than about 15 cm, and should be regularly turned. They can be spread out on plastic sheets on the ground, taking care to erect barriers around the drying area to collect the seed when it dehisces. Re-wetting of pods once dry (by rain or dew) should be avoided. If green pods are dried too slowly then the pods do not dehisce spirally, but lose moisture gradually and never split, making seed extraction extremely difficult. Seed that has been collected when not completely mature can germinate successfully with good after-ripening but its long-term viability may be reduced. From 50 kg of freshly harvested green pods, Sumberg (1984) obtained about 2.3 kg of seed.

Once pods have been collected and field-dried, extraction of seed is relatively easy. The temptation to open pods manually should be avoided as seed will dry too quickly (Hughes, pers. comm.). Pods should be allowed to open naturally and then can be threshed manually in sacks to separate the seed from the pods (Sumberg, 1984). Insect predation is low for *G. sepium* seed but the removal of trash and damaged or infected seed will minimize the risk of future pest and disease infestation and will also improve germination rates in the nursery (Bonner *et al.*, 1994).

Storage

Seed moisture content and temperature are the critical factors in ensuring the viability of seeds over long periods in storage. Orthodox seeds, such as *G. sepium*, can tolerate a very low moisture content of less than 10% (Bonner *et al.*, 1994). The lower the seed moisture content the lower the temperature at which the seed can be stored. Cold storage is advantageous because it decreases the rate of deterioration of the seed. Harrington (1972) observed that within a temperature range of 0° to 50°C, every 5°C lowering of storage temperature doubled the life of the seed. The optimal moisture content for *G. sepium* is in the region of 6-10% for seed stored at 4°C. Under these conditions, seed can retain up to 90% germination for over ten years. If seed is to be stored in polythene bags it must be properly dried beforehand to avoid deterioration. Storage bags should ideally not allow seeds to rehydrate following drying. Seed to be stored should be properly labelled for future identification.

For farmer-collected seed, however, there will be little time between collection and sowing since seed will mature towards the middle or end of the dry season. As long as seed is properly dried it can be stored at room temperature in a dry place.

A further important consideration related to moisture content is the fact that seed collected from trees before it is fully mature, even after sun drying, will have a higher moisture content than seed collected from the ground. Moisture content and ripeness of the seed also affect its weight, which could be one reason why there is such a large range in the numbers of seed per kilogram reported for *G. sepium*. Seed size is also affected by genetic, maternal and environmental influences, and this will also affect the number of seeds per kilogram, which Hughes (1987a) places in the range 4700 to 11000.

5.2 Propagation and establishment

One of the advantages of *G. sepium* is the ease with which it may be propagated vegetatively (Glover, 1989). Within much of tropical America and its exotic range this is the principal method of propagation, especially in areas where seed set is limited because there is no pronounced dry season. Where seed is available, it can either be sown directly at the planting site or raised in the nursery as container seedlings, bare root seedlings or stump cuttings. Selection of propagation technique will depend upon various factors such as the objective of the planting, environmental factors such as soil fertility, the resources available, labour and transport constraints.

Standard propagation methods, particularly nursery techniques, are well reported elsewhere (*e.g.*, Weber, 1977; Rojas, 1987; Shanks and Carter, 1995), so propagation methods are discussed only in so far as they are specific to, or important for achieving the best results with, *G. sepium*.

Seed preparation

Gliricidia sepium is an easy species to raise in the nursery. Pretreatment (scarification, hot water or nicking) of the seed is not necessary, particularly where fresh seed is used. Whiteman *et al.* (1986) observed no improvement in germination rates when seeds were scarified. The seed coat of *G. sepium* is not as hard as that of other legumes and seeds germinate readily once they come into contact with water (Hughes, 1987b). Some authors (*e.g.* CATIE 1991) recommend soaking seed in water at room temperature for 24 hours prior to sowing if the seed is over a year old. Seed does not require hot water treatment to enhance germination as Gupta (1993) suggests. Seed that has been stored under appropriate cold storage conditions should maintain viability for many years, as described in Section 5.1.

Inoculation

Gliricidia sepium fixes atmospheric nitrogen through a symbiotic relationship with *Rhizobium* bacteria in nodules on the roots. This symbiosis is essential for healthy plant development, especially on nitrogen-deficient soils. If *G. sepium* is to be established in countries where it is not native or naturalized, it is advisable to inoculate seeds or seedlings in the nursery (Plate 5D) with suitable strains of

Rhizobium. This is because early survival and growth is superior where nodules are present. Whiteman *et al.* (1986) observed poor performance of non-inoculated seedlings planted in Queensland, Australia. In trials in Malawi, Ngulube (1989) observed greater shoot and root growth in inoculated seedlings. Some authors, however, have observed that plants can establish themselves satisfactorily without inoculation; (Cobbina *et al.*, 1990; CATIE, 1991) by nodulating with local microsymbionts present in the soil. *Rhizobium* from *Calliandra* and *Leucaena* species can be effective in forming nodules on the roots of *G. sepium* (Turk and Keyser, 1992) and successful nodulation has also been achieved by using *Rhizobium* isolated from species from different continents such as *Sesbania* species (MacDicken, 1994). Little, however, is known regarding the capability of different provenances to nodulate with or without their specific strains of *Rhizobium;* Dart (pers. comm.)[2] observed notable differences in Pakistan. Relying on the possibility of locally compatible strains of *Rhizobium* already existing in the soil of an exotic site can, therefore, be a risk.

Inoculum can be obtained from Agroforester Tropical Seeds in Hawaii[3]. The inoculum is stored in sterile dry peat and must be kept sealed and refrigerated, and used within six months. Inoculum can be applied as a coating to seed using 50 g of inoculum per kg of seed, or can be applied to seedlings as a slurry using 5 g, mixed with water, per 1000 seedlings (Hughes, 1987b; Glover, 1989).

Direct sowing

Although direct sowing may appear to be an attractively cheap and easy method of establishment, results can be very variable. Whilst Hernandez (1983) reported survival rates of 75% to 85% using fresh seed in Costa Rica, trials in Honduras (Barrance, pers. comm.)[4], Cameroon (Tonye *et al.*, 1994) and Nicaragua (Foletti, 1994) resulted in survival rates of 31%, 52% and 31% respectively. Barrance also observed a significant variation in germination depending on the age of the seedlots used. It is therefore important to use fresh or well-stored seed. Direct sowing requires large amounts of seed, usually three or more times the amount required to produce the same number of plants in the nursery. Given the limited availability of good quality *G. sepium* seed, it is not therefore recommended unless large amounts are available locally.

Direct sowing can, however, be a successful method of establishment, especially when it is incorporated into the farming system, as in contour hedgerows within agricultural fields or in alley cropping. Aken'Ova and Sumberg (1986) obtained good results from direct sowing hedges in southwest Nigeria, and successful contour hedgerow establishment by direct seeding has also been achieved by farmers in the Philippines. This method of establishment has also proved popular with farmer researchers in the Republic of Benin (Versteeg and Koudokpon, 1993). Foletti (1994) found that even though survival in direct-sown contour hedges in Nicaragua was only 31%, farmers were more satisfied with this method of establishing contour hedgerows than the previously used method of stump cuttings which resulted in lower survival. In this instance, direct sowing was successful compared to the other methods tried.

Direct sowing of *Gliricidia sepium*

- No seed pre-treatment is required.
- Use fresh seed wherever possible, or seed that has been well stored.
- Ploughing the area to be sown will improve survival and reduce weed growth.
- Sow the seed just after the start of the rainy season.
- Three seeds should be sown per hole at a depth of 1-2 cm.
- Regular weeding, preferably hoeing, is required until trees become established.
- Generally not suitable for superior (selected) seed, as large amounts needed.

Direct sowing requires good land preparation, preferably ploughing, which eliminates early weed competition at the time of sowing and assists germination. In a trial in Nigeria, survival and growth of *G. sepium* directly sown in guinea grass pasture was assessed using different establishment and maintenance techniques (Cobbina, 1994). Survival and subsequent growth was much better if disc-ploughing was used to prepare land, and hoeing was carried out to weed the trees, than if hoeing was used for land preparation and no weeding took place. Seed is normally sown superficially at a depth of 1 to 2 cm. Trials by Barrance (pers. comm.) in Honduras showed better germination and survival from seed sown superficially rather than more deeply.

Seed should be sown at the start of the rainy season and when soil is more than just superficially humid. Heavy rain storms can uncover seed sown close to the surface; Laurie (1974), with reference to African savanna conditions, recommended waiting until the rains are established before sowing so as to avoid the initial heavy storms often associated with the onset of the rainy season. Seeds can be

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[2] *P. Dart, University of Queensland, Brisbane, Australia.*

[3] *Agroforester Tropical Seeds, P.O. Box 428, Holualoa, Hawaii 96725, USA.*

[4] *A.J. Barrance, Fferm Nanteos, Moriah, Aberystwyth, Dyfed SY23 4EA, UK.*

sown by hand, seed drill or hand-jabber directly into cultivated soil. Three seeds per hole are recommended (Glover, 1989; CATIE, 1991).

The main cause of mortality after direct sowing is seed predation. Apart from this, weeding after sowing is probably the key factor in survival. Weeding, and later thinning of plants to the desired spacing, can place a heavy burden on labour which is already stretched in those areas with a strongly seasonal agricultural calendar. At least three or four weedings may be required in the first season alone. In farmer-managed experiments in Honduras, for example, it was shown that *G. sepium* was difficult to establish by direct sowing unless several weedings were carried out (Kowal, pers. comm.)[5].

Nursery seedlings

Seed can be sown directly into containers or into nursery beds to produce bare-root seedlings and stump cuttings. Given the reliability of germination in *G. sepium* (usually 80-90%), and the manageable size of the seed, it is not necessary to use germination beds. Seeds can be sown directly into containers or nursery beds, thus avoiding the disturbance to the root system which may occur during pricking-out. Container seedlings are more expensive to produce but have a higher survival rate once planted out.

Containers

A wide range of nursery containers is available. They must be large enough to provide sufficient space for root development and for free drainage. In the case of polythene pots or tubes, black is preferable as it minimizes the growth of algae that is common in clear plastic containers. Pots of 10 cm x 15 cm laid flat have been used widely and successfully (Plate 5E).

Soil mixture

Standard methods for preparing potting mixtures are well developed in most nurseries. The mixture should have enough cohesion to form a root ball that does not disintegrate on removal of the container, but be friable enough to allow water to infiltrate and roots to penetrate. Soils with a high clay content should be avoided as *G. sepium* does not tolerate waterlogging.

If no inoculum is available and planting is going to take place in an area new to *G. sepium*, soil should be collected from under other leguminous species with the chance that suitable strains of *Rhizobium* may be present. This soil should be added to the potting mixture (5-10% by volume) after soil sterilization, so as not to kill the *Rhizobium*.

Sowing

Two seeds per container should be sufficient given the high germination rate for the species. They should be sown to a depth of 1 cm. In nursery beds, seed is sown either 30 cm x 10 cm apart or 15 cm x 15 cm apart (Glover, 1989; CATIE, 1991). Germination normally begins in three to four days and usually is complete after 12 to 15 days (Hughes, 1987b; CATIE, 1991). Once seedlings have reached 5 to 6 cm in height, the first leaves begin to appear. At this stage, where germination has been good, seedlings can be pricked out and used to beat up areas of the nursery beds or containers where germination has been poor (CATIE, 1991).

Management

Shading is particularly important in the early stage of seedling development, especially after pricking out. In Nigeria, Cobbina (1990) observed poor performance of *G. sepium* seedlings exposed to direct sunlight in the nursery. Liyanage and Jayasundera (1989) also reported that seedling performance was superior under shading compared to direct sunlight. In a trial that varied the intensity of shading, they found some genetic variation in tolerance to shade. Generally, however, *G. sepium* does not perform well under heavy shade; a dappled and adjustable shading system is preferable. Excessive shading can be as damaging as none at all, by reducing photosynthesis and therefore growth. A few weeks before planting out, all shade should be removed to allow the plants to harden off.

Gliricidia sepium grows quickly in the nursery and roots may perforate containers. It is therefore recommended that containers arranged on the ground should be moved regularly to prevent the roots from penetrating the ground. Some root pruning may be necessary, particularly if seedlings have been in the nursery for a long time.

Planting out

Gliricidia sepium grows fast and is normally ready to plant out in the field after 10 to 12 weeks, when seedlings should ideally be 30 to 40 cm tall. A common problem with raising *G. sepium* in containers is that seedlings spend too much time in the nursery and become 'leggy'. Container-grown seedlings of over 50 to 60 cms tall should be cut back to about 10 cm before planting.

Container-grown seedlings, provided they have been well looked after in the nursery and planted out correctly, usually give excellent results in terms of survival. Planting practice for seedlings is well known but it is worth mentioning that, because of the strong root development in *G. sepium* seedlings, root pruning probably will be necessary before planting. Planting should take place at the start of the rainy season (in bimodal climates, at the start of the longer rainy season). Planting holes ideally should be twice the height of the container (usually 30 cm x 30 cm x 30 cm) but in harsh

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[5] *T. Kowal, ODA Technical Officer, Proyecto CONSEFORH, Aptdo. 45, Siguatepeque, Honduras.*

conditions, such as stony sites, larger planting holes are recommended. Mulching and micro-catchments can also improve survival in less favoured environments (see Weber, 1977; Carter, 1987; Khosla and Puri, 1993).

The usual measures to protect newly-established trees from fire, weed competition and browsing animals should be taken, but it is worth mentioning that *G. sepium* appears to tolerate fire damage (Section 3.1) and in general to be palatable only to animals that are accustomed to it (Section 4.5). In countries with no tradition of using *G. sepium* as fodder, animals are unlikely to browse it and there is less need to protect young trees from livestock (*e.g.* Versteeg and Koudokpon, 1992).

Site Requirements

- *G. sepium* does not tolerate frost.
- Avoid planting in areas where night temperatures fall below 5°C.
- Avoid soils that are heavily compacted or prone to waterlogging.
- *G. sepium* will tolerate acidity but not where there are high levels of aluminum in the soil.
- Rainfall requirements for *G. sepium* are not exacting. It can tolerate 6-8 months of dry season and rainfall as low as 600 mm.

See Section 3.1 for a more detailed discussion of habitat.

Bare root seedlings and stump cuttings

Bare root seedlings and stump cuttings are prepared from seedlings raised in nursery beds. Their chief advantage, besides the cheapness of production costs relative to container seedlings, is their ease of transport. Experiences in Central America suggest that stump cuttings in particular are an appropriate and successful method of propagation for *G. sepium* (CATIE, 1991). Salazar (1988) reports 80% survival rates for stump cuttings established in Costa Rica and Barrance (pers. comm.) also reports good survival rates (69%) in a trial in southern Honduras. A further advantage of stump cuttings is that if the planting season is poor or plants are left over, they can be kept in the nursery until the next year. Experience of planting bare root seedlings is rather limited with *G. sepium.*

Bare root seedlings need to stay in the nursery for at least three to five months until they have reached 60 cm to 90 cm in height and 1cm to 2 cm in diameter. Plants for stump cuttings often need up to a year in the nursery. Unused bare root seedlings can therefore, be planted out as stump cuttings at a later date. At planting time, seedlings are removed from the nursery beds by wetting them thoroughly and carefully uprooting them. It is important to keep the seedlings moist until they are planted; Glover (1989) recommends smearing the roots with mud to reduce moisture loss during transport to planting sites. Stump cuttings are produced from older plants with diameters of at least 2 cm (CATIE, 1991). The stem is cut 10 to 20 cm above the root collar and the roots are cut 15 to 20 cm below the root collar. If the cuttings are placed in sacks or polythene bags and kept damp (*e.g.* packed with moss), they can last for up to two weeks in storage (Salazar, 1988).

Bare root seedlings need no preparation before planting and should be planted as soon as possible after having been dug up, at the start of the rainy season. Stump cuttings, on the other hand, should be wounded by making cuts with a sharp knife just before establishment, so as to stimulate growth, and are usually planted one to three weeks before the start of the rains, thus taking advantage of their dormant state (CATIE, 1991). The principal concern with transplanting stump cuttings, and bare root seedlings in particular, is the possibility of damaging the roots. Planting holes must be large enough to allow the roots to hang freely and not spiral or bunch up prior to filling. The same size planting hole as for container seedlings is recommended by CATIE (1991).

Vegetative propagation

Gliricidia sepium is propagated most commonly by cuttings and indeed the ease with which leafless cuttings root is considered to be one of its most desirable features. Striking percentages can be greater than 90% (Litzow and Shelton, 1991). It is because of this characteristic that it has earned the name 'quick stick' in Jamaica and the Philippines, and has become so important for live fencing. Furthermore, the labour input required to prepare the stakes is minimal in comparison to other propagation methods, and the stakes can be planted for fencing, contour hedges, shade or crop supports some time before the rainy season when demand for labour in strongly seasonal environments is not so intense. Cuttings, however, may not always be the most appropriate method of establishing *G. sepium* on poor soils, acid ones in particular. Maclean *et al.* (1992) report that on acid upland soils in the Philippines, seedling survival was much higher for seedlings (70-100%) than for cuttings (0-43%). They found that aluminum in the soil induced drought stress, which increased the susceptibility of the cuttings to termite attack. Evensen *et al.* (1994) also report poor cutting survival (11% after four years) on acid upland soils with high aluminum saturation levels in Indonesia.

Individual trees and provenances differ tremendously in the number of cuttings that they can produce per year and the productivity of the regrowth. It is also likely that certain clones (or provenances) root more easily than others. The main disadvantage of cuttings has been the narrow genetic base from which so many trees have been propagated, not exploiting fully the available genetic variation. Dawson *et al.* (1995), using molecular analyses (see Chapter 7), found that five individuals they sampled in a fence line in Guatemala were identical and originated from a single clone. The cutting is genetically identical to the tree from which it has been cut and this has implications for maintaining sufficient diversity to protect against disease or insect attack.

Within tropical America, large *G. sepium* stakes are most commonly established at wide spacing to support barbed wire in live fences, usually associated with extensive cattle ranching, whereas on smallholder farms in Asia, for example in the Philippines, Sri Lanka and Indonesia, much smaller cuttings are planted at very close spacings to erect a dense and impenetrable stock-proof fence.

Preparation and establishment

Age, diameter, length, planting depth, season of preparation and phase of the moon are some of the factors taken into consideration by farmers when they prepare and plant cuttings. Cuttings can be prepared just a few days before planting, or earlier if well stored. Most farmers in tropical America cut and prepare their stakes one full lunar phase prior to planting in order both to cut and to plant the stakes during a waning moon (Baron *et al.*, 1987). Establishment failures have been attributed to the cutting and preparation of stakes under a waxing moon. Baron *et al.* (1987) conducted a trial to examine the effects of timing of cutting and planting on establishment. They found that if stakes were prepared and then immediately planted, it made no difference to establishment which phase of the moon the stakes were cut under. Where stakes were stored before planting, however, they did appear to perform better when cut and prepared under a waning moon.

Jolin and Torquebiau (1992) describe the preparation of cuttings in northwest Costa Rica. Farmers identify the trees from which they are going to prepare cuttings well in advance of planting. Selected shoots should be straight, with no branches, and are best selected from two-year-old regrowth (Otárola and Torres, 1994). According to Salazar (1988), stakes are best cut when the tree is leafless in the dry season. Although Jolin and Torquebiau (1992) report that trees with strong shoots of at least 15 cm in diameter and that can be trimmed to 2.5 m long, are selected, such large diameters are not always used; around 6 cm is more common (Glover, 1989; CATIE, 1991; Otárola and Torres, 1994). In Central America they are cut in March (late in the dry season) and stacked horizontally in the shade for one week, after which they are stacked vertically for a further three weeks with the planting end downwards. Stakes are cut in various ways (see Otárola and Torres, 1994) but most commonly are slanted at the sprouting end and wounded at the base by making several cuts with a sharp knife to stimulate root growth. Planting takes place in April, four weeks after preparation, just before the first rains begin. Stakes of 2 m or more are commonly used in live fencing and pasture planting so that the foliage sprouts out of reach of browsing livestock (Sauer, 1979). Larger stakes of this type are used to support barbed wire in live fences or for shading crops such as cocoa. They can also be used as supports for pepper, vanilla, and yam (see Section 4.6).

Preparing stakes and cuttings

Stakes to support barbed wire:

- Select shoots that are 1.5-2.0 years old, about 6 cm in diameter and 2.5 m long.
- Selected shoots should be straight and free of branches, the bark a brownish-green colour.
- Stakes should be cut with a slant at the sprouting end to prevent rotting, and wounded at the planting end to promote rooting.
- Stakes should be planted upright to a depth of roughly 40 cm.

Smaller cuttings for stockades:

- Select shoots of at least 6 months of age and 50 cm in length.
- The cuttings should be given a slanting cut at the sprouting end and should be wounded at the planting end.
- Cuttings can be planted at an angle to stimulate root growth, 10-20 cm apart.

Smaller stakes are used for establishing closely spaced fences, hedgerows and contour hedges. Litzow *et al.* (1991) tested a variety of ages and lengths of cutting material and found that the age of the cutting had a major influence on the initiation of root development. They also found that longer cuttings provided more bud sites and therefore better shoot growth; this was also observed by Yamoah and Ay (1986) in Nigeria. Litzow *et al.* (1991) concluded that for optimal results, cuttings should be from material older than six months, longer than 50 cm and with a diameter of at least 1-2 cm. The speed with which cuttings can take root and begin to produce biomass is particularly important in hedgerow systems. Palmer (pers. comm.)[6] found that in the first year after establishment, hedges grown from seedlings produced 3.1 kg m^{-1} hedge of biomass whereas cuttings produced 4.1 kg m^{-1}. Performance slows down in the second year but the advantages of early returns, in terms of a high initial production are substantial. Muschler *et al.* (1993) reported high initial biomass production, in the first years

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[6] *J.R. Palmer, Tropical Forestry Services, 3 Beechcroft Road, Oxford OX2 7AY, UK.*

after establishment. Preston (1992), however, reported greater survival and leaf biomass production of trees derived from seedlings than of those derived from cuttings. Stakes have been used in soil conservation programmes because of their ease of propagation, and when closely planted they help to form a physical barrier against erosion, but according to Bennison and Paterson (1993), plants established from cuttings have a poorer root system than seedling plants and therefore are less appropriate for erosion control. Hellin (pers. comm.)[7] found that in the reclamation of slopes exposed during road construction in Trinidad, fascines of *G. sepium* (bundles of stems 3-4 m in length) laid out along contours provided a physical barrier to erosion as well as proving to be a successful method of propagation.

Hernandez (1983) recommends planting stakes before the rainy season because they will rot if exposed to too much water before rooting commences. The top of the stake needs to be cut at a slant so that water does not collect and create potential sites for attack by pests or pathogens. It is very important to reduce competition for water early on in establishment. Otárola *et al.* (1985) recommend weeding strips along the line of establishment. Studies by Baggio (1982) with farmers in Costa Rica suggested that depth of planting has a significant influence on successful establishment. The optimal planting depth for large stakes in this study was 30 to 35 cm: too shallow, and the stakes were liable to falling over; too deep, and rotting was a problem. In general, a quarter to a fifth of the length of the stake should be buried. Otárola *et al.* (1985) recommend placing organic matter in the base of the planting holes to aid rooting.

When live fences are established in Honduras, stakes are placed at regular spacing between large diameter 'mother posts' which are placed at larger intervals, usually on corners or where there is a change of direction, to support the barbed wire until the stakes have established themselves and can support the wire on their own (Otárola *et al.*, 1985). A number of species are used for 'mother posts' including *Lysiloma* sp., *Caesalpinia* sp., *Mimosa* sp., as well as *G. sepium* (Colindres *et al.*, 1995). In southern Honduras, large diameter posts are at a premium and therefore it is common for most of them to be removed after three or four years and reused in the establishment of other live fences. Shoots will normally develop from the stakes one month after establishment (Salazar, 1993).

Stakes for shade over cocoa are usually established at the same time as the crop. Their rapid growth make them ideal for the provision of shade within a short time. Where stakes are used as crop supports, establishment will vary depending upon the crop. In the case of yams, for example, they are usually established the year before planting the crop, because the yams require shade at establishment. The management of shade for different crops is discussed in Section 5.3.

In the case of smaller hedgerow stakes, Duguma (1988) experimented with different ages of stake, depth of planting and planting angle and found that age was much more important than planting depth. Older stakes taken from near the base of the stem showed the best survival. Survival was also improved if stakes were planted at an angle rather than perpendicular. It is possible that by planting at an angle, growth hormones responsible for root formation concentrate on the lower side of the stake, thus improving root growth. In Indonesia, cuttings are sometimes planted very close together (10 cm apart) with alternate cuttings slanted at 45° and interwoven with the upright cuttings thus producing a very strong and impenetrable fence (Shelton, 1994).

Spacing

The spacing at which *G. sepium* should be established will depend upon the products and services required within the context of the physical and socio-economic environment in which it is to be grown. Research on spacing in alley cropping and hedgerow systems is well documented in the literature (*e.g.*; Friday and Friday, 1990; Maclean *et al.*, 1992; Haggar and Beer, 1993; Karim *et al.*, 1993; Kang and Gutteridge, 1994) whereas the literature pertaining to pure block planting is less extensive (*e.g.* CATIE 1986, 1991). This section provides an overview of the considerations when planning the spacing of plantations of *G. sepium* for different end uses.

Spacing options are classified here according to the primary objective of the planting. Obviously, secondary objectives are also important and plantations established primarily for service functions such as live fencing or crop support may also be managed to yield wood or leaf biomass as an important secondary function. Table 5.1 shows spacings recommended in the literature for various primary establishment objectives.

The principal question that arises when deciding upon the spacing of a plantation for wood production is whether maximizing biomass production alone should be the most important consideration or whether aspects of quality are also important. For wood production, diameter or form may be of importance if the desired end product is poles or construction posts. Quality usually is an important consideration and spacing must take this into account. Smaller spacings tend to be used where the objective is to produce large amounts of biomass, regardless of dimension or quality, over short rotations. Wider spacings, usually managed over longer rotations, are recommended for the production of larger diameter wood products and shading of crops. In a spacing experiment in Nicaragua, Maravilla and Vásquez (1995) found that wood production (dry weight) was greatest at the closest spacing tested (2.0 m x 1.5 m) but

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[7] *J.J. Hellin, NRI, Chatham Maritime, Kent ME4 4TB, UK.*

diameters were greater at the widest spacing tested (2.0 m x 3.0 m).

Andi and Blair (1989) reported that in Indonesia, higher densities (up to 40000 trees per hectare) were preferable to lower densities (down to 5000 trees per hectare) for leaf and wood biomass production. In leaf fodder production from protein banks, Gómez *et al.* (1990) found that over a range of provenances tested, all produced more biomass if spaced at 0.5 m x 0.5 m (40000 trees per ha) than at 1.0 m x 1.0 m (10000 trees per ha). Where the objective is to maximize the production of *G. sepium* biomass (leaf, wood or both) from a unit of land, as in protein banks, very close spacing is recommended. Lower individual tree productivity is compensated for by higher plant density.

If companion crops are grown with trees, however, not only density of trees is important, but also the layout, particularly in the case of hedgerows. This was demonstrated clearly by Karim *et al.* (1993) in a trial in Sierra Leone. *Gliricidia sepium* was planted in hedgerows 2 m, 4 m, 6 m, and 8 m apart, inter-cropped with maize. Within the hedgerows, trees were planted 25 cm, 50 cm and 100 cm apart. Once management was introduced in the form of pruning, the hedgerows planted 2-4 m apart with intra-row spacing of 0.5 m resulted in double the yield of the associated maize crop relative to alleys 8 m wide with intra-row spacing of 0.25 m, even though the number of *G. sepium* plants per hectare was the same. The implication is that wider distance between rows cannot be compensated for in terms of leaf biomass by closer spacing within rows. Competition within rows reduces the productivity of individual trees and can cause high mortality at establishment. This suggestion is supported by Sumberg (1986) who observed that competition between trees within rows in an alley farming system in Nigeria began if there were more than 12 seedlings established per metre of hedge, recommending a maximum of 10 trees per metre of hedge (a spacing of 10 cm between trees) within a row. Although low productivity on an individual tree basis can be compensated for by high plant densities, (as in the example of the protein bank) this assumes low mortality. According to Sumberg (1986) however, mortality can be higher than 40% for plants at less than 10 cm spacing. Karim *et al.* (1993) recommend 50 cm as a minimum within-row spacing.

In the case of contour hedgerows, very high densities of trees within a hedge (as little as 2-3 cm apart; Glover, 1989) are used, because the formation of a physical barrier is just as important as the production of leaf biomass for mulch. Productivity is therefore sacrificed to some degree. Maclean *et al.* (1992) however, found that competition between trees for nutrients in poor soils had a major effect on biomass production in contour hedges in the Philippines and therefore recommended the use of wider spacings where soil fertility is low and acidity high.

Numerous management practices will interact with spacing, including coppicing height and frequency, how and when the trees are pruned, and at what size and age they are harvested. In production systems where crops and trees are grown together, at narrower spacings, a choice has to be made between the potential benefits of high biomass production and weed suppression, and the more intensive management required to control competition for light between tree and crop. Intensity of management is a very important consideration, particularly when promoting tree planting to farmers with limited access to labour. Yamoah *et al.* (1986), for example, found that farmers in a trial in Nigeria would have preferred to plant *G. sepium* yam supports at a wider spacing than was recommended. This was because they were not only worried about tree roots interfering with the tubers, and excessive shading; they also felt that they could not commit sufficient labour to managing such a fast-growing species at the recommended spacing of 4 m x 1 m. Selecting appropriate spacing and layout may therefore involve a compromise between maximizing productivity or service provision (such as shade) and minimizing the socio-economic costs (principally labour).

The orientation of plantations is important in hedgerow establishment where agricultural crops are to be grown between the alleys of trees. Hedges should be aligned in an east - west direction so as to minimize the effect of shading and so that the crops benefit from as much sun as possible.

Table 5.1 Establishment objectives and recommended spacing options

Primary objective of planting		Recommended spacing (m)
Leaf Production	Alley cropping (line planting in hedges)	**Food crops:** 4.0 x 0.10 (Kang and Mulongoy, 1987) 2.0-6.0 x 0.10-0.50 (Atta-Krah and Sumberg, 1987) **Pasture grasses:** 4.0 x 0.30 (Cobbina, 1994) 4.0 x 1.5 (Ezenwa *et al.*, 1995)
	Intensive leaf production (blocks at close spacing)	1.0 x 0.25 (Nitis *et al.*, 1987) 1.0 x 3.0 (CATIE, 1991) 0.50 x 0.50, 1.0 x 1.0 (Gómez *et al.*, 1990)
Wood production	Poles (blocks at wide spacing)	2.5 x 2.5, 3.0 x 3.0 (CATIE, 1991) 2.0 x 2.0, 2.0 x 2.5 (Maravilla and Vásquez, 1995)
	Fuel (blocks at close spacing)	1.0 x 1.0 - 3.0 x 3.0 (CATIE, 1991) 1.5 x 2.0 (Wiersum *et al.*, 1982; Maravilla and Vásquez, 1995) 1.0 x 1.0, 1.0 x 2.0 (Ryan, 1994)
Live fences	Fences to support wire	0.75-2.0 apart (Otárola *et al.*, 1985) 1.0 - 1.5 apart (Otárola and Torres, 1994)
	Stockades	0.2 apart (Glover, 1989) 0.1 apart (Shelton, 1994)
Shade and Support	Support and shade for climbing crops	**Yams:** 4.0 x 1.0 (Yamoah *et al.*, 1986) **Vanilla:** 2.0 x 2.0, 3.0 x 3.0 (Morera *et al.*, 1993) **Pepper:** 2.5 x 2.5 (Seibert, 1987b; Gunaratne and Heenkende, 1993)
	Shade for perennial crops	**Cocoa:** 6.0 x 6.0 - 12.0 x 12.0 (Sánchez and Dubón, 1994) 3.0 x 3.0 - 6.0 x 6.0 (Seibert, 1987a) 1.5 x 3.0 (Alvim, 1988) **Coffee:** 2.0 x 2.5 (Gunaratne and Heenkende, 1994) 5.5 x 5.5 (Salazar, 1984) **Tea:** 6.0 x 6.0 (Wadasinghe and Sheikh, 1994)
	Shade for cattle	10.0 x 10.0 over pasture (Bennison and Paterson, 1993)
Erosion control	Contour hedges	2.0-3.0 x 0.5 (Bennison and Paterson, 1993) 4.0-6.0 x 0.15-0.2 (Nuberg and Evans, 1993)

5.3 Management

Management is determined largely by the objectives of the planting and the spacing and layout used. The frequency of management, although also influenced by which product (or products) is desired, is determined to a greater extent by biological considerations such as growth rates and the ability of the tree to recover after cutting, and by labour availability. Two key characteristics of *G. sepium* are its ability to resprout after cutting and to root from vegetative cuttings; systems of management have developed to exploit these characteristics. Little is known about possible provenance variation in rooting ability but some data are available on the response of different provenances to repeated cutting (see Section 8.2).

The productivity of different management systems has been discussed in some detail in Chapter 4, so in this section systems of management are described and yields are only presented to illustrate the advantages of certain management practices.

Pruning and pollarding are the two main management activities associated with *G. sepium*. The distinction between the two techniques is a fine one, the difference generally being the objective of the management. Pruning (cutting at 0.3 - 1.5 m) is usually carried out to stimulate leaf production, as in hedgerow cultivation or fodder protein banks, whereas pollarding (cutting at 2 m or above) typically is for the production of wood biomass, as in the maintenance of live fences. Other management systems include short rotation woodlots managed for fuelwood by coppicing (cutting at ground level), and live fences managed for fodder by frequent pollarding. Trees managed with shade or crop support as the primary objective can also produce leaf biomass or woody biomass, or sometimes both. It is, however, simplest to divide management techniques used for different plantation systems into the two broad categories of leaf and wood production.

Leaf biomass production

Management options

Gliricidia sepium is most commonly managed for leaf biomass in the form of hedgerows as part of alley cropping or alley farming systems and associated methods for erosion control (*i.e.* Sloping Agricultural Land Technology (SALT), developed in the Philippines). The layout and spacing of these hedgerows will be determined by whether the leaf biomass is to be used for green manure or fodder, and whether erosion control is a primary objective. Management regimes will vary accordingly and although alley cropping has been the focus of much of the literature and research effort (especially in the 1980s), management of *G. sepium* for green manure can be applied to many different farming systems. Other beneficial outputs such as weed suppression and fuelwood production can also result, depending upon the intensity of the management system employed.

In many of these management systems, availability of labour is a key consideration. The SALT system as practised in the humid tropical conditions of the Philippines, for example, entails the pruning of hedgerows as frequently as every month at a height of 0.4 -1.0 m. This system can provide substantial yields of biomass (10 t ha^{-1} yr^{-1} dry matter yield) but at the cost of high labour input. Laquihon and Pagbilao (1994) stress that labour requirements reduce as the system establishes itself and requires less maintenance. Contour hedgerow management can be more labour-efficient than other methods of erosion control. As described in Section 4.4, establishing and managing contour hedgerows (using very closely-spaced trees) is a less costly and more effective way of creating physical barriers against soil erosion than terrace construction, as well as contributing organic material to the soil.

The way in which hedgerow technologies affect, and are affected by, within-household processes (the division of labour, responsibilities and differing interests) is increasingly being shown to make the adoption of hedgerow technologies very difficult (David, 1995). Farmers may appear to be convinced of the benefits of hedgerow intercropping and applying green manure but often do not feel that the long-term benefits are worth the extra labour requirements. Hedgerows have proved to be particularly difficult to adapt to farmer conditions in drier areas, where the sale of labour off-farm is a critical survival strategy. In such environments, where labour is at a premium, labour-intensive hedgerow technologies may not be appropriate. Competition for water between the hedgerow and the crop may also be a problem in drier areas. In practice, the intensity of management in hedgerow systems will often entail a compromise between optimal management and the ability of producers to provide the necessary labour.

Hedgerows are not the only management option for the production of green manure and mulch; alternative less labour-intensive systems are also possible. In an experiment in Sri Lanka, *G. sepium* was grown under coconut plantations to improve soil fertility. The hedgerows were pruned to a height of 1.5 m every three to six months and prunings were incorporated into the soil via quarter circle trenches 30 cm from the base of the coconut palms (Liyanage and Wijeratne, 1987).

Fodder production under smallholder conditions usually takes the form of opportunistic harvesting from fence lines or hedges. The potential for more intensive fodder production systems appears to be limited by land and, to a lesser extent, labour availability. Intensively-managed protein banks are therefore a management option for larger-scale farms which have sufficient land to establish numerous protein banks with rotational harvesting. These protein banks are established at close spacing and harvested at short intervals with the objective of maximizing edible biomass per unit area. In Nigeria, Cobbina (1994) and Ezenwa *et al.* (1995) tested hedgerows of *G. sepium* established in strips in guinea grass pastures as a means of enhancing dry season fodder availability and quality. These hedgerows are managed in much the same way as hedgerows inter-cropped with agricultural crops.

Cutting regimes: age at first cut, interval and height

One of the key management considerations in leaf biomass production, and other systems involving pruning, is the age at which the first cutting takes place. *Gliricidia sepium* does not recover well from very early and heavy pruning. Most authors recommend that trees are at least one year old (or 2 m tall) before cutting commences. In general, a longer initial establishment period gives higher biomass production later (Ella *et al.*, 1991) as well as better tolerance of repeated cutting (Glover, 1989). Although studies by Muschler *et al.* (1993) and Erdmann *et al.* (1993) have not been able to find a close relation between the amount of carbohydrate concentrated in a stem and the diameter of the stump it appears that a more mature tree can accumulate sufficient carbohydrate reserves to ensure lower mortality rates and demonstrate a greater resprouting ability than younger trees. The disadvantage of having an establishment phase is that it prohibits the cultivation of companion crops in the first year because of shading. Very little information exists on the best time of year for first cutting, but experience in the seasonally dry climates of Central America suggests that the end of the dry season may be the best time (Picado and Salazar, 1984; Glover, 1989; CATIE, 1991; Otárola and Torres, 1994). In areas with no clear dry season, it is likely that the timing of the first cutting will be influenced by the requirements of the agricultural cycle.

Subsequent pruning will be determined largely by whether an agricultural crop is cultivated in intimate mixtures with the trees. If a companion crop is cultivated, as in alley cropping systems, the intensity of pruning will have to reflect a balance between minimizing shading, optimizing weed suppression and maximizing the production of leaf biomass and the companion crop; all dependent upon the spacing and layout of the trees, and their growth rate. The nature of the companion crop will also influence management regimes; crops of lower stature such as cowpeas are more prone to shading than other crops, and trees will therefore require more frequent pruning even if this means foregoing some of the biomass production that would be possible under a less intensive management regime.

Maximization of leaf biomass production does not necessarily increase crop yields in the alleys between the hedgerows. Duguma *et al.* (1988) showed that with pruning heights of 25, 50 and 100 cm, and pruning frequencies of one, three and six months, the highest total leaf biomass was obtained by six-monthly cutting at 100 cm. However, although this regime also gave the highest nitrogen yield from the prunings, the highest crop yields (maize and cowpea) were obtained by monthly pruning at 25 cm. The lower crop yields under regimes favouring *G. sepium* leaf biomass production are attributed to the shading of the crop. Thus in an alley cropping system (*i.e.* one where all the leaf biomass is returned to the crop) leaf biomass production may have to be sacrificed to avoid excessive shading. However in a system where the leaf production is not in intimate association with the crop, for instance in India where *G. sepium* is grown for mulch on the bunds of rice paddies, a longer cutting cycle and higher pruning will usually be preferable.

Recommended cutting interval and height for leaf biomass production

It is assumed that the maximization of leaf biomass yield is not the only objective. These intervals and heights therefore, reflect a balance between the yield of leaf biomass, the quality of leaf biomass, the yield of associated crops and the labour input.

Management system	Cutting Interval (months)	Cutting Height (m)
Hedgerows	1-2 (inter-cropped)	0.4-1.0
	3-6 (not inter-cropped)	1.0-1.5
Live fences, shade and support trees	6-12 (live fences)	2.0-2.5
	8-12 (shade trees)	2.0-3.0
	4-8 (support trees)	2.0-2.5
Fodder banks	2-3	0.4-0.9
	4	0-0.2

Intervals will vary depending upon climatic conditions and growth rates. In fodder banks, if lower cutting heights are chosen a longer recovery period is required.

In alley cropping systems, below-ground interactions can also be influenced by management. Schroth and Zech (1995) studied tree and crop root interactions and found that whilst frequent pruning during the cropping season sacrificed root mass and therefore some of the root system's ability to improve soil fertility, competition with the crop for water and nutrients was reduced. Sanginga *et al.* (1995), however, found that pruning could enhance below-ground contributions to soil fertility by promoting nodule senescence and decay shortly after pruning while new nodules form to continue fixing atmospheric nitrogen during shoot regrowth. Thus although it is known that high concentrations of nutrients are found in the roots, the best management to enhance root contributions to soil fertility remains unclear. It is also possible that management of root growth could have an effect on soil structure.

Where no agricultural inter-crop exists, usually in fodder banks or alley farming systems with a livestock component, the emphasis is on striking a balance between yield and quality. Longer cutting intervals may, for example, result in greater biomass production, but beyond a certain interval the additional yield consists mainly of woody material which is not desirable if leaf biomass production is the objective (Stür *et al.*, 1994). In a cutting interval trial for fodder production, Stür *et al.* found that maximum edible yield could be obtained by cutting at any time during a one month period from two to three months after the previous cut. Yield before two months was too low because the hedges had not yet had enough time to recover from the previous cutting, and yield after three months had a higher proportion of woody material in relation to edible biomass. In intensive fodder systems, therefore, it is common to find densely planted trees managed with very short cutting intervals; every six to twelve weeks is recommended in humid tropical conditions. In fodder bank experiments conducted by Gómez *et al.* (1990) in the Cauca Valley, Colombia closely-spaced trees (0.5 m x 0.5 m - 1.0 m x 1.0 m) were cut at three-monthly intervals at a height of 45 cm. The percentage of leaf biomass was found to increase as a proportion of the total biomass produced with successive prunings. If the cutting interval is short enough, regrowth consists mainly of leafy biomass and tender stems.

Cutting interval (frequency) is one of the most critical management decisions determining the productivity of species grown for green manure and fodder, and as already demonstrated, it also has an important effect on the productivity of any companion crop. Experiments by Ezenwa *et al.*. (1990) in Nigeria, with cutting intervals of one, two and three months, showed that too-frequent cutting (every month) at 5 cm from ground level, resulted in a hedge mortality rate of 50%. Root development was observed to be poor in the trees cut most frequently. They concluded that pruning reduced root weight by mobilizing sugars and amino acids from the roots to support the development of new leaf tissue. The trees cut every month also showed a low level of nodulation which, it is suggested, is related to the increased demand on roots and nodules for carbohydrates and amino acids. This finding is supported in a recent study by Schroth and Zech (1995) in which it was observed that repeated energy losses as a result of pruning led to a loss of root mass during the cropping season; too frequent pruning can lead to excessive energy depletion and root death. Ezenwa *et al.*, (1990) therefore suggest that a two to three month cutting interval is the most appropriate. In a trial which cut trees at 25 cm height every three or six weeks, results indicated that the three week cutting interval gave much less biomass than the six week interval (1.9 versus 8.3 t ha $^{-1}$) (Erdmann *et al.*, 1993).

Studies by Erdmann *et al.* (1993) also found that starch and sugar concentrations vary over the year, indicating that there must be times of the year when reserves are low and cutting should be avoided. Equally, there may be periods of high reserves when cutting should be done if maximum regrowth is the objective. This study also found that, after pruning, *G. sepium* used carbohydrates from stems to support initial regrowth as well as root reserves. This implies that cutting interval and cutting height together influence successful regrowth. The relationship between cutting height and length of recovery period will of course also be dependent upon climatic and site factors, and these vary from year to year.

Cutting height appears to influence the recovery period of pruned trees, which in turn affects cutting interval. Lower cutting heights require a longer recovery and growth period and therefore a longer cutting interval. Glover (1989) for example, recommends 40-90 cm with cutting intervals of two to three months for fodder bank biomass production whereas CATIE (1991) recommend cutting at ground level with a four-monthly cutting interval. Stür *et al.* (1994) recommend leaving some stump so as to provide more sites for regrowth. Ultimately, however, selecting a cutting height is often an ergonomic choice. Farmers in Kenya, for example, preferred to cut higher than was recommended by research results, simply because it was easier with the tools that they were using.

Green manure from hedgerows

In alley cropping, where soil conservation and enhancing agricultural crop yields are the major objectives, pruning should take place at the time when it is most likely to benefit the companion agricultural crop. This corresponds to crop establishment and periods of high nutrient demand. Large quantities of nitrogen are harvested with prunings but Sanginga *et al.* (1995) found that nitrogen recovery by the companion crop was often very low. In an experiment in Nigeria they found that of more than 300 kg N ha $^{-1}$ harvested from hedgerows, only 40-70 kg N ha $^{-1}$was contributed to the companion maize crop , a recovery of just 30%. Sanginga *et al.* (1995) partly attribute this poor recovery to a lack of synchronization between release and the demands of the associated crop. Experience with other -fixing trees popular in hedgerow systems has revealed that mixing the prunings with lower quality litter can delay the release of (Sanginga *et al.*, 1995). Jabbar *et al.* (1992) and Mulongoy *et al.* (1993) recommend applying green manure just before planting as it has the biggest impact on crop yield at this time. Lehmann *et al.* (1995) studied the synchronization of nutrient release with crop requirements and uptake and found that the peak period for demand in maize is four to six weeks after establishment, and therefore recommend applying prunings in the first two weeks after sowing. Applying mulch or manure one or two weeks before establishing the crop, however, minimizes any allelopathic effect that the leaves may have on the companion crop (Tian and Kang, 1994). The attributes of *G. sepium* mulch and its effect on crop yields are discussed in Section 4.4. The economics of mulching, however, will depend upon whether there is a discernible response from the crop. If crop response to mulching is poor, higher economic returns can be made from managing the hedgerows for fodder rather than green manure (Jabbar *et al.,* 1992). This is discussed further below.

Prunings can be laid out on the surface as mulch or incorporated into the soil as green manure. In Sri Lanka and India, *G. sepium* is laid on top of flooded paddies (Plate 4C) one or two weeks before transplanting the rice which, because of the standing water, is sufficient time for the mulch to decompose. In coconut plantations in Sri Lanka, the best results were obtained by incorporating the green manure into the soil (Liyanage and Wijeratne, 1987). CATIE (1991) also recommend this, particularly when soil is moist, although Mulongoy *et al.* (1993) report no discernible advantage in doing so. Lehmann *et al.* (1995) do not recommend the incorporation of prunings with a high proportion of twigs as green manure where termites are a problem, because they break down the matter very quickly. They recommend instead applying prunings as mulch, a method which is also less labour-intensive than incorporation, especially if carried out frequently, and gives the additional benefits of moisture retention and weed suppression. Again, the choice of management will be determined by the priorities of the producer. In older trees, woody material can constitute a significant proportion of the biomass produced. In order to reduce the labour needed to separate the firewood from the green manure, Glover (1989) recommends leaving all the prunings on the site for one or two weeks during which time the leaves fall off and the woody material can be collected easily.

Rippin *et al.* (1994) observed that *G. sepium* is not as effective in weed suppression, and that mulching is not as long-lasting, as with other species such as *Erythrina* spp. because the leaves decompose very quickly. Budelman (1988) reported that they have a half-life of only 22 days. Weed suppression will improve in shadier conditions; although management of shade is largely precluded in alley systems, this is an additional benefit in systems where *G. sepium* is used as a shade tree for valuable crops such as cocoa and coffee.

Green manure from shade trees and crop supports

Although shade is the primary function of trees established over crops such as cocoa, tea and coffee, some management systems include leaf biomass production for mulch as an important objective. Alvim (1988) describes an alley management system from Brazil for shading cocoa which relies heavily on the mulch produced by the *G. sepium* shade trees. Trees are established at 1.5 m x 3.0 m and alternate rows are pollarded every eight to twelve months to a height of 2-3 m. The prunings are incorporated into the soil and the remaining trees are gradually thinned to final spacing for permanent shade. Liyanage and Wijeratne (1987) describe another system over tea in Sri Lanka, in which trees are established 18 months before the tea is planted so that adequate shade and protection are already in place. Trees are usually planted at close spacings and are later thinned. They are pollarded or lopped twice a year, at the start of the monsoon rains, for the production of green manure which is applied to the soil. In dry areas where shade trees can compete with the companion crop for water, *G. sepium* is pruned at the start of the dry season before competition sets in. This minimizes losses through transpiration and supplies a layer of mulch to the soil to conserve moisture (CATIE, 1991).

Gliricidia sepium makes an excellent support for crops because of its upright branching habit after pollarding and generally slender branches. The management of *G. sepium* for crop supports depends very much on the nature of the associated crop. Budelman and Pinners (1987) describe a method of using *G. sepium* to support yams. The stakes are planted a year in advance so that they can establish roots and grow shade ready for the establishment of the yams. Yam requires heavy shade in the early stages of its development, and the farmers also appreciate working under shady conditions. The living poles are found to be more resistant to wind and to the weight of the crop than the dead posts previously used. Trees are gradually lopped and pollarded as the tubers develop and the yams require more light. They can also be girdled to reduce the shading gradually. In an experiment to compare *G. sepium* with *Erythrina berteroana* as a live support for yam in Costa Rica, Jímenez *et al.* (1992) found that yam tuber production was much higher under *G. sepium* than under *E. berteroana*. The authors ascribed this to the lighter and narrower crown formation of *G. sepium* which provided the correct dappled shade for the yam.

The attributes of a light and narrow crown are also important in the use of *G. sepium* for crop supports. Muschler *et al.* (1993) found that although *G. sepium* contributed less than *Erythrina* species, it provided a more open shade suitable for pepper production. Support stakes do, however, need regular pruning so as not to compete with the crop they are supporting. Once established, pepper, for example, requires more light than vanilla. In Sri Lanka, an experiment to determine leaf production of 10-year-old support poles pollarded every one to six months revealed that a four-month cutting interval provided the most leafy biomass relative to woody biomass, but that a clear relationship between pepper production and cutting interval existed. Pepper production was at its highest (4.5 kg per vine) when pruning took place once a month and was at its lowest (1.3 kg per vine) when pruning took place every six months (Gunaratne and Heenkende, 1993). Alvim (1988) found that pepper yields in Brazil were highest when dead supports were used. It is necessary therefore to sacrifice some of the biomass yield of *G. sepium* in order to maximize the productivity of the more valuable associated crop if it is light-demanding. Vanilla, however, requires moist and shady conditions, so live *G. sepium* supports are preferred and these also require less frequent pruning (Glover, 1989).

Fodder

In smallholder farming systems, fodder is usually produced in fences, boundary hedges and occasionally in small blocks, from which it is periodically lopped under cut-and-carry systems of management. Versteeg and Koudokpon (1993) observed that goats did not browse directly from hedges in an on-farm alley farming experiment in the Republic of Benin. This may have something to do with the palatability of fresh leaves (see Section 4.5 for a discussion of palatability). Cut-and-carry systems, which allow the leaves to wilt before feeding, are therefore the most appropriate method of feeding *G. sepium* to livestock.

Although *G. sepium* is not used much for fodder within tropical America, the flexibility of management which is possible with live fences means that they can be managed to provide substantial amounts of fodder as a secondary product. Experiments by CATIE (1991) resulted in up to 5 t km $^{-1}$ (dry weight) of fodder being produced from a mature live fence (see also Section 4.3). Muschler *et al.* (1993) undertook studies of leaf biomass production from trees shading cocoa plantations in Costa Rica and found that trees pollarded twice a year, at 4 m x 4 m spacing, produced 2.3 t ha $^{-1}$ dry weight.

More intensive systems of fodder production include fodder protein banks and alley farming systems which incorporate fodder as a desired end product from hedgerow management. In protein banks, trees are planted at very close spacing, to maximize productivity per unit area, and therefore require regular pruning. These systems, fodder banks in particular, cannot produce high yields of leaf biomass indefinitely and can deplete a site of nutrients. This is because the leaves, which are being removed from the site, have the highest nutrient content. The return of animal manure to the trees can help to prevent a decline in fertility but entails a significant labour input where cut-and-carry systems are in operation. Once yield begins to decline, pruning should cease, the site should be left to recover and production should rotate to another protein bank. Protein banks,therefore, are not the most appropriate method of fodder production for smallholder farmers who do not have enough land to devote areas to fodder production, and also suffer from labour constraints. Protein banks have beenestablished on larger farms such as the dairy farms of the Cauca Valley in Colombia where *G. sepium* is grown at close spacing in blocks managed by regular pollarding (Gómez *et al.*, 1990).

The concept of alley farming is similar to alley cropping (see above), except that part of the leaf biomass is fed to animals instead of being returned directly to the alleys (Reynolds and Jabbar, 1994). The relative benefits of using the *G. sepium* foliage as green manure or as fodder have been the subject of several studies by ILCA (now ILRI) in Nigeria (*e.g.* Jabbar *et al.*, 1992; Larbi *et al.*, 1993). In general, where crop yields and/or responses to mulching are low, removal of some of the foliage as fodder becomes an economically viable option. Larbi *et al.* (1993) found that maize yields in an alley cropping system increased by 54% (compared to an unmulched control) where 50% of the prunings was returned to the alleys, and by 89% when 100% was returned. In this case the proportionately lower response to the higher rate of mulching suggests that 50% could be returned to the alleys and 50% removed for fodder.

In seasonally dry tropical areas, timely cutting is a very important management tool because it can provide fodder well into the dry season, a time when uncut trees lose their leaves and feed is scarce. Trees left uncut for four to six months before the start of the dry season will generally lose their leaves. Coppicing shortly before the rainy season ends will promote growth of leaves in the dry season and if the cutting is staggered, fodder production can be guaranteed well into the dry season. In areas where a cool dry season persists, however, Gutteridge and MacArthur (1988) found that irrespective of previous coppice management, *G. sepium* lost its leaves. One option to retain feed through the dry season is to dry leaves for later use (see also Section 4.5 on silage production).

Ezenwa *et al.* (1995) have experimented with an alternative alley farming system (which they term a feed garden) in which hedges of *G. sepium* are inter-cropped with pasture grasses and cutting interval is varied during the year, depending upon the season, in an attempt to achieve year-round fodder production. Pruning every three months in the wetter part of the year produced better grass yields in the dry season by reducing shading in the period of maximum growth for grass. It also promoted tree growth (leaf biomass) in the dry season. Tree foliage made a greater contribution to total forage in the dry season than in the rainy season.

Fodder trees established at wide spacing over pasture provide valuable shade to livestock and can be an important fodder supplement in the dry season if lopped in time to produce fresh growth. Leaf fall can also provide some mulch to benefit the pasture grass (Bennison and Paterson, 1993).

Woody biomass production

Although some woody biomass is produced as a by-product of hedgerow management, it is more commonly produced from woodlots managed as coppice or as a result of the maintenance of live fences and shade trees. Most of the woody biomass produced from these systems is either for firewood or stake material to establish live fences, shading systems and crop supports. The systems are therefore self-sustaining, each tree producing woody material for the propagation of others. Where trees are left to mature, larger diameter poles and posts can be produced. As woody biomass is produced from all these systems, each is discussed below.

Woodlots

Coppicing for firewood or pole production obviously requires a longer cutting interval than leaf biomass production and, as with fodder banks, trees cannot coppice indefinitely without a reduction in yield. Site depletion can also occur. Ryan (1994) recommends that in woodlots managed for firewood production, no leaf material is removed from the site. In Timor, Indonesia, *G. sepium* is managed in woodlots cut every two to four years on ten-year cycles which means that a maximum of five harvests can be made before trees need to be replaced. So long as leaf material is not removed from the site, site deterioration can be minimized, but if land is available a period of fallow for the site is advisable. Site quality will influence growth rates and therefore rotation length. On better sites, a coppicing rotation of three years is common, whereas on poorer sites rotations of five years or more may be necessary (CATIE, 1991). Growth models for *G. sepium* developed by Hughell (1990), based on the analysis of 128 permanent sample plots in Central America, showed that trees planted on a 'good' site at 2.0 m x 2.0 m spacing (2500 trees per ha) can produce up to 16.5 t ha^{-1} on a three-year rotation, having reached maximum mean annual increment in the third year. On poorer sites, however, trees planted at the same density produce only 6.5 t ha^{-1} on a three-year rotation, not having yet reached maximum mean annual increment, and therefore requiring a longer rotation.

As in hedgerow management, the same principles of age and size of the tree at first coppicing apply, the only difference being that cutting height is generally lower, no more than 20-30 cm above the ground, so as to concentrate wood production in just a few resprouts. Subsequent management will depend upon the diameter of wood required. If larger diameter poles are wanted, then selection of shoots is recommended. This concentrates growth in the most robust and promising shoots. Experiments at CATIE (Picado and Salazar, 1984) with coppice regrowth found that retention of four shoots gave the best survival and diameter growth. If too few sprouts are selected, there is a higher risk of mortality through a reduction in photosynthetic ability, whereas if too many sprouts are selected, poor diameter growth results. Height appears not to be affected by the number of sprouts selected.

In experiments by Harrington and Fownes (1993, 1995), coppice-managed stands produced more biomass in the first nine months of growth after cutting and had a much higher stocking density than seedling stands, because of the numerous resprouts. This meant, however, that competition set in sooner than in seedling stands, resulting in the production of much smaller diameter woody biomass. Where larger diameters are required, coppice stands therefore have to be thinned to the same densities used in the establishment of seedling stands. The thinning regime will depend upon the initial spacing, growth rates, and diameters required.

Recommended cutting interval and height for wood biomass production

Woody biomass production is only a primary objective in the case of woodlot management. In the other systems it is a secondary objective and management can vary in accordance with the requirements of the other components in the system.

Management system	Cutting interval (years)	Cutting height (m)
Woodlots (managed as coppice)	Small diameter fuelwood 2-4 years	0-0.2
	Larger diameter fuelwood/poles 6-10 years	0-0.2
Live fences	every year for fuelwood	2-3
	every 2 years for stakes	2-3
Shade trees	every year (crop-dependent)	2-3
	At time of replacement of companion crop	0-0.2

Intervals will vary depending upon climatic conditions and growth rates.

In its native range, *G. sepium*'s colonizing ability makes it a common sight in disturbed areas of secondary forest and agricultural fallows (Plate 3A). Management of trees by natural regeneration is an important source of wood products in much of the Pacific region of Meso-America. This can consist of opportunistic use of whatever trees happen to regenerate on fallow land, or the selection and management of desired species. In some areas *G. sepium* is favoured over other species as a fallow tree because farmers report that it restores fertility to even the most difficult sites. During this fallow period the trees are managed for fuelwood, usually on six to eight-year rotations (*i.e.* the duration of the fallow) (Ugalde and Otárola, 1983). Martínez (1985) reported a yield of 12.3 t ha^{-1} fresh weight of fuelwood from a three-year-old fallow with a density of 630 trees ha^{-1} in Gualán, Guatemala.

At the end of the fallow period, in the dry season, the trees are cut to a height of 20 cm and the ground prepared for the agricultural crop. The better regrowth shoots are selected three to six months later (Campos *et al.*, 1990). The coppice regrowth has to be cut periodically through the farming period, to reduce shading, and the prunings can provide small amounts of either fuel or leaf biomass which is usually left on-site. Cropping typically continues for two to three years, after which the land is left fallow and the trees are managed for fuelwood once more. Farmers periodically nurture naturally regenerated seedlings to replace trees that have been coppiced many times and are beginning to deteriorate. Unlike timber species such as *Cordia alliodora*, *G. sepium* is rarely maintained in fields beyond the fallow period to grow to maturity. It is therefore uncommon to see large mature trees except in some cases where they have been maintained uncoppiced as high shade trees over crops such as coffee (see below). No reports exist to suggest that *G. sepium* is a nuisance through weediness; unwanted trees and shrubs are eliminated at the end of fallow periods during land preparation by covering stumps with soil and, because they are pruned regularly, they do not set seed.

Live fences

In Central America, the management of live fences has received a lot of attention as a low-cost system for multiple product and service provision. Otárola and Torres (1994) identified two distinct management phases, which they termed the establishment phase and the productive phase. The establishment phase can last for three to four years during which time all regrowth from the stake is removed. This ensures that a clean straight fence post is maintained but also, by reducing weight at the top of the post, stability is maintained and root development encouraged. Otárola and Torres (1994) recommend a total, or near total, prune once a year for the first three years. This phase will provide the producer with leafy and small diameter woody biomass, but because the tree has to be pollarded every year it precludes the production of larger diameter wood. By the third year after establishment the posts should be ready to support the barbed wire and, if well established, to enter into a more flexible production system.

Various management options are available for this 'productive phase' depending upon whether leaf biomass, fuel, shade or stakes for future fence establishment are required. Where fodder or green manure is the desired product, multiple resprouts are desirable but in fuelwood or stake production, the better shoots must be selected. Harvesting of fuelwood usually takes place on a yearly basis. In the native range of *G. sepium*, pollarding normally takes place at the end of the dry season when there are no leaves and when wounds are believed to heal much faster. Regular prunings of undesirable regrowth is necessary between these harvests. Living fences around agricultural fields may require regular pruning in order to control shading. Around cattle farms, however, shade is a very desirable function of the live fence, and rotations for fuel and stakes can be three to four years. Stakes for future fence establishment generally need to be at least two years old before they can be harvested. At the time of harvest, pollarding can be complete or partial, leaving a few shoots. Yields will increase as the trees mature and live fencing can remain productive for up to 30 years.

The management of live fences is flexible and can range from being carefully planned, as described above, to very informal where farmers make use of the products and services that their live fences provide, as and when they need them.

Shade trees

The ability of *G. sepium* to resprout vigorously makes it an ideal shade tree because the intensity of shading can be regulated. *Gliricidia sepium* is usually planted at close spacing to provide early shade to young plantations of cocoa and coffee and is then thinned or pollarded in such a way as to leave a final stocking density suitable for permanent shading of the crop. Sánchez and Dubón (1994) describe a system of shading for cocoa in Costa Rica where *G. sepium* is planted at 6 m x 6 m spacing (278 trees per ha). The rapid growth of the trees and the relatively close spacing means that it does not take long for adequate shade to be provided. After three years, the trees are thinned to 6 m x 12 m spacing (139 trees per ha) and then after five or six years to 12 m x 12 m (69 trees per ha). *Gliricidia sepium* is sometimes established at final spacing with bananas to provide the temporary shade for the cocoa (Seibert, 1987a). In Indonesia, closely-spaced trees (3 m x 3 m) are pollarded to 3 m at three years of age and then every year thereafter, providing a regular supply of fuelwood and mulch. This management system provided a woody biomass yield of 5.1 t ha^{-1} dry weight: enough fuelwood to dry beans from 1 ha or more of cocoa plantation (Seibert, 1987a). Where pollarding is very frequent, to maintain a light shade, trees have to be replaced every eight to twelve years.

Thinning and pollarding must be carried out with great care so as not to damage the crop underneath. At thinning, it is common for farmers to lop off the branches to lighten the crown before felling. Ring barking or girdling is also commonly practised but there is a long lag time before the leaves fall and a reduction in shading occurs, which makes this method suitable where a gradual decrease in shading is required, such as in yam production. Regular pruning and pollarding is recommended to maintain light branching. When trees are thinned, unwanted resprouting can be a problem. It is recommended that cutting takes place as close to the ground as possible and that the stumps are covered with soil to prevent regrowth (Sánchez and Dubón, 1994).

Salazar (1984) describes a system of establishing *G. sepium* high shade over coffee in Costa Rica. This system entails the establishment of trees at 5.5 m x 5.5 m (330 trees per ha). No pollarding takes place in this system, allowing trees to grow to over 19 m when mature, and without pollarding the crown remains narrow (5 m in diameter), thereby minimizing management costs. Trees are harvested when the coffee crop is replaced, which can be every 20-30 years or more. The resulting harvest of large diameter *G. sepium* timber (an average of 26 cm in Salazar's study) is prized for rural house construction. The disadvantage of this system is that only a single harvest is achieved and the farmer does not benefit from a sustained supply of firewood and leaf biomass. Salazar claims that the trees can be managed as coppice regrowth once the new crop of coffee is established but little information exists on the coppicing ability of more mature trees.

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6 Diseases and Insect Pests

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6.1 Diseases

More than thirty fungal pathogens are listed for *Gliricidia sepium* (Lenné, 1990, 1992; Boa and Lenné, 1994). Although widely grown throughout the tropics, *G. sepium* has apparently remained free of serious diseases (Lenné, 1992). Its deciduous character in seasonally dry environments may reduce the development of foliar epidemics. However, surveys by the authors, in 1992 and 1993, of natural populations and nearby managed trees in Central America and Mexico revealed two previously unknown diseases, loosely classified as virus-like (mottle and shoestring leaves) and little leaf disease. These are reported briefly in Boa and Lenné (1994). This does suggest the possibility that significant problems may exist elsewhere which have not been identified because of a lack of specialist attention to diagnosis of disease and pest problems on *G. sepium.*

Foliage disease

Cercosporidium gliricidiasis, chocolate leaf spot, causes small, light brown, rounded spots with dark brown borders and is widely recorded on *G. sepium* throughout Central and South America, the Caribbean (Lenné, 1990), Africa (Lenné and Sumberg, 1986), Southeast Asia and the Pacific. Recent surveys confirmed its common occurrence in Honduras and Guatemala (Lenné and Boa, 1994). Under humid conditions, it causes defoliation. Recent unpublished observations via ICRAF suggest that chocolate leaf spot is an increasing problem in East and Southern Africa. Leaf spot caused by *Colletotrichum gloeosporioides*, expressed as small, dark, rounded leaf spots, is more common than *C. gliricidiasis* in Nigeria (Lenné and Sumberg, 1986).

Sirosporium gliricidiae is another widespread leaf disease from the Caribbean region, Central and South America, India and Southeast Asia (Ellis, 1976; Boa and Lenné, 1994). It differs from chocolate leaf spot in that the symptoms are more diffuse, forming less definite spots and more general yellow patches visible on the upper surface of leaves. Below, dark sporing areas of the fungus with irregular outlines can occur over much of the surface. Conidia are also produced on the adaxial surface but not from superficial mycelia. *S. gliricidiae* is often associated with poorly-growing trees, on which attacks can result in moderate defoliation.

Gliricidia sepium was defoliated by *Cladosporium* sp. in Costa Rica (Glover and Heuveldop, 1985) and the pathogen has also been recorded in Jamaica and Venezuela (Lenné, 1990). Scab (*Sphaceloma* sp.), manifest as brown scab-like lesions on petioles and stems, was found for the first time on *G. sepium* in Honduras during recent surveys (Lenné and Boa, 1994). Its relation to other legume scabs is being determined. More recent unpublished observations in 1995 in Honduras, Guatemala and El Salvador show that scab is widespread on natural and planted populations. It does not appear to result in major disease losses.

Colletotrichum truncatum causes an anthracnose on *G. sepium* in India and Venezuela (Boa and Lenné, 1994). Unpublished observations from disease surveys in Honduras, Guatemala and El Salvador from 1992 to 1995 show that anthracnose is a widespread and occasionally damaging condition on young stems. Shallow necrotic patches along the length of the stem result in leaf and petiole blight. *C. truncatum* was isolated from one specimen from Guatemala.

In humid environments, or where the dry season is not well defined, seed production problems have been observed (Sumberg, 1986). These may be related to pod and seed rots of unknown cause.

Branch, trunk and root diseases

Pink disease affects *G. sepium* in Papua New Guinea (Lenné, 1990). Twig, stem and branch dieback caused by *Botryosphaeria*, *Nectria* and *Phomopsis* spp. have been recorded on *G. sepium* in Central America, Asia and Africa (Lenné, 1990) but their importance has not been documented. Collar rot caused by *Armillaria mellea* in Malawi, root rot by *Rosellinia pepo* in El Salvador and *Botryodiplodia theobromae* in India, and stinking root rot by *Sphaerostilbe repens* in Malaysia have been observed but there is no information about their importance (Lenné, 1990). De Zoysa *et al.* (1990) reported a dieback of *G. sepium* in Sri Lanka which was linked to infections by two fungi, *Merimbla* sp. and *Fusarium pallidoroseum.* The disease affected pruned or mechanically damaged trees in dry regions and began with leaf yellowing and wilting which eventually led to defoliation, dieback and stem rot.

Plate 6

- A - Tree with little leaf disease showing symptoms of yellowing foliage, reduced leaf size and dieback, Jutiapa, Guatemala
- B - Tree with little leaf disease showing characteristic bunches of yellowing leaves in only part of the crown, El Progreso, Honduras
- C - Tree with virus-like disease, La Garita, Honduras
- D - Trees at different stages of leaf loss and dieback due to little leaf disease, Gualán, Guatemala
- E - Close-up of new shoots showing abnormal leaf shoot production
- F - Comparison of healthy and diseased leaves from the same tree affected by a virus-like disease, Nuevo Concepción, Guatemala

Little leaf and virus-like symptoms

Recent wide-ranging surveys in Central America noted the common occurrence of serious little leaf disease (thought to be caused by a phytoplasma) in fence line and natural populations of *G. sepium*, especially in Honduras and Guatemala (Lenné and Boa, 1994). This was associated with extensive dieback and tree death, particularly in Honduras. A continuation of these surveys in 1995 confirmed the widespread distribution of little leaf, to include the Petén region of Guatemala around Tikal and along an approximate west-east transect through El Salvador. The condition is characterized in its early stage by a proliferation of new leaves, some of which may be distorted, and all of which are much reduced in size (Plate 6E). Observations indicate that shoots like these do not survive for long and dieback occurs (Plate 6D). Affected leaves are yellow, though the intensity may vary according to the time of year. Crown yellowing may be more pronounced at the beginning of the wet season (June-August), although there is some doubt whether this symptom by itself represents little leaf (Plate 6A). In its most distinctive form, little leaf disease results in small bunches of affected leaves which stand out against a backdrop of what may appear to be otherwise healthy foliage (Plate 6B). In its final stage, before the death of the tree, only small bunches of leaves on branches remain and have the superficial appearance of birds' nests. The cause of the disease is still unknown.

Virus-like symptoms, including leaf curl, shoestring leaves, foliar distortion, mosaic, and mottle have been noted in several natural stands of *G. sepium* in Central America (Lenné and Boa, 1994). Plate 6C shows a tree with thin, shoestring leaves, a widely distributed but relatively uncommon condition associated with a virus-like disease. It appears to be less serious in mature trees than in young seedlings. Another virus-like disease reported from Central America causes reduced leaf size, flecking and yellowing (Plate 6F). Other symptoms can include mottling and ringspot on the leaves but the disease appears to have only a mild to moderate impact on affected trees. Viruses are potentially very serious to future development of *G. sepium*, especially if they are seed-borne. Virus symptoms have also been identified in Colombia (F. Morales, pers. comm.)[1].

6.2 Insect pests

In comparison to the information available on diseases of *G. sepium*, there is a noticeable dearth of observations concerning insect pests. Standard texts concerned with forest entomology in India, for example Beeson (1941), contain no reference to *G. sepium*. Roberts (1969) notes several insects, mostly beetles, on *G. sepium* in Nigeria but none of these records is of any economic significance.

A recent account of insect pests on trees in Central America lists a number of named defoliators attacking young (less than three years old) and older trees, including *Erynnis* sp., *Hylesia lineata, Spodoptera* sp. and several other unidentified larvae, but none of these are serious problems (Hilje *et al.*, 1991). The aphid *Aphis craccivora* has been recorded widely, from India (Patel and Patel, 1971), Uganda (Davies, 1972), Trinidad (Bennett, 1985) and the Philippines (Villacarlos and Robin, 1992) but the only serious attack was that noted by Schmutterer *et al.* (1990) in the Dominican Republic. *A. craccivora* is a known vector of plant viruses, for example groundnut rosette.

Severe infestations by the striped mealybug *Ferrisia virgata*, occurred in Nigeria (Kadiata *et al.*, 1992) but only within the confines of the IITA screenhouse. Other recent records of insects on *G. sepium* record it as a food plant for pests which attack other crops. Concoctions of *G. sepium* are used to combat many insect pests and this might suggest that the tree has natural defence mechanisms which discourage insect attack. However, a review of insect pests on neem (*Azadirachta indica*) whose products are also widely applied for their natural insecticidal properties, indicates that this is a false assumption (Boa, 1995).

6.3 Other symptoms not associated with pest and disease attack

The interpretation of symptoms and diagnosis of diseases of trees is particularly difficult. Smith and Vanden Berg (1992) clearly illustrate changes to foliage of *G. sepium* that occur as a result of various nutrient disorders, thus permitting a comparison and distinction with the symptoms of conditions such as little leaf disease. The symptoms of nutrient disorders range from inter-veinal discolouration, associated with lack of zinc, to pronounced leaf yellowing and marginal necrosis caused by boron toxicity. Boron deficiency results in leaf and shoot tip blight.

Surveys in Central America demonstrate that there is a much wider insect fauna on *G. sepium* that has not yet been fully documented. It would be unwise to assume on the basis of the limited studies and observations on *G. sepium* so far that it is not very prone or susceptible to insect attack. A similar conclusion and warning should be made concerning diseases of the tree, particularly in the light of the 'recent' discovery of little leaf disease. The process of selecting superior trees for forestry and agriculture rarely takes into account any detailed consideration of pest and disease risks, which are usually poorly quantified. It is therefore important to stress the need for an adequate awareness to ensure that emerging problems are identified and dealt with swiftly. Further emphasis on maintaining vigilance arises from the distribution of new germplasm from the centre of diversity for *G. sepium* to other countries and thus the new opportunities for pests and diseases to develop.

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7 Molecular Analysis of Genetic Variation

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7.1 Rationale

Knowledge of the underlying level, structure and origin of genetic variation within and between plant populations is crucial for scientific approaches to their utilization and conservation (Yeh, 1989; Hamrick, 1993). Determinants of the level and structure of genetic variation within plant species include mating system, evolutionary history, life-history characteristics, population density and mechanisms of gene flow (Schaal, 1980; Loveless and Hamrick, 1984; Hamrick *et al.*, 1992; Loveless, 1992). In addition to the within-species issues, potentially complex interactions among species must be considered (Rieseberg and Brunsfeld, 1992; Rieseberg and Wendel, 1993). Although morphological characters and various production traits have traditionally been used to characterize levels and patterns of diversity, these traits alone represent only a small portion of the genome and are also influenced by environmental factors, thereby limiting their utility in describing the potentially complex genetic structures which may exist within and among taxa (Avise, 1994). To overcome these constraints, various molecular approaches for the detection of variation have been devised, including the use of isozymes (Tanksley and Orton, 1983), restriction fragment length polymorphisms (RFLPs) (Bernatsky and Tanksley, 1989) and, more recently, the polymerase chain reaction (PCR) (Bachmann, 1994). These 'markers' of genetic variation are generally independent of environmental factors and more numerous than phenotypic characters, thereby providing a clearer indication of the underlying variation in the genome of an organism (Avise, 1994).

The purpose of this chapter is to discuss the application of molecular markers to questions regarding the biology and distribution of *Gliricidia* which are otherwise difficult to resolve by more conventional approaches. For those readers not familiar with molecular approaches to analysis, the techniques employed are summarized briefly in Section 7.2, while Section 7.3 describes their specific application in the genus. Data are summarized in terms of implications for (a) optimum resource collection, evaluation and *ex situ* conservation; (b) *in situ* conservation; (c) seed orchard design; and (d) release of germplasm in exotic locations. Section 7.4 addresses areas for future work using molecular analyses.

7.2 Molecular approaches to analysis

Isozyme analysis

Isozyme analysis relies on the movement of enzyme molecules through an acrylamide or starch gel medium in response to an applied electric current (Tanksley and Orton, 1983). If an enzyme occurs in different forms, with different amino acid compositions, then differences in the overall ionic charges of the molecules can result, causing variation in their electrophoretic mobilities in the gel medium. Different levels of migration are subsequently detected by chemical staining of the gel for the enzyme in question. Because different enzyme forms (isozymes) are inherited co-dominantly at individual loci[1], it is possible to determine the genotype of an individual from its electrophoresis profile (Brown, 1979; Weeden and Wendel, 1990; Avise, 1994).

Isozyme analysis has been applied more than any other molecular technique to characterize patterns of genetic diversity and differentiation in plant species. The reasons for this are manifold, but include the relative simplicity of the approach, which allows data to be collected quickly from a large number of samples, the low cost compared to other molecular techniques, and its early recognition and availability in the history of marker development (Avise, 1994). Studies with tree species include those on *Cordia alliodora* (Chase *et al.*, 1995) and *Populus tremuloides* (Jelinski and Cheliak, 1992).

RFLP analysis

Restriction fragment length polymorphism (RFLP) analysis relies on the ability of enzymes (restriction endonucleases) to cut DNA at specific recognition sites within the genome of an organism (Bernatsky and Tanksley, 1989). If individuals differ in their distribution of recognition sites, so that fragments of DNA of different lengths are created after digestion, then polymorphisms can be resolved as mobility differences during agarose gel electrophoresis. Detection of variation at individual loci normally requires DNA fragments resolved by electrophoresis to be blotted on to nylon membranes and probed by a radioactively labelled

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[1] *In this case, a locus is the site in the genome encoding a particular enzyme; if a diploid individual is heterozygous at that locus, it possesses two different forms of the gene (alleles) coding for two forms of the enzyme (isozymes).*

DNA sequence complementary to the locus in question. The probe binds specifically to corresponding nucleotide sequences on the membrane, allowing that locus to be detected by autoradiography (see Avise, 1994 for details).

Although limited in use by the requirement for relatively large amounts of DNA and the long and technically demanding method of detection, RFLP analysis has been used to study genetic variation in many plant genera, including *Capsicum* (Prince *et al.*, 1992), *Leucaena* (Hughes and Harris, 1994), *Lycopersicon* (Miller and Tanksley, 1990) and *Vicia* (van de Ven *et al.*, 1993). The use of RFLP analysis in tropical trees has been reviewed by Neale *et al.* (1992).

PCR analysis

Polymerase chain reaction analysis (PCR) is a technique which allows the selective *in vitro* amplification of DNA. The logic of PCR is simple in principle. The first step in the reaction is the binding of short DNA sequences (oligonucleotides) to complementary sequences in the DNA of an organism. This is followed by synthesis of new DNA primed (initiated) by these oligonucleotides and catalysed by DNA polymerase, using supplied deoxyribonucleotide triphosphates (dNTPs), the 'building blocks' of DNA, as substrates. DNA amplification, to produce much greater amounts of the DNA than originally present, is then brought about by repeated temperature-controlled cycling through three basic steps: (1) melting of double-stranded DNA to produce two complementary single strands; (2) annealing (binding) of the oligonucleotide 'primers' to target sequences in the single-stranded DNA; and (3) extension of the primers using the target DNA as a template, thereby producing new double-stranded copies of the original DNA. Automation of the amplification process is facilitated by employing thermal cycling machines and an extremely thermostable enzyme, *Taq* polymerase, which is capable of surviving incubation at 95°C, the temperature required to melt double-stranded DNA. This obviates the requirement to add enzyme after each amplification cycle (see Vosberg, 1989 for details).

Based on PCR, a wide range of approaches has become available for the detection of genetic variation in plants and animals (Bachmann, 1994). Methods differ in the type of primers used for analysis, which can be targeted to specific regions of the genome or, alternatively, chosen at random to amplify unspecified regions. Targeted approaches include cleaved amplified product (CAP) analysis, in which the detection of variation relies on restriction endonuclease digestion of PCR products in a manner similar to RFLP analysis, but avoiding the requirement for large initial quantities of DNA or radioactive detection (*e.g.* Karl and Avise, 1992 in *Crassostrea virginica*); single-strand conformation polymorphism (SSCP) analysis, in which differences are detected as changes in secondary structure between single-stranded DNAs on non-denaturing gels (*e.g.* Orita *et al.*, 1989 in *Homo sapiens*) and simple sequence repeat (SSR) analysis, in which length variation is assessed across short iterative repeats in the genome (*e.g.* Terauchi and Konuma, 1994 in *Dioscorea tokoro*). Of the approaches based on unspecified targeting, random amplified polymorphic DNA (RAPD) analysis is the most common, relying on primers of arbitrary sequence to detect polymorphisms as the presence or absence of amplified products between individuals. In this case, the basis of polymorphism apparently reflects differences in complementarity at potential primer binding sites, either allowing or preventing binding and amplification (Williams *et al.*, 1990). RAPD analysis has been applied widely to assess genetic variation in plants, including *Eucalyptus globulus* (Nesbitt *et al.*, 1995) and *Populus* (Liu and Furnier, 1993).

PCR is particularly suitable for genetic studies of tropical tree species because very small quantities (mg) of low quality leaf material can supply the DNA required. Apart from facilitating collection in the field, this allows leaf fragments from previously collected herbarium specimens to be analysed.

7.3 Application of molecular analyses in *Gliricidia*

Molecular approaches have been used to address a number of important biological questions at different levels of geographical scale in *Gliricidia*. Analyses can be grouped under four main areas: (1) assessment of inter-specific interactions between *G. sepium* and *G. maculata*, (2) ecogeographical variation within *G. sepium*, (3) metapopulation structure in *G. sepium*; and (4) reproductive biology. Each of these areas is considered separately below, indicating the implications of the data for improved genetic resource management within the genus and the inter-relationship of data with morphological and production trait analyses.

Inter-specific hybridization between *G. sepium* and *G. maculata*

Ecogeographical, morphological and chloroplast DNA studies of *Gliricidia* suggest that the natural distribution of *G. sepium* is restricted primarily to lowland tropical dry forest areas of the Pacific coast and inland valleys of southern Mexico and Central America. In addition, a second distinct yet inter-fertile species, *G. maculata*, appears to show a separate and localized distribution in the Yucatan Peninsula (see Section 3.2; Hughes, 1987; Lavin *et al.*, 1991; Lavin and Sousa, 1995).

Although natural gene flow between coastal Pacific and more inland populations of *Gliricidia* appears unlikely due to intervening highland and rain forest regions (Lavin *et al.*, 1991), interactions within the genus resulting from the influence of man are possible yet poorly understood. There is some evidence, from a field trial in Honduras of progeny from a controlled crossing experiment, that hybrids of *G. sepium* and *G. maculata* may show reduced vigour relative to the parent species (Simons, pers. comm.[2]). If anthropogenic dispersal leads to hybridization between the species, followed by backcrossing to *G. sepium* (introgression; Anderson and Hubricht, 1938), the genetic integrity of important natural populations of *G. sepium*, which are periodically collected as seed for distribution to users (particularly Monterrico and Retalhuleu; see Chapter 8), could become threatened. Assessment of potential interactions is important, therefore, in order to define appropriate germplasm management strategies within the genus.

During ecogeographical surveying in 1993 (Dawson *et al.*, 1996), populations displaying morphological characteristics of both *G. sepium* and *G. maculata* (such as intermediate flower colour: Plate 2E) were identified, indicative of possible hybridization between the species. Evaluation of populations in the field is difficult, however, and examples from other species suggest that the complex genetic relationships which often underlie hybridization between taxa are best addressed by molecular as well as morphological analyses (Rieseberg and Brunsfeld, 1992). To investigate further the possibility of hybridization, Dawson *et al.* (1996) collected leaf material from at least five individual trees from each of 15 sites across the known natural distributions of both *G. sepium* and *G. maculata* for molecular analysis (Figure 7.1). For the Monterrico and Retalhuleu populations, twenty individuals of each were sampled. Sites were chosen in order to resolve macrogeographic interactions between the species, and included apparently 'pure' populations of *G. sepium* and *G. maculata*, as well as sites of apparently mixed ancestry, as defined by morphological characters (see Section 3.2, and legend to Figure 7.1).

Screening a range of individuals with PCR-based molecular approaches identified a set of 16 markers which were species-diagnostic (13 RAPDs, two CAPs and one maternally-inherited mitochondrial SSCP), and these were therefore employed to assess populations for inter-specific hybridization. The distribution of two RAPD markers in a subset of populations is shown in Plate 7.1. Overall, three sites, which occupied geographical positions intermediate to the known native distributions of *G. sepium* and *G. maculata* (Palenque, Belize City and Poptún), revealed combinations of markers consistent with inter-specific hybridization. This hypothesis was further supported at Palenque and Belize City by morphological observations made at the time of collection, which indicated characters of both species in these populations. At Poptún, however, molecular analysis did not correspond with morphological data, since the latter suggested the population to be of *G. sepium*. Although unexpected, other studies indicate disparity between the molecular and phenotypic classification of hybrids (Rieseberg and Brunsfeld, 1992), demonstrating the importance of supplementing morphological data with molecular approaches in order to delimit accurately the distribution of taxa within *Gliricidia*. Data at a single CAP locus, which are indicative of the overall pattern of variation among populations, are shown in Figure 7.2. Data were summarized in the form of an hybrid index, in which scores are based on the proportion of *G. sepium*-diagnostic products individuals contained. 'Pure' *G. sepium* individuals are expected to score 1 and 'pure' *G. maculata* individuals 0. Consistent with a hybrid origin, individuals from Palenque, Belize City and Poptún demonstrated intermediate values (averages for populations being 0.61, 0.35 and 0.65, respectively), while other populations had values of 1 or 0.

Taken together, the molecular data provide the first clear evidence for a hybrid zone between *G. sepium* and *G. maculata*, the presence of which is consistent with range-wide extension within the genus, under the influence of man. The occurrence of inter-specific hybridization in *Gliricidia* indicates a potential mechanism for the loss of species integrity of important genetic resource populations of *G. sepium*, such as Monterrico and Retalhuleu, especially if this is followed by introgression (backcrossing to *G. sepium*). Although the implications of such a loss in integrity are difficult to predict, the reduced vigour of artificially produced inter-specific hybrids suggests that the performance of provenances in future generations could be adversely affected. Significantly, however, 20 individuals sampled from both Monterrico and Retalhuleu displayed no evidence of gene exchange with *G. maculata*, suggesting these populations to be genetically intact at the species level (Figure 7.2), although a white-flowered mutant of *G. sepium*, ascribed to *G. maculata*, was found near Retalhuleu. To maintain the future integrity of these important populations, management strategies should strongly discourage field testing of *G. maculata* in Pacific coastal regions of Meso-America. Furthermore, if a wide genetic base is to be maintained within the genus to meet potential changes in selection requirements, conservation strategies should stress, as a priority, collection of 'pure' populations of each species positioned close to the identified hybrid zone, since as a result of anthropogenic dispersal these are the most threatened by inter-specific gene flow.

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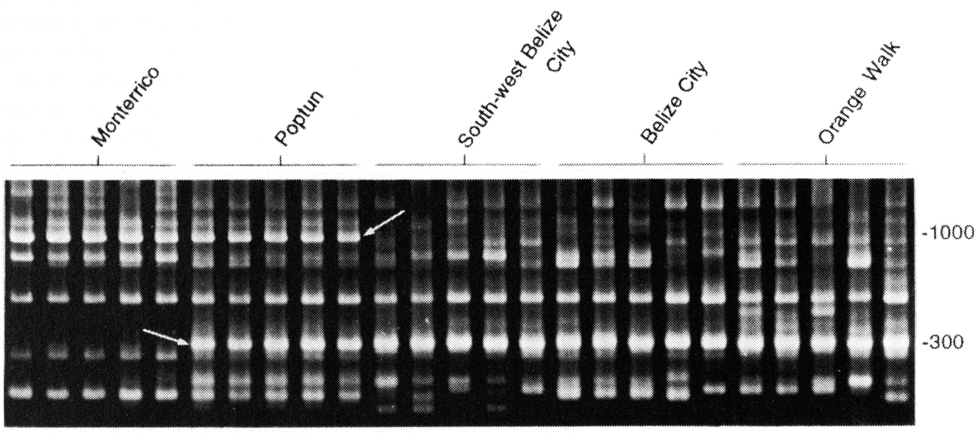

Plate 7.1 *G. sepium*- and *G. maculata*-diagnostic RAPD markers generated in a single PCR. Individual profiles from a subset of five populations are shown. Products diagnostic of *G. sepium* (1000 bp) and *G. maculata* (300 bp) are indicated. Individuals from Poptún contain both markers, indicating their hybrid character between these loci

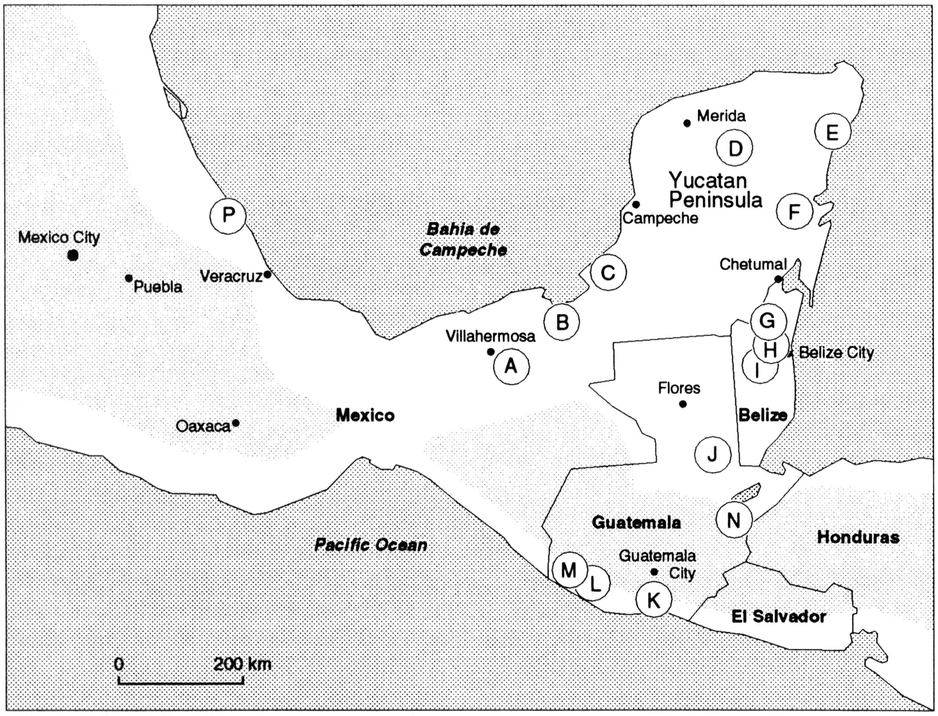

Figure 7.1 Geographic distribution of sampling localities for *Gliricidia* in Meso-America. **A** Macuspana (Gs), **B** Palenque (Gs/Gm), **C** El Aguacatál (Gm), **D** Holca (Gm), **E** Playa del Carmen (Gm), **F** Tancan (Gm), **G** Orange Walk (Gm), **H** Belize City (Gs/Gm), **I** south-west Belize City (Gm), **J** Poptún (Gs), **K** Monterrico (Gs), **L** Retalhuleu (Gs), **M** Ocosito (Gs), **N** Gualán (Gs), **P** Palmasola (Gs). Codes in parentheses indicate the designation of populations based on morphological descriptors at the time of collection. Gs = *G. sepium*, Gm = *G. maculata*, Gs/Gm = characteristics of both species. Precise morphological characterization of individual plants within populations was not possible in the field, owing primarily to sporadic flowering. Populations **K** (Monterrico) and **L** (Retalhuleu) from the Pacific coast represent important natural resources of *G. sepium* for distribution to farmers and other users (see Chapters 8 and 9). Hatched areas indicate land over 1200m in altitude intervening between Pacific coastal and more northern populations of *Gliricidia*

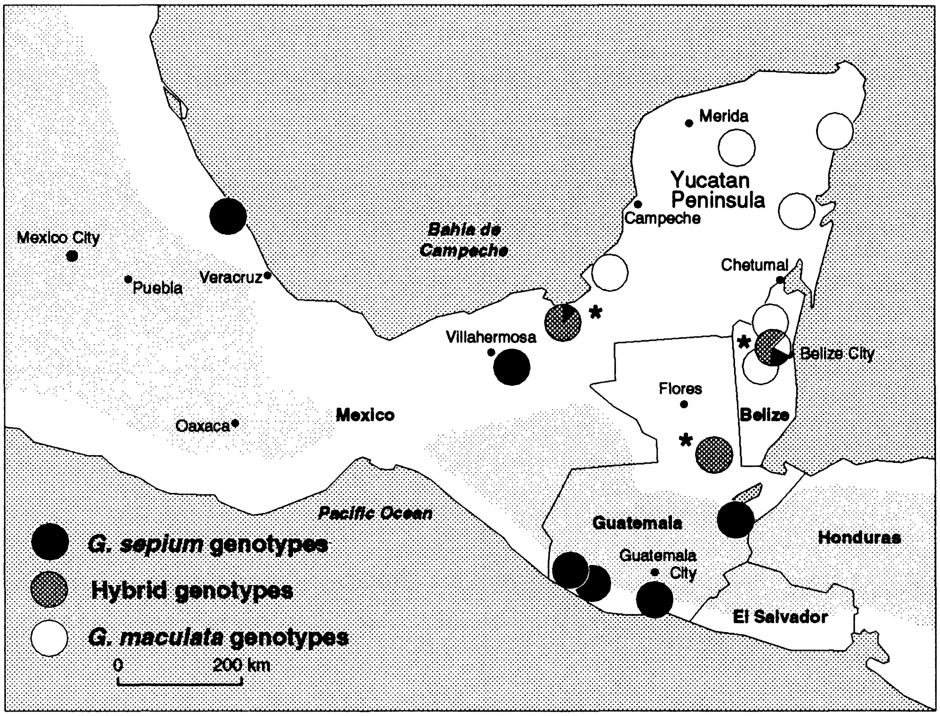

Figure 7.2 Macrogeographic distribution of G. sepium- and G. maculata-diagnostic polymorphisms in populations of Gliricidia sampled from Meso-America. Data are shown at a single CAP locus. Pie diagrams indicate the proportion of types at each site. Three populations where hybrid genotypes occurred are indicated *. Other diagnostic markers showed similar overall distributions

Ecogeographical variation within *G. sepium*

Fundamental to the efficient utilization and conservation of *G. sepium* is an understanding of the relative partitioning of genetic variation within and between populations or regions across a wide ecogeographical range. In addition to this information, knowledge about absolute levels of variation within populations is crucial for outbreeding tree species such as *Gliricidia*, since this has implications for the sustainability of resource utilization after release to farmers. This is because heterozygosity and performance may be linked in outbreeding tree species (Park and Fowler, 1982; Griffin and Lindgren, 1985; Mitton and Jeffers, 1989), and the release of genetically diverse *G. sepium* may therefore be necessary to prevent inbreeding depression during future generations, as farmers distribute seed from initial introductions to their neighbours. In addition, high diversity is important because it may provide an adaptive capacity to varying farmer requirements and promote sustainability under varying environmental conditions (Simons *et al.*, 1994).

Chloroplast RFLP analysis across geographical regions

In order to assess patterns of variation within *Gliricidia* at an ecogeographical level, Lavin *et al.* (1991) employed probes taken from a mung bean library to detect chloroplast RFLPs among 42 populations sampled from the native and exotic distribution of the genus, including the whole of southern Mexico and Central America. In total, 106 individuals were sampled. From a pilot study of selected individuals, 11 enzymes which revealed RFLPs were chosen for analysis of the populations. Cladistic analysis of RFLP data revealed five distinct chloroplast genomes. Two genomes were unique to three populations sampled from the Yucatan Peninsula, and could therefore be ascribed to *G. maculata*. The other three genomes, ascribable to *G. sepium*, showed distinct regional distribution patterns, such that genome types could be defined as "Mexico", "Mexico West" and "Central America", indicating clear differences in *G. sepium* across its ecogeographical range.

Isozyme analysis within and among populations

In order to assess the partitioning of genetic variation within and among populations of *G. sepium* over a wide ecogeographical range, Chamberlain (1993; see also Chamberlain and Galwey, 1993) employed isozyme analysis on eight populations collected from diverse locations in Meso-America (Table 7.1). For each population, eight seeds were tested from each of 20 mother trees. Preliminary screening of a range of individuals identified eight polymorphic enzyme loci (*Aat*-1, β-*Est*-1, *Idh*-1, *Lap*-2, *Pgi*-1, *Pgi*-2, *Pgm*-3 and *Sdh*-1) and these were therefore employed to assess populations. Estimates of diversity within populations (H_0), calculated according to Nei (1978), are shown in Table 7.1. In a randomly mating population, H_0 is the proportion of individuals observed to be heterozygous, averaged across all loci. A high value for H_0 implies a high level of genetic diversity. Of the populations sampled, Monterrico was the most diverse, with those from San Mateo, Retalhuleu and Ocosito also exhibiting high heterozygosity values. The least diverse population was from Pedasí, Panama. This population appears to be naturalized (*i.e.* introduced to the area rather than truly native) and may have been established from a very narrow genetic base. Overall, the relatively high level of diversity detected by isozymes in the important genetic resource populations of Retalhuleu and Monterrico indicates the potential for sustainable utilization of *G. sepium* based on these populations. Generally, there was good agreement between observed heterozygosities in populations and those expected assuming Hardy-Weinberg equilibrium (Table 7.1), suggesting that the populations are close to equilibrium with near-random mating. The populations from Belen Rivas and Masaguara, however, exhibited heterozygosities significantly lower than expected. In these cases, the apparent departure from random mating could be due to population substructuring resulting either from the introduction of germplasm from other populations or from mating between related individuals. At Masaguara, the population consists of trees on farmland which may be derived from many different introductions of germplasm, while at Belen Rivas seed was collected from trees in a planted woodlot and fence lines. The latter, in particular, are likely to have been propagated from cuttings and therefore could well be related or even of clonal origin (Hughes, pers. comm.)[3]. In these ways, human influence on the establishment and subsequent management of these populations could account for the disequilibrium observed.

Partitioning of genetic variation within and among populations according to Wright's *F*-statistic (Wright, 1951) indicated that most variation occurred within rather than among the eight populations, in accordance with predictions for outcrossing, insect-pollinated plant species (Loveless and Hamrick, 1984; Hamrick, 1989). This indicates the importance of extensive and systematic intra-population sampling for the optimal capture of diversity during seed collection of *G. sepium*. The level of differentiation among populations was still significant, however ($F_{ST} = 0.172$, *i.e.* 17% of the total detected variation), and substantially greater than the average value observed in other tropical trees ($F_{ST} = 0.119$; Hamrick *et al.*, 1992). The isozyme data thus concur with the RFLP data (above), which also showed clear differences between populations sampled from different regions; and with production data from field trials which indicated substantial differences between provenances (see Chapter 8). It is clear from all these studies that extensive ecogeographical collection is important for the optimal capture, conservation and utilization of genetic variation.

Metapopulation structure in *G. sepium*

During field trial assessment, the populations of *G. sepium* from Monterrico and Retalhuleu were identified as the most promising provenances for collection and distribution to farmers (see Chapter 8). The optimal genetic management of individual *G. sepium* populations, however, requires a detailed knowledge of local genetic structure (Yeh, 1989). The partitioning of genetic variation in *G. sepium* in both the Monterrico and Retalhuleu regions has therefore been studied in detail by isozyme (Chamberlain, 1993) and PCR-based (Dawson, 1995; Dawson *et al.*, 1995) analyses.

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Table 7.1 Collection site data and mean heterozygosities averaged over eight isozyme loci for eight populations of *G. sepium* sampled from a wide ecogeographical range in Meso-America (number of individuals per family and standard errors for heterozygosities, in parentheses)

Population	Country	Lat. (N)	Long. (W)	OFI identity no.	No. of families	Mean heterozygosities (H_0)	
						Observed	Expected
Monterrico	Guatemala	13°54'	90°29'	17/84	20 (12)	0.361(.075)	0.364(.076)
Vado Hondo	Guatemala	14°44'	89°30'	59/87	20 (8)	0.210(.063)	0.234(.073)
Retalhuleu	Guatemala	14°33'	91°39'	31/92	20 (8)	0.281(.076)	0.297(.076)
Ocosito	Guatemala	14°32'	91°46'	99/92	20 (8)	0.304(.077)	0.306(.075)
Masaguara	Honduras	14°16'	87°58'	25/84	14 (8)	0.213(.118)	0.295(.092)
San Mateo	Mexico	16°13'	94°58'	35/85	20 (8)	0.303(.065)	0.308(.069)
Pedasí	Panama	7°32'	80°04'	13/86	10 (8)	0.017(.004)	0.016(.003)
Belen Rivas	Nicaragua	11°37'	85°48'	14/86	20 (8)	0.216(.074)	0.260(.081)

Genetic structure at Monterrico

The Monterrico provenance of *G. sepium*, located close to the coastal town of the same name in southern Guatemala, was identified as an important genetic resource population during production trials because of superior leaf biomass production (see Chapter 8). Whilst trial evaluation was underway, however, further exploration within the Monterrico region indicated a much wider distribution of *G. sepium*, along a narrow (1 km wide) coastal strip, approximately 40 km in length, so that the original Monterrico population could be considered as only part of a larger and semi-continuous metapopulation. To assess whether the material sampled for testing in trials was representative of variation within this wider overall distribution, *G. sepium* was sampled for molecular analysis from an additional three locations located at 8 km intervals from the Monterrico population (Figure 7.3). This study would indicate whether the entire range could be treated as a single unit for the purpose of future sampling and evaluation.

From an initial survey of selected individuals from each site, Dawson *et al.* (1995) identified 27 RAPD and three CAP (two nuclear and one mitochondrial) markers which could be used to assess genetic variation within and between locations. In all, ten seeds from each of five trees were tested from each of the four locations. A phenogram based on all 27 RAPD markers, grouped by location, is shown in Figure 7.4, indicating a degree of genetic differentiation among locations and a direct relationship between this variation and geographical distance (compare with Figure 7.3). The Puerto Viejo region was least similar to the others. Nuclear CAP markers indicated significant allele frequency deviations among locations ($P < 0.001$) and grouped the locations in a similar way to the RAPD data (Dawson, 1995). Analysis of single individuals from each family with a maternally-inherited mitochondrial CAP marker indicated the Puerto Viejo region to be unique (Figure 7.4), confirming the genetic subdivision already indicated by the RAPD data.

Complementary to an isozyme analysis of genetic variation in the original Monterrico population (see above), Chamberlain (1993) estimated H_0 values in each of the three additional locations sampled from the metapopulation. To provide an accurate indication of diversity, 12 seeds from each of 20 trees were tested at each site. Levels of variation at the sites differed significantly, with the Monterrico population the most diverse (observed H_0 = 0.361; see Table 7.1), followed by El Banco, Puerto Viejo and then El Garitón, with H_0 values of 0.326, 0.218 and 0.171 respectively.

Overall, the combined data from both the PCR-based and isozyme analyses indicate that the Monterrico population tested in production trials cannot be considered representative of overall variation within the wider metapopulation. This has important implications for genetic management. Significant differentiation exists within the metapopulation; absolute levels of variation also differed significantly between sampled sites. In order to evaluate fully the potential of the metapopulation, therefore, future trials should involve stratified sampling of the entire area (at intervals of 8 km or less), followed by independent evaluation of each subpopulation. Until this information is available, seed collection for immediate distribution to farmers, or for the establishment of seed production orchards, should concentrate only on the original trial collection site and not the adjacent area, since the genetic differences observed here may be reflected in lower levels of performance (Yeh, 1989). In addition to the implications of the data for utilization and *ex situ* conservation, the degree of structuring observed suggests that overall *in situ* conservation of *G. sepium* resources within this region may require at least the maintenance of the four locations assessed here.

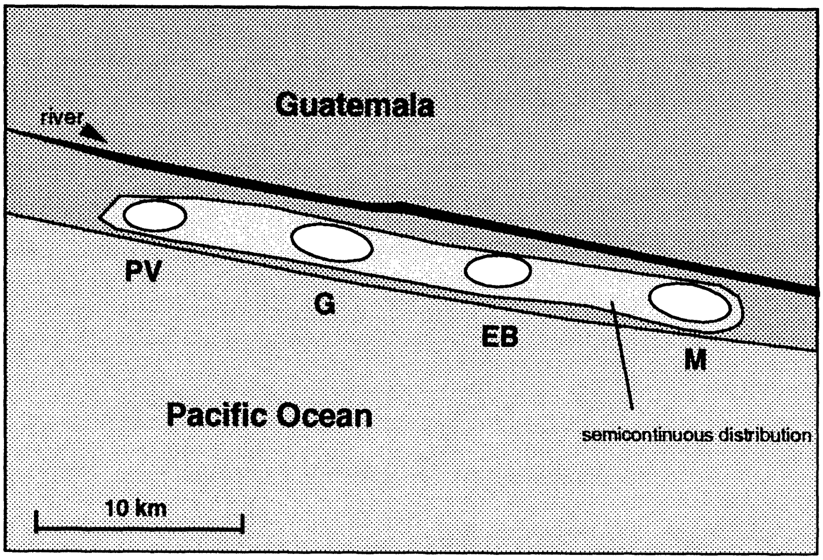

Figure 7.3 Schematic representation of sampled localities for *G. sepium* at Monterrico, Guatemala. Populations: **PV** Puerto Viejo, **G** El Garitón, **EB** El Banco, **M** Monterrico. Provenance trials have included **M** only, but **PV**, **G** and **EB** all occur within a wider semi-continuous distribution of *G. sepium*, which can be considered as forming a single metapopulation

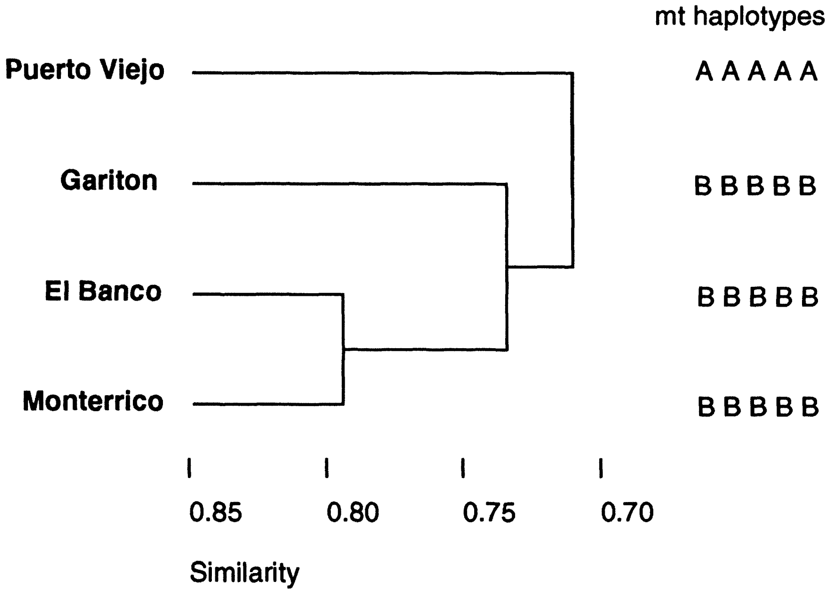

Figure 7.4 Phenogram based on RAPD differences between four localities within a single metapopulation of *G. sepium* at Monterrico, Guatemala. Mitochondrial DNA haplotypes at five individuals per population (**A** or **B**), which show a subpopulation-specific distribution and indicate the Puerto Viejo site to be unique, are also shown

Genetic structure at Retalhuleu

The Retalhuleu provenance of *G. sepium*, located close to the Pacific coast of Guatemala, was identified as an important genetic resource population during field trials because of superior wood and leaf biomass production (see Chapter 8). The subsequent demand for seed from this provenance has been very high, so since 1991 annual seed collections have been made at Retalhuleu.

The population occupies a relatively small region of secondary forest, approximately 450 m square, on a river flood plain site. The population is bisected by a river course, approximately 100 m wide, into two subpopulations of equal area, one of which is on an island in the river. Despite this subdivision, seed collection from Retalhuleu for provenance and progeny trials, and for direct distribution to users, has made no distinction between the subpopulations, assuming both to be similar in composition. Potentially, however, the effect of the intervening river on population structure could be considerable. To evaluate this, leaf material was collected from every tree in the population for molecular analysis. In all, 59 trees were collected on the mainland and 79 trees from the island site. The geographical position of every tree was also recorded. From an initial survey of selected individuals from both sites, Dawson *et al.* (1995) identified 15 RAPD markers, two CAPs and a single SSR marker which could be used to assess genetic variation within the population. These were used to assess all parental trees. Estimates of diversity within and between subpopulations, based on RAPD data, were obtained from Shannon's information index, expressed as $\Sigma p_i \, ln(p_i)$, where p_i is the RAPD product frequency (Lewontin, 1973; Saghai-Maroof *et al.*, 1984). Although the data indicated the island subpopulation to be more diverse than the mainland site (Shannon's index values of 0.335 and 0.290, respectively), less than 5% of the variation was between subpopulations, indicating little genetic differentiation. CAP and SSR markers also indicated no significant genetic differentiation between sites.

The collection and conservation of genetic resources from the Retalhuleu population is particularly important owing to severe physical erosion by river flooding and cutting for firewood by man. The low level of genetic differentiation between the mainland and island sites indicates that this population can be considered as a single unit, allowing seed from both sites to continue to be pooled during future collection.

Comparison between Monterrico and Retalhuleu

In contrast to Retalhuleu, significant structuring was observed among sites in the Monterrico region. This difference is consistent with the geographical scale of sampling at the two sites: within an area of 450 m x 450 m at Retalhuleu, no genetic differentiation was observed, whereas at Monterrico there were significant differences between four populations sampled at 8 km intervals. Overall, therefore, these data give an indication of the general relationship which may be expected between geographical and genetic distances in *G. sepium* populations, and provide a guide for sampling at other sites. Further sampling of the Monterrico population at closer intervals would indicate the distance at which genetic differentiation becomes apparent.

Mating system and gene flow

Information on the mating system and patterns of gene flow of *G. sepium* is essential because these influence population genetic structure and the way in which populations will develop following introduction by users into exotic locations (Schaal, 1980; Loveless and Hamrick, 1984).

Investigation of the mating system of G. sepium

To assess the degree of outcrossing in *G. sepium*, Chamberlain (1993) analyzed data for eight isozyme loci in eight seed of each of 20 mother trees from the Monterrico population (see above). The mixed mating model of Brown, Barrett and Moran (1985) was used, employing a maximum likelihood approach (Ritland and Jain, 1981) and the MLT computer program (Ritland, 1990). Two population outcrossing rates were estimated: t_m the multilocus outcrossing rate, in which data from all loci are analyzed together; and t_s the single locus outcrossing rate, where each locus is analyzed separately. Single locus outcrossing rates for the population are shown in Table 7.2. Neither the mean t_s over all loci, nor t_m (estimated as 1.106 (SE 0.058)), differ significantly from 1, indicating *G. sepium* to be strongly outcrossing and suggesting the existence of a strong self-incompatibility mechanism. This confirms observations on pollination by Simons (Section 3.2), which indicated the inability of self pollen to produce seed. There were, however, significant departures from the mixed mating model at two loci, β-*Est*-1 and *Lap*-2, where an excess of homozygous offspring suggests a low level of inbreeding due to mating between related individuals (rather than selfing, since in this case all loci would have been equally affected). The data therefore suggest some degree of neighbourhood structuring or assortative mating within the Monterrico population, which could lead to inbreeding. Such structuring may be caused by the limited dispersal of seed in *G. sepium* (see Section 3.2). For an outbreeding species it is desirable to minimize related matings because of potential inbreeding depression. In the establishment of seed production orchards, therefore, seed must be collected from widely-spaced mother trees in the original population, to reduce the likelihood that they are related.

Table 7.2 Maximum likelihood estimates of gene frequencies in the pollen and ovule pools; single locus outcrossing rates (t_s) with estimated standard errors (SE); and chi-squared tests for fit to the multilocus mixed mating model. Data refer to eight individual loci in a population of *G. sepium* sampled at Monterrico, Guatemala

Locus	**N**	**Allele**	**Gene frequencies**		t_s	**SE**	χ^2	**df**
			Pollen	**Ovule**				
Aat-1	240	1 2	0.42 0.58	0.45 0.55	1.024	0.011	3.53	1
β-*Est*-1	240	1 2 3	0.04 0.62 0.34	0.13 0.50 0.37	0.821	0.169	21.02*	9
Idh-1	240	1 2	0.01 0.99	0.05 0.95	1.109	0.008	1.23	1
Lap-2	240	1 2	0.60 0.40	0.60 0.40	0.752	0.032	21.90*	1
Pgi-1	240	1 2	0.84 0.16	0.73 0.27	1.211	0.009	5.25	1
Pgi-2	240	1 2	0.26 0.74	0.48 0.52	0.925	0.03	5.55	1
Pgm-3	240	1 2 3	0.55 0.11 0.34	0.60 0.15 0.25	0.823	0.036	10.44	1
Sdh-1	240	1 2	0.05 0.95	0.13 0.87	1.109	0.008	3.60	1

* significant effect at $P<0.05$.

Pollen-mediated gene flow

Pollen-mediated gene flow is recognized to play an important role in determining the genetic structure of populations and has important *ex situ* implications for *G. sepium*. Its estimation by observations of pollinator movement, however, are both difficult and unreliable because of the phenomenon of 'carry-over', by which pollen may be transferred across several plants before final deposition on the stigma (Levin, 1978; Schaal, 1980). In order to provide a reliable estimate of pollen-mediated gene flow, therefore, Dawson *et al.* (1995) employed SSR analysis to assess progeny arrays (families) collected from the Retalhuleu population (see Plate 7.2). In all, 20 progeny from each of 20 parental trees were analyzed at a single SSR locus, sampling from both mainland and island sites (see above for details of population structure). Since every parental tree in this population had previously been characterized at this locus, and since the geographical position of every tree was also recorded, comparison of progeny data with parental data allowed calculation of pollen flow distances by paternity exclusion analysis. Using only those SSR alleles which appeared to be rare in the parental population, the data indicated that while most pollen-mediated gene flow took place over relatively short distances, a small but significant proportion (6%) of observable events occurred over 75 m, with a maximum observed distance of 289 m. While it is likely that most long-distance transfer occurred by 'carry-over', the latter event occurred from mainland to island sites, with no intervening trees for at least 100 m. This observation provides a possible explanation for the lack of differentiation between mainland and island subpopulations at Retalhuleu, as even a low level of long-distance gene flow can prevent population divergence (Hartl and Clark, 1988). In addition, the data are consistent with the behaviour of solitary bees, such as *Xylocopa fimbriata*, which are capable of long flight distances, sometimes of several kilometres (see Section 3.2).

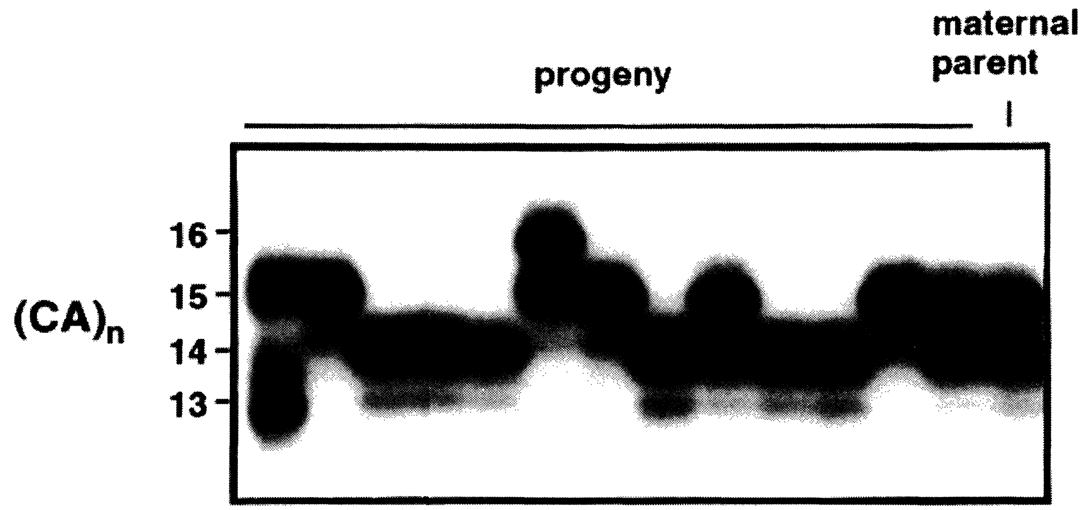

Plate 7.2 Allelic variation revealed at a single SSR locus in progeny taken from a single *G. sepium* tree at Retalhuleu, Guatemala. The genotype of the maternal parent is also shown. Alleles not present in the maternal parent (in this case CA$_{16}$ and CA$_{13}$) can be assigned a minimum pollen flow distance by paternity exclusion of neighbouring trees. In this case, minimum pollen flow distances of 11 and 32 m can be assigned respectively

Although insect-mediated pollen flow can be idiosyncratic (Handel, 1983; Ellstrand *et al.*, 1989), the results from SSR analysis, in addition to their direct implications for the Retalhuleu population, have important consequences for the management of *G. sepium* in other situations, including seed production orchards. One requirement of such orchards is to maintain provenance genetic integrity (Xie and Knowles, 1994), and this is normally ensured by an exclusion zone which separates orchard trees from neighbouring stands of the same species. For *G. sepium*, the maximum pollen transfer distance of more than 250 m observed at Retalhuleu suggests that exclusion zones should be at least this wide if integrity is to be maintained. In addition, the pollen flow data has implications for the introduction of superior provenances into exotic locations where local sub-optimal land races already exist because trees less than 250 m apart could exchange pollen. Although the full implications of such interactions in *G. sepium* are not presently well understood, one result could be a dilution of favourable gene complexes in subsequent generations, leading to a gradual loss of advantage over the pre-existing material (see also Section 9.2).

Key findings from molecular analysis, and their implications

Hybridization between *G. sepium* and *G. maculata*

● PCR-based analyses indicated inter-specific hybridization at three sites located between the native distributions of *G. sepium* and *G. maculata* .

Implication: possible loss of genetic integrity in important native populations of *G. sepium*, especially if hybridization is followed by backcrossing.

Genetic variation within and between native populations of *G. sepium*

● RFLP analysis indicated three distinct chloroplast genomes, with different regional distributions.

● Isozyme analysis of eight populations (spanning native range from Mexico to Panama) showed:
(a) generally good agreement between observed and expected heterozygosities, *i.e.* populations close to equilibrium with near-random mating. Departures from equilibrium at two sites suggest population structuring arising from human influence.
(b) 83% of observed variation within populations, 17% between populations.

Implications: importance of thorough sampling within populations, as well as extensive exploration and collection throughout native range, for optimal capture of available genetic variation (whether for conservation or utilization).

Metapopulation structure

● Sampling at 8 km intervals in a continuous coastal population (Monterrico) showed significant variation (using PCR-based analyses) between four subpopulations.

● A much smaller population (Retalhuleu, 450 m x 450 m), divided by a river into two parts, showed little genetic differentiation between the two parts.

Implication: indication given of relationship between geographic and genetic distances in *G. sepium*.

Mating system and gene flow

● Outcrossing (with strong self-incompatibility mechanism), and some mating of related individuals, indicated by isozyme analysis of Monterrico population.

Implication: important to minimize related matings to avoid inbreeding depression; so seed for establishment of multiplication stands must be collected from widely-spaced trees.

● Pollen movement usually 75 m or less, but occasionally more than 250 m, allowing gene flow over this distance.

Implication: seed orchards and introductions of superior genetic material should be separated from existing populations by at least 250 m.

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8 Provenance and Progeny Trials

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8.1 Introduction

Since 1987, the Oxford Forestry Institute (OFI) has coordinated a network of field trials to assess variation between and within populations of *Gliricidia sepium* in terms of their ability to provide useful products under cultivation. To identify the best populations (provenances), whether in terms of productivity (growth and yield) or product quality, the full range of available genetic variation had first to be systematically sampled and evaluated.

The first provenance collections of *G. sepium* were made in Costa Rica and Guatemala (Chang and Martinez, 1985; Sumberg, 1985). From 1984 to 1986, systematic exploration and seed collections were carried out by OFI, under ODA-funded projects, throughout the native range in Mexico and Central America. This seed was used to establish an international series of provenance trials throughout the tropics to assess genetic variation in the provenances from the native range, and to compare their performance with local land races.

As discussed in Section 3.1, *G. sepium* has a very wide exotic distribution. Most established exotic populations, however, are of unknown origin. Introductions may have been single or multiple; from the native range or from another land race (exotic) population; by seed or by cuttings; and from many or few trees. In most cases little or nothing is known about the history of exotic populations, as most introductions were not documented. Their genetic composition is therefore generally unknown. As well as the possibility that they are derived from provenances of inferior performance, they may also have a narrow genetic base, reducing environmental adaptability (for instance, to pests and diseases), and possibly resulting also in inbreeding depression. There is therefore likely to be considerable scope for improvement through correct selection of a robust, genetically diverse seed source with characteristics of proven superiority to the local land race.

Range-wide exploration and seed collection

The first aim of the exploration of *Gliricidia sepium* populations throughout the species' distribution in tropical America was to define the species' native distribution and ecological amplitude (see Chapter 2, Map 3; and Section 3.1), so that subsequent provenance seed collections could be planned to sample and capture as much as possible of the available genetic diversity, including sites at the environmental limits of the native range (Hughes, 1987a).

Twenty-eight provenances were collected: these are listed in Table 8.1, and the collection sites are shown in Map 4. Most are from the Pacific coastal areas and dry inland valleys where *G. sepium* is thought to be native, but a few probably represent naturalized populations arising from introductions for cultivation. These include Palmasola and Barrosa on the Atlantic coast of Mexico, Masaguara in central Honduras, and the collections from Panama, Colombia and Venezuela (Pedasí, Pontezuela and Mariara, respectively). Even within the native range, however, none of the populations is free of human interference; all *G. sepium* genepools have been profoundly disturbed by centuries of domestication. Provenance variation as a response to environmental variation has therefore been heavily overlaid by variation resulting from a variety of human activity over long periods, including possible mixing of populations by movement of germplasm from one area to another, and local selection of desirable phenotypes.

Another important aspect of sampling populations of multipurpose trees is that it is not appropriate to select superior individuals in the field, as may be done with some single-use species: for instance timber trees may be readily selected by eye on the basis of stem form. For *G. sepium*, however, there are several potential end uses requiring quite different attributes. For most of these, product quality (such as nutritive value of fodder) may be the most important attribute and this cannot be easily evaluated at the time of seed collection. For these reasons, in the OFI seed collections, trees were randomly sampled, without phenotypic selection, but with wide spacing between sampled trees (at least 50 m) to avoid as far as possible collection from related individuals. All the collections (except the Barrosa land race) were from at least 25 individuals and, in populations with low seed set, up to 200 individuals were sampled (Hughes, 1987a). This sampling strategy was used in all the collections, to make them as comparable as possible.

For most of the populations, seed from all trees was bulked into a single collection, but in some cases collections were also made from individual trees (open-pollinated families) for establishment of progeny trials (see Section 8.4) and family-based seed orchards.

Map 4 OFI seed collection sites (after Hughes, 1987a).

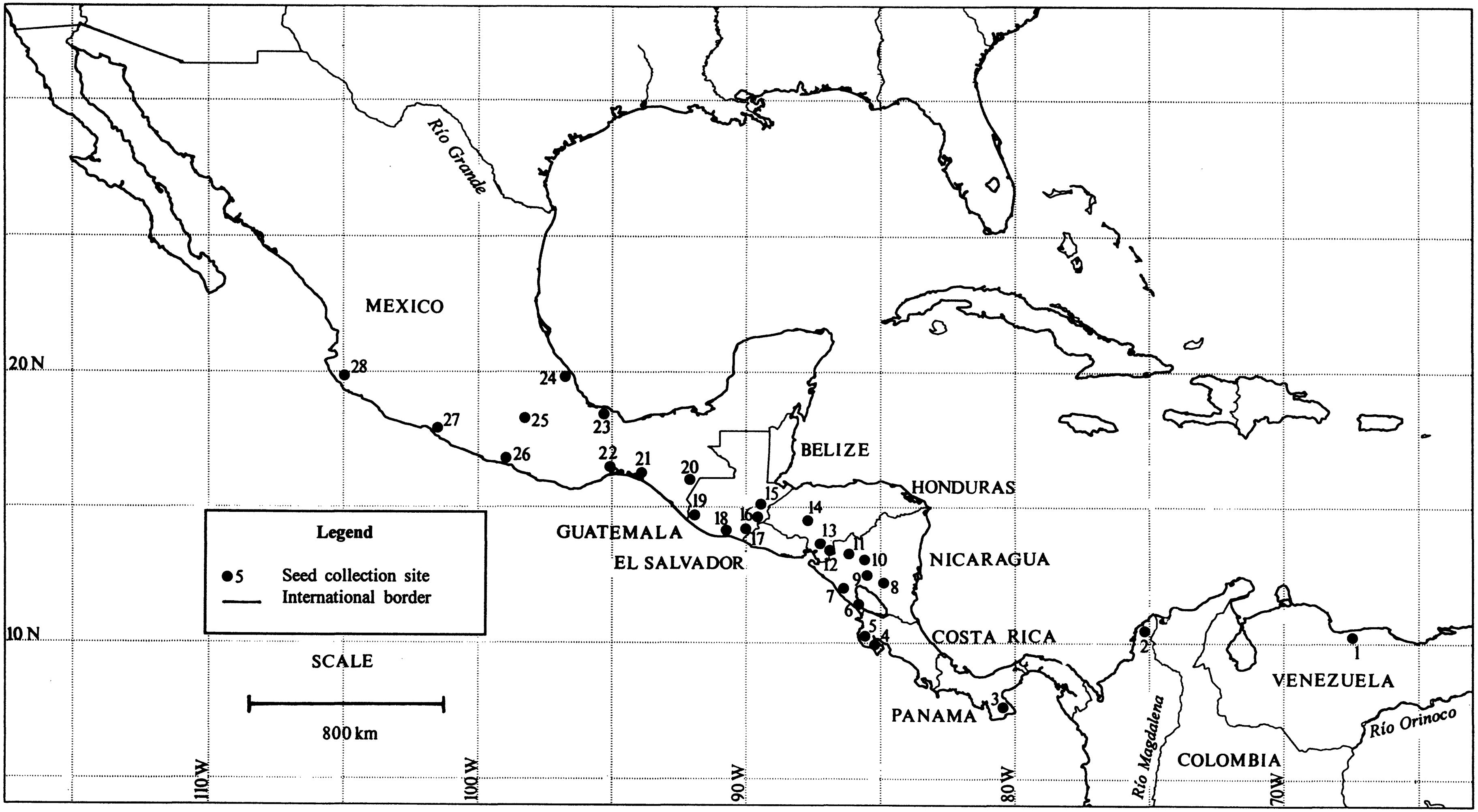


Table 8.1 Provenances included in the OFI *Gliricidia* international trial series

Site no.	OFI no.	Provenance	Country	Altitude (m)	Rainfall (mm)
1	1/86	Mariara	Venezuela	520	800
2	24/86	Pontezuela	Colombia	20-50	950
3	13/86	Pedasí	Panama	0-20	850
4	11/86	El Roblar	Costa Rica	20-100	1000
5	12/86	Playa Tamarindo	Costa Rica	0-10	1500
6	14/86[1]	Belen Rivas	Nicaragua	75	1650
7	31/84	Mateare	Nicaragua	60	1100
8	29/84	Ojo de Agua	Nicaragua	220	900
9	13/82	Laguna Tecomapa	Nicaragua	380	900
10	31/83	Ciudad Darío	Nicaragua	450	900
11	30/84	Estelí	Nicaragua	605	800
12	24/84	Guayabillas	Honduras	480	1400
13	10/86	La Garita	Honduras	450	1200
14	25/84	Masaguara	Honduras	825	1100
15	15/84	Gualán	Guatemala	150	700
16	16/84[2]	Vado Hondo	Guatemala	400	830
17	13/84	Volcán Suchitán	Guatemala	950	1060
18	17/84[3]	Monterrico	Guatemala	5	1650
19	14/84[4]	Retalhuleu	Guatemala	330	3500
20	37/85	Tzímol	Mexico	600-700	1030
21	40/85	Arriaga	Mexico	30	1800
22	35/85	San Mateo	Mexico	10-30	950
23	36/85	Barrosa	Mexico	100-150	1500
24	34/85	Palmasola	Mexico	10-50	1130
25	33/85	Los Amates	Mexico	1100	650
26	39/85	San José	Mexico	30	1400
27	38/85	Playa Azul	Mexico	0-30	900
28	41/85	Chamela	Mexico	60-100	900

[1] also 126/91

[2] also 59/87

[3] also 58/87, 13/89, 124/91

[4] also 60/87, 12/89, 125/91, 31/92, 82/94, 10/95

Table 8.2 Trial details and site descriptions of 34 provenance trials in the OFI *Gliricidia* international trial series (LP = line planting design; PP = pure plot design)

Country	Trial Code	Collaborating Organization	Design	Site Location (lat., long.)	Site Details			References known to the authors
					Altitude	Rainfall	Soil pH	
Australia	Utchee Creek, AUS	CSIRO (Tropical Crops & Pastures), Queensland, Australia	LP	17°45′S, 146°0′E		3500mm	5	Bray *et al.* (1993).
Benin	Abomey, BEN	Université Nationale du Benin, Abomey-Calavi, Benin	LP			1210 mm	6.6	
Burundi	Gihanga, BRN	ISABU (Institut des Sciences Agronomiques du Burundi), Bujumbura, Burundi	LP		830 m	816 mm		
Cameroon	N'kolbisson, CMR	IRZ (Institut de Recherches Zootechnique), Yaoundé, Cameroon	LP					
Ghana	Kumasi, GHA	Forest Products Research Institute, Kumasi, Ghana	LP	6°45′N, 1°40′W	150 m	1520 mm	5.8	Britwum (1988).
Ghana	Nyankpala (1), GHA	Crops Research Institute, Nyankpala, Ghana	LP	9°25′N, 0°58′W	175 m	1250 mm		
Ghana	Nyankpala (2), GHA	Crops Research Institute, Nyankpala, Ghana	PP	9°25′N, 0°58′W	175 m	1250 mm		
Haiti	Bois Laurence, HAI	Mennonite Central Committee, Port-au-Prince, Haiti	LP	19°19′N, 71°52′W	780 m	1593 mm	6.3	
India	Mettupalayam, IND	Tamil Nadu Agricultural University, Mettupalayam, India	PP	11°19′N, 76°56′E				
India	Urulikanchan, IND	BAIF Development Research Foundation, Pune, India	PP					
India	Vellanikkara, IND	Kerala Agricultural University, Vellanikkara, India	PP					
Indonesia	Denpasar, INO	Department of Nutrition & Tropical Forage Science, Udayana University, Denpasar, Bali, Indonesia	LP		150 m	1000 mm		
Indonesia	Sei Putih, INO	CSIRO (Tropical Crops & Pastures), Queensland, Australia	LP	3°30′N, 99°0′E		1900mm	5	Bray *et al.* (1993).
Kenya	Maseno, KEN	ICRAF, Maseno, Kenya	PP					
Malaysia	Semongok, MLY	Agricultural Research Centre, Semongok, Sarawak, Malaysia	PP					
Nepal	Adabhar, NEP	Nepal-UK Forestry Research Project, Babar Mahal, Nepal	PP		250 m			Neil (1990).
Nepal	Butwal, NEP	Nepal-UK Forestry Research Project, Babar Mahal, Nepal	LP		140 m			Neil (1990).
Nigeria	Ibadan (1), NGR	ILRI, Ibadan, Nigeria	PP	7°30′N, 3°54′E		1500 mm	6.2	
Nigeria	Ibadan (2), NGR	ILRI, Ibadan, Nigeria	LP	7°30′N, 3°54′E		1500 mm	6.2	Cobbina and Atta-Krah (1992).
Pakistan	Tando Jam, PAK	Atomic Energy Agricultural Research Centre, Tando Jam, Pakistan	LP					
Peru	Yurimaguas, PER	Yurimaguas Experiment Station, Loreto, Peru	LP	5°45′S, 76°5′W	180 m	2200 mm		
Rwanda	Gituza, RWA	CARE International au Rwanda, Kigali, Rwanda	LP	1°38′S, 30°18′E	1500 m	1071 mm		
Senegal	Ziguinchor, SEN	Direction des Recherches sur les Productions Forestières, Ziguinchor, Senegal	LP	12°28′N, 16°16′W	26 m	1500 mm	5.7	
Sierra Leone	Njala, SLE	Department of Soil Science, Njala University College, Freetown, Sierra Leone	LP					

Country	Trial Code	Collaborating Organization	Design	Site Location (lat., long.)	Site Details			References known to the authors
					Altitude	Rainfall	Soil pH	
Sri Lanka	Madampe, SRL	Coconut Research Institute, Lunuwila, Sri Lanka	LP	8°2′N, 79°50′E	2 m	1596 mm	5.2	Liyanage and Jayasundara (1991).
Tanzania	Hai, TAN	Hai Afforestation Scheme, Hai, Tanzania	PP			800 mm		
USA	Waimanalo, USA	NFTA, Waimanalo, Hawaii, USA						
Zaïre	Mulungwishi, ZAI	United Methodist Church, Kitwe, Zambia	LP	10°48′S, 26°36′E	1200 m	1240 mm	6.5	
Zaïre	M'vuazi, ZAI	PRONAM, Kinshasa, Zaïre	LP			1500 mm	5	
Zambia	Chipata, ZAM	ICRAF, Chipata, Zambia	PP	13°39′S, 32°34′E	1030 m	900mm	5	Kwesiga (1994).

8.2 Provenance variation in growth and yield

The OFI provenance trial network

Seed from the collections described above was sent to collaborators throughout the tropics for a network of provenance trials (Plate 8C). The many different end uses of *G. sepium* (Chapter 4) are reflected in the variety of management techniques employed by farmers (lopping/coppicing regimes, spatial arrangement *etc.*: see Chapter 5). Generally, however, it is managed primarily for production of either wood (fuelwood or poles) or leaves (fodder or green manure), the latter requiring more frequent cutting to increase the leaf:wood ratio. To reflect this, seed was sent out for two main types of trial: a pure plot design for production of wood, and a line planting (alley cropping) design for leaf production.

The pure plot design consisted of a randomized complete block design with four replications and 64-tree square plots at 1.5 m x 1.5 m spacing. The central 36 trees in each plot were the assessment plot; the outer trees formed border rows to minimize interactions between plots, primarily competition effects. It was intended that half the trees should be removed at canopy closure by systematic thinning of alternate diagonal rows, leaving 32 trees per plot at a final square spacing of just over 2 m x 2 m. The line planting design was also in randomized complete blocks, but with six replications and only 12 trees per plot. These trees were arranged in single lines with 0.5 m spacing between trees, and 4 m between rows (adjacent plots). The area in the alleys between the rows was to be planted with a local arable crop such as maize or sorghum. The rows of *G. sepium* were to be lopped repeatedly to evaluate not only leaf production *per se*, but also its seasonality and its sustainability over time.

Seed for over 160 trials was sent to 55 countries (Pottinger, 1992), and approximately equal numbers of each type of trial were established. As far as possible, trial layout was standardized across sites by distributing a detailed "Trial Protocol" (Hughes, 1987b) with the seed. This described both layouts in detail; most collaborators did follow the recommended designs as far as practicable under their particular conditions, although only a few reported results from repeated assessments as was intended in the line planting design.

The results from the trials from which reports and/or data were received formed the basis of the evaluation of provenance performance. The analyses presented here are based on results from 30 trials within the OFI *G. sepium* international trial series. All 28 of the OFI-collected provenances were represented in one or more of the trials. Table 8.1 gives a list of the provenances evaluated, and Table 8.2 gives details of the trials included in the analysis, including the type of design used. The trials encompassed an extremely wide range of environmental conditions, ranging from sea level to 1500 m altitude, 30°N to 20°S latitude, and with mean annual rainfall from 800 mm to 3500 mm. Age at the time of assessment varied from 4 to 36 months. Provenance representation was also very unequal. None of the provenances was planted in all the trials; the most commonly occurring provenance was represented on 23 sites, whilst one provenance was planted on just two sites.

Assessment methodology

In both types of trial the most commonly assessed trait was stem length, being relatively simple to measure (Plate 8A) and useful as a basic indicator of growth that is readily comparable across sites. Rarely, however, is this the trait of most importance to farmers growing *G. sepium*. The species is used for poles in some areas, but this is not often the primary use; more often it is used for firewood, as a green manure or as fodder. For most farmers, wood or leaf production is therefore of more interest than stem length. These two traits, however, require more complex assessment (Plate 8B) and were not measured in so many of the trials; their combined analysis is therefore based on far fewer data. Although the pure plot trials were designed to measure wood production, and the line planting trial leaf production, in practice most of the biomass data reported for both these traits are from line planting trials.

Most data were also from a single assessment, or total *per annum* values, and they did not give information about seasonal and annual variation as had been intended in the line planting design. To provide an insight into these aspects, a detailed analysis of a line planting provenance trial, in Bali, Indonesia, is also included here. Fifteen provenances were compared, together with the local land race of *G. sepium*. The trial site lies at an altitude of 100 m and has a mean annual rainfall of 1000 mm, with an eight month dry season from April to November. The trial had a randomized complete block (RCB) design with six replications. A block consisted of four rows, each containing four provenances represented by 12 trees. The first lopping was carried out at age 10 months. The lopping height was 1 m and both stems and branches were lopped. At each subsequent lopping, the four innermost trees of each plot were assessed, to minimize the effects of inter-provenance competition. These loppings were carried out in January, March, July and November each year, corresponding to the middle and end of both the wet and dry seasons. The provenances were compared on the basis of leaf biomass (fresh weight) production.

The unequal representation of provenances in the trials, combined with the fact that complete datasets (*i.e.* those reported on an individual tree basis) were available for only eight of the sites, made a combined analysis of all thirty trials impossible. In order to ompare the results from different trials, and to provide an overall measure of provenance performance, the provenance means were converted to *relative performance values*, using the formula:

$$\text{relative performance} = 100\times((\bar{x}_{ip}/\bar{x}_i)-1)$$

where $\bar{x}_{ip}$ is the mean of provenance p on site i, for a given trait, and $\bar{x}_i$ is the overall mean performance for that trait of all provenances on site i. This provides a measure of the performance of each provenance on each site, relative to the other provenances on that site, and therefore takes into account differences due to factors such as site quality and assessment age. The mean relative performance values for each provenance, across all trials in which they were represented, were used to identify the best provenances in terms of stem length, leaf production and wood production.

A possible problem with mean relative performance values across sites is that values from individual sites are dependent on the set of provenances represented at that site, and if trials have very few, possibly atypical, provenances, they may give a misleading result. To investigate this, a more detailed combined analysis was undertaken for stem length at the eight sites for which complete datasets were available. This was done using the REML (Residual Maximum Likelihood) statistical package (Robinson, 1987), which is designed for the analysis of unbalanced datasets. This gives unbiased estimates of provenance performance at each site, and estimates performance of missing provenance-trial combinations using information on the overall relative performances of the provenance and site. The expected mean stem lengths from this analysis were compared with the mean relative performance values, and a correlation of 0.93 between the two measures was obtained. This suggests that the mean relative performance values do provide an accurate measure of provenances' overall performance.

The stability of each provenance's performance across a range of environments is also of great importance, since successful uptake by farmers depends on there being low risk attached to any investment in new material. Stability of performance was estimated using the relative performance values, for all provenances that were represented on five or more sites. If it is assumed that each provenance's relative performance values come from a normal distribution, then the expected frequency of above average performance (*i.e.* of an above-zero relative performance value) can be calculated and used as a measure of that provenance's reliability. The higher (or lower) this expected frequency value, the greater the stability of that provenance's performance, whether good (for high values) or bad (for low values). However it should be noted that intermediate values do not give any indication of stability, as they could arise either from stable, average performance or from variable performance.

Trial results

Survival

The survival of all provenances was very good in most of the trials: generally above 90%, with little variation between provenances. *Gliricidia sepium*, however, is not frost tolerant; the natural distribution follows the frost-free limits, and survival was drastically reduced at frost-prone sites (see Section 3.1). Although survival rates varied more between provenances at sites where there was frost damage, none of the provenances displayed any consistent frost tolerance. In a provenance trial on a site in Nepal with occasional frosts (data not included here), all provenances showed severe dieback (Sherpa *et al.*, 1992). Even minimum temperatures as high as 3 °C can result in severe dieback, if not death, so in general *G. sepium* should not be considered as an option for cold sites.

Stem length

Gliricidia sepium is a fast-growing species, with early growth rates of over 3 m per year observed in some trials, and attaining a height of seven metres in 13 months in a trial in Sri Lanka (data not included here). Table 8.3 shows the mean stem length for each provenance at each site on which it was planted, with the pooled standard error of provenance means shown for comparison between provenances. The overall mean stem length for each trial is also given, together with the age at the time of assessment, for comparison between trials. It is clear from Table 8.3 that there was considerable variation in stem length between provenances at each site, between sites, and also between individual provenances' performances on different trial sites (*i.e.* provenance x site interactions).

Figure 8.1 shows the mean relative performance value for stem length, for all provenances represented at five or more sites. There was an overall variation between provenances of 40% around the mean, implying that the tallest provenance had a stem length approximately 1.5 times that of the shortest. The best provenance overall, in terms of stem length, was Retalhuleu, Guatemala. All the Guatemalan provenances had above-average stem length, with the exception of Monterrico. Similarly the Nicaraguan provenances, with one exception (Ojo de Agua), were above average for this trait, whilst the provenances from Mexico were amongst the slowest-growing. An interesting exception amongst the Mexican seed sources was Barrosa, which had greater stem length than Retalhuleu on some sites (but is not included in Figure 8.1 as it was very poorly represented in the trials). However this provenance was collected from live fences in an area where it is doubtful whether *G. sepium* is native (Hughes, 1987a).

Table 8.3 Summary of results for 28 seed sources of *Gliricidia sepium* at 30 trials in the international trial series: stem length (m)

Provenance Code Trial code, age at assessment (months), trial mean (m) and pooled standard error of provenance means				24/86 Pontezuela	11/86 El Roblar	12/86 Playa Tamarindo	13/84 Volcán Suchitán	14/84 Retalhuleu	15/84 Gualán	16/84 Vado Hondo	17/84 Monterrico	24/84 Guayabillas	25/84 Masaguara	10/86 La Garita	33/85 Los Amates	34/85 Palmasola	35/85 San Mateo	36/85 Barrosa	37/85 Tzimol	38/85 Playa Azul	39/85 San José	40/85 Arriaga	41/85 Chamela	13/82 Laguna Tecomapa	31/83 Ciudad Darío	29/84 Ojo de Agua	30/84 Estelí	31/84 Mateare	14/86 Belen Rivas	13/86 Pedasí	1/86 Mariara
Utchee Creek, AUS		3.15	0.13	2.87	3.37	3.47	3.23	3.60	3.33	3.27	3.07	3.03	3.10	3.30	2.83	2.87	3.03	3.43	3.17	2.97	3.07	2.83	2.70			3.07	3.40	3.43	3.13	3.10	3.10
Abomey, BEN	12	2.31	0.28				2.37	2.34	2.26	2.39	1.69	2.34	2.16												2.50	2.14	2.58	2.61			
Gihanga, BRN	12	2.11	0.14	2.13			2.71	2.50	2.27	2.34			2.38		1.83		1.50			1.80			1.92				2.43			1.54	
N'kolbisson, CMR	10	1.64	0.14				1.57	1.73	1.84	1.86	1.56	1.50	1.76												1.33	1.49	2.09	1.42			
Kumasi, GHA	8	1.82	0.07				1.63	2.01	1.87	1.78	1.28	1.98	1.66												2.09	1.94	1.91	1.85			
Nyankpala (1), GHA	5	1.68	0.14						1.93						1.64	1.48	1.59		1.48	1.81	1.86	1.62	1.61				1.80				
Nyankpala (2), GHA	5	1.58	0.18				1.80		1.73	2.08					1.44	1.28	1.13	1.95	1.50	1.28	1.67	1.48	1.48				1.73				
Bois Laurence, HAI	13	1.37	0.05			1.36		1.64			1.13																				
Mettupalayam, IND	36	3.23	0.09	3.73		2.71	3.66	3.97	3.53		2.32			3.90	2.83	2.85	2.88			3.24	3.36								3.93	2.74	2.87
Urulikanchan, IND	28	3.45	0.08			3.81	3.44		3.98						2.78														3.45		
Vellanikkara, IND	11	0.88	0.09			0.67		1.11		0.81	0.92																				
Maseno, KEN	14	2.49		2.57		2.08		2.95		2.59	2.28																				
Semongok, MLY	6	1.30	0.06	1.83		1.17		1.80		1.44	1.15						0.83		0.88												
Adabhar, NEP	18	2.95	0.09			2.82	3.25		2.97				2.71			2.43				3.03				3.15		2.88	3.14				
Butwal, NEP	20	1.78	0.07			1.67			2.04							1.72				1.85				2.07		1.93				1.17	
Ibadan (1), NGR	20	6.01	0.31				7.00	6.50	6.00	5.60	5.60	5.80	5.60												5.80	5.90	6.30	6.00			
Ibadan (2), NGR	9	2.28	0.21	2.54	2.32	1.96	2.64	2.81	2.25	2.51	1.98	2.50	2.42	2.60	1.95	1.83	2.08	2.06	2.04	2.53	2.17	2.34	2.27			2.11	2.27	2.19	2.51	2.12	2.26
Tando Jam, PAK	15	2.02		2.36		2.04	2.21	2.20	2.24		1.77			2.20	2.04	1.82	2.00			1.96	1.93								2.07	1.35	2.10
Yurimaguas, PER	6	1.00	0.07		1.09	0.73	0.93	1.63				0.75	1.16	1.16							0.66					0.82		1.12	0.98		
Gituza, RWA	14	1.75	0.10				1.35	2.19					1.70	1.69												1.84					
Ziguinchor, SEN	4	0.99	0.09				0.99	1.26	0.76	1.20	0.75	0.96	0.89												1.23	1.11	0.95	0.76			
Njala, SLE	12	1.81	0.23				1.62	1.43	1.58	1.45	1.33	1.96	1.67												2.19	1.55	1.77	1.83			
Madampe, SRL	12	3.17	0.11	3.27		2.94	3.54	3.63	3.33		2.96		3.28	3.67	2.81		2.78		2.99	2.96											3.04
Hai, TAN	15	1.75	0.09	1.92		1.70		1.78		1.53	1.81																				
Waimanalo, USA	12	3.39	0.06					3.78				3.38			2.64												3.57	3.69			3.29
Mulungwishi, ZAI	18	1.77	0.14	1.88		1.44		2.18		1.82	1.68						1.63		1.63												
M'vuazi, ZAI	6	2.98	0.21				3.13	3.07	2.89	3.18	2.35	2.98	2.89												2.99	3.04	3.16	3.15			
Chipata, ZAM	24	3.51	0.44	4.30		2.81	3.47	4.57	3.22		3.25			4.34	3.45	2.91	3.23			3.17	3.77								3.56	2.81	3.86

Figure 8.1 Stem length: mean relative performance across all sites

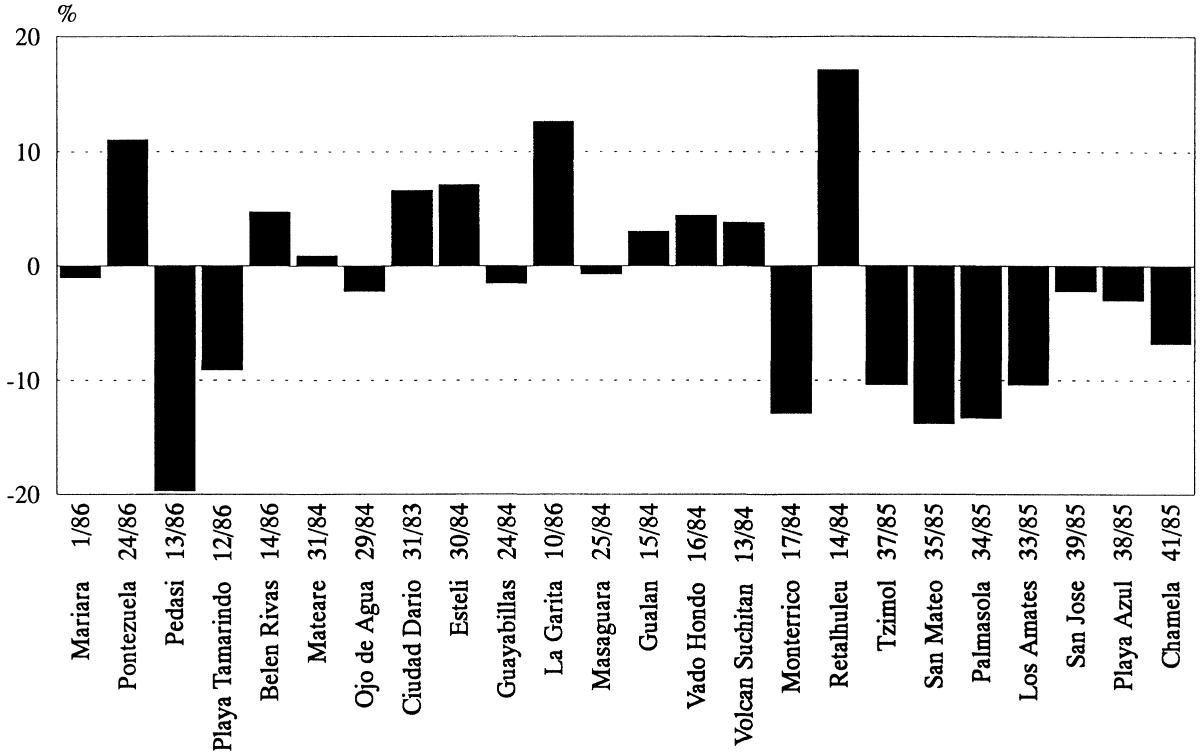
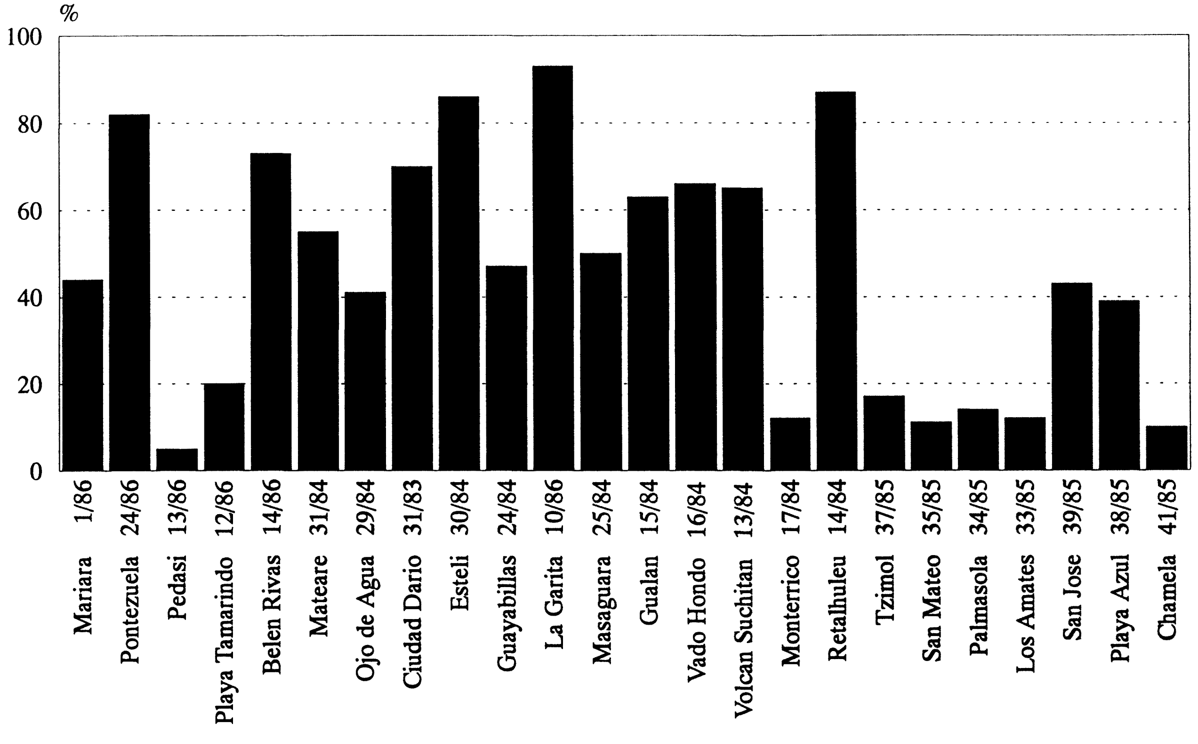


Figure 8.2 Stem length: expected frequency of above average performance



It is interesting to note the poor performance of the Costa Rican provenance Playa Tamarindo; Atta-Krah (1989) found a composite of four Costa Rican lines to be the best performer at ILCA. This composite, however, comprised populations collected from live fences in Costa Rica (Chang and Martinez, 1985). The other Costa Rican provenance included in the OFI trial series, El Roblar (not included in Figure 8.1), was slightly above average for stem length in each of the three trials in which it was planted.

Figure 8.2 shows the stability of the provenances' performance over a range of sites, as measured by the expected frequency of above-zero relative performance values. La Garita was the most stable provenance by this criterion, closely followed by Retalhuleu and Estelí, then Pontezuela, although the mean performance of Retalhuleu was considerably superior to these other provenances, making it overall the 'best bet' provenance where stem length is the criterion of choice.

Leaf production

Table 8.4 shows the mean leaf production, expressed either as fresh weight or dry weight, for each provenance, together with the pooled standard error of provenance means, overall site mean, and age at the time of assessment. Leaf production is greatly affected by management intervention, particularly in relation to season, and this trait would therefore be expected to produce a greater degree of site-provenance interaction than stem length. One source of between-site variation is the difference in the way the trials were managed prior to assessment. Some were repeatedly lopped, with the leaf production reported being either from one harvest or from several harvests, whilst other trials were assessed at the time of first cutting. There may well be variation between the provenances in their reaction to repeated lopping. Pedasí, for example, performed well at Mettupalayam (a continuous-growth woodlot trial), but poorly at Sei Putih and Denpasar (both repeatedly lopped trials). Provenance differences in leaf production may also be due to variation between provenances in leaf phenology, which is unquantifiable in this across-site analysis.

Provenance rankings for leaf production did vary greatly from trial to trial. Few provenances were consistently good leaf producers, with all provenances below average on at least one site. Overall, the mean relative performance for leaf production (Figure 8.3) shows that Retalhuleu produced the highest leaf yields of the well-represented provenances, followed by Belen Rivas and Monterrico. The high leaf yield of Monterrico is notable, as this provenance was well below average in terms of both stem length and wood production. Most of the Nicaraguan provenances performed more poorly for leaf production than for the other traits analyzed. All the Mexican provenances were poor leaf producers.

Figure 8.4 shows the provenances' stability of leaf production, which reflects the increased site-provenance interaction mentioned above: only Retalhuleu and Belen Rivas have greater than an 80% expectation of an above-average leaf yield, indicating stable, high leaf production; and only three provenances (Tzímol, San Mateo and Palmasola) performed consistently badly, with expected frequencies of above-average performance lower than 20%.

A more detailed analysis of a line planting provenance trial in Bali, Indonesia, gives useful information on seasonal variation in leaf production from regrowth after repeated cutting. Figure 8.5 shows the fresh weight of leaf biomass for two years, each divided into wet and dry season totals. Each value is the sum of yields from two cuttings, in the middle and end of the wet and dry season respectively: a total of four loppings per year. There is considerable between-provenance variation, not only in overall leaf production but also in the seasonal distribution of production. As expected, leaf production was much lower for all provenances in the dry season than in the wet season: this seasonal reduction was much more pronounced in the second year. In the first year there was less variation between provenances in wet season production than dry season production. The best provenances, in terms of total leaf biomass per year, were Retalhuleu, Monterrico, Pontezuela, Playa Tamarindo, Mariara and Belen Rivas, and it is important to note that most of the additional production by these was in the dry season, when demand for green leaf material, particularly for fodder, is highest. There was much less variation in dry season production in the second year, although Retalhuleu did produce somewhat more leaf biomass than any of the other provenances, suggesting that it could be a useful provenance for areas with a pronounced dry season. This result is surprising given that this provenance come from an area with an average rainfall of 3500 mm. In general, dry season leaf production is a trait of great interest as this is the time when demand for green fodder is highest.

It is uncertain why there was a universal decline in leaf yield in the second year. The second year had a lower total annual rainfall and a longer dry season, but too-frequent pruning during periods of water deficit in later harvests may also have reduced production. This point highlights the need to consider gains in genetic improvement alongside possible changes in the way the trials are managed, since a different lopping regime (height or frequency) might have reduced, or even prevented, the decline. Thus it may be that for dry season leaf production, greatest gains can be achieved through the adoption of a different management regime, rather than simply selecting particular provenances.

Two papers have been published reporting provenance variation in response to repeated cutting. Neither of these datasets are included in the across-site analysis reported here. Gomez *et al.* (1990), testing six provenances (Arriaga, Retalhuleu, Playa Tamarindo, Pontezuela, Monterrico and Vado Hondo) in a trial in the Cauca Valley of Colombia, measured production of edible biomass (leaves and tendershoots) from four successive cuts at three-monthly intervals.

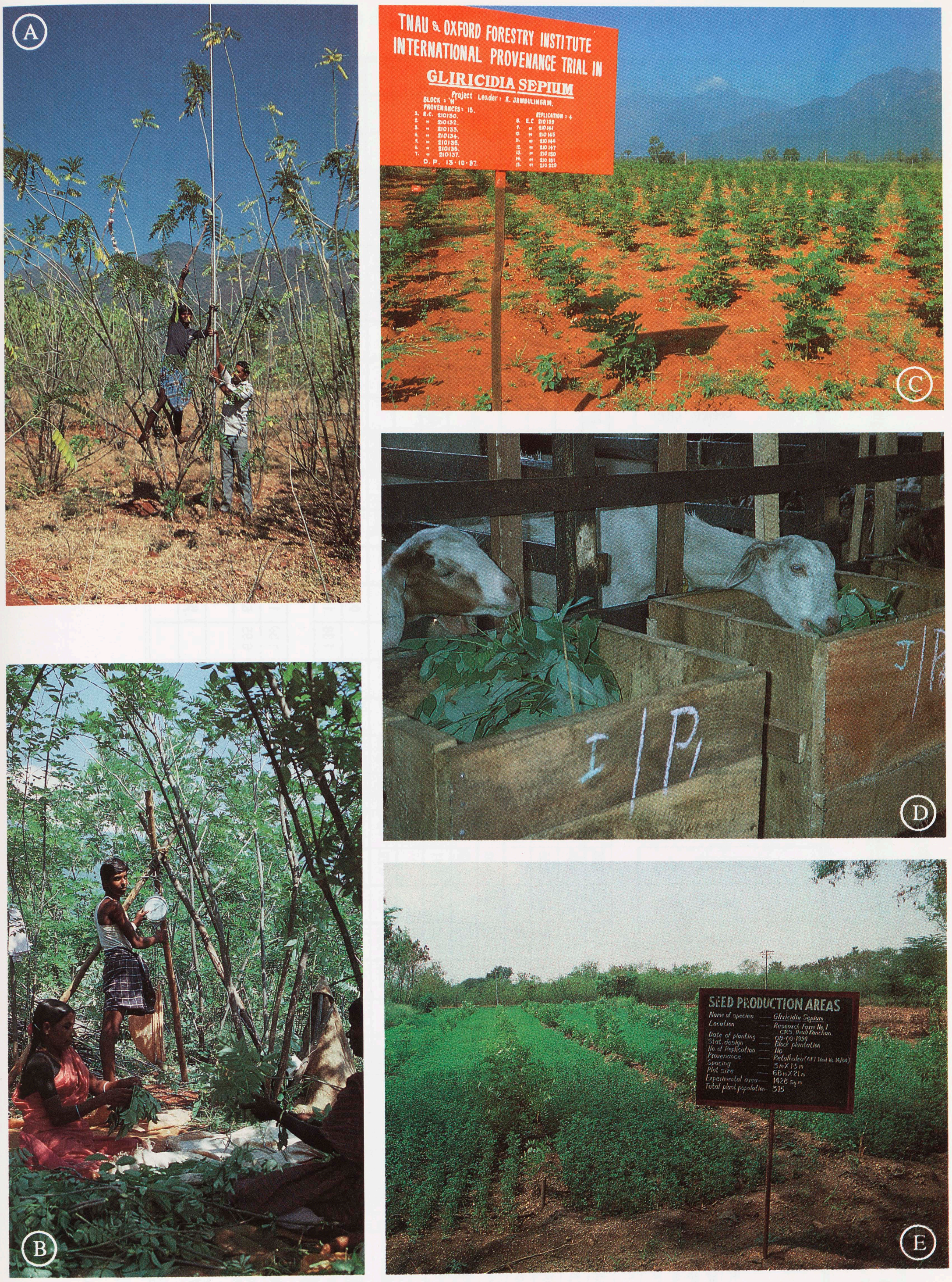


Plate 8

A - Measuring stem length in a trial at TNAU, Tamil Nadu, India

B - Partitioning of tree for biomass assessment, TNAU

C - One of the OFI network provenance trials, TNAU

D - Goats in an intake trial, UP, Sri Lanka

E - Bulk seed production area, BAIF, Pune, India

Table 8.4 Summary of results for 28 seed sources of *Gliricidia sepium* at 16 trials in the international trial series: leaf production (kg/tree)

Provenance Code Trial code, age at assessment (months), trial mean (kg/t) and pooled standard error of provenance means (kg/t). *p.a.*: *per annum* values.				24/86 Pontezuela	11/86 El Roblar	12/86 Playa Tamarindo	13/84 Volcán Suchitán	14/84 Retalhuleu	15/84 Gualán	16/84 Vado Hondo	17/84 Monterrico	24/84 Guayabillas	25/84 Masaguara	10/86 La Garita	33/85 Los Amates	34/85 Palmasola	35/85 San Mateo	36/85 Barrosa	37/85 Tzimol	38/85 Playa Azul	39/85 San José	40/85 Arriaga	41/85 Chamela	13/82 Laguna Tecomapa	31/83 Ciudad Darío	29/84 Ojo de Agua	30/84 Estelí	31/84 Mateare	14/86 Belen Rivas	13/86 Pedasí	1/86 Mariara
DRY WEIGHT																															
Utchee Creek, AUS		1.08	0.25	0.90	0.81	1.44	1.27	1.78	0.98	1.35	1.59	0.86	1.15	0.99	0.67	0.98	0.81	1.14	1.03	1.27	0.78	0.79	0.62			1.37	1.16	1.32	1.35	0.54	1.16
Abomey, BEN	12	0.58	0.16				0.56	0.57	0.57	0.50	0.54	0.62	0.52												0.57	0.51	0.71	0.67			
Kumasi, GHA		0.33					0.37	0.36	0.32	0.35	0.46	0.30	0.31												0.27	0.31	0.26	0.31			
Bois Laurence, HAI	13	0.35	0.04			0.24		0.50			0.31																				
Sei Putih, INO	*p.a.*	1.16	0.13	1.29	1.04	1.01	1.22	1.68	1.25	1.31	1.40	1.19	1.12	1.24	1.31	0.85	1.06			1.07			0.51			0.79	1.23	1.21	1.50	0.74	1.39
Semongok, MLY	7	0.58	0.16	0.58		0.46		1.07		0.68	0.57						0.36		0.35												
Ibadan (2), NGR	*p.a.*	0.95	0.08	0.97	1.03	0.97	0.98	1.32	0.97	1.11	1.18	1.07	1.07	0.92	0.93	0.77	0.93	1.09	0.85	0.97	0.94	0.86	0.58			0.91	0.88	0.86	1.04	0.75	0.83
Yurimaguas, PER	19	0.30	0.11		0.37	0.29	0.27	0.51				0.21	0.40	0.30		0.22					0.23					0.30		0.25	0.27		
Ziguinchor, SEN		0.77					0.60	0.86	0.51	0.79	1.04	1.05	0.63												0.81	0.67	0.81	0.66			
Madampe, SRL	12	0.71	0.05	0.73		0.77	0.79	1.10	0.64		0.89		0.65	0.69	0.52		0.64		0.48	0.64											0.69
Chipata, ZAM	24	1.58	0.33	2.12		1.47	1.45	2.05	1.12		1.77			1.58	1.39	1.38	1.46			1.28	1.66								1.72	1.45	1.73
FRESH WEIGHT																															
Mettupalayam, IND	36	1.80	0.14	1.71		1.54	1.65	1.76	1.94		1.55			1.77	1.87	1.39	1.72			2.15	1.87								2.51	2.22	1.32
Denpasar, INO	*p.a.*	7.00	0.63	8.20		8.15	6.88	8.16	6.42		8.32				5.28	6.95	6.98			5.33	6.71	5.38							7.95	5.75	8.09
Njala, SLE	12	0.86	0.25				0.79	0.56	0.77	0.66	0.95	1.16	0.93												1.06	0.91	0.64	0.97			
Mulungwishi, ZAI	18	0.69	0.10	0.64		0.45		1.03		0.67	0.71						0.64		0.61												
M'vuazi, ZAI	8	1.87	0.38				1.77	2.69	1.44	2.00	1.95	1.46	1.73												1.61	1.67	1.98	2.32			

Figure 8.3 Leaf production: mean relative performance across all sites

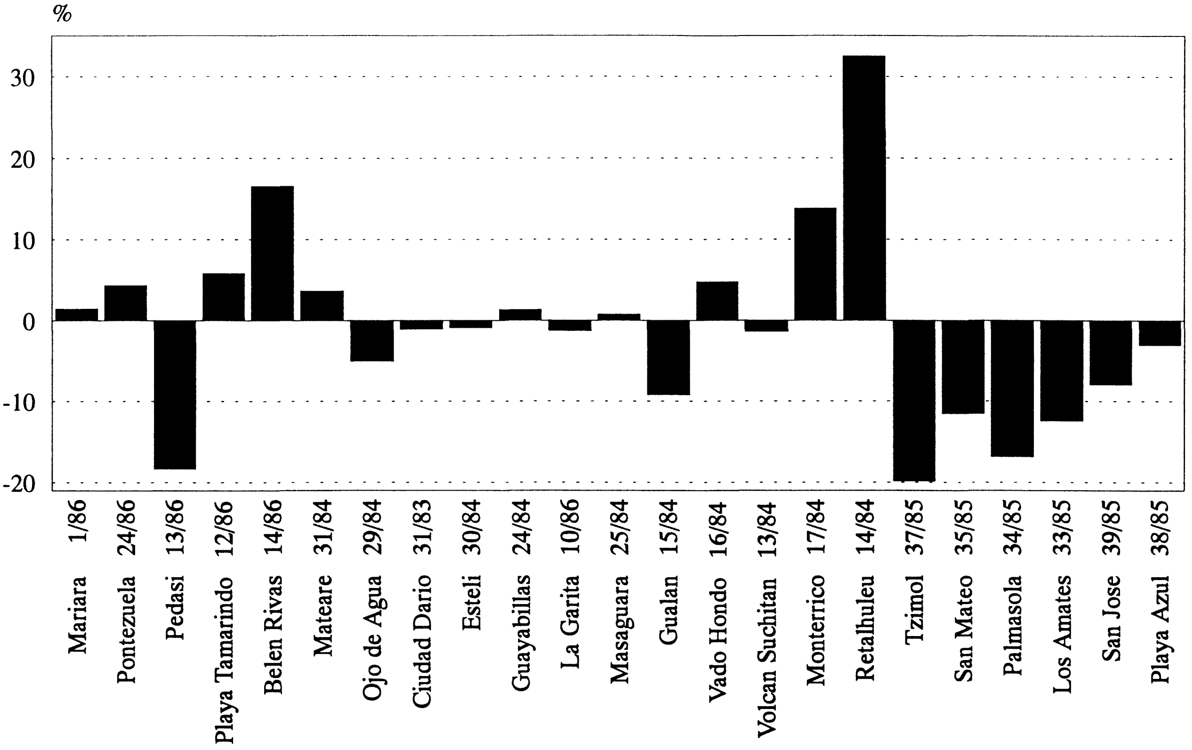


Figure 8.4 Leaf production: expected frequency of above average performance

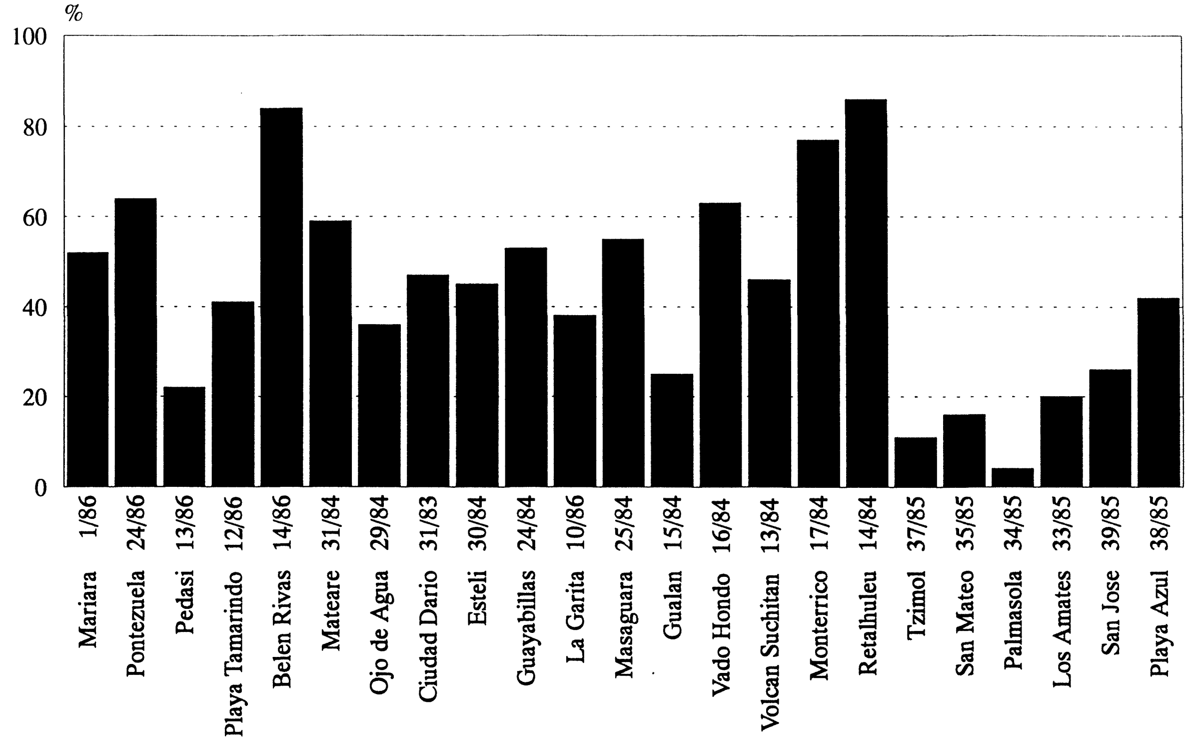
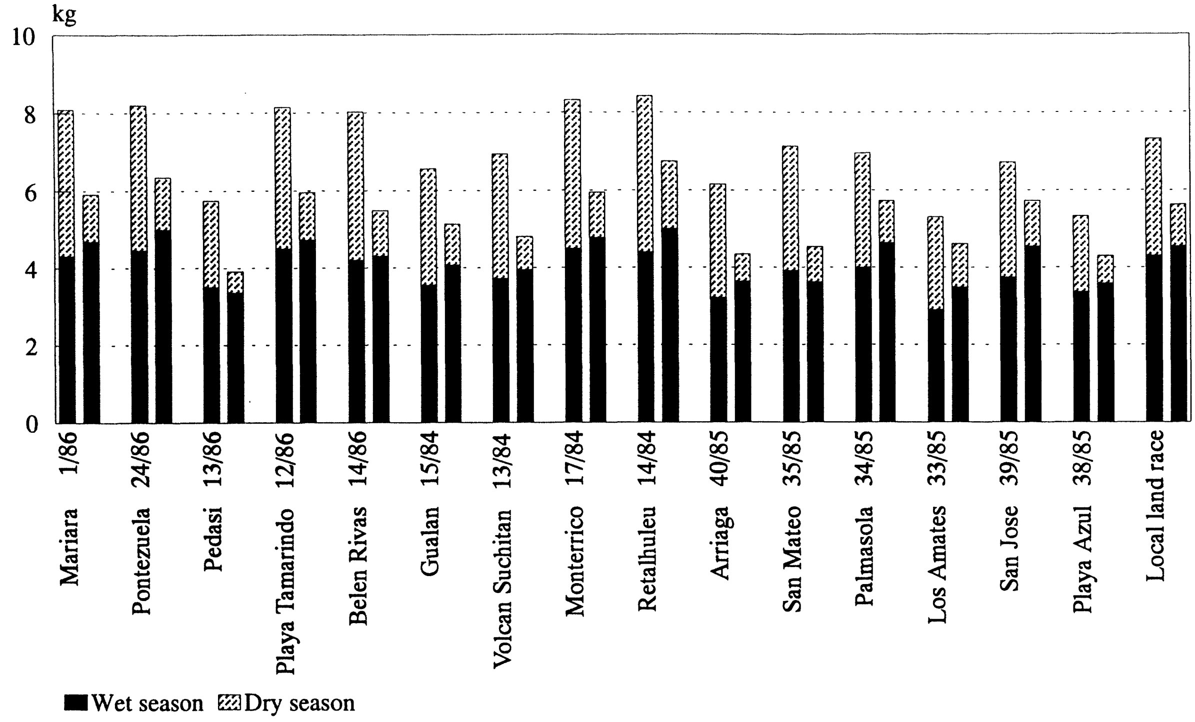


Figure 8.5 Mean leaf fresh weight: wet and dry season over two years



The ranking of the provenances varied greatly from harvest to harvest, and the overall ranking was also atypical, with Retalhuleu and Vado Hondo the highest biomass producers and Monterrico, generally a productive as well as a stable provenance in the OFI trials, giving much lower total production than any other provenance. Ngulube (1994), evaluating nine provenances in a line planting trial in Malawi for leaf and wood biomass production over three years (two cuts per year), also reported results that differ profoundly from the overall relative performances fround in the across-site analysis: while Retalhuleu, as expected, produced the highest mean yield of both wood and leaf, Monterrico was again among the poorest performers. An even more unusual result was the high leaf production of Tzímol provenance (mean production over three years almost as high as that of Retalhuleu), which was the poorest of all the provenances tested in the across-site analysis (see Figure 8.3). The differences between the results from these studies over several lopping cycles and the results from the across-site analyses (which in most cases used data from a single assessment) underlines the importance of response to lopping and the need for more data on provenance variation in sustainability of biomass production over time.

Wood production

Wood production (Table 8.5) was the most variable of the traits measured. There was also considerable variation from site to site, in terms of both absolute wood biomass production values and the relative performance of the provenances. Some of the apparent variation between sites may be due to the differences in the assessment method used; some of the results were reported as fresh rather than oven-dry weights, and in most of those studies where dry weights were reported, the wood was not partitioned into size classes. Stewart (1989) found large differences in the dry matter content of different size classes of wood for *G. sepium* (typically 30% and 55%, for wood under 1 cm and over 5 cm in diameter), and this could have a major effect on the calculation of total dry weights. Comparisons between provenances in terms of wood dry matter production may also be affected by differences between provenances in moisture content.

The box opposite gives the results of a more detailed assessment of wood biomass production in a trial in India, and shows how provenance ranking can change over time.

Wood biomass production: changes over time

One trial, with 15 *Gliricidia sepium* provenances in a pure plot design in Mettupalayam, India, had two detailed assessments of wood biomass production at two and three years after planting. This trial gives some interesting insights into the way that relative provenance performance can change over time.

The trial was laid out according to the standard OFI design for a pure plot ('woodlot') trial: square plots of 64 trees at 1.5m × 1.5m spacing, with three replications in a randomised complete block (RCB) design. Two assessments were carried out, at 24 months and 36 months, each based on the destructive sampling of 18 of the 36 trees in the inner plot, sampled in a systematic manner. Both assessments were of previously uncut trees rather than resprouts.

There was significant provenance variation in wood production at both assessments. Provenance means and ranks are given below. On this site Belen Rivas provenance was the highest wood biomass producer at both ages, but the overall ranking of provenances changed considerably from one assessment to the next. This suggests that some provenances have faster early growth, with others catching up later. Retalhuleu provenance, for instance, ranked second at 24 months, but fifth at 36 months. Since all the other assessments of wood biomass reported in this chapter were at 24 months or less, it is possible that the overall superiority of Retalhuleu may become less marked in older trees. The change in rankings also suggests that different provenances may follow different growth curves, giving different optimal harvest times. These are both aspects on which further research is needed.

It is also noticeable that the increase in biomass is generally greater in the more productive provenances. This suggests that differences between fast- and slow-growing provenances will tend to increase with age, but may also reflect a competition effect: as the trees were at 1.5m x 1.5m spacing until the first assessment at 24 months, the larger provenances must have been suffering more severe competition than the smaller ones, and this would have been alleviated by the 50% thinning at the first assessment.

Provenance means, with standard errors, for wood production of 15 provenances of *Gliricidia sepium* growing in a woodlot trial at Mettupalayam, India, assessed 24 and 36 months after planting.

Provenance	Mean wood fresh weight (kg/tree)		Rank	
	24 months	36 months	24 months	36 months
24/86 Pontezuela	3.79	5.42	6	2
12/86 Playa Tamarindo	3.11	3.46	10	13
13/84 Volcán Suchitán	4.23	4.51	3	8
14/84 Retalhuleu	4.42	5.14	2	5
15/84 Gualán	4.11	4.95	4	7
17/84 Monterrico	2.28	2.89	15	15
10/86 La Garita	3.70	5.31	7	3
33/85 Los Amates	3.42	4.04	9	10
34/85 Palmasola	3.09	3.63	11	12
35/85 San Mateo	2.89	3.74	14	11
38/85 Playa Azul	3.86	5.21	5	4
39/85 San José	3.69	4.37	8	9
14/86 Belen Rivas	4.68	6.84	1	1
13/86 Pedasí	3.04	5.00	12	6
1/86 Mariara	3.00	3.40	13	14
Standard error of provenance mean	0.27	0.35		

Table 8.5 Summary of results for 28 seed sources of *Gliricidia sepium* at 15 trials in the international trial series: wood production (kg/tree)

Provenance Code Trial code, age at assessment (months), trial mean (kg/t) and pooled standard error of provenance means (kg/t). *p.a.: per annum* values.				24/86 Pontezuela	11/86 El Roblar	12/86 Playa Tamarindo	13/84 Volcán Suchitán	14/84 Retalhuleu	15/84 Gualán	16/84 Vado Hondo	17/84 Monterrico	24/84 Guayabillas	25/84 Masaguara	10/86 La Garita	33/85 Los Amates	34/85 Palmasola	35/85 San Mateo	36/85 Barrosa	37/85 Tzímol	38/85 Playa Azul	39/85 San José	40/85 Arriaga	41/85 Chamela	13/82 Laguna Tecomapa	31/83 Ciudad Darío	29/84 Ojo de Agua	30/84 Estelí	31/84 Mateare	14/86 Belen Rivas	13/86 Pedasí	1/86 Mariara
DRY WEIGHT																															
Utchee Creek, AUS		0.77	0.16	0.84	0.59	0.81	1.12	1.33	0.84	0.94	0.97	0.66	0.74	0.83	0.46	0.46	0.69	1.01	0.55	0.68	0.63	0.49	0.40			0.83	0.81	1.09	0.90	0.49	0.82
Bois Laurence, HAI	13	0.23	0.02			0.21		0.32			0.17																				
Semongok, MLY	7	0.85	0.34	1.00		0.42		1.52		1.31	0.71						0.54		0.48												
Ibadan (1), NGR	20	15.8	2.9				18.5	38.7	9.2	15.3	11.9	11.8	12.1												14.1	9.0	17.2	15.6			
Ibadan (2), NGR	*p.a.*	0.80	0.06	1.00	0.68	0.76	0.94	1.21	0.71	0.90	0.85	0.94	0.75	0.67	0.94	0.63	0.73	0.86	0.69	0.87	0.74	0.72	0.52			0.72	0.71	0.80	0.98	0.65	0.92
Yurimaguas, PER	19	0.32	0.13		0.46	0.22	0.33	0.80				0.14	0.35	0.34		0.15					0.16					0.29		0.32	0.29		
Ziguinchor, SEN		2.12					2.11	2.10	1.56	2.94	2.13	2.55	1.71												2.12	2.04	2.59	1.44			
Madampe, SRL	12	0.47	0.04	0.52		0.47	0.67	0.53	0.47		0.47		0.44	0.55	0.42		0.38		0.35	0.48											0.41
Chipata, ZAM	24	5.98	1.66	9.27		3.67	4.89	10.8	4.93		5.29			5.76	5.63	3.82	5.44			5.28	6.73								6.36	4.56	7.30
FRESH WEIGHT																															
Abomey, BEN	12	1.58					1.60	2.07	1.48	1.55	1.40	1.82	1.16												1.45	1.26	1.66	1.95			
Mettupalayam, IND	36	4.50	0.31	5.42		3.46	4.51	5.14	4.95		2.89			5.31	4.04	3.63	3.74			5.21	4.37								6.84	5.00	3.40
Denpasar, INO	*p.a.*	4.66	0.50	6.02		5.36	4.59	6.37	4.72		4.39				3.44	4.00	3.40			3.37	4.19	4.08							6.27	3.44	6.24
Njala, SLE	12	0.59	0.18				0.58	0.50	0.45	0.52	0.58	0.66	0.52												1.04	0.45	0.64	0.56			
Mulungwishi, ZAI	18	0.48	0.12	0.58		0.32		0.71		0.61	0.37						0.37		0.26												
M'vuazi, ZAI	8	0.78	0.12				0.63	1.22	0.61	0.95	0.96	0.68	0.60												0.72	0.54	0.77	0.89			

Figure 8.6 Wood production: mean relative performance across all sites

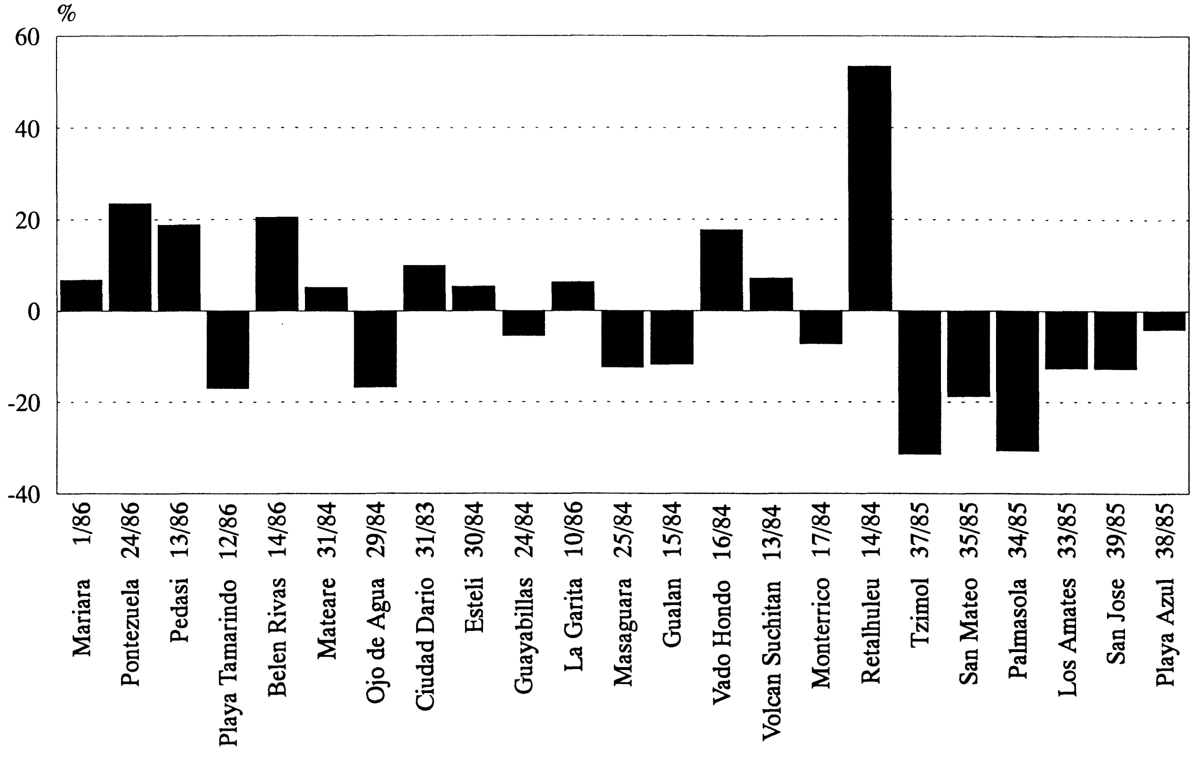
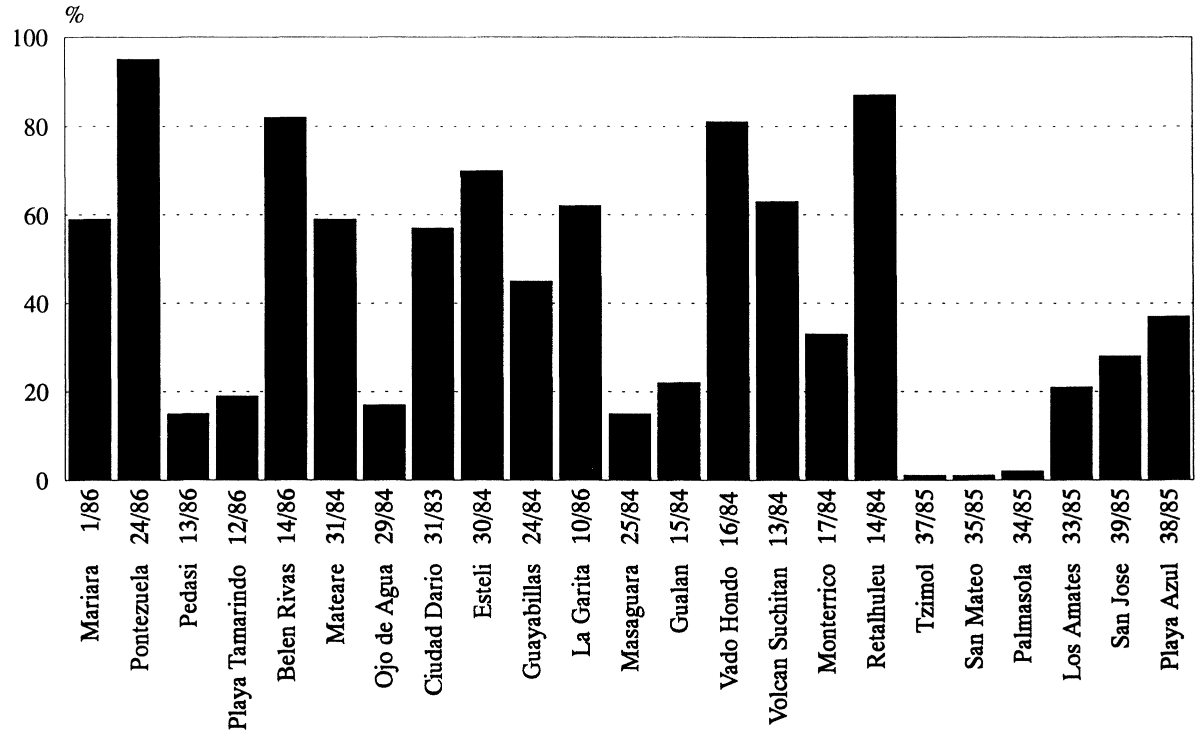


Figure 8.7 Wood production: expected frequency of above average performance



The overall mean relative performance for wood production (Figure 8.6), shows Retalhuleu greatly outperforming all other provenances. The Guatemalan provenances were not as consistent in their wood production as in their performance for the other traits analyzed, but the Nicaraguan provenances were all above-average wood producers except Ojo de Agua. The Mexican provenances generally gave low wood production, again with the exception of the less-represented Barrosa.

In terms of stability of performance (Figure 8.7), Pontezuela showed the highest likelihood of an above-average yield (95%), with Retalhuleu, Belen Rivas and Vado Hondo also showing good stability across sites. The clear dominance of Retalhuleu provenance in terms of mean relative performance values, combined with its stability of performance, shows it to be by far the best of the provenances tested in terms of wood biomass production.

Conclusions

The most promising provenances for each of the three traits evaluated, in terms both of relative performance and of stability (expected frequency of above-average performance) are shown in the box below. Retalhuleu provenance emerges clearly as a superior and stable provenance for all the traits. The other top-performing provenances, however, have each shown superiority in some traits but not in others, suggesting that they could be recommended for particular uses, but not as universally as Retahuleu. Thus La Garita, a provenance with an unusually arboreal form, produces long stems suitable for pole production but is close to average in wood biomass production and even slightly below average in leaf biomass yield. Monterrico, in contrast, has a bushy and highly-branched habit, making it one of the poorest of all provenances in terms of stem length, and below average for wood biomass, but one of the best for leaf biomass. From the across-site analysis, therefore, Monterrico can be recommended specifically for leaf production. The conflicting results of Gomez *et al.* (1990) and Ngulube (1994) for Monterrico (see above) should also be noted, however, as these cast some doubt on the response of this provenance to repeated lopping. Belen Rivas is unexceptional in terms of stem length but is one of the best biomass producers, for both wood and leaf, in the across-site analysis. Neither Gomez *et al.* (1990) nor Ngulube (1994) included Belen Rivas in their experiments.

Seasonality is an essential aspect of leaf production, particularly for fodder where dry season production is the yield trait of greatest interest in the semi-arid tropics. Detailed seasonal production data are only available for one site, in Bali, but these suggest that Pontezuela, Playa Tamarindo and Mariara provenances also have potential to provide dry season fodder, in addition to the three provenances shown in the box. However it must be stressed that these results are from only one site, and that none of these additional three provenances show high stability of performance (Figure 8.4). Further studies on the interaction of provenance with management and site effects would give a more complete picture of suitability of different provenances for particular farming systems and agroclimatic conditions.

The OFI *Gliricidia sepium* provenance trial network: key findings

Trait	Top three provenances (overall performance across all sites)	Most stable provenances (above-average performance predicted on >80% of sites)
Stem length	1. Retalhuleu, Guatemala (17%) 2. La Garita, Honduras (13%) 3. Pontezuela, Colombia (11%)	1. La Garita, Honduras 2. Retalhuleu, Guatemala 3. Estelí, Nicaragua 4. Pontezuela, Colombia
Leaf production	1. Retalhuleu, Guatemala (33%) 2. Belen Rivas, Nicaragua (17%) 3. Monterrico, Guatemala (14%)	1. Retalhuleu, Guatemala 2. Belen Rivas, Nicaragua
Wood production	1. Retalhuleu, Guatemala (53%) 2. Pontezuela, Colombia (24%) 3. Belen Rivas, Nicaragua (21%)	1. Pontezuela, Colombia 2. Retalhuleu, Guatemala 3. Belen Rivas, Nicaragua 4. Vado Hondo, Guatemala

Values in brackets show provenance' mean relative performance across all sites, *i.e.* percentage by which each provenance's performance exceeds mean performance of all provenances tested.

8.3 Provenance variation in fodder quality

The *Gliricidia sepium* provenance trial network was intended primarily to test provenances' adaptability to a range of sites in terms of survival, growth and yield, but leaf material from a few trials was also used to investigate provenance variation in fodder quality.

The possibility that genetic variation in *G. sepium* could influence its palatability was first suggested by the selective feeding behaviour of howler monkeys (Glander, 1979) and moths (Janzen, 1983) in natural populations of *G. sepium* in Costa Rica. Both studies suggested avoidance of less palatable individuals within populations. The first study specifically to investigate provenance variation in palatability was conducted by Larbi *et al.* (1993). Freshly-harvested leaves of 28 seed sources of *G. sepium* were offered simultaneously to sheep in a cafeteria-type preference test. These included 26 provenances from the native range, the local Nigerian land race, and the ILCA 'high-yielding bulk' (HYB) composite derived from four Costa Rican provenances. Over ten four-hour periods, there was a five-fold difference in intake between the most and least palatable provenances. The Nigerian land race was among the most highly preferred, confirming the observation that accustomization plays a major part in feeding behaviour with *G. sepium*. Among the provenances from Central America and Mexico, there was a strong geographical association with palatability: with few exceptions, palatability increased the further south the original seed source. All the least palatable provenances were from Mexico, the most northern part of the species' native range. The provenances from Costa Rica and Colombia (the latter is probably a land race originating from Panama or Costa Rica) were the most palatable. This also concurs with the perceived high palatability of *G. sepium* in Colombia.

Recent research coordinated by the Oxford Forestry Institute has compared the fodder quality of Retalhuleu, Monterrico and Belen Rivas provenances, identified as the highest biomass producers in the provenance trial network, and two land races from areas where palatability is, and is not, perceived as a problem (Nigeria and Colombia respectively); as discussed in Section 4.4, perceptions of palatability of *G. sepium* differ widely in different parts of the tropics. Fodder blocks of these five seed sources were established for feeding trials at the following five livestock research institutions in countries where *G. sepium* is used as fodder to a greater or lesser extent:

- ILRI, Ibadan, Nigeria
- CATIE, Turrialba, Costa Rica
- CIPAV, Cali, Colombia
- BALITNAK, Ciawi, Indonesia
- University of Peradeniya, Sri Lanka

In the first of these feeding trials, conducted by CIPAV in Colombia, sheep were offered all five provenances simultaneously and *ad libitum*, either as a sole feed, with sugar cane tops, or with cane tops plus urea-molasses block (Benneker and Vargas, 1994). The intake of the *G. sepium* varied significantly between provenances, with the Colombian land race highly preferred over the other provenances in all three diets (Table 8.6).

Table 8.6 *Ad libitum* dry matter intake of *Gliricidia sepium* leaves in three diets, Cauca Valley, Colombia (source: Benneker and Vargas, 1994)

Provenance/ land race	**Daily *ad libitum* intake of *Gliricidia sepium* (g dry matter)**			
	***G. sepium* only**	***G. sepium* + sugar cane tops**	***G. sepium* + sugar cane tops + urea-molasses block**	**Mean of all three diets**
Monteria, Colombia (32/92)	294	277	266	279 c[1]
Monterrico, Guatemala (124/91)	110	103	91	101 a
Retalhuleu, Guatemala (125/91)	130	116	111	119 ab
Belen Rivas, Nicaragua (126/91)	168	171	154	164 b
Ibadan, Nigeria (4/92)	136	149	145	143 ab

[1] Different letters indicate significant differences at 1% probability level by Duncan's multiple range test.

Another notable finding in this experiment was that the intake of all five provenances was much higher than expected: the usual dry matter intake by ruminants is around 3% of body weight per day, but dry matter intake of *G. sepium* in this trial was over 4% of body weight. Previous studies by CIPAV have shown that the optimum economic level of supplementation of cane tops with *G. sepium* is about 25% of 'normal' daily intake, which is well below the intake level of even the least palatable of the five provenances in the feeding trial. A subsequent trial in which each sheep received a single provenance, fed at this 'economic' level as a supplement to sugar cane tops, revealed no differences between provenances in live weight gain over 18 weeks (Vargas, pers. comm.[1]). Like the experiment of Larbi *et al.* (1993), the results of Benneker and Vargas (1994) show that sheep can discriminate between provenances of *G. sepium*, and find some more palatable than others. The subsequent experiment, however, demonstrated that none of the provenances was so unpalatable as to be avoided if no choice was offered; moreover, there was no difference between them in their effect on animal production.

Unpublished results from the other four trials support these findings. The feeding trial at CATIE, Costa Rica also allowed the animals (in this case, goats) a choice between provenances, and again the local land race was highly preferred over the other, less familiar accessions. In the CATIE trial, the lowest intake was of the Colombian land race (although this was not significantly different from the other non-Costa Rican material). This suggests that while sheep and goats can detect genetic variation in taste/odour of *Gliricidia*, their preference seems to be determined mainly by adaptation to a particular provenance or land race, rather than by some genotypes being inherently more palatable than others.

In two of the feeding trials (ILRI, Nigeria and University of Peradeniya, Sri Lanka) goats were fed *G. sepium* leaves *ad libitum* as the sole feed, and each animal received only one of the five provenances (*i.e.* no choice was offered). Neither trial showed any effect of provenance on intake (Plate 8D). In a second trial at ILRI, and in trials at CIPAV and BALITNAK, the *G. sepium* was fed as a supplement to a low-protein basal feed: *Pennisetum purpureum* in Indonesia, *Panicum maximum* in Nigeria and sugar cane tops in Colombia. In these trials live weight gain was measured rather than intake of *G. sepium*, as the latter was limited and the animals in all cases ate all the *G. sepium*, of whatever provenance, that was offered. Again, no provenance effect was found in most cases, except in the first of two trials in Indonesia, where the effect of provenance on live weight gain was significant ($p<0.01$) with Retalhuleu provenance and the local land race giving the lowest weight gain over a seven week period. In a second, twelve-week trial at the same site, however, the effect of provenance was not significant. Overall, therefore, these provenance-based feeding trials give no evidence of a strong provenance effect on nutritive value in *Gliricidia sepium*; and while it has become clear that ruminants can and do distinguish between provenances, their preference appears to be for material to which they are accustomed rather than for particular provenances. The chemical basis of their ability to distinguish between provenances remains unknown.

8.4 Progeny trials

As well as the large network of provenance trials coordinated by OFI, a number of progeny tests were established under the same programme to estimate genetic parameters and so to determine which traits of interest are under good additive genetic control and therefore amenable to selection. Each trial comprised a large number of families of a single provenance, to give precise estimates of genetic parameters.

In this section, results are reported from three of the trials, planted in Honduras, Nicaragua and Zambia. Variance components are presented for each of the trials, and the heritabilities and genetic correlations calculated from these. There follows a brief discussion of the implications of the results for genetic gain in traits of interest in *G. sepium*. An example is also given of the calculation of genetic gain for one trait, branch cross-sectional area of regrowth after lopping.

Methods

Table 8.7 gives details of the three trials. They are broadly similar in design, each consisting of 50-63 families of a single provenance, planted in 5- or 6-tree lines replicated across 9 or 10 blocks. However the Monterrico trial in Honduras differs from the other two in that an incomplete block design was used with the 50 families arranged in 10 sub-blocks of 5 families within each replication. This is a resolvable alpha design that could improve the precision of family comparisons compared to a randomized complete block design, where there is a large number of treatments creating large replications.

The assessment schedules were different for each trial and comparison of traits is therefore not always possible across trials. The trait measurements followed a standard procedure. The stem measurement was that of the longest stem. The number of stems and the diameters of all stems larger than 1 cm diameter were measured at 30 cm above ground before coppicing, and at 50 cm after coppicing. The diameter (d) measurements were used to calculate cross-

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[1] *J.E. Vargas, CIPAV, Cali, Colombia.*

sectional area (csa) according to the formula:

$$csa = \frac{\pi}{4} \sum d^2$$

Variance components and genetic parameters were estimated for all the traits measured. The replications and families were considered random effects.

Results

In the trial in Honduras there was no significant effect of sub-block within replications, so analysis of this trial as an alpha design did not add to the precision of the results. All three trials were therefore analyzed as randomized complete block designs. Overall means for each trait in each of the three trials are shown in Table 8.8. There were significant family differences and replication differences for all traits in the three trials. The families change rank dramatically across the replications, showing that the large number of replications (9-10) in all the trials was necessary.

Variance components estimated from the three trials are given in Table 8.9, and genetic parameters (heritabilities and genetic correlations) in Table 8.10. The heritability was estimated as:

$$h^2 = \frac{4\,\sigma_f^2}{V_p} \quad where \quad V_p = \sigma_f^2 + \sigma_r^2 + \sigma_{rf}^2 + \sigma_e^2$$

(see also key to Table 8.9)

Low standard errors were associated with all parameters, showing that they are estimated with acceptable precision because an adequate number of families (50-63) was planted in each trial (earlier progeny trials using fewer families had resulted in estimates being swamped by their standard errors). However it has been assumed that the open-pollinated families are half-sibs and that there are no full-sibs present. It is therefore possible that the heritabilities are over-estimated if covariance between the members of a family is due to a relationship closer than that of half-sib.

Discussion

It is not possible to compare directly the genetic parameters obtained for the different provenances, as the effect of provenance will be confounded with effects of site and age of assessment; the results from the trial in Honduras clearly show that the parameters change with age. All the traits, however, showed moderate values of heritability at all three sites, and would therefore respond to selection. For all provenances stem length is more highly heritable than either number of stems or cross-sectional area. This suggests that, for a given selection intensity, greater gains could be achieved in stem length than in traits such as branch cross-sectional area which are more closely related to biomass production. Although stem length *per se* is rarely a trait of great interest to farmers, it is highly genetically correlated with stem cross-sectional area, suggesting that gains obtained through control over stem length should also yield gains in biomass.

The traits of greatest interest are those measured after coppicing, especially the total branch cross-sectional area, as this gives an indication of potential biomass production from trees managed by repeated cutting, the most usual form of management for *G. sepium* trees grown on farms. Unfortunately there is only information about this from one trial (in Honduras). In this trial there is a high genetic correlation (r_g= 0.75) between stem length at six months and branch cross-sectional area at 30 months (six months after coppicing), suggesting that early selection for wood biomass production may be possible on the basis of stem length measured as early as six months after planting. However, it must be emphasized that this is a preliminary finding, based on data from only one trial, and it should therefore be interpreted with caution. Moreover, such early selection would be done before the trees had flowered, so variation in pod production could not be taken into account (see also Section 9.3).

Progeny tests are frequently transformed into seed orchards when no further results are required. The field design of these tests would best be adapted by thinning to one tree per plot from the original six trees. This would give an average within-row spacing of 6 m, and minimize relatedness among adjacent trees. The tree with the best phenotypic value for the trait to be improved would be selected in each plot. A modest additional gain would be achieved by also removing the worst families.

The genetic gains resulting from selection for different traits, and the implications for dissemination strategies to farmers, are discussed further in Section 9.3. Using data from the trial in Honduras, the calculation of estimated genetic gain from selection for one trait, branch cross-sectional area after coppicing, is shown in the box. This example gives an insight into the methodology and into the potential gains achievable in *G. sepium* using a relatively low selection intensity which would be typical for a progeny trial undergoing conversion to a seed orchard.

Table 8.7 Site details and experimental design of three progeny tests of *Gliricidia sepium*

Site	**Provenance**	**Latitude Longitude**	**Altitude**	**Annual rainfall (mm)**	**Number of families**	**Number of reps.**	**Spacing**	**Trees per plot**
Comayagua, Honduras	Monterrico	13°39' S 13°39' S	600	880	50	10	1m x 4m	6
La Lucha-Léon, Nicaragua	Belen Rivas	12°22'N 86°48'W	80	1300	63	9	1m x 3m	6
Chipata, Zambia	Retalhuleu	13°39' S 32°34' E	1030	900	50	10	1m x 4m	5

Table 8.8 Mean values of the traits assessed in the three progeny tests of *Gliricidia sepium* (standard errors of the means in brackets)

Site	**Traits assessed, and assessment age (months from planting)**		
	6 months	18 months	30 months (6 months after coppicing)
Comayagua Honduras	longest stem (m) 1.20 (0.02) number of stems 5.16 (0.07)	longest stem (m) 2.29 (0.04) number of stems 4.54 (0.05) cross-sectional area at 30cm (cm^2) 21.0 (0.9)	number of stems 13.5 (0.3) cross-sectional area at 50 cm (cm^2) 35.3 (0.3)
	12 months	24 months	
La Lucha-Léon Nicaragua	longest stem (m) 2.21 (0.03) number of stems 2.84 (0.05)	longest stem (m) 4.04 (0.04) number of stems 3.17 (0.05) cross-sectional area at 30 cm (cm^2) 27.2 (0.5)	
	6 months		
Chipata Zambia	longest stem (m) 1.21 (0.02) number of stems 5.47 (0.08)		

Estimates of genetic gain in total branch basal area from direct and indirect selection

In this example, the trait to be improved is total branch cross-sectional area at 50 cm above ground level, 30 months after planting and six months after coppicing to 30 cm above ground level. The branches measured in the 30 month assessment therefore represented six months' regrowth. In order to remove adjacent related trees the selection strategy requires one tree per family plot to be selected, an intensity within family of 1 in 6. Additional gain is achieved by removing the worst 10% of families, leaving the better 45 out of 50.

Genetic gain from within-family selection is given by:

$$\Delta G_2 = i_2(n+3)\left(\frac{h^2}{4n(4+h^2(n-1))}\right)^{½}\sigma_A$$

where σ_A^2 = the additive genetic variance = 4 σ_f^2
h^2 = heritability
ΔG = genetic gain

The selection intensity within families is 1 in 6, $i_1 = 1.267$
$n = 6$

The within-family selection intensity, i_1, is defined as the standardized expected gain resulting from selection of a certain proportion of families (Falconer and Mackay, 1996). In this case, the proportion is the best one out of six individuals. The standardized expected gain for populations of sizes between 1 and 400 is read from tables of selection intensity (*e.g.* Becker, 1975; Lindley and Scott, 1984).

Although the total family size is 54 trees, the selection takes place within plots and the gain results from choosing the best one out of six trees in each of nine plots.

Genetic gain from between-family selection is given by:

$$\Delta G_1 = i_1\left(\frac{n-1}{n}\right)^{½}\left(\frac{h^2}{4-h^2}\right)^{½}\frac{3\,\sigma_A}{2}$$

The selection intensity between families is 45 in 50, $i_2 = 0.19$
$n = 54.$

The effective family size (n) for between-family selection is 54, that is, the family mean is estimated from all 54 family members.

Table 8.11 Genetic gain from direct selection on total branch cross sectional area at 30 months, 6 months after coppicing

h^2	σ_A^2	**Trait mean** (cm^2)	ΔG_1 **(within-family)** (cm^2)	ΔG_2 **(between-family)** (cm^2)	**Total gain** (cm^2)	**% gain**
0.13 (0.04)	81.0 (27.9)	44.9 (0.4)	2.9	0.7	3.6	8

Table 8.9 Variance components estimated from three open pollinated progeny tests of *Gliricidia sepium* (standard errors in brackets)

	σ_r^2	σ_f^2	σ_{rf}^2	σ_e^2
Provenance: Monterrico, Guatemala Trial: Comayagua, Honduras				
stem length (m) at 6 months	0.0109 (0.0058)	0.0059 (0.0021)	0.0282 (0.0028)	0.0604 (0.0019)
stem length (m) at 18 months	0.045 (0.025)	0.0507 (0.0151)	0.1592 (0.0148)	0.262 (0.008)
number of stems at 6 months	0.197 (0.105)	0.201 (0.055)	0.249 (0.045)	2.085 (0.064)
number of stems at 18 months	0.212 (0.110)	0.092 (0.028)	0.069 (0.030)	1.893 (0.058)
number of stems at 30 months	1.32 (0.72)	0.88 (0.32)	1.11 (0.46)	28.42 (0.87)
total branch cross sectional area (cm^2) at 18 months	15.95 (8.65)	9.15 (3.40)	38.21 (4.84)	159.92 (4.92)
total branch cross sectional area (cm^2) at 30 months	31.52 (16.67)	12.50 (4.58)	28.43 (6.57)	340.4 (10.5)
Provenance: Belen Rivas, Nicaragua Trial: La Lucha-Léon, Nicaragua				
stem length (m) at 12 months	1.25 (0.72)	4.08 (0.99)	3.93 (0.70)	31.28 (0.95)
stem length (m) at 24 months	5.01 (2.64)	4.10 (1.09)	5.30 (0.96)	44.07 (1.34)
number of stems at 12 months	0.033 (0.02)	0.017 (0.009)	0.092 (0.019)	0.910 (0.028)
number of stems at 24 months	0.053 (0.03)	0.055 (0.017)	0.055 (0.021)	1.276 (0.039)
total branch cross sectional area (cm^2) at 24 months	10.78 (5.69)	4.15 (1.51)	4.43 (2.22)	141.3 (4.3)
Provenance: Retalhuleu, Guatemala Trial: Chipata, Zambia				
stem length (m) at 6 months	0.0115 (0.0058)	0.0072 (0.0024)	0.0304 (0.0034)	0.1166 (0.0034)
number of stems at 6 months	0.160 (0.0083)	0.208 (0.056)	0.407 (0.060)	2.085 (0.064)

σ_r^2 = variance component due to replications

σ_f^2 = variance component due to families

σ_{rf}^2 = variance component due to replication x families

σ_e^2 = within families variance

Table 8.10 Genetic correlations estimated individually from three open-pollinated progeny trials of *Gliricidia sepium* (standard errors in brackets)

Provenance: Monterrico, Guatemala

Trial: Comayagua, Honduras

	stem length (m) at 6 months	**stem length (m) at 18 months**	**number of stems at 6 months**	**number of stems at 18 months**	**number of stems at 30 months**	**total branch area (cm^2) at 18 months**	**total branch area (cm^2) at 30 months**
stem length (m) at 6 months	0.24 (0.07)						
stem length (m) at 18 months	0.98 (0.02)	0.42 (0.10)					
number of stems at 6 months	-0.31 (0.17)	-0.42 (0.15)	0.32 (0.08)				
number of stems at 18 months	-0.42 (0.17)	-0.48 (0.15)	0.86 (0.07)	0.18 (0.05)			
number of stems at 30 months	-0.19 (0.19)	-0.32 (0.17)	0.69 (0.12)	0.64 (0.13)	0.14 (0.05)		
total cross-sectional area (cm^2) at 18 months	0.93 (0.04)	0.90 (0.04)	-0.15 (0.18)	-0.28 (0.19)	-0.02 (0.22)	0.18 (0.05)	
total cross-sectional area (cm^2) at 30 months	0.75 (0.10)	0.68 (0.11)	0.22 (0.19)	0.14 (0.21)	0.33 (0.19)	0.75 (0.10)	0.13 (0.04)

Provenance: Belen Rivas, Nicaragua

Trial: La Lucha-Léon, Nicaragua

	stem length (m) at 12 months	**stem length (m) at 24 months**	**number of stems at 12 months**	**number of stems at 24 months**	**total cross-sectional area (cm^2) at 24 months**
stem length (m) at 12 months	0.40 (0.09)				
stem length (m) at 24 months	0.91 (0.04)	0.28 (0.07)			
number of stems at 12 months	0.21 (0.21)	0.13 (0.13)	0.06 (0.04)		
number of stems at 24 months	-0.19 (0.18)	-0.30 (0.17)	0.98 (0.08)	0.15 (0.05)	
total cross-sectional area (cm^2) at 24 months	0.70 (0.11)	0.64 (0.12)	0.45 (0.22)	0.07 (0.22)	0.10 (0.04)

Provenance: Retalhuleu, Guatemala

Trial: Chipata, Zambia

	stem length (m) at 6 months	**number of stems at 6 months**
stem length (m) at 6 months	0.17 (0.06)	
number of stems at 6 months	-0.64 (0.12)	0.24 (0.06)

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9 Seed Orchards and Breeding

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9.1 Germplasm demand

To justify investment in large-scale seed or clonal production or in a formal breeding programme, there needs to be a strong demand for the species. It has been estimated that between 150 and 200 million people use *Gliricidia sepium*, the majority of whom live outside its native range in areas where *G. sepium* trees are largely cultivated rather than natural regenerants in farmers' fields or in secondary vegetation. Seed may therefore be in demand either to replace existing material with improved germplasm, or to expand into new areas (locally or regionally).

Replacements

Economically, *G. sepium* is a low-value tree; farmers are likely to place greater emphasis on the improvement of higher-value species such as timber or fruit trees. Where *G. sepium* trees already occur in farmers' fields they are seen as a ready source of material for replacements by seed or cuttings. Under suitable environments *G. sepium* seeds early (from six months of age), prolifically and annually. The Tanzanian Forestry Research Institute now only handles about 3 kg of seed per year, since farmers have become self-sufficient in germplasm. For clonal propagules, trees as young as 12 months old in Sri Lanka have been shown to provide up to 22 cuttings each, and older trees or trees pollarded in fence lines can produce far more. Availability of material for replacements, for those farmers who already cultivate *G. sepium*, is therefore not likely to be a problem.

A key question is whether farmers would buy improved material when they have the option of collecting their own seed or cuttings. Street (1992) carried out an economic analysis of growing *G. sepium* in Haiti and concluded that when farmers had to pay for seedlings the net present values were negative irrespective of the economic product (charcoal, poles, *etc.*). To stimulate demand for improved replacements (free or otherwise) the new *G. sepium* germplasm would have to be markedly and demonstrably superior.

Expansion

Following good performance in species evaluation trials, *G. sepium* is being highlighted as a species for greater cultivation particularly for newer technologies (*e.g.* contour hedgerows, mixed intercropping). It is difficult, however, to apportion this demand among various sectors (individual farmers, farmer groups, NGOs, national and international programmes). New introductions can avoid some of the problems encountered with previous land races (*e.g.* a narrow genetic base and sub-optimal material). Clearly, the first need is to ensure that a productive, stable and diverse provenance is chosen (see provenance trial results in Chapter 8).

The other possibility for expansion is at the local level, where farmers want to grow more *G. sepium* on new areas of land or to replace other species (*e.g. Leucaena leucocephala* following psyllid infestations). As with replacements, farmers would need to see a clear benefit from using new germplasm.

Farmers' criteria and thresholds for improvement

The OFI international trial network tested range-wide provenance collections of *G. sepium* on sites throughout the tropics, although unfortunately farmers were not involved in their evaluation. It was assumed that the traits farmers would be interested in were: (1) survival; (2) leaf or wood biomass growth; (3) stability of production across years and sites; and (4) number of stems produced.

Assuming farmers were interested in, for example, greater wood biomass production, how small a difference could they discern between germplasm sources? Given the multi-stemmed nature of *G. sepium* and the poor correlation of height with woody biomass, there would probably need to be a difference in wood biomass of at least 30% for farmers to appreciate it. A similar threshold for improvement might be required for leaf biomass production. It is important, therefore, to weigh up the biological threshold for improvement (genetic gain) versus the farmers' threshold for improvement (the minimum difference perceivable by farmers).

Only where the biological threshold is greater than the farmers' threshold is there scope for promoting the use of improved material. For qualitative traits (*e.g.* product quality, degree of bushiness, degree of aphid attack, *etc.*) it is much harder to define farmers' criteria and their ability to discern differences.

Real versus perceived demand and incentives

How much of the real demand from individual farmers and farmer groups is reflected in the perceptions of NGOs, national and international programmes is unclear. In essence, it is unknown whether the demand is real or perceived. For example, the Forestry Research Institute of Malawi has recorded a demand from within the country of more than 150 kg per year since 1988. There is no corresponding evidence, however, of greater cultivation of *G. sepium* (Minae, pers. comm.)[1]. In Indonesia, 10 tonnes of seed are sold annually for use within the country by one organization alone (Pangkalredjo, Semarang), and apparently the demand for seed of this species still remains high (Nitis, pers. comm.)[2].

Demand for germplasm of a particular species in agroforestry development projects has often been stimulated by the provision of incentives (cash, livestock, food, fertilizer, *etc.*). In these instances, it is difficult to dissociate the real demand from that created by the incentives.

In cases where it can be shown that it is farmers who are articulating the demand, as in community nurseries in Bolivia which are raising seedlings of *G. sepium* (Lawrence and Carter, 1994), there is little, if any, appreciation of intraspecific diversity. Demand is expressed at the species level. Why then do farmers distinguish between varieties of maize or tomato but do not generally extend this distinction to non-industrial trees like *G. sepium*? Is it that they are unaware of choices available to them, or that they have little interest or need to make distinctions?

A clear prerequisite for catalyzing a demand for useful intraspecific variation is attaching a label to that variation. Both alphanumerics (*e.g.* IR8 rice variety) and names (*e.g.* King Edward potato variety) have been successful for agricultural crops. For *G. sepium*, it is unlikely that the name Retalhuleu would catch on because of problems of pronouncing this Mayan word (*e.g.* corrupted to 'Rooter' in Malawi; J. Maghembe, pers. comm.)[3]. The alphanumeric (OFI 14/84) would also be problematic, as other alphanumerics describe seed collections from the same provenance in subsequent years (*e.g.* OFI 57/87; OFI 125/91). Consequently, releases of seed of Retalhuleu provenance for establishment of seed orchards or for delivery to farmers were latterly referred to by the author as the 'Mayan Type'.

9.2 Potential for improvement

The potential for improvement of *G. sepium* can be considered at a number of different levels, including provenance, family, individual and clone. It is worth placing these in context to evaluate the appropriateness of various types of improvement. Simons *et al.* (1994) argue that improvement opportunities are dependent upon whether the species in question is exotic or indigenous, propagated sexually or vegetatively, of low or high economic value, for home or market use, and new to or pre-existing in the area.

Although *G. sepium* is described as a multipurpose tree, it is typically cultivated by farmers for a single, or perhaps dual, purpose. The farmer recognizes the other benefits and products but does not necessarily demand or desire them. The adjacent farmer may want the tree for a different primary purpose. For *G. sepium*, the concept of a single ideotype fulfilling all purposes is illusory.

Provenance level

The provenance trial results presented in Chapter 8 indicate a high degree of provenance differentiation in *G. sepium* (see Section 8.2). Tree species that show high levels of provenance differentiation do so for one of three reasons: (a) they contain different genes; (b) they contain the same genes but at different frequencies; or (c) they contain the same genes but 'packaged' in different ways (co-adapted gene complexes). The molecular analyses reported in Chapter 7 indicate that although there are a few locally common but generally rare alleles (forms of a gene), most of the provenance differences are due to (b) or (c).

It is important when evaluating provenances that unbiased comparisons are made. Provenances should be collected in the same way and from a sufficient number of trees. Furthermore, all variation in a provenance should be included, with no selection being carried out in the nursery. To estimate provenance means accurately, Cotterill (1990) estimates that for poorly inherited traits 200 individuals per provenance should be measured; this could be reduced to 100 for highly heritable traits. Fortunately, such considerations were taken into account in the international provenance trial series of *G. sepium*, and thus provenance comparisons are valid and meaningful.

The provenance is an ideal level at which to distribute germplasm of *G. sepium* to farmers. In terms of wood biomass production, by choosing Retalhuleu provenance an average gain of 65% would be realized relative to choosing another provenance. The actual gain depends upon the alternative selected and ranges from 27% gain relative to Belen Rivas to 170% gain relative to Tzímol provenance. The mean figures mask what might happen at any particular site, but for *G. sepium* the superior provenances showed remarkable stability across the wide range of sites tested.

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For leaf biomass production, Retalhuleu provenance is also the best and provides an average gain of 36% over any other provenance. As with wood biomass, the actual gain depends upon the particular provenance selected and ranges from 7% gain relative to Belen Rivas provenance to 88% gain relative to Palmasola provenance. Very few trials, however, included repeated assessments of leaf biomass, and results from one trial in Indonesia (Bali) showed the inconsistency of provenance ranks over a two-year period (see Section 8.2).

In general, the average gains in leaf and wood biomass production from selecting Retalhuleu provenance, relative to local land races, were greater than those observed relative to other provenances from the native range. This confirmed suspicions that early exotic introductions were made from sub-optimal founder material which has become inbred.

The gains quoted above assume that it is possible to deliver sufficient quantities of seed of the best provenances to farmers. It also assumes that this gain will be sustainable over future generations of seed collected from these trees. If trees of other provenances or land races are present in the area then they can pollinate trees of the superior provenance creating inter-provenance hybrids. Depending on the underlying reason for provenance differentiation, the mixing of provenances could have different effects. Although the value of interspecific hybrids has been confirmed for many species, there are conflicting data on the performance of inter-provenance hybrids (Barnes and Simons, 1994). These, together with the unknown effects on genetic equilibrium and diversity, suggest a cautious approach to mixing provenances. Isozyme studies by Chamberlain (1994) suggested that Masaguara provenance may be of mixed origin resulting from multiple introductions (see Section 7.3); and this provenance was neither stable nor superior in the international provenance trial series. Obviously this would not be an important consideration if vegetative propagules were used.

The greatest problem with respect to the sustainability of the performance of an incipient land race derived from a superior provenance such as Retalhuleu is the manner in which farmers collect seed. Given that individual trees can produce several thousand seeds annually, there is the temptation to collect seeds from one or a few trees; this could lead to inbreeding in future generations. Inbreeding in cross-pollinated species almost invariably leads to a loss of vigour and fecundity (Barnes and Simons, 1994) and should definitely be avoided in *G. sepium*. Arguably, the greatest improvement in *G. sepium* that could be made is the promotion of an extension message to advise farmers to collect seed from at least 20 trees.

Family level

Selection at the family level (see Sections 8.1 and 8.4) requires the establishment of progeny trials. For quantitative traits such as biomass production, family heritabilities are likely to be higher than individual heritabilities (low to moderate), but to achieve any substantial gain a high selection intensity would need to be imposed. For Retalhuleu provenance, however, the natural stand only contains approximately 150 trees and seed can only be collected from perhaps 60 trees if an adequate minimum distance (50 m) between trees (to reduce co-ancestry) is to be maintained. Given that it is desirable to retain at least 20-30 families in a seed orchard, this provides little scope for family selection. Moreover, there might be family x site interactions which would necessitate progeny trials on a range of sites.

Individual level

Selection of superior individuals can be on either a phenotypic or a genotypic basis. Phenotypic selection can be carried out in native populations, in farmers' fields or amongst superior families in progeny trials, whereas genotypic selection can only be performed with progeny trial information. Pitcher (1982) found phenotypic selection of *Prunus serotina* trees in natural stands to be ineffective in predicting family performance. Ying and Morgenstern (1979) also found phenotypic selection in *Picea glauca* to be ineffective. Phenotypic selection in *Pinus radiata*, however, was shown to provide a 19% realized increase in volume at age 7 years (Eldridge *et al.*, 1977).

No such information on the efficiency of phenotypic selection is available for *G. sepium* but it is clear that phenotypic selection for quantitative traits would be questionable in native populations or farmers' fields since the previous management history (*e.g.* lopping, coppicing, *etc.*) and age of individual trees is uncertain. The comparison of within-family selection methods (phenotypic and genotypic) in *G. sepium* should therefore be confined to progeny trials. Cotterill (1986) reviewed a number of breeding strategies and concluded that strategies that rely solely on within-family selection produced relatively poor gains per generation and per year, although this was somewhat dependent on the heritability of the trait in question. The value of each of these two methods will therefore depend on the genetic parameters of traits and the accurate estimation of family means. There are often family x site interactions so caution will be needed if selection is in only one environment (Johnson and Burdon, 1990). The efficiency of various methods of breeding have been reviewed by a number of authors although it is unlikely that questions of economic and genetic efficiency carry as much weight for *G. sepium* as for commercial species.

The genetic parameters of a trait are specific to a certain population growing at a particular site. Woolaston *et al.* (1990) found large differences in *Pinus caribaea* both in genetic parameters for a single population planted on different sites and between different populations planted on the same site, which could not be related to site quality. Examination of the genetic parameters for *G. sepium* provenances reported in Section 8.4 shows some variation for quantitative traits of interest but the effects of site and provenance are confounded and impossible to discern from the existing trials.

Where *G. sepium* is used in contour hedgerows or alley cropping it is impossible to determine the effect of individual trees on soil erosion or fertility. In such cases, individual selection is inappropriate.

Clonal level

Apart from the advantage of using vegetative propagules if *G. sepium* does not set seed in a given environment, cloning also offers other benefits. Cloning will produce exact copies of the mother tree (ortet) since both additive and non-additive genetic variation can be captured (Leakey, 1991). Non-additive variation cannot be captured through breeding. Vegetative propagation also allows the capture of combinations of traits that might otherwise be difficult to achieve (*i.e.* where there were negative genetic correlations between traits). Randall and Cooper (1973) found significant clone x environment interactions in *Populus deltoides*, so selection of clones might have to be site-specific.

One concern in using vegetative propagation is that clones which produce high numbers of cuttings per year can dominate the composition of clonal populations. For instance, for three clones A, B and C, producing respectively 2, 3 and 4 cuttings per year, the proportion of each clone in the population would change drastically in only a few cycles of vegetative propagation. After 10 years, clones A, B and C would have 1024 (0.1%), 59,049 (5.3%) and 1,048,576 (94.6%) copies each, respectively.

In relation to the spread of certain diseases, clones could be either advantageous or problematic. Seed-borne diseases would be avoided if cuttings were used, but mechanically-transmitted diseases (such as some viruses) could easily be spread on the tool used to take cuttings.

9.3 Predicted gains from breeding

Breeding of most commercial forest tree species has been in progress for less than 40 years (Barnes and Simons, 1994). Using a strategy of recurrent selection for general combining ability, and seed production from progeny-tested clonal orchards, average gains of around 20% were attained in the first generation of selection in pines (Barnes and Simons, 1994). Is this a strategy that should be followed for non-industrial trees like *G. sepium*?

Irrespective of the strategy followed, a key question is "Whose strategy is it?" The most important question for genetic improvement of *G. sepium* is whether farmers are setting the breeding objectives, or agencies such as governments, research projects and international organizations. It is fair to say that most literature on the improvement of non-industrial trees, *G. sepium* included, equates superiority with greatest growth, yet it is recognized that product quality is often more important then yield, and farmers may also value stable production above enhanced but variable production (Simons, 1992). In essence, is biggest the best? Kanowski (1993) concluded that there has been a "northern temperate bias" to tropical tree improvement and that there is a need to re-evaluate breeding methods.

Assuming that longer stem length (for poles), greater wood biomass (for firewood) or increased leaf biomass (for fodder) are traits preferred by farmers, the progeny trial results from Honduras (Section 8.4) can be used to estimate the response to selection for these traits. This assumes that biomass can be predicted from branch cross-sectional area, the trait actually measured. Heritabilities of stem length at 18 months, cross-sectional area at 18 months and cross-sectional area at 30 months (six months after coppicing) were 0.42, 0.18 and 0.13 respectively (Table 8.10). This trial was set up with six-tree line plots and by selecting the best tree per plot these heritabilities would result in genetic gains of 14% for stem length at 18 months, 14% for cross-sectional area at 18 months and 8% for cross-sectional area at 30 months. The branch cross-sectional area of uncut trees (at 18 months) is known to be a good predictor of wood biomass (Stewart *et al.*, 1992), and cross-sectional area of resprouts after coppicing (30 month data) may be related to leaf biomass production. Although the heritabilities were accurately estimated, they were low to moderate and this, combined with a low selection intensity, resulted in relatively small gains.

By selecting for stem length at 18 months there would be selection against a high number of stems, since these two traits were negatively correlated ($r_g = -0.48$)[4]. An interesting aspect to emerge was the strong genetic correlation between stem length at 6 months and stem length at 18 months (r_g=0.98), cross-sectional area at 18 months (r_g=0.93) and cross-sectional area at 30 months (r_g=0.75). This suggests scope for indirect selection of the latter traits using stem length at 6 months; however, given that in this trial the ultimate objective was to produce seed, selection at this age would be unwise because the trees would not have flowered and no indication of pod set would be available.

In the absence of survey information about what farmers want from improved *G. sepium* it seems prudent to pass on as much genetic variation to them as possible. Wei and Lundgren (1991) called for development of breeding methods that combine the goals of gain and diversity. Gain is associated with economic return whilst diversity is a more nebulous concept. The loss of diversity is dependent on the selection method used and the selection intensity (Wei and

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[4] *r_g = genetic correlation.*

Lundgren, 1991). For four of the families present in a progeny trial in Honduras, the genetic diversity was estimated using 42 randomly amplified polymorphic DNA products (RAPDs). Following selection for leaf biomass at 30 months, where the best tree per plot was chosen (*i.e.* 1 in 6), the genetic diversity within a family was reduced by up to 40%. Clearly, this loss of diversity would be a high price to pay for the modest gain of 8% in leaf biomass. This study, however, used dominant molecular markers (*i.e.* RAPDs) whereas using co-dominant markers (isozymes) Cheliak and Pitel (1988) sampled phenotypic selects and trees at random in *Picea glauca* and found that 75% of alleles were present in the selected phenotypes. Mitton and Jeffers (1989), also using isozymes, found in *Picea engelmannii* that selected individuals had higher heterozygosity.

Given the low gains from a single cycle of selection there seems little prospect for advanced generation breeding in *G. sepium*. Indeed, there is little merit in selection beyond the provenance level and all the variation should be passed on to farmers so that they may carry out their own selections if they wish (see box).

A model for provision of superior seed to farmers

- Identification of farmer requirements and desired traits.
- Rangewide provenance collections.
- Provenance evaluation and selection.
- Establishment of seed orchards using bulk seed of selected provenances.
- No further selection within seed orchard: all available variation passed on to farmers.
- Distribution of seed or cuttings for planting by farmers or establishment of further multiplication stands.

Step 2 is carried out centrally (in the case of *G. sepium*, by OFI); steps 1, 4 and 5 locally; and step 3 locally but with central coordination.

9.4 Seed orchards

From surveys of both buyers and suppliers of *G. sepium* seed it is clear that we are dealing with an undiscerning market. There is no premium paid for quality (physical or genetic) and there is little appreciation of intraspecific diversity. One large supplier in Europe was obtaining seed from Gualán, Guatemala which is a provenance shown in trials to be of below average leaf and wood biomass production. Seed, however, is marketed almost without exception under the species name only. No instances of the sale of cuttings were found. Seed can be purchased for as little as US$1.50 per kg in Indonesia, and some suppliers in India carry stocks of up to 1000 kg for sale at US$4.00 per kg. Other suppliers in Europe quote prices of up to US$120 per kg. In Haiti, 400 kg was being imported from southern Honduras at a price of $7 per kg. A bilateral project in Kenya found an annual demand of 300 kg of seed in East Africa which was being satisfied from various suppliers. Some national organizations maintain a price differential for local or international sales so the market value of *G. sepium* seed is variable.

It is uncertain how long demand for seed of *G. sepium* will continue, and this is crucial to the way seed orchards should be set up. If the demand is satisfied by inferior material from either the native range or exotic land races before seed orchards are productive then there will be difficulty in promoting seed from orchards unless it is markedly superior or has some beneficial qualitative trait (*e.g.* insect resistance).

A great advantage of *G. sepium* is that it does set seed early (from six months of age) and regularly each year. Individual trees can produce up to 1 kg of seed per year and more than 95% of trees set seed. A well established seed orchard could produce 50-100 kg of seed per hectare. Who, however, should bear the costs of establishment; and could a seed orchard be self-financing from sales? The answers to these questions are unclear because they depend on a number of factors, including location and size of the orchard, uses of *G. sepium* in the region, whether the seed is for local or international use, and the response of suppliers and buyers to quality seed. At present, there are few cases of farmers buying *G. sepium* seed. It is NGOs, national and international institutions and donor projects that purchase seed to pass on to farmers. There are cases of farmers and farmers' groups producing their own seed, but this is generally not for sale.

Seed orchards may either be large centralized entities or at a village-level scale. Advantages of a large seed orchard are the quantities of seed that can be derived from them, ease of management and security over the seed orchard, and the ease of monitoring quality and composition of the seed produced. Disadvantages include distance to users, uncertainty of quantities required and the infrastructure needed. Village- or farm-produced seed has the advantage that farmers can take part in the production of seed and no transport or storage facilities are required. There is often, however, a lack of extension information on village-level seed production.

Seed orchard design and management

Seed orchards should contain a minimum of approximately 50 trees derived from a broadly-based seed collection and a well-documented seed source. Trees can be left intact to grow tall or be managed as coppiced or pollarded trees.

Intact trees will produce seed for several decades but pod collection will become difficult as the trees get large. The final spacing for intact trees should be about 6 m x 6 m, so that they can develop full crowns. They will attain a height of 6-10 m after 2-5 years. Initial spacing might be 2 m x 2 m, allowing for some selection of good trees at an intensity of one in nine. Unless the identity of half-sib families is retained there is a danger of leaving individuals from only a few families which would result in future inbreeding. This should not be a problem if more than 1000 trees are planted initially. There will be little genetic gain from this selection but it would allow for selection of trees that produced more seed. Experiments in Honduras, however, showed low correlation in pod production between successive years.

Seed trees that are to be coppiced or pollarded can have a final spacing of 2 m x 2 m. The greatest advantage of managing trees by coppicing is that pod collection is easier and safer. Moreover, seed production may be increased by coppicing, since flowers are produced on new wood.

To facilitate good seed set, pollinators can be encouraged to nest in the seed orchards. The primary pollinator of *G. sepium* in its native range is *Xylocopa fimbriata*. This is a solitary bee that nests in rotten or sound wood, and posts can be placed in the orchard as nesting sites. In exotic locations with a favourable climate for flowering and fruiting, other species of solitary bee will serve as pollinators. Honey bees (*Apis* spp.) are very poor pollinators of *G. sepium* and so beehives will not greatly assist pollination although they may provide useful income.

To ensure good seed production from seed orchards it may be worth fertilizing them. A seed orchard of Retalhuleu provenance in Indonesia responded well to fertilizer application which increased the proportion of trees flowering from 44% to 71%. Although 44% of trees flowered without fertilizer, less than one-third of these set pods. In an extreme case of a poorly-fertilized seed orchard of Retalhuleu provenance in Malawi, boron deficiency was recorded that led to symptomatic problems of tip dieback, curling of leaves and slight chlorosis (Smith and Vanden Berg, 1992). This seed orchard produced no seed at all as a consequence.

Seed of superior provenances is now becoming available from seed orchards in Brazil, Guatemala, Hawaii, Honduras, India (Plate 8E), Indonesia, Malawi, Nicaragua, the Philippines, Sri Lanka and Zambia by a variety of institutions (including universities, bilateral projects, NGOs, government research stations). In most cases the seed produced by these organizations is for local use but because such institutions often have their own client farmer groups, access to high quality seed is rarely uniform within a locality. These seed orchards will rarely satisfy demand fully but will rather produce nucleus amounts of germplasm which can be used to set up more seed orchards and to serve as founder material for newly developing land races (*e.g.* in Malawi). It is expected that these seed orchards will have a five- to ten-year lifespan before most demand will be met. Organizations or individuals hoping to generate continued income from such seed orchards should be aware of this fact.

Gliricidia sepium has proved to be a useful model for studying the genetic improvement of a non-industrial tree which, although widely used, is of little commercial value. It was recognized early on that supplying sufficient quantities of quality seed to meet demand would be difficult. Although largely unquantified, it is known that much of the demand for *G. sepium* seed has been met by the supply of inferior germplasm. This will have a major impact on the performance of incipient land races. It is recommended, therefore, that a more proactive approach to the multiplication of germplasm for dissemination be taken. This would entail the establishment of seed orchards of several provenances early on in the provenance testing process so that, once the results become available, seed of the most desirable provenances is already available to meet demand. This approach may seem wasteful of resources, in that some seed orchards may never be used, but it would provide seed several years earlier and reduce the proportion of demand satisfied by inferior germplasm.

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