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Naturally-regenerated *Cordia alliodora* in Costa Rica, growing as an overstorey above coffee.

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Cordia alliodora

A promising tree for tropical agroforestry

by
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Foreword

As awareness increases of the importance of tropical forests to the wellbeing of humanity, so too do demands for the effective conservation of those resources. Tropical forest conservation in its true sense, that is the wise and sustained use of the resource, can only be achieved if there is access to adequate information on the trees that make up the forests. Many species have been studied and numerous valuable data recorded, but much of the information is scattered throughout large numbers of publications and reports. In these circumstances the forest manager seldom has an opportunity to benefit from the vast store of information that has been built up over a century or more. Owing to ignorance of existing facts numerous mistakes are repeated, there is unnecessary failure and avoidable environmental degradation continues.

Much more could be done to help tropical forest conservation if known facts were collated, reviewed and made available in an easily-read form. The Oxford Forestry Institute (OFI), with its unrivalled library and broad professional experience of tropical forestry, is uniquely placed to prepare efficiently such reviews. This was recognized 20 years ago when Alan Lamb wrote the first of a series of monographs on fast-growing timber trees[1]. The OFI's policy is to continue publishing these reviews in support of its long-running research concerning the conservation and improved use of tropical forest genetic resources. Thus, this publication not only summarizes the results of OFI work, supported by the Overseas Development Administration (ODA), on provenance variation in *Cordia alliodora* but it also reviews all the information on the species published up to 1987.

A preliminary stage in the preparation of this review was the joint publication with the CAB International Forestry Bureau of an annotated bibliography of 198 references covering literature from 1922 to 1987, which includes substantial summaries of the papers and reports cited here[2]. Reference to both publications will give the reader a thorough introduction to the known facts. However, if further details are required copies of the original papers can be purchased through the Plant Sciences and OFI Library[3], within the provisions of copyright legislation.

This review is not written as a technical manual on how to grow and use *C. alliodora*. It is intended to provide the manager with an insight into past experience with the species, including both successes and failures, and to draw attention to the range of management options that are available. It is the responsibility of the manager to identify what is relevant to his or her own circumstances, to modify where appropriate, and to incorporate it in a realistic management regime according to the principles of good forestry practice.

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[1] Published in the series *Fast Growing Timber Trees of the Lowland Tropics*. Later replaced by *Tropical Forestry Papers*. Both published by the Oxford Forestry Institute.

[2] *Cordia alliodora. Annotated Bibliography, CAB International, Wallingford, UK* (1988) F40, 28 pp.

[3] Details available on request from the Library and Information Service, Oxford Forestry Institute.

Summary

Cordia alliodora is a fast-growing tree with a high-quality wood. The species is widely distributed in continental tropical America from central Mexico to northern Argentina, a range in latitude of some 50° from approximately 25°N to 25°S. There is also a wide occurrence among the Caribbean islands.

Not only does the tree produce high-quality timber but the persistant, tall, straight stem, self-pruning habit and compact crown make it suitable for growing in combination with many agricultural crops. This, combined with the ease with which the species regenerates naturally on cleared sites, has led to its incorporation in numerous agroforestry systems throughout its natural range.

C. alliodora can also readily be regenerated artificially by using either seedlings or stumps. Good growth as a plantation species has been achieved in the neotropics, trials in Africa have been promising and it is the basis of a plantation programme in Vanuatu. On suitable sites dimensions of 30–35 m height and 40–55 cm diameter breast height are predicted for rotations of 20–25 years. However, the choice of provenance is important. Provenance variation over the whole of the species' natural range has not been assessed but substantial data are available for Central America. These show that, in exotic environments, provenances from the seasonally-dry Pacific watershed develop more rapidly at the seedling stage than do provenances from the more humid Atlantic watershed, but within two years of planting in the field this ranking is reversed. The Atlantic group then shows superior growth rates up to 10 years, the greatest age for which information is available.

Evidence from plantations exposed to hurricanes and cyclones indicates that *C. alliodora* probably has above average resistance to stembreak and windthrow, compared with other plantation species, especially during the early years. In the species' natural range, stem canker caused by the rust fungus *Puccinia cordiae* is economically damaging on some sites. Other pests and diseases have been recorded as problematical locally but not sufficiently to detract from the tree's widespread popularity. Outside its natural range *C. alliodora* appears to have few serious pests and diseases but mortalities due to a root disease attributed to the fungus *Phellinus noxius* have given rise to concern in Vanuatu.

The timber seasons easily with little degrade. It is dimensionally stable when dry, moderately durable compared with other tropical hardwoods when exposed to fungus attack, and resistance to termites is good. The wood works easily with little dulling of cutting edges to give a very smooth finish. Polishing and staining characteristics are satisfactory. The decorative heartwood has somewhat similar mechanical properties to *Swietenia macrophylla*. These characteristcs have resulted in the timber being widely used in the countries where the species occurs naturally. The wood is popular for light construction, as well as for furniture- and cabinet-making. It is also used for veneer manufacture, turnery and a wide variety of carvings.

As many of the properties of *C. alliodora* wood are similar to those of *S. macrophylla*, it might be an acceptable substitute in uses such as boat planking and other boat parts. The resistance to decay indicates a possible role as an alternative timber to several species of cedar in situations requiring durability. An investigation of plantation-grown samples from Vanuatu concluded that although the wood is not strong for construction purposes, the combination of stability and durability make it suitable for both indoor and outdoor work. The appearance suggests a use in furniture construction and panelling, and it should be acceptable for flooring where there is light traffic.

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1. Introduction

Cordia alliodora is a fast-growing forest tree with a wide-ranging natural distribution in the neotropics. International attention was first drawn to the species because of its desirable timber properties. However, long before the timber trade took an interest, the tree was well known throughout its natural range. Here it was, and still is, preferred for many uses where ease of working, durability, dimensional stability and attractive appearance are required.

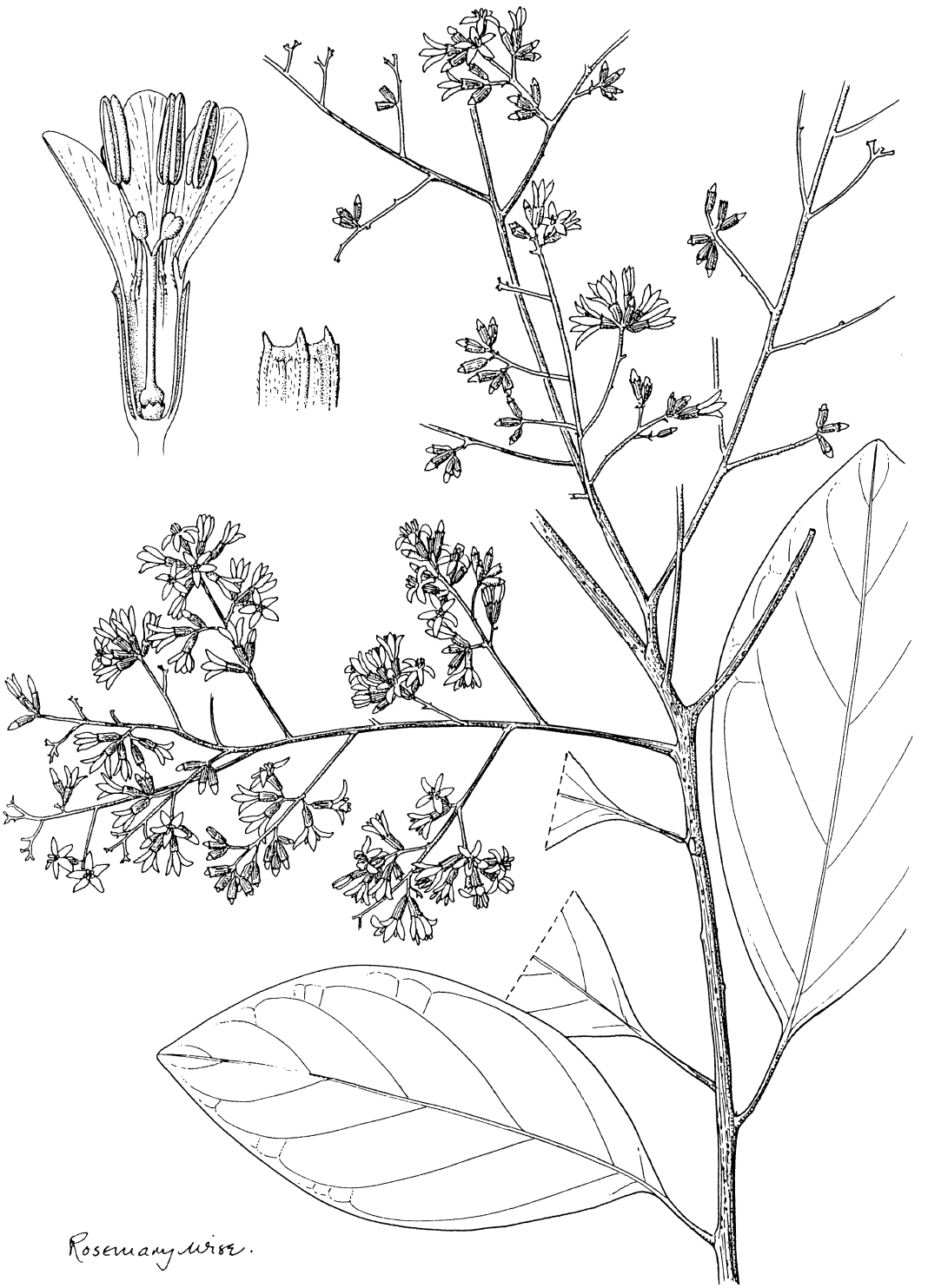
It was probably in Trinidad during the 1920s that *C. alliodora* was first investigated by the forestry profession. Although the species is common in parts of the island, few extensive sites could be found where artificial regeneration succeeded. Consequently, at that time it did not receive acclaim as a tree suitable for widespread planting. Nevertheless, some useful silvicultural observations were recorded. In later years profuse natural regeneration was found to occur in old cocoa plantations, a fact that prompted Lamb (1955) to advocate systematic management on such sites because of the substantial revenue that was likely to accrue from medium-length rotations.

Long before *C. alliodora* received this attention, the usefulness of the prolific natural regeneration that often springs up on cleared forest sites was already recognized throughout much of Latin America. The practice of retaining selected trees whilst raising crops around them has persisted to the present day, not only because the presence of trees may benefit the crops but also because there are many areas where the trees are a valuable source of supplementary income. In this way *C. alliodora* has become part of many pasture and cultivation systems. One widespread practice is to manage the species to provide part or all of the necessary shade over cocoa and coffee plantations. Such use covers an estimated 4.5 million ha in Colombia alone. This confers the benefits referred to above as well as assisting nutrient cycling and maintenance of fertility.

C. alliodora has, therefore, a long-standing reputation throughout its natural range as a highly desirable tree with an above average range of useful characteristics. Elsewhere a few very promising exotic trials were established around the middle of the century but these failed to stimulate large-scale planting. There was little incentive to attempt this while large logs of fine hardwoods were in plentiful supply from natural forests. Moreover, *C. alliodora* requires the kind of fertile site that has a tendency to be cleared for agriculture. A further deterrent to attempting to establish plantations was the erroneous belief that the seed is difficult to store and transport.

In recent years, as traditional sources of tropical hardwoods declined, there has been increased interest in *C. alliodora*. The tree produces an abundant supply of seed from an early age and seedlings are easily raised in nurseries. Plantations and line plantings can be readily established using normal silvicultural practices. It is especially attractive for incorporating in agroforestry systems to provide peasant farmers with additional income. Moreover, such systems have the potential for making a substantial contribution to buffer zones around natural forest reserves.

The few plantation schemes started recently have been very promising, but unless there is adequate information on provenance variation there is always the danger that the success of a plantation will be severely compromised by using an unsuitable seed source. This situation existed until 1978 when the Oxford Forestry Institute (OFI) began a programme of provenance exploration and evaluation for *C. alliodora*. Now that more is known about provenance variation, it is an appropriate time to review all knowledge of the species to encourage its efficient and sustained use.



(a) Flowering branchlet of *Cordia alliodora* showing leaves and inflorescence; (b) vertical section of flower; (c) calyx.

2. Description of the species and its natural distribution

2.1 General description

On good sites *C. alliodora* typically achieves a diameter at breast height (d.b.h.) of 70–80 cm, although it may exceed 1 m. It is capable of growing to a height of 30–35 m (Perez Figueroa, 1954). The bole is generally straight, cylindrical and often clear of branches for 50–60 percent of the total tree height, even when growing in the open. Other notable characteristic features are the horizontal layers formed by the branch whorls and the garlic odour emitted by the leaves when they are crushed[1], hence the species' Latin name. During the flowering season the tree is readily recognized by the masses of white flowers (Little & Wadsworth, 1964).

2.2 Nomenclature

Family: Boraginaceae
Sub-family: Cordioideae
Genus: *Cordia* Linn.
Section: Cerdanae
Latin name: *Cordia alliodora* (Ruiz & Pavon) Oken

The genus *Cordia* is pantropical in its distribution and consists of about 300 species, all of which are trees or shrubs. The modern classification of these species is based on the treatment originally devised by Johnston (1930). This identified seven sections which have been widely accepted by most authors, although there have been some name changes and minor revisions. The following five sections are currently recognized: Cerdanae; Cordia; Micranthae; Rhabdocalyx; and Varroniae.

Miller (1985) reviewed in detail the systematics of the genus *Cordia* in Mexico and Central America. He recorded that the section Cerdanae is confined to the neotropics and made up of about 30 species. Among these 13 are found in Mexico and Central America of which two extend beyond this region. One, *C. gerascanthus*, also occurs in the West Indies. The other, *C. alliodora*, is found in both the West Indies and in most mainland countries from Mexico to Argentina.

Carpanezzi *et al.* (1982), partly citing Guimaraes *et al.* (1971), recorded that the *C. alliodora* type specimen from Peru was originally described by Ruiz & Pavon in 1799 as *Cerdana alliodora*. It was transferred to the genus *Cordia* by Oken in 1841. This substituted combination is frequently attributed to Chamisso who was incorrectly cited as the authority by De Candolle in 1845. The correct botanical nomenclature, as given by Miller (*loc. cit.*) is: *Cordia alliodora* (R. & P.) Oken, Allg. Naturgesch. 2(2):1098 (1841); A. DC., Prodr. 9: 472 (1845) (incorrectly as *C. alliodora* (R. & P.) Cham.); I.M. Johnston, J. Arnold Arbor. 3: 181 (1950); *Cerdana alliodora* R. & P. Fl. Peruv. 2: 47, t. 184 (1799); *Cordia cerdana* (R. & P.) R. & S., Syst. Veg. 4:467 (1819); *Lithocardium alliodorum* (R. & P.) Kuntze, Revis. Gen. Pl. 2: 976 (1891). TYPE: Peru.

This does not give the full nomenclatural history of the species which is very confused. Miller (*loc. cit.*) drew attention to the numerous synonyms or misapplied names published by many early authors and gave the following 15 examples:

Cordia gerascanthus Jacq., Select. Stirp. Amer. 43. 1976, not *Cordia gerascanthus* L. 1759.

Cordia gerascanthus var. *domingensis* Cham., Linnaea 8: 121. 1833; DC. Predr. 9:472. 1845; *Lithocardium gerascanthus* var. *domingense* (Cham.) Kuntze, Revis. Gen. Pl. 3(2): 206. 1898.

Cordia velutina Mart. (Herb. Fl. Bras. pg. 165, no. 268) Flora Regenb. xxi. Bd. 2, Beibl. 85. 1838.

Cordia alliodora var. *glabra* DC., Prodr. 9:472. 1845.

Cordia gerascanthus var. *subcanescens* DC., Prodr. 9:472. 1845.

Cordia gerascanthus sensu Griseb. Fl. W. Indies 478. 1861.

Varronia tuberosa S. & M., Pl. N. Hisp. 30. 1888; ed. 2, 28. 1893.

Lithocardium gerascanthus var. *alliodorum* Kuntze, Revis. Gen. Pl. 3(2):206. 1898.

Cordia gerascanthus forma *martinicensis* Chodat, Bull. Soc. Bot. Geneve, Set. 2, 12:210. 1920.

Cordia gerascanthus forma *micrantha* Chodat, Bull. Soc. Bot. Geneve, Ser. 2, 12:210. 1920.

Cordia alliodora var. *boliviana* Chodat and Vischer in Chodat, Bull. Soc. Bot. Geneve, Ser. 2, 12:211. 1920.

Cordia andina Chodat, Bull. Soc. Bot. Geneve, Ser. 2, 12:211. 1920.

Cordia chamissoniana var. *complicata* Ruiz & Pavon ex. Chodat, Bull. Soc. Bot. Geneve, Ser. 2, 12:215. 1920.

Cordia goudoti Chodat, Bull. Soc. Bot. Geneve, Ser. 2, 12:215. 1920.

Cordia macrantha Chodat, Bull. Soc. Bot. Geneve, Ser. 2, 12: 215. 1920.

According to Miller (*loc. cit.*) this is by no means a complete list. Moreover proper typification of many of the names is not possible without examining the herbarium material.

There is uncertainty concerning the nomenclature and taxonomic status of the populations at the southern end of the species' natural distribution. In his early studies, Johnston attempted to keep large-flowered specimens from Argentina, Paraguay and Brazil to the east and south of the Amazon basin as a

[1] In the literature there is much reference to this alleged garlic odour, but the second author of this review failed to detect it during the several months that he spent in the field assessing *C. alliodora* provenance trials and studying the natural populations.

distinct species called *Cordia trichotoma*. These large-flowered specimens also lack the usual ant domatia. Later he concluded that these differences alone did not justify this separation and that the taxon was best classified as a variety named *Cordia alliodora* var. *tomentosa* A. DC. (Johnston, 1935).

This issue was recently re-examined by Gibbs & Taroda (1983). They noted that in Brazil trees essentially similar to the type are found in the northern and western parts of the country. In the central, eastern and southern regions these are replaced by plants that have larger flowers and no ant domatia. Studies of 230 herbarium specimens revealed that these two taxa also differ in their expression of heterostyly. The floral morphology of *C. alliodora* is homostylous, whereas in *C. trichotoma* there are distinct short-and long-style morphs as well as homostyles. This suggests that the two taxa should be treated as separate species and not merely as allopatric races that differ only in flower size and presence of ant domatia.

Throughout its wide natural range *C. alliodora* is known by many local names, of which the following are listed by Little & Wadsworth (1964): varía, varía prieta, varía colorada, varía amarilla (Cuba); bois soumis, chene caparo (Haiti); capá, capá prieto, guacimilla, capá de sabana, capá de olor (Dominican Republic); spruce (Antigua); bois de rose, bois de Rhodes (Guadeloupe); laurier cypre (Dominica); cypress (Tobago); cypre, cyp (Trinidad); onion cordia (USA, commerce); hormiguero, bojón, tambor hormiguero (Mexico); laurel (Central America); laurel blanco (Central America, commerce); salmwood, salaam, bohun, laurel blanco (Belize); bojon (Guatemala); laurel negro (Honduras, Nicaragua, Costa Rica); laurel macho (Nicaragua); solera, canalete de humo, laurel negro (Colombia); pardillo, tacuaí (Venezuela); brown silver balli (Guyana); louro, louro amarello, uruazeiro (Brazil); laurel negro, laurel prieto, laurel macho, laurel (Ecuador); árbol del ajo (Peru); ajo (Bolivia).

2.3 Botanical description

The mature tree may or may not have buttresses. If present, they are usually small but on shallow soils they may extend 1–1.5 m up the trunk (Johnson & Morales, 1972). On young trees the bark is smooth with a greenish colour. On mature trees it is a greenish-black and may be smooth or narrowly fissured. The thin, tough, pale underbark darkens rapidly on exposure (Marshall, 1939).

The leaves, like those of all *Cordia* species, are simple, petiolate and alternate. Detailed botanical descriptions indicate that they range up to 5 cm in width and 18 cm in length. They are short- or long-pointed at the base. The upper leaf surface may have scattered hairs when young but it becomes smooth at maturity. The lower surface is covered with stellate (i.e. star-shaped) hairs. The petioles are 1–2 cm long and, like the greenish twigs, they are slender and sparsely hairy (Little & Wadsworth, 1964; Marshall, 1939; Miller, 1985).

A notable feature of *C. alliodora* is the presence of nodal swellings, or domatia, on all the smaller branches and twigs. Throughout the species' natural range these are invariably colonized by ants.

Another conspicuous feature at certain times of the year are the large conspicuous panicles, 10–30 cm across, of many small white flowers. Every flower's expanded tubular corolla is almost 1 cm long, and slightly over 1 cm wide measured across the five widely-spreading, oblong and rounded lobes.

The cylindrical grey-green calyx is about 6 mm long, 10-ribbed, 5-toothed and densely covered with minute stellate hairs. It contains the ellipsoid, thin- and fibrous-walled fruit that is the main characteristic of the Cerdanae. The fruit, with its single seed, swells only slightly during development within the calyx which, although it may stretch to enclose the fruit, is not accrescent (i.e. does not continue to grow after pollination). The mature fruit is shed complete with persistent calyx and marcescent (i.e. withers but remains attached) corolla. The corolla acts as a parachute during seed fall and may assist wind dispersal (Little & Wadsworth, 1964; Miller *loc. cit.*).

C. alliodora displays epigeal, germination. The hypocotyl is pubescent with long white hairs. The cotyledons have a border of hairs and are rounded and leaf-like. They are glabrous on the upper surface and pulverulent on the lower. The venation is palmate with three principal veins and inconspicuous secondary veins (Amo R., 1979).

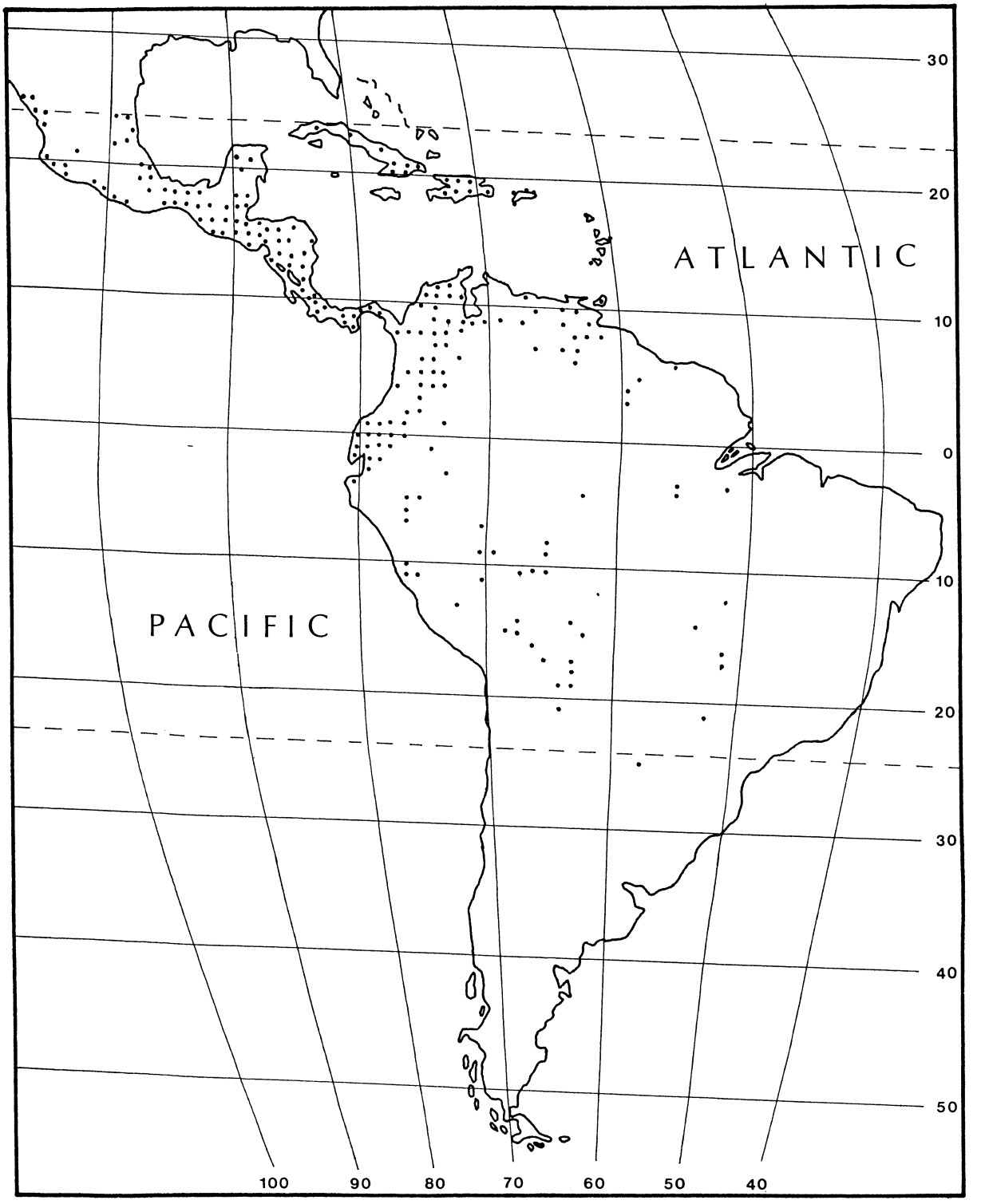
According to Miller (*loc. cit.*), the unique botanical characteristics of *C. alliodora* among the Cerdanae are its ant domatia at the nodes, and the indumentum of stellate hairs on the leaves. The species is also homostylous and partly self-compatible while all other members of the Cerdanae are distylous. This partial self-compatibility is a possible explanation for the species' wide-ranging natural distribution in terms of both distance and habitat; a characteristic that is not shared with other members of the Cerdanae.

2.4 Natural distribution and habitats

C. alliodora is widely distributed in continental tropical America from central Mexico to northern Argentina. There is also a wide occurrence among the Caribbean islands where it is found in Cuba, Hispaniola, Puerto Rico, the Virgin Islands, throughout the Lesser Antilles and in Trinidad and Tobago.

The species is found on a wide range of sites at altitudes from sea level to 2000 m. The best growth occurs where the mean annual rainfall exceeds 2000 mm and the mean annual temperature is about 24°C. The tree is also common in drier areas. It will tolerate a mean annual rainfall as low as 1000 mm but under these conditions growth is slower and the stem and crown form poorer.

C. alliodora is a light-demanding species that readily colonizes exposed fertile soil. In primary forest it regenerates where natural gaps occur in the canopy. Where such gaps are predominantly small the trees tend to be found in small groups or as solitary



Recorded sources of *Cordia alliodora* herbarium specimens.

mature specimens. The most abundant regeneration occurs on sites cleared by man. It is on such sites that extensive, almost pure stands are encountered. They may occur either as an early stage in secondary forest succession following logging or as an invasion of land cleared for agriculture. A range of diverse soil types are tolerated but fertile, freely-drained conditions are preferred. The tree is most often found on slopes and hillsides rather than on level sites susceptible to seasonal waterlogging.

C. alliodora reaches the northern limit of its natural distribution in Mexico. In this country it is found along the Pacific coast as far north as the middle of the state of Sinaloa. On the Caribbean lowlands the species spreads from Quintana Roo, Yucatán and Campeche on the Yucatán peninsula through Vera Cruz to San Luis Potosí (Barajas Morales & Echenique-Manrique, 1976). In the Pacific regions *C. alliodora* is common in both deciduous and semi-deciduous forest, as well as being a major component of secondary forest. On these sites the tree seldom exceeds 12 m in height and 20 cm in diameter, whereas in the moist forests adjacent to the Caribbean heights up to 25 m are reached (Miller, 1985).

The natural distribution extends southwards from Mexico into Central America. Here the species is particularly widespread and is found in many areas of Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica and Panama (Gentry & Janos, 1974).

In Belize *C. alliodora* is said to be frequent in forest (Standley & Record, 1936). The species is listed among the common trees of 'advanced forest', and is also described as being found typically in the early stages of secondary rain forest succession following cultivation (Stevenson, 1928).

The distribution in Costa Rica was described in detail by Perez Figueroa (1954). Here *C. alliodora* is common, and grows well, in the humid forests of the Atlantic zone. Also, Standley (1938) recorded occurrences in two regions on the Pacific side of the country at altitudes up to 1200 m. In Guanacaste, where rainfall is low, the species is rare and grows poorly. The other region comprises Parrita, Queyos and Golfito. Here precipitation is higher and the development of the tree is moderate.

In Panama *C. alliodora* is found throughout the hills but rarely close to streams (Anon., 1926). It is common in the Canal Zone (Standley, 1928).

Beyond Panama the distribution extends eastwards and southwards across South America to northern Argentina, but it is not continuous. Detailed descriptions of the occurrence of the species are available for only those areas in the north where it is relatively abundant compared with other parts of the continent.

C. alliodora occurs in 24 departments of Colombia, in areas both with and without severe dry seasons and at altitudes from sea level to 1900 m. It is especially common in the areas drained by the Rio Cauca and the Rio Magdalena, including the slopes of the Cordillera Occidental, Cordillera Central and Cordillera Oriental. Here the species is abundant at 1100–1900 m altitude (Venegas Tovar, 1978).

In Venezuela *C. alliodora* is found mostly in the forests of the warm areas, but it also occurs on the hills and ridges up to altitudes of 1300–1400 m. The species is most common on the western plains, where it reaches its largest dimensions, but well-developed trees are found only in isolation or in small groups and never in abundance (Lamprecht, 1955).

Fanshawe (1961) recorded *C. alliodora* as being found occasionally in the savanna woodland and seasonal forest of the Kanuku Mountain foothills of Guyana. Here the tree attains a height and diameter up to 36 m and 90 cm respectively.

In Brazil, Carpanezzi *et al.* (1982) listed 20 locations where *C. alliodora* has been found in Brazilian Amazonia. The mean annual temperature at these sites lies between 24° and 27°C and the mean annual rainfall ranges from about 1500 mm to 2300 mm.

Although *C. alliodora* occurs on many Caribbean islands, information about the habitats in which it is found is available for few of them. In Puerto Rico natural populations occur on the humid limestone hills of the north coast. Elsewhere on the island the tree is found in the lower montane regions, especially on the soils derived from volcanic tuffs. At these locations heights and diameters up to 20 m and 50 cm respectively are achieved. Populations also occur on the neighbouring island of Vieques as well as on St. Croix, St. Thomas, St. John and Tortula in the Virgin Islands (Little & Wadsworth, 1964).

C. alliodora occurs in parts of Trinidad and Tobago, as well as on Chacachacare in the neighbouring Gulf of Paria. Some trees are found in rain forest but the species occurs mainly in semi-deciduous and dry evergreen forests. It is mostly confined to the hills

Table 1. Maximum *C. alliodora* dimensions observed in natural forests.

Country	Height (m)	Diameter b.h. (cm)	Data source
Columbia	24	64	Curran (1929)
Guyana	36	90	Fanshawe (1961)
Mexico:			
eastern	12	20	Miller (1985)
western	25	—	Miller (1985)
Nicaragua	30	46	Record (1929)
Puerto Rico	20	50	Little & Wadsworth (1964)
Trinidad	30	90	Marshall (1931)
Venezuela	30	80	Lamprecht (1955)

where the best growth appears to be achieved on sites with a mean annual rainfall between 1270 and 1900 mm (Marshall, 1931; 1939). Throughout Trinidad and Tobago *C. alliodora* is generally rare in the natural forests, although it is abundant in parts of Tobago where it thrives on rich soils derived from igneous rocks (Lamb, 1955).

2.5 Life history and development

General characteristics

C. alliodora will survive under light shade but full overhead light is necessary for full vigour. The species is capable of rapid early growth. A strong taproot is produced at an early stage but a spreading rooting system also develops (Marshall, 1930), which allows the tree to withstand exposed conditions. Young and middle-aged trees coppice readily and suckers are sometimes abundant (Marshall, 1931).

Ant domatia

C. alliodora and other *Cordia* species may form galls on their shoots as a consequence of insect attack. Subsequently these galls may be inhabited by ants. However, a distinctive characteristic on the shoots of *C. alliodora* are pre-formed swellings or domatia. These domatia and the ants that colonize them were investigated in detail by Wheeler (1942), with particular reference to field observations in Guyana and Panama. He observed that young specimens of *C. alliodora* less than 2 m in height usually have a very symmetrical appearance with regularly-spaced whorls of branches along the stem. Except in the youngest seedlings of less than 30 cm height, every node is almost invariably swollen to form a closed capsule. These capsules are perfectly regular in their arrangement and position. When the plants have grown to 1.0–1.5 m the walls of the domatia begin to lignify. They are then perforated and entered by ants at one or more points below the node where the wall is thinnest. A domatium continues to grow after its occupation, possibly as a result of the effect of the numerous coccids that attach themselves to the walls of the cavity. Growth does not continue indefinitely and the domatia are eventually obscured on the oldest parts of the branches and trunk as more wood is laid down. Johnston (1949) remarked that in the West Indies the twigs of *C. alliodora* are less deformed by ant domatia than they are in north-western South America.

Wheeler (*loc. cit.*) also recorded that in Mexico, Central America, Peru and Bolivia 54 species of ant are known to be associated with *C. alliodora*. Of these, 44 have been found nesting in the domatia but only four are known to be obligate tenants. The most common of these is *Azteca longiceps*, which occupies 85 percent of the domatia. Numerous insects feed on the tissues of *C. alliodora* but no evidence was found that they are attacked by any of the ants. On the contrary, the ants attend many of the coccids and derive nutrition from their exudates. Therefore, there is no indication that *C. alliodora* derives any benefit from the ants that are associated with it. It is interesting to note that when planted in exotic locations the species continues to produce these nodal swellings, although they are seldom, if ever, inhabited by ants.

Phenology

C. alliodora may commence flowering when it is only two years old. According to Johnston (1950), in Mexico and Central America the conspicuous masses of white flowers appear early in the dry season. Flowering begins at the northern end of the range in December and about a month later in southern Central America. According to Stead (1980), in this region the fruits are mature in April. On the seasonally-dry Pacific slope of Costa Rica flowering occurs over a six-week period from January to February, although the flowering of individuals is somewhat asynchronous (Opler *et al.*, 1975). Lamprecht (1955) recorded that in Venezuela flowering takes place in December and January and the seeds mature during February & March. Similarly, in Trinidad flowering occurs between January and March (Marshall, 1930) and the seeds are mature in May (Lamb, 1955).

In Colombia there are conflicting reports on the phenology of *C. alliodora*. Melchior (1977) drew attention to the diverse accounts concerning the times of flowering and fruiting, which appear to vary widely in different parts of the country. In the coffee-growing region of Ulloa flowering is reported to take place in January, while in the vicinity of the Rio Mira in Tumaco it is said to occur in August and September.

Table 2. Times of *C. alliodora* flowering and seeding.

Location	Flowering time	Seeding time	Data source
Mexico	December	—	Johnston (1950)
Southern Central America	January	—	Johnston (1950)
	—	April	Stead (1980)
Costa Rica			
—Pacific watershed	January–February	—	Opler *et al.* (1975)
Venezuela	December–January	February–March	Lamprecht (1955)
Trinidad	January–March	May	Lamb (1955)
Colombia			
—no dry season	all year	—	Neyra Román (1981)
—dry season	—	March	Neyra Román (1981)

The time between flowering and maturation of the fruit also appears to vary from place to place. In the vicinity of Putumayo the process is reported to take four weeks, but in Ulloa it extends over a far longer period. A possible explanation of these differences is given by the results of studies undertaken in Colombia by Neyra Román (1981). Distinct variations were noted between two sites in terms of flowering characteristics. At La Espriella in the Rio Mira region, where there is no distinct dry season, there was more or less constant flowering throughout the year. On the other hand, at Las Teresitas, where there is a distinct dry season, flowering and fruiting took place over definite periods. In the latter instance most of the fruits matured in March. The influence of climate on phenology was also noted by Venegas Tovar (1971) from observations in Colombia. He reported that in years with atypical weather flowering may be late and fruiting delayed.

Reproductive biology

The reproductive characteristics of several *Cordia* species, including *C. alliodora*, were described and their evolutionary significance discussed by Opler *et al.* (1975). They suggested that there has been divergence from an ancestoral type that was presumably characterized by a basic chromosome number of eight, heterostyly and fleshy fruitedness. Several dioecious taxa appear to have evolved independently from polyploid derivatives of this type. There seems to be a strong emphasis on outcrossing in the *Cordia* genus. All *Cordia* species are heterostylous with associated self-incompatibility, or they are dioecious. The exception to this is *C. alliodora*, which is homostylous with a variable degree of self-compatibility.

This intra-specific variation in the self-compatibility of *C. alliodora* probably maintains heterozygosity by cross-pollination, while also allowing seed to be set by self-pollination. As in other *Cordia* species, Lepidoptera are mostly responsible for the pollination of *C. alliodora*. However there was no observed specificity of particular species of pollinating insects to *C. alliodora*.

3. *C. alliodora* as a plantation species

3.1 Suitability for plantations

Marshall (1939), when discussing the ecology of *C. alliodora* in Trinidad, referred to the large quantities of seed that are produced by a mature tree. The seed is readily dispersed by wind and germination is usually good. Nevertheless, in the absence of adequate light few seedlings develop into mature trees. This situation prevails throughout the species' natural range. However, when land is cleared in the vicinity of seed-bearing trees natural regeneration is frequently prolific, especially when the soil is disturbed. If there is no interference with the growth of such regeneration, a dense even-aged stand may result that is suitable for management as a plantation.

Often, land clearance is a prelude to the cultivation of crops. Under these circumstances much natural regeneration of *C. alliodora* will be weeded out but the desirable characteristics of the species give the farmer an incentive to retain some trees. Not only does the tree yield a decorative high-quality timber but its tall straight stem, self-pruning habit and compact crown make it suitable for growing in combination with many agricultural crops. This has led to the evolution of numerous agroforestry systems throughout the species' natural range, several of which were described by Beer *et al.* (1981) and Combe & Budowski (1979). The tree is particularly suitable as a shade tree in coffee plantations and is widely used for this purpose, especially in Colombia (Venegas Tovar, 1978), Costa Rica (Beer *et al.*, 1981) and Venezuela (Lamprecht, 1955).

3.2 History as a plantation species

The earliest attempts to establish *C. alliodora* plantations probably took place in Trinidad. The Forest Department annual report for 1921 recorded that of the 454 ha of plantations planted up to the end of that year, 20 percent were *C. alliodora* (Trinidad and Tobago, 1922). Small-scale planting continued up to 1974 at least (Dardaine, 1974) but these efforts failed to establish a substantial resource. It appears that planted stock only survive on the better soils and the species is susceptible to canker diseases on sites where there is prolonged high humidity. On the other hand, natural regeneration succeeds on a greater range of soils. Similar tendencies are shown by several other light-demanding species in Trinidad. All of these, including *C. alliodora*, regenerate freely on the sites of over 60,000 ha of former hardwood forest that was converted to cocoa and coffee plantations. Lamb (1955; 1960) suggested that such regeneration is a valuable source of additional revenue. He advocated that it should be retained in the overstorey as all that the landowner has to do is to select the trees. These then reach maturity over 40–50 years.

In Puerto Rico, Marrero (1950) reported that of the 46 species planted over 6500 ha between 1920 and 1949, *C. alliodora* was regarded as one of the most promising. The best growth was achieved on soils derived from diorites and shales, especially where satisfactory soil conditions had been maintained by the preservation of a forest cover. There are indications that it is capable of making early rapid growth when planted under light shade. Therefore, it appears to be suitable for underplanting. However, in an earlier report (Marrero, 1948) the species was not recommended for large blocks because of the pests and diseases to which is is susceptible.

In recent years plantations of *C. alliodora* have been established in Colombia. Here performance was outstanding among the 17 native and 11 exotic species that were investigated as plantation species for the Pacific coast of the Department of Nariño (Peck, 1976). Neyra Román (1980) considered it to be one of the most promising reforestation species for the country.

C. alliodora was introduced to Surinam in 1967 when trials were set up in the vicinity of Mapane. The area planted in this region reached 570 ha in 1975 and by 1977 the annual rate of planting had increased to about 300 ha (Vega, 1977).

Outside the neotropics, Streets (1962) briefly summarized the results of introducing the species to three countries in Africa. The first plantings in Nigeria took place in 1922 and produced well-formed trees 12 m high at age 14 years. In 1959 it was reported that there were excellent stands in Mauritius that were regenerating freely. It was also introduced into Sierra Leone where it was reported to be growing well. Kriek (1968f), reporting on species trials in Uganda, rated the performances of six underplanting trials in tropical high forest as satisfactory or very good. Similarly, a trial in *Celtis-Holoptelea* forest was described as vigorous (Kriek, 1968c). Poor results were given by trials in *Combretum* and mixed savanna (Kreik, 1967), *Celtis-Cynometra* woodland (Kriek, 1968a), *Pennisetum* grassland (Kreik, 1968b), *Piptadeniastrum-Albizia-Celtis* forest (Kriek, 1968d), and *Chlorophora-Pennisetum* grassland (Kriek, 1968e).

C. alliodora has also been introduced to the Pacific region. Trials were laid down on 10 sites in Hawaii during the 1960s but the species only showed promise at one of these (Whitesell & Walters, 1976). It has also been introduced to Fiji where it has been planted on a small scale but it is in Vanuatu that the largest plantations have been established. Here land owners have been given support for establishing plantations, mainly of *C. alliodora*, provided that they dedicated 100–200 ha for this purpose and agreed to abide by the Government's guidelines. The 24 small plantation schemes that have been developed in this way since 1975 should bring about self-sufficiency in sawn timber after 15–20 years (Bennett, 1980). *C. alliodora* was first planted in Vanuatu in 1972 using seed acquired from Fiji. It is the most promising of the 50 species and provenances that have been evalued for plantation establishment. The area planted up to 1984 was 700 ha, which was expected to increase to

1100 ha by the year 1990. The plantations are generally on the southeastern windward slopes of the islands where the mean annual rainfall is 2500–4000 mm. Most are below 200 m altitude on young, fertile soils (Hudson, 1984). According to Neil (1984), the greatest growth rates are achieved on humic, weakly-unsaturated, ferralitic soils where the mean annual rainfall exceeds 2500 mm.

4. Plantation establishment and management

4.1 Seed collection and storage

Until recently *C. alliodora* seed was widely regarded as having a low germination percentage and short viability, especially if it was not stored at a low temperature (Lamb, 1955; Neyra Román, 1980). Seed collected from the tree over a period of three weeks before the time of natural seed fall was reported by Tschinkel (1967) to have satisfactory viability. Nevertheless, he found that germination percentage still declined by half over one year, even though the seed was dried to 12–18 percent moisture content and stored at 5°C. Further evidence of the importance of seed collection timing was given by Marshall (1930) who noted that the first fruits to ripen had the lowest fertility. Vega (1977) stated that the best time for seed collection was a few days before the onset of total seed fall. He found that more than 70 percent of the seed collected at the optimum time was likely to germinate. Such seed also had a short germination period of 8–15 days, whereas seed collected at the beginning of the maturing period required 25–28 days to germinate.

Salas & Valencia (1979) described how the time for collecting seed of maximum viability is indicated by the flower panicles turning from yellow to brown without appearing burnt, the colour being that of the persistant corolla. If seed is collected before this time, and maturation is incomplete, it ceases to ripen when it is separated from its branch. A single tree yields up to 8 kg of seed, but the usual yield is 0.5–3 kg. Among the seed lots collected by the OFI, those with a germination percent of 80 or more comprised 55,000–75,000 viable seeds per kg.

Stead (1979) refuted previous descriptions of the seed as being difficult to store for more than three months. He found that if branches are shaken, mature seed of optimum viability will drop off. It can be easily collected by spreading plastic sheets on the ground beneath the tree. Seed collected in this way and dried to below 10 percent moisture content, then stored at 2°C, suffered little or no loss in viability over a year. Recent re-testing of this seed showed that there had been little deterioration over 10 years.

4.2 Nursery practice

Types of planting stock

The use of bare-root planting stock is rare. Marshall (1939) stated that in Trinidad *C. alliodora* seedlings a few months old were found to transplant easily when their roots were protected with a ball of earth. However, the method was found to be expensive. Similar planting material was used in an experiment to investigate the success of dry season planting using dormant stock. Although survival was good, most of the plants became unhealthy and many died back to within 30 cm of the ground.

Hanmer & Branney (1982) reported the occasional use of bare-root striplings in Vanuatu. The ideal size appeared to be a shoot length of 30 cm, a root length of 12–25 cm and a root collar diameter of 6 mm. These dimensions were achieved at the same time as the bark became impermeable. The results with this stock were usually disappointing. There was a general tendency for the soft stem apex, and the uppermost pair of leaves left on the stem, to wilt. This happened within a few hours and recovery was rare. Striplings may be suitable for use where they occur as natural regeneration very close to the planting site. In these circumstances the plants can be lifted and re-planted in a short time to reduce the danger of wilting.

Potted stock has occasionally been used in several countries. After planting out in the field, the initial growth rate may be superior to that achieved with other planting stock. If this results in reduced establishment costs, the high expenditure required for raising, transporting and planting potted stock may be justified. Normally its use is only economically viable when there is easy access between the nursery and the planting site.

Stumps (produced by pruning the roots and shoots back to short lengths) are the most widely-used planting stock because of their robust qualities and the ease and economy with which they can be produced. They require longer in the nursery than potted stock but they are less sensitive to adverse conditions during transport and storage. They are also more resilient to drought immediately after planting out in the field. Salas & Valencia (1979) reported that on lowland sites in Colombia the survival rate for pot-raised planting stock was 85–90 percent, whereas for stumps it was 95 percent.

Sowing and germination

Irrespective of the kind of planting stock that is to be produced, seedlings are first raised in germination beds. Standard nursery techniques are appropriate. However, in Trinidad it was found that when beds of stiff clay had to be used, burning slash on them before sowing had a beneficial effect on the survival and health of the seedlings (Trinidad and Tobago, 1939).

Neyra Román (1980) described *C. alliodora* as a species with seed that germinates rapidly and is suitable for broadcast sowing. The use of this method appears to be widespread. Carpanezzi *et al.* (1982) gave an account of how in Brazil seed was broadcast sown onto shaded germination beds at a rate of 40–50 g/m^2. It was then covered to a depth of about 0.5 cm. Under these circumstances germination occurred within 17–20 days. Venegas Tovar (1971) reported a similar germination period in Colombia after seed was sown along drills 10 cm apart and 2 cm deep.

Past difficulties with collecting and storing seed of satisfactory viability sometimes resulted in poor results after broadcast sowing in conventional nursery germination beds. As plantation trees produce an abundance of seed from an early age, an alternative method was devised. This relies on natural regenera-

tion in beds located close to seed trees. Vega (1977) referred to the use of this system in Surinam but its application in Vanuatu was described in greater detail by Hanmer & Branney (1982). Here *C. alliodora* plantations over 3–4 years old produce adequate amounts of seed. Natural regeneration beds are located downwind of the seed trees and where there is least shade. Provided that all vegetation is removed in November, a carpet of regeneration results by March.

Stump planting stock

The usual practice for producing stump planting stock is first to transfer seedlings from germination beds to transplant beds. They are then left to grow to a suitable size before being root and shoot pruned immediately before planting out in the field. Vega (1977), when describing a system used in Surinam, advocated that seedlings should be transplanted into polythene pots when they were 4–6 weeks old. At this stage they were 5–8 cm high. The transplants were then kept under medium shade for 5–8 months until they attained the necessary root collar diameter of 1 cm. Two weeks before planting out the stems were pruned back to 15 cm and at the time of planting the roots were lightly pruned.

Judging from experiences elsewhere it appears to be unnecessary to use pots when raising stump planting stock. Venegas Tovar (1971), in an account of nursery practice in Colombia, described how seedlings were transplanted into beds using a spacing of 10 × 10 cm. They were then kept under shade for 7 days. After 10–12 months they achieved a root collar diameter of 2 cm. Immediately before planting out they were pruned to leave 2 cm of shoot and 12–20 cm of root.

An alternative method also used in Colombia was described by Salas & Valencia (1979). When seedlings had developed a pair of leaves they were transplanted into beds at 15 × 15 cm. Shade was maintained at 80 percent for the first 15 days and then progressively removed. Over 6–12 months the seedlings grew to heights of 1.8–2.2 m and a mean diameter of 2.5 cm. At this stage they were root and shoot pruned to give 30-cm stumps.

Hanmer & Branney (1982) reported that in Vanuatu seedlings were kept in natural regeneration beds for 2 years. They were then large enough to give stumps 0.8–1.0 cm in diameter at the root collar. These were pruned to a length of 15–20 cm, of which two-thirds were root and one-third shoot.

All these methods have given adequate success but some may be more successful than others. Where seed-producing trees are conveniently available, the use of seedlings from natural regeneration beds has obvious advantages. Seed collection and storage operations are avoided and nursery procedures are not dependent on the success of these activities. On the other hand, the time of seed fall dictates to a considerable extent the age and size of the stumps that are ultimately produced. There are some indications that these factors influence the viability and sprouting vigour of the stumps. Thus Hanmer & Branney (*loc. cit.*) advised that growth is reduced if stumps more than 1 cm in diameter are used. They suggested that this is because large plants become checked in the natural regeneration beds, or the bark is too thick for rapid bud development. Also, smaller-diameter stumps were regarded as unsuitable because their bark is too thin to prevent the stumps from drying out.

Further support for the use of stumps approximately 1 cm in diameter was given by Silva Herrera *et al.* (1985). In a replicated experiment, the influence of initial stump diameter on subsequent survival and height growth was assessed. After two years there were no statistically-significant differences ($P>0.05$) among the 0.5–1.4 cm, 1.5–2.4 cm and 2.5–3.4 cm diameter classes. However, the mean values for height and survival were greatest for the 0.5–1.4 cm class and least in the 2.5–3.4 cm class. It was recommended that *C. alliodora* planting stock should consist of stumps that are 0.5–1.4 cm in diameter owing to the results outlined above. In addition, the production, handling and transportation costs of such stumps are more favourable when compared with those of stumps of greater diameter.

Hanmer & Branney (*loc. cit.*) emphasized the importance of culling, which may result in the rejection of many plants. It is particularly important to avoid using plants with poorly developed root systems. The same authors also stated that stumps of *C. alliodora* do not store well. They should be transported in damp hessian sacks but after being kept under these conditions for about a week their viability rapidly declines. If there has to be a delay between producing the stumps and planting them, they are best kept in holding beds with their roots covered in moist earth.

Potted planting stock

Although the successful use of potted planting stock is subject to the conditions discussed earlier, such stock can be raised in a shorter period than is required for the production of stumps. Seedlings are first grown in germination beds, or they are selected from young natural regeneration. In Colombia, Venegas Tovar (1971) described how seedlings 7–10 cm high were transplanted into polythene pots and kept shaded for 7 days. After 6–8 weeks the seedlings reached a height of 20–30 cm. At this stage they were judged to be ready for planting out in the field. Also in Colombia, Salas & Valencia (1979) reported that a slightly longer time of 2–3 months was required to raise suitable stock, while Carpanezzi *et al.* (1982) stated that 4–6 months was required in Brazil. Here, in Amazonia, seedlings 5 cm tall were transplanted into 15 × 20 cm plastic bags. Overhead shade was given but progressively removed over 30 days. After 6 months the plants reached heights of 20–25 cm and they were planted out in the field.

These differences in the time required in the nursery probably reflect different nursery practices and climates. When there are distinct wet and dry seasons, seedling growth is likely to be fast during the rains. Seedlings transplanted into pots at the begin-

Table 3. Recommended dimensions of planting stock.

Planting stock type	Country	Shoot length (cm)	Root length (cm)	Root collar diameter (cm)	Age (months)	Data source
Striplings	Vanuata	30	12–25	0.6	—	Hanmer & Branney (1982)
Stumps	Vanuata	5–7	10–15	1.0	24	Hanmer & Branney (1982)
Stumps	Colombia	2	10–20	2.0	10–12	Venegas Tovar (1971)
Stumps	Colombia	10	20	2.5	6–12	Salas & Valencia (1979)
Stumps	Surinam	15	—	1.0	6–9	Vega (1977)

ning of the rainy season may be acceptable for planting out during the second half of the rains. However, this is unlikely to achieve the best survival in the field. It is preferable to time nursery operations so that plants of the optimum size are hardened off, preferably over a dry season which they survive in a dormant condition. Then they can then be planted out at the beginning of the rains as growth is resumed. Stumps are more easily produced under such a regime but in some circumstances, such as research plot establishment, the use of unpruned potted stock may be preferable.

4.3 Methods of establishment and management

Direct sowing

The earliest records of afforestation with *C. alliodora* using direct sowing are for Trinidad and Tobago. According to Marshall (1930), direct sowing with a light covering of earth gave good results. A simple and successful way of achieving this is was to scratch the ground with a machete point, drop a few seeds on it, and mix the seeds with the earth using the point of the machete (Marshall, 1939). In later years, direct sowing in lines was investigated as a means of converting cocoa plantations to timber plantations (Trinidad and Tobago, 1955). Results were unsatisfactory, apparently because of a late sowing date (July) and excessive shade. The evidence indicated that the cocoa plantation should first be cleared of weed growth to allow more light to reach the ground. Early sowing was considered advisable to take advantage of the lighter shade at the end of the dry season. Also, regeneration in groups was suggested as an alternative to line planting to take advantage of breaks in the canopy. Several years later it was reported that direct sowing in groups was being used successfully. (Trinidad and Tobago, 1959).

More recently, the effectiveness of direct sowing was investigated in Costa Rica using a method employed with success for hardwoods in the Congo. On a site that was mostly covered with the grass *Panicum maximum*, the natural vegetation was cut and piled into mounds about 40 cm high and 1.2 m in diameter. These mounds were located at intervals of about 4 m along the contour. They were lightly covered with earth, left to dry for 10 days, then the entire site was burned. After the mounds of ash and soil were raked level, each was sown early in the rainy season with 10–30 *C. alliodora* seeds. The soil was then lightly raked and firmed. Four weeks later seedlings were growing on about three-quarters of the mounds (Budowski, 1958).

After two years there were wide variations in tree vigour among the sites of the mounds. Some trees had diameters and heights that exceeded 7.5 cm and 5 m respectively, but in all the places where the grass *Melinis minutiflora* was prevalent the trees were mostly checked. It was noted that if the *M. minutiflora* became suppressed by more aggressive species (*Panicum* sp., *Paspalum* sp.) there was an improvement in the *C. alliodora*. It was concluded that although direct sowing on burnt mounds is an appropriate way of introducing *C. alliodora* on degraded sites, it is undoubtedly difficult to establish the species in this way if *M. minutiflora* is present (Budowski, 1960).

Also in Costa Rica, *C. alliodora* was direct sown onto prepared plots to investigate the influence on percentage germination and subsequent survival of time of sowing, protection from wildlife and several different site preparations. A large proportion of unprotected seed was destroyed by wildlife, presumably birds. Sowing to coincide with the rainy season resulted in better germination and survival than sowing at the time of natural seed fall. The most promising results were achieved by ploughing and covering the seeds lightly. However, in all treatments there was prolific weed growth with which the seedlings could not compete in the long term (Tschinkel, 1965).

Planting

Some of the earliest recommendations concerning the establishment and management of *C. alliodora* plantations were made by Marshall (1931). He advised that the planting espacement should be at least 1.8 × 1.8 m, and that there should be a thinning to half this density after 3–4 years. Later, Wadsworth (1948), referring to conditions in Puerto Rico, recorded that *C. alliodora* is one of several species that can be used for underplanting beneath an existing forest canopy, provided that the overstorey is carefully regulated to control the shade. Side shade is necessary but there should be an opening directly overhead. Liberation

activities carried out during the dry season need to be light to avoid excessive exposure at a time when many trees of the natural forest are leafless. Marrero (1950) regarded 7.6 × 7.6 m as a suitable planting espacement under these circumstances.

The suitability of *C. alliodora* for underplanting led to a method for regenerating *Casuarina equisetifolia* plantations (Puerto Rico, 1951; 1953). These are widely used throughout Puerto Rico to protect degraded soils. Excessive exposure of the soils needs to be avoided, but *C. equisetifolia* does not regenerate naturally because ants destroy the seed and planted seedlings of this species are intolerant of shade. However, *C. alliodora* was one of several species that were found to grow better beneath *C. equisetifolia* on these sites than when planted in the open.

In Surinam, Vega (1977) described how *C. alliodora* was planted on forest sites 2 years after they had been exploited and the remaining trees poisoned. Stumps were planted in groups of three with a triangular espacement of 10 × 5 m among the groups. This gave an initial density of 200 trees/ha, with the intention of producing a final crop of 130–150 trees/ha. After three years the plantations were thinned to favour the best tree in every group. Alternatively, planting was undertaken along cleared strips 1.5 m wide and 10 m apart.

Venegas Tovar (1971) recommended a planting distance of 2 × 2 m, but Peck (1976) noted that plantations densely planted at 2.5 × 2.5 m or less had a tendency to become checked. He recommended an espacement of 4 × 4 m. This was also favoured by Salas & Valencia (1979) on sites prepared by hand clearing, with or without burning according to local conditions.

Neil (1984) described how a standard procedure in Vanuatu was to plant stumps at 2.5-m intervals along lines 10 m apart cut through unlogged natural forest. This gave a planting density of 400 trees/ha. Between the lines the canopy was gradually removed by a combination of felling, girdling, poisoning and burning to avoid excessive weed growth. Weeds tended to be exceptionally vigorous along the planting lines and this necessitated intensive weeding for the first three years.

Although these examples of planting prescriptions differ in some details, all are successful provided that the planting and subsequent tending operations are adequately supervised. Success is usually determined not by the choice of method alone, but also by the adoption of modifications according to local conditions. This was illustrated by Neil & Hudson (1983) who referred to the practice in Vanuatu described above. In their opinion, the recommended prescription of 2.5 × 10 m line planting and subsequent overstorey canopy removal was satisfactory for natural forest, provided that adequate numbers of experienced staff were available for implementing it. Secondary and disturbed forest require earlier capture of the site to avoid prolonged intensive weeding operations. It was suggested that this would be facilitated by reducing the distance between the lines to 5 m.

Weeding, cleaning and tending

In the earlier section of the text concerned with direct sowing, attention was drawn to the adverse influence that the grass *Melinis minutiflora* has on the growth of young trees. Further investigations into this effect were performed by Marinero (1964). He found that the growth of one-year-old potted *C. alliodora* plants was inhibited when they were treated with root or leaf extracts of *M. minutiflora*. The growth of the potted *C. alliodora* was also inhibited when it was grown in close association with *M. minutiflora*. These results are indicative of a harmful allelopathic effect on *C. alliodora* by *M. minutiflora*. Therefore, even a moderate density of *M. minutiflora* might have a detrimental effect, whereas a similar density of some other species may be more tolerable. It follows that site preparation and weeding prescriptions should not only be formulated according to the density of the vegetation, but note should also be taken of the vegetation's species composition.

It is of paramount importance that young plants should not become smothered by climbers or other weeds. These not only retard growth but there is also a danger that stems will become misshapen. The necessity for avoiding such intense competition between weeds and trees was emphasized by Hanmer & Branney (1982) who, for the conditions in Vanuatu, prescribed spot weeding at least every month during the first 6 months after planting. Compared with line cleaning, this is a relatively cheap operation. Line cleaning needs to be done less often and mainly from year two. Frequent and rapid spot weedings are more effective than occasional large, expensive operations.

In Colombia, Salas & Valencia (1979) prescribed pruning after 2 months to favour the best shoot per stump, and periodic cleanings up to the third year. They found that cleaning may be necessary three and two times in the first and second years respectively, and once in the third. Peck (1976) noted that the trees are sensitive to invasion of the plantations by the grass *Paspalum vergatum*. Also in Colombia, *Convolvulus* sp. climbers need to be cut back in the fourth year, otherwise they may completely cover the trees and occasionally break the stems (Venegas Tovar, 1971). If climbers distort stem growth within a few years of planting the trees can be coppiced. However, if this is done when the trees are 4 years old or more, the new shoots are unable to catch up with the main crop unless the weeding operations are prolonged (Neil, 1984).

Thinning

A general lack of experience with the management of *C. alliodora* plantations through to rotation age has resulted in only general advice on thinning regimes being available. Marshall (1931) suggested a heavy thinning after 3–4 years that would reduce the stocking by half after initial close planting at 1.8 × 1.8 m. Hanmer & Branney (1982) advised thinning between 5 and 10 years in Vanuatu, the

actual year of the operation being influenced by the growth rate and stocking. Here trees are expected to reach timber height by this age. If thinning is delayed, the trees are likely to become increasingly susceptible to windblow.

The self-pruning habit of *C. alliodora* avoids the need to maintain a high stocking to achieve a clean stem. In these circumstances thinning can be directed primarily at maintaining vigour according to standard silvicultural principles.

5. Protection

5.1 Wind

Accounts of wind damage to *C. alliodora* are available from observations in Puerto Rico, the Solomon Islands and Vanuatu. Wadsworth & Englerth (1959) described the effects of Hurricane Betsy after it passed over Puerto Rico in 1956. Local and exotic species were listed according to whether they were susceptible to windthrow, susceptible to stembreak or resistant to wind damage. *C. alliodora* was assigned to the resistant category.

In the Solomon Islands 31 species in arboretum plots were assessed in terms of their resistance to storm damage after a cyclone passed over trial plots on Kolombangara, Baga Island and Gizo in 1967 (Self, 1968). The results are merely indicative because many plots were only 0.04 ha in area and the heights of adjacent plots were often irregular. Only one plot of *C. alliodora* was available. Few stems were broken, which could be interpreted as a sign that the species is probably fairly resistant to wind damage, but the evidence is not conclusive.

In January 1985 two cyclones passed over the northern half of Vanuatu causing severe damage to the forest plantations on the islands of Espiritu Santo, Ambae and Pentecost. The plantations were mostly *C. alliodora*, which was line planted between 1977 and 1985, as well as a variety of species trials which were planted mainly between 1972 and 1978. An assessment of the damage was carried out immediately after the cyclone (Barrance, 1985). The extent and nature of the damage were apparently related to tree size, rooting depth, local topography and disease. Very young *C. alliodora* trees appeared to have considerable flexibility and readily bent in very high winds. However, this action progressively loosened the roots and caused trees to fall over. Lack of flexibility in older trees sometimes resulted in the stems breaking or in entire trees being uprooted. On deep soils the species had developed a vigorous tap root which contributed to its stability, but if the development of the tap root had been prevented, as on shallow coralline soils, there was increased susceptibility to windthrow. Conversely, very deep friable soils did not provide adequate anchorage and entire root systems were pulled out of the ground. Extensive windthrow occurred in some areas where roots were damaged by the fungus *Phellinus noxius*.

Another form of storm damage to *C. alliodora* in Vanuatu was not evident until several weeks after the cyclones when some branches and leading shoots failed to recover from defoliation. This was apparently the result of damage to the tissues caused by excessive bending. Some trees were seen on which the bark had separated from the wood towards the base of the stem. This was possibly a consequence of high twisting forces. These injuries caused loss of apical dominance of branches and leading shoots. Subsequently there was profuse epicormic growth at lower levels in the crown or along the length of the stem. Overall, *C. alliodora* was classified as having moderate resistance to both windthrow and stembreak.

5.2 Pests and diseases

The earliest reports of an economically damaging disease on *C. alliodora* were from Trinidad. It was observed that under conditions of high humidity cankers were likely to develop on the bark. Briton-Jones (1930) identified the rust fungus *Puccinia cordiae* as the primary agent responsible for this disease. Occasionally cankers may occur on young green shoots, but the most evident and damaging effects of the disease are large cankers on the trunks. The cortical tissues are attacked, which results in an open wound. Continuous spread outwards of the initial infection is usually prevented by callus formation but secondary infections increase the damage by attacking the wood. The cankers are usually confined to one side of the tree but several may coalesce to girdle the stem.

The role of high humidity in predisposing the trees to infection may result in wide variations in susceptibility over short distances. Thus, the young branches on the exposed crowns of tall old trees may be completely free of the disease, while on the same site most of the small young trees may be killed outright. It was recommended that if *C. alliodora* plantations were to succeed in Trinidad they should be planted on sites exposed to the sun and wind, and managed to avoid overcrowding. The influence of site conditions on the incidence of canker was confirmed some years later. It was found that experimental plantings in the Southern Watershed Reserve remained free of the disease on the drier northern and eastern aspects (Trinidad and Tobago, 1936).

It is difficult to reconcile these observations with those made by Pawsey (1970) who reported on the pests and diseases of forests in Trinidad. He found only one instance of canker on *C. alliodora* that was caused by *P. cordiae*, despite previous reports of the widespread nature of the disease. He suggested that basal cankers 1 m or more in length are unlikely to be caused by direct or indirect infection by *P. cordiae*.

Spaulding (1961) reported that *P. cordiae* has also been found on *C. alliodora* in Guatemala and Puerto Rico, where entire trees are sometimes killed. Johnson & Morales (1972) also noted the existence of the same, or similar, disease in Costa Rica.

Other early reports from Trinidad referred to damage to *C. alliodora* by pests. On some sites mole crickets destroyed over 50 percent of direct sowings, but lacewing bugs (*Corythucha gossypii*) were the cause of more serious damage. These insects completely defoliated many young trees on several experimental plots, and twig dieback was also associated with their attack (Trinidad and Tobago, 1936). Similar damage was noted at an early date in Puerto Rico where high infestations of the Spanish elm

Table 4. Recorded pests and diseases.

Country	Causal agent	Symptom	Data source
	Pests:		
Trinidad	Mole crickets	Defoliation	Trinidad & Tobago (1936)
Trinidad	*Corythucha gossypii* (lacewing bugs)	Defoliation	Trinidad & Tobago (1936)
Puerto Rico	*Monanthia monotropidia*	Defoliation	Martorell (1940)
Colombia	*Dictyla monotropidia*	Defoliation	Berrio (1978)
Colombia	*Atta* sp. (leaf-cutting ants)	Defoliation	Salas & Valencia (1979)
Costa Rica	Bruchid beetles	Seed destruction	Opler *et al.* (1975)
Costa Rica	*Phoradendron robustissium* (mistletoe)	Parasitization	Opler *et al.* (1975)
	Diseases:		
Trinidad	*Puccinia cordiae*	Stem canker	Briton-Jones (1930)
Guatemala	*Puccinia cordiae*	Stem canker	Spaulding (1961)
Puerto Rico	*Puccinia cordiae*	Stem canker	Spaulding (1961)
Costa Rica	*Puccinia cordiae*	Stem canker	Johnson & Morales (1972)
Colombia	*Phytophthora* sp.	Damping off	Peck (1976)
Vanuatu	*Phellinus noxius*	Root rot	Neil (1986)
Vanuatu	*Rigidporus vinctus* var. *vincta*	Root rot	Barrance (1986)
Vanuatu	*Corticium salmonicolor* (Pink's disease)	Root rot	Barrance (1986)

lacewing bug (*Monanthia monotropidia*) were the cause of complete defoliation of many trees (Martorell, 1940). It was reported that the defoliation may be particularly injurious during dry years (Marrero, 1948).

Recently-established plantations of *C. alliodora* in Colombia have suffered attack by *Dictyla monotropidia*, as well as injury from another defoliator (Lepidoptera, Pyralidae) of unknown identity (Berrio, 1978). *D. monotropidia* is found on the backs of the leaves where it sucks the sap after perforating the midrib and sometimes other parts of the lamina. Necrosis develops at the site of the perforation. This leads to the deformation of the leaf and eventually to leaf fall.

The unknown defoliating insect was only seen as a reddish-brown larva, which apparently is active at night. The first signs of damage are some leaves with parts of the laminas missing and others that are rolled up. At a later stage, groups of dry, twisted leaves can be seen. It is among these that the larvae are found, protected by a network of threads.

Trees of all ages suffer from both insects. Those that are stressed, usually as a result of having been planted on adverse sites, suffer most and may be completely defoliated. Trees may die from both forms of damage but usually there is vigorous re-growth of the leaves.

Also in Colombia, seedlings in the nursery may suffer from attack by a leaf miner or from a fungus infection (*Phytophthora* sp.). However, neither of these occurs as epidemics (Peck, 1976). In the same country, plagues of leaf-cutting ants (*Atta* sp.) have been known to defoliate *C. alliodora*. They have been controlled by applying 5 percent 'Mirex' (Salas & Valencia, 1979) or a 1 percent emulsion of 'Ciclordin' (Venegas Tovar, 1971) to the ant hills.

Opler *et al.* (1975) referred to the destruction of large amounts of seed in Costa Rica by host-specific bruchid beetles, but Echandi (1958) reported that the most widespread problem of *C. alliodora* in that country is parasitization by mistletoe. *Phoradendron robustissimum* is the most abundant species and it has been known to kill the host tree. Attempts to identify a herbicide that could be used systemically to control the mistletoe were unsuccessful. Neither the mistletoe nor the tree was affected by injections into the tree's vascular system with 2-methyl,4-dichlorophenoxyacetic acid (2,4-D), 2-methyl,4,5-trichlorophenoxyacetic acid (2,4,5-T) or 2-methyl,4-chlorophenoxyacetic acid (MCP).

Outside its natural range *C. alliodora* appears to have few serious pests and diseases at present but mortalities from a root disease in the Vanuatu plantations have caused concern (Neil, 1986). The first symptom of the disease is a general yellowing and wilting of the foliage, soon followed by the death of the tree. At the same time, the base of the stem becomes covered with a dark brown encrusting mat with a lighter edge. This mat is a continuation of a yellow-brown fungal sheath that covers the main roots. It is unusual for trees less than 2 years old to be attacked. The first deaths in a plantation usually occur close to old stumps of forest trees. The disease appears to spread by root contact with the result that infected trees tend to occur in groups. These symptoms are attributed to *Phellinus noxius*, a fungus that is widespread throughout the Pacific region. It causes deaths of tree crops planted on cut-over forest sites where old stumps are susceptible to inocula-

tion. These subsequently serve as sources of infection.

In 1983 a survey of the disease was carried out in all the *C. alliodora* plantations throughout Vanuatu. It was found that the incidence of infected trees usually did not exceed 5 percent except on Pentecost Island where losses were much higher. There was no clear cause of this, but a possible explantion was the high density of the natural forest tree species *Mystica fatua* and *M. fatua* var. *papuana*. Apparently these are susceptible to infection by *P. noxius* and they may serve as an abnormally large reservoir of the disease. If this is confirmed it may be possible to control the disease by appropriate management techniques. There are indications (Neil, 1983b) that it is most common on sites that receive more than 3000 mm annual rainfall.

Other, less widespread fungus diseases have also been recorded on *C. alliodora* in Vanuatu (Barrance, 1986). *Rigidporus vinctus* var. *vincta* has a similar mode of attack to *P. noxius*. It possibly infects *C. alliodora* on Erromango. *Corticium salmonicolor* (Pink's disease) occurs on Espiritu Santo where 5 percent of the trees were severely affected in one plantation.

6. Growth and yield

6.1 Mensuration

Few mensurational studies on *C. alliodora* have been published. Perez Figueroa (1954), after studying data that were mostly from Costa Rica, noted that the form factor for the commercially-utilizable trunk was seldom less than 0.8. He also reported that, not surprisingly for a wide-ranging species, there was a wide variation in the length of the commercially-utilizable trunk as well as in the ratios of height to age and d.b.h. to height.

McCaffrey (1972) prepared a volume table for *C. alliodora* growing in northern Costa Rica. It covers the total height and d.b.h. over bark ranges of 0.8–24.2 m and 10–76 cm respectively.

Tschinkel (1966) found that annual growth rings could not be identified on increment cores taken from trees of known age in Costa Rica. However, they could be detected on stem disks when they were dried, polished and then viewed while the surface was covered by a film of water. Similarly, Rosero & Gewald (1979) discovered that increment cores were inadequate for determining tree age but it could be determined by stem analysis that used disks from felled trees.

6.2 Site relationships

Few studies have been made to compare the growth of *C. alliodora* on different sites. The available data indicate that the species is site sensitive to a degree that is likely to be of considerable influence on the management of most plantations. However, this is not necessarily apparent during the early years. Thus Vega (1977) found that in Surinam the height increment during the first 3 years of plantation growth exceeded 2.5 m/year irrespective of the site. On well-drained soils this vigorous growth was maintained and dominant heights of 18–20 m, with 11–14 m of clear stem, were achieved after 7 years. On the other hand, growth became relatively slower on heavy soils and dominant height at the same age ranged from 14 to 15.5 m with 9–13 m of clear stem. The difference in diameter increment was even more pronounced. On good sites this varied from 2.1 to 3.5 cm/year and at age 7 years d.b.h. frequently exceeded 22 cm. On poor sites the annual diameter increment was reduced to 0.6–1.1 cm.

Peck (1976) also drew attention to the site sensitivity of *C. alliodora* in Colombia. He stated that the species did not thrive on soils that were either low in organic matter or suffered from impeded drainage. In contrast, markedly different results were achieved on well-drained fertile soils. On such sites there was very rapid early growth and it was possible for 3-year-old trees to have mean heights and diameters of 12 m and 12 cm respectively.

Salas & Franco (1978) also investigated site relationships in Colombia with the aid of 20 0.1-ha sample plots in plantations aged from 2 to 5.5 years. No clear relationship was found between the soil chemical properties and tree growth, as measured by the heights and diameters of the dominant trees. It was concluded that *C. alliodora* was influenced more by the physical than by the chemical properties of the soil. Those aspects of the soil profile that control drainage and rooting depth were particularly important.

The OFI-coordinated international provenance trial (see section 10.2), although not primarily designed to evaluate site relationships, yielded useful data on this aspect of growth and yield. Intensive assessment data were collected from 15 of the contributing trials: six were in Latin America, six in West Africa and three in the southern Pacific region. All the West African trials were on sites with distinct dry seasons, while the remainder were at locations where there was rainfall throughout the year.

Only at three sites in southern Brazil, at latitudes greater than 20°, did climate appear to have the dominant influence on growth. Here the low minimum winter temperatures, together with soils of low fertility, resulted in the best provenances achieving mean heights of only 2–6 m at age 5 years. However, the survival was as high as that achieved on more favourable sites, which demonstrates the species' remarkable ability to survive under adverse conditions.

Elsewhere, at latitudes less than 18°, and at altitudes below 700 m (the parameters set by the trial), soil fertility appeared to be the main factor that determined rate of growth, irrespective of the rainfall regime. Impoverished soils gave poor results, but trials established on forest sites produced good growth, even on those that would have been expected to be marginal to the species' requirements. A notable example was in the Ivory Coast at a site where the mean annual rainfall over the 8.5-year trial period was only 1190 mm. Despite a six-month dry season the best provenance (19/77) achieved a mean height of 20.3 m.

Some of the most vigorous growth was encountered at Ikom, Nigeria, where there was a mean annual rainfall of 3000 mm and a four-month dry season. Here, at age 8.5 years, provenance 19/77 attained a mean height of 21.0 m, while the best provenance in the trial (33/77) reached 25.2 m, the largest value recorded throughout the assessment.

6.3 Flowering and seeding

Trees in plantations are reported to have begun flowering at an early age, just as they do in natural stands. Viable seed was produced in Vanuatu 3–4 years after planting and this gave rise to profuse natural regeneration (Neil, 1983a).

In the vicinity of Mapane, Surinam, a provenance from Costa Rica gave better results than one from Venezuela. It began flowering at age 4 years and produced viable seed after 5 years. Intensive observa-

tions on 10 seed trees over a 3-year period revealed that some individuals could be found in flower at any time during the year, with the exception of the September-October dry season. However, most trees flowered during the short rainy season (December-January) and the seeds formed in the short dry season (February-March). They ripened over a period of about 30 days from mid-March to mid-April. Therefore, this observed phenology of the species when planted in Surinam was similar to that which has been encountered in most natural stands (Vega, 1977).

6.4 Growth trends, productivity and rotation length

On a suitable site, early rapid growth of *C. alliodora* is assured. Annual diameter increment invariably exceeds 1 cm and frequently it is greater than 2 cm. This impressive increment is, however, a characteristic of early growth. There is evidence that it is not necessarily maintained in later years. Perez Figueroa (1954) plotted d.b.h./age curves from measurements of growth rings on trees in the humid tropical forest zone in Costa Rica. He found that, on average, the diameter increment increased rapidly over the first 6–10 years, after which it began to decline. The most profitable rotation under these conditions was calculated to be 25 years.

Further evidence of a decline in diameter increment early in the life of the tree is given by data from Puerto Rico (1952). It was found that the mean annual diameter increment of the 32 dominant and co-dominant trees on a growth plot was 1.2 cm at age 12 years. At 14 years the current annual diameter increment had declined to 0.5 cm. There was no obvious external influence to explain this. The basal area of the stand was only 7.3 m^2/ha and the climate over the measurement period was favourable.

Nevertheless, various authors have predicted that trees will achieve substantial dimensions over a medium-length rotation, although it is not clear if those responsible for the predictions took a decline in diameter increment into account in their calculations. Thus Vega (1977) estimated that in Surinam, if growth trends up to age 7 years were maintained, most sites would yield trees greater than 30 m in height and at least 40 cm in diameter on a 25-year rotation. At Tumaco in Colombia, Salas & Valencia (1979) extrapolated growth data from trees aged 8–10 years. They calculated that a 20-year rotation would result in a final crop of 200 trees/ha, 20 m in height and 40 cm in diameter, to give a final yield of 200–250 m^3/ha.

Greater yields have been predicted for Vanuatu. Hudson (1984) found that trees on the better sites attained 15 m height and 12 cm d.b.h. at 5 years. This increased to 23 m height and 27 cm d.b.h. at 10 years. It was predicted that a rotation of 20 years would produce trees 35 m in height and 55 cm in diameter.

The data referred to above were derived from either natural regeneration or plantations. Recent evidence from the OFI-coordinated international provenance trial indicates that correct provenance selection is likely to result in greatly increased growth rates. This is discussed in Section 10.0.

Table 5. Observed growth rates and predicted rotations.

	Observed			Predicted			
Country	Height (m)	d.b.h. (cm)	Age (yr)	Height (m)	d.b.h. (cm)	Rotation (yr)	Data source
Surinam	18–20	22	7	30	40	25	Vega (1977)
Colombia	—	—	—	20	40	20	Salas & Valencia (1979)
Vanuatu	23	27	10	35	55	20	Hudson (1984)

7. Agroforestry systems

C. alliodora is not merely a fast-growing species that yields a valuable timber; it has other useful traits. The species may be grown without close competition from neighbouring trees and still produce a single stem that is self-pruning for 50–60 percent of its height. Moreover, as the tree ages the crown becomes thinner and casts less shade. These characteristics have resulted in the species being incorporated into numerous agroforestry systems.

Taungya is an agroforestry system on which several authors have reported favourably as a means of reducing expensive establishment costs. Aguirre (1963) described how, in Costa Rica, taungya was compared with other methods of plantation establishment that do not involve the simultaneous cultivation of crops. *C. alliodora*, *Cupressus lusitanica*, *Swietenia humilis* and *Tectona grandis* were evaluated in terms of survival, early growth and establishment costs. *C. alliodora* and *T. grandis* were particularly successful under the taungya system, which was both economically viable and socially desirable in the conditions under which it was tested.

Vega (1978) reported how an adaptation of traditional shifting cultivation practices to include the planting and tending of trees was seen as a means of reducing high *C. alliodora* plantation establishment costs in Surinam. The productivity, financial returns and the influence of agricultural crops on the growth of trees were examined. It was concluded that the taungya method was less costly to implement than other establishment systems, which involve line planting and four years of intensive cultural operations. It was also an efficient means whereby rural populations may be settled and their living standards improved.

In Vanuatu, because most of the land is under customary ownership, there is a need to reconcile agriculture with timber production if the latter is not to be regarded as competing with the former. Persuading the farmers to accept agroforestry systems has been the answer and several demonstration trials were set up to assist the attainment of this objective. Preliminary observations after one year indicated that there was no reduction in the yield of either the trees or the food crops raised among them. Cattle-grazing under *C. alliodora* also showed promise. The bark appeared to be unpalatable to the animals and the trees were not damaged, provided they were old enough to avoid being trampled (Neil & Jacovelli, 1985).

Another system that combined timber production with cattle-grazing was described by Bishop (1979). In the Amazon region of Ecuador, pasture was improved by growing the velvet bean (*Mucuma pruriens* var. *utilis*) for one year. Then, vegetative propagation material of the forage grass *Brachiara humidicola* and stumps of *C. alliodora* were planted at 1 × 1 m and 5 × 5 m respectively. The grass was kept fallow until the trees were 3 m high. Two years after the *C. alliodora* was planted it was thinned to 200 stems/ha. A second thinning took place at age 4 years to leave the best 100 trees/ha.

Although a combination of pasture and tree crops is an attractive proposition, there is the possibility that the quantity and quality of herbaceous vegetation is reduced by the shade of the trees. This was investigated in Costa Rica by Daccarett & Blydenstein (1968). In a replicated experiment, plots of *C. alliodora*, *Erythrina poeppigiana*, *Gliricidia sepium* and *Pithecelobium saman* were planted at an espacement of 13 m. Seven years later the ground vegetation, which consisted of *Digitaria decumbens*, *Homolepis aturensis*, *Panicum maximum* and *Paspalum fasciculatum*, was sampled and analysed. There was no significant reduction in dry matter production beneath any of the tree species compared with the unshaded plots. However, the unshaded plots did have a significantly higher percentage of fibre. The protein content of the herbage under *C. alliodora* and on the unshaded plots was significantly lower than under the other species.

Beer *et al.* (1981) reviewed traditional agroforestry practices in part of the wet tropical zone of Costa Rica. The data that they assembled led them to the conclusion that *C. alliodora* was an excellent choice of tree for combinations with crops. It has been incorporated with pasture, often in mixture with other woody species such as *Erythrina* spp. It has also been grown with sugar cane but its most important use has been as a shade tree for coffee, frequently in combination with *E. poeppigiana*. In coffee plantations the optimum density for the *C. alliodora* appeared to be 200 stems/ha for saplings, decreasing to 100 stems/ha for mature trees. The *C. alliodora* may have adversely affected the coffee yield, especially at densities greater than 100 mature trees/ha, but typically the value of the timber more than offset this limitation.

Bermúdez (1979) also recorded that coffee plantations cultivated without shade were potentially capable of yielding 10 percent more than those with shade, but in the former larger investments were needed for weeding, fertilizing and controlling diseases. Also, losses of soil, nutrients and water were greater without an overstorey.

The success of a system that combines an understorey of coffee with an overstorey of trees is not just beneficial in terms of protecting the site and providing a supplementary timber crop. The combination may bring about improved nutrient cycling. Glover & Beer (1986) studied the mineral nutrient cycling of plantations of coffee (*Coffea arabica*) with an overstorey of *E. poeppigiana*, and of coffee with both *E. poeppigiana* and *C. alliodora*. They found, among other things, that there were large differences between the systems in the amounts of nutrients recycled by the trees. Nevertheless, overall, the nutrients recycled by both systems reached the recommended level of fertilizer required for coffee production. However, the inclusion of *C. alliodora* resulted in a more even distribution of nutrient inputs over the year.

Rosero & Gewald (1979) assessed the timber production in traditional agroforestry systems. These comprised naturally-regenerated *C. alliodora* growing in combination with pasture and perennial crops. Their findings are summarized in Table 6.

A more detailed investigation was undertaken by Somarriba & Beer (1987) who assessed annual growth for 5–8 years on 12 permanent agroforestry plots in Costa Rica. The d.b.h./height relationship of the trees did not vary between sites or between plots where different associated crops were grown. The d.b.h. data indicated that the growth of *C. alliodora* was influenced by the crops and that it increased in the order: pasture, sugar cane, coffee, cacao. Thirty-four years was calculated to be the rotation of maximum volume production. It was estimated that agroforestry stands with the average tree stocking reported in this study (68–290 trees/ha) would yield a total over-bark volume of 298–690 m^3/ha, or a utilizable stem volume of 191–442 m^3/ha, at the end of a 34-year rotation. These data apply to the humid region of Costa Rica at altitudes below 650 m where the mean annual rainfall is 2600–4000 mm without a well-defined dry season. However, after comparisons with other growth data, the authors suggested that these findings are applicable over a wide range of sites.

Despite the advantages of traditional agroforestry systems that incorporate *C. alliodora*, there is evidence that modern aids to weeding are placing these systems in jeopardy. Most, if not all of the systems rely on natural regeneration of *C. alliodora* and other desirable tree species. The method of weed control often determines whether or not trees are grown at the same time as agricultural crops. The farmer now has improved means at his disposal to combat weeds but sometimes the methods are detrimental to trees. Thus, the increasing use of herbicide sprays in coffee plantations is likely to reduce the numbers of valuable tree species that would normally be encouraged as part of the agroforestry system (Beer, 1979).

Table 6. *C. alliodora* timber yield from agroforestry systems (Rosero & Gewald, 1979).

Age (yr)	Associated crop	Stems per ha	Mean d.b.h. (cm)	Mean ht. (m)	Standing vol. (m^3/ha)
15	Coffee	228	29	22	162
20–25	Cacao	120	41	34	271
15–20	Cacao	180	35	35	308
25–30	Pasture	200	37	34	380

8. Wood properties

8.1 Anatomy

Several accounts are available of the anatomy of *C. alliodora*. All agree on the main characteristics but there are some differences in the fine detail. In particular, there are variations in some of the recorded cell dimensions, although most are of the same order of magnitude. Such differences undoubtedly reflect not only the variation between trees on the same site, but also especially the variation between trees from different parts of the natural range.

Jane (1952) and Johnston (1955) gave short descriptions of the anatomy but did not state the source of their data. More-detailed data, based on samples from Mexico, were given by Barajas Morales & Echenique-Manrique (1976) and Barajas Morales (1981).

The most comprehensive description was made by Peralta & Abbate (1981) for wood grown in Panama, which is summarized as follows:

GROWTH RINGS: indistinct, wood diffuse porous.

VESSELS: moderately scarce (mean frequency 7/mm^2); many solitary; rounded shape; very short; transverse diameter from 84 to 160 μm, mostly 100–140 μm, with a mean of 125 μm; radial diameter from 100 to 200 μm, mostly 130–150 μm, with a mean of 140 μm; length from 90 to 280 μm, mostly 150–190 μm, with a mean of 180 μm; transverse walls horizontal or slightly oblique, with simple perforations; inter-vascular pits large (mean diameter 9 μm), with a horizontal orifice and an almost round border.

PARENCHYMA: (a) paratracheal (i.e. associated with the pores) vasicentric (i.e. forming a complete sheath concentric with a pore)—usually a single cell, sometimes two or three, tending towards aliform (i.e. with wing-like extensions)-confluent; (b) apotracheal (i.e. independent of the pores)—diffusely aggregated in tangential or short radial lines which gives a banded pattern; (c) radial—in moderately numerous rays, always multi-seriate (2–8 series), height 10–64 cells (mean 26).

FIBRES: short, thick-walled with a tendency towards an arrangement in radial series; length from 990 to 1800 μm, mostly 1400–1500 μm, with a mean of 1400 μm; diameter from 16 to 32 μm, mostly 24–27 μm, with a mean of 24 μm; wall mean thickness 3 μm; lumen mean diameter 18 μm.

INCLUSIONS: thick gum deposits on the vessel walls; numerous polyhedral crystals.

8.2 Physical and mechanical properties

C. alliodora trees in Puerto Rico were described by Longwood (1961) as having heartwood that, when freshly cut, was light greenish-brown to olive-brown with dark streaks. On seasoning it turned a pale golden brown to brown and the streaks became more conspicuous. Small rays gave quarter-sawn surfaces a slightly mottled appearance. The sapwood was lighter than the heartwood but the boundary between the two was not sharply defined. The wood was usually straight-grained with a fine to medium texture and a medium to high lustre. There was seldom any odour or taste except that the dark wood from very old trees occasionally had a spicy aroma.

This description is in general agreement with less detailed accounts that refer to wood from Guyana (Fanshawe, 1961) and western Mexico (Barajas Morales, 1981). Other authors made similar descriptions but they differed over the degree of contrast between the heartwood and the sapwood. Thus, trees from Ecuador were reported to have a greyish-brown sapwood and a variable brown heartwood (Timber Development Association, 1948). On the other hand, in timber from Mexico, Barajas Morales & Echenique-Manrique (1976) noted a creamish-yellow or uniformly white sapwood and a greyish-brown heartwood.

Record (1927) and Standley (1938), referring to material from Honduras and Costa Rica respectively, described the wood of some trees as being greyish or greyish-white. Others were stated to have the darker wood, similar to walnut in appearance. It was suggested that these differences may have reflected the ages of the trees or the site conditions where they grew. Alternatively, there may have been two species, which were not distinguished in the field.

The only report on plantation-grown wood was made by Brazier & Moore (1984) who studied samples from five 10-year-old trees in Vanuatu. They found a wide band of pale sapwood that made up a considerable proportion of the cross section in the upper parts of the stem. It contrasted sharply with the grey-brown heartwood, which had an irregular outline because of fluting on the logs. The heartwood was lighter and less uniform in colour than that of older trees from the Americas but it had an attractive appearance despite the presence of knots, some of them large.

The moisture content of *C. alliodora* in the green condition is of the order of 106 percent (Kukachka, 1970) to 122 percent (Volkart, 1965). The green weight is in the range 929 kg/m^3 (Volkart, *loc. cit.*) to 1089 kg/m^3 (Longwood, 1961).

Basic density (oven dry weight/green volume) shows wide variation. Volkart (*loc. cit.*) collated test data from several sources in Central America and the Caribbean. He recorded an average figure of 0.42 g/cm^3. Wangaard & Muschler (1952) produced values of 0.38–0.52 g/cm^3 for samples from Belize, Honduras, Nicaragua, Panama and Venezuela. Barajas Morales (1981) reported 0.73 g/cm^3 for a single specimen from western Mexico.

The most intensive density study of naturally-regenerated trees was implemented by Howe (1974) who investigated trees on different sites in Costa

Rica. These represented six life zones according to the Holdridge ecological classification system. They varied from tropical dry forest to tropical wet forest, and covered a range in mean annual rainfall of 1650–5080 mm. Basic density, as determined for the first 35 mm from the bark on increment cores taken at breast height, ranged from 0.384 to 0.624 g/cm^3. Values were greater for the tropical dry and premontane moist zones than they were for the tropical moist, premontane wet and tropical wet zones. There was also a highly positive correlation of density with diameter breast height, and a highly negative correlation with crown percent.

The investigation by Brazier & Moore (*loc. cit.*) included an assessment of basic density. The full range of values encountered was 0.265–0.525 g/cm^3. Mean values for individual trees varied from 0.384 to 0.445 g/cm^3.

Among the accounts of the mechanical properties of the wood is a report of tests performed on samples from a single tree in Venezuela (Kynoch & Norton, 1938). Compared with some United States species in the same weight class, the timber showed less shrinkage but higher values in several important strength properties. However, it was low in toughness, hardness and shear resistance.

More comprehensive results were given by Wangaard & Muschler (*loc. cit.*) following tests on samples from Belize, Honduras, Nicaragua, Panama and Venezuela. Considerable variation was recorded in the air-dry strength properties among these sources, mostly associated with differences in basic density (0.38–0.52 g/cm^3). These properties were similar to those reported for *Swietenia macrophylla*. Exceptions were resistance to shock, which was higher for *C. alliodora*, and compression across the grain, tension across the grain and cleavage which were lower. Most of the *C. alliodora* strength properties improved moderately on air drying. The greatest proportional increase was in elastic resilience, followed by compression strength parallel to the grain, bending strength, end hardness, compression across the grain, stiffness and shear. There was no change in side hardness. Decreases occurred in tension across the grain and cleavage resistance. *C. alliodora* appeared to be more permeable to moisture than *S. macrophylla*, and it was only fair in its steam-bending characteristics.

8.3 Chemistry

Some chemical analyses of *C. alliodora* wood have been made, mostly to investigate the possible influence of its chemical composition on its resistance to decay. Wise *et al.* (1951) found that samples from trees grown in Honduras contained a small amount of a fragrant essential oil, no tannin, some starch and a high nitrogen content. These results were regarded as inconclusive in terms of whether the wood is likely to be durable or not. More positive evidence of possible chemical influence on durability was reported by Stevens & Jurd (1976). They found that extraction of dry *C. alliodora* heartwood yielded a crystalline quinol-terpenoid compound. This was shown to be a derivative of geranylhydroquinone, for which the name alliodorin was proposed. This newly discovered compound belongs to a class of natural terpenoids, consisting of a terpenoid system joined to resorcinol, quinol or quinone units, many members of which have been shown to have biocidal properties.

Table 7. Basic density recorded for *C. alliodora* wood.

Country	Basic density (g/cm^3)	Data source
Natural forests		
Panama	0.49	Wangaard & Muschler (1952)
Belize	0.49	Wangaard & Muschler (1952)
Honduras	0.40	Wangaard & Muschler (1952)
Nicaragua	0.38	Wangaard & Muschler (1952)
Venezuela	0.52	Wangaard & Muschler (1952)
Mexico	0.73	Barajas Morales (1981)
Costa Rica	0.38–0.62	Howe (1974)
Plantations		
Vanuatu	0.38–0.44	Brazier & Moore (1984)

9. Utilization

9.1 Seasoning

Two brief references to the seasoning characteristics of *C. alliodora* wood stated that it seasons satisfactorily (Anon., 1952) and that it dries with little degrade (Brown, 1979). More detailed information was provided by Dickenson *et al.* (1949) based on the study of samples from Belize, Honduras and Nicaragua. They classified the air-seasoning characteristics of the wood as fast under the conditions prevailing during April to November at New Haven, Connecticut in the USA. Drying to 16 percent moisture content was achieved in less that 120 days. The degree of warp in terms of crook, bow, cup and twist resulted in less than 5 percent waste. There was a similar degree of wastage due to splitting and end- and surface-checking. Case-hardening did not occur. Wangaard & Muschler (1952) found that wood from Belize, Honduras, Nicaragua, Panama and Venezuela air-seasoned easily with little defect. Rapid drying resulted in only slight checking and warping. Volumetric shrinkage varied from 7.8 to 10.6 percent, depending on the origin of the test material.

Brazier & Moore (1984) tested plantation-grown samples from Vanuatu and found that they kiln-dried satisfactorily using kiln schedule E, although there was considerable splitting. The linear shrinkage on drying from the green condition to 12 percent moisture content was 3.2–5.4 percent in the tangential direction and 1.2–2.3 percent in the radial direction.

9.2 Durability

A short, general account of *C. alliodora* wood described it as not resistant to rot (Anon., 1952) but other evaluations of the wood's durability disagreed with this. Shank (1948) described how a hurricane in 1933 had uprooted *C. alliodora* trees on the Atlantic coastal plain of Nicaragua. About 15 years later the sapwood of these trees had rotted away but the heartwood remained in sound condition. Scheffer & Duncan (1947) also noted that the sapwood was distinctly more susceptible to decay that the outer heartwood. They reported that, following heartwood decay tests in soil in Costa Rica and Panama, the species was described as resistant to decay and outstandingly resistant to termite attack. Following tests in the USA the same author described it as very resistant to both decay in soil and to decay induced by pure cultures of white- and brown-rot fungi. Mayorca (1972) listed *C. alliodora* among six species that suffered no fungus or termite attack out of 115 Venezuelan species evaluated in a 6-year graveyard test. On a scale of one to five, indicating decreasing resistance to termites, Volkart (1965) gave the wood a value of two. Brazier & Moore (1984) classified samples from 10-year-old plantation-grown trees as moderately durable when exposed to fungus and as having a good resistance to termites.

In an investigation in Mexico, Perry & Lima (1964) compared the durability of treated and untreated *C. alliodora* fenceposts. The posts were 5–15 cm in diameter and uniformly yellowish throughout without any visible evidence of heartwood formation. The bark was easily stripped off with a machete to leave the wood clean and smooth. Treatment was by the 'hot and cold' bath method using a 5 percent solution of pentachlorophenol in diesel oil. The preservative penetrated about 6 mm. After five years the posts had suffered only superficial termite attack at ground level, but the action of wood-destroying fungi at the same level caused 84 percent of the posts to break. The preservation treatment increased overall durability by about 9 percent.

In terms of resistance to marine borers, *C. alliodora* wood samples from Puerto Rico showed little resistance after 6–9 months submergence in Honolulu harbour, Hawaii (Edmondson, 1948). *C. alliodora* was also one of 113 Panamanian timber species that were tested for marine-borer resistance at three locations in the Panama Canal Zone (Southwell & Bultman, 1971). Wood samples were exposed for periods up to 90 months at underwater sites in the Pacific Ocean, the Caribbean Sea and the brakish waters of Miraflores Lake. *C. alliodora* was susceptible to teredo attack in the lake, but it showed a high restance to teredo and limnoria at the ocean sites. It was not resistant to pholads. It was suggested that the wood should be suitable for marine construction in northern temperate waters where pholads are not a problem.

9.3 Uses

C. alliodora is recorded as having medicinal properties. Standley (1924) referred to the use in Mexico of a decoction of the leaves as a tonic and a stimulant, especially in cases of catarrh and lung infections. Reference was also made to the pulverized seeds being used in the West Indies in the treatment of cutaneous diseases.

In the Caribbean *C. alliodora* flowers are known to bee-keepers as a major source of nectar (Crane *et al.*, 1984) that gives a viscous extra-white honey (Mulzac, 1979).

However, it is as a timber-producing species that *C. alliodora* is renowned. The wood is usually straight grained and easily worked with little dulling of cutting edges to give a very smooth finish. Its polishing and staining characteristics are satisfactory (Brown, 1979). These qualities, combined with the fact that the wood seasons easily with little degrade, its dimensional stability when dry, and its strength and durability properties reviewed earlier, have resulted in the timber being widely used in the countries where it occurs naturally.

An early report by Marshall (1930) noted that in Trinidad it was in considerable demand for building construction, flooring, furniture, boat timbers and oars. Almost 50 years later Ramdial (1978) recorded

that *C. alliodora* was one of the eight preferred species of the numerous furniture factories operating on the island. Record (1929) stated that it was widely used in Nicaragua for building construction, flooring and railway sleepers. Perez Figueroa (1954) regarded *C. alliodora* as one of the most important timber trees of Costa Rica. This was because of the plentiful supply of good quality wood and its widespread use. It has also been recorded as being the preferred species for cabinet work and furniture-making in Venezuela (Lamprecht, 1955) and Guyana (Fanshawe, 1961), while in Mexico it is used for furniture and veneer manufacture, turnery and a wide variety of carvings and artists' equipment (Barajas Morales & Echenique-Manrique, 1976).

In a review of the properties of *C. alliodora* wood, Dickenson *et al.* (1949) noted that, in addition to its traditional uses, it also appeared to be suitable for pattern-making, turnery, instruments and veneers. Many of its properties are similar to those of S. *macrophylla*, for which it might be an acceptable substitute in uses such as the planks and other parts of boats. Its resistance to decay indicated that it is a possible alternative timber to several species of cedar in situations requiring durability. Brazier & Moore (1984), after studying plantation-grown samples from Vanuatu, concluded that although it was not a strong wood in terms of resistance to bending, its combination of stability and durability made it suitable for both indoor and outdoor joinery work. Its appearance suggested a use in furniture construction and panelling, and it would be suitable for flooring where there was light traffic.

10. Genetic variation

10.1 Evidence from the natural populations

Throughout the natural populations of *C. alliodora* there is considerable phenotypic variation. Attention has already been drawn to the relatively low stature of the trees on the seasonally-dry Pacific seaboard of Central America and Mexico, compared with those on the wetter Atlantic coastal plains (Section 2.4). However, it is not only stem and crown form that vary. Miller (1985) reviewed the descriptions of numerous herbarium specimens collected throughout Central America and Mexico, and found large ranges in the dimensions of several morphological characteristics. Thus, for example, leaf length was said to vary between 5.2 and 17.0 cm, but extremes of 3.5 cm and 20.5 cm had also been recorded.

Phenotypic differences are not confined to the morphology of the tree. Typically, the wood is sharply differentiated into a pale sapwood and a relatively darker heartwood, but trees have been found that are a uniform pale colour throughout the stem (Standley, 1938). When there is a darker heartwood it is not unusual to find differences among trees in its shade, as observed by Record (1927) in Honduras. Here, and in other regions, *C. alliodora* is known locally as 'laurel blanco' or 'laurel negro'. The heartwood of the former is greyish or yellowish. In the latter it is a darker, variegated, brown colour.

Record was not able to differentiate laurel blanco and laurel negro in the field, but foresters in Colombia and Ecuador have maintained that they can (McCarter, 1988). They have alleged that laurel blanco is the typical form and the only one that is found on the Pacific lowlands of these two countries. Farther to the east in Amazonia laurel blanco grows in intimate mixture with laurel negro. It is said that the leaves and flowers of the latter are two to three times the size of those of the former and that this can be used for distinguishing the two forms. On this basis, it has been claimed, the colour of the heartwood can be safely predicted before the tree is felled. The second author could not detect any differences in the gross morphologies of the two forms and he suggested that they are the same taxa.

The phenotypic differences detected in *C. alliodora* are unlikely to reflect the genotypic variation alone. Environmental conditions undoubtedly have a modifying influence, nevertheless the evidence presented is an indication that the populations in some broad geographical zones are genetically distinct from those elsewhere. This is to be expected for a wide-ranging species. However, data from systematic and more intensive botanical sampling would be necessary before clinal or ecotypic patterns of variation could be suggested for the whole of the species' extensive natural range.

10.2 Evidence from provenance trials

Variation among provenances

In 1977 and 1978 the OFI acquired *C. alliodora* provenance seed collections representative of most of the species' natural range (see Table 8). The collections were made in naturally-regenerated stands that occurred either in the forest or as shade trees over agricultural crops and pasture. These provenances represent a wide range of sites, at altitudes from just above sea level to 2000 m, over which mean annual rainfall varies from 850 mm to 3550 mm (Stead, 1980). Six land races were also acquired from three countries.

Distribution of provenance seed samples for an international provenance trial commenced in 1977. Owing to poor germination of some of the Caribbean and South American provenances, a fact attributed to incorrect seed collection and processing techniques rather than genetic variation, the composition of the trials was heavily biased in favour of the Central American provenances. Consequently, trial assessments and evaluations produced conclusive evidence of the pattern of genetic variation in Central America only.

Early observations by collaborators in the international trial revealed distinct differences among the provenances. In Costa Rica, Boshier (1984) noted that provenances from areas with a pronounced dry season, that is from the Pacific watershed of Central America, germinated more quickly and showed more vigorous seedling growth than provenances from the areas with a less-marked dry season that drain into the Atlantic. Similar observations were made in the Ivory Coast by Delaunay & Grolleau (1978). These differences were also apparent elsewhere, although to a lesser extent, notably in the Solomon Islands (Miller & Chaplin, 1981) and Brazilian Amazonia (Kanashiro *et al.*, 1980).

Several early reports also referred to provenance differences in the morphology of the seedlings and young trees. Thus Delaunay & Grolleau (*loc. cit.*) commented on differences in the shape, size and colour of the leaves, as well as in the rate of development and size of the nodal swellings that serve as ant domatia. Again, the provenances from the Pacific watershed in Central America were distinct from the others, in this instance by showing the most rapid development of domatia.

However, this early ranking of the two groups of provenances, in which those from the Pacific watershed showed superior early development, was not maintained. Despite a slower start in the nursery, the growth rates of the Atlantic provenances improved in the field and the ranking soon reversed. This was apparent at Shark Bay on Espiritu Santu, Vanuatu, two years after planting. Among the seven provenances in the trial there was only one from the Pacific

group. Twenty-six months after planting this provenance (14/77) had achieved a mean height and diameter of 9.8 m and 10.1 cm respectively. Nevertheless, it was conspicuously smaller, with poorer form and less self-pruning ability than the others. All six remaining provenances were from the Atlantic group. Without exception they were rated good to excellent for both their stem form and growth traits. The best (34/77) had a mean height of 11.5 m and a mean diameter of 14.1 cm (Neil & Aru, 1987).

The superiority of the Atlantic group was established in all trials, usually within two years of planting. This occurred regardless of the rainfall, altitude or other environmental factors at the trial site.

In 1985 the status of the *C. alliodora* international provenance trial was reviewed with a view to carrying out a standardized intensive assessment across a wide range of sites. Fifteen trials were identified that had been adequately managed for them to make a meaningful contribution to such an assessment. This was implemented during 1986 and 1987 (see Table 9). At every trial 16 trees per replicated provenance plot were either measured or scored for 12 growth traits. In addition, observations were made on the phenology of the trees and the incidence of pests and diseases present. Also, bark-to-bark cores were extracted at breast height so that an examination of density variation across the stem could be made with the assistance of optical desitometry.

Data from these intensive assessments showed that after the early years there was little change in provenance ranking up to age 10 years, the age of the oldest trials available for assessment. The data also confirmed the overall superiority of provenances in the Atlantic group in terms of growth traits. However, in almost every case the slower-growing Pacific provenances had a higher basic density.

Despite the division of the provenances into two groups, there were still highly significant differences within and between these groups at many of the sites in almost all growth traits and wood density. Interestingly, the fastest growing provenances in each of the groups (i.e. those with the largest mean d.b.h.) did not always have the lowest density.

Survival was the only trait measured for which there was little or no significant difference among provenances at most sites. In general, survival was remarkably good, even on the worst sites.

The intensive assessment also showed that the impressive early growth rates referred to earlier in section 6.4 are not exceptional. During the first two years the annual diameter increment of the best provenances was 5–7 cm. Over the third and fourth

Table 8. Provenances represented in the *C. alliodora* international provenance trial intensive assessment.

Provenance identity number	Provenance source details						Number of trials
	Country	Site	Latitude	Longitude	Altitude (m)	Mean annual rainfall (mm)	
	Natural populations						
22/77	Belize	Silk Grass	16°58'N	88°23'W	65	2256	2
10/77	Guatemala	Finca el Chilero	14°23'N	90°28'W	1350	1300	15
30/78	Guatemala	Retalhuleu	14°27'N	91°46'W	120	2901	6
9/77	Honduras	Tres Piedras	13°02'N	87°04'W	110	1850	13
19/77	Honduras	Finca la Fortuna	15°36'N	87°58'W	210	1373	16
20/77	Honduras	San Francisco	15°40'N	87°02'W	50	2858	14
14/77	Nicaragua	Esteli	13°02'N	86°19'W	850	848	15
18/77	Nicaragua	La Pineda	12°45'N	84°45'W	750	1374	15
33/78	Nicaragua	Nueva Guinea	11°43'N	84°26'W	220	2588	6
32/77, 51/78	Costa Rica	Turrialba	09°53'N	83°38'W	602	2660	8
33/77, 52/78	Costa Rica	Limon	09°57'N	83°02'W	50	3550	8
34/77, 53/78	Costa Rica	San Carlos	10°22'N	84°32'W	140	3270	3
16/78	Puerto Rico	Arecibo	NA	NA	200	1200	1
17/78	Puerto Rico	Caguas	NA	NA	100	1400	1
13/77, 21/78	Colombia	Ulloa	04°41'N	75°46'W	1600	2129	4
35/77	Ecuador	Lago Agrio	00°17'S	77°02'W	230	3013	2
	Land races						
1/77	Ivory Coast	Yapo (ex Belize)	NA	NA	NA	NA	4
37/77	Solomon Is.	Mt. Austen (ex Trinidad)	NA	NA	NA	NA	1
13/78	Fiji	Nukurua (ex Belize)	NA	NA	NA	NA	1
38/76	Fiji	Nansori (ex Belize)	NA	NA	NA	NA	1
40/76	Fiji	Nabontini	NA	NA	NA	NA	1

Table 9. Provenance trials selected for intensive assessment.

Country	Site	Latitude	Longitude	Altitude (m)	Mean annual rainfall (mm)	Number of dry months (<70 mm)
Americas						
Brazil	Bebedouro	20°57′S	48°30′W	570	1296	5
Brazil	São Jose do Rio Preto	20°49′S	49°23′W	488	1240	5
Brazil	São Luiz Antonio	21°40′S	47°49′W	550	1280	5
Colombia	Sautata	7°50′N	77°07′W	50	2070	4
Colombia	Tumaco	1°22′N	78°34′W	20	2139	0
Costa Rica	Turrialba	9°53′N	83°38′W	602	2681	0
Africa						
Ghana	Pra Anum	6°15′N	1°15′W	150	1324	4
Ivory Coast	La Sangoué	6°20′N	5°30′W	200	1194	6
Liberia	Cavalla	6°09′N	8°11′W	250	1800	4
Nigeria	Awi	8°02′N	4°58′E	63	2800	5
Nigeria	Ikom	8°45′N	6°00′E	119	3000	4
Nigeria	Sapoba	6°01′N	5°46′E	100	1799	5
Pacific						
Fiji	Nukurua	17°53′S	178°27′E	140	3600	0
Fiji	Nukurua	17°35′S	178°27′E	140	3600	0
Solomons	Poitete	7°52′S	157°07′E	30	3500	0

years it averaged 3–6 cm. Thereafter the annual increment was reduced, probably due to the intense competition that arose at the standard trial espacement of 3 × 3 m. In comparision, the poorest provenances seldom achieved diameter increments greater than 3 cm/yr over the first and second years, and this was often reduced to less than 1 cm/yr by the fourth year. As a consequence, by the time the trials were seven to eight years old the heights and diameters of the Pacific group were often less than half those of the Atlantic group.

All the results from the intensive assessments were confounded by planting distance, management and age of the trials. If a wide planting distance had been used, such as 5 × 5 m rather than the 3 × 3 m generally employed, the phenotypic characteristics of the Atlantic provenances would have been less suppressed by competition. This would undoubtedly have led to even more pronounced differences between the Pacific and Atlantic groups than were observed. An indication of this is that when analyses were based on just the three trees of greatest d.b.h. per plot, provenance means for height and d.b.h. in the Atlantic group increased mostly by 50–100 percent, whereas in the Pacific group it was only 25–40 percent.

Phenological traits, such as leaf fall and flowering period, showed little variation among provenances. However, such was the large degree of variation within provenances that this may mask differences among them. In general, the Pacific group appeared to flower at a younger age and more prolifically than the Atlantic group.

Although the provenances representing the Caribbean and South American *C. alliodora* populations, as well as several land races around the world, were poorly represented in the international provenance trial an examination of the few data available is informative.

The only Caribbean provenances were two from Puerto Rico (16/78, 17/78). These were included in one trial at Nukurua in eastern Viti Levu, Fiji. Neither did well compared with the other eight provenances in this trial. At age 5.5 years 16/78 was last in the order of ranking for height and d.b.h. The mean d.b.h. was less than 40 percent of that of the best provenance (33/78, Nicaragua). Provenance 17/78 came half way down the order of ranking for height and d.b.h. The stem form of both these provenances was also very poor.

Assessment data were obtained for two South American provenances. Of these, a Colombian provenance from an altitude of 1600 m, the highest represented in the international trial, occurred at four sites: two in Fiji, one in Colombia and one in Ghana. Its performance relative to other provenances was poor in every case. In terms of vigour and stem form traits it came at or near the bottom of the order of ranking in the Colombian trial. In the other three trials it was placed in the bottom half or third of the ranking table.

The other South American provenance (35/78), and the only one from the southern hemisphere represented in the intensive assessment, was from a Pacific lowland source in Ecuador. It was present in two trials. In Ghana, where the experiment had been badly damaged by fire, it ranked first for stem form and second for d.b.h. Just before the fire, at age 54

months, it had ranked fifth for d.b.h. This provenance did less well in the Solomon Islands where it ranked fourth (out of eight) for height, fifth for d.b.h. and last for stem form. However, plantation trees raised from seed of this provenance in Ecuador show exceptionally good vigour and stem form.

Two land races were available for assessment. One from the Solomon Islands, which was established using seed from Trinidad, performed very poorly compared with the Central American provenances in a trial on Kolombangara in the Solomons. The other land race was represented by four trees at the Yapo Experimental Station in the Ivory Coast, which are believed to have been grown from seed collected in Belize. This land race occurred in four trials: Fiji, Colombia, Ivory Coast and Ghana. At every location it was among the best provenances, except in Ghana where out of 10 provenances it was half way down the ranking tables for all traits. However, this was the trial referred to above that was damaged by fire four years before the assessment. Prior to the fire the Yapo provenance was by far the best with a mean height and d.b.h. of 19.3 m and 18.3 cm respectively at only 54 months. At that time survival was 97 percent. The superiority of this provenance had been apparent from the first assessment at 17 months. Of the trees measured in the intensive assessment, 81 percent were coppice regrowth that arose after the stems were killed by the fire.

Variation within provenances

Very great between-tree variation within provenances was observed at almost all sites for almost all traits. For example, within a 4 × 4 tree assessment plot, height and diameter varied by up to 1500 percent and wood density at breast height by up to 200 percent. The general trend was for density to increase gradually with distance from the pith but in some trees this trend was reversed.

There were also great phenological differences between trees within provenances, especially on sites without a marked dry season. Under such conditions leaf fall and flowering were recorded as occurring at all times of the year. Individual trees of the same provenance dropped their leaves, flushed and flowered independently of one another.

Provenance–environment interaction

The general differentiation of provenances into Atlantic and Pacific coastal groups was affected little by site, but the better the site the greater and more statistically significant were the differences between the two groups.

Although the ranking of provenances was not constant within each group, the provenance–site interaction term was not significant for most traits. Consequently, one can be reasonably confident in making recommendations concerning the provenances that should be planted on lowland sites, which were typical of the trial locations. Two provenances in particular performed outstandingly well on all sites: Limon from Costa Rica (33/77) and San Francisco from Honduras (20/77). Generally, the latter had the greater volume production but the former had the best stem form. However, in general all the Central American Atlantic watershed provenances gave acceptable results.

11. Discussion and conclusions

C. alliodora is a species of considerable socio-economic importance throughout its natural range in Latin America and the Caribbean. Not only is the timber highly valued in local commerce but the tree's silvicultural characteristics allow many peasant farmers to raise it in agroforestry systems. In the past, most of the trees utilized for these purposes were grown from the profuse natural regeneration that is often found on cleared ground in the vicinity of seed trees. Now it has been demonstrated that there are not any technical obstacles to artificial regeneration.

The earlier belief that the seed is short lived has been dispelled and, provided that simple precautions are taken, viability is retained for at least 10 years in cold storage. This opens the way for wider use of the species as an exotic. The available evidence from species introduction trials and the OFI-coordinated international provenance trial has shown that very promising plantations can be established on tropical lowland sites at latitudes up to 18° and at altitudes up to 700 m. Economically-viable plantations are probably feasible at higher altitudes but wider-ranging investigations are needed to confirm this.

However, *C. alliodora* is very site sensitive with regard to soil conditions. Not only does it benefit from deep soils free of seasonal waterlogging, as do most species, but it is very demanding in terms of nutrients. *C. alliodora* is predominantly a species for planting on recently cleared forest sites, and degraded soils should be avoided.

The pattern of annual rainfall distribution is unimportant and sites with marked dry seasons are likely to be as productive as sites that receive rainfall throughout the year. Although satisfactory growth has been achieved when the mean annual rainfall during the trial period was as low as 1200 mm, the use of this type of site is likely to be hazardous because the species is unlikely to tolerate the inevitable years when the rainfall is substantially below average. It is probably advisable to seek sites with a mean annual rainfall of at least 1800 mm.

The species' simple nursery requirements and the ease with which plantations can be raised from seedlings, stumps, or even direct sowing in some circumstances, are important factors greatly facilitating plantation management. Furthermore, early rapid growth helps to reduce establishment costs, although these may still be considerable on sites where frequent tending operations are necessary to prevent the trees from being distorted by vigorous climber regrowth.

The fine details of *C. alliodora* plantation management remain to be resolved but it is known that if close spacings, such as 3 × 3 m, are used early heavy thinnings will be necessary to prevent excessive competition developing. If this sets in and the trees become checked they are unlikely to recover when the canopy is opened up. Wide planting espacements are usually avoided in conventional plantation practice with most species because of, among other things, the unacceptable deterioration in stem and branch form that this brings about. Fortunately this is not the case with *C. alliodora*. Even when grown as a solitary tree in the open it maintains a single persistent stem and narrow crown, as well as its ability for self-pruning to about two-thirds of its total height. It is these qualities, plus the fact that the crown casts only light shade, that encourages its use as an agroforestry species.

The early growth rates reported for existing plantations are impressive. For example, on the better sites in Vanuatu trees have attained heights and diameters of the order of 23 m and 27 cm respectively at 10 years. It is projected that in these circumstances trees of 35 m height and 55 cm d.b.h. will be produced on a 20-year rotation. However, the recently completed international provenance trial assessment has revealed that the correct choice of provenance results in even greater vigour.

The design of the international provenance trial permitted firm conclusions to be reached concerning the relative merits of Central American provenances for plantations on lowland sites throughout the humid tropics. In these environments provenances from the Atlantic watershed of Central America were found to be superior to those from the Pacific watershed of the isthmus in terms of vigour and stem form. Unfortunately, high-altitude trials were not available for assessment, neither were provenances from the Caribbean and South American populations well represented. Nevertheless, in the few comparisons that could be made these provenances were inferior to the Atlantic provenances from Central America. On the evidence available, the Atlantic watershed of Central America is the recommended seed source for exotic plantations on humid tropical lowland sites at altitudes below 700 m.

The wide variation encountered within provenances is a strong indication that considerable gains could be achieved by a tree improvement programme. The contribution that individual parent trees make to this variation is unknown but early results from progeny trials now under way in Costa Rica indicate that from a very early age there is pronounced variation among the different families. Further work of this kind is needed before an appropriate tree improvement scheme can be planned. More information is also needed on the species' pollination mechanism, as well as its suitability for vegetative propagation.

Although it would be advantageous to expand and refine the knowledge on *C. alliodora* there is no justification for delaying wider use of the tree as a plantation species, at least on a trial basis. Pests and diseases have been the only important drawback to date. These have not caused problems sufficient to deter the use of natural regeneration and the establishment of plantations in the species' natural range. However in exotic plantations, *Phellinus noxius* in Vanuatu merits further investigation with the aim of

controlling the disease by either cultural means or the selection of genetically resistant planting stock.

There are no obstacles to the use of *C. alliodora* timber. Throughout the species' natural range it is held in high esteem owing to ease of seasoning and working, dimensional stability when dry, satisfactory mechanical characteristics, resistance to decay and an attractive finish. These qualities have earned the wood a reputation as being suitable for a wide range of utility and decorative uses where high strength is not important. Data from provenance trials show that density remains within acceptable limits despite high growth rates. Furthermore, the intensive physical and mechanical testing of a consignment of plantation-grown timber did not reveal any deterioration in the characteristics described above when the species was grown as an exotic.

In conclusion, there is much to commend the wider use of *C. alliodora*. Improved awareness of provenance variation, combined with this review of the information available on all aspects of the species, comes at a time when there is worldwide concern over the excessive exploitation of tropical hardwoods and the irreversible depletion of the forests in which they are found. One way of alleviating such forest degradation is to create alternative sources of high-quality timber. Although not all forest trees are adaptable to plantation management, it is possible for some through systematic observation and scientific study. *C. alliodora* is an example of one such species that is eminently suited to both commercial plantations and agroforestry systems. Its wider use in these ways would not only help to reduce demands on the remaining tropical forests but would also be of direct benefit to the rural poor.

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