

Calliandra calothyrsus: Implications of Plant Taxonomy, Ecology and Biology for Seed Collection

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SUMMARY

The Oxford Forestry Institute has recently begun seed collections of *Calliandra calothyrsus* for eventual inclusion in international provenance trials. The importance of the species in agroforestry throughout the tropics is described. Information on the species taxonomy, habit, ecological amplitude, and reproductive biology is presented and its implications for the seed collection strategy are discussed. Guidelines for sampling are included and the process of provenance delimitation is described. Specific details including topographical, political, climatic, edaphic, and ecological maps of the provenance sites are given. The ability to achieve real improvement in species performance is discussed in relation to the perceived potential and limitations of the species in agroforestry systems.

RÉSUMÉ

L'Institut de Foresterie d'Oxford a commencé récemment à rassembler des graines de *Calliandra calothyrsus* destinées finalement à être utilisées dans des tests de provenance internationaux. On décrit l'importance de l'essence dans l'agroforesterie partout sous les tropiques. On présente des renseignements sur la taxonomie, le port, l'amplitude écologique et la biologie de reproduction de l'essence et l'on considère les conséquences de ces renseignements pour la stratégie de rassembler des graines. On présente des lignes directrices pour l'échantillonnage et l'on décrit le processus de délimitation des provenances. Parmi les détails précis fournis sont des cartes topographiques, politiques, climatiques, édaphiques et écologiques des sites de provenance. On considère la capacité d'obtenir une véritable amélioration de la performance de l'essence par rapport à ce que l'on tient pour les possibilités et les limites de l'essence dans les systèmes agroforestiers.

RESUMEN

Calliandra calothyrsus: Implicaciones de la Taxonomía, Ecología y Biología en la colección de semillas de esta especie. El Instituto de Silvicultura de Oxford ha iniciado recientemente colecciones de semillas de *Calliandra calothyrsus* para incluirlas, de manera definitiva, en estudios internacionales de variedades de esta especie. En este trabajo se describe la importancia de *C. calothyrsus* en agronomía forestal en todas las zonas tropicales. Se presentan datos de taxonomía, hábitat, amplitud ecológica y biología reproductiva de la especie, y se discuten las consecuencias que de ellas se derivan para la colección de semillas. Se incluyen además, algunas instrucciones para llevar a cabo el muestreo y se describe el proceso completo de delimitación de variedades. Asimismo, se muestran detalles específicos que incluyen mapas topográficos, políticos, climáticos, edáficos y ecológicos. Finalmente, se discute la posibilidad de lograr una mejora real de la especie, en relación con el potencial observado y las limitaciones de los sistemas de agronomía forestal.

Key words: *Calliandra Calothyrsus*, biology, provenance, seed collection

INTRODUCTION

Calliandra calothyrsus Meissn. (Leguminosae – Mimosoideae) is a small, thornless tree native to Central America and Mexico. Although rarely used within its native range, *C. calothyrsus* was introduced in 1936 to Java from Southern Guatemala as a possible substitute for *Leucaena leucocephala* (Verhoef, 1939). At several sites in Indonesia since 1939 *C. calothyrsus* has been evaluated in comparison with *C. tetragona* primarily for use as a shade plant or intercrop hedgerow (Satjaprada and Sukandi, 1981). The promising growth rate, disease resistance and drought tolerance of *C. calothyrsus* prompted further trials of the species in plantation in 1950 (Soerjono and Suhaendi 1981), although the first extensive reforestation project was not initiated until 1965. In 1974 village-based trial plots were set up to assess *C. calothyrsus* and other fast growing species for their suitability in the reforestation of eroded, poor quality land around villages (NAS, 1983). *C. calothyrsus* was ranked first among the species tested which resulted in co-operative planting by village chiefs and forest guards and later in spontaneous planting and seed distribution.

The species has received much favourable publicity

within Indonesia as a source of fuelwood (FPRI, 1977), pulp and paper (Kasmudjo, 1982), forage (Panjaitan, 1988), honey (Nadiar, 1979), shellac (Kasmudjo, 1978) and as an ornamental. Moreover, it is prized as a source of green manure (Baggio and Heuvelod, 1984) and as a means by which soil can be protected and rehabilitated (Hadipoeromo, 1979). By 1983 an estimated 170,000 hectares had been planted in Indonesia alone.

With an increasing international emphasis on the use of nitrogen fixing trees to support rural needs in developing countries (Westoby 1985), *C. calothyrsus* has been the subject of much attention. Although included in various lists such as 'economically important nitrogen fixing tree species' (Brewbaker and Styles, 1982), *C. calothyrsus* was not included for testing with a group of 25 Central American dry zone trees chosen by the Oxford Forestry Institute (OFI) (Hughes and Styles, 1984) since it is an insignificant shrub in its native habitat and local people disregard it (Hughes*, pers. comm.). Nevertheless, the spread of this

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species has continued and agroforestry trials have already been initiated in the following countries: Australia (Bray *et al.*, 1988); Bolivia (Lawrence*, pers. comm.); China (Zhou and Han, 1984); Colombia (Graf, 1987); Costa Rica (Baggio and Heuvelodp, 1984); Guinea (Catinot, 1984); Haiti (Ochoa†, pers. comm.); Hawaii (MacDicken and Brewbaker, 1983); India (Swaminath and Vadiraj, 1988); Indonesia (Kasmudjo, 1982); Kenya (Chavangi *et al.*, 1985); Nigeria (IITA, 1986); Papua New Guinea (Saroa, 1988); Philippines (Durst, 1987); Rwanda (Egger, 1986); Sri Lanka (Liyana *et al.*, 1988); Thailand (Chantrasiri, 1987); Taiwan (Hu *et al.*, 1983); Western Samoa (Kidd and Taogaga, 1984); Zimbabwe (Maasdorp and Gutteridge, 1986). Seed for such experimentation came primarily from Indonesia (based on the original 1936 Guatemalan acquisition of probable narrow genetic base), Oxford Forestry Institute (two Guatemalan, two Honduran and one Indonesian source), and CATIE (Guatemalan and Costa Rican sources; see Chang and Martinez, 1984).



Alley Cropping Trial at Maseno, Kenya (ICRAF)

The international interest in *C. calothyrsus* has been apparent from the extensive network of trials worldwide. To date, however, all such trials have, firstly, been based on limited seed sources, and secondly, been conducted in formats unrelated to one another so as to negate the possibility of comparing seed source performance in different ecological, geographical or climatic regions. It is self-evident that the users of multipurpose trees (MPT) will desire that ideotype of the tree which performs best in their environment, under their management regime, in those aspects for which they have chosen it. It is equally clear from past experimentation that the greatest, quickest and cheapest improvement in that performance can be achieved through the selection of the ideal species and seed source within that species (Zobel and Talbert, 1984). Despite this, no systematic genecological investigations to define the distribution of *C. calothyrsus*, or to sample its rangewide genetic variation, have yet been carried out. In response to these factors, and to an ever increasing demand for seed of *C. calothyrsus*, OFI proposed an Overseas Development Administration (ODA) project to explore the natural dis-

tribution of the species, to collect seed for assessment in standardized trial sites throughout the tropics and to test the ability of *C. calothyrsus* to tolerate acid soils. The objectives of the project are: to explore and map the natural distribution of the species; to explore and collect material of close relatives; to assemble provenance seed collections of the above; to design experiments to test the species potential; and to distribute seed for provenance trials.

TAXONOMY

Calliandra calothyrsus Meissner was first described in 1848, based on the collection of Kegel in Surinam (Kegel #1465). This collection was almost certainly based on introduced material (Breteler, 1989). Considerable past confusion has been generated by the use of two later synonyms of *C. calothyrsus*, *Calliandra confusa* Sprague & Riley and *Calliandra similis* Sprague & Riley, described simultaneously from Guatemala and Costa Rica respectively in 1923 (Sprague and Riley, 1923). Studies of the relevant herbarium material have led to the conclusion that the latter two names had to be placed in synonymy under *C. calothyrsus* (Hernandez, in press) as have field observations in the regions where collections of the two were made (Macqueen, unpublished).

The genus *Calliandra* is a member of the subfamily Mimosoideae (Elias, 1978) and is placed within the tribe Ingeae (Nielsen, 1978). The generic name *Calliandra* Benth has been conserved over *Anneslia* Salisbury, despite subsequent changes to the type (Bunting, 1967; Hernandez and Nicolson, 1986). Benth (1844, 1875) subdivided the genus into five sub-genera which were founded chiefly on foliage and inflorescence characters. More recently, Hernandez separated all the members of one subgroup (Laetevirentes), and two members of another (Macrophyllae) into a new genus, *Zapoteca* (Hernandez 1986, 1989).

The morphology of *C. calothyrsus* clearly places it in the sub-genus *Racemosae*. Within this group there are approximately ten closely related species which occur from the north of Mexico to Panama (and arguably one species, *C. parviflora*, in Brazil). The centre of diversity of the subgroup appears to be in southern and central Mexico and three species, *C. houstoniana* (Mill.) Standley, *C. grandiflora* (L'Her.) Benth. and *C. calothyrsus*, are the most widespread, well known and, possibly, phylogenetically central within the group (Hernandez, in press).

The bases for distinction between members of the group have been differences in: numbers of pinnae and leaflets; shape of leaflets; leaflet venation; state of pubescence; rachis length; peduncle length; and coloration of the staminal filaments (Benth, 1875; Britton and Rose, 1928; McVaugh, 1987; Standley and Steyermark, 1946; Hernandez, in press). Of these characters, pubescence is highly unreliable, pinnae and leaflet numbers are highly variable, and staminal filament coloration is also variable (Macqueen, unpublished). Field identifications are generally based on plant architecture, shape, coloration and waxiness of leaves and leaflets, and the form of the inflorescence and flowers.

C. calothyrsus is most closely allied to *C. acapulcensis* (Britton & Rose) Standley, the latter being separated geographically from the recognized populations of *C.*

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calothyrsus by the isthmus of Tehuantepec. Differences between the two are slight, *C. calothyrsus* having more robust peduncles and rachi (the rachis arguably longer and pinnae numbers greater, Hernandez, in press). Population-based studies are being carried out to examine the significance of these differences.

C. calothyrsus co-exists in certain areas with both *C. houstoniana* and *C. juzepczukii* Standley. Hernandez (in press) presents evidence from various herbarium specimens that hybridization between *C. houstoniana* and *C. calothyrsus* can occur. Recent field observations, based on inflorescence characteristics rather than unreliable pod pubescence, support this (Macqueen, unpublished). Field trials within the whole group are being conducted at Siguatepeque, Honduras to resolve questions on hybridization.

The complications of possible hybridization and taxonomic confusion create difficulties in seed collection. Clearly, it is necessary to avoid making collections from populations of possible hybrid origin if traits of a particular species are to be captured. Fortunately, most of such sites are in areas of artificial disturbance in which the species have entered as colonizers. Such sites are not natural in terms of ecology and potentially contain very narrow 'colonizer' genetic bases. If hybridization is a possibility, then it follows that it must be prevented in the species' natural distribution by geographical, ecological, seasonal, diurnal, or pollinator behavioural barriers. If this were not the case continued intercrossing would eventually eliminate species differences. Consequently, it might be considered advisable that collections be made only from sites epitomising a species' natural habitat (discussed for *C. calothyrsus* in the following section). This strategy would avoid both the collection of hybrid seed and collection of potentially narrow genetic resources.

An alternative viewpoint lies in the speculation that the very large differences between the provenances of other MPTs, such as those of *Gliricidia sepium* (Jacq.) Walp., are largely a reflection of the inclusion of narrow colonizer genetic bases (Attah-Krah, 1987). For *G. sepium* one provenance (Retalhuleu, 14/84) is proving to be superior at many sites in the tropics (Simons, in press), yet this population is suspected to be based on escapes from planted trees in nearby fields (Simons*, pers. comm.). While most collections should, therefore, come from the species' natural habitat it would be wise also to sample extensive secondary populations, taking care to state their genetic position by appropriate qualifying documentation. Some populations in bush fallows, or under cultivation, may have suffered considerable artificial selection which could also be capitalized on. These too could be sampled as secondary populations.

The elucidation of the taxonomic difficulties in the group is a priority in making accurate collections for future distribution. Close relatives of *C. calothyrsus*, such as *C. acapulcensis*, while displaying similar morphology may have vast differences in agroforestry potential. There appears to be no rational reason why *C. calothyrsus* was selected above some of the other close relative species. Therefore, it will prove instructive to test *C. acapulcensis* also in the forthcoming trials. Similarly, testing the performance of certain

hybrids might prove interesting. The ability to distinguish accurately between the species is important in providing predictable trial results.

HABIT AND HABITAT

C. calothyrsus can be classified as a small tree or a large, often multiple stemmed shrub, 1.5-10m tall. Bark colour varies from white to dark red-brown and is normally glabrous, but occasionally can be finely pubescent. Shoots may be ridged and coloured with anthocyanin. The canopy is dense with mid-green, alternate, petiolate, bipinnately compound leaves, 10-28cm long and without an upper waxy sheen. Pinnae vary in number from 5-20 pairs and possess 25-65 pairs of linear, acute or obtuse, 5-10mm leaflets. The 8-30cm floral racemes are held vertically above the foliage in an erect position with few or numerous flower heads. The raceme axis has 13-19 nodes at which an average of four umbelliform sub-inflorescences are clustered, each with an average of 6 floral buds. The buds may or may not be tinged with anthocyanin. The calyx is 1.5-2mm long, and the corolla 5-6mm long, both glabrous yellow-green with subacute lobes. The 30-45 staminal filaments project 48-65mm from the flower base where they are formed into a short tube. They are generally basally white and apically pink, though more rarely completely scarlet or apically white. The single pale pink or scarlet style projects 60-77mm above the flower base. The legume pods are 8-13cm long, 11-16mm wide, long attenuate to the base and sharply acute at the apex. They are thick margined and brown in coloration, glabrous or with fine white or red pubescence, and held in upright clusters at various stages of maturity.

C. calothyrsus is found in its natural habitat as a colonist of river margins and alluvial or shingle deposits. Initially, it may occur in dense stands, but is normally distributed at a low density over many kilometres. In later successional stages it is quickly outcompeted, and it seems only to exist in areas of recurrent disturbance. In areas of artificial disturbance such as roadside verges or rotational cultivation *C. calothyrsus* may invade as a temporary colonist.

DISTRIBUTION

Despite the wide use of *C. calothyrsus* in other parts of the tropics, the natural range of the species in the Central American isthmus is still well defined. This stems primarily from the fact that, in its native environment, *C. calothyrsus* is not perceived as having any practical value. Such is the disdain for this small tree that it has various nicknames such as 'camaron' (the shrimp) and 'gran hierba' (the big weed). Consequently, the species' native range is not obscured by human disturbance as is the case for *Gliricidia sepium* (Hughes, 1987). Nevertheless, exploring and mapping the range of this species is complicated by: (i) the taxonomic confusion, which renders precise definition of *C. calothyrsus* difficult. In particular, the extension of the range to the north and west of the Tehuantepec isthmus in Mexico is in doubt because of the confusion between *C. calothyrsus* and *C. acapulcensis*; (ii) the extensive forest clearance, which renders any precise delimitation of the original range hazardous. Fortunately, *C. calothyrsus* is almost entirely riverine in habitat. Most native sites are

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thus sufficiently inaccessible (or agriculturally unsuitable) to avoid destruction; (iii) destruction of parts of the range and colonization into newly disturbed areas. New areas of colonization suffer from the additional problem of containing an uncertain parentage of a possibly very narrow genetic base. Once again, it is fortunate that for *C. calothyrsus* such situations are very rare since the species is a poor competitor in later successional stages. Nevertheless, traits such as early flowering (after one year in some cases), and early seed set, do present the possibility of expansion into areas which are periodically disturbed. This has been documented for sites such as roadside populations or rotational cultivation; (iv) areas of deliberate introduction such as the site at Hojancha, Costa Rica (Campos, 1986) and San Juan de Flores (Kowal*, pers. comm.). As has been stated earlier, however, such sites of deliberate introduction are extremely rare in Central America due to the low perception of the species' usefulness.

In spite of the above restrictions, it can be seen that it is indeed possible to delineate accurately the natural distribution of *C. calothyrsus*. Meticulous exploration and the use of Herbarium data from Mexico City, Mexico (MEXU); Forest Herbarium Oxford, UK (FHO); Kew Botanic Gardens, UK (K); British Museum, UK (BM); Missouri Botanic Garden, USA (MO); New York, USA (NY); Chicago, USA (F); Tegucigalpa, Honduras (EAP); and San Jose, Costa Rica (CR); has allowed the construction of a distribution map (Figure. 1) which follows those of Hernandez (in press) and Macqueen (in press). From this map it is clear that *C. calothyrsus* extends from 19°20'N to 9°20'N and 96°40'W to 79°50'W. The most northerly population at Veracruz is unusual in that it bridges the otherwise restrictive barrier of the Tehuantepec isthmus. The high morphological variation observed over the species wide distribution suggests that significant variation between provenances will be found and justifies their collection and separation during testing.

ALTITUDE

In addition to the wide latitudinal variation and longitudinal variation, *C. calothyrsus* also tolerates a broad variety of edaphic and climatic environments. It inhabits an altitudinal range from sea level to an upper limit of 1860m (see Table 1). In terms of temperature within its native range *C. calothyrsus* occupies areas with an annual mean of (20) 22-28°C with a mean maximum temperature of 24-30°C and a mean minimum temperature of 18-24°C (Wiersum, 1989). The areas in which it grows are frost free.

SOILS

The species exists on a wide range of soils throughout Central America. The bulk of the herbarium acquisitions

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TABLE 1. Percentage of *C. calothyrsus* herbarium specimens within chosen altitude bands

Altitude (m)	1-200	201-400	401-600	601-800	801-1000	1001-1200	1201-1400	1401-1600	1601-1800
% of specimens	13.7	11.2	8.7	14.8	18.9	16.3	9.2	4.6	2.6

come from areas of three principal soil types: (i) Cambisols (a widespread, reasonably fertile group of soils in the early stages of soil development with an ochric A horizon and a cambic B horizon) are found under 37.4% of recorded specimens. These soils tend to have slightly acid to mildly alkaline pH values; (ii) Acrisols (extremely weathered, leached, and relatively infertile soils of old landscapes with an argillic B horizon and base saturation less than 50%) are found under 19.6% of all recorded specimens. The soils are often mildly acidic; (iii) Nitisols (deep, clayey, red, fertile soils with an argillic B horizon) occur under 18.8% of specimens. They have variable pH values.

Other soil types on which recorded specimens occur include volcanically formed andosols (9%), luvisols with high base saturation (8%), shallow calcareous rendzinas with pH close to neutrality (3.6%), recent, fertile, alluvial deposit fluvisols (2.7%), and wet mineral gleysols (0.9%). Such figures, based on examination of map locations, probably underestimate the number of specimens on fluvisols since observations in the field have demonstrated that almost all natural populations occur by rivers. Many of the soils on which *C. calothyrsus* occurs have relatively high pH values (e.g. Georgesville, Belize). Collection from populations with acid tolerance will be important for testing in tropical areas facing acidity related problems with other MPTs such as *Leucaena leucocephala* (Tilo *et al.* 1981; Blair *et al.*, 1988).

CLIMATE

The range of climates occupied by *C. calothyrsus* is wide, but there is a tendency to find field and herbarium specimens in areas with 2-4 months dry season (less than 50mm rainfall (Table 2)), and 1000-4000mm rainfall (Table 3).

TABLE 2. Percentage of *C. calothyrsus* herbarium specimen records from geographical zones with known dry season lengths

Dry season (months)	0-2	2-4	4-6	>6
% of specimens	15%	53%	20%	12%

TABLE 3. Percentage of *C. calothyrsus* herbarium specimen records from geographical zones with known annual rainfall

Ann. rainfall (mm)	<1000	1-2000	2-3000	3-4000	>4000
% of specimens	8.6%	37.5%	21.0%	31.3%	1.6%

VEGETATION

The majority (60.2%) of the recorded specimens of *C. calothyrsus* are found in what is classified by Holdridge as 'wet' and 'very wet premontane forest' (CATIE, 1986).

C. calothyrsus occupies the very early stages of succession, often being replaced by other colonist species such as

Acacia farnesiana, *Mimosa pigra*, *Leucaena shannonii*, *L. leucocephala*, and *Trema micrantha*. Several other species commonly co-occur with *C. calothyrsus*, *Acacia angustissima* being the most notable. These two species occupy almost identical habitats in Costa Rica, Nicaragua, and Honduras, and the latter is also an excellent MPT used for fuelwood, fodder, and green manure on similar soils to that of *C. calothyrsus*. Additional co-occurring trees are *Mimosa alba*, *M. pigra*, *Acacia farnesiana*, *A. pennatula*, *Lysiloma divaricata*, *Leucaena shannonii*, *L. leucocephala*, and non-legumes such as *Trema micrantha*, *Cecropia* sp. and *Alvaradoa amorphoides*.

In any seed collection programme it is essential to encompass as much of the geographic, altitudinal, edaphic, climatic, and ecological variation as possible (Hughes, 1987). The underlying presumption is that areas which differ in any of the above factors will subject populations of a species to different selection pressures over time. It must, therefore, be considered likely that such different areas will contain populations with differing genetic composition, provided that there is no gene flow between them. It is consequently a fundamental prerequisite of any seed collection strategy that ample exploration of the range (and variation within the range) be completed prior to the initiation of collection so as to outline areas of potentially interesting adaptation. In many instances time constraints imposed by recipients of seed, or more often by the funding bodies of seed collection, curtail adequate exploration and reduce the chance of interesting adaptive complexes being picked up. The current project endeavours to postpone seed dispatch until seed collections from the entire range have been completed.

PHENOLOGY

Calliandra calothyrsus exhibits the typical syndrome of seasonally dry forest species, losing its leaves during the dry season and flushing with the onset of the rain, though in its particular case the flowering and fruiting process occurs just prior to leaf fall.

The actual dates of flowering and fruiting are extremely variable both within and between populations. Precocious flower opening begins as early as July throughout the native range. Peak flowering occurs between September and December in more northerly latitudes, and between late July and November in Nicaragua, lowland Costa Rica and Panama. The end of the flowering season is late March, although there remains a residual low level of flowering throughout the year in areas of high rainfall and reduced dry season. There appear to be slight correlations between the following: long dry season or low rainfall and early flowering; low altitude and early flowering; and low latitude and early flowering. Despite such general trends, however, for the purposes of seed collection, flower and fruit ripening are sufficiently irregular as to demand individual pre-emptive observation at each site. Furthermore, within-population irregularity is such that repeated visits to any one site are needed to collect seed from all the desired trees.

Within a single tree, the period of flowering may last as long three months, though it is usually somewhat shorter. Long flowering racemes open basipetally, and in *C. calothyrsus* during a single night 4-26 (mean of 11) flowers

open simultaneously to give an almost circular floral display. The sequential nature of flowering in *C. calothyrsus*, and the small numbers of flowers open at any one time, is most probably an evolutionary strategy based on a number of component selective forces: firstly, it forces vector movement between trees without which they could not obtain sufficient nutrition thus stimulating outcrossing; secondly, it maintains the opportunity for pollination events over several months in the case of irregular pollinators or irregular climatic conditions suitable for pollination; thirdly, it allows a long sequence of fruit maturation and seed dispersal maximizing the chances of some seed escaping bruchid predators and ripening in favourable climatic conditions; lastly, it offers the option of floral abortion in some of the fruit maturation period so as to conserve vital reserves in times of climatic irregularity.

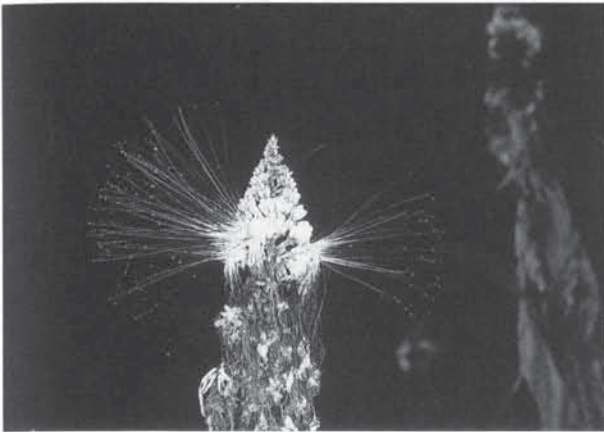
The time between flowering and fruit maturity ranges from 55 to 90 days and is dependant on environmental conditions during the ripening phase thus making the exact timing of seed collection unpredictable. Within any one tree, fruit ripening is sequential following the basipetal flowering pattern. At any one time, it is common for only a small proportion of the fruit to be ripe. Nevertheless, there is a tendency for relatively concise areas of the raceme rachis to develop fruit. Boland and Owour (in press) suggest that this may either be due to the episodic nature of good pollination, or to an abortion strategy of the plant to maximize seed produced for resources available. A period of 3-7 days elapses during which the seed is sufficiently ripe to be collected, and before the tension in the pod due to desiccation causes explosive apical dehiscence. No studies have been carried out on the viability of seed picked in an unripe state and artificially ripened. Fruit ripening begins in November, with the peak almost entirely between January and March in most populations.

Several instances of unusually low seed production have been observed. Zygote abortion was found throughout one population in Cofradia, Cortés, Honduras, in 1991 despite ample pod production. Abnormally high rainfall in December 1990 and January 1991 may have prevented pod drying, allowing an observed fungal infestation to proliferate perhaps causing zygote abortion. *Calliandra houstoniana*, however, in the close vicinity did show normal pod development and seed production. In another population at San Francisco de la Paz, Olancho, Honduras, no pod production occurred during 1991, perhaps due to similar climatic irregularity. In the non-native tropical plantations of *C. calothyrsus* in Africa poor seed set has also been recorded (Boland and Owour, in press).

The combined effects of: ripening failure; variable ripening time across, and within, sites; the small quantities of seed per tree; the small numbers of trees in certain populations; rapid ripening; and explosive fruit dehiscence impose difficulties on the seed collector. It is difficult to obtain good collections of *C. calothyrsus* and the quantities of seed tend to be limited in comparison with other MPT species such as *Leucaena* and *Gliricidia*.

BREEDING SYSTEMS

An understanding of the breeding systems of MPTs is essential to the process of devising a rational collection



Night Flowering of *Calliandra calothyrsus*

strategy. The ideal sampling unit of such a strategy is a panmictic group of individuals among which the probability of a mating event between any two individuals is equal (i.e. a population). Individuals within a population will exhibit similarities of genetic constitution owing to gene flow between them. Gene flow is limited, firstly, by the range and behaviour of the pollinating organism or vector, and secondly, by the distance of seed dispersal. Each of these two aspects is examined below for *C. calothyrsus*.

Pollination

The inflorescence of *C. calothyrsus* consists of a conical raceme held vertically above the foliage. Of the small numbers of flowers open on any one night a small portion appeared to be functionally male following the common Mimosoid legume trait of andromonoecy (Arroyo, 1981). Both the functionally male flowers, and the much more abundant hermaphrodite flowers, were seen to produce nectar and pollen, and the function of the former may be to increase the pollen to ovule ratio so as to ensure pollination.

Floral opening throughout the natural distribution occurs between 3-5pm. The staminal filaments and single style are fully erect by 7pm. The lifecycle of one flower is a single night, the staminal filaments wilting by 12.30pm the following day. The flowers are slightly protandrous and this, coupled with the observed 10mm differences in style and stamen lengths, suggests outcrossing (Boland and Owour, in press). The overall brush type floral syndrome suggests adaptation to a number of non-specialist pollinators (Faegri and Van der Pijl, 1979). Nectar production starts almost simultaneously with flower bud burst (approximately 4pm) and reaches a peak at the time of full filament extension being exuded into a droplet at the base of the staminal filaments. The quantity of nectar produced in one night is approximately 62.9µl (±12.9µl) and it has a sugar concentration of 13.1% (Hernandez, in press). The production of nectar does not stop until early the next morning (6-7am), thus allowing repeated visits by pollinators during the night.

Observations from Nicaragua, Honduras, and Guatemala support those of Hernandez in Mexico in allowing the delimitation of illegitimate and legitimate visitors.

Of the illegitimate visitors, prior to nightfall in Central America, honey bees (*Apis mellifera*) were seen to rob the emerging nectar while positioned on the side of the corolla tube clearly remaining out of contact with the anthers. In the morning after anthesis, humming birds were also seen to extract any remaining nectar with little contact to the wilting anthers. During 1988 and 1990 in Mexico, prior to nightfall, Hernandez recorded two moths (*Palpita flegia* and *Letis vultura*) and honey bees (*A. mellifera*) acting as robbers positioned to the side of the floral cup.

Of the legitimate visitors, the principal vectors in Nicaragua and Guatemala appeared to be bats (*Glossophaga soricina*, Dobat and Peikert-Holle, 1985). Bats visit regularly every 20 minutes appearing incautious of the red staminal brush which may be undetected by sight and radar. They alight forcibly on the cream coloured corollas of the raceme removing nectar with their tongues, their underneath becoming smeared by pollen. Numerous small moths were also observed as a component of more localized pollen dispersal. In Mexico Hernandez (in press) observed both bats and the sphingid moths (*Eumorpha vitis* and *Erimyis ello*) commencing visitation at 7pm. A more comprehensive study of the species of bat and sphingid moth within the pollination fauna is in progress.

At the pollination event one polyad has the potential to fertilize almost all of the average 8.7 ovules per ovary (Hernandez, in press). A pollen/ovule ratio of approximately 320 will be increased by the presence of andromonoecy and is indicative of non-specific pollination of the type described above.

Points of importance to be drawn from an analysis of the species pollination are the following: (i) The trees are almost certainly outcrossing and will therefore have sizeable populations within which gene flow occurs; (ii) The pollinators are a mixture of short and long distance vectors making population size relatively large. In particular the river corridors along which *C. calothyrsus* grows will provide potential gene flow over kilometres in a linear format which sampling should reflect; (iii) When sampling from a single tree, pods from all positions in the crown should be selected so as to avoid high genetic similarity of progeny due to pollination by a single vector.

Seed Dispersal

The dispersal mechanism of *C. calothyrsus* seed is that of explosive apical dehiscence generated by drying tensions in the pod walls. Seed is released from the funicle during dehiscence with a spinning motion akin to that of a discus and the mechanism has a range of 0-10m. Water may then take the seed downstream for a further unspecified distance. The potential for relatively long distance dispersal is again indicative of a large population size. As before, however, the exact extent of a genetic population is difficult to define.

The relatively long distance pollination and seed dispersal potential of *C. calothyrsus* suggests that populations (in which gene flow maintains genetic similarity) may extend over many kilometres. In order to maintain a broad genetic base for future breeding populations Namkoong *et al.* (1980) suggest that selected populations should contain a minimum of 50 trees. Ideally, trees from which seed is

collected should be sufficiently far apart as to avoid being directly related to one another. A distance of 100m has been suggested arbitrarily by Callaham (1964). The long distance gene flow in *C. calothyrsus* indicates that individuals may be directly related to one another over greater than 100m. Sampled populations should therefore consist of 50 individuals spaced at greater than 100m apart. The confines of real observed populations has, however, imposed compromise on such theoretical ideals. Where individual tree collections have been made the guidelines have been rigidly followed, but bulk collection has had to involve all available individuals so as to achieve the required quantities of seed. All individuals from which seed is collected are chosen at random due to the inability to differentiate between genetically and environmentally caused variation in the field.

BASIS FOR A GENETIC IMPROVEMENT STRATEGY

The genetic improvement of *C. calothyrsus* is in its initial stages. The high morphological variation observed and wide ecological amplitude of the species suggest significant variation will be found between different geographic areas. It is generally acknowledged that the geographical area from which genetic material is collected has great significance with respect to the subsequent performance in comparative trials (Turnbull, 1983). Striking examples of differences in 'provenance' performance are frequent in the literature (FAO, 1979; Atta-Krah, 1987) and are acknowledged to be highly repeatable (Boyle and Yeh, 1987). In species with broad natural distributions over a rich variety of environments the differences are commonly 5-15% (Willan, 1988) but may exceed 200% (Simons, in press). When compared to the expected 10-30% in subsequent tree breeding programmes (Carlisle and Teich, 1978) the importance of the initial sampling strategy becomes apparent. A dilemma consequently arises in the species selection phase in that it is not worth collecting provenances unless a species is worthwhile, yet often worthwhile species cannot be identified unless all the provenance variation is included in the assessment. Given that *C. calothyrsus* is highly regarded, however, it is necessary to define the location and extent of the 'provenances' to be used. The confusion surrounding the definition of 'provenance' has been amply discussed (Jones and Burley, 1973; Turnbull and Griffin, 1986) with the latter authors concluding that 'it is incumbent upon the user to provide the appropriate definition'. Consequently, for *C. calothyrsus* the following definition has been adopted:

A clearly delimited geographical area in which the species grows and is native, which contains, through similarity of past and present natural selection pressures and gene flow within its boundaries, individuals more broadly genetically and phenotypically similar to each other, than to individuals in neighbouring areas.

PRACTICAL STAGES IN PROVENANCE DELIMITATION FOR *C. CALOTHYRSUS*

Having elected the above provenance concept as the rational basic unit with which we ought to sample the genetic

variation of *C. calothyrsus* over its range, it would be profitable to discuss the practical steps needed for provenance elucidation. Such steps may be used as a framework for the pragmatic delimitation of provenance in other species.

1. An accurate map of the distribution of the species should be drawn as far as can be gleaned from herbarium records and field exploration. (Previous literature is often inaccurate and incomplete for the precise definition required). Areas of taxonomic confusion should be clearly marked or omitted. This distribution map will form the basic scaffolding from which accurate 'available provenances' can be delimited (see Fig. 1). Units within which gene flow is a distinct possibility should be marked (for example populations spread along a single river valley).

2. Key topographic features should be added to a map of the geographic area used in the distribution map. In particular, all features which are likely to impede or prevent gene flow (such as mountain ranges above 1500m for *C. calothyrsus*) should be included. These additions will identify probable units between which there will be no gene flow. It is important to emphasize, however, that there is no immediate reason why gene flow within the unit may not also be impeded by distance or ecological factors (see Fig. 2).

3. In addition to geographical features which may act as confines to a subsection of the species range, it must also be remembered that for collecting purposes, political barriers also act as boundaries to possible collecting. These boundaries should be drawn on the maps and may divide acceptable single biological provenance units into two political provenance halves. Where rivers form borders in the range of *C. calothyrsus* access to one side of a population may be denied. Major rivers have also been included in Figure 3.

4. Soils are likely to play a major role as selective forces moulding the genetic constitution of populations over an evolutionary timescale. For *C. calothyrsus* the populations adapted to acidic soils will be particularly interesting in trials at planting sites with high acidity. A soil map should be drawn which will allow the subdivision of geographical units should a single unit contain two markedly different soil types. The soil map shown in Figure 4 was based on the FAO UNESCO world soil map series.

5. Ecological pressures on survival are affected by the prevailing vegetation type and individual species with which the chosen species is competing. While it is impossible to map precise species competitors, a vegetation map based on climate can be drawn and may serve to further subdivide geographical units within which there are grave vegetational dichotomies. While several climatic classifications are available, including those of Koppen, Thornthwaite, Gaussen, and Holdridge (Robbins and Hughes, 1983), the latter has been chosen for use in this particular study (Fig. 5).

6. Rainfall within provenance regions also has an important impact as a factor controlling plant growth and development. Where areas with marked differences in total rainfall occur adjacent to one another it is likely that the existing populations will display some degree of adaptation to their particular rainfall regime. Consequently, it would seem prudent to use annual precipitation to further subdivide geographical areas of otherwise similar status. Figure 6 depicts the annual rainfall pattern for Central America.

7. In addition to the impact of the total annual rainfall,

the seasonal distribution of rainfall is also an important force acting on plant survival. Areas with longer dry seasons will contain plants that are more adapted to that particular climatic regime (Fig. 7). Therefore, length of dry season can also be used to subdivide areas of otherwise similar status.

8. Having delineated areas covering sources of genetic material it should be decided which of these areas will furnish sufficient seed to meet the current demand. Areas with the required sufficiency are the current available provenances. Provenances with only a few individuals should either be eliminated from trials or used to establish seed production orchards from which seed demands can be met. The narrow genetic base of such orchards should generate caution and is only advisable in proven exceptional provenances.

9. It is important in the acquisition of genetic material and its incorporation in trials that material is kept to a manageable quantity. This prevents unnecessary expense and minimises technical confusion in the fragile network of world provenance trials. In view of this, the original total number of available provenances should be reduced to an arbitrary acceptable number between 10-20. These provenances should cover the entire geographical range of the species and as much of the edaphic, biotic, and climatic range as possible. Such provenances will then form the core of subsequent research into improvement. A map of the research provenances for *Calliandra calothyrsus* is included (fig. 8) and a brief description of the 14 chosen for initial trials is given in Appendix A.

DISCUSSION

Any single MPT introduced as an exotic to solve problems of soil erosion, soil impoverishment, shortages of fodder, fuelwood, food or construction material faces the risk of failure. Failure may result from incompatibility with the soil or climate, the impact of a pest or disease, or rejection by the local populace due to the new plant's ecological, social and political implications (for example with regard to such factors as weediness or land tenure). The introduction of MPTs over large areas, as a single option, in an extremely short time scale is likely to amplify the risk considerably. *C. calothyrsus* is a fast growing species with potential for soil stabilization and improvement, and the production of fuelwood, pulp and paper, fodder, honey and lac. While it does exhibit astonishing growth in some farming systems (FPRI, 1977) and is widely regarded as an excellent small dimension fuelwood, it is neither the only fuelwood species, nor the most suitable for growth in all environments (Gutteridge and Akkasaeng, 1985). With regard to fodder, reports of poor digestibility have been widely published (Baggio and Hueveldop, 1984; Blair *et al.*, 1988; Panjaitan, 1988). The value of *C. calothyrsus* as a source of nitrogen-rich manure has also been called into question (Gutteridge, 1990). While major pests on the scale of the *Leucaena* psyllid infestation have not been documented, several pests may cause problems. Among these a stemborer, similar to *Hypsipyla robusta* which attacks Mahogany, has devastated 40% of a population in the Philippines (Luego, 1989). In Kenya, a coleopteran, *Pachnoda ephippiata*, feeds on the flowers, fruits and foliage of *C. calothyrsus* causing floral

abortion and the lack of seed production (Kaudia, 1990). Within its native range bruchid seed predators and various defoliators have also been recorded though not formally identified.

In the light of the above points, attempts to introduce and improve *C. calothyrsus* should proceed only after several important prerequisites. These include: (i) a clear analysis of the complex problems in each individual ecosystem where the plant is to be used; (ii) an assessment of locally native species which might provide the desired solutions (in view of the advantages of local species listed in Von Maydell, 1986); (iii) detailed genecological studies of the species in its natural range to provide information necessary to evaluate the likely outcome of an introduction; (iv) the inclusion of several alternative species, such as *Acacia angustissima*, so as to minimize the risks associated with any one component.

Only after these steps have been taken is the testing of provenances a logical strategy. It is important in that it facilitates the introduction of the provenances suited to a suite of local environmental factors and of proven high performance within them. It fosters a systematic approach to species introduction which minimizes risk to potential users. It also acts as a firm foundation for future breeding work should that be appropriate.

The acquisition of germplasm, currently progressing under ODA research project R. 4485, will make available different germplasm sources for testing in a range of exotic environments. International cooperation at trial sites throughout the tropics will ensure that the most suitable source of germplasm is introduced at each region. In addition the systematic and comprehensive nature of the initial collections will provide a firm base for future breeding and selection. Early and abundant production of seed, ease of vegetative reproduction, and short rotation lengths for production assessment will enable rapid selection and improvement. In the context of *C. calothyrsus*, therefore, it is clear that improvement is possible in the near future, but that careful consideration needs to be paid both to the uses for which it is suitable and to the need for diversity within agricultural systems.

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APPENDIX A. *Table of provenances for Calliandra calothyrsus.*

Provenance	State	Country	Grid ref.	Altitude
1. Agua Azul	Chiapas	Mexico	18°00' N 91°48' W	200m
Along the waterfalls of the Rio Azul, in disturbed forest 60km north of Palenque.				
2. Sumidero	Chiapas	Mexico	16°50' N 93°10' W	1300m
At the canyon of the Sumidero National Park, in deciduous forest at km 14 above Tuxtla.				
3. Santa Cruz	Toledo	Belize	16°16' N 89°00' W	500m
On the road from San Antonio to Santa Cruz on roadside verges and field boundaries.				
4. Flores	Peten	Guatemala	16°55' N 89°52' W	220m
On the flat plain around the west of Lago Peten Itzan on the road from San Benito to San Antonio.				
5. Coban	Alta Verapaz	Guatemala	15°28' N 90°15' W	1300m
To the west of Coban on the deviation to Guatemala City on the hill facing the military base.				
6. Santa Maria	Quezaltenango	Guatemala	14°45' N 91°32' W	1500m
In secondary vegetation 23km from Retaluleu on the road to Quezaltenango, just before Santa Maria.				
7. La Ceiba	Atlantida	Honduras	15°43' N 86°50' W	80m
On the banks of the Rio Cangrejal and Rio Danto, either side of La Ceiba, into the Pico Bonito National Park.				
8. Meambar	Comayagua	Honduras	14°48' N 87°46' W	450m
At km 10 to the north of Meambar on the road to Los Globos, in secondary regrowth of a bush fallow system.				
9. San Ramon	Matagalpa	Nicaragua	12°54' N 85°48' W	850m
On the road to Yucul, 10km to the south of San Ramon, colonizing road verges and hillside fields.				
10. La Puerta	Chontales	Nicaragua	12°12' N 85°17' W	600m
On the riverbanks of a stream 12km from Juigalpa on the road past La Puerta to La Pradera.				
11. Fortuna	Alajuela	Costa Rica	10°30' N 84°49' W	85m
On the road to Palma, 2km from Fortuna along moist ditches and adjacent fields.				
12. Salitres	San Jose	Costa Rica	9°53' N 84°11' W	900m
Thickets on steep roadside banks 1.5km to the north west of Salitres, 22km north east of Puriscal.				
13. San Isidro	San Jose	Costa Rica	9°25' N 83°42' W	1000m
Above Rivas and San Isidro by the Rio Talari and larger Rio General towards the village of Canaan.				
14. Rio Maje	Panama	Panama	9°04' N 78°44' W	45m
On the banks of the Rio Maje from the waterfalls near Bayano Lake to a farm 3.5km upstream.				

