PLANT SUCCESSION ON DEGRADED LAND IN SINGAPORE

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CORLETT, R.T. 1991. Plant succession on degraded land in Singapore. The course of secondary succession on land degraded by prolonged cultivation is described. On the most degraded sites, the pioneer vascular flora consists of only 13 non-parasitic species and is independent of the proximity of forest seed sources. This pioneer community is replaced after 20 to 50 *y* by a secondary forest with 35 to 64 species > 2 *cm* dbh in a 0.1 *ha* plot (more species-rich than any extra-tropical forest), dominated by the families Guttiferae, Myrtaceae, Elaeocarpaceae, and Lauraceae. After 50 to 100 *y* this forest still contains no Dipterocarpaceae or other poorly-dispersed members of the local rain forest flora. This study suggests that plant succession on degraded land is initially controlled by edaphic factors - nutrient deficiency or periodic water stress - and later by seed dispersal.

Key words: Succession - degraded land - pioneers - rain forest - Singapore - southeast Asia

Introduction

Soils degraded by intensive agriculture cover vast areas of the humid tropics while seed sources of primary forest trees have become increasingly restricted. Succession in such areas will clearly be very different from the succession in natural forest gaps and smaller man-made clearings. Understanding such successions seems likely to be an essential prerequisite for the restoration of forest on degraded land.

The existence of a distinct successional sequence on severely degraded sites in the Malay Peninsula has been recognised previously (Symington 1933, 1943, Wyatt-Smith 1963, 1964) but only fragmentary studies have been made before now. In Singapore, Holttum (1954) described the pioneer community on a degraded site, while Burkill (1919), Gilliland (1958) and Gilliland and Jabil (1958) described the composition of older (and rather atypical) secondary forests. In Malaysia, Kochummen and Ng (1977) described the succession after farming on a partly degraded site at Kepong. In this paper, I describe the course of secondary succession on severely degraded land in Singapore and attempt to derive some general principles which can be applied in similar situations elsewhere.

The Republic of Singapore lies just north of the equator at the southern tip of the Malay Peninsula, from which it is separated by a shallow strait, 0.6 *km* wide at the narrowest point. It has a typical equatorial climate with a mean annual rainfall of 2375 *mm* and no month with a mean rainfall of less than 100 *mm.* When the modern settlement was founded in 1819, the island was entirely forested except for coastal cliffs and beaches and a small inhabited area at the mouth of the Singapore River (Corlett 1991a). By 1883, more than 90% of this forest had been cleared for agriculture and half the cleared area abandoned to lalang (*Imperata cylindrica*) (Cantley 1884). From the late nineteenth century onwards, however, an increasing area in the centre of the island was protected as a water catchment, mostly in the period 1899 to 1906. Today this protected area totals 2000 *ha* and is largely covered in secondary forests of various ages (Wee 1964). Small patches of primary forest, disturbed to varying extents, occur throughout the water catchment, but the largest and least disturbed area is in the adjacent 70 *ha* Bukit Timah Nature Reserve (Corlett 1988, 1990, 1991b). Scattered around the main island, and on several offshore islands, are areas of younger secondary forest and scrub, mostly less than forty years old.

As far as can be determined, all secondary forest in Singapore is on land which was cultivated repeatedly over a period of decades. The major nineteenth century crops were gambier (*Uncaria gambir*) and pepper, although coconuts, pineapple, tapioca and other crops covered significant areas (Corlett 1991a). Cultivation continued until the soil was exhausted. In the first half of this century, rubber and pineapple were the major crops. Plantation agriculture declined rapidly in the 1950s for economic reasons.

Methods

In the absence of long term observations of a single site, the course of succession had to be inferred from the comparison of stands of different ages. Moreover, the

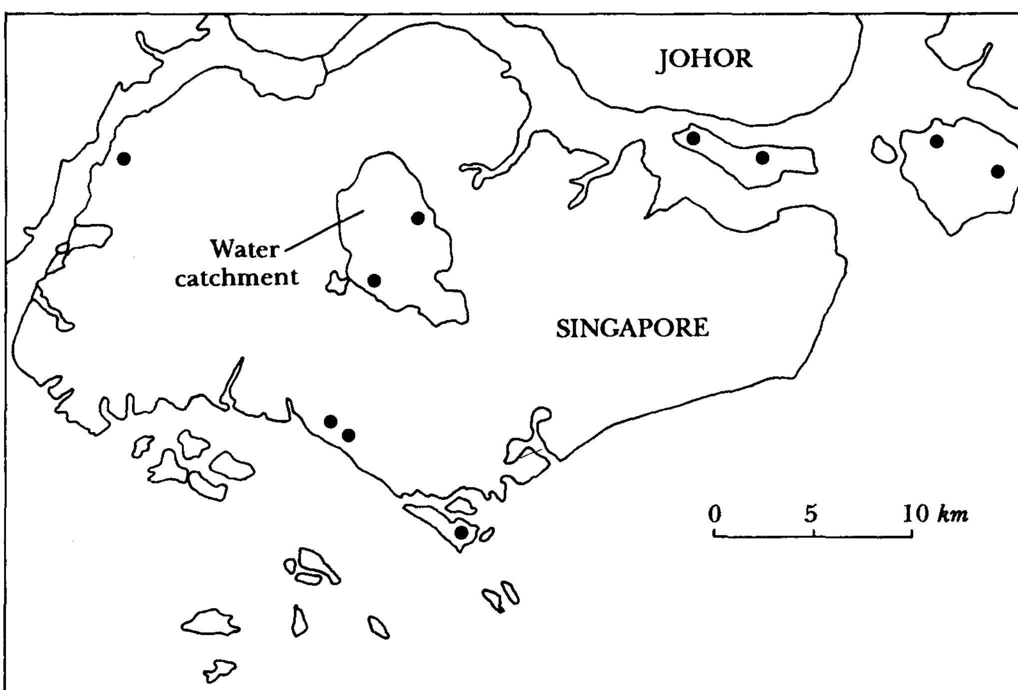

Figure 1. Map of Singapore showing sites (indicated by ●) where the early stages of secondary succession on degraded land were studied

relative ages of some of the secondary forest stands have had to be inferred, in part, from the vegetation present, although historical evidence of varying precision was available in most cases. This procedure is unsatisfactory but unavoidable.

The early stages of woody succession on severely degraded land can be observed at many sites in Singapore (Figure 1). Because of the relative uniformity, species-poverty and impenetrability of this stage, only qualitative observations were made. The older, taller secondary forests in the centre of the island are, in contrast, more variable, much more species-rich and relatively easily entered. Fifteen 50 × 20 *m* plots were studied in this area at sites chosen for the absence of recent disturbance, physiognomic uniformity, and geographical spread (Figure 2). The diameters of all plants more than 2 *cm* dbh were measured and, as far as possible, all measured plants were identified. Basal area was used as a measure of the abundance of each species in each plot. Other plant species present were listed and notes taken on the vertical structure of the forest. Plant names follow Keng (1990).

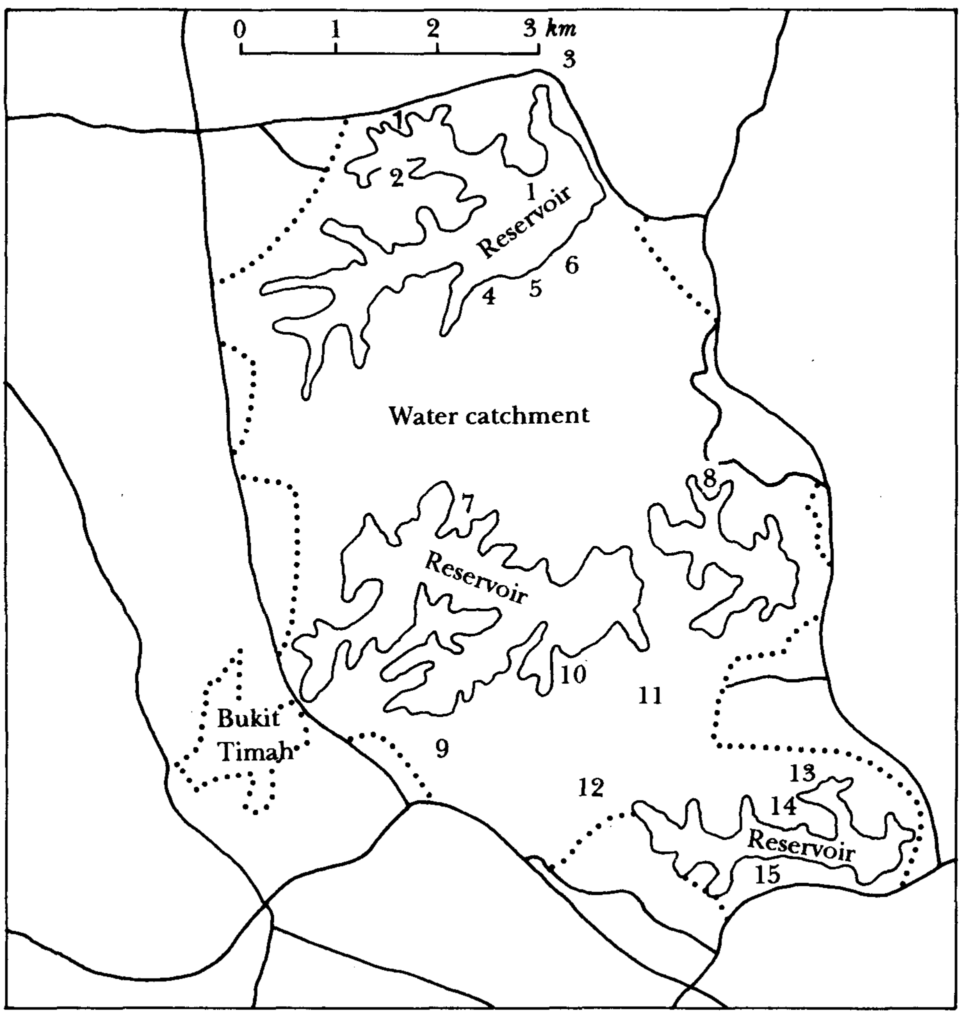

Figure 2. Map of the central water catchment showing locations (indicated by numerals) of the 15 tall secondary forest plots studied

The species abundance data were analysed by detrended correspondence analysis (DCA) (Hill 1979, Hill & Gauch 1980) and the sites plotted on the first two axes (Figure 3). Species occurring in less than three sites were excluded and the range of abundance values of the remaining 138 species compressed by a logarithmic transformation, following standard practice (Gauch 1982). Ordinations with untransformed data were more difficult to interpret ecologically. Standardisation by sample and species total is implicit in DCA.

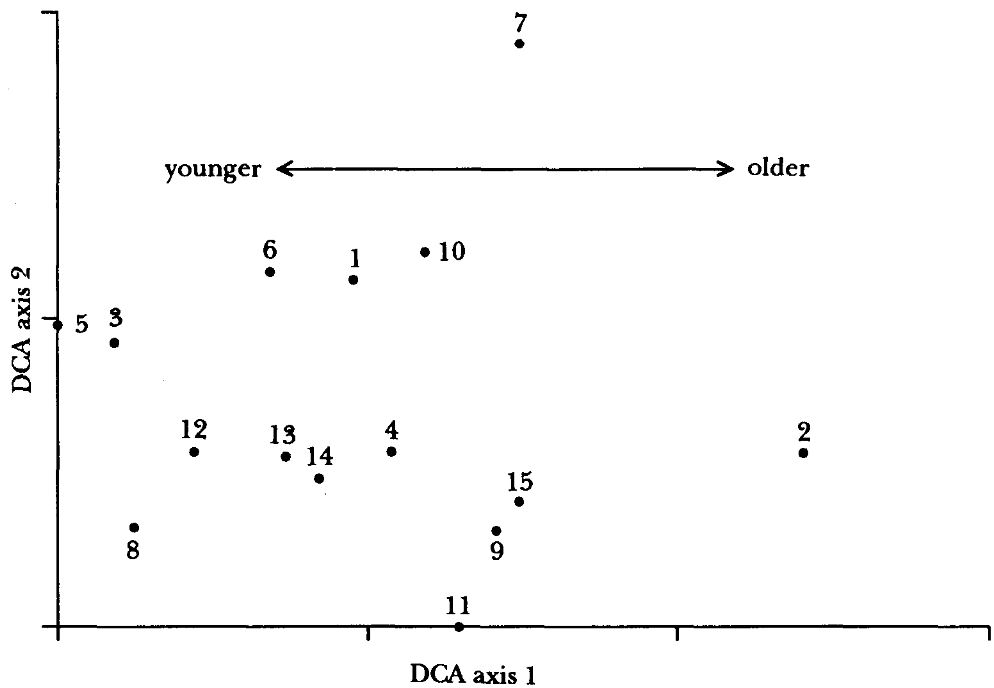

Figure 3. First 2 axes of DCA ordination of 15 tall secondary forest plots; the first axis is apparently related to successional development

Results

It is convenient to divide the succession on degraded land into four stages. In Stage 1, the abandoned site is invaded by herbaceous and woody pioneers and the woody canopy is still incomplete. In Stage 2, the woody pioneers form a closed canopy, eventually eliminating the herbaceous species and the lower growing shrubs. Stage 3 is a transition period, during which the woody pioneers are superseded by a different set of species which form the taller (15 - 24 *m*) secondary forest of Stage 4 - hereafter referred to as Tall Secondary Forest. Stages 1 and 2 are widespread in Singapore and can be found on soils derived from a variety of parent materials. Stages 3 and 4 are, for historical reasons, confined to the protected central water catchment area, which is underlain by granite, with recent alluvium in the deeper valleys.

Stage 1

The composition, structure and persistance of this stage is variable but a core group of species are found at all sites. The influence of soil parent material is not obvious: very similar pioneer communities are found on soils derived from granite, conglomerate, sandstone and quartzite. Moreover, there is no consistent difference between sites adjacent to tall secondary forest or within 150 *m* of primary rain forest, and sites more than 10 *km* from the nearest forest.

The simplest community is found on eroded slopes with shallow soil and, in places, exposed bedrock. Here the pioneers consist of one grass species, *Eriachne pallescens*, the sedge, *Gahnia tristis*, the scrambling ferns, *Dicranopteris linearis* and *D. curranii*, *Lycopodium cernuum* and six tree and shrub species, *Adinandra dumosa*, *Dillenia suffruticosa*, *Fagraea fragrans*, *Myrica esculenta*, *Ploiarium alternifolium*, *Rhodamnia cinerea* and *Rhodomyrtus tomentosa*. *Adinandra* is usually most abundant. The insectivorous *Nepenthes gracilis* and *N. rafflesiana* are common climbers and species of *Dendrophthoe*, *Macrosolen* and *Viscum* occur as parasites, largely on the *Adinandra*. Other species are very sparse and probably confined to favourable microsites. Initial vegetation development is very patchy, with clumps of trees, 4 *m* or more tall, interspersed with herbaceous vegetation and bare soil.

On deeper soils, in valleys and on gently sloping ground, a number of other pioneer species are also present and may attain local dominance. The most important additional woody species are *Acacia auriculiformis*, *Macaranga heynei*, *Melastoma malabathricum* and *Vitex pinnata*. *Acacia* is an exotic from the more seasonal climates of the Torres Straits, introduced as an ornamental and now widely naturalised. On recently abandoned sites it often seems to exclude the native species. *Eupatorium odoratum*, which is so prominent on similar sites further north, has only recently reached Singapore and has a very restricted distribution. *Melastoma* is often the pioneer woody species in fire-protected *Imperata* grasslands. In some places there are dense thickets of the ferns *Dicranopteris linearis* and *D. curranii*. These are probably the result of cutting *Adinandra* for poles or firewood (Burkill 1961) and are very persistant. These thickets appear to prevent the establishment of tree seedlings and their eventual elimination seems to depend on there being sufficient trees already established to form a closed canopy.

Stage 2

As soon as a closed canopy is formed, the herbaceous pioneers are shaded out. At undisturbed sites, there are no seedlings or saplings of any species, presumably as a result of the deep shade, although the slowly decomposing litter layer may be a contributory factor. As the canopy height increases, the shorter woody species are also gradually shaded out. *Melastoma* dissappears early but *Dillenia*, after attaining its maximum height of 3 to 5 *m*, persists for years as an increasingly sparse, non-flowering understorey. Eventually, only the tallest species remain. *Adinandra* usually dominates, with a varying representation of *Eugenia* spp., *Myrica* and *Rhodamnia* and scattered individuals of *Fagraea*, *Ploiarium* and *Vitex*.

How long the pioneer phase on degraded sites persists depends on the quality of the site. The eroded slopes studied by Holttum (1954), 36 years ago, are still occupied by the same flora. A dense, *Adinandra*-dominated forest has replaced some of the open scrub he described but other areas are no different from the vegetation illustrated in his Figure 1. Several other sites in Singapore support a pioneer vegetation at least 30 *y* old and nowhere near its maximum development. On deeper, presumably more fertile, soils succession may be considerably faster. The large areas of *Adinandra* forest in the central water catchment area 30 years ago, described by Holttum (1954) and Burkill (1959), have now been replaced by tall secondary forest.

Fire is a complicating factor at this stage. The pioneer species burn easily in exceptionally dry weather and, although they coppice readily, the increased light and, presumably, nutrient supply, permits the invasion by seed of species of *Macaranga* and *Trema* which (with the exception of *M. heynei*) are unable to establish directly on degraded sites. *Trema* is shaded out rapidly but the *Macaranga* species persist into the next stage. Many of the largest *Adinandra* and *Rhodamnia* trees in the water catchment forests are multi-trunked, probably as a result of post-fire coppicing. However, there is no evidence that the *Adinandra*-dominated community is a "fire climax" anywhere in Singapore. Fire does not seem to have the major role in woody succession in Singapore that it does in the northern Malay Peninsula, where dry periods are more regular and pronounced.

Stage 3

As *Adinandra* reaches its maximum height of around 15 *m*, the canopy opens out and there is a second period of establishment of new individuals. Most of the pioneers appear unable to regenerate under their own shade and a new group of taller, more shade-tolerant species begins to take over. As the surviving pioneers sink below the rising canopy, they develop sparse, narrow crowns before eventually dying. *Adinandra* and *Myrica* persist longest and dead or dying trees of these species are common in the younger parts of the catchment forests. Scattered individuals of *Fagraea*, *Ploiarium* and *Ixonanthes* persist into the next stage, and *Rhodamnia*, which has more shade-tolerant seedlings, increases its representation.

Stage 4

The 15 tall secondary forest plots are in areas that were, as far as could be determined, previously dominated by *Adinandra*. The youngest forest is probably about 50 *y* old (from cessation of cultivation or grassland fires) and the oldest less than 100 years. The first two axes of the DCA ordination are shown in Figure 1. The spread of the sites along the first axis is only 2.4 SD units (average standard deviation of species turnover), showing the floristic similarity of the sites: a full turnover in species composition occurs in about 4 SD units (Gauch 1982). The first axis is related to successional development. At one extreme are the three sites (5, 3, 8) with forest of the lowest stature (15 *m*) and the greatest abundance of surviving

Adinandra and *Myrica* while, at the other extreme, are the three sites (7, 15, 2) with the highest stature (18 - 24 *m*) where the pioneer species have been entirely eliminated. The second and subsequent axes have no obvious ecological interpretation. No axis shows any relationship with topography or the spatial distribution of the sites. Nor is there any obvious relationship with plot species richness, which ranges from 35 to 64 species > 2 *cm* dbh per plot and shows no consistent trend with successional development.

The tall secondary forest is dominated by members of the families Guttiferae (*Calophyllum* spp., *Garcinia* spp.), Lauraceae (*Lindera lucida, Litsea* spp.), Myrtaceae (*Eugenia* spp., *Rhodamnia cinerea*), and Elaeocarpaceae (*Elaeocarpus* spp.). These four families account for 57.6% of the total basal area in the plots. Other common species are listed in Appendix 1. More than 240 tree species were recorded at least once. *Calophyllum pulcherrimum, Garcinia parviflora* and *Rhodamnia cinerea* were the only species found in all tall secondary forest plots.

The similarities in floristic composition between plots were most marked at the generic level. Groups of congeneric species, most noticeably in *Calophyllum* (*C. pulcherrimum, C. tetrapterum, C. ferrugineum* and several rarer species), *Garcinia* (*G. parvifolia, G. eugeniifolia*) and *Litsea* (several incompletely identified species), seem to be interchangeable and to play equivalent ecological roles.

Woody climbers are not abundant or diverse. The commonest species are *Fibraurea chloroleuca* and *Rourea mimosoides.* Epiphytes are rare and strangling *Ficus* absent.

Origins and characteristics of the Secondary Forest Flora

The degraded land pioneers are not normal components of the rain forest flora of Singapore and the Malay Peninsula and do not occur in tree-fall gaps or other sites opened temporarily by disturbance. Their natural (*i.e.* before the arrival of man) habitats are permanent open sites, such as cliffs, riverbanks and sandstone or quartzite ridges. I have seen all the common herbaceous and woody pioneers in such habitats in Johor, Malaysia, within 150 *km* of Singapore. Unlike the typical softwooded, fast growing pioneers of undegraded sites, the timbers of *Adinandra, Eugenia longiflora, Fagraea, Ploiarium, Rhodamnia* and *Vitex* are all described as hard, durable or heavy in Burkill (1966), and all species are relatively slow growing. Their leaves are generally smaller than typical pioneers (with the exception of *Dillenia*), thicker, and borne on much-branched axes. Their reproductive characteristics, however, are typical of all pioneer trees: continuous or frequent flowering from a young age and the production of small-seeded, small fruit. *Adinandra, Fagraea* and possibly other species are dispersed internally by *Cynopterus* fruit bats (Phua & Corlett 1989). Most of the other species are dispersed internally by small, open-country birds. *Ploiarium* is exceptional in being wind-dispersed, which may explain its patchy distribution.

The tall secondary forest has a much richer and more variable flora, although the dominant genera are similar at all sites studied. All the characteristic species - with the exception, possibly, of *Rhodamnia* - are also normal components of lowland rain forest in the region. The most obvious shared characteristic of the flora is efficient seed dispersal. Again most species are bird or bat dispersed, although both seeds and fruits tend to be larger than in the pioneers. The few wind-dispersed species (*Alstonia* spp., *Ixonanthes reticulata*) are very patchily distributed, despite their small seeds. Even the oldest areas of secondary forest are very different from the primary forest remnants within the water catchment area and the adjacent Bukit Timah Nature Reserve. On aerial photographs, the high, uneven canopy of the primary forest contrasts sharply with the lower, relatively smooth canopy of the secondary forest. The primary forest is much more species-rich, with > 100 tree species in 50 x 20 *m* plots and very low floristic similarities between adjacent plots (Corlett unpublished). The family Dipterocarpaceae, which dominates the upper canopy and emergent layers of the primary forest is completely absent in the secondary forest, as are other species with large, wind dispersed seeds (*e.g. Gluta wallichii, Heritiera simplicifolia, Pentace triptera*). Moreover, the generally large-seeded, animal-dispersed families, Anacardiaceae, Burseraceae, Meliaceae, Leguminosae, Myristicaceae and Sapotaceae are either very rare or represented only by exceptionally small-seeded species, for example *Campnospermum auriculatum* in the Anacardiaceae and *Santiria apiculata* in the Burseraceae.

Discussion

It is not clear what factor or factors at degraded sites determine the occurrence of the distinct pioneer community. The independence of geology suggests that, if the explanation is nutritional, it is more likely to be lack of some nutrient associated with the organic component of the soil than the mineral component, most probably nitrogen. An alternative explanation is the physical conditions of the soil: shallowness, compaction, poor aeration and, probably, poor water holding ability. Jordan (1985) points out that high stress, whatever its nature, tends to result in vegetation with low biomass, productivity and diversity. As a result, it is often difficult to distinguish the effects of different types of stress. Jordan (1985) follows Whitmore (1984) in using the term 'oligotrophic' to characterise such vegetation, despite the limnological connotations. I propose that the succession on degraded land be termed the 'oligotrophic succession', in contrast to the typical 'eutrophic succession' on undegraded sites.

The edaphic factors which limit the flora of the pioneer stage seem to have been largely overcome by the time the pioneers are replaced by the succeeding phase. After less than 100 years of succession, the tree flora is already richer than any extra tropical forest (Gentry 1988). The tall secondary forest seems to be a well-dispersed subset of the rain forest flora. However, it must be emphasised that many rain forest species which might be expected to be well-dispersed, such as most of the understorey Euphorbiaceae and Rubiaceae, are also confined in the catchment area to relict patches of primary forest. Possibly these species require an internal microclimate which has not yet developed in the secondary forest.

In conclusion, this study suggests that plant succession on degraded land is initially limited by edaphic factors - probably nutrient deficiency or periodic water-stress - and later by seed dispersal. An experimental approach will be essential to separate these factors. It seems probable that dispersal efficiency will continue to control the course of the succession in the future and that restoration of the original rain forest will take many hundreds of years without human assistance.

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Appendix 1. Tree species > 2 *cm* dbh found in five or more of the 15 forest plots

Species	Number of plots
Adinandra dumosa	11
Alstonia angustifolia	7
Antidesma cuspidatum	6
Aporusa symplocoides	7
Aquilaria hirta	6
Archidendron clypearia	6
Artocarpus elasticus	6
Bhesa paniculata	9
Calophyllum pulcherrimum	15
Calophyllum tetrapterum	10
Calophyllum teysmannii	7
Calophyllum wallichianum	10
Campnosperma auriculatum	10
Canthium sp.	5
Champereia manillana	6
Diospyros styraciformis	8
Elaeocarpus ferrugineus	6
Elaeocarpus mastersii	12
Elaeocarpus petiolatus	13
Eugenia grandis	9
Eugenia longiflora	8
Eurycoma longifolia	5
Garcinia eugeniifolia	7
Garcinia griffithii	5
Garcinia parvifolia	15
Gironniera nervosa	9
Guioa pubescens	5
Gynotroches axillaris	11
Ixonanthes icosandra	7
Ixonanthes reticulata	6
Knema latericia	6
Licania splendens	6
Lindera lucida	12
Litsea firma	7
Macaranga conifera	5
Macaranga triloba	7
Porterandia anisophylla	11
Prunus polystachya	8
Pternandra echinata	7
Rhodamnia cinerea	15
Timonius flavescens	14
Xylopia ferruginea	9
Xylopia malayana	9