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Restoration of a Sri Lankan rainforest: using Caribbean pine *Pinus caribaea* as a nurse for establishing late-successional tree species

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Summary

1. In the moist tropics, studies have demonstrated poor seedling establishment of late-successional trees on lands cleared of forest. Our study examined the potential for establishing late-successional tree species that dominate the canopy of rainforest by planting within and adjacent to experimental openings that were created within a *Pinus caribaea* plantation.

2. We tested five canopy tree species (*Dipterocarpus zeylanicus*, *Mesua ferrea*, *Shorea disticha*, *S. megistophylla* and *S. trapezifolia*) of tropical forest in south-western Sri Lanka. Seedlings were monitored for 2 years within treatments that removed either three rows or one row of *Pinus* canopy, a canopy edge treatment and a control that left the canopy intact.

3. The greatest growth and dry mass for all species were in the canopy removal treatments. In particular, *S. trapezifolia* and *S. disticha* exhibited the greatest height growth in these treatments. In the three-row canopy removal treatment, *M. ferrea* had a significantly lower dry mass than the other species.

4. Differences were shown in the number and area of leaves among species. *Shorea trapezifolia* and, to a lesser degree, *S. disticha* increased area by increasing leaf production. *Dipterocarpus zeylanicus* and, to a lesser degree, *M. ferrea* increased area by increasing the size of individual leaves.

5. Guidelines based on results from this study recommend that species grow best when seedlings are planted within openings created by the removal of three rows of *Pinus* canopy. Where planting without canopy removal is required, *S. disticha* or *S. megistophylla* should be selected because of greater shade and drought tolerance.

6. This experiment demonstrated that *Pinus* can be used as a nurse for facilitating the establishment of site-sensitive tropical forest tree species that are late-successional. In particular, results have application for similar mixed dipterocarp forest types in south-east Asia.

Key-words: *Dipterocarpus zeylanicus*, enrichment planting, *Mesua ferrea*, *Shorea disticha*, *S. trapezifolia*.

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Introduction

Sinharaja Man and the Biosphere Reserve (6°21′N, 80°21′E) is Sri Lanka's only remaining relatively intact hill rainforest. This rainforest is part of the mixed-dipterocarp type that dominates the forested regions of south and south-east Asia (Whitmore 1984). High tree species endemicity (64% as defined by Gunatilleke & Gunatilleke 1985) and the biogeographic significance of the island as a relic of Gondwanan origin (Ashton & Gunatilleke 1987) make protecting the Sinharaja forest and nearby logged forests managed by the Sri Lanka Forest Department important. However, private land surrounding these forests has almost all been converted to plantation crops (tea, rubber) (Ishwaran & Erdelen 1990). Much of the remaining government land that borders these forests can be described as abandoned agricultural lands that were formerly forested and that have now reverted to fire-maintained shrublands dominated by kekilla fern *Dicranopteris lineariz* Gleicheniaceae (Cohen, Singhakumara & Ashton 1995). Some *Pinus caribaea* var. *hondurensis* (Sénécl) Barr. et Golf. has been planted on kekilla in the hill regions of central and south-western Sri Lanka. The rationale for doing this was to initiate a small pulpwood industry, and to protect the upper watershed catchments from erosion and the consequent sedimentation of soil at dam sites downstream.

New mandates by the Forest Department of Sri Lanka call for the renewed protection of all rainforest reserves, including Sinharaja. Government policies now prevent encroachment of remaining rainforest, and call for restoration of their floristics and structure where these forests have been degraded. However, the late-successional canopy tree species that create the habitat for fauna and the environment for many subcanopy plants of the mature rainforest, require particular conditions for their early growth and establishment. Research has demonstrated that differences in canopy opening sizes within rainforests promote differences in regeneration survival and growth of late-successional canopy tree species (Hartshorn 1978; Oldeman 1978; Whitmore 1978; Denslow 1980, 1987; Bazzaz 1984; Raich & Gong 1990; Turner 1990). Studies have also shown that the variation in micro-environment (e.g. light quality and quantity; soil moisture and nutrient status) (Chazdon & Fetcher 1984; Canham *et al.* 1990; Ashton 1992) can affect seedling survival and growth within the opening itself and beneath the adjacent forest canopy (Brandani, Hartshorn & Orians 1988; Uhl *et al.* 1988).

For Sri Lanka, studies have demonstrated this variability in survival and growth for the late-successional canopy trees of the Sinharaja rainforest in relation to light and soil moisture (Ashton & Berlyn 1992; Ashton 1995; Ashton, Gunatilleke & Gunatilleke 1995) and soil nutrient status (Gunatilleke *et al.* 1996). Results showed that these tree species are site specific and require protection from the desiccating effects of full sun. Though critical for the restoration of key attributes of rainforest habitat and structure, these species cannot be planted in the open or in any exposed position (Ashton *et al.* 1995; Gunatilleke *et al.* 1996).

Studies have demonstrated the ability of pioneer rainforest trees to establish beneath *P. caribaea* (Parrotta 1995). Many studies have also demonstrated the use of partial shade provided by the rainforest canopy for the enrichment planting and release of slower growing late-successional trees that were not represented in the composition of a future stand (Wormald 1992). Only a few studies have examined the effectiveness of planting fast-growing plantation species to assist below-canopy establishment of late-successional tree species on cleared lands (Dawkins 1949; Wormald 1992). No studies have examined the use of *Pinus* for promoting the establishment and successional development of tropical late-successional tree species on formerly cleared and then abandoned sites.

Evidence from the documentation of land abandonment and successional development of forests of temperate regions (Raup 1966) supports our supposition that this idea should be tested in the tropics. In temperate circumstances of eastern North America, colonization by conifers on abandoned farmland has facilitated the understorey initiation (*sensu* Oliver & Larson 1990) of many angiospermous tree species that would be considered mid- to late-successional (Lutz 1928; Billings 1938; Oosting 1942; Bormann 1953; Bowman 1979; Chapman *et al.* 1982).

Examples of temperate studies that have examined the use of *Pinus* plantations to assist the establishment of late-successional tree species have been mostly restricted to the former German Democratic Republic where *Quercus petraea* (Mattuschka) Liebl. was planted beneath *P. sylvestris* L. (Ebling & Hansen 1988), and *Fagus sylvatica* L. was planted beneath *P. sylvestris* (Dittmar & Knapp 1986). These plantings were done beneath the existing forest canopy. Results from these studies have been mixed with species showing satisfactory establishment, but relatively slow growth, except for the more shade- and drought-tolerant *F. sylvatica* which showed reasonable growth in comparison to advanced regeneration under similar canopy light environments.

Our study examined the potential for establishing late-successional tree species that dominate the canopy of the Sinharaja rainforest by planting within and adjacent to experimental openings that were created within a *P. caribaea* plantation.

Methods and materials

SITE DESCRIPTION

The study was located in a *P. caribaea* plantation bordering the Sinharaja MAB reserve in south west Sri Lanka. The rainforest adjacent to the study site has been described as belonging to the *Mesua-Shorea* type (De Rosayro 1942; Gunatilleke & Ashton 1987). Mean monthly temperature ranges between 18°C and 27°C with an annual rainfall of between 3500 and 6000 mm. The topography of the region is one of ridges and valleys with altitudinal ranges between 600 and 1000 m. The soils are classified as red-yellow podsols (Moorman & Panabokke 1961) or ultisols (USDA, Soil Conservation Service 1975), underlain by khondalitic gneiss (Cooray 1967).

The study site was located on the lower part of a midslope (30° slope, southern aspect) that was originally cleared of forest for swidden cultivation in the 1950s and subsequently abandoned. Repeated fires promoted the establishment of kekilla fernland. In 1978 the Forest Department of Sri Lanka planted the site with *P. caribaea* at a 2 × 2-m spacing. Before commencement of our experiment, samples of mineral soil were taken from the top 15 cm, air dried (27°C), crushed and sieved. Soil was then measured for pH, total soil nutrients were extracted using a Kjeldahl digest, and organic carbon was measured in the manner used by Walkley & Black (1934). Available nutrients were extracted to 1 N ammonium acetate buffered to pH 7. Soil data from the *P. caribaea* plantation were compared with soil data collected in the same manner by Ashton *et al.* (1995) from valley and midslope sites of the Sinharaja MAB reserve (Table 1). No significant differences exist among sites for amounts of soil K, but the valley site had significantly higher amounts of Mg than the *Pinus* or midslope sites. Percentage carbon, percentage nitrogen and amount of Ca in the *Pinus* soil were significantly greater than both of the rainforest sites. We speculate that this might be related to the slower decomposition of the needle litter in the *Pinus* soil as compared to the leaf litter of the rainforest sites.

EXPERIMENTAL DESIGN AND ENVIRONMENTAL MEASUREMENTS

Tree species for the experiment were chosen based on knowledge gained from previous experiments that examined establishment patterns (Ashton *et al.* 1995; Gunatilleke *et al.* 1996). Five tree species were selected that grow on the mid- to lower slopes and that dominate the canopy of mature phase rainforest (*sensu* Watt 1947; Whitmore 1984). The species were *Dipterocarpus zeylanicus* Thw., *Mesua ferrea* L., *Shorea disticha* (Thw.) Ashton, *S. megistophylla* (Thw.) Ashton and *S. trapezifolia* (Thw.) Ashton. Except for *M. ferrea* (Clusiaceae), all other species in this experiment are in the timber tree family Dipterocarpaceae.

The lower slopes and smaller valleys with large streams support *S. megistophylla*. *Shorea trapezifolia* characteristically occupies the deep soils of midslopes and ridges, but can occur with *S. megistophylla* in the smaller valleys. *Shorea disticha* predominates on the same kind of sites as *S. trapezifolia*, but can also occur on more rocky ridges or with *S. megistophylla* on the lower slopes. *Dipterocarpus zeylanicus* occurs on bottomlands and larger valleys with small rivers. It can occur with *S. megistophylla*, but usually dominates the canopy of stands along larger water courses. *Mesua ferrea* occurs as a canopy or subcanopy tree with *S. megistophylla* and is usually associated with the larger water courses along which *D. zeylanicus* can also be found. It is slower growing and more shade tolerant than the other study species (Holmes 1957, 1958).

Species growth was evaluated over a 2-year period in four treatments. Three of the treatments involved the removal of a part of the *P. caribaea* canopy (15 m in height). The fourth was an under-planting beneath a closed canopy of *P. caribaea* where no trees were removed. The three canopy removal treatments comprised (i) one row of *P. caribaea* removed (4-m strip width); (ii) three rows of *P. caribaea* removed (8-m strip width); and (iii) under-planting beneath three rows of *P. caribaea* adjacent to three rows of *P. caribaea* canopy removal. To avoid the environmental effects of canopy removal, the under-planting treatment where no canopy trees were removed was located at least 20 m away from any of the canopy removal treatments. All treatments were aligned north–south. *Pinus* rows were therefore removed parallel to the direction of the slope and resembled narrow clearcut strips that were 140 m in length. All four treatments were also blocked together within the *Pinus* plantation at three different locations.

Measures of daily photosynthetic photon flux (DPPF) were made using a data logger (LI-1000, LiCor, Lincoln, Nebraska) and quantum sensors (LI-190Z, LiCor, Lincoln, Nebraska). Sensors were placed at the centre of each treatment 1 m above the ground surface to avoid shading from ground vegetation. This height was usually above the tallest planted seedlings. In certain situations where taller seedlings were above the sensor, the sensor was moved along the centre of the treatment to a position that avoided shading from the seedling canopy. Measures of DPPF were recorded at 10-s intervals and stored as a mean every 10

Table 1. Soil pH, organic carbon and nutrients in the *Pinus caribaea* plantation with comparative data from valley and midslope sites of the Sinharaja MAB rainforest. K = available potassium; Mg = available magnesium; Ca = total calcium. Data are means with standard errors in parentheses. Data from rainforest valley and mid-slope sites were from samples collected by Ashton *et al.* (1995). Letters qualitatively indicate significant differences (a > b > c) according to Duncan's multiple range test ($p < 0.05$)

	P. caribaea	Valley	Midslope
pH	4·31 (0·02)a	4·37 (0·13)a	3·87 (0·18)b
% carbon	6·02 (0·21)a	2·05 (0·42)b	1·44 (0·29)b
% nitrogen	0·16 (0·02)a	0·12 (0·01)b	0·10 (0·01)b
K ($\mu g\ g^{-1}$)	21·71 (0·60)a	29·00 (2·00)a	27·50 (3·00)a
Mg ($\mu g\ g^{-1}$)	18·04 (1·44)b	37·50 (1·10)a	20·50 (3·40)b
Ca ($\mu g\ g^{-1}$)	111·81 (9·83)a	77·00 (6·50)b	59·50 (6·50)b

min over the course of a 12-h period (06:00–18:00 hours). Measurements were repeated on three sunny days for each treatment plus the control during the months of January and February 1993.

The amount of DPPF received at the centre of the three-row canopy removal treatment ($X = 22{\cdot}13$ mol m^{-2} day^{-1}, $S_x = 0{\cdot}78$) was similar to the amount received at the centre of a 450-m^2 canopy opening in the Sinharaja rainforest (Ashton 1992). The DPPF received at the centre of the one-row canopy removal treatment ($X = 10{\cdot}35$ mol m^{-2} day^{-1}, $S_x = 0{\cdot}95$), the three row under-planting ($X = 4{\cdot}95$ mol m^{-2} day^{-1}, $S_x = 2{\cdot}06$) and the closed canopy under-planting ($X = 3{\cdot}31$ mol m^{-2} day^{-1}, $S_x = 1{\cdot}29$) were, respectively, the same as that at the centre, the outside edge and the inside edge of a 250-m^2 canopy opening in the Sinharaja rainforest (Ashton 1992; Ashton *et al.* 1995). No treatment in our study had amounts of DPPF that were as low as that measured at the ground surface beneath the closed canopy of the Sinharaja rainforest. Measurements of DPPF beneath the closed canopy of Sinharaja rainforest made by Ashton (1992) have generally not exceeded 0·92 mol m^{-2} day^{-1}.

For each treatment, single seedlings of each species were planted together at one location to evaluate comparative performance. Five individuals were therefore planted in randomly assigned positions at the corners of a square, with one additional individual at the centre. For a group, 1-m spacing was used among all seedlings except the centre which was slightly less. Groups were planted at 5-m intervals along a single transect. Each transect was positioned in the centre of each treatment and aligned north–south along the length of the treatment. Twenty seedling groups were therefore planted along a single transect within a treatment. To avoid shading at the northern and southern ends of each treatment, plantings started and stopped 20 m inside the strip edge. There were therefore three transects per treatment, each being represented in a different block, with a total of 60 planted seedling groups. All seedlings were 1-year-old stock collected from the 1989 mast year and grown in polythene pots (20 cm diameter across the top; 30 cm depth) under 50% shade and in well-watered conditions at the nursery of the Sinharaja field station. Seedlings selected for planting were of approximately the same height ($X = 25$ cm, $S_x = 3$ cm) with no sign of leaf damage from herbivore or pathogen.

GROWTH MEASUREMENTS

All treatments were planted in August 1991 and clean weeded at regular intervals over a 2-year period. At the end of 2 years (August 1993) measures of height, basal stem diameter and number of leaves were taken on surviving individuals, and mortality was recorded.

Also at that time, a sample of 12 seedlings was taken for destructive sampling from each species and treatment. Seedlings were selected equally, but at random from each block and treatment. All were dug up and the roots carefully washed free from soil in a bucket of water. They were then taken to the laboratory at the University of Peradeniya. Areas were measured using a LiCor 3100 (Lincoln, Nebraska) for three randomly selected mature leaves per seedling. Subsequently, all seedling parts (leaves, stem, roots) were dried at 80°C for 48 h. Dry mass for each species and treatment were then recorded for seedling parts. Total leaf area for a seedling was calculated by multiplying the mean leaf area for a given species and treatment by the leaf number for a seedling.

Analyses of variance using SAS (Ray 1982) were carried out on seedling mortality, height, basal stem diameter, number of leaves, leaf area of individual leaves, total leaf area, total dry mass, and dry masses of leaf, stem and roots. Analyses were with factorial combinations of the four treatments, the three blocks, and the five species. Where appropriate, Duncan's multiple range test was used to test for differences among treatments for each species ($P < 0{\cdot}05$).

Results

MORTALITY

Analysis of variance showed significant differences in mortality among treatments ($F_{(3,24)} = 5{\cdot}33$; $P < 0{\cdot}01$), and among species ($F_{(4,24)} = 4{\cdot}38$; $P < 0{\cdot}01$). No significant difference was found in the interaction among treatments and species, or among treatment blocks. Mortality after 2 years was greatest for *S. trapezifolia* in the canopy underplanting (CU) treatment (Fig. 1). Apart from the relatively poor survival of *S. trapezifolia* in the CU, almost all other treatments and species had less than 10% mortality after 2 years. *Shorea megistophylla* and *D. zeylanicus* had lower mortality than the other species in the canopy removal treatments. For *D. zeylanicus*, mortality increased with treatments associated with lower amounts of DPPF. For all treatments mortality of *M. ferrea* was consistently 8–10%.

HEIGHT AND BASAL STEM DIAMETER

Analysis of variance showed significant differences in height among treatments ($F_{(3,1180)} = 180{\cdot}57$; $P < 0{\cdot}0001$) and among species ($F_{(4,1180)} = 48{\cdot}57$; $P < 0{\cdot}0001$). Analysis of variance showed no significant difference in interaction among treatments and species, or among treatment blocks.

For all species greatest height was attained in the three-row (3R) canopy removal treatment and least height was attained in the closed canopy under-planting (CU) (Fig. 2). However, the *Shorea* species showed no significant difference in height between the 3R, the one-row (1R) canopy removal treatment, and the three-row under-planting (3U) treatment (Table 2). For *D. zeylanicus* and *M. ferrea*, the 3R treatment was sig-

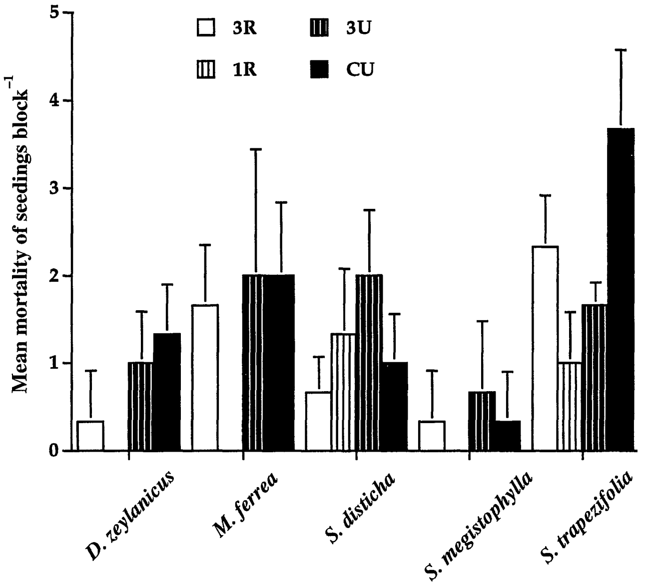

Fig. 1. Seedling mortality by species and treatment after 2 years: 3R, three-row canopy removal; 1R, one-row canopy removal; 3U, three-row under planting; CU, closed canopy under-planting. One block contains 20 seedlings per species. Bars indicate 1 standard error of the mean.

nificantly different in height from the 1R, 3U and CU treatments. For the treatments that promoted the greatest heights, comparisons among species revealed *S. trapezifolia*, *S. disticha* and *S. megistophylla* to have attained significantly greater height than *D. zeylanicus* and *M. ferrea*. In the CU treatment the same trend was noticeable, but *M. ferrea* attained significantly greater height than *D. zeylanicus*. Both species were again shorter than the *Shorea* spp. in the CU treatment (Fig. 2).

Analysis of variance also showed significant differences in basal stem diameter among treatments ($F_{(3,1180)} = 110{\cdot}53$; $P < 0{\cdot}0001$), among species ($F_{(4,1180)} = 11{\cdot}04$; $P < 0{\cdot}0001$) and in interaction among species and treatments ($F_{(12,1180)} = 3{\cdot}28$; $P < 0{\cdot}01$). No significant differences were found among treatment blocks.

The greatest basal stem diameter for all species was again in the 3R treatment. *Shorea trapezifolia* and *D. zeylanicus* had significantly thicker stems in this treatment as compared to the other species. However, in the CU treatment, analyses revealed that *S. megistophylla* had the thickest stem diameter, and *D. zeylanicus*, *M. ferrea* and *S. trapezifolia* had the thinnest stem diameters (Fig. 2).

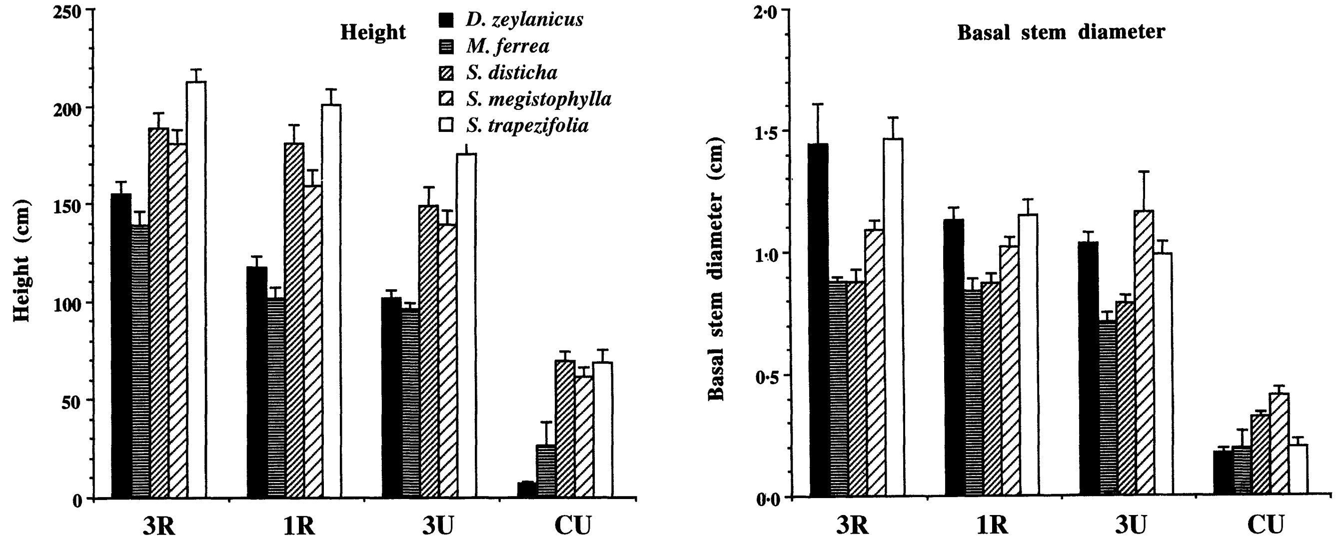

Fig. 2. Seedling height and basal stem diameter after 2 years: 3R, three-row canopy removal; 1R, one-row canopy removal; 3U, three-row under planting; CU, closed canopy under-planting. Bars indicate 1 standard error of the mean.

Table 2. Differences in height, basal stem diameter, leaf number, leaf area, total leaf area, total dry mass and component dry masses (root, stem, leaves) and dry mass ratios (root, stem, leaves) between treatments for each species. Letters qualitatively indicate significant differences (a > b > c) according to Duncan's multiple range test ($p < 0.05$). Treatments: 3R, three row removal; 1R, one row removal; 3U, three row underplanting; CU, closed canopy underplanting

	Height				Basal stem diameter				Leaf number				Leaf area			
	3R	1R	3U	CU	3R	1R	3U	CU	3R	1R	3U	CU	3R	1R	3U	CU
D. zeylanicus	a	b	b	c	a	ab	b	c	a	a	a	a	a	a	b	c
M. ferrea	a	b	b	c	a	ab	b	c	a	b	b	c	a	a	a	a
S. disticha	a	a	a	b	a	a	a	b	a	a	a	b	a	a	a	a
S. megistophylla	a	a	a	b	a	a	a	b	a	ab	b	c	a	a	a	a
S. trapezifolia	a	a	a	b	a	a	a	b	a	ab	b	c	a	a	a	a

	Total area				Total dry mass				Root dry mass				Stem dry mass			
	3R	1R	3U	CU	3R	1R	3U	CU	3R	1R	3U	CU	3R	1R	3U	CU
D. zeylanicus	a	a	a	b	a	b	b	c	a	ab	ab	b	a	b	b	c
M. ferrea	a	ab	a	b	a	b	c	d	a	b	b	c	a	b	bc	c
S. disticha	a	a	a	b	a	ab	ab	b	a	ab	ab	b	a	ab	ab	b
S. megistophylla	a	a	ab	b	a	bc	b	c	a	ab	b	c	a	b	b	c
S. trapezifolia	a	b	ab	c	a	ab	bc	c	a	ab	b	c	a	ab	b	c

	Leaf dry mass				Root mass ratio				Stem mass ratio				Leaf mass ratio			
	3R	1R	3U	CU	3R	1R	3U	CU	3R	1R	3U	CU	3R	1R	3U	CU
D. zeylanicus	a	b	b	c	a	a	a	a	a	a	a	a	a	a	a	a
M. ferrea	a	b	c	d	a	a	a	a	a	a	a	a	b	b	b	a
S. disticha	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
S. megistophylla	a	b	b	c	a	a	a	a	a	a	a	a	b	ab	a	ab
S. trapezifolia	a	ab	bc	c	a	a	a	a	a	a	a	a	a	a	a	a

LEAF NUMBER, INDIVIDUAL LEAF AREA AND TOTAL LEAF AREA

Analysis of variance for number of leaves showed significant differences among treatments ($F_{(3,220)} = 18{\cdot}38$; $P < 0{\cdot}0001$), among species ($F_{(4,220)} = 75{\cdot}30$; $P < 0{\cdot}0001$), and in interaction among species and treatments ($F_{(12,220)} = 8{\cdot}70$; $P < 0{\cdot}0001$). No significant difference was found among treatment blocks. Unlike measures of height and basal stem diameter, number of leaves had an F-value for differences among species that was much larger than the F-value for differences among treatments. This suggested that leaf number was a measure that better described differences in species morphology compared to differences in growth among treatments.

In all treatments *S. trapezifolia* had the greatest number of leaves followed in order by *S. disticha*, *S. megistophylla*, *M. ferrea* and *D. zeylanicus* (Fig. 3, Table 2). The greatest number of leaves was in the 3R treatment and the least was in the CU.

For areas of individual leaves, analysis of variance revealed differences among treatments ($F_{(3,220)} = 20{\cdot}40$; $P < 0{\cdot}0001$), among species ($F_{(4,220)} = 220{\cdot}96$; $P < 0{\cdot}0001$) and in interaction among species and treatments ($F_{(12,220)} = 17{\cdot}35$; $P < 0{\cdot}0001$). F-values for leaf area differences reflected similar trends to those for number of leaves. This again suggested that leaf area better described differences in species morphology than differences in performance of species among the treatments. Again, no significant difference was found for differences among treatment blocks.

Trends in areas of individual leaves among species were different compared to trends among species for leaf number. *Dipterocarpus zeylanicus* had the largest leaves followed in order by *S. megistophylla*, *M. ferrea*, *S. disticha* and, lastly, *S. trapezifolia* (Fig. 3, Table 2). This trend is virtually the reverse of that for leaf number. The only exception was for *M. ferrea*, which had both relatively smaller leaves and a low number. Except for *D. zeylanicus* and *M. ferrea*, leaf area did not vary noticeably across treatments for the other species.

Analysis of variance for total leaf area showed significant differences among treatments ($F_{(3,220)} = 43{\cdot}43$; $P < 0{\cdot}0001$), among species ($F_{(4,220)} = 28{\cdot}80$; $P < 0{\cdot}0001$), and in interactions among treatments and species ($F_{(12,220)} = 3{\cdot}83$; $P < 0{\cdot}0001$). No significant difference was found among treatment blocks.

Total leaf area of an individual plant, being a multiple of individual leaf area and leaf number, showed much greater F-values for treatment differences compared to the F-values for differences among species. This composite measure of area based on the product

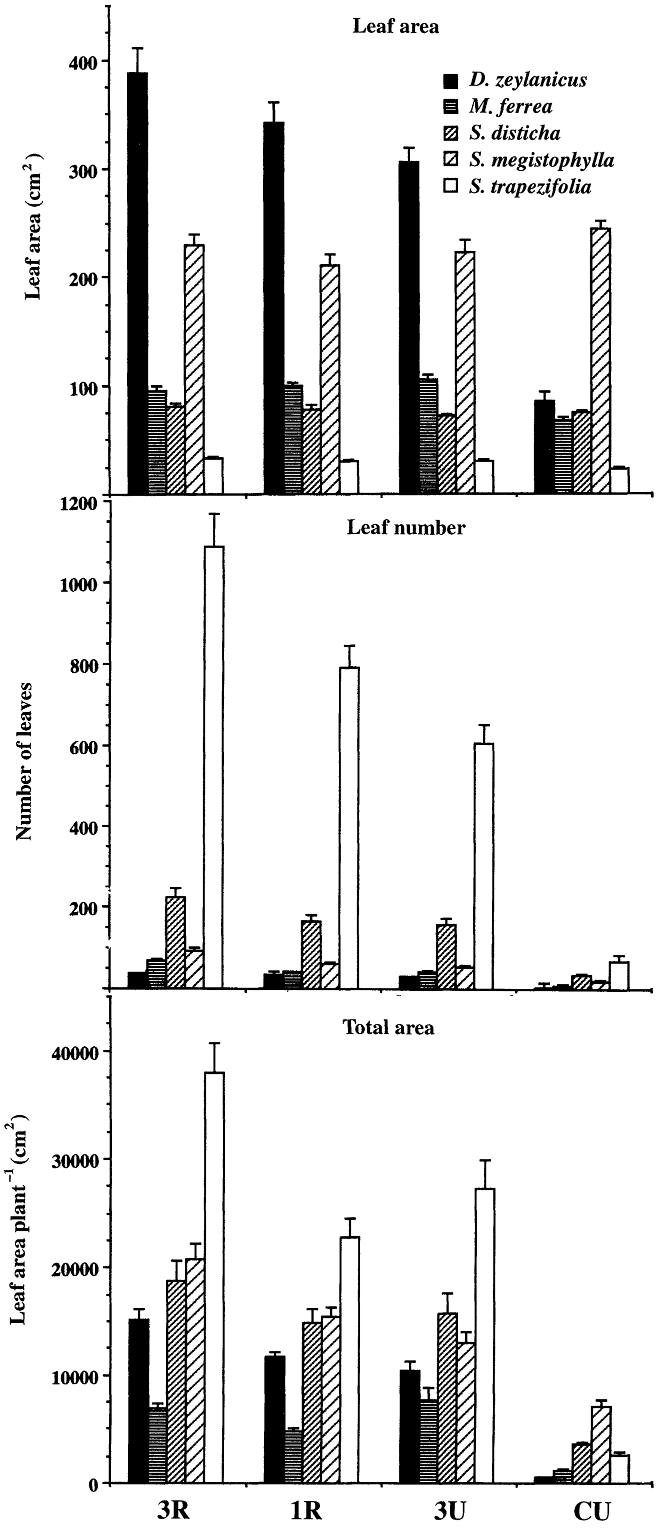

Fig. 3. Area of individual leaves, leaf number and total leaf area for seedlings after 2 years: 3R, three-row canopy removal; 1R, one-row canopy removal; 3U, three-row under-planting; CU, closed canopy under-planting. Bars indicate 1 standard error of the mean.

of individual leaves and number of leaves was therefore a better reflection of comparative growth performance of species among treatments.

For all treatments except CU, *S. trapezifolia* had the greatest total leaf area, followed in order by *S. megistophylla* and *S. disticha*, *D. zeylanicus* and, lastly, *M. ferrea* (Fig. 3). In the CU treatment, *S. megistophylla* had the greatest total leaf area and *D. zey-*

lanicus exhibited the least. All species had the greatest total leaf area per plant for the 3R treatment and the least total leaf area per plant for the CU treatment.

DRY MASSES OF ROOTS, STEMS AND LEAVES

Analysis of variance for total mass and its component parts of roots, stem and leaves, revealed significant differences among treatments and among species. No significant difference was shown among blocks (Table 3).

For three of the species, total dry mass was greatest in the 3R treatment followed in descending order by 1R, 3U and lastly CU (Fig. 4, Table 2). An exception to this trend was exhibited by *S. disticha* which only showed significant differences between the CU and all other treatments, and *S. megistophylla* which showed a significantly greater total dry mass for the 3U treatment compared to the 1R treatment.

In the 3R treatment, *M. ferrea* had a significantly lower dry mass than the other species. However, for the CU treatment, *S. megistophylla* had the greatest total dry mass, followed in descending order by *S. disticha*, *S. trapezifolia*, *D. zeylanicus* and *M. ferrea* (Fig. 4). Differences among species for the component parts (roots, stem, leaves) revealed similar trends to that of total dry mass (Table 2). Differences among treatments for all component masses were less marked for *S. disticha* than for the other species.

Proportional allocation to roots, stem and leaves for each species are depicted by treatment (Fig. 5). Proportional dry mass allocation to roots in most of the treatments was greater for *M. ferrea*, *S. trapezifolia* and *D. zeylanicus* compared to *S. disticha*. However, these differences were not significant among treatments for any of the species. For all species, greater allocation was made to leaves in treatments that received lower amounts of DPPF, but again this was not significantly different in most cases. In most instances, *S. megistophylla* allocated noticeably more dry mass to leaves than the other species.

Discussion

Other studies in this region and elsewhere have demonstrated the ability of pioneer tree and shrub species of rainforests to colonize and establish within *P. caribaea* (Guariguata, Rheingans & Montagnini 1995; Parrotta 1995; Gamage 1997). This study has demonstrated that seedlings of late-successional canopy tree species can also be established on formerly cleared forest by planting beneath the canopy of a *P. caribaea* plantation.

After 2 years, canopy removal treatments had greater height growth and dry masses for all tested species compared to those in the *Pinus* underplanting. For all these species the 3R treatment was the best, but in most instances was not significantly different from the other removal treatments. Many factors could account for differences in seedling performance among treatments. These include below-ground competition for water and nutrients with *P. caribaea*, possible allelopathic effects of terpenes and phenolics from pine needles, or availability of light. We suggest that for satisfactory establishment, seedlings should be exposed to amounts of DPPF that are at least half that found in the open and about 4–5 times that beneath a closed *Pinus* canopy. These results emphasize the importance of openings for establishing plantings and suggest that these manipulations emulate natural for-

Table 3. *F*-values and significance (*$P < 0·05$; **$P < 0·01$; ***$P < 0·001$; NS, not significant) for analyses of variance of total dry mass, root dry mass, stem dry mass and leaf dry mass. Degrees of freedom are given in parentheses. 3R, three-row canopy removal; 1R, one-row canopy removal; 3U, three-row under-planting; CU, closed canopy under-planting

Main effects	Total	Root	Stem	Leaves
Treatments (3)	42·54***	29·22**	40·96**	20·54***
Treatment × blocks (6)	1·63 NS	1·79 NS	1·04 NS	1·19 NS
Species (4)	8·90***	5·27*	10·09***	6·73***
Treatments × Species (12)	1·18 NS	1·24 NS	0·86 NS	0·54 NS
Block (2)	1·20 NS	1·00 NS	1·13 NS	0·93 NS
Subeffects				
By species among treatments (3)				
D. zeylanicus	19·54**	3·88 NS	24·90***	20·66**
M. ferrea	41·43***	56·22***	18·23**	55·13***
S. disticha	3·93 NS	3·95 NS	4·30 NS	1·75 NS
S. megistophylla	12·33**	11·87**	23·45**	16·23**
S. trapezifolia	11·26**	12·63**	10·55**	9·80**
Among species within each treatment (4)				
3R	2·07 NS	1·44 NS	2·07 NS	1·33 NS
1R	4·28*	17·40***	5·60*	3·07 NS
3U	6·33*	3·77 NS	5·63*	8·38**
CU	11·11**	21·79***	9·26**	10·83**

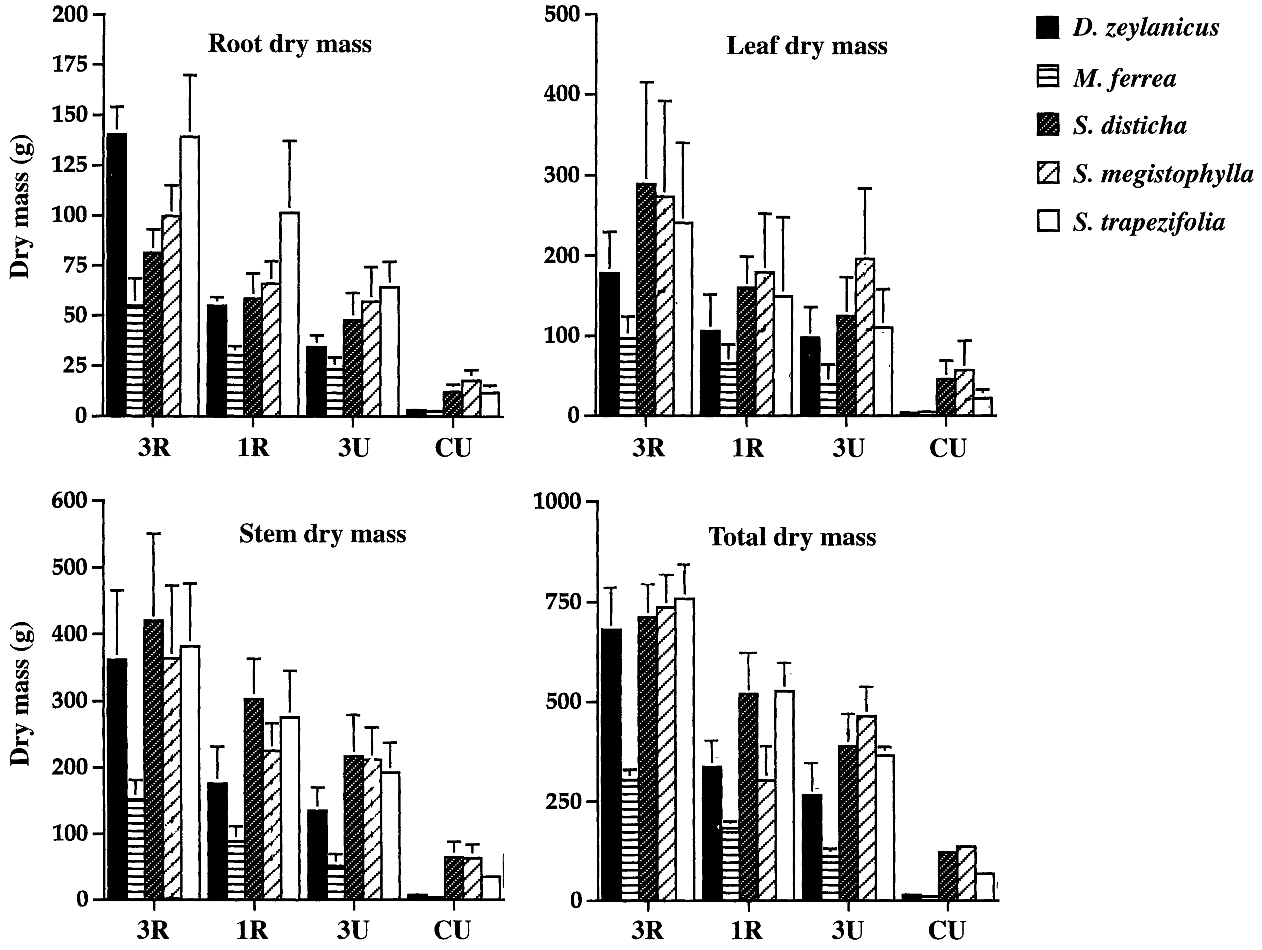

Fig. 4. Total dry mass and dry mass of roots, stem and leaves of seedlings after 2 years: 3R, three-row canopy removal; 1R, one-row canopy removal; 3U, three-row under-planting; CU, closed canopy under-planting. Bars indicate 1 standard error of the mean.

est disturbance regimes that release advance regeneration (Denslow 1980, 1987; Ashton, Gunatilleke & Gunatilleke 1993).

Based on this study, 2-year-old seedlings can be planted beneath openings that are three rows wide (8 m) and that are orientated in a N–S direction to facilitate periods of direct radiation. For our study site, the greatest height growth was shown by *S. trapezifolia*, *S. disticha* and *S. megistophylla*. All are dominant canopy trees of the mid- and lower slopes. The poorest height growth was shown by *D. zeylanicus* and *M. ferrea*, both predominantly valley bottom species. Further studies should be undertaken to test plantings beneath wider openings and in the full sun, as well as within man-made openings to compare the effects of opening direction (N–S–E–W).

D. zeylanicus and the *Shorea* spp. had noticeably greater dry mass in the 3R treatment compared to

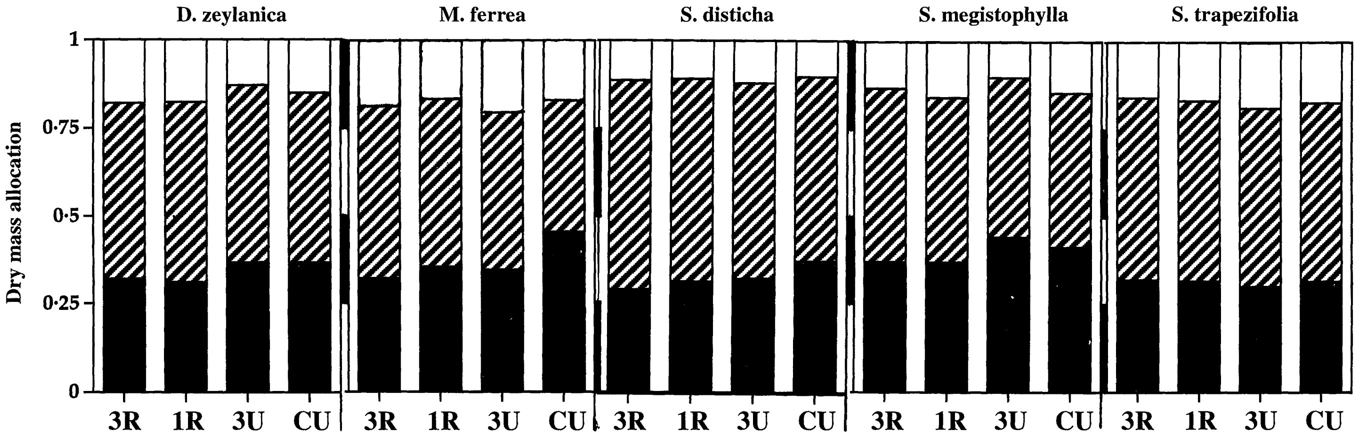

Fig. 5. Proportional dry mass allocation to roots, stem and leaves after 2 years: ■, leaves; ▨, stem; □, roots.

that of *M. ferrea*. The ratio between species height and dry mass suggests that, relative to the other species, seedlings of *D. zeylanicus* and *S. megistophylla* were thick-stemmed and stocky. Total leaf area reflected similar trends as dry mass for the different species. Species differences were shown in the arrangement and display of leaf area. *Shorea trapezifolia* and *S. disticha*, species that have slender stems and branches, increased plant leaf area by increasing leaf production. *Shorea megistophylla* and *D. zeylanicus*, species that are stocky, increased plant leaf area by increasing leaf size.

This result is supported by other studies that have compared leaf morphology of shade and sun leaves for these species (Ashton & Berlyn 1992; B.M.P. Singhakumara & P.M.S. Ashton, unpublished data). These studies reveal that *S. megistophylla* and *D. zeylanica* have significantly thicker cuticles and leaves, higher rates of net photosynthesis (P_N) and allocate greater proportions of their dry mass to roots compared to the other species in full sun environments. In these studies, *S. megistophylla* and *D. zeylanicus* have also been demonstrated to be the most water-use efficient and sun-tolerant relative to the other species. Because of these attributes, both *S. megistophylla* and *D. zeylanicus* may be more suited to planting on sites prone to greater desiccation above-ground, but where soil water is freely available.

In circumstances where under-planting without canopy removal is desired, *S. disticha* and *S. megistophylla* should be selected for enrichment beneath *P. caribaea* rather than *S. trapezifolia*. Experiments have demonstrated the susceptibility of *S. trapezifolia* to drought in forest understorey conditions (Ashton 1995; Ashton *et al.* 1995). In these circumstances, *S. trapezifolia* has poor root development. For example, in these studies, *S. trapezifolia* allocated proportionately less to roots compared to the other *Shorea* species in the understorey, and also exhibited up to a five-fold decrease in root mass between seedlings in the understorey of a ridgetop site compared with those seedlings in the understorey of a valley site (Ashton *et al.* 1995).

Results from this experiment can be used to develop enrichment planting protocols on sites similar to this study. However, further experimentation should be undertaken using the same design, but in different topographic positions (valley, ridge) and with larger opening sizes, including full open conditions, in order to verify the site performances of the late-successional tree species and to develop more fully species selection criteria for enrichment planting. Also, it should be recognized that this existing study should continue to be monitored for a longer period to verify the findings after 2 years.

The results from this study demonstrate that a plantation species, such as *P. caribaea*, can play an important role in the establishment of late seral tree species in *Mesua–Shorea* rainforest. These rainforest tree species would ordinarily take much longer to re-establish on abandoned agricultural lands, if at all. The results from this study also imply that plantations such as *P. caribaea* on this site, that do not have the capability of reproducing viable seed in this environment, may be useful for the development of successional plantation analogues in other regions.

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