

Ecology of Two Selected Liana Species of Utility Value in a Lowland Rain Forest of Sri Lanka: Implications for Management

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Calamus ovoideus Thw. and *Coscinium fenestratum* Colebr. are economically important, naturally growing liana species in the disturbed habitats of lowland rain forests in Sri Lanka. Harvesting their mature stems has jeopardised their survival and led to dwindling populations. Growth performance, population sizes and the eco-physiology of these species were examined under three different canopy removal treatments and a closed canopy control of a *Pinus caribaea* buffer zone plantation of the Sinharaja forest. Population studies of *Calamus* spp. and *C. fenestratum* revealed that they survive and regenerate naturally in disturbed habitats compared to undisturbed forest.

After nine years, both liana species grew poorly in the *Pinus* understorey (control) compared to the canopy removal treatments. During the study period, height increment of *C. ovoideus* was best in the three-row canopy removal treatment. In contrast to *C. ovoideus*, the eco-physiological features of *C. fenestratum* varied little among the canopy removal treatments, suggesting that they tolerate a wider range of light levels.

The study revealed that both species could be successfully introduced to the *Pinus caribaea* buffer zones, degraded areas of lowland rain forests in Sri Lanka, in order to conserve them in the wild and manage them sustainably.

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INTRODUCTION

THE RAIN FORESTS of Sri Lanka are of considerable interest in the historical biogeography of South and South-East Asia (Gunatilleke and Ashton 1987). Sri Lanka also has a wealth of economically important timber and non-timber forest species. Much of the original forests in Sri Lanka have been cleared for settlement, cultivation and production of timber, and only about 8 per cent of the original lowland rain forests now remain on the island. These forests, recognised as among the floristically richest terrestrial biomes in South Asia, are fragmented, degraded and isolated throughout the lowland wet zone in Sri Lanka (Gunatilleke et al. 1996). The remaining government land that borders these forests can be described as abandoned agricultural lands that were formerly forested and have now reverted to fire-maintained scrublands or degraded lands. Therefore, restoration of these degraded lowland rain forests is an immediate necessity.

In the past, natural forests were largely used for the extraction of timber. Little attention was then paid to other useful resources, largely non-timber resources, which were being extracted and used by peripheral communities around forests. Nonetheless, some rural communities in Sri Lanka continue to have a tradition of conservation practised in harmony with, and partial dependence on, the natural forest. This provides an excellent setting to examine how these tropical rain forests can be managed for multiple uses following a system that is socially acceptable, ecologically sustainable and economically viable (Gunatilleke et al. 1994). It also becomes imperative to understand the ecology of rain forest species, which have a utility value other than timber, so that they can be sustainably managed for non-timber forest products based on scientific criteria. The need to select species that will be protected, planted and encouraged has been emphasised in studies on regeneration and restoration. It is essential to understand the ecological, biological, physiological and silvicultural requirements of such species; the lack of understanding of the requirements of individual species has been considered as the greatest gap in our knowledge (Gómez-Pompa and Burley 1991).

Calamus ovoideus Thw. and *Coscinium fenestratum* Colebr. are naturally growing economically important liana species around the disturbed sites of Sinharaja Man and Biosphere (MAB) Reserve, Sri Lanka. *Coscinium fenestratum* (family Menispermaceae) is a wide spread dioecious woody climber that occurs in the lowland wet zone of Sri Lanka. It is locally known as 'weniwalgeta' and grows along forest edges, and in gaps and disturbed habitats. The woody stem of this well-known medicinal liana contains the active compounds berberine, jatrorrhizine and palmatine and has antibiotic properties (Jayaweera 1982). It is extensively used in indigenous medicine as a bitter tonic for the treatment of fever and tetanus (Senerath 1990). The stems of *C. fenestratum* are also used locally for cordage as a substitute for rope. Most populations of this species have been exploited on a substantial scale in its natural habitats and it has not been cultivated so far. *Calamus ovoideus* (family Arecaceae, subfamily Calamoideae), is a thorny liana locally known as 'tuda rena' or 'sudu wewel.' It is an endemic climbing cane species, or

rattan, that occurs in the wet zone of Sri Lanka (de Zoysa and Vivekanadan 1991). The stems of this liana have become an increasingly popular raw material for rural industries. It is used to make furniture, baskets, ornaments, house and kitchen utensils, and also as a binding material. Most rattans are collected from natural forests and cultivation is very rare. According to the Sri Lanka Forestry Sector Master Plan (Anon 1995), except for two rattan species (*C. rotang* and *C. thwaitesii*), rattan resources are greatly depleted and are now confined almost exclusively to protected areas in the lowland rain forests of Sri Lanka. However, due to the illicit harvesting of good quality, large diameter rattan (*C. ovoides*), which is preferred by the cane industry, even these protected populations are on the verge of near extinction in Sri Lanka (de Zoysa and Vivekanadan 1991). This article presents information on the ecological and silvicultural strategies of the liana species, *Coscinium fenestratum* and *Calamus ovoides*, which grow naturally in the Sinharaja rain forest of Sri Lanka. Our study addressed the following questions: (a) What is the population size and size class distribution of individuals of each of these species in forests that have been selectively logged in the past and are at present regenerating? (b) Do these species perform differently in selectively logged forest and in undisturbed forest? (c) Do these two species respond differently to different-sized canopy gaps in a *Pinus* buffer zone enrichment stand? (d) Do they show differences in their mortality, growth rates and eco-physiology in different-sized gaps?

The answers to these questions will provide insights into the silvicultural strategies that can be used to promote these two liana species in restoration trials of lowland rain forests of Sri Lanka.

MATERIALS AND METHODS

Study Sites

The study was carried out in and around the Sinharaja (MAB) Reserve (6° 21' N, 80° 21' E) in south-west Sri Lanka (hereafter, Sinharaja). The total conservation area of Sinharaja comprises 11,187 ha, which includes about 5,000 ha of primary forest with over 60 per cent of the tree species endemic to the island (Gunatilleke and Gunatilleke 1996), secondary forests, and fernlands. The rain forest adjacent to the study areas has been described as a mixed dipterocarp forest and belongs to the *Mesua-Shorea* forest type (Gunatilleke and Ashton 1987). The climate of this region is characterised as aseasonal and perhumid. Mean monthly temperature ranges between 18 and 27° C, with an annual rainfall of between 3,500 and 6,000 mm (Ashton 1992).

Populations of the study species were examined in disturbed forest sites and in some selected areas of the forest fringe, where these species grow well. The disturbed area of the reserve was logged for timber for the supply of plywood between 1972 and 1977.

Growth performance of the two liana species in different size gaps was investigated in the enrichment trial set up in part of a *Pinus caribaea* var. *hondurensis* (Sénécl) Barr. et Golf. plantation in the buffer zone bordering the north-western part of Sinharaja. This enrichment trial was established in 1991 in the *P. caribaea* buffer zone plantation (Gamage 1998), which had been planted in 1978 and protected for the last twenty-three years. Before plantation establishment, this area was abandoned agricultural land (Ashton et al. 1997). The average slope of the study site is about 44°. The *P. caribaea* trees were planted at a spacing of 2×2 m in rows aligned north-south as described in Ashton et al. (ibid.).

Sampling for Population Density and Size Distribution in the Disturbed Forest

In part of the selectively logged forest, permanent plots (nine for *C. fenestratum* and fifteen for *Calamus*) were established in 2000 and 2001. Sampling sites were selected in different areas of the forest where these two species were present. Within a site, plots were randomly demarcated and the perimeter of each plot was marked by painting a ring around the stem of the border trees using water resistant yellow paint. In these plots all the enumerated individuals of the study species were permanently tagged and numbered. For *C. fenestratum*, sampling was carried out in three different sites in the disturbed forest, and in the forest fringe due to scarcity of this species in other areas; the forest-fringe site was close to a village on the perimeter of the reserve. For *C. ovoideus*, five different sites were sampled.

For each species three transects per site, each 100×4 m, were sampled. Since well-grown cane lianas have a smooth woody stem once the leaf sheaths at the base perish, it is not possible to identify them to their respective species, as it is the arrangement of spines on the leaf sheath that enables their identification. The apex of the plants was high above the ground (>20 m) and as stems of the different species were intermingled it was difficult to discern the identity of the individuals. *Calamus* enumerated, therefore, was one of three species that occur in this forest, namely, *Calamus ovoideus*, *Calamus zeylanicus* Becc. & Hook. f., and *Calamus thwaitesii* Becc. & Hook. f. Each individual was tagged at the root collar for future monitoring. For the cane species, the root collar diameter, shoot diameter (1 m above the root collar) of each of the stems in a clump and the number of stems per individual clump were recorded. In the case of *C. fenestratum*, the root collar diameter and shoot diameter (1 m above the root collar) were measured for each individual.

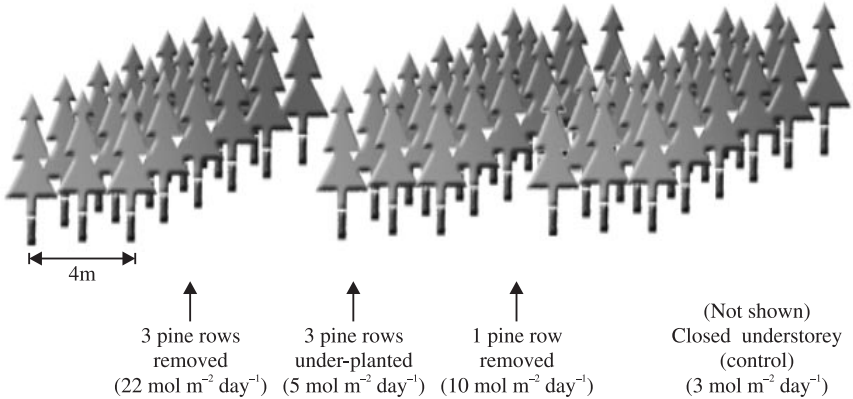
Size variation among individuals of the study species based on root collar diameter and shoot diameter was investigated. For both species, the site variation was tested using GLM (General Linear Model) procedure of Statistical Analysis System (SAS), version 6.12 (SAS Institute Inc., Cary, NC).

Eco-physiological Investigations in the Pinus Enrichment Trial

The *Pinus* enrichment trial was the study site for eco-physiological investigations of these two liana species. This enrichment trial had been set up as a two-factor

split-plot design with three replicate blocks. The main factor in the experiment is the light treatment, including the control, created by removal of the *Pinus* trees in 1991. The sub-factor in the experiment is represented by the different study species (Gamage 1998). The light treatments were obtained by the removal of a part of the *P. caribaea* canopy. In two of the treatments, three rows and one row of pines were removed respectively, with a distance of three pine rows between these two treatments (Figure 1). We considered the three-pine-row gap between the two removal treatments as a third light treatment for our study. The closed canopy of *P. caribaea* served as the control treatment. This control was located away from the canopy removal treatments to avoid any edge effects influencing the under-planted seedlings. In May 1992 twenty individuals of each study species, *Calamus ovoideus* and *Coscinium fenestratum*, were initially planted in all four treatments in the three replicate blocks.

Figure 1
Stand Profile of Canopy Removal Treatments



Note: Stand profile of the canopy removal treatments and control (note shown here) of one block of the *Pinus* enrichment trial in the buffer zone of Sinharaja MAB Reserve, with their respective light intensities (within parenthesis) at the ground level in 1991, when the trial was set up.

The daily photosynthetic photon flux densities (PPFD) received at ground level by the treatments were as follows: three rows removed ($22 \text{ mol m}^{-2} \text{ day}^{-1}$), one row removed ($10 \text{ mol m}^{-2} \text{ day}^{-1}$), three rows under-planted ($5 \text{ mol m}^{-2} \text{ day}^{-1}$) and the closed canopy control ($3 \text{ mol m}^{-2} \text{ day}^{-1}$). Growth performance and physiological attributes of *C. fenestratum* and *C. ovoideus* plants established under the three different light regimes created by canopy removal and in the closed canopy control were examined.

The growth measurements of the study species have been annually recorded over nine years (1992–2001) since the inception of the enrichment trial. Their root collar diameters (RCD) were recorded using vernier calipers initially, and diameter tape once they grew bigger. Heights of the surviving individuals were recorded

only up to 1998 due to the difficulty of measuring the accurate height of the grown-up plants. Height was measured from the ground to the highest point of the plant using a surveying staff. Annual increments of RCD and height were calculated from measurements made between 1992 and 2001, and 1992 and 1998 for all the existing individuals respectively. Dead seedlings were counted and recorded at each sampling period. Since randomly selected seedlings were taken for destructive sampling two years after establishment of the trial (August 1994), seedling mortality was calculated during the period 1995–2001 for both species.

The physiological measurements (photosynthetic rates and stomatal conductance) of the study species were recorded in February 2001. Gas exchange measurements were obtained using a closed system LiCor 6200 portable infrared gas analyser (LiCor, Lincoln, Nebraska) following the method described in Ashton and Berlyn (1992). From each block, three representative plants per species per treatment were randomly selected for these studies. In each of these plants a single fully exposed, expanded, undamaged, intact leaf at about 2 m above ground level was selected for subsequent physiological measurements. All measurements on these selected leaves were made under ambient conditions (CO_2 concentration of approximately $340 \mu\text{mol mol}^{-1}$, relative humidity 50–55 per cent and photon flux density between 250 and $1,200 \mu\text{mol m}^{-2} \text{s}^{-1}$). For sampling, the 1 litre leaf chamber without the artificial light source was used. The leaf area of the chamber was set at 10 cm^2 for the broad-leafed *C. fenestratum* and at 6 cm^2 for narrow-leafed *C. ovoides*. The airflow rate was maintained at $500 \mu\text{mol m}^{-2} \text{s}^{-1}$ and the stomatal ratio was kept at 0.5. To avoid bias from diurnal effects, sampling was done between 9.00 A.M. to 3.00 P.M. on sunny days as described in Ashton and Berlyn (ibid.) and Tennakoon et al. (1997). The study species did not show any midday closure of stomata during the period gas exchange measurements were taken. Each gas exchange measurement took place during a 40–90 enclosure of the leaves of a species, taking care to avoid periods of rapidly changing light conditions before or during measurements. The three replicates of each species in each light treatment were sampled within one day to avoid any sampling errors. Each replicate plant was sequentially measured six times over this time period. Each measurement of a leaf comprised a set of three sequential readings. The net photosynthetic rate and stomatal conductance were determined from these measurements.

Differences in mean per cent seedling mortality, growth over nine years, annual growth increments between 1992 and 2001, and leaf physiological measurements were analysed by the analysis of variance (ANOVA) using the generalised linear models (GLM) procedure of SAS (version 6.12; SAS Institute Inc., Cary, NC). The effects of light treatments, species and the interactions between treatments and species were examined at the 5 per cent level of significance. Owing to some seedling mortality and missing values in growth parameters of some individuals, data were analysed as an unbalanced ANOVA. Multiple comparisons among treatments, and between species, were made using Duncan's multiple range test (at $p < 0.05$). All data on per cent seedling mortality were arcsine transformed

prior to analysis; data on growth over nine years, growth increments and physiological measurements, which were not normally distributed, were log-transformed prior to the analyses. Where appropriate, means of the untransformed data were used to plot graphs.

RESULTS

Population Studies in the Disturbed Forest

A total of 199 individual clumps and 669 stems of *Calamus* spp. were found within the 0.6 ha sampled in the disturbed sites (study plots in the selectively logged area) of the Sinharaja forest. The number of individuals and stems varied considerably among the five sites. The highest number of individuals (sixty-three) and stems (183) were recorded within Site 1 (Table 1). Except at one site (Site 3), more than 50 per cent of the individuals had multiple stems. The number of stems per clump ranged between two and eighteen, with most individuals having four to five stems per clump. Mean RCD ($p = 0.021$) and mean shoot diameter ($p = 0.019$) of the *Calamus* stems varied significantly among the five sites.

Table 1
Population Size and Growth Parameters of Calamus spp.

	Site 1	Site 2	Site 3	Site 4	Site 5	Sites 1–5
Total no. of individuals/0.12 ha	63	43	31	30	32	199
Total no. of stems/0.12 ha	183	127	94	136	129	669
No. and % of individuals with multiple stems	32 (51)	24 (56)	11 (35)	20 (67)	22 (69)	109 (55)
Mean RCD/stem (cm)	2.7 ^a	2.6 ^{ab}	2.5 ^b	2.6 ^{ab}	2.6 ^{ab}	2.6
Mean SD/stem (cm)	2.1 ^a	1.9 ^b	2.0 ^a	2.0 ^a	2.1 ^a	2.0

Note: *Calamus* spp. sampled in five different sites of the disturbed forest in Sinharaja MAB Reserve, Sri Lanka. Percentage of stems having multiple stems is given in parentheses. Letters qualitatively indicate ($a < b < c$) the significant differences among the sites at $p < 0.05$.

More than 50 per cent of all *Calamus* stems in all sites were in the 2–2.99 cm RCD class (Figure 2). The proportion of stems with RCD between 3 and 3.99 cm was more than 20 per cent. The proportion of stems in the 1.0–1.99 cm and 4.0–4.99 cm RCD classes were only 9.1 per cent and 6.3 per cent respectively (Figure 2).

In *C. fenestratum*, within the three different sites sampled in the disturbed forest, 100, 102 and sixty-one individuals were recorded. For all individuals sampled, the mean root collar diameter per individual was 3.0 cm and the mean shoot diameter per individual was 2.1 cm. Among the three different sites, the mean RCD of the individuals did not vary significantly ($p = 0.142$), but the mean shoot diameter was significantly higher in Sites 1 and 2 compared to that in Site 3 ($p = 0.006$; see Table 2).

Figure 2
Root Collar Diameter Distribution of *Calamus* spp. in Five Different Sites of the Disturbed Forest in Sinharaja MAB Reserve, Sri Lanka

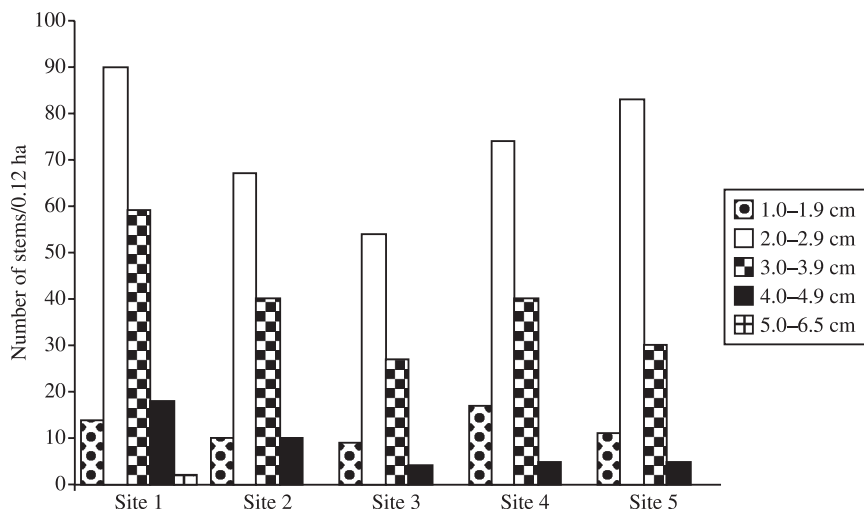


Table 2
Population Size and Growth Measurements of *Coscinium fenestratum*

Measurements recorded	Site 1	Site 2	Site 3
No. of individuals/0.12 ha	100	102	61
Mean RCD (cm)/individual	3.0 ^a	3.1 ^a	2.9 ^a
Mean SD (cm)/individual	2.2 ^a	2.2 ^a	1.8 ^b

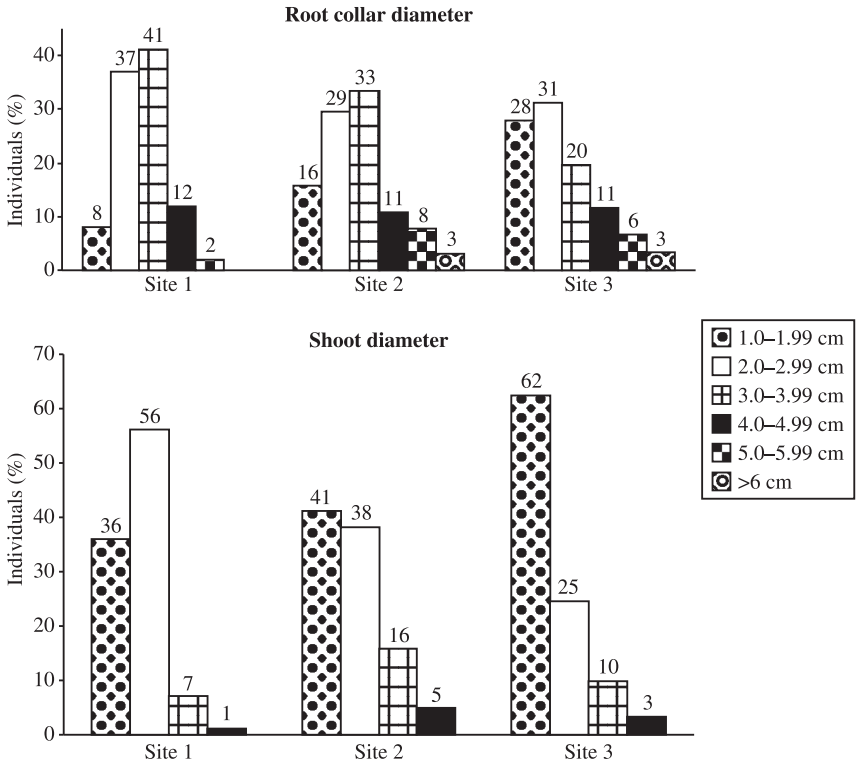
Note: *Coscinium fenestratum* sampled in the three different sites of the disturbed forest in Sinharaja MAB Reserve, Sri Lanka. Letters indicate the significant differences among sites at $p < 0.05$.

The proportions of individuals of *C. fenestratum* in different RCD classes showed that Site 3 had a higher proportion of small individuals (28 per cent) in the RCD size class 1.0–1.99 cm relative to Sites 1 and 2. Between 59 and 78 per cent of individuals in each site had RCD of 2.0–3.99 cm. However, individuals over 6 cm RCD were present only in Sites 2 and 3, where they represented 3 per cent of each of these populations (Figure 3). In each of the three sites, in contrast to RCD, the shoot diameters in 79–92 per cent of individuals ranged between 1.0 and 2.9 cm, whereas the proportions of individuals between 3.0 and 4.99 cm was less than 21 per cent (Figure 3).

Population Sizes of the Liana Species in the Selectively Logged and an Undisturbed Forest

In the 25 ha forest dynamics plot demarcated for the long-term monitoring of the growth of species in an undisturbed area of the Sinharaja forest, only fifty-six

Figure 3
Root Collar Diameter and Shoot Diameter Distributions of
***Coscinium fenestratum* in the Sinharaja MAB Reserve, Sri Lanka**



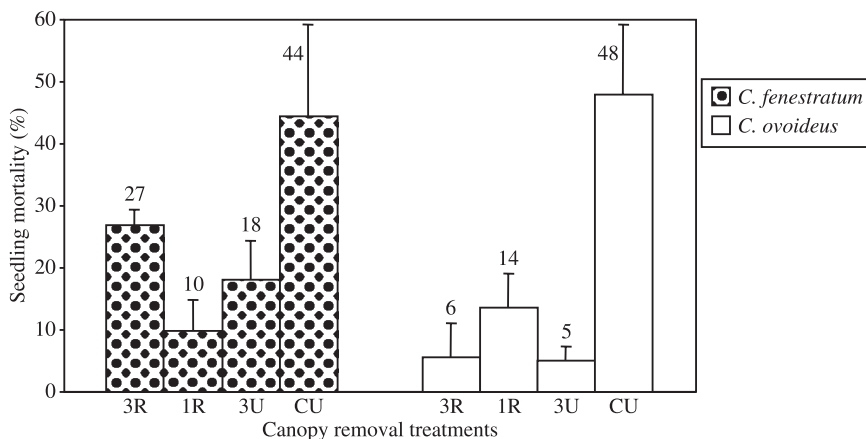
Note: Sites 1, 2 and 3 (where $n = 100, 102$ and 61 respectively) in part of the selectively logged and regenerating forest in the Sinharaja MAB Reserve, Sri Lanka. Values above bars indicated the proportions of individuals in each size class in each site.

individuals of the cane species and none of the *C. fenestratum* were recorded (C.V.S. Gunatilleke and I.A.U.N. Gunatilleke, unpublished data). In the present study, in contrast, we recorded as many as 199 individuals of *Calamus* spp. and 263 individuals of *C. fenestratum* in just 0.2 ha of the selectively logged forest.

Seedling Mortality and Growth Performance in Different Sized Canopy Gaps

Results of seedling mortality during 1995–2001 failed to show any significant differences among canopy removal treatments. The per cent mortality of both study species in the closed canopy control was highest compared with the canopy removal treatments in the *Pinus* enrichment trials (Figure 4).

Figure 4
Mean Percentage Mortality of *C. fenestratum* and *C. ovoideus*
under Different Canopy Removal Treatments (1995–2001)



Note: 3R: three rows removed; 1R: one row removed; 3U: three rows under planting; CU: closed canopy control. Bars indicate the standard error of the mean. Values above show the mean percentage mortality of each species under each treatment.

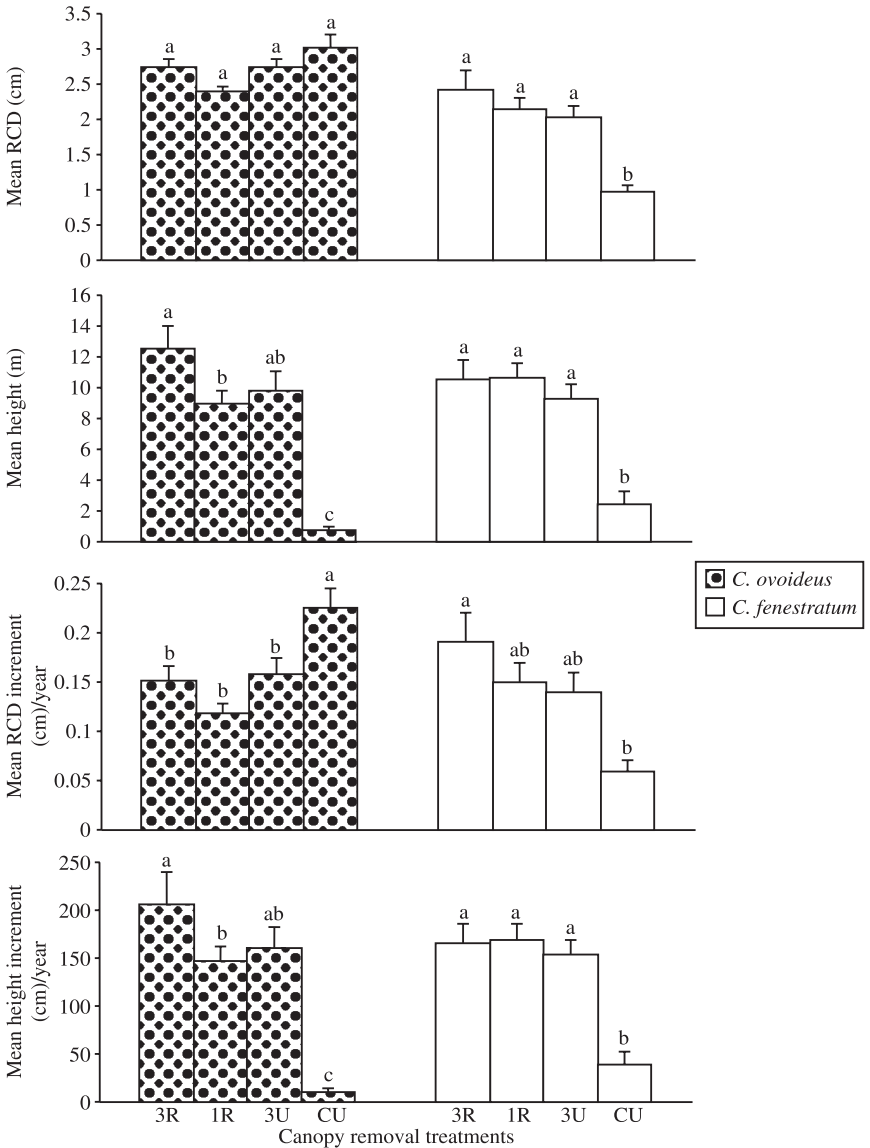
As depicted in Figure 5, mean RCD, mean height and their increments of *C. fenestratum* after nine years were significantly higher in canopy removal treatments compared to the closed canopy control. The differences of *C. fenestratum* among the canopy removal treatments were not significant except in the case of the annual RCD increment, which was significantly higher in the three-rows-removed treatment compared to the other two canopy removal treatments. The results showed that mean height, and its increment per year, were significantly higher in canopy removal treatments than in the closed canopy control for *C. ovoideus*. The mean annual RCD increment of *C. ovoideus*, on the other hand, was higher in the closed canopy control.

Leaf Physiological Investigations

The results suggest that each of the species had its best net photosynthetic rate under a different canopy removal treatment (Figure 6). The highest mean net photosynthetic rate recorded for *C. ovoideus* was in the one-row-removed treatment; the highest mean photosynthetic rates recorded for *C. fenestratum*, on the other hand, were in the three-rows-removed and the control treatments. Stomatal conductance reflected different trends between species and among the canopy removal treatments. Stomatal conductance was significantly higher in the three-rows-removed treatment for *C. ovoideus*, and in the one-row-removed and three-rows-underplanted treatments for *C. fenestratum* (Figure 6).

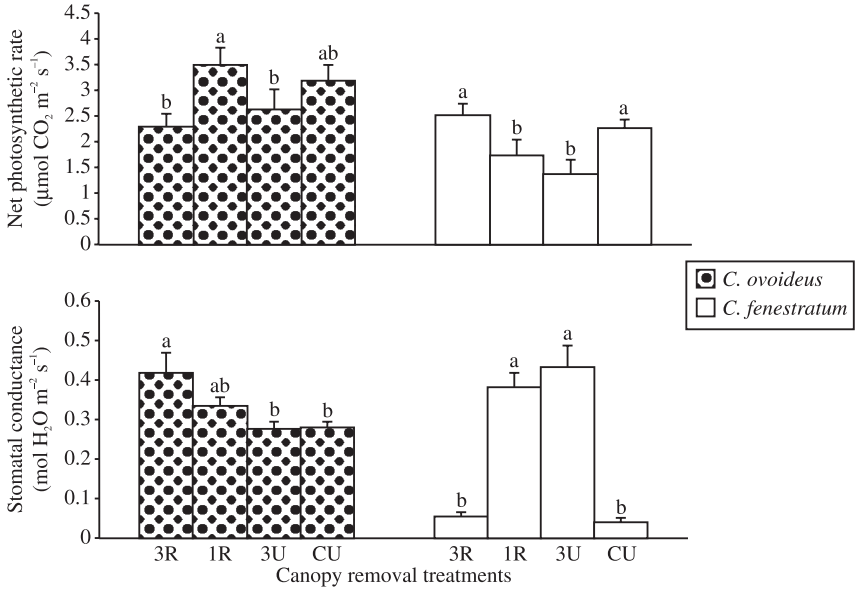
Figure 5

Mean Root Collar Diameter, Mean Height and Their Increments per Individual per Year of *C. ovoideus* and *C. fenestratum* in the Sinharaja MAB Reserve, Sri Lanka



Note: *C. ovoideus* and *C. fenestratum* after nine years growth under different canopy removal treatments in the *Pinus* enrichment trial in the buffer zone of Sinharaja MAB Reserve, Sri Lanka. 3R: three rows removed; 1R: one row removed; 3U: three rows under planting; CU: closed canopy control. Bars indicate the standard error of the mean. Letters indicate significant differences among treatments for each species according to Duncan's multiple range test ($p < 0.05$).

Figure 6
Net Photosynthetic Rate and Stomatal Conductance of C. ovoides and C. fenestratum in the Sinharaja MAB Reserve, Sri Lanka



Note: *C. ovoides* and *C. fenestratum* under different canopy removal treatments in the *Pinus* enrichment trial in the buffer zone of Sinharaja MAB Reserve, Sri Lanka. 3R: three rows removed; 1R: one row removed; 3U: three rows under planting; CU: closed canopy control. Bars indicate the standard error of the mean. Letters qualitatively indicate significant differences ($a > b > c$) among treatments for each species according to Duncan's multiple range test ($p < 0.05$).

DISCUSSION

Although commercial selective mechanised logging and disturbances associated with it caused some extent of destruction to the forest, the present study, carried out twenty years after logging, showed that the study species could regenerate naturally and survive in the disturbed sites of the Sinharaja forest.

Results of this study further showed that regeneration of *Calamus* spp. in their natural habitats could have occurred either by seeds or vegetatively by buds at the rooting points. Single-stemmed individuals may have possibly arisen from seeds dispersed by bats, polecats and other dispersers to sites far away from their mother plants. Seeds of both species have a pulp that attracts mammalian and bird dispersers. On the other hand, individuals with multiple stems could have arisen from vegetative shoots at the rooting point, or from those plants that may have been dormant at the time of logging. The growth rates of these multiple- and single-stemmed cane plants and their relationship with age in these habitats should be monitored to test for their growth differences, if any. The similar RCD distributions

shown by individuals in different sites depicts the low variability among sites. In contrast to cane, the natural regeneration of *Coscinium fenestratum* is known to be difficult due high moisture content of the seeds (>25 per cent) and their inability to withstand low humidity conditions (Bandara et al. 2004).

The performance of *C. fenestratum* varied among the three different sites sampled. Sites 1 and 2 were located within the forest reserve and Site 3 was located in the forest fringe, bordering the reserve. All the growth measurements made at Site 3 were lower than measurements made at the two sites that were within the forest. The differences between Site 3 and the other two sites could be attributed to the degree of disturbance in them due to removal of mature lianas by villagers living in the vicinity. These results further showed that the mean RCD of plants growing in all three natural forest habitats was greater than the maximum RCD (2.4 cm) recorded after nine years growth in the three-rows-removed treatment of the *Pinus* buffer zone enrichment trial. Studies carried out by Senerath (1990) showed that mean density of the *C. fenestratum* in the forest fringe at Sinharaja was fourteen individuals per 125 m². However, the present study showed a reduction in the density of the individuals in the forest edge, where the value was ten and eleven individuals per 125 m² in Sites 1 and 2 respectively. According to a study conducted ten years before the present investigation (ibid.), a large proportion of the individuals sampled in the forest fringe of the Sinharaja forest had a shoot diameter ranging between 1.0 and 1.9 cm. In contrast, in the present study, more than half (56 per cent) of the individuals sampled were represented by a shoot diameter of 2.0–2.9 cm, which could be due to the growth of individuals over the last ten years.

The trends in most of the leaf physiological attributes in both species, and among treatments may be due to the comparatively similar light conditions (2.5–6.4 mol m⁻² day⁻¹) at 2 m above the ground, the height at which the leaves were harvested for physiological studies. The spatial and temporal light variation of the understorey is a major factor that affects the physiological processes of the two species investigated. The study also demonstrates the changes between the initial light intensities at the commencement of the experiment (in 1992) and at the time of measurement (in 2001) due to the growth of the introduced plants, and how these changes have affected the physiological responses of these plants. The existing average total daily photosynthetic photon flux densities 2 m above the ground were found to be 6.44, 4.31, 3.27 and 2.5 mol m⁻² day⁻¹ for the three-rows-removed, one-row-removed, three-rows-underplanted and control treatments respectively.

The results of this study provide important information on the survival, growth and physiological responses of two native liana species in an enrichment trial of the *P. caribaea* buffer zone plantation. Previous studies (Gamage 1998) have shown that 3-year-old seedlings of these species can be established under suitable gap sizes of *P. caribaea* plantations. The results of this study confirm the ability of 9-year old plants of the two study species (*C. fenestratum* and *C. ovoideus*) to

grow successfully under suitable-sized gaps in the *P. caribaea* plantation in the buffer zone of the Sinharaja MAB Reserve.

When one considers the two liana species, *C. fenestratum* and *C. ovoideus*, plant height is a good measure of growth as well as of the quantity available for extraction because in both species the stem is harvested for its utility value. The results demonstrate that, even after nine years of growth, *C. fenestratum* and *C. ovoideus* grew poorly in the *Pinus* understorey compared with the canopy removal treatments, but they showed different growth strategies. The best height after nine years for *C. ovoideus* was observed in the three-row-removed treatment compared to all the other treatments tested in this study. In contrast to cane, *C. fenestratum* showed only a small variation, mostly non-significant, in terms of growth and other eco-physiological features among the canopy removal treatments. This depicts that *C. fenestratum* has a wider tolerance of a range of light conditions. Although not significant, results showed that both liana species had poor per cent survival under the lowest light treatment (that is, the control) compared to any of the *Pinus* canopy removal treatments. The heights of both species and the root collar diameter of *C. fenestratum* increased considerably with the increased initial light level from 3 to 5 mol m⁻² day⁻¹. This suggests that 9- to 10-year-old plants of *C. ovoideus* and *C. fenestratum* are shade intolerant. Increases between 5 and 22 mol m⁻² day⁻¹, however, did not lead to much variation in these growth parameters. Based on the results, both liana species can be grown economically and successfully in *Pinus* stands, where every fourth row of pines is removed. In these pine stands the lianas could be grown in the gaps created by removing rows as well as in the understorey of the intervening rows.

The ecological, physiological and silvicultural findings of these native non-timber forest species should also be examined in the light of their production, and sustainable extraction levels in this type of manipulated mixed-species plantation. Continuation of this investigation should provide valuable information on some of the economical aspects of these species and the production levels under these manipulated conditions.

The National Forest Policy (1995) of Sri Lanka (Anon 1995) proposes the sustainable management of state forests for multiple uses, through involvement of local people who will participate in planning and implementing, and will benefit from natural forest management. According to the recent forest classification (ibid.), Class III forests are mainly to be used for multiple uses such as sustainable production of wood and NTFP for the benefit of the local communities. This includes the buffer zones that protect strictly conserved or preserved forests for non-extractive uses, that is, Class I and Class II forests. Class IV forests comprise plantations and agro-forestry systems on state lands that would be managed for production of wood and NTFP. Therefore, the results of the species investigated in the present study provide insights into the best ways in which these species can be introduced or cultivated in the mixed-species buffer zone plantations in the lowland wet zone in Sri Lanka. They also provide insights into the subsequent

management strategies that could be adopted in the lowland wet zone forests that are assigned for production with the help of community participation. In addition, the findings of this study are invaluable when drawing up suitable silvicultural guidelines to enhance the growth of these species in their natural forest fringe habitats or in degraded forests. The information on population sizes of *Coscinium fenestratum* and *Calamus* spp. could be useful in developing silvicultural systems for these species that are applicable to degraded and selectively logged forest habitats in the lowland wet zone of Sri Lanka. This study indicates that there is much variation in the densities of the two liana species and, in turn, the availability of these resources in different sites of the selectively logged forest and the forest fringe. This information is imperative to draw up guidelines for their sustainable extraction from the wild. The continued monitoring of the permanent plots demarcated in this study over a long period would further provide valuable information on the rate of growth, mortality and regeneration of these two liana species in their natural habitats.

References

- Anon. (1995), Sri Lanka Forestry Sector Master Plan, Colombo: Ministry of Agriculture, Land and Forestry.
- Ashton, P.M.S. (1992), 'Some Measurements of the Microclimate Within a Sri Lankan Tropical Rainforest', *Agricultural and Forest Meteorology*, 59: 217–35.
- Ashton, P.M.S. and G.P. Berlyn (1992), 'Leaf Adaptations of Some *Shorea* Species to Sun and Shade', *New Phytologist*, 121: 587–96.
- Ashton, P.M.S., S. Gamage, I.A.U.N. Gunatilleke and C.V.S. Gunatilleke (1997), 'Restoration of a Sri Lankan Rainforest: Using Caribbean Pine *Pinus caribaea* as a Nurse for Establishing Late Successional Tree Species', *Journal of Applied Ecology*, 34: 915–25.
- Bandara, M., K.U. Tennakoon and C.V.S. Gunatilleke (2004), 'Seed Biology of the Medicinal Liana *Coscinium fenestratum*', *Proceedings of the Forestry and Environment Symposium*, 10: 27.
- de Zoysa, N.D. and K. Vivekanadan (1991), *The Bamboo and Rattan Cottage Industry in Sri Lanka*. Colombo: Forest Department and IDRC.
- Gamage, S. (1998), 'Feasibility Studies on Underplanting Multiple Use Species in Buffer Zone Pine Plantations of the Sinharaja MAB Reserve', M. Phil. thesis. Sri Lanka: University of Peradeniya.
- Gómez-Pompa, A. and F.W. Burley (1991), 'The Management of Natural Tropical Forests', in A. Gómez-Pompa, T.C. Whitmore and M. Hadley (eds), *Rain Forest Regeneration and Management*, (volume 6), pp. 3–18. Paris: UNESCO; Carnforth: Parthenon Publishing Group.
- Gunatilleke, C.V.S. and P.S. Ashton (1987), 'New Light on Plant Geography of Ceylon, II. The Ecological Biogeography of Lowland Endemic Tree Flora', *Journal of Biogeography*, 14: 286–307.
- Gunatilleke, C.V.S., I.A.U.N. Gunatilleke and P. Abeygunawardena (1994), 'An Interdisciplinary Research Initiative towards Sustainable Management of Forest Resources in Lowland Rain Forest of Sri Lanka', *Journal of Sustainable Forestry*, 4: 95–114.
- Gunatilleke, I.A.U.N. and C.V.S. Gunatilleke (1996), *Sinharaja: World Heritage Site*. Colombo: National Science Foundation.
- Gunatilleke, I.A.U.N., P.M.S. Ashton, C.V.S. Gunatilleke and P.S. Ashton (1996), 'An Over View of Seed and Seedling Ecology of *Shorea* (Section Doona) Dipterocarpaceae', in I.M. Turner, C.H. Dlong, S.S.L. Lim and P.K.L. Ng (eds), *Biodiversity and the Dynamics of Ecology*, (DIWPA Series 1), pp. 81–102.

- Jayaweera, D.M.A. (1982), *Medicinal Plants Used in Ceylon: Part IV*. Colombo: National Science Council of Sri Lanka.
- Senerath, D.M.B.D. (1990), 'Biological Studies on *Coscinium fenestratum* Colebr. (Menispermaceae)', M. Phil. thesis. Sri Lanka: University of Peradeniya.
- Tennakoon, K.U., J.S. Pate and D. Arthur (1997), 'Ecophysiological Aspects of the Woody Root Hemiparasite *Santalum acuminatum* (R.Br.) A. DC. and its Common Hosts in South Western Australia', *Annals of Botany*, 80: 245–56.