Tropical Ecology **41**(2): 143-154, 2000 ISSN 0564-3295

Abundance and distribution of lianas in tropical lowland evergreen forest of Agumbe, central Western Ghats, India

ARJUN PADAKI & N. PARTHASARATHY*

Salim Ali School of Ecology and Environmental Sciences, Pondicherry University, Pondicherry 605 014, India

Abstract: Species diversity and density of all woody climbers (lianas) 5 cm gbh were inventoried in three one-hectare plots (at 650 m, 200 m and 100 m elevations) in the tropical lowland evergreen forest of Agumbe, in central Western Ghats, India. In all a total of 1,138 lianas belonging to 40 species were recorded. Mean liana density was 379 stems ha^{-1}. Plots 1, 2 and 3 contained 211, 668 and 259 lianas ha^{-1} respectively. Their corresponding species richness was 15, 24 and 24. The number of lianas twining over individual trees ranged from 1 to 3, but majority of the hosts supported only a single liana. Rutaceae and Papilionaceae were the most species-rich plant families of lianas followed by Annonaceae, Arecaceae, Caesalpiniaceae, Connaraceae, and Piperaceae. Twiners formed the bulk (>70%) of liana types followed by rattans and root climbers, while tendril and hook climbers were rare. Greater proportion of individuals was represented in the lower girth classes in all the plots. There was aggregated distribution of lianas on host trees in all the plots. Very few liana species showed any kind of association with host trees in the three plots indicating that the selection of hosts was largely random.

Resumen: Se realizaron inventarios de la diversidad de especies y la densidad de todas las trepadoras leñosas (lianas) $\geq$ 5 cm pap en tres parcelas de una hectárea (a altitudes de 650, 200 y 100 m) en el bosque tropical perennifolio de tierras bajas de Agumbe, porción central de los Gaths Occidentales, India. Se registraron en total 1,138 lianas pertenecientes a 40 especies. La densidad promedio de las lianas fue de 379 tallos ha^{-1}. Las parcelas 1, 2 y 3 tuvieron 211, 668 y 259 lianas ha^{-1}, respectivamente. Sus correspondientes riquezas específicas fueron 15, 24 y 24. El número de lianas trepadas sobre cada árbol varió entre 1 y 3, aunque la mayoría de los hospederos soportaban una única liana. Rutaceae y Papilionaceae fueron las especies de plantas más ricas en especies de lianas, seguidas por Annonaceae, Arecaceae, Caesalpinaceae, Connaraceae y Piperaceae. Las enredaderas conformaron la mayoría (70%) de los tipos de liana, seguidas de los ratanes y las trepadoras con raíces, mientras que las trepadoras con zarcillos y ganchos fueron raras. Una gran proporción de los individuos estuvo representada en las clases perimétricas bajas en todas las parcelas. En todas las parcelas hubo una distribución agregada de las lianas sobre sus hospederos. Muy pocas especies de lianas mostraron algún tipo de asociación con los árboles hospederos en las tres parcelas, indicando que la selección de hospederos es en gran medida aleatoria.

Resumo: A diversidade específica e a densidade de todas as trepadeiras lenhosas (lianas) com um PAP$\geq$ 5 cm foram inventariadas em três parcelas de 1 ha (650 m, 200 m e 100 m de elevação) na floresta sempre verde das zonas baixas de Agumbe na zona central dos Gates Ocidentais na Índia. No seu conjunto foram registadas 1138 lianas pertencendo a 40 espécies. A densidade media de lianas foi de 379 caules.ha^{-1}. As parcelas 1,2 e 3 continham 211, 688 e 259 lianas.ha^{-1}, respectivamente. A riqueza específica correspondente foi de 15, 24 e 24. O número de lianas entrelaçando-se em árvores individuais oscilou entre 1 a 3 se bem que a maioria das

**Corresponding Author:* E-mail: partha@pu.pon.nic.in

árvores só suportassem uma simples liana. As espécies mais representadas pertenciam à família das Rutacea e Papilionaceae seguindo-se as Annonaceae, Arecaceae, Caesalpinaceae, Connaraceae e Piperaceae. As enterlaçadoras formam a maior parte (>70%) dos tipos de liana, seguindo-se as rotins e trepadores radiculares, enquanto as lianas com gavinhas e as trepadeiras enganchadoras eram raras. A maior proporção de indivíduos estava representada na classe de perímetro mais baixa em todas as parcelas. Em todas as parcelas havia uma distribuição agregada de lianas nas árvores hospedeiras. Muito poucas lianas mostraram qualquer tipo de associação com árvores hospedeiras nas três parcelas de estudo indicando que a selecção de hospedeiros era, na sua maioria, casual.

Key words: Association, climbing mechanism, diversity, forest ecology, lianas, population structure.

Introduction

Lianas are woody climbing plants that rely on other plants for mechanical support. Their axes have reduced amounts of supporting tissue and they are highly light demanding. Lianas are a conspicuous and characteristic life-form in tropical rain forests and their high abundance is an important physiognomic feature differentiating tropical from temperate forests (Gentry 1991). There is an average ten-fold difference in liana density between temperate and lowland tropical forests, with a three-fold difference between the most liana-rich temperate forests and the most liana-poor lowland tropical ones (Gentry 1982). Forest locality and type appear to influence the distribution of climbers (Balfour & Bond 1993; Grubb 1987). Variations in reproduction, dispersal, climbing methods or phenology strategies help in sharing gaps and permit efficient resource partitioning between the liana species (Oldeman 1990).

A few quantitative ecological studies on lianas are available from the forests of Sarawak (Proctor *et al.* 1983; Putz & Chai 1987), Sabah, East Malaysia (Campbell & Newbery 1993), Queensland, Australia (Hegarty 1989, 1990), Hunter Valley, New South Wales (Chalmers & Turner 1994), Knysna, South Africa (Balfour & Bond 1993), Ituri, Congo (Makana *et al.* 1998), Costa Rica (Lieberman *et al.* 1996), Barro Colorado island, Panama (Putz 1984) and in the subtropical humid forest of Bolivia (Pinard *et al.* 1999). Such studies are lacking from Indian forests, except for the two recent works in the forest of Anamalais, Western Ghats (Muthuramkumar & Parthasarathy 2000; Srinivas & Parthasarathy 2000) and from the Kalrayan hills, Eastern Ghats (Kadavul & Parthasarathy 1999). Caballe (1998) analysed growth strategies of lianas with information gathered from over 400 liana species growing in 40 tropical forest sites in America, Africa and Mayotte, focussing on their growth strategies, anatomy and habitat features.

The main objectives of the present study were to compare the diversity, density and distribution of lianas as well as host trees in three different plots and to check for possible associations between lianas and host trees.

Study area

The study was carried out in the tropical lowland evergreen forest of Agumbe (13°31 N & 75°06 E) in Dakshina Kannada district of Karnataka state, India (Fig. 1a). These forests are classified as tropical wet evergreen forests of the *Dipterocarpus indicus - Humboldtia brunonis - Poeciloneuron indicum* type (Pascal 1988). Champion & Seth (1968) have classified these as 'west coastal tropical evergreen forest'.

Three 1 ha plots, situated at different altitudes, were inventoried (Fig. 1b). Plot 1, which was at an altitude of 650 m was the highest point near Agumbe town. The plot was relatively undisturbed with no signs of recent anthropogenic activities such as felling or burning. Plot 2 located at 200 m, was subjected to certain degree of disturbance due to illegal logging. The proximity of this plot and plot 3 to the nearby town, Someshvara may have been a determining factor for such exploitation. Plot 3 was located in the valley region at an altitude of 100 m and there were evidences of litter removal, grazing and logging. Each year, forest litter is removed periodically prior to the

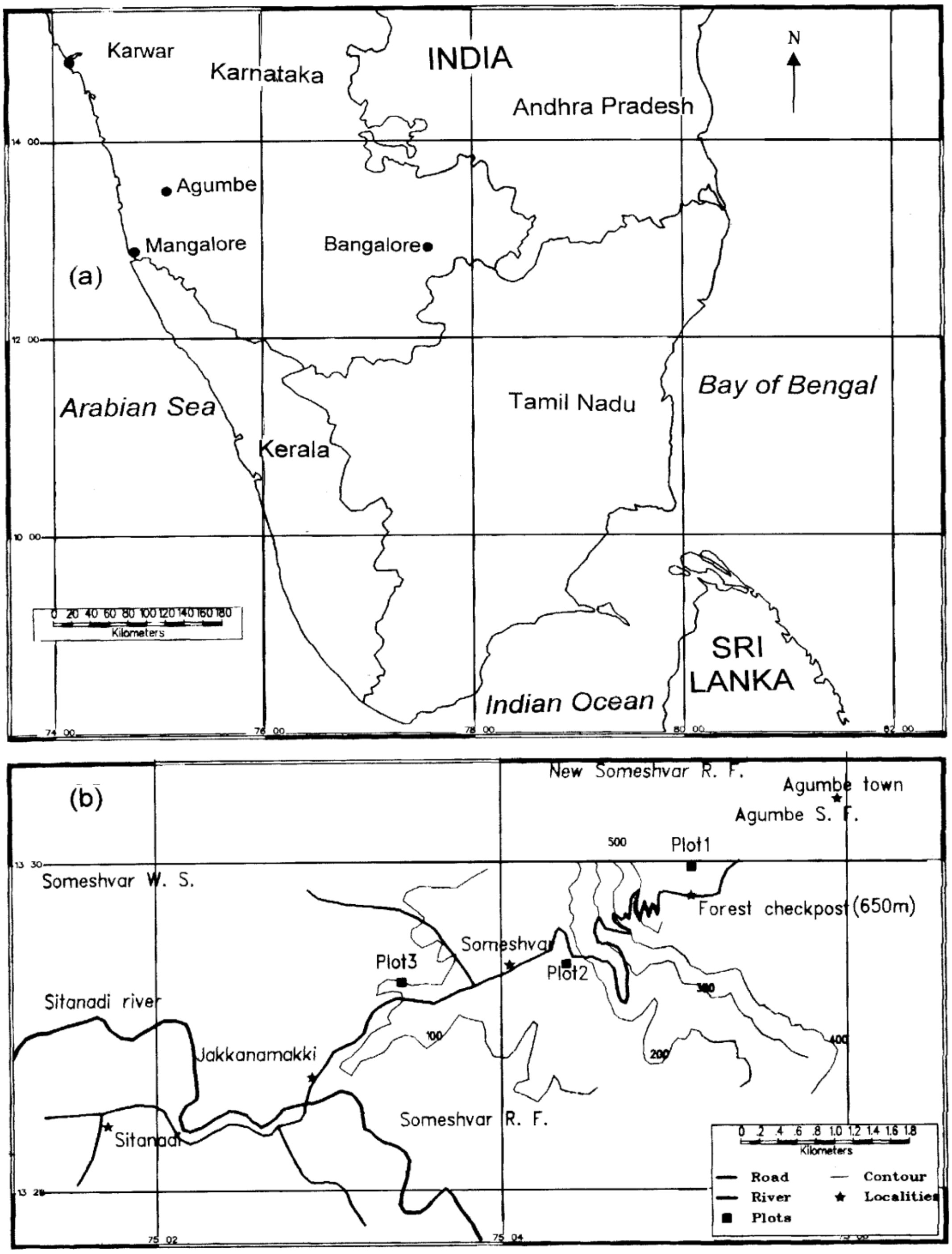

Fig. 1. (a) Locality map of Agumbe in south India; (b) Distribution of the three study plots.

onset of monsoon rains and used as organic manure for lands.

Climate

The climate of peninsular India is largely controlled by the monsoons. The southwest monsoon begins at Agumbe in the first week of June. Precipitation is much greater in the latitude of Agumbe. The mean annual rainfall in the Agumbe region is between 7000-7500 mm. The rains last up to November. During the wet season, there is almost continuous cloud cover and high humidity. The dry period lasts for duration of nearly five months.

The mean annual temperature at Agumbe is 22°C. During the dry season, the dominant winds are from the north-east corresponding to dry trade winds which blow over India. The winds are never violent in these regions and the average wind velocity is between 3.8 km h^{-1} and 8.8 km h^{-1}.

Methods

The study was conducted within three 1 ha plots of lowland evergreen forest. Each one ha plot was subdivided into one hundred 10 m x 10 m contiguous grids. Liana stems 5 cm gbh were examined on every tree 10 cm gbh within the grids. Girth measurements of lianas were made at 1.3 m from their base. Rattans were omitted for girth measurement due to practical difficulties induced by their spiny nature. Voucher specimens were collected, identified using regional and local floras (Cooke 1967; Gamble & Fischer 1915-35; Hooker 1872-1897; Pascal & Ramesh 1987) and lodged in the herbarium of Salim Ali School of Ecology, Pondicherry University. Climbers that were encountered were categorized as follows:

(a) *Twiners*: these include stem as well as branch twiners where, either the tip of the young stem is able to revolve so that the plant becomes securely wound round its supports or the leaf bearing branches twine around the supports.

(b) *Hook climbers and stragglers*: these possess hooks that passively assist them in climbing or lean on the hosts without attachment.

(c) *Rooting climbers*: attachment is by means of aerial roots and they cling to the surface over which the plant grows.

(d) *Tendril climbers*: possess organs of varied morphology, sensitive to contact with a support to which they fix themselves actively, usually by curling round it.

(e) *Rattans (climbing palms)*: possess recurved spines, which help in attachment to supports.

Liana stems were recorded as individuals only if they rooted within the sampling grid and not otherwise. All trees 10 cm gbh, which provided any means of support (such as the trunk or branches) to liana stems, were considered as hosts.

Diversity was estimated using the Shannon index (H) as in Krebs (1989):

$$H = - {}_{i\quad 1}^{\quad s} (pi)\,(\log_2 pi)$$

where, s = No. of species, pi = Proportion of total sample belonging to i^{th} species

Evenness was calculated as in Krebs (1989) :

$$\text{Evenness} = \frac{Ni}{S}$$

where, Ni = eH = No. of equally common species, S = No. of species observed in sample

The Jackknife estimate (Heltshe & Forrester 1983) was used to determine the total species richness in each of the three plots. Spatial patterns of liana species with >15 individuals were arrived at using the variance-mean method as per Krebs (1989). The degree of inter-specific association between lianas and hosts was also determined (Ludwig & Reynolds 1988). The bark texture of host tree species was determined and classified as (1) smooth and (2) rough, the surface being scaly or with fissures, along with occasional flaking. Associations between the different climbing types of lianas and rough or smooth barked nature of host trees were established.

Results

Lianas

Density and basal area

A total of 1138 lianas 5 cm gbh were enumerated in the three plots. The mean liana density was 379 stems ha^{-1} on trees 10 cm gbh. Plot 2 had greater abundance of lianas than the other two plots (Table 1). The basal area of lianas in plot 1 was least (0.109 m^2 ha^{-1}) whereas in plot 2 and plot 3 they were more or less equal (0.417 $m^2 ha^{-1}$). This is three-fold more than that of plot 1.

Diversity

Species-area curves were plotted by sequential summing of 100 x 10 m (0.1 ha) subplots by serpenting between one side to the other (as in Annaselvam & Parthasarathy 1999; Parthasarathy 1999). The curves varied for the three plots (Fig. 2). Only in plot 1, the curve reached an asymptote at the 1 ha scale, while it did not stabilize in plot 2 and plot 3.

A total of 40 species of lianas were enumerated (Appendix 1) of which three remained unidentified. The Shannon diversity index was greatest for plot 1, intermediate for plot 3 and least for plot 2 (Table 1). The evenness measures followed a similar trend, with plot 1 having higher evenness. The Jackknife estimate of the range of species richness for plot 1 is 16 to 24 (var = 4.7) for plot 2 it is 15 to 25 (var = 4.7) for plot 2 it is 15 to 25 (var = 6.4) and 14 to 26 (var = 9) for plot 3.

Table 1. Floristic comparison of lianas and host trees in the three study plots of tropical lowland evergreen forest in Agumbe, central Western Ghats, India.

	Plot 1 650 m	Plot 2 200 m	Plot 3 100 m
Lianas			
Density (stems ha^{-1})	211	668	259
Number of species	15	24	24
Number of families	11	20	23
Basal area (m^2 ha^{-1})	0.142	0.417	0.417
Shannon diversity index	0.764	0.686	0.759
Evenness	0.650	0.497	0.550
Host trees			
Number of individuals	205	164	132
Number of species	15	25	28
Number of families	12	19	18
Percentage trees as hosts	13.0	26.2	13.2

Similarity

Of the 40 species encountered in the three plots only 10% were common to all plots. The number of species common to plot 2 and plot 3 (41%) was greater than that of plot 1 and plot 2 (22%), and plot 1 and plot 3 (19%). The number of unique species (occurring in only one plot) in plot 1, plot 2 and plot 3 was 6, 7 and 8 respectively. The species composition with respect to evergreen and deciduous species differed in the three plots. There was a predominance of evergreen species in each of the plots. Deciduous species were absent in plot 1 and low numbers were found in plot 2 and plot 3.

Spatial patterns and frequency distribution of lianas

In plot 2 the variance mean ratios were high for the three species irrespective of the area under consideration, suggesting clumped distributions. The spatial patterns of species in plot 1 and plot 3 varied at differing scales (Table 2).

Table 2. Spatial patterns of lianas in the three plots reflected by variance/mean values.

	Variance/mean value and dispersion pattern		
Area (ha)	0.16	0.64	1.0
Plot 1			
Kunstleria keralense	0.50(r)	1.33(c)	1.33(c)
Ventilago madraspatana	1.44(c)	1.14(c)	1.06(r)
Calamus gamblei	3.32(c)	1.84(c)	1.71(c)
Rourea santaloides	0.95(r)	1.20(c)	1.14(c)
Plot 2			
Calamus thwaitesii var. *canarana*	1.39(c)	1.64(c)	2.07(c)
Ancistrocladus heyneanus	1.39(c)	1.65(c)	1.72(c)
Smilax sp.	1.58(c)	2.58(c)	2.56(c)
Piper nigrum	1.52(c)	1.19(c)	1.34(c)
Plot 3			
Canthium angustifolium	1.1(r)	1.9(c)	2.0(c)
Alangium salvifolium subsp. *hexapetalum*	0.9(r)	1.3(c)	1.0(r)
Piper nigrum	0.9(r)	1.1(r)	1.0(r)
Strychnos dalzellii	1.4(c)	1.2(c)	1.0(r)

c = clumped, r = random

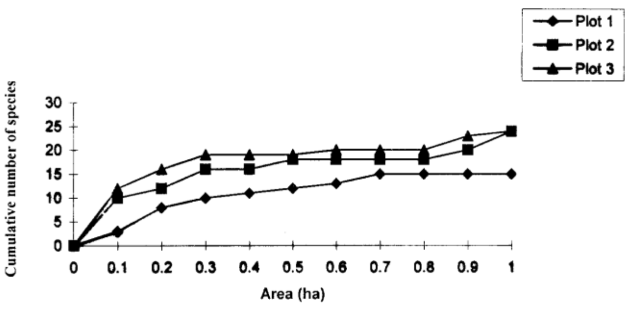

Fig. 2. Species-area curves for the three plots in Agumbe, central Western Ghats, India.

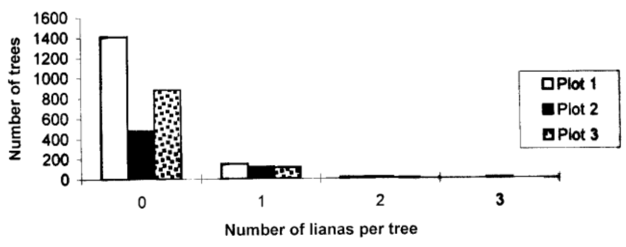

Fig. 3. Frequency distribution of lianas on trees 10 cm gbh for the three plots in Agumbe, Western Ghats, India.

The frequency distribution of lianas on trees 10 cm gbh (Fig. 3) shows that the number of lianas per tree ranged from 1 to 3 with most of the trees supporting only a single liana. The mean number of lianas per tree was 1.16 in plot 1, 1.86 in plot 2 and 2.2 in plot 3. When the frequency distribution of lianas on host trees was compared with that of the Poisson distribution using the chi-square goodness of fit test, there found to be marked departures from randomness in all the three plots (Plot 1, ^{2} = 2.58; df = 2; P <0.05; Plot 2, ^{2} = 4.8; df = 2; P <0.05 and Plot 3, ^{2} = 2.71; df = 2; P <0.05). The measures of departure from the Poisson distribution suggested possible clumping or aggregation and this was corroborated by the parameter k of the negative binomial distribution which indicated high degrees of liana aggregation on host trees in all three plots (Table 3).

Table 3. Degree of liana aggregation on trees 10 cm gbh in the three plots as determined by the parameter k of the negative binomial distribution and the ^{2} test.

	Plot 1	Plot 2	Plot 3
n	1576	625	1001
$\bar{x}$	0.112	0.262	0.121
s^2	133.1	96.9	110.1
k	2.52	4.94	3.96
^{2}	0.96	2.23	4.43

Girth-class distribution

Greater proportions of individuals in the stand were represented in the lower girth classes in all the plots (Fig. 4a, b & c). The girth-class distribution of individual species did not vary much from that of the whole forest stand. Most of the species had lower girth class representation of individuals and in some the higher girth classes were not represented at all (Fig. 5a, b, c, d, e & f).

Climbing nature of lianas

There was a significant variation in the number and types of climbers in the three plots (Table 4). All the five climbing types were represented in plot 2 and plot 3 and three in plot 1. Twiners, rooting climbers and rattans occurred in all three plots and hook climbers together with tendril climbers were present only in plot 2 and plot 3. There was a greater proportion of twiners in plot 1 (88%) and plot 3 (85%) where as in plot 2, rattans contributed the most (61%). Among the twiners, *Alangium salvifolium, Moullava spicata, Mimosa intsia, Canthium angustifolium, Paramignya monophylla* and *Luvunga sarmentosa* possess spines, which aid in climbing. There were only few species which frequently attained canopy height and these included *Bauhinia phoenicea, Gnetum ula, Opilia amentacea* and *Smilax* sp.

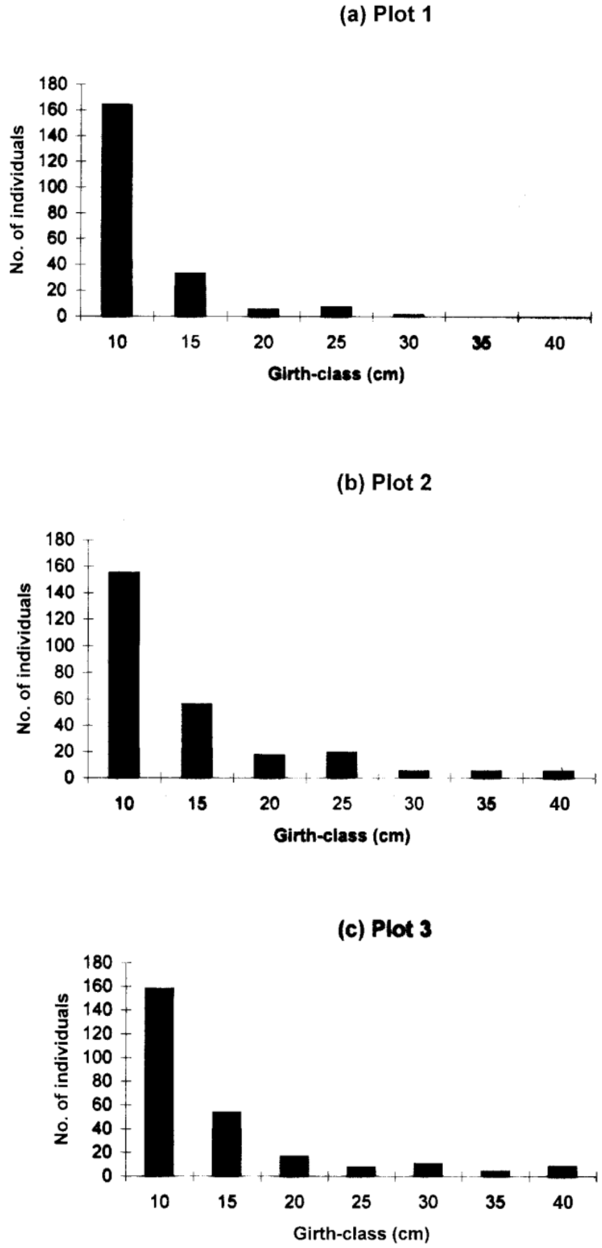

Fig. 4 (a-c). Girth-class distribution of liana individuals in plots 1, 2 and 3 respectively in Agumbe, Western Ghats, India.

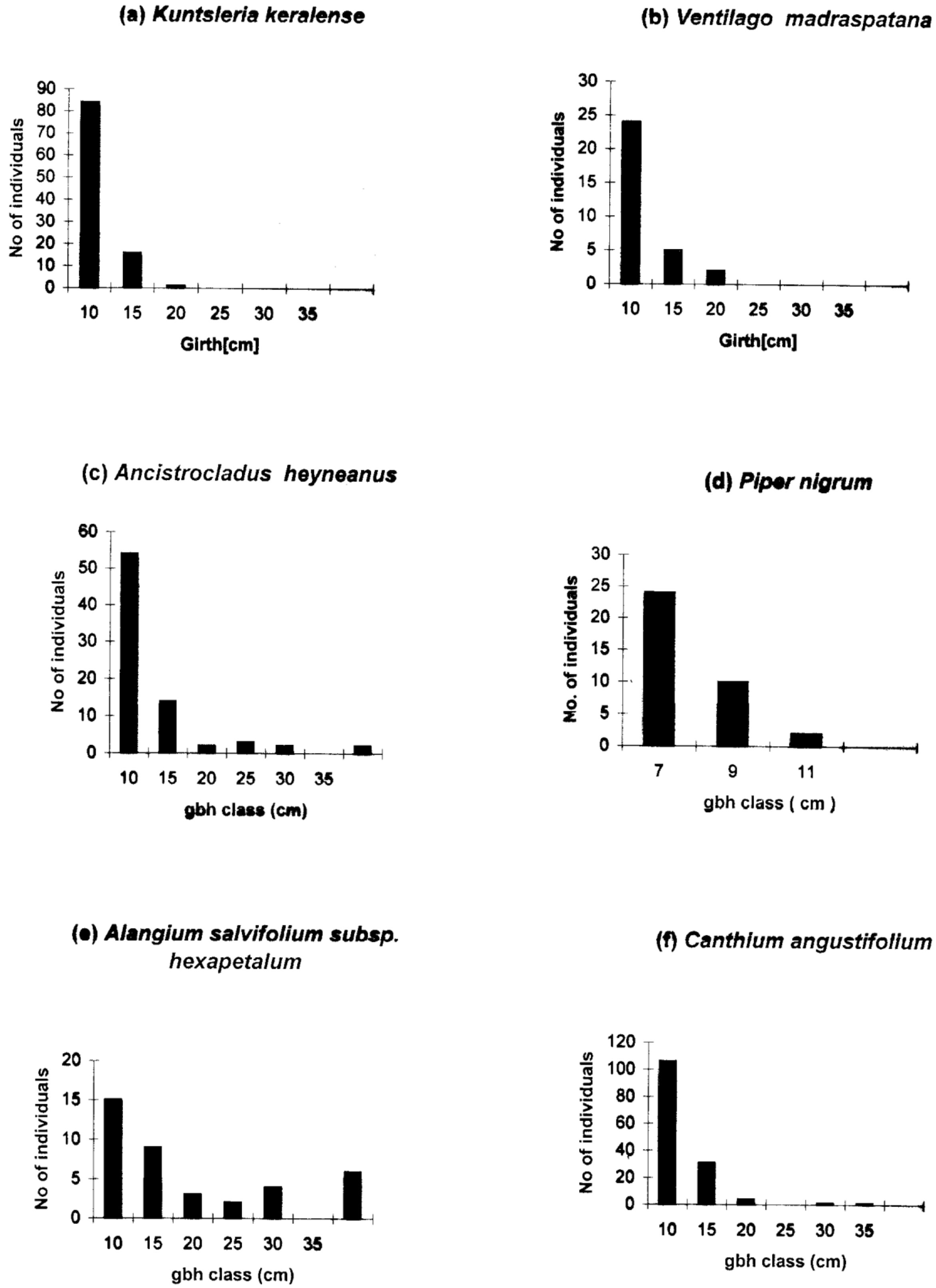

Fig. 5 (a-f). Girth-class distribution of liana species in plots 1, 2 and 3 in Agumbe, Western Ghats, India.

Trees

Host composition

The total number of trees (10 cm gbh) enumerated in the three plots was 3202 (Srinivas & Parthasarathy 2000). Of these, the total number of hosts 10 cm gbh in the three plots was 501. Their density and species richness varied (Table 1). *Poeciloneuron indicum* was the dominant host in plot 1 followed by *Reinwardtiodendron anamallayanum* and *Palaquium ellipticum*. In plot 2, *Knema attenuata* and *Dimocarpus longan* were more abundant followed by *Hydnocarpus pentandra* and in plot 3 the predominating hosts included *Hopea parviflora* and *Nothopegia beddomei* (Table 5).

Table 4. Percentage individuals belonging to different climber types and to different bark types of host trees.

	Percentage individuals		
	Plot 1	Plot 2	Plot 3
Climber type			
Twiner	88	14	85
Hook	0	15	2
Tendril	0	5	5
Root	3	6	8
Rattan	9	61	1
Host tree bark type			
Smooth	95	53	54
Rough	5	47	46

Table 5. Dominant host tree species in the three one hectare plots.

	Species	% trees as hosts
Plot 1	*Poeciloneuron indicum*	23
	Palaquium ellipticum	11
	Reinwardtiodendron anamallayanum	9
Plot 2	*Hydnocarpus pentandra*	93
	Dimocarpus longan	71
	Knema attenuata	66
Plot 3	*Knema attenuata*	26
	Nothopegia beddomei	22
	Hopea parviflora	20

Liana-host associations

Liana-host associations were reflected only in plot 1 and plot 3. In plot 1 the exclusive co-occurrence of *Poeciloneuron indicum* and the liana *Kunstleria keralense* suggested possible associations between the two. The association analysis, based on presence-absence data for the two species revealed a positive association (^{2} = 24.83, df = 1, P <0.05). Further, when their proportions were compared a high degree of association was indicated (^{2} = 18.54, df = 9, P <0.05). None of the other species showed any association with host trees.

In plot 3, *Canthium angustifolium* showed high degrees of association with *Nothopegia beddomei* (^{2} = 34.96, df = 9, P <0.05) and *Memecylon terminale* (^{2} = 20.61, df = 9, P <0.05).

Associations between the various liana climbing types and the bark texture of host trees revealed that in plot 1, twiners and smooth-barked trees showed positive associations (^{2} = 2.58; df = 2; P <0.05), whereas in the other two plots such associations were not reflected.

Discussion

The higher density of lianas in plot 2 (Table 1) is largely due to the presence of the rattan, *Calamus thwaitesii* var. *canarana* which contributed to 60% of all lianas in the plot. In addition, disturbances due to anthropogenic activity such as selective logging of *Vateria indica* were greater in plot 2. This supports the view that most lianas are light demanding and grow well in natural and man-made clearings, especially in logged forests (Putz 1984).

A wide variation in research objectives, methods used, plot size and the diameter considered, makes comparison of liana data across the tropics difficult. Table 6 compares the abundance of lianas in Indian and Malaysian forests. The species richness of lianas in each of the Agumbe plots falls within the ranges of the Jackknife estimate with increasing variance from plot 1 to plot 3. The Shannon diversity index was used specifically, since this index rates the rare species more heavily than those abundant.

More number of species were common to plot 2 and plot 3 (41%) than between the other plots, indicating lower variation of species between these two plots. Also, the number of unique species did not vary significantly between the three plots. The

Table 6. Liana abundance stratified by dbh in Indian and Malaysian forests.

Author(s)	Location and forest type	Liana (no. ha^{-1})		
		>1cm	>2cm	>5cm
Proctor *et al.* (1983)	Gunung Mulu National Park, Sarawak, Malaysia			
	1. Dipterocarp forest (ridge)	440		
	2. Dipterocarp forest (valley)	1960		
Putz & Chai (1987)	Lambir National Park, Sarawak, Malaysia			
	1. Dipterocarp forest (ridge)	228	164	2
	2. Dipterocarp forest (valley)	554	348	52
Campbell & Newbery (1993)	Lowland rain forest of Sabah, East Malaysia			
	1. Dipterocarp forest (Plot 1)		928*	
	2. Dipterocarp forest (Plot 2)		836*	
Muthuramkumar & Parthasarathy (2000)	Tropical evergreen forest	373		
	Varagalaiar, Anamalais, Western Ghats, India			
Kadavul & Parthasarathy (1999)	Tropical semi-evergreen forest			139
	Kalrayan hills, Eastern Ghats, India			93
Present study	Agumbe, central Western Ghats, India			
	Plot 1			211**
	Plot 2			668**
	Plot 3 (valley)			259**

* 2 cm gbh ** 5 cm gbh

predominance of evergreen species in all the plots may be indicative of the high amount of rainfall the area receives.

The clumped distribution of lianas in plot 2 may be attributed to the overall high density of the plot. On the other hand the spatial patterns of lianas in plot 1 and plot 3 do not follow a density gradient. The high degrees of liana aggregation on host trees in each of the plots may suggest that lianas present on a given host influence other lianas in infesting the same host.

The girth-class distribution of lianas (Fig 4a, b & c) follows a typical reverse J-shaped distribution. Higher proportions of individuals are represented in the lower girth classes in all the plots, indicating the low girth potential of lianas, as compared to trees within the same forest. Lianas are known to have extremely slow stem diameter increments because they allocate more resources for vertical growth (see also Putz *et al.* (1989). Large woody climbers were found to occur only in plot 2 and plot 3. The girth-class distribution of selected liana species (Fig. 5a-f) does not vary much from that of the combined pattern of all lianas in the forest stand. In some, the higher girth classes have not been represented at all probably indicating that the forest stand is either young or has attained the maximum girth limit. In Plot 3 there were 141 saplings and these predominantly included *Ancistrocladus heyneanus* and *Canthium angustifolium*. This probably indicates early stages of recovery following new recruitment of individuals.

A liana's climbing technique and the distance it can span between supports determine the forest structure required for successful growth to the canopy (Putz 1984). Five types of climbers were encountered in plot 2 and plot 3 whereas in plot 1 only three of these were represented. This difference in the number of climbing types between the plots corresponds with the difference in species richness of lianas and hosts. Rattans were more abundant in plots 1 and 2 than in plot 3 which was located in the valley. This is supportive of the findings of Putz & Chai (1987) wherein they reported greater abundance of rattans in the valleys of Malaysian rain forest.

The species composition of host trees varied among the plots. The dominance of *Poeciloneuron indicum* in plot 1 and its susceptibility to liana invasion may be attributed to a combination of many factors such as the presence of characteristic stilt roots providing easy access to the main trunk, proximity between individuals and the sheer abundance of the species in the stand. It was observed that the number of liana stems reaching trees from other trees was quite low in all the three plots indicating that most lianas reach tree crowns from the ground or from lower-stature trees rather than from neighbouring trees of similar stature.

Inter-specific association analysis based on presence-absence, as well as that based on the proportions of lianas and hosts, both, reflect high degrees of association between *Kuntsleria keralense* and *Poeciloneuron indicum* in plot 1. The monodominance of *Poeciloneuron indicum* (49% of stand tree density) could be a likely factor. In plot 3, *Canthium angustifolium* was not found to climb emergent species and had high degrees of association with *Nothopegia beddomei* and *Memecylon terminale*, both occurring in the understorey layer. None of the other liana species were indicated to have any sort of preference for a particular host tree species. The selection of hosts of particular species was thus concluded to be largely random.

Many of the existing liana inventories in tropical lowland rainforests are from the forests in Malaysia (Table 6). Very few inventories are available from the Western and Eastern Ghats of India. The Agumbe plots tend to have greater abundances of lianas compared to Lambir National Park, Malaysia.

Disturbance usually leads to the proliferation of lianas (Putz 1984; Putz & Chai 1987; Webb 1958; Wyatt-Smith 1954). In the study carried out by Proctor *et al.* (1983) in Gunung Mulu N.P. lianas were found to be extremely abundant and one of the possible factors was explained to be treefall frequency due to river water inundation. Plots 2 and 3 were subjected to logging and may partly explain the increase in diversity and abundance of lianas in these plots. Other influencing factors may include soil fertility, site history and rainfall.

References

Annaselvam, J. & N. Parthasarathy. 1999. Inventories of understorey plants in a tropical evergreen forest in the Anamalais, Western Ghats, India. *Ecotropica* **5**: 197-211.

Balfour, D.A. & W.J. Bond. 1993. Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* **11**: 93-99.

Caballe, G. 1998. Self-supporting capacity of tropical lianas: growth strategies. *Canadian Journal of Botany* **76**: 1703-1716.

Campbell, E.J.F. & D. McC. Newbery. 1993. Ecological relationships between lianas and trees in lowland rain forest in Sabah, East Malaysia. *Journal of Tropical Ecology* **9**: 469-490.

Chalmers, A.C. & J.C. Turner. 1994. Climbing plants in relation to their supports in a stand of dry rainforest in the Hunter Valley, New South Wales. *Proceedings of the Linnean Society* NSW **114**: 73-89.

Champion, H.G. & S.K. Seth. 1968. *A Revised Survey of the Forest Types of India*. Government of India Press.

Cooke, T. 1967. *The Flora of the Presidency of Bombay*. 3 Vols. (Rep. ed.) Botanical Survey of India, Calcutta.

Gamble, J.S. & C.E.C. Fischer. 1915-35. *Flora of the Presidency of Madras*. 3 Vols. Secretary of State for India, London.

Gentry, A.H. 1982. Patterns of neo-tropical plant species diversity. *Evolutionary Biology* Vol. 15. *In*: M.K. Hecht, B. Wallace & G.T. Prance (eds.) Plenum Publishing Corporation.

Gentry, A.H. 1991. The distribution and evolution of climbing plants. pp. 3-49 *In*: F.E. Putz & H.A. Mooney (eds.) *The Biology of Vines*. Cambridge University Press, Cambridge.

Grubb, P.J. 1987. Global trends in species-richness in terrestrial vegetation: a view from the northern hemisphere. pp. 24-27. *In*: J.H.R. Gee & P.S. Giller (eds.) *Organization of Communities - Past and Present*. Blackwell Scientific Publications, Oxford.

Heltshe, J.F. & N.E. Forrester. 1983. Estimating species richness using jackknife procedure. *Biometrics* **39**: 1-11.

Hegarty, E.E. 1989. The climbers - lianes and vines. pp. 339-353. *In*: H. Leith & M.J.A. Werger (eds.) *Tropical Rainforest Ecosystems: Biological and Ecological Studies*. Ecosystems of the world. Vol. 14B, Elsevier, Amsterdam.

Hegarty, E.E. 1990. Leaf life span and leafing phenology of lianes and associated trees during a rainforest succession. *Journal of Ecology* **78**: 300-312.

Hooker, J.D. 1872-1897. *The Flora of British India*. Vols. I-VII L. Reeve & Co. London.

Kadavul, K. & N. Parthasarathy. 1999. Lianas in two tropical semi-evergreen forest sites on the Kalrayan hills, Eastern Ghats, South India. *Tropical Biodiversity* **6**: 197-208.

Krebs, C.J. 1989. *Ecological Methodology*. Harper and Row, New York, USA.

Lieberman, D., M. Lieberman, R. Peralta & G.S. Hartshorn. 1996. Tropical forest structure and composition on a largescale altitudinal gradient in Costa Rica. *Journal of Ecology* **84**: 137-152.

Ludwig, J.A. & J.F. Reynolds. 1988. *Statistical Ecology*. Wiley, New York.

Makana, J.R., T.B. Hart & J.A. Hart. 1998. Forest structure and diversity of lianas and understorey treelets in monodominant and mixed stand in the Ituri forest, Democratic Republic of the Congo. pp. 429-446 *In*: F. Dallmeir & J.A. Comiskey (eds.) *Forest Biodiversity Research Monitoring & Modeling: Conceptual Background and Old World Case Studies*. Parthenon Publishing Co., Paris.

Muthuramkumar, S. & N. Parthasarathy. 2000. Alpha diversity of lianas in a tropical evergreen forest in the Anamalais, Western Ghats, India. *Diversity and Distributions* **6**: 1-14.

Oldeman, R.A.A. 1990. *Forests: Elements of Silvology*. Springer-Verlag, Hiedelberg.

Parthasarathy, N. 1999. Tree diversity and distribution in undisturbed and human-impacted sites of tropical wet evergreen forest in southern Western Ghats, India. *Biodiversity and Conservation* **8**: 1365-1381.

Pascal, J.P. & B.R. Ramesh. 1987. *A Field Key to the Trees and Lianas of the Evergreen Forests of the Western Ghats (India).* French Institute, Pondicherry, India.

Pascal, J.P. 1988. *Wet Evergreen Forests of Western Ghats of India: Ecology, Structure, Floristic Composition and Succession*. Ph.D. Thesis, University of Toulouse, France.

Pinard, M.A., F.E. Putz & J.C. Licona. 1999. Tree mortality and vine proliferation following a wildfire in a subhumid tropical forest in eastern Bolivia. *Forest Ecology and Management* **116**: 274-252.

Proctor, J., J.M. Anderson, P. Chai & H.W. Vallack. 1983. Ecological studies in four contrasting lowland rain forests in Gunung Mulu National Park, Sarawak. I. Forest environment, structure and floristics. *Journal of Ecology* **71**: 237-260.

Putz, F.E. & P. Chai. 1987. Ecological studies of lianas in Lambir National Park, Sarawak. *Journal of Ecology* **75**: 523-531.

Putz, F.E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **65**: 1713-1724.

Putz, F.E., H.A. Mooney & S.H. Bullock. 1989. Biology of vines. *Trends in Ecology and Evolution* **4**: 224.

Srinivas, V. & N. Parthasarathy. 2000. Comparative analysis of tree diversity and dispersion in the tropical lowland evergreen forest of Agumbe, Central Western Ghats, India. *Tropical Biodiversity* **7**: (in press).

Webb, L.J. 1958. Cyclones as an ecological factor in tropical lowland rainforest, North Queensland. *Australian Journal of Botany* **6**: 220-228.

Wyatt-Smith, J. 1954. Storm forest in Kelantan. *Malaysian Forester* **17**: 5-11.

Appendix 1. List of liana species and their climbing mechanism recorded in the three study plots in Agumbe, central Western Ghats, India.

Family	Species	Climbing mechanism
Alangiaceae	*Alangium salvifolium* (L.) Wang Subsp. *hexapetalum* (L.) Wang	Twining
Ancistrocladaceae	*Ancistrocladus heyneanus* Graham	Hook
Annonaceae	*Unona viridiflora* Bedd.	Twining
	Artabotrys zeylanicus J.D. Hook & Thoms.	Hook
Apocynaceae	*Chonemorpha fragrans* (Moon) Alston	Twining
Araceae	*Raphidophora laciniata* (N. Burm.) Merrill	Rooting
	Pothos scandens L.	Rooting
Araliaceae	*Schefflera venulosa* (Wight & Arn.) Harms	Twining
Arecaceae	*Calamus gamblei* Becc.	Rattan
	Calamus thwaitesii var. *canarana* Becc. & J.D. Hook	Rattan
Caesalpiniaceae	*Moullava spicata* (Dalz.) Nicolson	Twining
	Bauhinia phoenicea Wight & Arn.	Twining
Celastraceae	*Salacia beddomei* Gamble	Twining
Combretaceae	*Calycopteris floribunda* (Roxb.) Poir	Twining
Connaraceae	*Rourea santaloides* Wight & Arn.	Twining
	Connarus sclerocarpus (Wight & Arn.) Schellenb.	Twining
Gnetaceae	*Gnetum ula* Brongn.	Twining
Icacinaceae	*Sarcostigma kleinii* Wight & Arn.	Twining
Liliaceae	*Smilax* sp.	Tendril
Linaceae	*Hugonia ferruginea*	Hook
Loganiaceae	*Strychnos dalzellii* C.B. Clarke	Tendril
Malpighiaceae	*Hiptage benghalensis* Kurz	Twining
Menispermaceae	*Coscinium fenestratum* Colebr.	Twining
Mimosaceae	*Mimosa intsia* L.	Twining
Opiliaceae	*Opilia amentacea* Roxb.	Twining
Papilionaceae	*Derris heyneana* (Wight & Arn.) Benth.	Twining
	Derris thyrsiflora Benth. var. *eualata* (Bedd) Thoth.	Twining
	Kunstleria keralense (C.N. Mohanan & N.C. Nair)	Twining
Piperaceae	*Piper nigrum* L.	Rooting
	Piper sp.	Rooting
Rhamnaceae	*Ventilago madraspatana* Gaertn.	Twining
Rubiaceae	*Canthium angustifolium* Roxb.	Twining
Rutaceae	*Paramignya monophylla* Wight	Twining
	Paramignya armata (Thw.) Oliver	Twining
	Luvunga sarmentosa (Blume) Kurz	Twining
Tiliaceae	*Grewia rhamnifolia* Heyne ex Roth	Twining
Vitaceae	*Cayratia* sp.	Tendril
Unidentified 1		Twining
Unidentified 2		Twining
Unidentified 3		Twining