

THE NATURAL HISTORY OF LIANAS ON BARRO COLORADO ISLAND, PANAMA¹

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Abstract. Liana (woody vine) abundance, height, diameter, and climbing mode were studied in the mature tropical moist forest on Barro Colorado Island, Panama (BCI). Because lianas are capable of extended horizontal as well as vertical growth, sample plots were 100-m² cylinders extending from the ground up to the treetops. The plots were randomly located in areas representing different stages of regeneration following treefalls. In order to examine canopy lianas closely, trees in or adjacent to the sample plots were climbed freehand or with the aid of mechanical rope ascenders.

Lianas are abundant on BCI and play important roles in forest dynamics. A hectare of old-growth forest had 1597 climbing lianas distributed among 43% of the canopy trees. Trees with at least one liana had a higher than random probability of having more than one liana, and individual lianas connected an average of 1.56 canopy trees. In the understory, 22% of the upright plants <2 m tall were lianas, and, depending on the species, between 15 and 90% of these plants were vegetative offshoots (ramets) and not true seedlings (genets). Lianas were most abundant in recent treefall gaps and decreased in abundance with time since last disturbance.

Trellis availability was found to be a major factor limiting liana access to the forest canopy. Experimental manipulation of supports and experimental planting of *Dioclea reflexa* seedlings revealed that trellises consisting of small diameter, closely spaced supports are most abundant on the edges of treefall gaps. Tree and liana stems on the edges of treefall gaps provided a major pathway to the canopy for climbing plants.

Trees carrying lianas suffered higher mortality rates and upon falling caused more other trees to fall than did liana-free trees. Few lianas died when their host tree fell, and many grew back to the canopy using the abundant trellises that occur on the edges of treefall gaps. Tree sapling growth rates in treefall gaps and *Luehea seemannii* growth rates in the canopy were slower where lianas were abundant.

Key words: forest dynamics; forest ecology; gaps; lianas; tropical ecology; vines.

INTRODUCTION

Lianas (woody vines or climbers) epitomize tropical forests. Although present in temperate forests, lianas are more abundant, are more diverse, and present a wider variety of shapes and sizes in the tropics (see, for example, Schenck 1892, Spruce 1908, Bates 1910, Givnish and Vermeij 1976). Because of the problems of working in species-rich forests on extremely tall plants that grow horizontally as well as vertically, ecologists have paid little attention to lianas.

Approximately one-half of the families of vascular plants contain climbing species (Schenck 1892). In some families nearly all of the species are climbers, Hippocrateaceae and Vitaceae being familiar examples. The climbing habit apparently evolved independently in a diverse array of taxa including the Gymnospermae (Gnetaceae), Monocotyledonae (e.g., Palmae), and the Dicotyledonae (e.g., Bignoniaceae).

In tropical forests there are generally many lianas representing many different species. For example, Croat (1978) lists 175 species of lianas on Barro Colorado Island, Panama, 45% of the recorded plant species that grow to be >10 m tall. Although liana biomass generally represents <10% of total forest biomass, up to 40% of the leaves in a forest can be liana leaves (Ogawa

et al. 1965, Klinge and Rodrigues 1974, Kato et al. 1978, Putz 1983b).

Most lianas are light-demanding and grow well in natural and man-made clearings, especially in logged forests. Abundant lianas are a nuisance to tropical foresters, and the tropical forestry literature abounds in accounts of liana damage to advanced growth during felling (Fox 1968) and suppression of tree regeneration after logging (e.g., Nicholson 1958, Dawkins 1961, Kochummen 1966, Fox 1968). The silvicultural treatment usually recommended for liana control is to cut and poison all climbers after logging (Foggie 1960, Taylor 1962, Smith and Smithson 1975). This expensive operation (Liew 1973) is often ineffective because of the ability of lianas to sprout roots and shoots from fallen and cut stems (Gentry 1978). There is also the problem of contamination from the poisons. Knowledge of how trees regenerate in liana-rich forests after natural disturbances could lead to the design of effective, inexpensive, and ecologically sound liana control techniques.

This paper concerns some of the roles lianas play in mature tropical forest. I present data on the abundance of lianas in the forest on Barro Colorado Island and on how liana abundance and species composition change as forest regenerates in treefall gaps. I then discuss how liana trellis requirements and forest structure interact to influence both the horizontal and the ver-

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tical distribution of lianas in the forest. Finally, I examine the effects of lianas on tree growth, tree mortality rates, and the sizes of gaps opened by falling trees.

STUDY SITE

The study was conducted on Barro Colorado Island (BCI), a 15.6-km² island isolated from the mainland between 1911 and 1914 when Gatun Lake was created during the construction of the Panama Canal. The central part of the island is a plateau underlain by basalt. The flanks of the island are underlain by sedimentary and intruded volcanic rock (Bennett 1929). The prevalent soil on BCI, present in all my sampling areas, is a red clay loam known as Frijoles Clay (Bennett 1929). Frijoles Clay is well drained, well aerated, friable when moist, and fairly rich in nutrients (Bennett 1929, Knight 1975).

The vegetation of BCI is classified as tropical moist forest in the Holdridge Life Zone System (Holdridge et al. 1971). The forest is semideciduous: a large fraction of the canopy trees lose their leaves sometime during the mid-December to mid-April dry season. The flora of BCI consists of 1369 species of vascular plants of which 659 are herbs, 211 are trees > 10 m tall, 271 are shrubs and small trees, 94 are herbaceous vines, and 175 are lianas (Croat 1978). In a typical 1-ha plot there are roughly 170 trees > 20 cm dbh of over 50 species (Thorington et al. 1982).

The recent history of the island's vegetation varies greatly from place to place, but the area on the central plateau where I worked appears not to have been cleared by humans for at least 200 yr (Foster and Brokaw 1982). The largest trees in the area exceed 40 m in height and 3 m dbh (diameter either at 1.3 m or above buttresses). The average canopy height is \approx 30 m, but because of frequent treefalls, the forest structure is extremely heterogeneous; on the average, \approx 1% of the trees > 20 cm dbh die each year (Putz and Milton 1982). Understanding the effects of lianas on forest dynamics requires detailed background information on tree mortality rates, the size and spatial distribution of treefall gaps, and the species composition and rate of tree regrowth in gaps. Barro Colorado Island is one of the few places in the world for which much of this information is available (e.g., Brokaw 1982, Putz and Milton 1982, Garwood 1983, Putz 1983a, Putz et al. 1983).

METHODS

Liana abundance

The major goals of this study were to determine liana abundance in the forest as a whole and to examine changes in liana abundance as forest regenerates in treefall gaps. Liana sampling schemes must take into account the fact that lianas are not restricted to growing vertically. Therefore, I sampled cylindrical volumes rather than horizontal areas of forest. Each circular 100-m² plot had imaginary walls extending from the

ground to above the canopy. Branches of trees rooted in a plot but growing through the plot's imaginary walls were included in the sample; branches of trees rooted outside but growing into the plot were disregarded. The same scheme was used for sampling lianas, with the following elaborations. When a liana from outside a plot grew into a tree rooted in the plot, its diameter was measured (or estimated) where it crossed the plot's boundary or, in the case of tree branches outside the plot, where it entered the branches. Lianas rooted inside the plot but growing entirely on trees rooted outside the plot were not included.

Overall liana abundance in the forest was determined by a complete inventory of lianas in 10 randomly located 40 \times 25 m (0.1-ha) plots on the central plateau. It was thought that large plots would provide a better estimate of liana abundance than would an age-weighted combination of the not strictly randomly located 100-m² plots.

To characterize forest structure, to assess the abundance of upright (free-standing) lianas, and to determine what supports were available on which climbing lianas could grow, I counted and measured all woody plants in 100-m² plots in forest of different stages of recovery after treefalls. Trees and tree seedlings were grouped into eight size-classes (0.1–2 m tall, > 2 m tall but < 5 cm dbh, 5–10 cm dbh, 10–20 cm dbh, 20–40 cm dbh, 40–80 cm dbh, 80–120 cm dbh, and > 120 cm dbh). Plants < 10 cm tall were not included because during the dry season they could be buried in the litter, and their abundance fluctuates widely depending on the season (Garwood 1983). In addition to measuring the diameter at breast height (or diameter at the plot boundary) of all lianas, I estimated their maximum height above the ground with a range finder, determined the species (nomenclature follows Croat [1978]), and recorded the species of the trees supporting each liana. When a liana climbed into a plot, the habitat type from which it came was recorded (e.g., growing into a gap edge plot from a gap). For data on the horizontal extent of individual lianas, each liana rooted in the plot was followed no matter how far it grew outside the plot, and the number and size of the trees on which it grew were recorded.

Changes in the abundance, size, and species representation of lianas after treefalls were assessed in a series of different-age treefall gaps. The ages of gaps < 10 yr old were provided by N. Brokaw and R. B. Foster (*personal communication*) and other researchers on BCI. For gaps > 10 yr old I estimated the ages based on tree heights, diameters, and species composition (Brokaw 1982a). Forest age-classes based on known or estimated years since last major treefall were as follows: 1–5, 5–10, 10–20, 20–50, 50–100, and > 100 yr.

For sampling forest of different ages, 90 of the previously described circular 100-m² sample plots were randomly located along 10 500 m long parallel transect lines placed at 40-m intervals from a randomly located

baseline. Where a potential sample plot contained forest of mixed age (e.g., old forest and part of a recent treefall gap), its boundaries were shifted so as to sample a stand as uniform in age as possible. Within 100–300 m² gaps, sample plots were located at random; smaller gaps were sampled in their entirety, but gaps <80 or >300 m² were not sampled. I divided my sampling efforts equally among different-age areas in the forest and rejected potential plots if they fell in forest of an age-class with an already complete set of 15 samples. A further departure from strictly random sampling was that gaps of known age were included wherever they occurred. Also, gap centers and gap edges were sampled separately because they constitute distinct physical and biological environments (Gysel 1951, Ranney 1978).

Several operational definitions of gaps have been proposed (e.g., Runkle 1981, Brokaw 1982*b*). I used the “canopy gap” of Runkle (1981), which is defined as a vertical projection in the forest inside the crown edges of trees around the edges of a gap (trees >20 cm dbh).

To assess the importance of trees and lianas on the edges of young (<10-year-old) treefall gaps as trellises for lianas climbing to the canopy, special plots were used for sampling gap edges. Gap edges were defined as bands of forest starting at points directly under the tips of branches hanging into treefalls (i.e., the drip line) and extending 5 m into the forest. For sampling purposes I divided each of the 30 gaps in half along the longest axis and randomly located a 5 × 10 m rectangular plot in the edges of opposite sides of the gap. Plots wider than 5 m often included forest that did not appear to be affected by the increased light available from the gap. Plots >10 m long would have had to be curved to stay on the edges of small gaps.

Because of restrictions on destructive sampling on BCI and the decomposition of vegetative connections between ramets (branches), it was generally impossible to determine with any certainty whether a liana was a sexually produced individual (genet) or a vegetative offshoot (ramet). Where connections between stems were visible, the relationship was recorded, but in this study, an individual was considered to be an independently climbing or upright (self-supporting) stem. Thus, branches of lianas that fell to the ground, rooted, and then grew upward were tallied as separate individuals.

To determine the predominant modes of propagation (i.e., from seed or vegetative offshoot) of the common liana species, 20 individuals <50 cm tall of each of the five most common species were excavated along randomly located transects on Gigante Peninsula, near BCI, in forest similar in species composition and structure to the main study area. In the few cases when I was uncertain whether the excavated liana was a true seedling or a vegetative offshoot from a rhizome, stolon, or fallen stem, the plant in question was excluded from the census.

To identify lianas and the trees upon which they

grew, it was often necessary to climb into the canopy. Once a sample plot was located, I shot a fishing line into the treetops with a line-throwing gun, pulled up a climbing rope, and then climbed up with the aid of mechanical rope ascenders. From up in the canopy it was generally possible to see clearly even the tallest lianas in the 100-m² sample plots; larger plots would have necessitated climbing more than one tree per plot.

Trellis requirements and liana distribution

In addition to wanting to know how liana abundance changes as forest regenerates after treefalls, I wanted to know how representation of liana species and morphological types change with time. The high species richness of lianas coupled with the mechanical nature of the questions concerning the relationship between lianas and forest dynamics made it both necessary and advantageous to examine the data on the basis of both species and climbing mechanisms. Several schemes for classifying lianas by growth habit have been proposed (e.g., Darwin 1867, von Marilaun 1895, Obaton 1960). Each system was designed in reference to a particular flora, but no one classificatory system yet proposed is suitable for all the lianas in the world. Furthermore, because the climbing habit has independently evolved in diverse taxa, classificatory systems based on habit alone seldom reflect evolutionary relationships. The following categories were selected with the flora of Panama in mind and are based on the character of most interest in this study: how lianas climb.

- 1) Tendril climbers: modified leaves, leaflets, or stipules twine around supports.
- 2) Twiners: major axis coils around supports. Included here is *Omphalea diandra* (Euphorbiaceae) in which the main stem twines around supports and is replaced by a lateral branch.
- 3) Branch twiners: leaf-bearing branches twine around supports. The main stem may also twine but most of the support derives from the branches.
- 4) Root climbers and adhesive-tendril climbers: attach to the sides of trees with glandular secretions or by growing into cracks and crevices in the host's bark.
- 5) Sprawlers, scramblers, and hook climbers: lean on but do not attach to supports.

This system is not perfect (several species fall into more than one category), but I am satisfied that most species are reasonably classified.

A liana's climbing technique and the distance it can span between supports determine the forest structure required for successful growth to the canopy. The maximum sizes (diameters) of supports and the maximum distances spanned between supports were determined by keeping records for each species in the 100-m² sample plots. Only the largest supports and inter-support distances were measured. Because trellis dimensions may change while a liana remains holding on, only

supports to which young liana shoots had recently attached were measured.

To determine where tree stems and branches are most often arranged into suitable trellises for canopy-bound lianas, *Dioclea reflexa* (Leguminosae) seedlings were planted in recent treefall gaps, on the edges of recent treefall gaps, and in closed forest. *D. reflexa* was chosen for assessing the availability of supports because its seeds are large (≈ 7 g fresh mass) and readily available, and the seedlings are fast-growing twiners. *D. reflexa* seedlings were sorted by height-class (range 8–18 cm) at the time of planting, so there was no initial height difference among the seedlings planted in the three habitats. In what I judged to be a typical gap edge, treefall, and area of closed forest, I planted 20 tagged seedlings at random points on subjectively located sample lines and remeasured heights and lengths after 1 yr.

The hypothesis that limited availability of supports restricts height growth of lianas was tested with a field experiment. Adjacent pairs of conspecific lianas of approximately the same height and growing under what were judged to be uniform environmental conditions were selected. The flip of a coin determined which of each liana pair was experimentally attached to a trellis in the form of a nearby sapling or a pole driven into the ground. After 1 yr the maximum height from the ground attained by each plant was measured. I also noted whether the originally unsupported (control) plant attached to a support during the 1-yr period.

Effects of lianas on trees

Lianas can influence tree growth and mortality rates in at least five ways: (1) by competing with trees for light and thereby slowing tree growth, (2) by increasing tree mortality rates by weighting down tree crowns and increasing mechanical strain (torque) on the stem and roots, (3) by increasing the number and size of trees pulled down when liana-laden trees fall, (4) by slowing rates of tree sapling height growth in treefall gaps through the combined effects of shading and mechanical damage, and (5) by binding trees together and thereby increasing the stability of the individual trees.

Testing the hypothesis that lianas slow host tree diameter growth rates required long-term (e.g., 10 yr) growth rate estimates for a large number of conspecific trees of similar size. Such data were provided by G. E. Lang and D. H. Knight (*personal communication*) for *Luehea seemannii* (Tiliaceae) growing in a 1.5-ha plot on Barbour Peninsula on BCI. *L. seemannii* is a pioneer (shade-intolerant) species that lacks most of the characteristics of other pioneers. For example, it has neither large leaves nor a strong monopodial or excurrent growth form. Consequently, it often supports heavy liana loads (Putz 1984). For each of the 26 *L. seemannii* trees (30–50 cm dbh) in the plot, I measured the stem diameter (dbh or diameter at the point of crown entry) of all the lianas carried.

Tree sapling heights in gaps of known age were used

to test the hypothesis that lianas interfere with tree regeneration. If lianas interfere with sapling growth, then the average height of saplings in a given-age gap should be shorter where lianas are abundant. I measured the height of the tallest sapling within a 1-m radius of eight randomly selected points within the 100-m² sample plots in 150–300 m² treefall gaps of known age. I tested the influence of liana abundance (as expressed by basal area) on sapling height after first statistically removing the effect of gap age, using a stepwise multiple regression.

To test whether lianas influenced the number of trees falling down together, treefalls on the central plateau on BCI were monitored from July 1979 through December 1980. In every treefall discovered during the study period, I measured the dbh of all fallen trees > 10 cm dbh and determined which tree was the gapmaker (the causal tree). Usually the gapmaker was obvious by its size and location in the pile of fallen trees. However, in a few cases, the gapmaker was assumed to be the largest tree. By crawling through the treefall, I located, identified, measured, and marked all the lianas > 2 cm diameter carried by the gapmaker and the other fallen trees. At least 8 mo later, each treefall was revisited to determine which lianas survived.

To test the hypothesis that lianas increase tree mortality rates, the loads (total basal area) of lianas on recently fallen trees were compared with the loads carried by standing trees. The standing trees were located in a 1-ha plot in the center of my general study area, while the fallen trees were scattered throughout the forest. The 1-ha plot was selected as representative of mature forest on the plateau (Putz and Milton 1982). This test suffers from the inherent weakness that dying trees may allow more light to pass through their crowns and consequently may have larger lianas and may carry lianas more frequently than do healthy trees. However, I doubt that this is often the case for three reasons. First, most lianas enter the crowns of large trees by climbing over from adjacent trees, not by climbing up the larger trees themselves. Rather than increase liana access to the crown, branch loss should make a tree less susceptible because lost branches represent lost potential supports for invading lianas. Second, lianas generally grow on top of their host trees; loss of tree leaves probably has little direct effect on liana growth. Finally, few trees die slowly on BCI; most are blown over in storms and show no signs of trunk deterioration prior to dying (Putz et al. 1983). Because lianas generally grow slowly in diameter (Putz 1983b), their response to the weakening of their hosts would not be detected unless this condition persisted for many years.

RESULTS AND DISCUSSION

Liana abundance

In 10 randomly located 0.1-ha plots, there were 1597 climbing lianas and 1568 self-supporting (upright) lianas > 10 cm tall (Table 1), representing 65 species. The

TABLE 1. Size-class frequency distribution of climbing lianas and the total number of self-supporting lianas in 10 randomly located 1000-m² plots.

	Sample plot										No. lianas/ha
	1	2	3	4	5	6	7	8	9	10	
	No. self-supporting lianas										
	282	123	81	165	103	118	94	207	223	172	1568
	No. climbing lianas > 1 cm dbh										
dbh (cm)											
<1	127	81	63	107	85	98	73	65	106	19	824
1-2	51	47	4	62	19	51	26	34	9	41	344
2-3	31	39	3	19	16	44	20	28	7	29	236
3-4	19	26	3	8	13	3	7	3	11	16	109
4-5	4	5	2	8	3	0	5	1	12	1	41
5-6	2	4	3	1	1	0	2	0	2	0	15
6-7	1	3	0	1	0	0	2	1	2	0	10
7-8	0	2	1	0	0	0	0	0	1	0	4
8-9	1	2	0	0	1	0	2	1	0	0	7
9-10	0	2	0	0	0	0	1	1	0	0	4
10-15	0	1	0	0	1	0	0	0	1	0	3
Total climbing lianas > 1 cm dbh	109	131	16	99	54	98	65	69	45	87	773
Grand total	518	335	160	371	242	314	232	341	374	278	3165

20 most common species (Table 2) account for 64% of the total of 3165 lianas/ha. It is surprising that the two most common species seldom reached the canopy and frequently reproduced in the understory (Table 2). Neither the abundance nor even the existence of this group of shade-tolerant woody vines was anticipated at the outset of this study.

Many of the small upright woody plants in the forest are liana seedlings, not tree seedlings. Most species of lianas have seedlings that go through an upright stage during which they are superficially indistinguishable

from tree seedlings. Upright individuals of some species (e.g., *Connarus panamensis*, Connaraceae) grow to > 2 m before requiring support, while others (e.g., *Aegiphila cephalophora*, Verbenaceae) grow as lianas or as small shrubby trees depending on whether they are in the forest or in the open. On BCI, 22% of the upright plants < 2 m tall were lianas. Other tropical seedling surveys in which liana seedlings were differentiated from tree seedlings report similarly high proportions. Rollet (1969) and Putz (1983b) found that 18 and 20% of the seedlings were lianas in wet lowland forests in

TABLE 2. The numbers of upright (self-supporting) lianas > 10 cm tall and climbing lianas in 10 randomly located 0.1-ha sample plots. *Combretum decandrum*, in addition to twining, has spines that aid in climbing. Asterisks mark species that rarely attained canopy height and regularly reproduced in the understory.

Species	Family	Climber type	No./ha		
			Upright	Climbing	Total
* <i>Hiraea reclinata</i>	Malpighiaceae	twining	394	187	581
* <i>Paullinia turbacensis</i>	Sapindaceae	tendrils	187	283	370
<i>Petrea aspera</i>	Verbenaceae	twining	143	27	170
<i>Maripa panamensis</i>	Convolvulaceae	twining	39	101	140
<i>Dolioscarpus major</i>	Dilleniaceae	twining	86	21	107
<i>Phryganocydia corymbosum</i>	Bignoniaceae	tendrils	56	41	97
<i>Coccoloba parimensis</i>	Polygonaceae	twining	65	28	93
<i>Pleonotoma variabilis</i>	Bignoniaceae	tendrils	21	73	94
<i>Paullinia fibrigera</i>	Sapindaceae	tendrils	36	26	62
<i>Prionostema aspera</i>	Hippocrateaceae	branches	17	36	53
<i>Dolioscarpus dentatus</i>	Dilleniaceae	twining	31	19	50
<i>Abuta racemosa</i>	Menispermaceae	twining	34	17	51
<i>Paullinia baileyi</i>	Sapindaceae	tendrils	23	13	36
<i>Paragonia pyramidalis</i>	Bignoniaceae	tendrils	11	23	34
<i>Arrabidaea patellifera</i>	Bignoniaceae	tendrils	5	27	32
<i>Arrabidaea verrucosa</i>	Bignoniaceae	tendrils	11	9	20
<i>Serjania mexicana</i>	Sapindaceae	tendrils	3	17	20
<i>Clitoria javitensis</i>	Leguminosae	tendrils	8	7	15
<i>Combretum decandrum</i>	Combretaceae	twining	2	3	5
<i>Anthodon panamense</i>	Hippocrateaceae	branches	1	3	4
Other species			395	736	1331
Total			1568	1697	3165

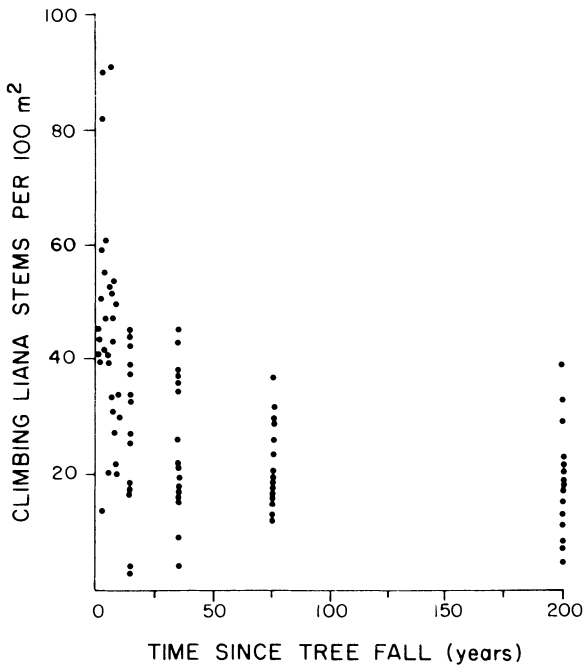


FIG. 1. Number of climbing liana stems in sample plots as a function of time since last treefall. Exact ages of forest < 10 yr old are known; after 10 yr the ages were estimated and plotted at age-class midpoints.

Venezuela. Wyatt-Smith (1963) reported that 11% of the seedlings were lianas in mixed dipterocarp forest in Malaysia.

Results from seedling excavations showed that although true seedlings of all liana species were found, vegetatively produced plants predominated in many species. Results for the individual species were as follows: *Paullinia turbacensis* (Sapindaceae) 10% true seedlings, *Acacia hayesii* (Leguminosae) 30% true seedlings, *Coccoloba parimensis* (Polygonaceae) 45% true seedlings, *Doliocarpus major* (Dilleniaceae) 65% true seedlings, *Maripa panamensis* (Convolvulaceae) 85% true seedlings.

As the forest grows back after treefalls, there are surprisingly few changes in the species composition of the liana flora. A few species, however, appear to be more common in recent (i.e., <5-yr-old) treefalls than in older forest. Because of extremely high species diversity and the small sample size, it would be difficult to suggest with certainty that any species actually drop out as the forest matures, but the following appear to be early successional species: *Aegiphila cephalophora* (Verbenaceae), *Mesichites trifida* (Apocynaceae), and *Mendoncia littoralis* (Acanthaceae). (The last two species mentioned might be considered herbaceous vines.)

Lianas were most abundant in several young treefall gaps, and liana density decreased with time since last disturbance (Fig. 1; $r = -0.39$, $N = 90$ 100-m² plots;

$P < .01$). However, inspection of the data (Fig. 1) and observations in the forest revealed large between- (and within-) plot variance in the number of climbing lianas even in forest of the same age. To some extent lianas appear particularly abundant in young forest because, in full sun and in the absence of supports (trees), lianas grow to be extremely long. Up in the canopy they are also long, but because they do not interfere with pedestrians, their abundance is rarely noted.

When a tree falls in the forest, small trees often survive in the center of the new treefall gap. Many of these small trees are quickly covered by lianas, which proliferate in the improved light conditions. This is reflected in the high proportion of trees that carry lianas in 0–5 yr old gaps (Fig. 1). After 5 yr and especially between 10 and 20 yr after gap formation, saplings of pioneer tree species (e.g., *Cecropia* spp., *Zanthoxylum* spp., and *Trema micrantha*) may emerge from the liana tangle or from open areas within the gaps (Fig. 3). These pioneer species rarely have lianas; this is apparently due to their monopodial growth form, large leaves, flexible trunks, rapid growth rates, and, in the case of *Cecropia* spp., the liana-removing activities of *Azteca* ants (Janzen 1969, Putz 1984). The presence of these species is largely responsible for the slightly lower proportion of trees that carry lianas in the 10–50 yr old forest (Fig. 2). After 20–30 yr the *Cecropia* spp. trees start to die, and the other pioneers probably do not

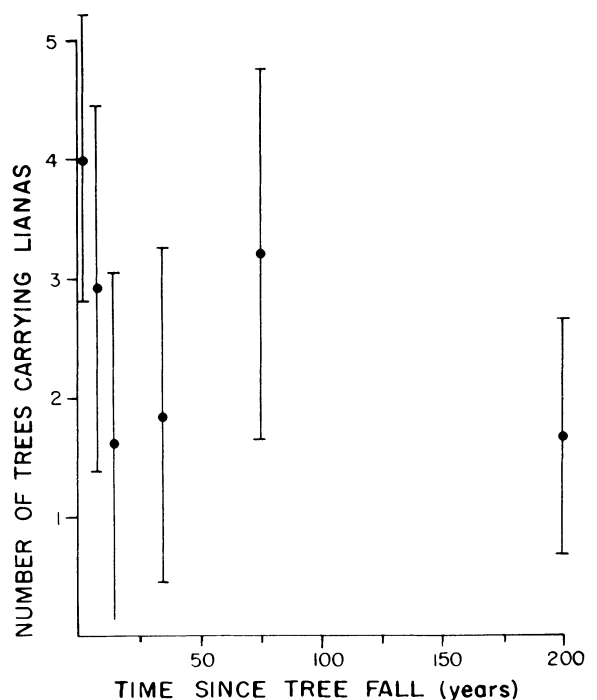


FIG. 2. The mean (± 1 SD) number of trees (out of the five with greatest dbh) carrying lianas in the 100-m² plots. Values are plotted at the midpoints of the age-classes; the first three bars represent 0–5, 5–10, and 10–20 yr old treefall gaps. 15 plots were sampled in each treefall age-class.

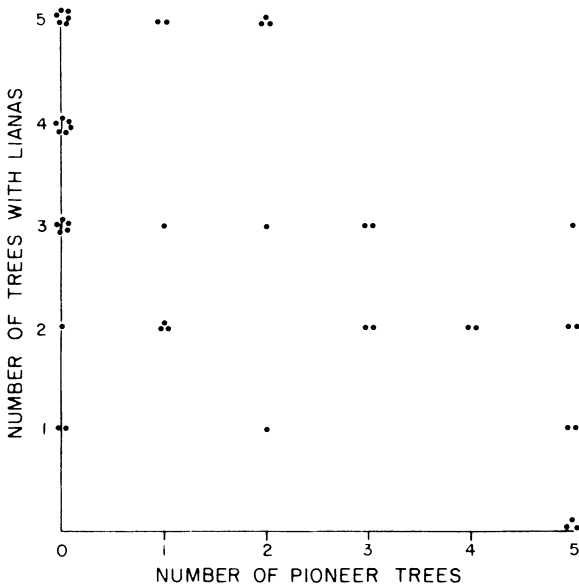


FIG. 3. The number of trees (of the five with greatest dbh in each 5–50 yr old treefall-gap plot) that carried lianas as a function of the number of pioneer trees in each five-tree sample. Pioneer species included *Cecropia* spp., *Zanthoxylum* spp., *Trema micrantha*, *Croton bilbergianus*, and *Trichospermum mexicanum*. ($r = 0.59$, $N = 45$ 100-m² plots, $P < .05$.)

live >100 yr at most. However, the data indicate that many trees in 50–100 yr old forest carry lianas. With the replacement of liana-free pioneer tree species by trees that are more susceptible to lianas, the proportion of large trees carrying lianas would be expected to increase.

The proportion of trees infested with lianas indicates a great potential for liana impact on the forest. In the 100-m² sample plots, 43% of the trees >20 cm dbh carried lianas. In the 1 ha of forest in which liana loads were measured on all trees >20 cm dbh for the standing vs. fallen tree comparison, 89 of the 165 trees (47%) carried lianas. Knight (1975) also censused lianas but located his plots so as to avoid treefall gaps. He found that 32% of the trees >10 cm dbh had lianas and 17% of the trees had lianas >5 cm dbh. Montgomery and Sunquist (1978) found that ≈50% of the trees >15 cm dbh growing in young (<200-yr-old) forest on BCI carried lianas. The similarity of these three independent estimates indicates that on BCI somewhere between 30 and 50% of the canopy trees carry lianas. The only other estimate of this kind of which I am aware is from a lowland rain forest growing on an Oxisol near San Carlos de Rio Negro, Venezuela, where 42% of the trees >10 cm dbh carried lianas (Putz 1983b).

Trees often carry more than one liana. Lianas were significantly aggregated on trees in the 100-m² sample plots, with more trees having two or more lianas than would be expected by chance ($P < .05$, chi-square goodness-of-fit test with expected numbers based on the Poisson distribution). In some cases, trees seemed

particularly prone to liana infestation due to their size, shape, and location in the forest. Another important way lianas climb into the crowns of large trees is by climbing on other lianas already in the canopy.

Because of the limited availability of tall supports of small diameter, lianas generally climb up to the forest canopy on series of successively taller trees (trellises). Thus, during their lives, lianas are supported by more than one tree. The major exceptions to this pattern are the rare root and adhesive-tendrils climbers and lianas that climb on other lianas. Once in the canopy, lianas often pass from one tree to another. On the average, canopy lianas in the 100-m² sample plots grew on 1.6 trees >20 cm dbh before either returning to the ground or failing to bridge the gap between trees. An extreme case of intercanopy passage was a 51 cm dbh *Entada monostachya* (Leguminosae; outside of the sample plots) that connected the crowns of 22 canopy trees, fell to the ground and rooted, and went on to climb on an additional 27 canopy trees over an area of ≈0.5 ha. There are reports in the literature of lianas covering extensive areas (Richards 1952, Caballé 1977, 1980), but as far as I am aware, this *Entada* holds the size record. Lianas that connect tree crowns provide inter-canopy pathways much travelled by arboreal animals (Montgomery and Sunquist 1978, Emmons and Gentry 1983).

Trellis requirements and liana distribution

Trellis (support) requirements and forest structure (especially tree size-class frequency distributions) together influence the distribution of lianas in the forest and the probability of lianas successfully growing up into the canopy. Potential trellises must be strong enough to support a liana's mass, but otherwise there do not appear to be minimum diameter limits for usable support structures. The mechanism used by a liana

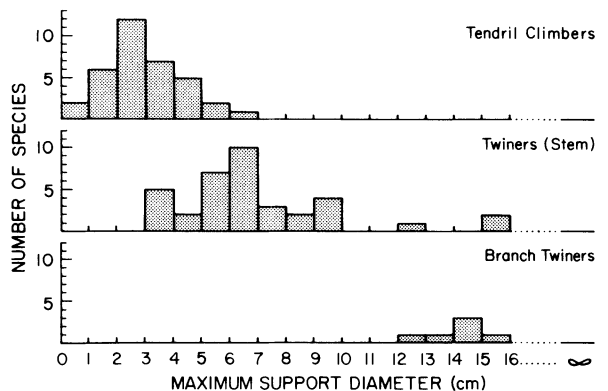


FIG. 4. Distribution of the averages of the three maximum recorded support (trellis) diameters for the species of four types of lianas. Only recently climbed supports were used. All lianas can climb on supports smaller than those reported here. Root and adhesive-tendrils climbers can climb on supports of any diameter.

for climbing determines the maximum diameter of supports it can use. For example, tendrils rarely exceed 10 cm in length; most tendril climbers require supports \ll 10 cm in diameter (Fig. 4) because for a tendril to anchor a liana's stem in place it must wrap itself around the support. Darwin (1867) pointed out that, as a partial compensation for this restricted range in suitable support diameters, tendril climbers invest relatively little in support structures (e.g., roots or extra lengths of stem for twining). This may allow tendril climbers to grow more rapidly than other types of climbers when suitable supports are available.

Twiners can climb larger diameter supports than tendril climbers (Fig. 4). The rigidity, length, and mass of the elongating portion of the twiner's stem determine the maximum usable support diameter. Twining plants are held up by a combination of internal support (rigidity) and friction between the climber and its trellis. Twiners can increase the maximum diameter support on which they can climb by increasing friction between the liana and its support. *Doliocarpus major* (Dilleniaceae) does this with dense hooked trichomes, while *Mariapa panamensis* (Convolvulaceae) and *Abuta racemosa* (Menispermaceae) increase friction by flattening their stems against supports. Trees with rough (but not flaky) bark appear more easily ascended than smooth-barked trees by twining lianas. Ascent angle (pitch) of the liana decreases with increases in the diameter of the support, and eventually, at a shallow and species-specific angle, internal support strength is exceeded, and the climber slips down, producing the liana coils sometimes found around the bases of trees.

Except for root and adhesive-tendril climbers, which climb trees regardless of their diameter, branch twiners have the widest ranges in sizes of supports used (Fig. 4). The final category, the sprawlers and hook climbers, depend more on dense arrangements of supports than on supports of a restricted diameter. They climb most successfully in young forest and gap-edge tangles because branches are usually closely spaced near the ground only while trees are small.

Twining and tendril-climbing lianas generally climb to the canopy on series of successively taller supports. After reaching the top of one support, they produce long leafless leader shoots, which grow up into the air over the support. Endogenous circular or elliptical movements (circumnutation) of liana stems and tendrils have attracted much attention from physiologists (see Baillaud [1962a, b] and Johnsson [1979] for reviews) after being first noticed by naturalists (e.g., Dutrochet 1837, Darwin 1867). Elliptical circumnutation movements with the long axis of the ellipse oriented toward potential supports (Tronchet 1945, 1946, Miège 1958) and enhanced by the wind may increase the probability of lianas finding support. More often than not, however, there are no suitable supports nearby, and the leader falls over and either starts up a support nearer the ground or is replaced by another vertical

leader. Maximum erect leader lengths are species specific. Scramblers and hook climbers generally produce thicker and longer leaders than other climber types. The distance that a liana can traverse between supports is determined by the length of stem it can hold erect out of the top of a support. The maximum distances lianas spanned between supports ranged from 0.3 m (*Cissus rhombifolia* Vitaceae) to $>$ 3.0 m (*Combretum decandrum* Combretaceae). For the 43 species for which I have good records, the average maximum inter-support span was just under 1 m (\bar{x} = 0.95 m, standard deviation = 0.62 m). Leaf expansion on leader shoots generally proceeds only when attached to a support (Raciborski 1900, French 1977). This allows leaders to remain light in mass and hence easy to support (Troll 1938). Knowing the required size and distance between trellis members, I next tried to determine where in the forest lianas are most likely to find proper trellises.

Gap edges are the sites most likely to fulfill the trellis requirements of lianas. After 1 yr, seedlings of the liana *Dioclea reflexa* planted along the edges of a recent tree-fall gap were an average of 1.5 m tall (SD = 0.6 m; N = 20), while seedlings in the gap center were 0.7 m tall (SD = 0.4 m; N = 20), and seedlings under closed canopy of mature ($>$ 100-yr-old) forest were 0.6 m tall (SD = 0.4 m; N = 20). The height of *D. reflexa* seedlings in the gap center was statistically indistinguishable (one-way analysis of variance; $P > .1$) from the height of seedlings in the forest interior. However, seedlings planted along the gap edge grew significantly taller ($P < .01$) than the seedlings in the gap center and the forest interior. This was because 90% of the seedlings on the gap edge found trellis supports, but in the center of the gap and in the forest interior, only 10 and 30%, respectively, of the seedlings found any support whatsoever. In contrast to other sites, on gap edges there was an abundance of supports provided both by the proliferation of tree growth and the presence of lianas pulled down by falling trees but still attached in the crowns of gap edge trees. It is important to keep the distinction between height growth and extension growth clear. *D. reflexa* seedlings growing in full sun in the center of gaps were greater in length than gap edge and forest interior seedlings; however, in terms of progress toward the canopy, seedlings on gap edges were considerably more successful. This demonstrates the importance of gap edges in providing small-diameter supports that can serve as major avenues for lianas climbing to the canopy. Since seedlings grew when planted under the shade of closed canopies in mature forest, lianas may well climb up through the forest interior if provided with trellises.

The suggestion that support availability rather than light, moisture, or nutrients is the major factor limiting the probability that forest understory lianas climb up through the forest to the canopy is further supported by the observation that forest understory lianas experimentally provided with trellises displayed marked

TABLE 3. Height growth of experimentally supported and nearby control seedlings of lianas in the understory of closed forest. Differences between the supported and the control groups were significant (Wilcoxon signed-ranks test; $P < .05$) for all species except *Paullinia turbacensis*. Values are means ± 1 SD.

Species	Type	N	Average annual height growth (cm)	
			Supported	Control
<i>Dolioscarpus major</i>	twiner	11	84 \pm 69	4 \pm 31
<i>Maripa panamensis</i>	twiner	7	57 \pm 88	14 \pm 25
<i>Hiraea reclinata</i>	twiner	11	94 \pm 88	6 \pm 17
<i>Paullinia turbacensis</i>	tendrils	12	15 \pm 24	11 \pm 37
<i>Pleionotoma variabilis</i>	tendrils	23	58 \pm 93	5 \pm 23

height growth responses (Table 3). Although experimental manipulation caused damage to many stems, after 1 yr, 53 pairs of conspecific lianas representing five species were intact. Only 3 out of the 64 lianas that were not experimentally provided with trellises found support during the 1-yr observation period. That supported stems grew taller than unsupported stems may not be particularly surprising, but the amount of growth in the shade of the understory and the failure of unsupported stems to find support on their own indicate that trellis availability is a major factor reducing the success of canopy-bound lianas. It should be pointed out that although only stems that looked like seedlings were used in this experiment, some may have been attached to larger stems that provided the resources required for growth.

Height growth of liana seedlings was limited by trellis availability, and *D. reflexa* seedlings found supports most frequently on the edges of gaps. However, to confirm that gap edges provide trellises all the way to the canopy, data on taller liana individuals are required. The height distribution of lianas provides indirect evidence for trellis distribution. Where lianas are in the process of successfully climbing to the canopy, there should be many intermediate-height liana stems.

Lianas were distinctly stratified by height in closed forest on BCI (Fig. 5: Forest interior); intermediate height-classes (4–24 m) were underrepresented. This suggests that few lianas reached the canopy by gradually climbing up through the interior of old forest. Although lianas can grow in the forest if provided with supports, considering the low light levels in the forest interior, it seems unlikely that the rarity of mid-height lianas was due to rapid growth through the intermediate height-classes. There were more intermediate-height lianas in plots on the edges of treefall gaps than in the interior of old forest (Fig. 5: Forest edge; $t = 21.6$; $df = 31$; $P < .0001$). This is no surprise given that gap edges, like river margins, often appear as if draped with an impenetrable curtain of lianas. Of the lianas growing up on the edges of 3–10 yr old gaps, 45 were rooted in the surrounding forest, while 195 grew

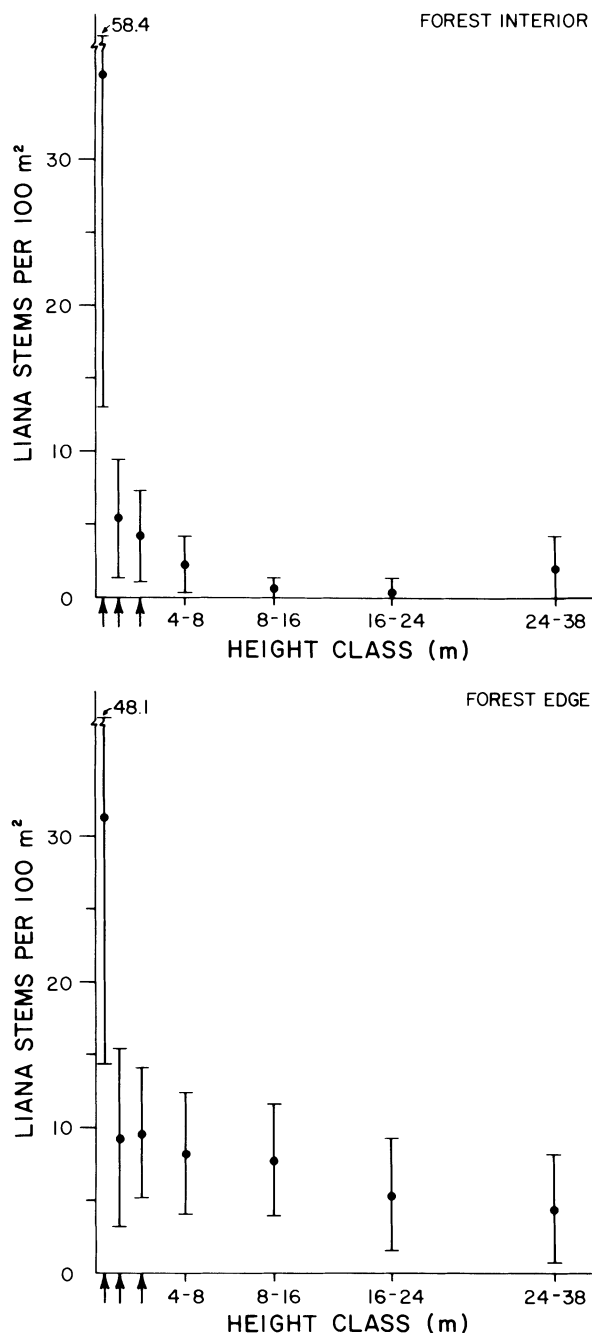


FIG. 5. The number of liana stems in 100-m² sample plots in (top) mature (> 100-yr-old) forest and (bottom) on the edges of treefall gaps, as a function of height. The arrows on the abscissa axis indicate the classes 0–1, 1–2, and 3–4 m. All frequencies are plotted at the height-class midpoints. Wider classes for taller plants reflect expected measurement errors. Plotted as the mean ± 1 SD.

to the gap edges from the gaps themselves (16 gaps, Wilcoxon signed-ranks test, $P < .01$). Approximately 40% of the lianas growing over from the gaps were sprouts of fallen lianas. The edges of treefall gaps thus

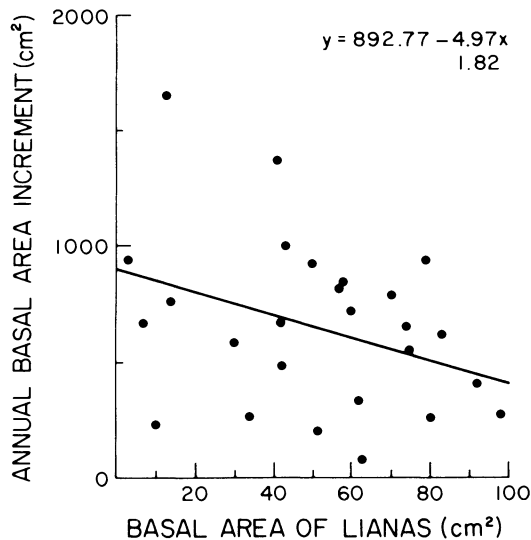


FIG. 6. Growth rates (in basal area) of 26 *Luehea seemannii* trees 30–50 cm dbh averaged over a 10-yr period as a function of the total basal area of lianas carried at the end of the 10-yr period. The standard error of the regression coefficient appears on the figure under the coefficient ($P < .05$).

often provide the supports required by canopy-bound lianas, and many lianas that successfully grow to the canopy start out as fallen stems in treefall gaps.

Effects of lianas on trees

Lianas generally grow on top of their host trees. In so doing they both shade and mechanically burden their hosts where the effects on torque (strain) are most severe. However, lianas may also bolster a tree's ability to withstand wind-induced mechanical stress by anchoring it to other trees (Smith 1973). In this section I present data on the effects of lianas on host tree growth and mortality rates and on the rate of sapling growth in recent (<10-yr-old) treefall gaps.

To test the hypothesis that stem diameter growth rates of trees are slowed by lianas, liana loads on 30–50 cm dbh *Luehea seemannii* trees were measured and tree growth rates compared. All 26 trees had lianas; some had so many as to make it difficult to see the tree leaves amidst the mass of liana foliage. Over the 10-yr observation period, stem basal area increments of 26 *L. seemannii* trees decreased with increasing liana loads (Fig. 6).

To see whether the presence of lianas increases tree mortality rates, I compared the liana loads on recently fallen trees with loads carried by standing trees in the 1-ha plot in the center of my study area. Of the 165 standing trees, 78 (47%) had lianas in their crowns; the average liana basal area per tree was 29 cm² (SD = 51 cm²). In contrast, of the 63 gapmaker trees, 51 (80%) carried lianas with an average liana basal area per tree of 50 cm² (SD = 63 cm²). Fallen trees carried lianas

more frequently ($\chi^2 = 21$, $P < .001$) and carried a higher total basal area of lianas ($t = 8.4$, $P < .001$) than standing trees. Lianas seemed to increase the probability of their host tree falling due to the combined effects of shading and mass loading. Even lianas with stems of small diameter can supply large leaf areas and hence cast considerable shade on their host trees (Putz 1983b). Shading should lead to less energy being available to root system growth and repair. However, lianas may be symptoms of other problems rather than the cause of tree deaths.

To evaluate the influence of lianas on treefall gap size, I measured all the trees and lianas involved in the 68 independent treefalls that occurred in the study area during a 1-yr period. When falling, liana-laden trees were expected to cause more other trees to fall than were liana-free trees. An average of 2.3 trees >10 cm dbh (SD = 2.6 trees) fell with each gapmaker (causal) tree. The total basal area (BA; in square centimetres) of trees that fell with the gapmaker (BA_O) depended on both the BA of the gapmaker (BA_G, $P < .001$) and the total BA of the gapmaker's lianas (BA_L, $P < .05$; $R^2 = 0.51$):

$$BA_O = 0.63 \times BA_G + 4.02 \times BA_L - 396.7.$$

Trees pulled down with the gapmaker often shared lianas with it, but some trees without lianas were pulled down when entangled by loops of liana stems attached to other trees. This evidence agrees with the contention of many tropical slash and burn agriculturalists that the easiest way to clear forest is to fell large liana-laden trees and let these pull others down. Some trees immediately adjacent to treefalls seemed to have been stabilized by liana connections with trees other than those that fell. Lianas may also, at least temporarily, reinforce trees by holding them together in groups.

Few lianas die when their host trees fall. Of the 92 fallen liana stems inspected 8–12 mo after falling, 83 (90%) were alive, and most were sprouting vigorously. In 27 recent (2–10 yr old) treefall gaps, an average of 55% (SD = 22%) of the independently climbing stems sprouted from fallen lianas. The densest liana tangles in the forest were in gaps caused by trees with heavy liana loads and in small gaps created when only lianas and their supporting branches fell.

Many of the lianas on BCI have stems with intruded phloem, included phloem, or abundant wood parenchyma (F. E. Putz, *personal observation*). Anomalous secondary thickening is not peculiar to but is certainly characteristic of many lianas (Obaton 1960). The isolation of bands of relatively thick-walled conducting tissue (xylem vessels) in a matrix of thin-walled parenchymatous tissues results in stems that are more flexible than would be predicted from their diameter and overall wood density. This flexibility increases the likelihood of lianas surviving the fall of their host trees. Because lianas that manage to survive falling sprout readily along their entire prostrate stem, an advantage

of anomalous secondary growth may be the mechanical flexibility it allows.

Through the combined effects of shading and mechanical damage, lianas appear to have the same negative effects on sapling growth as they do on canopy tree growth. Evidence for this came from 11 gaps (2–10 yr old) where the average height (in metres) of tree regeneration was very much affected by vigorous liana growth:

$$\text{Average sapling height} = 0.90 + 0.82 (\text{gap age}) - 0.02 (\text{BA lianas in gap}).$$

Gap age (in years) and liana basal area (in square centimetres) both made significant contributions to the regression ($P < .001$ and $< .05$, respectively; $R^2 = 0.51$). In several gaps the coefficient of variation of sapling height exceeded 50% because of a few fast-growing trees that emerged above the liana tangles. Saplings and small trees which were in the understory prior to gap formation remained standing in many gaps. In the cases in which these remnant trees were inaccessible to lianas due to their size and location, they seemed to respond well to the improved conditions. In many cases, however, remnant trees became inundated with lianas. Liana-entangled remnant trees often looked like guyed circus tents and may have suggested the idea that lianas grow up to the canopy as their supporting trees grow taller (e.g., Whitmore 1975, Della-Bianca 1978). Trees inundated with lianas have little chance of reaching the canopy, and lianas restricted to such trees are likewise restricted in their opportunities for rapid height growth.

CONCLUSIONS

Lianas rely on trees or other lianas for support; hence lianas invest less in support tissue than trees. This allows lianas to have extremely rapid extension growth rates but limits their growth upwards to places where supports are available. The number of stems and branches small enough in diameter to serve as supports is limited in the understory of mature forest. Although light, nutrients, and water undoubtedly restrict growth rates in the forest understory, when experimentally provided with suitable supports, lianas displayed substantial height growth rates. The edges of forests along water courses and human-caused openings generally have plentiful potential supports that provide ready canopy access for many lianas. The proliferation of lianas on forest edges is undoubtedly the basis for the oft-repeated description of tropical rain forests as impenetrable tangles of vegetation. Within forests canopy lianas should be abundant where there are frequent treefalls, and the success of lianas on the edges of treefall gaps should in turn lead to increased forest turnover rates. The particular forest structure that would best enhance (or prevent) liana proliferation depends on the climbing modes employed by the lianas in question. It is clear, however, that forest structure, and in particular

the vertical and horizontal distribution of small-diameter stems and branches, is among the major factors controlling liana success.

In several species in which vegetative offshoots abound, it is difficult to find a sexually produced offspring. Among the 175 liana species on BCI, the capability for vegetative expansion is the rule rather than the exception. In light of this observation, the importance of asexual reproduction of tropical rain forest plants needs to be reassessed and given due consideration when designing silvicultural systems for liana control.

In managing tropical rain forests for sustained yield of native hardwoods, lianas are often a major silvicultural problem (Fox 1968, Liew 1973). The observations in this study may very well aid in developing sound liana-control techniques. The frequency of intercrown liana connections and the propensity for lianas to sprout vigorously from fallen stems argue that cutting lianas before logging will serve to reduce both felling damage and liana abundance after logging. However, in any forest management program that includes liana control, the importance of lianas to animals should be taken into account.

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