

Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest

SAARA J. DEWALT¹, STEFAN A. SCHNITZER[†] and JULIE S. DENSLow^{‡,2}

* *Department of Biological Sciences, 202 Life Sciences Building, Louisiana State University, Baton Rouge, LA 70803*

[†] *Department of Biological Sciences, University of Pittsburgh, A234 Langley Hall, Pittsburgh, PA 15260*

[‡] *Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803*
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ABSTRACT. The abundance and diversity of lianas were examined along a tropical forest chronosequence at the Barro Colorado Nature Monument, Panama. Lianas ≥ 0.5 cm diameter were sampled along transects in two replicated stands in secondary (20, 40, 70 and 100 y after abandonment) and old-growth (>500 y) forests. Ordination of stands based on relative abundance, but not presence-absence, showed a significant separation of stands by age. Lianas were significantly more abundant and diverse (Fisher's α) in younger forests (20 and 40 y) than in older forests (70 and 100 y, and old-growth). The decline in liana abundance with stand age was offset by increased mean basal area per individual, resulting in a relatively constant total basal area and estimated biomass across stand age. The proportions of tendrill climbers decreased and stem twiners increased over stand age. Decline in liana abundance and changes in liana composition may be related to changes in support and light availability. Although lianas are recognized as playing an important role in the early secondary succession of many tropical forests, these results have shown that their important contribution to total basal area and biomass can continue as the forest matures, even as the number of established lianas declines.

KEY WORDS: Barro Colorado Nature Monument, climbing mechanisms, lianas, ordination, Panama, species diversity, succession

INTRODUCTION

Tropical wet forests are characterized by high abundance and diversity of lianas (Gentry 1991). Lianas are most conspicuous in naturally or anthropogenically

¹ Corresponding author. E-mail: sdewalt@unix1.sncc.lsu.edu

² Current address: Institute of Pacific Islands Forestry, USDA Forest Service, 23 E. Kawili Street, Hilo, HI 96720.

disturbed areas (Hegarty & Caballé 1991) but also contribute substantially to the diversity and structure of mature tropical forests (Gentry 1991). In neotropical lowland moist and wet forests, lianas may account for 18% of all stems ≥ 2.5 cm diameter (Gentry 1982) and as much as 25% of all woody stems (Gentry 1991; S. Schnitzer & W. Carson, unpubl. data). Furthermore, lianas contribute significantly to species richness, accounting for up to 25% of woody stem diversity (Gentry & Dodson 1987). Lianas also play a prominent role in tropical forest dynamics because they respond rapidly to canopy opening and may suppress sapling growth in treefall gaps (Putz 1984). Uhl *et al.* (1988) suggested that high vine dominance in abandoned pasture may impede forest succession. Despite their importance, liana communities have been described primarily in disturbed areas (e.g. Pinard & Putz 1994, Uhl *et al.* 1988) or primary forests (e.g. Appanah *et al.* 1993, Putz & Chai 1987); we know little about changes in liana abundance and diversity during tropical forest succession. Our purpose here is to describe patterns in the liana community along a forest chronosequence in central Panama.

One factor constraining liana growth is availability of support structures (Putz 1983, 1984; Putz & Chai 1987). The mechanism by which a liana climbs (e.g. tendrils, stem twining, branch twining or hooks) determines in part which trees are suitable supports (Peñalosa 1982, Putz 1984, Putz & Holbrook 1991); lianas climbing by different mechanisms are constrained to support diameters below different maxima (Putz 1984, Putz & Chai 1987). Putz & Holbrook (1991) suggested that tendril climbers would be better suited to gaps and forest edges, where smaller diameter supports are more common, than to forest interiors.

Light availability may also constrain liana establishment and growth (Castellanos 1991, Teramura *et al.* 1991). Lianas are thought to be light demanding because of their rapid growth in high light and their abundance in disturbed areas such as along waterways, treefall gaps (Putz 1984), and abandoned pastures (Uhl *et al.* 1998). Canopy height contributes to patterns in light availability (Brown & Parker 1994), and thus to liana density. The number of lianas decreases with increasing canopy height (Baars *et al.* 1998, Balfour & Bond 1993, Caballé 1976, Hegarty & Caballé 1991); energetic costs associated with ascent may be higher when the distance to the lit canopy is greater. Lianas may be most abundant, therefore, in early successional habitats before canopy closure. Thus, the liana community may be affected by changes in the tree community if the support availability or light environment differ along the successional sequence.

During tropical forest succession, we know that the forest structure and light environment change. The distribution of tree diameters becomes more variable, canopy height increases, and light levels at the ground decrease. Tree density also declines over stand age while basal area increases (Brown & Lugo 1990, Richards 1996, Saldarriaga *et al.* 1988). Thus, we would expect that the liana community will change in response to these other changes. Here we

address how liana abundance and species composition change across a forest chronosequence in central Panama. We relate differences in the liana community to the forest structure and environment. We predict that increasing tree diameters, decreasing light levels, and increasing canopy height over succession will be associated with a decrease in liana density and diversity and a change in species composition. Furthermore, we predict that tendril climbers will be more abundant in young forests, while stem and branch twiners will be relatively more common in later successional forests.

STUDY SITE

Study stands were located in Panama within the Barro Colorado Nature Monument (BCNM). The BCNM comprises Barro Colorado Island (BCI, 9°10'N, 79°51'W), a research station of the Smithsonian Tropical Research Institute, as well as several adjacent mainland peninsulas. The area receives *c.* 2600 mm of rainfall annually, predominantly during the 7-mo wet season from May through December. Detailed descriptions of the vegetation on BCI are found in Croat (1978) and Foster & Brokaw (1982).

The land use history of the BCNM is described by Leigh *et al.* (1996) and Denslow & Guzman (in press). Contemporary forests reflect a long history of human activity dating most directly from pasture and farms to support the French (1883–1889) and later American (1907–1914) crews working on construction of the Panama Canal. Subsequent to the filling of Lake Gatun and isolation of BCI in 1914, the land has been exploited for pasture, plantation, and swidden agriculture. Successive periods of abandonment of agricultural fields and pastures and the expansion of land under preserve protection have resulted in a mosaic of secondary vegetation and old-growth forest. Old-growth forest occupies approximately half of BCI and small areas at the bases of Gigante and Bohio Peninsulas. Secondary forests in the BCNM range in age between *c.* 15 and 100 y in fallow. No logging or farming has occurred on the island since the area became a research preserve in 1923.

Eight stands (two replicates each) representing secondary forests of approximately 20, 40, 70 and 100 y in fallow as well as two stands of old-growth forest (OG) were selected for intensive study (Figure 1). Study stands were at least 5 ha in size on relatively level topography. Stand ages were estimated by reference to early publications describing the establishment of Barro Colorado Island (Chapman 1938, Enders 1935, Kenoyer 1929, Standley 1933, and references in Foster & Brokaw 1982), aerial photographs dating from the late 1920s and from 1955 to 1983, and the dates of historical events affecting land use on the BCNM (Denslow & Guzman in press).

METHODS

Vegetation sampling

In nine of the 10 sites, vegetation was sampled in two parallel 160-m trans-

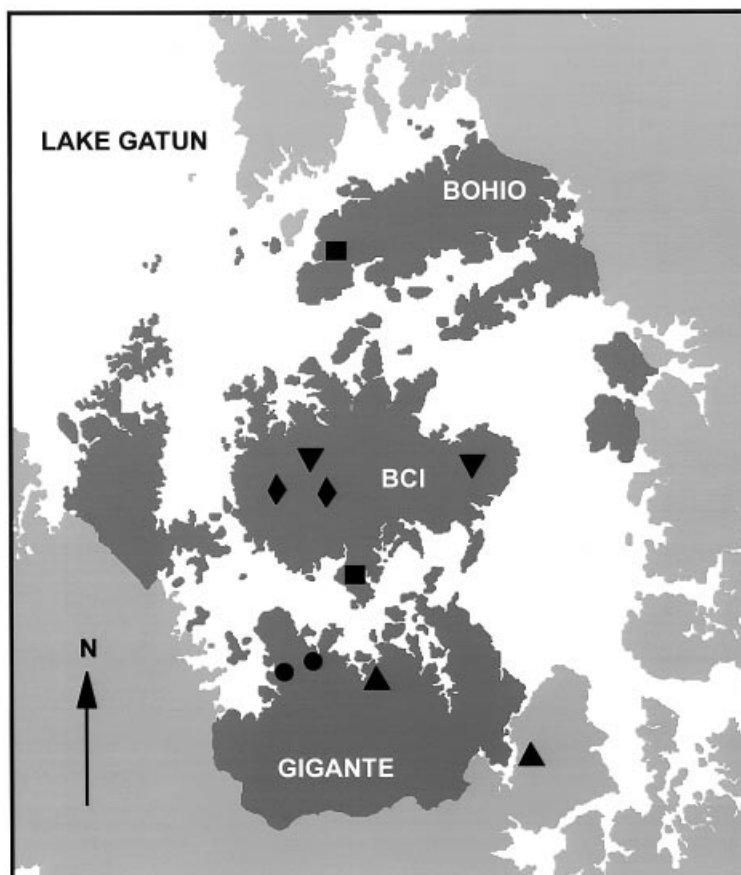


Figure 1. Map of the Barro Colorado Nature Monument showing the locations of the 10 forest stands in the chronosequence. BCI=Barro Colorado Island. The 20, 40, 70 and 100-y secondary forest stands are represented by triangles, circles, squares and inverted triangles, respectively. The old-growth stands are represented by diamonds.

ects composed of contiguous nested quadrats. Transects were located well inside forest edges and were separated by at least 20 m. The configuration of one 20-y site (Saino) was sufficient only for the establishment of a single transect, which was interrupted in two places by creeks. Trees (≥ 5 cm DBH) were sampled in 16 contiguous quadrats (10-m \times 10-m) in each transect and shrubs, saplings, and treelets (>1 m tall and <5 cm DBH) in 32 quadrats (5-m \times 5-m).

We sampled lianas in alternate 5-m \times 10-m quadrats along each transect (total of eight quadrats/transect, 400 m²). We pooled quadrats and transects by stand for analysis and used stand as the replication unit. We measured the diameters of all woody, dicotyledonous vines rooted in the quadrat, which were ≥ 0.5 cm diameter and ≥ 1.3 m in height. We measured apparent genets only once. When it was unclear whether stems were connected below ground, they were treated as distinct genets. The diameter of each liana was measured at its thickest point devoid of stem abnormalities if growing horizontally or at

1.3 m above the ground if growing only vertically. Thus, we measured the liana only once rather than summing multiple branch diameters. This methodology may provide a more representative measure of liana size than DBH when the main stem is horizontal but branches ascend vertically.

Lianas were identified in the field and verified at the Smithsonian Tropical Research Institute Herbarium. Lianas that could not be identified definitively ($n = 173$) were omitted from ordinations and calculations of diversity, although not from measures of abundance or size-structure. Nomenclature follows Croat (1978) except where recent revisions have modified names. In such cases they follow the working list of Panamanian plants compiled by W. D'Arcy and updated by M. Correa and R. Foster (unpubl.).

We classified species by climbing mechanism based on observations in the field and with reference to Croat (1978) and Putz (1984). We distinguished three categories: stem twiner, branch twiner and tendril climber. We found no root or adhesive-tendrill climbers. The main stem of stem twiners coils around supports; branch twiners have leaf-bearing branches, which twine around supports; and tendrill climbers have modified leaves, leaflets, or stipules, which coil around supports (Putz 1984). Species with stipular spines or other scrambling-type climbing mechanisms were rare in this survey and were therefore excluded in analyses of climbing type.

Analysis

We regressed liana density, basal area, average basal area per stem, diversity, and climbing mechanism on stand age. Regression was performed using PROC REG of SAS (6.12; SAS Institute, Inc. 1997). We assumed old-growth stands were 500 y old for the regression analysis. Liana density was scaled to a hectare basis, logarithmically transformed, and regressed against logarithm of stand age to normalize residuals. Total basal area and density of lianas of each climbing type were also scaled to the hectare. The proportions of lianas of each climbing type were arcsine transformed; we used analysis of covariance to examine differences across stand age (PROC GLM; SAS Institute, Inc. 1997). In that analysis, we only examined lianas < 1.5 cm diameter because small lianas are likely to be actively climbing, while larger lianas (> 1.5 cm) already may be established in the canopy. We expected a significant correlation between climbing mechanism and stand age only for actively climbing lianas, which would be responsive to changes in tree diameter. We estimated liana biomass (above-ground dry weight) from basal area as $\log y = 0.12 + 0.91(\log x)$, where $y =$ biomass and $x =$ basal area (Putz 1983). This equation was developed for 14 Venezuelan lianas ranging in diameter between 0.9 and 12.0 cm, a similar size range to that found in our study. Species diversity is reported as Fisher's log series α , an index of species diversity which is relatively unbiased by sample size (Magurran 1988).

We also compared liana densities, basal area, and diversity in young and old forest stands. We contrasted the four sites ≤ 40 y old with the six older sites

using analysis of variance (ANOVA). We used 70 y as a dividing age for the young and old sites because many fast-growing pioneer trees on BCI are projected to reach their maximum DBH before 70 y (Condit *et al.* 1993). Additionally, abundances of these species appear to decline after that age (J. Denslow, unpubl. data). ANOVA was performed using PROC GLM (SAS Institute, Inc. 1997) and P-values ≤ 0.05 were considered significant.

We examined patterns of liana composition using non-metric multidimensional scaling (NMS). Non-metric scaling is an iterative ordination technique based on ranked distances of n entities on k axes that seeks to minimize distortions caused by reductions in dimensionality (Minchin 1987). Ordinations were based on species that occurred in at least two stands (42 species) and used $1-D_s$, in which D_s is Sorenson's similarity index, as the distance matrix. Separate ordinations were based on relative abundances (abundance scaled to the total liana stems per site) and presence-absence. We used the SAS (6.12) routine PROC NMS with minimum acceptable final stress set at < 0.001 and maximum iterations set at 200 (SAS 1997). Solutions with 3 and 4 axes were examined, but two axes adequately decreased stress in both ordinations. Solutions using two axes are presented for easier interpretation.

RESULTS

Liana composition

We recorded a total of 1896 lianas ≥ 0.5 cm diameter from the ten stands. Unidentified lianas accounted for only 9% of all stems sampled. Our estimates of species diversity are conservative because the unidentified stems may have been rare species. The number of unidentified lianas per site ranged from 6–19% of total stems (Table 1). There was no significant difference in the number of unidentified stems among stand ages ($F = 1.63$, $df = 1, 8$; $P = 0.24$).

Lianas identified represented 89 different species from 22 families (Appendix 1). Predominant families encountered were the Bignoniaceae and Sapindaceae, represented by 21 and 13 species, respectively. The ten most abundant species, representing six families, accounted for 65% of all stems sampled (Table 2). The stem twiner *Maripa panamensis* (Convolvulaceae) was the most commonly sampled liana; it composed 11% of all stems and occurred in all stands. The most abundant species differed among stands, however (Table 3). The five most abundant species accounted for *c.* 50% of the total number of stems per stand. The total percentage contribution of these species per stand did not vary appreciably as a function of stand age ($r^2 = 0.06$, $n = 10$, $P = 0.51$).

Although less abundant than *M. panamensis*, *Prionostema aspera* (Hippocrateaceae) had the highest total basal area as summed over all stands (Table 2). *Maripa panamensis* had the second highest total basal area. The stem of *M. panamensis* usually grows flattened against tree boles. Because our basal area calculation is based on the radius of the flattened section of this liana, the basal area of *M. panamensis* was likely to have been overestimated.

Table 1. Site characteristics of the 10 stands in the Barro Colorado Nature Monument chronosequence. Numbers of individuals and basal area are not scaled to hectare. Site name codes are in parentheses. OG = old-growth forest.

Site	Stand Age (y)	Individuals sampled	Number of unidentified stems (% of number sampled)	Species recorded	Fisher's α	Basal area (cm ²)	Mean basal area (cm ² /liana)	Biomass* (t ha ⁻¹)
Pedro Gomez (PED)	20	348	38 (11)	38	11.37	1657	4.76	11.17
Saino (SAI)	20	114	22 (19)	21	8.50	271	2.38	4.05
Enders (END)	40	236	17 (7)	31	9.86	750	3.18	5.44
Foster (FOS)	40	363	20 (6)	35	9.75	1424	3.92	9.74
Bohio (BOH)	70	121	7 (6)	20	7.03	643	5.31	4.72
Poachers (POA)	70	167	10 (6)	25	8.38	988	5.92	6.98
Barbour (BAR)	100	147	15 (10)	25	9.13	1244	8.46	8.61
Pearson (PER)	100	149	21 (14)	21	7.14	1348	9.05	9.26
Armour (ARM)	OG	131	15 (11)	24	9.19	907	6.93	6.46
Zetek (ZET)	OG	120	8 (7)	20	7.09	583	4.86	4.33
Total across stands		1896	173 (9)	89		9815		

* Estimated above-ground dry mass as calculated with a formula in Putz (1983).

Table 2. Numbers of individuals and total basal areas of the 10 most abundant liana species summed over all stands across the chronosequence. Total area sampled was 3600 m².

Liana species	Family	Number of individuals	Basal area (cm ²)
<i>Mariipa panamensis</i>	Convolvulaceae	218	1053
<i>Prionostema aspera</i>	Hippocrateaceae	179	1638
<i>Petrea aspera</i>	Verbenaceae	155	306
<i>Clitoria javitensis</i>	Fabaceae	128	362
<i>Dolioscarpus olivaceus</i>	Dilleniaceae	124	423
<i>Dolioscarpus major</i>	Dilleniaceae	122	371
<i>Coccoloba parimensis</i>	Polygonaceae	84	338
<i>Davilla nitida</i>	Dilleniaceae	80	449
<i>Dolioscarpus dentatus</i>	Dilleniaceae	62	144
<i>Hippocratea volubilis</i>	Hippocrateaceae	59	476
Total of all species		1896	9815

Table 3. The most abundant species, the percent of the total liana stems composed by that species, and the percent of total stems composed by the five most abundant species in each stand. OG = old-growth forest.

Site	Stand age (y)	Most abundant liana species	Family	Percentage of total stems	Percentage of top five species
PED	20	<i>Clitoria javitensis</i>	Fabaceae	24	49
SAI	20	<i>Petrea aspera</i>	Verbenaceae	12	55
END	40	<i>Mariipa panamensis</i>	Convolvulaceae	20	52
FOS	40	<i>Mariipa panamensis</i>	Convolvulaceae	17	59
BOH	70	<i>Dolioscarpus major</i>	Dilleniaceae	22	64
POA	70	<i>Prionostema major</i>	Hippocrateaceae	16	58
BAR	100	<i>Coccoloba parimensis</i>	Polygonaceae	16	62
PER	100	<i>Dolioscarpus olivaceus</i>	Dilleniaceae	13	48
ARM	OG	<i>Petrea aspera</i>	Verbenaceae	18	47
ZET	OG	<i>Coccoloba parimensis</i>	Polygonaceae	18	69

Liana community structure

Liana abundance decreased significantly as a function of stand age (Figure 2a; $r^2 = 0.52$, $n = 10$, $P < 0.05$). Lianas were roughly twice as abundant in younger stands as in older stands ($F = 26.8$, $df = 1, 8$; $P < 0.0001$). Lianas were also a larger proportion of all woody stems > 1 m; they composed 25.4 and 19.0% of the stems in the younger and older forests, respectively.

In contrast to liana abundance, total liana basal area was independent both of stand age ($r^2 = 0.08$, $n = 10$, $P = 0.42$; Figure 2b) and relative age (young vs. old; $F = 0.29$, $df = 1, 8$; $P = 0.61$). The variance between stands in the younger forests was higher than in the older stands, however. Estimated mean liana biomass per stand was 7.1 t ha⁻¹.

Overall, mean liana size was greater in old than young stands (mean \pm SE: young = 3.56 ± 0.51 cm², old = 6.75 ± 0.70 cm²; $F = 11.07$, $df = 1, 8$; $P < 0.05$). Average liana basal area per stem increased from a mean of 3.6 cm² in 20-y stands to 8.8 cm² in 100-y stands. The average size in the old-growth forests (5.9 cm²) was lower than the 100-y stands. Average liana size over stand age increased over stand age, but was lower again in old-growth stands (Figure 2c).

Although the average size of lianas was greater in older stands, small lianas

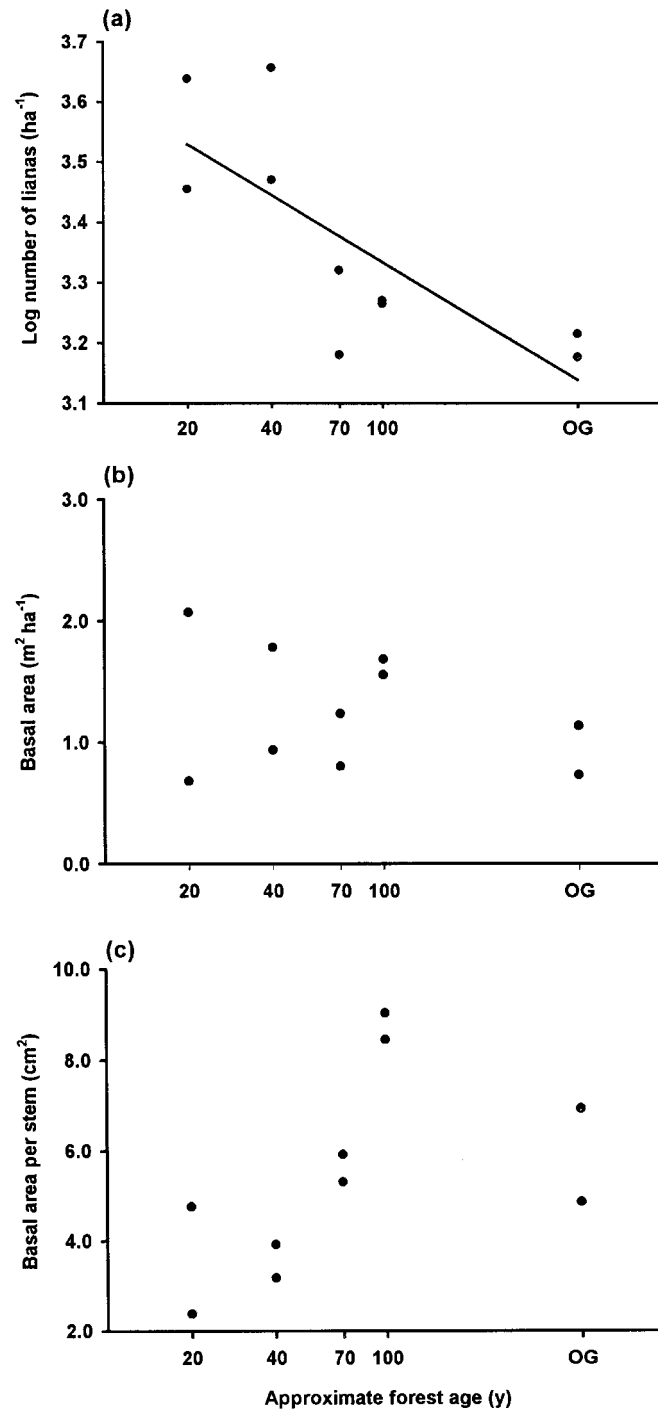


Figure 2. The relationship between (a) density of lianas, (b) liana basal area, and (c) mean basal area per stem, and forest age. Each point represents one stand. Only significant regression lines are shown ($P < 0.05$).

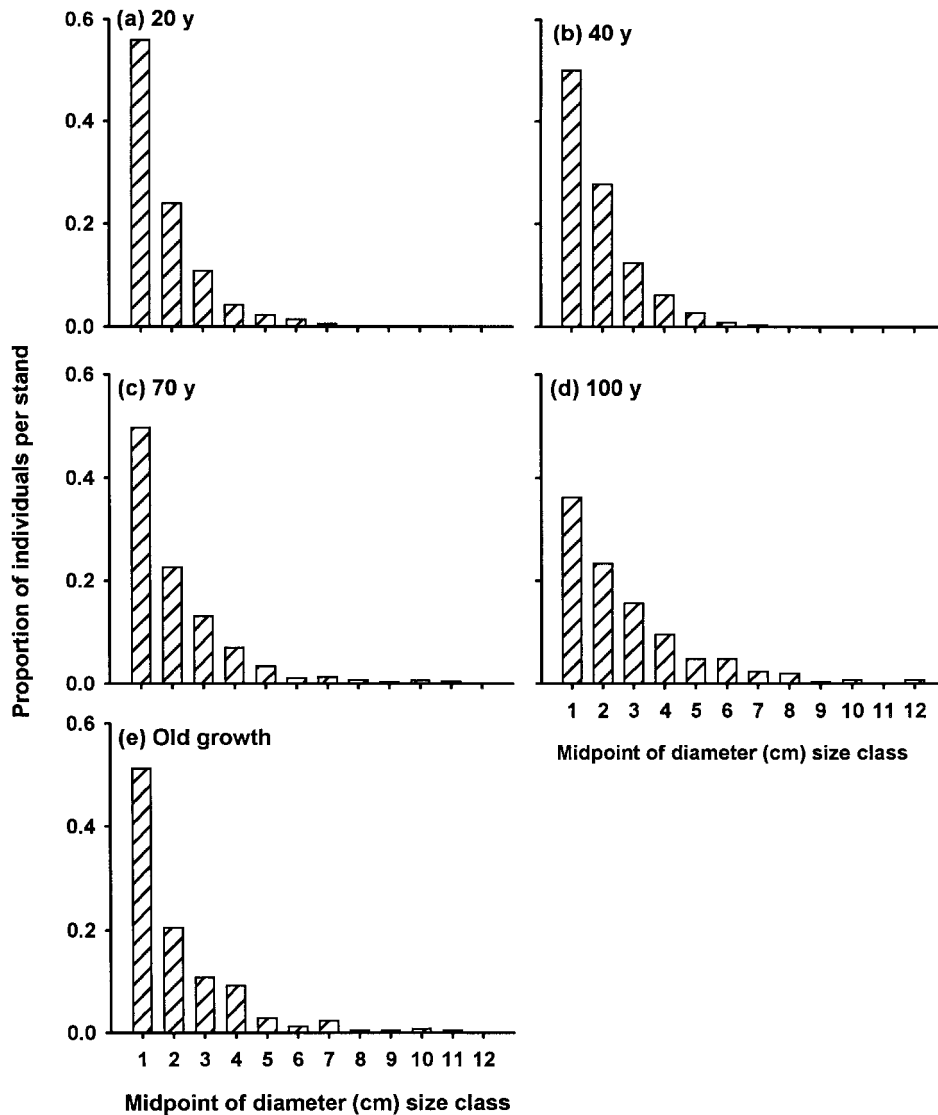


Figure 3. Size-class structure of the lianas in the different aged forest stands in the Barro Colorado Nature Monument.

(<1.5 cm) were always more abundant than medium or large lianas across stand age (Figure 3). Size class distributions did not differ greatly among stand ages. Nonetheless, small-diameter lianas were most abundant in the 20-y stands and the largest lianas were found in the forests ≥ 70 y old.

Liana diversity

Young stands (≤ 40 y) were significantly more diverse than older stands (≥ 70 y, $F = 7.13$, $df = 1, 8$; $P < 0.05$). Across stand age, however, no linear decline in diversity was apparent (Figure 4; $r^2 = 0.24$, $n = 10$, $P = 0.16$). Forests

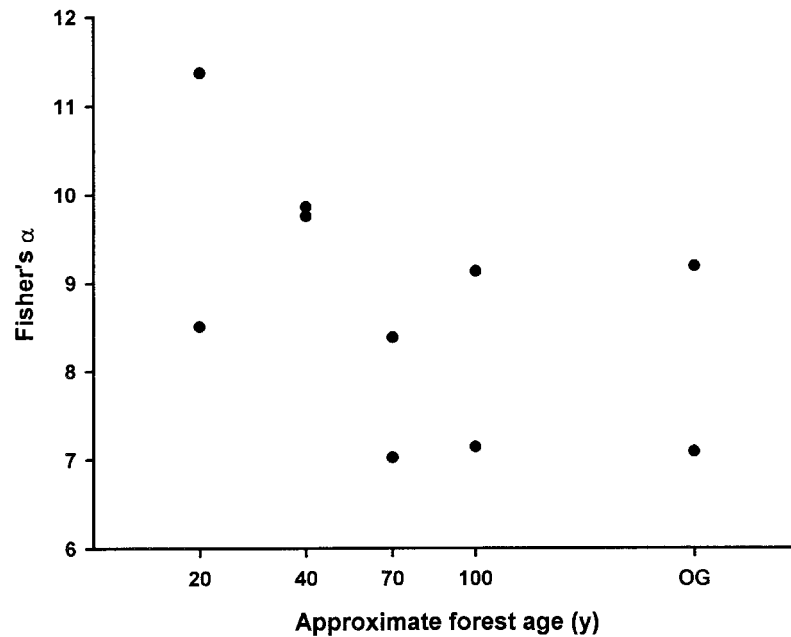


Figure 4. Relationship between Fisher's α log-series diversity index and forest age.

older than 70 y were similar in liana diversity. Because Fisher's α is a robust index of diversity and is relatively unbiased by sample size (Magurran 1988), the higher diversity of younger stands should not be a function of the high stem density. A strong correlation does exist, however, between liana abundance and the number of species sampled per stand ($r^2 = 0.92$, $n = 10$, $P < 0.0001$).

Species composition

The NMS ordination of stands based on relative abundance (Figure 5b), but not presence-absence (Figure 5a), of the liana species suggested a strong effect of stand age on composition. Stand position along the first dimension of the relative abundance ordination was correlated strongly with stand age (Spearman's rank correlation $r_s = 0.935$, $n = 10$, $P < 0.001$). The abundances of only four species were correlated significantly with stand position on the first dimension; three species were found more often in younger forests (*Clitoria javitensis*, $n = 128$, $r^2 = 0.42$, $P < 0.05$; *Phryganocydia corymbosa*, $n = 19$, $r^2 = 0.40$, $P < 0.05$; and *Smilax* sp.1, $n = 6$, $r^2 = 0.49$, $P < 0.05$) and one in older forests (*Cydista aequinoctalis*, $n = 7$, $r^2 = 0.48$, $P < 0.05$). Stand age was not significantly correlated with stand position on any axis when the ordination was based on presence-absence data. Stands separated by geographic locations in both ordinations (Figure 5).

Twining mechanism

Stem twiners predominated among all lianas sampled at all forest ages (1034 stem-twiners, 260 branch-twiners, and 360 tendril-climbers). Among lianas

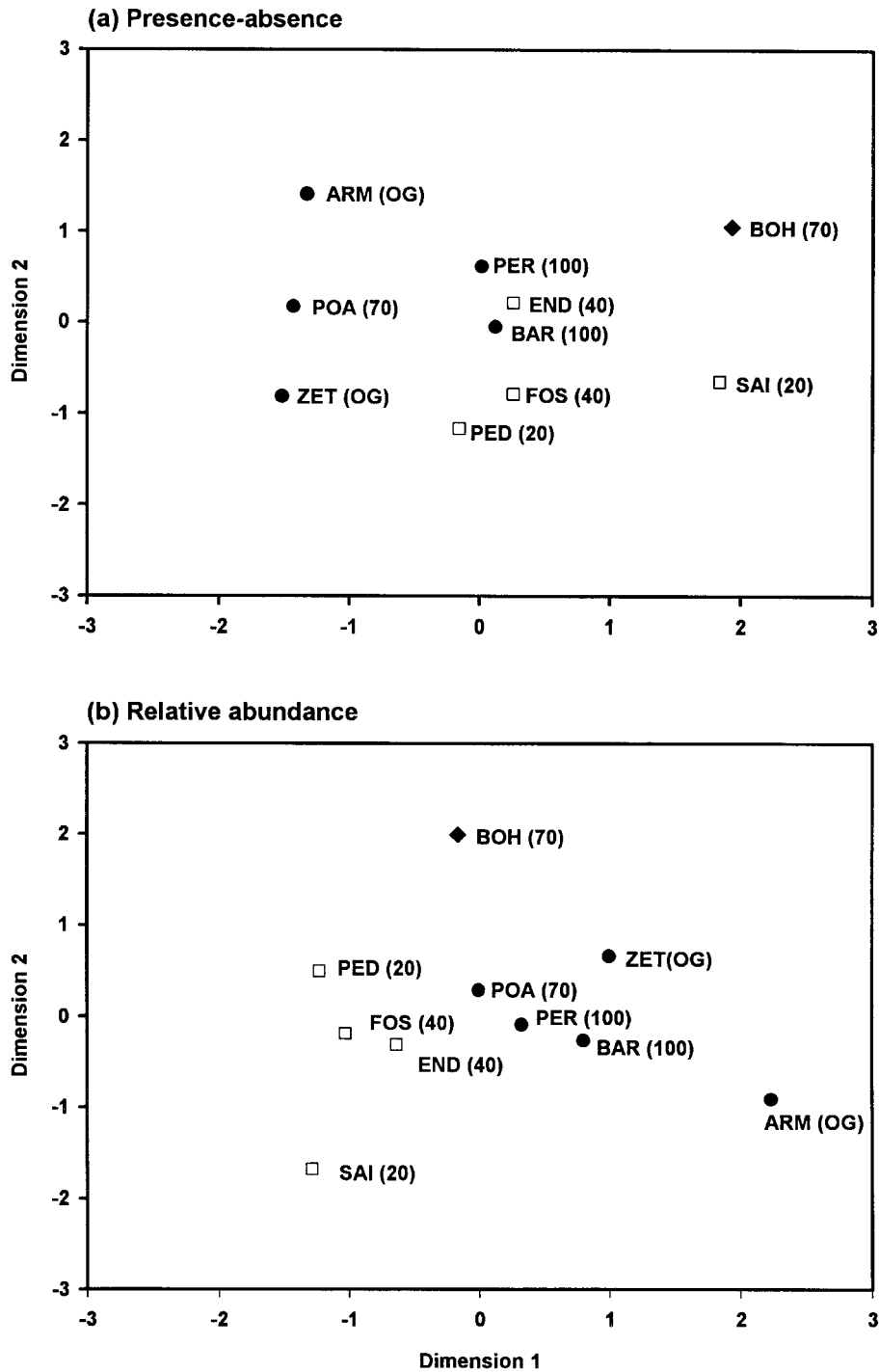


Figure 5. Non-metric multidimensional scaling ordination of the 10 forest stands using (a) presence-absence of 42 liana species (two-dimensional solution, stress = 0.11), and (b) relative abundance (two-dimensional solution, stress = 0.08). Stands are indicated by the stand code (see Table 1) and age is in parentheses. OG denotes old growth. Stands located on the Gigante Peninsula are shown as open squares, stands on Barro Colorado Island by filled circles, and the stand on the Bohio Peninsula by a filled diamond.

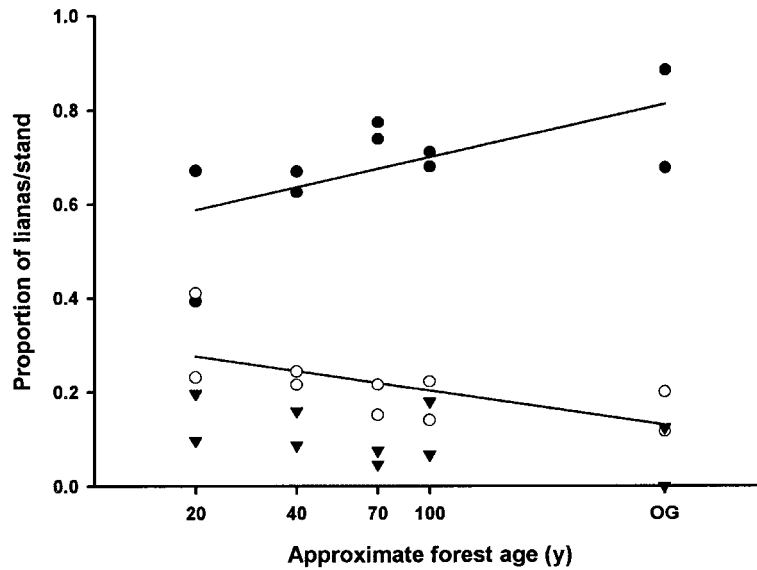


Figure 6. Proportion of lianas that are stem-twiners (black circles), tendrils (open circles) and branch-twiners (black inverted triangles) plotted against forest age. Only significant regression lines are shown ($P < 0.05$). Stem-twiners = $0.334 + 0.227x$ ($r^2 = 0.43$, $n = 10$, $P < 0.05$); tendrils = $0.423 - 0.1087x$ ($r^2 = 0.40$, $n = 10$, $P < 0.05$); where $x = \log$ of stand age.

<1.5 cm diameter, the relative proportion of the different climbing types changed across stand age (ANCOVA, $F = 7.96$, $df = 2, 24$; $P < 0.01$). Proportion of stem twiners significantly increased ($r^2 = 0.43$, $n = 10$, $P < 0.05$) while tendrils decreased ($r^2 = 0.40$, $n = 10$, $P < 0.05$) across stand age (Figure 6). Branch twiners did not show a significant trend ($r^2 = 0.20$, $n = 10$, $P = 0.20$).

DISCUSSION

Our approach of using a chronosequence to address questions of succession assumes that the forest stands differ only in their ages. However, variation in soils or microclimates, differences in land-use history, or consequences of isolation of BCI following the filling of Lake Gatun could confound the differences. Denslow & Guzman (in press) examined the assumptions of environmental and historical homogeneity over the chronosequence; they found no systematic variation in several environmental variables related to site productivity, including soil pH, standing litter mass, and soil bulk density that may have been confounded with successional patterns. Thus, even if differences in these variables were present at the time of field abandonment due to variation in land use history, they had diminished during the long fallow periods of stands used in this study.

Island-mainland differences in animal populations are another source of confounding variation. One 70-y stand and all of the 100-y and old-growth stands were located on Barro Colorado Island, while the young stands and one

70-y stand were located on the adjacent mainland (see Figure 1). Terborgh (1992) hypothesized that the absence of large carnivores on BCI has led to higher densities of mammalian seed predators and herbivores, which may in turn reduce seedling recruitment and density. A recent study in Lake Gatun, however, has shown little evidence for differences in seedling recruitment on island vs. mainland sites (Terborgh & Wright 1994). Additionally, seedling densities in the two 70-y stands were similar (Denslow & Guzman in press). We conclude that the observed patterns in stand structure were driven more by successional processes than by environmental or historical differences.

In general, the climbing habit seemed to be most successful in early successional communities. Liana abundance was highest in young stands, both absolutely and in relation to all woody stems. Species diversity was also highest in young stands even when the effect of density was removed. This suggests that a similar suite of environmental conditions promotes establishment of many liana species. High light early in succession is probably the strongest determinant of this pattern. Light availability is high after field abandonment and decreases rapidly as pioneer trees and other early-successional species close the canopy (Brown & Lugo 1990). At 20 y, relatively high light levels on the ground (about 6% full sunlight estimated from fish-eye photographs) reflect a low canopy and a sparse understorey (Denslow & Guzman in press). Canopy opening due to the senescence of the first cohort of pioneers probably occurs at about this time (Brown & Lugo 1990). Understorey light levels decline with stand age throughout the chronosequence (Denslow & Guzman in press). The high liana density in the young stands (20-y and 40-y) are likely to have resulted from relatively high understorey light levels early in succession.

Older stands are characterized by lower overall light levels and fewer microsites for seedling establishment (Denslow & Guzman in press), both of which may contribute to lower liana densities. Although lianas may establish under closed canopies in BCNM forests, few reach the canopy unless they are located in a treefall gap. Putz (1984) found that 10–85% of four common liana species were seedlings rather than vegetative sprouts. S. Schnitzer & W. Carson (unpubl. data) also found that lianas composed >17% of all seedlings in old-growth forest at BCNM. Nevertheless Putz (1984) found few lianas in intermediate size classes (4–24 m long) and suggested that few lianas successfully climb up through mature forest in the absence of gaps. These data suggest that small lianas may be abundant in the understorey but are not successful in reaching the canopy in older forests.

Liana composition likely is a function of both stand age and geographic location. Ordination based on relative abundance reveals both a successional sequence (stands arranged by age) and geographic separation of stands (BCI vs. Gigante Peninsula vs. Bohio). In the presence-absence ordination, the successional sequence is lost but the pattern due to geographic location is maintained. Thus, the relative abundances of species appear strongly affected by

successional processes, while species presence is affected by site distributions, probably due to dispersal limitations among sites separated by distance and water barriers.

Despite the fact that liana abundance was highest in young stands, no liana species were restricted to young forests. The failure of stands to separate by age in the presence-absence ordination suggests that few species were limited to a particular phase of succession. Some long-lived species establish early in succession and persist for many years. The observed increase in average liana size with stand age supports this idea. In addition, Putz (1990) found that genet mortality of lianas is low on BCI ($0.27\% \text{ y}^{-1}$), despite a high frequency of dislodgement of ramets from the canopy. In addition, species that require high light levels may establish early in succession and reappear in older forests by colonizing light gaps. Increases in liana abundance after disturbance have been well documented (Teramura *et al.* 1991) and gaps are known to be important sites for liana regeneration (Putz 1984, S. Schnitzer & W. Carson unpubl. data). For example, old gaps were thought to account for the spatially clumped pattern of lianas in a Gabonese rain forest (Caballé 1976). Thus, short-lived and long-lived species may contribute to liana diversity in both young and old-growth forest by recruiting into light gaps.

Successional changes in species abundances indicated by the relative abundance ordination may be caused in part by changes in availability of suitable supports. Climbing mechanism determines the maximum diameter support a liana can use. Tendril climbers are restricted generally to supports with diameters <10 cm and stem twiners to support diameters <30 cm (Putz 1984, Putz & Chai 1987). Branch twiners have higher maximum support sizes (Putz 1984, Putz & Chai 1987). Our results for small lianas (<1.5 cm diameter) support the predictions of Putz & Holbrook (1991), who suggested that tendril climbers would be more common when smaller diameter supports are available. As predicted, the proportion of stem twiners increased and tendril climbers decreased over stand age in this study. The recruitment of tendril climbers may be limited to the early stages of succession or to gaps during which time small diameter supports are available. This trend has also been found in Australian, West African, and other neotropical sites (Putz *et al.* 1989).

Total liana basal area, and thus estimated biomass, remained relatively constant over stand age. However, liana biomass is a higher proportion of total stand biomass in young than in old stands along the BCNM chronosequence because tree biomass increases with stand age (Denslow & Guzman in press). We did not measure liana leaf biomass, but this foliar component of biomass may be especially important to successional processes. Lianas >5.0 cm have higher leaf biomass/stem area than do trees (Putz 1983) and may contribute more than 20% to canopy leaf biomass in tropical forests (Hegarty 1988, Ogawa *et al.* 1965, Putz 1983). Moreover, some lianas have shorter leaf life-spans than trees (Hegarty 1990, Peñalosa 1984). Thus, the proportion of liana leaf litter

may be higher than that for trees in early succession when leaf turnover is most rapid. Hegarty (1990) found that lianas typical of early succession had higher leaf turnover rates than did lianas of mature forest in subtropical rain-forest in Queensland, Australia. Lianas may therefore contribute a disproportionately large component of leaf litter, and thus nutrients, in comparison to their biomass. This contribution may be especially important to reestablishment of nitrogen cycling processes, which occur early in succession (Reiners *et al.* 1994).

Results from this study suggest that lianas can be characterized as an early-successional guild of pioneer species. The high diversity and density of lianas in young forests indicate that lianas colonize quickly after land abandonment, given a proximate seed source. While the composition of the liana community appears to reflect changes in forest structure (support availability) and environment (light), we found little indication of old-growth specialists. Their importance in early successional communities suggests an important role in reestablishment of forest ecosystem processes.

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LITERATURE CITED

- APPANAH, S., GENTRY, A. H. & LAFRANKIE, J. V. 1993. Liana diversity and species richness of Malaysian rain forests. *Journal of Tropical Forest Science* 6:116–123.
- BAARS, R., KELLY, D. & SPARROW, A. D. 1998. Liane distribution within native forest remnants in two regions of the South Island, New Zealand. *New Zealand Journal of Ecology* 22:71–85.
- BALFOUR, D. A. & BOND, W. J. 1993. Factors limiting climber distribution and abundance in a southern African forest. *Journal of Ecology* 81:93–99.
- BROWN, M. J. & PARKER, G. G. 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Canadian Journal of Forest Research* 24:1694–1703.
- BROWN, S. & LUGO, A. E. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6:1–32.
- CABALLÉ, G. 1976. *Sur la biologie des lianes ligneuses en forêt Gabonaise*. PhD thesis, Université des Sciences et Techniques du Languedoc.
- CASTELLANOS, A. E. 1991. Photosynthesis and gas exchange of vines. Pp. 181–204 in Putz, F. E. & Mooney, H. A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.
- CHAPMAN, F. M. 1938. *Life in an air castle*. Appleton-Century, New York. 250 pp.
- CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1993. Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *Forest Ecology and Management* 62:123–143.
- CROAT, T. R. 1978. *The flora of Barro Colorado Island*. Stanford University Press, Stanford, California. 943 pp.
- DENSLOW, J. S. & GUZMAN G., S. In press. Variation in stand structure, light, and seedling abundance across a tropical moist forest chronosequence, Panama. *Journal of Vegetation Science*.
- ENDERS, R. K. 1935. Mammalian life histories from Barro Colorado Island, Panama. *Bulletin of the Museum of Comparative Zoology* 78:385–502.
- FOSTER, R. B. & BROKAW, N. V. L. 1982. Structure and history of the vegetation of Barro Colorado

- Island. Pp. 67–81 in Leigh, E. G., Jr., Rand, A. & Windsor, D. (eds). *The ecology of a tropical forest: seasonal rhythms and long-term changes* (1st edition). Smithsonian Institution Press, Washington, DC.
- GENTRY, A. H. 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* 15:1–84.
- GENTRY, A. H. 1991. The distribution and evolution of climbing plants. Pp. 3–49 in Putz, F.E. & Mooney, H.A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.
- GENTRY, A. H. & DODSON, C. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* 19:149–156.
- HEGARTY, E. E. 1988. *Canopy dynamics of lianas and trees in subtropical rainforest*. PhD thesis, University of Queensland.
- HEGARTY, E. E. 1990. Leaf life-span and leafing phenology of lianas and associated trees during rainforest succession. *Journal of Ecology* 78:300–312.
- HEGARTY, E. E. & CABALLÉ, G. 1991. Distribution and abundance of vines in forest communities. Pp. 313–335 in Putz, F.E. & Mooney, H.A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.
- KENOYER, L. A. 1929. General and successional ecology of the lower tropical rain forest at Barro Colorado Island, Panama. *Ecology* 10:201–222.
- LEIGH, E. G., JR., RAND, A. S. & WINDSOR, D. M. 1996. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. (2nd edition). Smithsonian Institution Press, Washington, DC. 503 pp.
- MAGURRAN, A. E. 1988. *Ecological diversity and its measurement*. Princeton University Press, Princeton, New Jersey. 179 pp.
- MINCHIN, P. R. 1987. An evaluation of relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107.
- OGFAWA, H., YODA, K., OGINO, K. & KIRA, T. 1965. Comparative ecological studies on three main types of forest vegetation in Thailand. II. Plant biomass. *Nature and Life in South East Asia* 4:49–80.
- PEÑALOSA, J. 1982. Morphological specialization and attachment success in two twining lianas. *American Journal of Botany* 69:1043–1045.
- PEÑALOSA, J. 1984. Basal branching and vegetative spread in two tropical rain forest lianas. *Biotropica* 16:1–9.
- PINARD, M. A. & PUTZ, F. E. 1994. Vine infestation of large remnant trees in logged forest in Sabah, Malaysia: biomechanical facilitation in vine succession. *Journal of Tropical Forest Science* 6:302–309.
- PUTZ, F. E. 1983. Liana biomass and leaf area of a 'tierra firme' forest in the Rio Negro Basin, Venezuela. *Biotropica* 15:185–189.
- PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713–1724.
- PUTZ, F. E. 1990. Liana stem diameter growth and mortality rates on Barro Colorado Island, Panama. *Biotropica* 22:103–105.
- PUTZ, F. E. & CHAI, P. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. *Journal of Ecology* 75:523–531.
- PUTZ, F. E. & HOLBROOK, N. M. 1991. Biomechanical studies of vines. Pp. 73–97 in Putz, F.E. & Mooney, H.A. (eds). *The biology of vines*. Cambridge University Press, Cambridge.
- PUTZ, F. E., MOONEY, H. A. & BULLOCK, S. H. 1989. Biology of vines. *Trends in Ecology and Evolution* 4:224.
- REINERS, W. A., BOUWMAN, A. F., PARSONS, W. F. J. & KELLER, M. 1994. Tropical rain forest conversion to pasture: changes in vegetation and soil properties. *Ecological Applications* 4:363–377.
- RICHARDS, P. W. 1996. *The tropical rain forest: an ecological study*. (2nd edition). Cambridge University Press, Cambridge. 575 pp.
- SALDARRIAGA, J. G., WEST, D. C., THARP, M. L. & UHL, C. 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology* 76:938–958.
- SAS INSTITUTE, INC. 1997. *SAS/STAT User's Guide. Version 6.12*, Cary, NC.
- STANDLEY, P. C. 1933. *The flora of Barro Colorado Island, Panama*. Volume 78. Smithsonian Miscellaneous Collection. 148 pp.
- TERAMURA, A. H., GOLD, W. G. & FORSETH, I. N. 1991. Physiological ecology of mesic, temperate woody lianas. Pp. 245–285 in Putz, F.E. & Mooney, H.A. (eds). *The biology of lianas*. Cambridge University Press, Cambridge.
- TERBORGH, J. 1992. Maintenance of diversity in tropical forests. *Biotropica* 24:283–292.
- TERBORGH, J. & WRIGHT, S. J. 1994. Effects of mammalian herbivores on plant recruitment in two neotropical forests. *Ecology* 75:1829–1833.
- UHL, C., BUSCHBACHER, R. & SERRÃO, E. A. S. 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *Journal of Ecology* 76:663–681.

Appendix 1. All identified liana species found in the 10 forest stands (3600 m²) along the Barro Colorado Nature Monument chronosequence with total number of individuals, total basal area, and climbing type of each species.

Family	Species	No. of stems	Basal area (cm ²)	Climbing type*	
Apocynaceae	<i>Forsteronia viridescens</i> S. F. Blake	7	91.7	S	
	<i>Prestonia acutifolia</i> (Benth.) K. Schum in Engler & Prantl	2	13.2	S	
Aristolochiaceae	<i>Prestonia obovata</i> Standl.	2	1.1	S	
	<i>Aristolochia chapmaniana</i> Standl.	3	5.4	S	
Bignoniaceae	<i>Arrabidaea chica</i> (H. & B.) Verl.	7	49.6	T	
	<i>Arrabidaea patellifera</i> (Schlecht.) Sandw.	1	9.3	T	
	<i>Callichlamys latifolia</i> (L. C. Rich.) K. Schum. in Engler & Prantl	1	7.8	T	
	<i>Ceratophytum tetragonolobum</i> (Jacq.) Sprague & Sandw.	1	0.8	T	
	<i>Cydista aequinoctalis</i> (L.) Miers	7	102.3	T	
	<i>Paragonia pyramidata</i> (L. C. Rich.) Bur.	11	65.0	T	
	<i>Phryganocydia corymbosa</i> (Vent.) Bur. ex K. Schum. in Engler & Prantl	19	48.2	T	
	<i>Pithecoctinium crucigerum</i> (L.) A. Gentry	1	5.9	T	
	<i>Pleonotoma variabilis</i> (Jacq.) Miers	16	15.0	T	
	<i>Xylophragma seemannianum</i> (O. Kuntze) Sandw.	5	66.6	T	
	Unknown Bignoniaceae 1-10	30	331.1	T	
	Boraginaceae	<i>Tournefortia cuspidata</i> H.B.K.	2	8.4	S
	Combretaceae	<i>Combretum decandrum</i> Jacq.	27	366.0	S
<i>Combretum laxum</i> Jacq.		8	107.5	S	
Connaraceae	<i>Connarus panamensis</i> Griseb.	52	299.9	S	
	<i>Connarus turczaninowii</i> Tr.	3	26.3	S	
Convolvulaceae	<i>Mariipa panamensis</i> Hemsl.	218	1052.9	S	
Dilleniaceae	<i>Davilla nitida</i> (Vahl) Kub.	80	448.8	S	
	<i>Dolioscarpus dentatus</i> (Aubl.) Standl.	62	144.2	S	
	<i>Dolioscarpus major</i> J. F. Gmel. in L.	122	370.5	S	
	<i>Dolioscarpus multiflorus</i> Standl.	10	53.7	S	
	<i>Dolioscarpus olivaceus</i> Sprague & L. O. Wms. ex Standl.	124	422.5	S	
	<i>Tetracera portobellensis</i> Beurl.	1	0.2	S	
	Unknown Dilleniaceae	1	1.7	S	
Euphorbiaceae	<i>Omphalea diandra</i> L.	4	94.0	S	
Fabaceae	<i>Bauhinia guianensis</i> Aubl.	1	11.3	T	
	<i>Bauhinia reflexa</i> Schery	3	126.8	T	
	<i>Bauhinia</i> sp.	1	44.2	T	
	<i>Clitoria javitensis</i> H.B.K.	128	362.4	T	
	<i>Machaerium kegelii</i> Meisn.	4	12.0	P	
	<i>Machaerium milleflorum</i> Pitt.	1	6.2	P	
	<i>Machaerium seemanii</i> Benth. ex Seem	3	6.6	P	
	<i>Machaerium</i> sp. 1-5	5	12.6	P	
Hippocrateaceae	<i>Anthodon panamense</i> A. C. Smith	2	13.5	B	
	<i>Cuervea kappleriana</i> (Miq.) A.C. Sm.	8	84.1	B	
	<i>Hippocratea volubilis</i> L.	59	476.0	B	
	<i>Hylenaea praecelsa</i> (Miers) A. C. Smith	8	86.7	B	
	<i>Prionostema aspera</i> (Lam.) Miers	179	1638.5	B	
	<i>Salacia</i> sp.	4	12.7	B	
	Unknown Hippocrateaceae 1-3	3	61.1	B	
	<i>Strychnos toxifera</i> Schomb. ex Benth.	4	2.9	T	
Loganiaceae	<i>Banisteriopsis cornifolia</i> (H.B.K.) C. B. Robinson ex Small	6	36.3	S	
	<i>Heteropterys laurifolia</i> (L.) Adr. Juss.	1	4.2	S	
	<i>Hiraea grandifolia</i> Standl.	8	27.6	S	
	<i>Hiraea quapara</i> (Aubl.) Sprague	9	9.7	S	

Appendix 1. *continued*

Family	Species	No. of stems	Basal area (cm ²)	Climbing type*
	<i>Hiraea reclinata</i> Jacq.	53	143.6	S
	<i>Mascagnia nervosa</i> Niedenzu	3	7.9	S
	<i>Stigmaphyllon lindenianum</i> Adr. Juss.	3	3.0	S
Menispermaceae	<i>Abuta racemosa</i> (Thunb.) Tr. & Planch.	21	67.3	S
	<i>Odontocarya tamoides</i> (Dc.) Miers. var. <i>canescens</i> (Miers) Barn.	1	0.6	S
Passifloraceae	<i>Passiflora auriculata</i> H.B.K.	4	6.9	T
Piperaceae	<i>Piper</i> sp.	1	14.5	U
Polygonaceae	<i>Coccoloba parimensis</i> Benth.	84	338.1	S
Rubiaceae	<i>Uncaria tomentosa</i> (Willd.) DC.	1	44.2	P
Sapindaceae	<i>Paullinia baileyi</i> Standl.	14	8.5	T
	<i>Paullinia bracteosa</i> Radlk.	17	19.1	T
	<i>Paullinia fibrifera</i> Radlk.	21	114.2	T
	<i>Paullinia glomerulosa</i> Radlk.	1	2.7	T
	<i>Paullinia pterocarpa</i> Tr. & Planch.	3	1.6	T
	<i>Paullinia rugosa</i> Benth. ex Radlk.	9	17.5	T
	<i>Paullinia turbacensis</i> H.B.K.	6	4.0	T
	<i>Paullinia</i> sp.	1	14.5	T
	<i>Serjania atrolineata</i> Suav. & Wright	1	0.5	T
	<i>Serjania cornigera</i> Turcz.	3	5.8	T
	<i>Serjania decapleuria</i> Croat	2	1.3	T
	<i>Serjania mexicana</i> (L.) Willd.	21	46.4	T
	<i>Thinouia myriantha</i> Tr. & Planch.	1	19.6	T
Smilacaceae	<i>Smilax</i> sp. 1	6	6.8	T
	<i>Smilax</i> sp. 2	1	2.7	T
Verbenaceae	<i>Petrea aspera</i> Turcz.	155	306.5	S
Vitaceae	<i>Vitis tiliifolia</i> H. & B. ex R. & S.	28	323.1	T

* B = branch twiner, P = spines used for climbing, S = stem twiner, T = tendril climber, U = climbing type not known.