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LARGE LIANAS AS HYPERDYNAMIC ELEMENTS OF THE TROPICAL FOREST CANOPY

OLIVER L. PHILLIPS,^{1,5} RODOLFO VÁSQUEZ MARTÍNEZ,² ABEL MONTEAGUDO MENDOZA,^{2,3}
TIMOTHY R. BAKER,^{1,4} AND PERCY NÚÑEZ VARGAS³

¹Earth and Biosphere Institute, School of Geography, University of Leeds, UK

²Proyecto Flora del Perú, Jardín Botánico de Missouri, Oxapampa, Pasco, Perú

³Herbario Vargas, Universidad Nacional San Antonio Abad del Cusco, Perú

⁴Max Planck Institute of Biogeochemistry, Jena, Germany

Abstract. Lianas (woody vines) are an important component of lowland tropical forests. We report large liana and tree inventory and dynamics data from Amazonia over periods of up to 24 years, making this the longest geographically extensive study of liana ecology to date. We use these results to address basic questions about the ecology of large lianas in mature forests and their interactions with trees. In one intensively studied site we find that large lianas (≥ 10 cm diameter) represent $< 5\%$ of liana stems, but 80% of biomass of well-lit upper canopy lianas. Across sites, large lianas and large trees are both most successful in terms of structural importance in richer soil forests, but large liana success may be controlled more by the availability of large tree supports rather than directly by soil conditions. Long-term annual turnover rates of large lianas are 5–8%, three times those of trees. Lianas are implicated in large tree mortality: liana-infested large trees are three times more likely to die than liana-free large trees, and large lianas are involved in the death of at least 30% of tree basal area. Thus large lianas are a much more dynamic component of Amazon forests than are canopy trees, and they play a much more significant functional role than their structural contribution suggests.

Key words: Amazonia; dynamics; liana; mortality; Peru; productivity; recruitment; soil structure; treefall; tropical forest; turnover.

INTRODUCTION

Lianas, or woody vines, are a significant component of most tropical forests (Schnitzer and Bongers 2002). They comprise from 15% to 25% of woody plant stems and species in forest sample plots around the tropics (Gentry 1991), and contribute up to 40% of forest leaf area and leaf productivity (Hegarty and Caballé 1991). Moreover, climbers are structural parasites on other plants (Darwin 1867, Stevens 1987) and as such may slow tree growth (Clark and Clark 1990), increase risk of death for host trees (e.g., Putz 1984a, b), and are a major pest in managed and plantation tropical forests (e.g., Appanah and Putz 1984). Lianas have been shown to delay and alter gap-phase regeneration processes through competitive interactions with juvenile trees (Schnitzer et al. 2000). Recent research also suggests that the abundance of lianas is changing. Long-term monitoring of populations in Amazonia (Phillips et al. 2002) and leaf fall in Central America (Wright et al. 2004) indicates that lianas are becoming more dominant and productive even in mature forests, possibly because higher CO₂ levels provide a competitive ad-

vantage to liana as opposed to tree species (Granados and Korner 2002).

In spite of their significance, lianas are persistently understudied, and even a basic understanding of population processes and macroecological patterns remains elusive. For example, several factors have been proposed to promote large liana abundance in forests, including soil fertility and seasonality (Gentry 1991), availability of suitable trellises (Hegarty and Caballé 1991), and prior human disturbance (Ballée and Campbell 1990); but few quantitative data are available to evaluate these claims. Those data that are available are rarely standardized, rendering large-scale comparative analysis of structure and composition, let alone dynamics, difficult (cf., Burnham 2004). Liana growth rates and turnover rates are rarely reported even though equivalent parameters for trees are now published from 100 sites in Amazonia alone (Phillips et al. 2004). The largest lianas that reach, and potentially dominate, the canopy of mature forests are especially understudied because of the difficulties in following a sufficiently large sample for a long enough time. One result is that lianas are ignored in models of forest processes and so the potential feedback of changing liana dominance and dynamics on stand-level biodiversity and carbon balance remain unexplored. Standardized structural and life history data are needed from a range of sites if the role of large lianas is to be better understood.

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⁵ E-mail: o.phillips@leeds.ac.uk



PLATE 1. Neotropical lianas of the genus *Bauhinia*. Photo credit: Yadvinder Malhi.

Here we report liana and tree structure and dynamics data from a series of upper Amazonian forest sites in Peru, representing the longest geographically extensive study of large liana dynamics in the world (see Plate 1). We use this long-term field effort to explore a set of key questions about the ecology of large lianas in mature forests and their interactions with trees. (1) Do large diameter lianas represent the canopy-dominant lianas? (2) What fraction of the tree community supports large lianas? (3) What structural/environmental factors affect the prevalence of large lianas? (4) How fast do lianas enter and exit the largest size class? (5) How do large liana turnover rates compare with tree turnover rates? (6) How are the deaths of large lianas and large trees associated with one another? (7) What factors control liana dynamics?

METHODS

Most lianas are small in diameter and often difficult to relocate. Complete liana censuses are therefore a time-consuming and error-prone method of evaluating liana population dynamics over long periods, especially when comparing multiple sites through time. By concentrating on lianas ≥ 10 cm diameter we aimed to focus on the dominant lianas and make possible exploration of liana dynamics at regional scales and through time (multiple sites, multiple censuses). We did not attempt to distinguish between ramets and genets because of the focus on aboveground biomass and

stem dynamics and the difficulties in making this distinction conclusively. Rather, the diameter of climbing stems rooted within our plots and ≥ 10 cm wide ("large lianas") was measured at 1.3 m (" $d_{1.3}$ ") above the ground and at the widest point within 2.5 m of the ground (" d_{max} "), and all lianas attaining at least 10.0 cm d_{max} were permanently marked. We focus here on results based on d_{max} , because these afford a larger sample size and therefore the sampling error associated with estimating density and dynamic parameters is lower.

To address the first question (do large diameter lianas represent the canopy-dominant lianas?), we quantified the relative importance of lianas ≥ 10 cm diameter in the context of a whole liana community of climbing stems ≥ 1 cm $d_{1.3}$. One 1-ha plot in southern Peru was selected at random when vegetation was fully hydrated at the start of the 2002 dry season and then systematically sampled in a predetermined grid of 13 20 m \times 20 m subplots, for a total of 0.52 ha. For each climbing liana encountered we recorded $d_{1.3}$ and d_{max} and visually estimated the median and maximum height at which it bore leaves, and recorded separately the canopy lighting environment of its leaves (emergent/canopy sun leaf/subcanopy/understory/ < 2 m above ground level). Aboveground dry biomass of each liana (stem plus leaves) was estimated allometrically from $d_{1.3}$ using a model of Chave et al. (forthcoming in S. A. Schnitzer, S. J. DeWalt, and J. Chave, *unpublished*

TABLE 1. Dynamics of lianas and trees in western Amazonian forests.

Site code	Census interval [†]	Tree ANPP (Mg C·ha ⁻¹ ·yr ⁻¹)	Dynamic rates, logarithmic model (% per year)					No. stems·ha ⁻¹ ·yr ⁻¹			
			Lianas, mortality rate λ	Lianas, recruitment rate μ	Liana turnover	All trees turnover	Trees >50 cm dbh turnover	Lianas lost	Lianas gained	Liana through put	Trees >50 cm dbh throughput
CUZ-01	14.35	9.88	5.96	5.60	5.78	2.35	1.68	2.16	2.02	3.90	0.70
CUZ-02	14.33	11.60	5.60	5.60	5.60	2.19	1.79	1.60	1.46	3.07	0.70
CUZ-03	14.34	11.46	4.10	4.83	4.47	2.44	1.70	1.60	1.88	3.49	0.70
CUZ-04	14.33	12.01	9.07	10.10	9.58	2.62	1.93	2.79	3.21	6.00	1.26
TAM-01	16.31	10.41	5.79	8.92	7.36	2.48	2.01	1.10	1.96	3.07	0.67
TAM-02	23.81	7.81	2.04	6.08	4.06	1.92	1.53	0.59	1.51	2.10	0.50
TAM-04	18.13	11.26	6.06	10.73	8.40	2.28	1.73	1.24	2.34	3.58	0.41
TAM-05	17.36	8.11	4.39	8.93	6.66	2.47	2.32	0.75	1.44	2.19	0.98
TAM-06	19.99	10.61	7.34	10.19	8.76	2.19	2.65	0.89	1.41	2.40	0.78
TAM-07	18.15	9.23	3.82	8.22	6.02	2.38	2.23	1.05	2.26	3.31	0.99
ALP-11	10.15	7.78	4.78	2.20	3.49	2.48	1.51	1.03	0.41	1.44	0.62
ALP-12	10.15	9.70	2.83	2.83	2.83	2.06	1.52	0.74	0.74	1.48	0.41
ALP-21	10.15	10.87	6.82	7.61	7.22	2.26	3.98	1.23	1.44	2.67	1.44
ALP-22	10.15	9.31	3.99	9.65	6.82	2.12	3.74	1.12	2.68	3.80	1.23
MSH-01	7.67	7.85	4.54	NA [‡]	4.54	1.46	1.46	0.65	NA [‡]	1.30 [§]	0.39
SUC-01	8.93	9.35	4.82	10.09	7.46	1.89	3.57	0.78	2.13	2.91	1.46
SUC-02	8.94	10.15	6.03	13.31	9.67	2.39	5.00	1.01	2.24	3.24	1.79
YAN-01	17.59	11.65	4.56	6.10	5.33	2.46	2.22	1.36	1.88	3.24	1.36
Mean	14.16	9.95	5.14	7.71	6.34	2.25	2.37	1.21	1.82	2.95	0.91
SD	4.51	1.41	1.66	2.97	2.02	0.28	1.04	0.56	0.68	1.11	0.42
95% CI	2.09	0.65	0.76	1.41	0.93	0.13	0.48	0.26	0.32	0.51	0.19

Notes: Values for lianas refer to lianas ≥ 10 cm d_{\max} . The diameter of climbing stems rooted within our plots and ≥ 10 cm wide ("large lianas") was measured at the widest point within 2.5 m of the ground (" d_{\max} ").

[†] Number of years of monitoring at the site.

[‡] Recruits were not recorded.

[§] Assuming that lianas recruited balance lianas lost.

manuscript). This uses available information on liana allometry from lowland tropical forests (224 individual lianas, mostly < 5 cm $d_{1.3}$ but including some lianas larger than those measured at our site, based primarily on sites in French Guiana, Brazil, Venezuela, and Cambodia, and estimates biomass as $1.604 \times e^{(-1.291 + 2.616 \times \ln(d_{1.3}))}$). Relative dominance of lianas ≥ 10 cm $d_{1.3}$ and d_{\max} was estimated on the basis of their proportion of (1) liana stems, (2) liana basal area (BA), (3) liana biomass, and (4) BA of lianas in the well-lit forest canopy. Inspection of census data across the region shows that the structural contribution of large lianas in this stand was typical of the regional mean values (Appendix A).

Remaining structural and dynamic questions were addressed using a total of 22 long-term plots in western Amazonia. Our core analysis is based on 11×1 ha long-term plots in seasonal tropical moist forest in southeastern Peru. Liana and tree populations have been monitored for up to 24 years (Table 1), probably the longest running liana monitoring study in the world. For analyses of forest structure we also use a series of 11×1 ha plots in northeastern Peru; here five plots have not yet been recensused and most others have been studied for a decade or less, so we have less confidence in their dynamic parameters. Detailed description of study areas and soil data are published elsewhere (Phillips et al. 2002, 2003). Three plots traversed by major

edaphic and drainage discontinuities (Tambopata plot 2, Allpahuayo plot A, Allpahuayo plot B; see Appendix A) are each treated as representing two sample points, following Phillips et al. (2004). Chemical and physical properties of soils were first normalized and then expressed as orthogonal principal components in two separate principal components analyses; first for all plots (Appendix B), then second for only those plots that had dynamic information (Appendix C). Recordkeeping of mode of death and of liana–host relationships has been uneven across sites, while becoming more comprehensive through time. We therefore use truncated monitoring periods for our southeastern Peruvian plots from the early 1990s through 2003 to test for effects of large lianas on host tree mortality. We separately evaluate tree death that is (1) directly associated with large lianas (i.e., host tree), (2) indirectly associated with large lianas (i.e., trees killed by the death of liana host trees), and (3) entirely independent of large lianas.

Liana and tree dynamic rates (mortality and recruitment, Table 1) were computed using standard logarithmic models (Phillips et al. 1994). Whole monitoring periods differ among sites, so that census interval effects (Sheil and May 1996, Phillips et al. 2004) may affect our dynamic results, although we note that these effects are now known empirically to be rather weak for tropical trees (Lewis et al. 2004a). To minimize any

TABLE 2. Relative importance of different diameter size classes in the liana community in 1 ha of seasonally moist Amazonian lowland forest, southeastern Peru (plot TAM-05).

Liana size range	BA (cm ² /ha)	Fraction (%) of basal area, by liana category				Dry mass (kg/ha)	Fraction (%) of biomass, by liana category			
		All lianas	Medium leaf height ≥ 10 m	Medium leaf height ≥ 15 m	Fully lit leaves		All lianas	Medium leaf height ≥ 10 m	Medium leaf height ≥ 15 m	Fully lit leaves
Diameter at 1.3 m ($d_{1.3}$)										
1.0–2.4 cm	738	10.1	3.8	1.6	3.9	596	4.2	1.5	0.6	0.2
2.5–4.9 cm	1896	25.9	20.9	12.9	21.4	2427	16.9	12.6	6.6	4.6
5.0–9.9 cm	2796	38.2	42.4	32.7	44.3	5399	37.7	37.9	26.1	38.1
≥ 10.0 cm	1888	25.8	32.9	52.7	30.4	5886	41.1	48.0	66.6	57.1
Maximum diameter (d_{max})										
1.0–2.4 cm	406	5.5	1.6	0.2	1.8	300	2.1	0.6	0.0	0.0
2.5–4.9 cm	1358	18.5	13.1	8.2	11.3	1558	10.9	7.2	3.6	1.5
5.0–9.9 cm	2600	35.5	36.4	23.5	38.1	4288	30.0	31.3	16.7	22.8
≥ 10.0 cm	2956	40.4	48.9	68.0 [†]	48.9	8163	57.0 [‡]	60.9	79.7 [§]	75.6
Total BA (cm ² /ha)		7319	5742	3190	6206					
Total dry mass (kg/ha)							14 309	12 845	8352	10 104

Notes: The diameter of climbing stems rooted within our plots and ≥ 10 cm wide (“large lianas”) was measured at 1.3 m (“ $d_{1.3}$ ”) above the ground and at the widest point within 2.5 m of the ground (“ d_{max} ”), and all lianas attaining at least 10.0 cm d_{max} were permanently marked. Basal area (BA) and biomass fractions were based on $d_{1.3}$ values; the biomass fractions assumed neotropical allometry (J. Chave, S. A. Schnitzer, and S. J. DeWalt, *personal communication*).

[†] Large lianas ≥ 10 cm d_{max} contribute two-thirds of the basal area of lianas that bear canopy leaves.

[‡] Large lianas ≥ 10 cm d_{max} contribute more than half of the liana biomass in the plot.

[§] Large lianas ≥ 10 cm d_{max} contribute four-fifths of the biomass of lianas that bear canopy leaves.

^{||} Large lianas ≥ 10 cm d_{max} contribute three-quarters of the biomass of lianas that bear fully lit leaves.

effect, for all plots we also use results from intermediate censuses to estimate liana and tree turnover rates in terms of absolute numbers of stems recorded as dying and recruiting per year, thereby including those recorded as both recruiting and then dying within the entire period. We do not explicitly correct for another potential problem, the secular trends towards increased tree and liana dynamics, density, and biomass, and the associated imbalances between stem recruitment and mortality rates (Phillips and Gentry 1994, Baker et al. 2004a, Lewis et al. 2004b, Phillips et al. 2004). In practice, impacts of such trends and imbalances may be small because most plots were monitored simultaneously (mid year of monitoring = 1994.7 ± 1.2 [mean and 95% CI]), but we minimize the potential impact by analyzing dynamics in terms of combined recruitment and mortality rates.

We develop regression models to explain statistically the total annual throughput of large liana stems (equal to the sum of stems recruiting and dying each year), with factors that describe tree structure (stem density, BA, large tree stem density, large tree BA), estimated aboveground net primary productivity (ANPP, estimated independently from tree growth rates following Malhi et al. 2004), and soil (chemical and particle size principal components). The best subsets of all candidate regression models were each evaluated by the contribution of each parameter to the adjusted R^2 , sum of squares, and whether they inflated variance (Belsey et al. 1980).

RESULTS

Structure

Do large diameter lianas represent the canopy-dominant lianas?—In the site selected for the liana community evaluation, TAM-05, density of large lianas (11/ha) was indistinguishable from the regional average (12.6 ± 3.0 lianas/ha; see Appendix A). Here the proportion of all liana stems with diameter ≥ 10 cm is very low: of 358 climbing lianas in 0.52 ha surveyed, only 6 lianas ≥ 10 cm $d_{1.3}$ (1.7%) and 16 lianas ≥ 10 cm d_{max} (4.5%) were encountered, but these few plants represent about half of the estimated biomass of climbing plants (Table 2). When large lianas are analyzed in terms of their canopy position, their ecological importance appears greater still (Table 2). Of the 289 lianas/ha with leaves in either emergent or fully lit canopy position (likely to be the most productive lianas) lianas ≥ 10 cm d_{max} represent 48.9% of BA. Of the 88 lianas/ha with median leaf height > 15 m and with fully lit canopies (“dominant canopy lianas,” likely to be the most competitive with trees) lianas ≥ 10 cm d_{max} represent 68.0% of BA, or 79.7% of the aboveground biomass of the canopy dominants. The larger the liana diameter class the higher the portion of the forest canopy occupied (Fig. 1). Finally, while the probability of any given liana being a canopy dominant is virtually zero for the smallest size class, it becomes 60–85% for lianas ≥ 10 cm diameter (Fig. 2). In our sites, trees ≥ 50 cm dbh were always established canopy residents, with

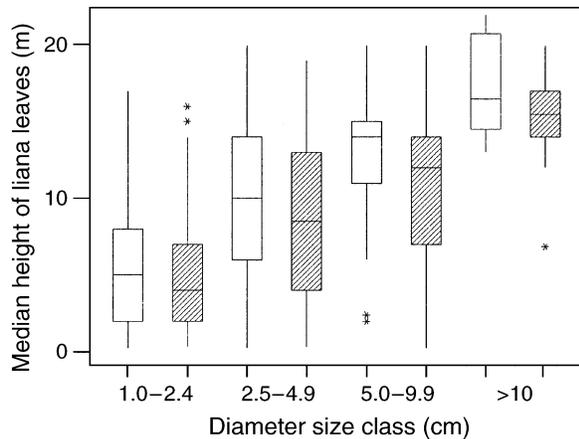


FIG. 1. Median canopy height of lianas as a function of diameter size class in plot TAM-05. Box plots represent the interquartile range. Open bars show diameter of lianas measured at 1.3 m ($d_{1.3}$) above ground; hatched bars show the diameter of lianas at the widest point within 2.5 m of the ground (d_{max}). The asterisks represent individual outliers.

a height of >25 m. Hemiepiphytic stranglers (*Ficus*, *Coussapoa*) also attained ≥ 10 cm diameter, but were very scarce (<2 /ha). In the analysis that follows we therefore treat trees ≥ 50 cm and lianas ≥ 10 cm diameter as the dominant canopy plants.

What fraction of the tree community supports large lianas, and what structural/environmental factors affect the prevalence of large lianas?—The large liana load borne by trees is strongly and nonlinearly related to tree size class (Fig. 3). Across all southeastern Peruvian plots the mean ratio of large lianas to trees increases from near zero for host trees <30 cm dbh to more than unity for trees ≥ 70 cm dbh; the difference among size classes is highly significant (Kruskal-Wallis nonparametric ANOVA, $H = 37.7$, $P < 0.001$ for lianas ≥ 10 cm d_{max}). Trees reach a threshold in large liana susceptibility at about 50 cm dbh (individual trees in the 30–50 cm dbh size class have a 0.14 ± 0.04 chance of being infested by lianas ≥ 10 cm d_{max} , compared to a 0.40 ± 0.09 chance for trees in the 50–70 cm dbh class).

Among all Peruvian plots, density of large lianas is positively associated with the BA of large trees ($r = 0.58$, $P < 0.01$). Our principal components analysis (PCA) of soils at all sites indicates that the main axis of soil variation (factor 1) is significantly and positively correlated with normalized Ca, K, and Mg concentrations and with the particle fraction <0.063 mm (Appendix B). After controlling for this factor, the partial correlation of lianas ≥ 10 cm d_{max} with BA trees ≥ 10 cm dbh is significant ($r = 0.48$, $df = 21$, $P = 0.02$). We used best subsets regression with the PCA factors to test whether accounting for the soil environment could improve our model. The best model, (lianas ≥ 10 cm d_{max}) = $16.7 + 1.91 \times (\text{BA trees } \geq 10 \text{ cm dbh}) + 1.68 \text{ soil PCA1}$, has low variance inflation and im-

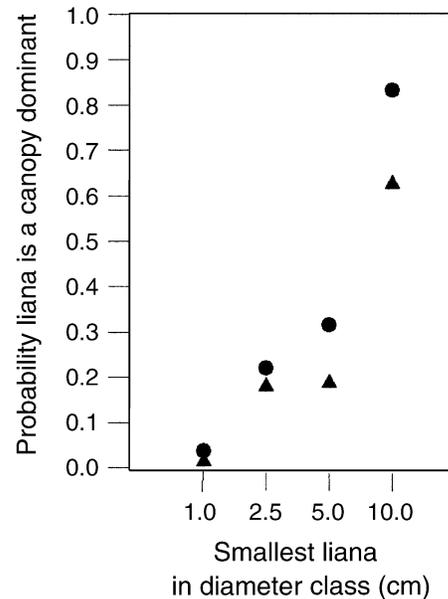


FIG. 2. Probability of a liana being a canopy dominant, as a function of the liana diameter size class, in plot TAM-05. Circles represent diameter at 1.3 m above ground; triangles represent diameter at the widest point within 2.5 m of the ground.

proves adjusted R^2 by 3.8% compared to the simple model with basal area of large trees alone. However, the contribution of the PCA factor to the model is only marginal ($t = 1.84$, $P = 0.08$); the partial correlation of lianas ≥ 10 cm d_{max} with soil PCA factor 1 controlling for BA trees ≥ 10 cm dbh is similarly weak ($r = 0.37$, $df = 21$, $P = 0.08$).

Dynamics

How fast do lianas enter and exit the largest size class?—Recruitment rates in southeastern Peru substantially exceed mortality rates ($t = 4.01$, $n = 10$, $P < 0.01$; paired t test). Long-term large liana turnover rates average $6.7 \pm 1.1\%$ per yr (mean and 95% CI). This implies a mean residence time of just 13.8 ± 2.7 yr, where residence time is estimated as initial stock divided by the annual mean of lianas recruiting and dying. Our smaller and shorter northern Peru data set provides an independent test of the generality of these results. Here, turnover rates average $6.1 \pm 1.4\%$ per yr and imply a residence time of 18.7 ± 6.1 yr.

How do large liana turnover rates compare with tree turnover rates?—By the standards of tropical forests as a whole and of Amazonia in particular, western Amazonian forests have unusually dynamic tree populations (Phillips et al. 1994, 2004). However, the liana populations are much more dynamic: here large lianas turn over three times as fast as the trees as a fraction of the initial population (Fig. 4), and the number of large lianas recruiting and dying (throughput) is three times greater than for large trees (Table 1). Across sites,

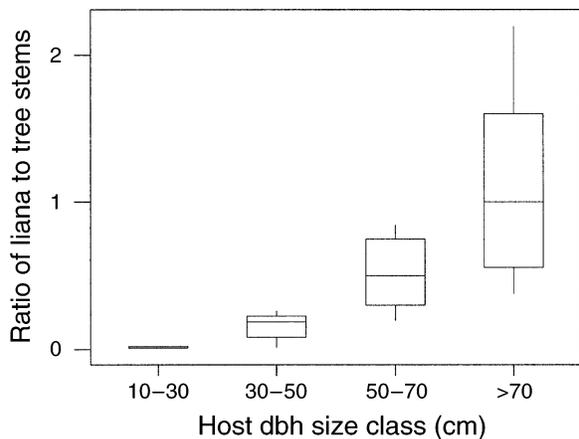


FIG. 3. Ratio of number of liana stems to number of tree stems as a function of tree dbh; all plots are in Amazonian southeastern Peru. Box plots represent the interquartile range.

large liana turnover is significantly associated with stand-level turnover of large trees ($r_s = 0.72$, $P = 0.001$), but not of all trees ($r_s = 0.33$, $P = 0.17$).

How are the deaths of large lianas and large trees associated with one another?—In forests in southeastern Peru, $21.0 \pm 4.1\%$ of large trees were infested with large lianas at the first census date in which liana infestation was reliably recorded. This fraction of the tree community suffers an elevated annual BA mortality risk ($2.8 \pm 0.5\%$ vs. $1.8 \pm 0.3\%$; $t = 2.70$, $P < 0.02$; paired t test, comparing infested vs. noninfested tree populations across sites). Compared to all trees, liana-infested trees experience an extra mortality risk by a factor of $56 \pm 41\%$ on a BA basis. However, large trees are much more likely to be infested with large lianas than are small trees, so examining mortality rates in large trees will provide a better indication of the actual risk associated with liana infestation. Among trees ≥ 50 cm dbh that are free of large lianas, annual BA mortality rates are $1.0 \pm 0.8\%$. Among trees ≥ 50 cm dbh that are infested with one or more large lianas, annual BA mortality rates are three times greater ($3.1 \pm 0.8\%$). Finally, among large liana stems whose mode of death was recorded, one third ($32 \pm 14\%$) died independently of trees, either senescing on the host or being broken by falling branches, while twice as many ($66 \pm 12\%$) died with their hosts in a fall.

When host trees fall, other, smaller trees are sometimes killed too, and this “collateral” death needs to be accounted for to assess the stand-level impact of host tree deaths. Accounting for these collateral deaths increases the liana-associated tree BA mortality rate modestly, from $2.8 \pm 0.5\%$ to $2.9 \pm 0.5\%$. This remains a conservative estimate as it ignores collateral deaths caused by liana-infested trees falling into the plot from outside, as well as direct and collateral death associated with lianas ≤ 10 cm d_{\max} . Overall, lianas ≥ 10 cm d_{\max} represent only $5.2 \pm 1.1\%$ of woody stems ≥ 10 cm

diameter, and just $1.0 \pm 0.2\%$ of stand basal area ≥ 10 cm $d_{1,3}$, but are involved in the death of at least $30.4 \pm 6.1\%$ of tree BA.

What factors control liana dynamics?—The sum of stems recruiting and dying each year provides a measure of the rate of “throughput” of plants through the forest. Our PCA of soils at only the dynamic sites indicates that the main axis of soil variation (factor 1) is significantly and positively correlated with normalized cation concentrations and with the particle fraction < 0.063 mm (Appendix C). Large liana throughput correlated only with tree aboveground net primary productivity (ANPP; $r = 0.654$, $P < 0.05$) and with soil PCA factor 1 ($r = 0.585$, $P = 0.07$); ANPP and soil PCA factor 1 are also correlated ($r = 0.774$, $P < 0.01$). The partial correlation coefficient of liana throughput with soil PCA factor 1 controlling for ANPP was 0.163 ($P = 0.67$); the partial correlation coefficient of liana throughput with ANPP controlling for soil was 0.392 ($P = 0.30$).

When the eight plots in northeastern Peru with liana throughput data are included in a combined data set, the relationships among variables change little. Thus large liana throughput correlated only with ANPP ($r = 0.663$, $P < 0.01$), and with soil PCA factor 1 ($r = 0.620$, $P < 0.01$); ANPP and soil PCA factor 1 are also correlated ($r = 0.552$, $P < 0.05$). Across our western Amazonian forests, soil, tree ANPP, and liana throughput are partly oriented along the same axis of ecological variation, but there is also an independent relationship between liana throughput and tree ANPP. The partial

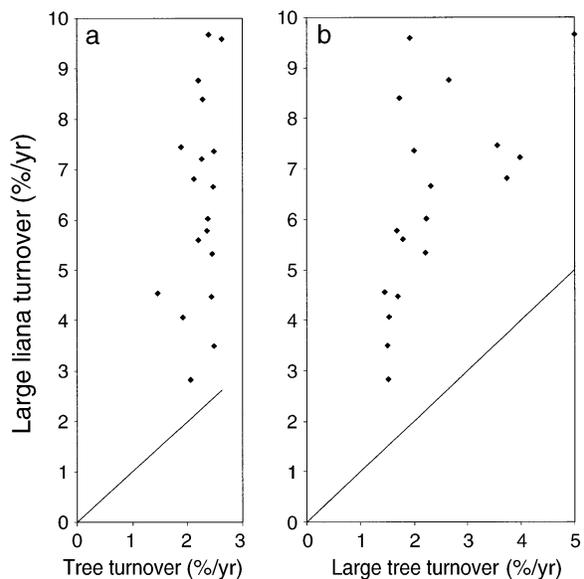


FIG. 4. Turnover rates of large lianas vs. turnover rates of trees (annual rates estimated using logarithmic models; see Phillips et al. 1994, 2004); all plots are in western Amazonia. The line represents the expected 1:1 relationship if liana and tree turnover rates are equivalent. Both graphs are plotted to the same scale. (a) Trees ≥ 10 cm dbh; (b) trees ≥ 50 cm dbh.

correlation coefficient of liana throughput with soil PCA factor 1 controlling for ANPP was 0.406 ($P = 0.11$); the partial correlation coefficient of liana throughput with ANPP controlling for soil was 0.491 ($P < 0.05$). Finally, path analysis shows reduced coefficients of nondetermination ($1 - R^2$) for hypotheses that include an effect of tree ANPP on liana throughput, whether ANPP is driven by soil (0.503) or independent of soil (0.504) compared to the hypothesis that liana throughput is affected only by soil (0.695).

DISCUSSION

This is the longest geographically extensive study of liana ecology. The permanent study plots, monitored for up to 24 years, represent the range of environmental conditions in western Amazonia from aseasonal to seasonal climate, and from white sands to rich alluvial soils.

Structure

As far as we are aware our work in the intensively sampled forest is the first to attempt to link liana diameter size distributions to height and canopy profile distributions. We find that a few large lianas represent a large fraction of total biomass, and comprise as much as 80% of the canopy dominant lianas. There are three caveats to this conclusion: (1) the liana allometric model suffers from having few data for very large lianas, so errors in estimated biomass may be large for lianas ≥ 15 cm $d_{1.3}$ (J. Chave, *personal communication*); (2) ground-based assessments of where liana foliage is displayed are subject to error since lianas tend to display leaves on and above host foliage; and (3) it will not hold where lianas are superabundant and suppress tree biomass and forest canopy height—these “liana forests” are characterized by dense tangles of mostly small- and medium-sized lianas (Gerwing and Farias 2000, Pérez-Salicrup et al. 2001). Nevertheless the results from our intensively sampled forest suggest that assessing long-term canopy processes at regional scales can be achieved by focusing only on the few, largest lianas.

Across our sites, large lianas depend on large trees to support them and provide access to high light environments. Results of partial correlation and regression analyses suggest that the relative dominance of large lianas is substantially determined by the large tree resource available (cf., Hegarty and Caballé 1991). There is weak evidence for an additional direct effect of soils, such that richer soils may favor a higher density of large lianas.

Dynamics

Large liana populations in southeastern Peru turn over very quickly. A smaller, independent, and more-or-less contemporaneous data set in northeastern Peru shows a similar result. This suggests that in western Amazonia, where tree populations are themselves dy-

namic by the standards of the tropical forest biome, large liana populations are exceptionally dynamic. Annual recruitment and mortality rates average $>6\%$, almost three times the equivalent rates of large trees with which they share the canopy (Table 1). These hyperdynamic large lianas constitute a major fraction of the turnover of canopy woody plants yet remain unrecorded by many forest monitoring efforts.

Liana infestation is associated with a greatly elevated risk of death for large trees. However, observational studies alone cannot disentangle cause and effect definitively. In this case we do not yet know the extent to which the association is merely coincidental (e.g., if trees that die are older and so have had longer for infestation to occur) or actively causal (large lianas shorten the life expectancy of host trees), or both. Others have noted evidence for negative impacts of liana infestation on growth and survival of trees (e.g., Clark and Clark 1990, Pérez-Salicrup 2001). Our results indicate the potentially substantial impact of large lianas on tree dynamics, and so on stand-level carbon balance and flux rates. How can we square the positive dependence of large lianas on large trees, on the one hand, with the negative feedback on large liana populations implied by the enhanced risk of death in liana-infested large trees? Clearly there is dynamic tension between the two effects, but that does not imply that one always counterbalances the other, nor that any equilibrium point cannot be shifted. Thus, recent work has shown a secular increase in liana densities and productivity in mature neotropical forests (Phillips et al. 2002, Wright et al. 2004). And some dramatically different stable states in moist tropical forests reflect how vital liana–tree interactions can be to ecosystem processes. For example, lianas may indefinitely arrest gap succession (Schnitzer et al. 2000), and “liana forests,” characterized by a superabundance of small lianas and an absence of large trees, are hyperdynamic communities with diminished carbon storage potential (Phillips et al. 2002, Baker et al. 2004b). Liana–tree interactions clearly have important emergent effects at stand and regional scales, and there is an urgent need for stand-level long-term experimental investigation to disentangle the mechanisms by which they interact (cf., Pérez-Salicrup and Barker 2000, Grauel and Putz 2004). Liana–tree interactions also represent a unique challenge to ecosystem modelers that has yet to be taken up.

Our results show predictability of liana behavior from broader environmental parameters. Thus, large liana throughput rates, tree aboveground net primary productivity (ANPP), and soil fertility all covary. The results are consistent with the direct effect of soil nutrient supply on tree ANPP across the neotropics (Malhi et al. 2004). Soil effects on liana throughput may be direct, or indirect via tree ANPP. There is also a separate relationship between tree ANPP and liana throughput, independent of soil. In the gap-rich envi-

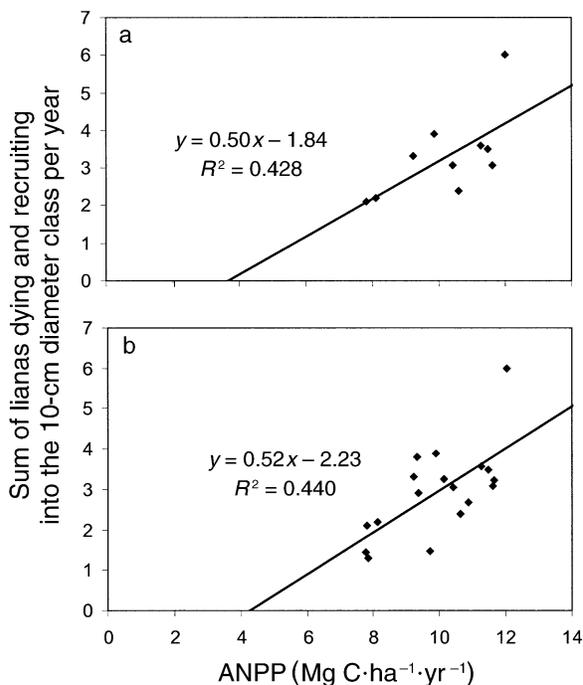


FIG. 5. Rate of large liana throughput (equals sum of large liana stems recruiting and dying annually per hectare) as a function of tree aboveground net primary productivity (ANPP; $\text{Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$). (a) Amazonian southeastern Peru; (b) western Amazonia.

ronment of productive, high-turnover western Amazonian forests, light-demanding tree taxa thrive (Baker et al. 2004b) and so, apparently, do lianas. Since liana infestation may accelerate the death of senescing trees, there also exists some potential for positive feedback of liana dynamics on stand productivity. Regardless, a consistent pattern emerges of relatively rich soils supporting forests with higher tree growth and high rates of liana turnover.

Based on the plots monitored thus far, the relationship of liana throughput to tree productivity appears to be steep (Fig. 5): large lianas recruit and die about twice as fast in forests with ANPP of $12 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ compared to forests with ANPP of $8 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. Extrapolation implies that in forests much below the minimum ANPP in our data set there may be very little large liana activity. This would be consistent with the known rapid drop-off in large liana density (and presumably dynamics) with increasing elevation in the tropics (Gentry 1991) and with latitudinal gradients in large liana density from the tropics to subtropics/warm temperate zone (Gentry 1991). Forests of western Amazonia are unusually productive by continental and global standards (Malhi et al. 2004). Large liana turnover data are still lacking for central and eastern Amazonia, but on the basis of the modeled relationship we predict that less productive forests in the highly weathered oxisols and spodosols of parts of eastern and northern

Amazonia, where ANPP is typically $\sim 4.5\text{--}7 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, will turn out to have much slower throughput of large lianas. The same may be true for pluvial tropical forests, such as the Chocó in western Colombia or the windward slopes of Hawaii, where productivity may be suppressed by excessive rainfall and/or reduced insolation (cf., Schuur 2003).

Conversely, substituting space for time, the steep relationship between large liana throughput and stand ANPP suggests that small increases in productivity could have disproportionate impacts on large liana dynamics. The unweighted average tree ANPP across 104 neotropical forests is $9.1 \text{ Mg C}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ (Malhi et al. 2004); we would anticipate that a 10% increase in tree productivity will engender an $\sim 20\%$ increase in the number of large lianas recruiting and dying. This projection is crude but it might help explain how large liana densities and growth rates appear to have increased in Amazonia faster than recent increases in tree productivity (Phillips et al. 2002, Lewis et al. 2004b), and faster than even the marked, direct response of lianas to elevated carbon dioxide would suggest (Granados and Korner 2002).

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APPENDIX A

A table describing the structure of western Amazonian forests is available in ESA's Electronic Data Archive: *Ecological Archives* E086-069-A1.

APPENDIX B

Principal components analysis of soil chemical and physical properties, for all sites with structural information, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-069-A2.

APPENDIX C

Principal components analysis of soil chemical and physical properties, for those sites with dynamic information, is available in ESA's Electronic Data Archive: *Ecological Archives* E086-069-A3.