

ARE LIANAS INCREASING IN IMPORTANCE IN TROPICAL FORESTS? A 17-YEAR RECORD FROM PANAMA

S. JOSEPH WRIGHT,¹ OSVALDO CALDERÓN, ANDRÉS HERNANDEZ, AND STEVEN PATON

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancón, Panama

Abstract. The relative importance of large lianas (woody vines) increased by 100% for stem enumerations conducted during the 1980s and 1990s in widely scattered Neotropical forests. We use three independent types of data to evaluate the hypothesis that lianas have increased in importance in old growth forests on Barro Colorado Island, Panama. Liana leaf litter production and the proportion of forest-wide leaf litter composed of lianas increased between 1986 and 2002. In contrast, liana seed production and liana seedling densities were much more variable through time with particularly high levels during and immediately after El Niño years. Longer time series will be required to detect shifts in life-form composition for highly dynamic seed and seedling communities. The Barro Colorado Island leaf production data are, however, consistent with the hypothesis that lianas are increasing in importance in Neotropical forests.

Key words: *Barro Colorado Island; El Niño; leaf litter; leaf production; lianas; seedlings; seeds; temporal trends; tropical forests.*

INTRODUCTION

The “changing dynamics of tropical forests” hypothesis attributes recent increases in turnover rates of trees and the basal area of trees and lianas to rising concentrations of atmospheric CO₂ (Phillips and Gentry 1994, Phillips et al. 1998, 2002b). The evidence for changing dynamics comes from enumerations of all woody stems in forest plots scattered widely across the Neotropics. This evidence has been controversial because several biases inherent to plot enumerations may alter apparent turnover rates and basal area estimates (reviewed by Phillips et al. 2002a). Due to its central importance and the ensuing controversy, independent tests of the “changing dynamics of tropical forests” hypothesis are to be expected. Surprisingly, the only independent tests have been eddy flux studies of net carbon sequestration and atmospheric inversion studies, both of which have proven to be equally controversial (Malhi and Grace 2000). Here, we use three independent types of data to evaluate the hypothesis that lianas are increasing in importance on Barro Colorado Island (BCI), Panama.

Lianas are large woody vines that reach their greatest diversity and biomass in tropical forests (Gentry 1991). The basal area of lianas larger than 10 cm in diameter at breast height (dbh) increased by 4.58% per year during the 1980s and 1990s in forest plots scattered widely across the Neotropics (Phillips et al. 2002b). Several biases influence plot-based estimates of tree turnover rates and basal area and may inflate the apparent im-

portance of lianas. Tree death, tree fall gaps, and forest edges all favor lianas (Putz 1984, Laurance et al. 2001, Schnitzer and Carson 2001). If plots were initially placed in majestic stands of large trees, future tree mortality rates would be biased upwards (Sheil 1996) favoring tree-fall gaps and lianas. Likewise, plots initially located deep inside forests may subsequently be overtaken by forest fragmentation and edge effects that favor lianas (Laurance et al. 2001). Tagging, climbing, and collecting herbarium samples from trees and compacting soil may also increase tree mortality favoring lianas. These potential biases associated with plot methods would tend to increase the apparent importance of liana basal area with time.

Phillips et al. (2002a) offered counterarguments to each of these potential biases. Rather than rehash this controversy, we ask whether lianas have increased in importance for three completely independent types of data. We have monitored species-level leaf litter production, seed production, and seedling density on BCI since 1986, 1987, and 1994, respectively. Phillips et al. (2002b) reported that the importance of liana basal area doubled relative to trees with the increase occurring almost entirely after 1986 in Amazonia (see their Figs. 2 and 3). We ask whether liana leaf, seed, and seedling production show similar strong increases for the same years in a Central American forest.

STUDY SITE AND METHODS

Study site

Barro Colorado Island (9°9' N, 79°51' W; BCI) supports old growth and secondary tropical moist forests. The old growth is now known to have escaped clearing for agriculture for at least 1500 years and to have a minimum age of 500 years with negligible human dis-

Manuscript received 9 December 2002; revised 14 April 2003; accepted 27 May 2003; final version received 3 June 2003. Corresponding Editor: F. He.

¹ Present correspondence address: Unit 0948, APO AA 34002-0948 USA. E-mail: wrightj@si.edu

turbance (Piperno 1990). This study took place entirely in old growth. Annual rainfall averages 2600 mm, and a four-month dry season begins in December. El Niño events bring low rainfall and sunny conditions, which favor seed production (Wright et al. 1999, Graham et al. 2003). Leigh (1999) further describes BCI.

Data sets

We monitored species-level leaf litter production, seed production, and seedling density for 17, 15, and 9 years, respectively. Both community- and species-level seed production and seedling recruitment are highly variable among years on BCI, and this variation is related to El Niño events (Wright et al. 1999, DeSteven and Wright 2002). This variation is likely to mask temporal trends for seeds and seedlings. Nonetheless, we present all three data sets to avoid selective publication of positive results.

Leaf litter

From November 1985 through December 2002, leaf litter was collected each week from 59 0.25-m² litter traps, oven dried to constant mass at 60°C, identified to species, and weighed (Wright and Cornejo 1990). We exclude partial data for 1985 and a sixtieth trap that was destroyed in 1989 and never replaced. Traps were randomly located in the central 1.44 ha of four 2.25-ha plots with a minimum distance of 15 m between traps. Two plots were irrigated for five dry seasons between 1986 and 1990. Leaf litter production was unaffected (Wright and Cornejo 1990, Cavelier et al. 1999). Leaf litter production (Mg·ha⁻¹·yr⁻¹) was estimated as leaf dry mass summed over calendar years and corrected for trap area. Species-level analyses were restricted to species with leaves captured in 10 or more traps in at least one year to insure that multiple individuals contributed.

Seed production

Seeds and fruits were collected each week from January 1987 through September 2002 and identified to species for 200 0.5-m² litter traps. Traps were located within a 50-ha plot at 13.5-m intervals along permanent trails, randomly between 4 and 10 m from the trail, and on alternating sides of the trail. The distance between neighboring traps averaged 18.9 m (equal to the hypotenuse of a right triangle with sides of 13.5 m and 8–20 m). Seed production (seeds·m⁻²·yr⁻¹) was estimated as the number of seeds captured plus the number of fruits captured multiplied by a species-specific mean number of seeds per fruit and corrected for trap area. To standardize timing, seed production was associated with the appropriate flowering event (seed dispersal occurs from three weeks to 11 months after flowering) and assigned to a meteorological year. Meteorological years began on 1 December to accommodate rainfall seasonality. Seeds associated with mean flowering dates between 1 December in calendar year *Z* and 30

November in calendar year *Z* + 1 were assigned to meteorological year *Z* + 1. Species-level analyses were restricted to species with seeds larger than the 1-mm trap mesh, identifiable seeds, more than 75 seeds captured, and seeds and/or fruits captured in at least 10 traps in at least one year. The final criterion insured that multiple individuals contributed seeds.

Seedling density

All woody seedlings less than 50 cm tall were tagged, identified to species, and censused each year from 1994 through 2002 for 600 1-m² plots (Harms et al. 2000). Seedling density (seedlings/m²) was estimated as the total number of seedlings corrected for plot area. The seedling plots were located 2 m from three sides of the 200 seed traps described above. The fourth side of each seed trap faced the nearby trail. Censuses took place between 1 January and 31 March. Virtually no seeds germinate during these dry season months. Species-level analyses were restricted to species with at least 50 seedlings.

Analyses

Temporal trends were first evaluated for life-forms (lianas vs. all other life-forms pooled). Each response variable (leaf litter production, seed production, and seedling density) was summed over all liana species and over all nonliana species. The proportional contribution of lianas was estimated as the ratio of the summed liana value to a final sum taken over all species regardless of life-form. Cross correlations with lag zero were performed between year and the summed liana value and between year and the proportional contribution of lianas for each response variable. Six cross correlations were performed, and the sequential Bonferroni procedure was used to correct significance levels. Significant, positive cross correlations comprise evidence for increasing lianas. The power of these cross correlations to detect a positive, linear trend with constant coefficient of variation was evaluated using TRENDS 3.0, the conservative *t* distribution and two-tailed tests at the 0.05 significance level (Gerrodette 1991).

The consistency of temporal trends was then evaluated for species-level data. The response variables were leaf litter production (Mg·ha⁻¹·yr⁻¹), seed production (seeds·m⁻²·yr⁻¹) and seedling density (seedlings/m²). Repeated-measures analyses of variance (ANOVAs) treated species as subjects, year as the repeated measure, and life-form as the grouping factor (lianas vs. all other life-forms). Response variables were logarithmically transformed. Significant year × life-form interactions are evidence that temporal trends were consistent across species within life-forms.

A second repeated-measures ANOVA was performed to evaluate spatial consistency across traps for leaf litter production. Small sample size at the scale of individual traps precluded similar analyses for seeds

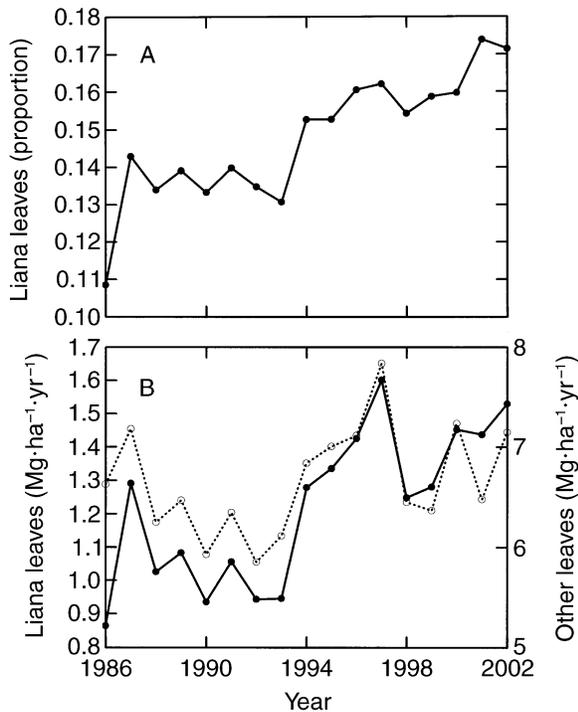


FIG. 1. The proportion of leaf litter dry mass contributed by lianas (panel A), leaf litter dry mass summed over all liana species (panel B, solid line), and leaf litter dry mass summed over all other species (panel B, dashed line) between 1986 and 2002.

and seedlings. The response variable was the angular or arcsine-square root transformation of the proportional contribution of lianas. The repeated-measures ANOVA treated traps as subjects and year as the repeated measure. There was no grouping factor. A significant year effect is evidence for a spatially consistent temporal trend.

Two-tailed statistical tests were used throughout. The Huynh-Feldt procedure protected significance levels against violations of the compound symmetry assumption of repeated-measures ANOVA. Power analyses were performed with TRENDS 3.0 (Gerrodette 1991 [available online]).² All other analyses were performed with SYSTAT 10.0 (SPSS, Chicago, Illinois, USA; SPSS 2000).

RESULTS

Power to detect temporal trends

The power to detect temporal trends depends on the length of the record and its coefficient of variation (Gerrodette 1991). Coefficients of variation (standard deviation divided by mean) calculated for 15, 9, and 17 years were 0.327, 0.154, and 0.099 for community-level (summed over all species) seed production, seed-

ling density, and leaf litter production, respectively. The basal area of large lianas increased by 4.58% per yr in Amazonian plots in the 1980s and 1990s (Phillips et al. 2002b). The probability of detecting a similar increase approached one for litter production but was just 0.39 for seedling density and 0.35 for seed production, which were characterized by shorter more variable time series (Figs. 1, 2, and 3).

Leaf litter

The 59 traps collected 206 kg of dried leaf litter representing 293 species between 1 January 1986 and 31 December 2002. All entire leaves were identified to species; however, unidentifiable leaf fragments averaged 4.1% of total leaf dry mass. This percentage showed no temporal trend ($r = 0.01$ for cross correlation with year). Unidentifiable leaf fragments were excluded from further analysis.

The proportional contribution of lianas to total leaf litter increased from 10.9% in 1986 to 17.1% in 2002 (Fig. 1A; $r = 0.88$, Bonferroni-corrected $P < 0.001$). Summed liana leaf dry mass also increased between 1986 and 2002 (Fig. 1B; $r = 0.76$, Bonferroni-corrected $P < 0.005$).

Forty-one liana species and 63 other species fulfilled the criteria to be included in species-level analyses (see *Methods: Leaf litter*). In the repeated-measures AN-

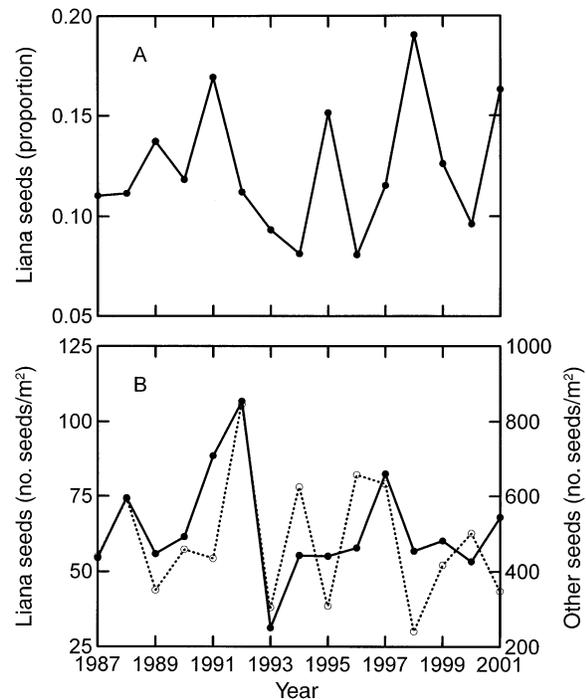


FIG. 2. The proportion of all seeds that were lianas (panel A), the density of seeds summed over all liana species (panel B, solid line), and the density of seeds summed over all other species (panel B, dashed line) between 1987 and 2001. Only seeds with a minimum dimension >1 mm were used in analyses.

² URL: <http://swfsc.nmfs.noaa.gov/prd/software/Trends.html>

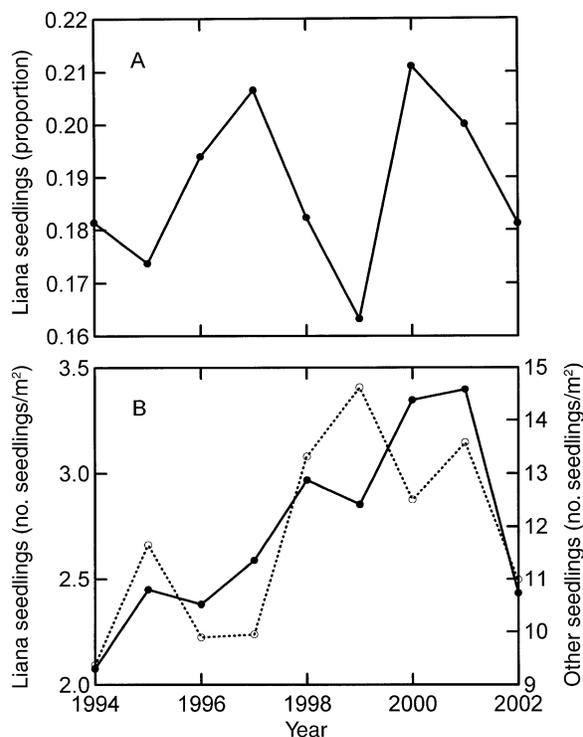


FIG. 3. The proportion of all seedlings that were lianas (panel A), the density of seedlings summed over all liana species (panel B, solid line), and the density of seedlings summed over all other species (panel B, dashed line) between 1994 and 2002. Only seedlings ≤ 50 cm tall were used in analyses.

OVA, the year \times life-form interaction was significant ($F_{15, 1530} = 2.40$, $P < 0.05$). The temporal trend observed for life-forms (Fig. 1) was consistent across species within life-forms.

Spatial consistency was evaluated in a trap-level analysis of the proportional contribution of lianas to leaf litter production. The year effect was significant ($F_{15, 870} = 6.70$, $P < 0.001$), indicating that the temporal trend was consistent across traps. Spatial consistency was also evident from cross correlations performed between year and the proportional contribution of liana leaf litter for each trap. These cross correlations were positive for 43 of the 59 traps (binomial test, $P < 0.001$).

Seed production

The 200 traps captured 495 497 seeds and 212 040 mature fruit representing 488 species between 1 January 1987 and 26 September 2002. All entire seeds and fruit were identified to genus, and $>99\%$ were identified to species.

The proportional contribution of lianas to seed production varied by a factor of two among years but lacked any temporal trend (Fig. 2A; $r = 0.17$, Bonferroni-corrected $P = 1.0$). Summed liana seed production varied by a factor of four among years and also

lacked any temporal trend (Fig. 2B; $r = -0.11$, Bonferroni-corrected $P = 1.0$). Summed seed production was greatest in the 1992 El Niño year for both lianas and nonlianas and was also relatively large in the 1997 El Niño year (Fig. 2B).

Fifty liana species and 69 other species fulfilled the criteria to be included in species-level analyses (see *Methods: Seed production*). Each seed is weighted equally in Fig. 2B. When instead species are weighted equally, enhanced seed production is clearly evident for both lianas and other life-forms during the 1992 and 1997 El Niño years (Wright et al. 1999, DeSteven and Wright 2002; S. J. Wright and O. Calderón, *unpublished data*). This El Niño effect contributed to a highly significant year effect ($F_{14, 1638} = 5.02$, $P < 0.001$) and to an insignificant interaction between year and life-form ($F_{14, 1638} = 0.58$, $P = 0.86$) in the repeated-measures ANOVA.

Seedling density

The nine annual censuses included 34 724 individual seedlings representing 370 species. The 652 seedlings that died before being identified were excluded.

The proportional contribution of lianas to seedling density varied by $<30\%$ among years and lacked a consistent temporal trend (Fig. 3A; $r = 0.20$, Bonferroni-corrected $P = 1.0$). Summed liana seedling density increased steadily from 1994 through 2001 then declined sharply in 2002 (Fig. 3B; $r = 0.65$, Bonferroni-corrected $P = 0.34$). Summed nonliana seedling density increased sharply in 1998 and 1999 (Fig. 3B).

Elevated seed production during the 1997 El Niño year caused the steep increase in nonliana seedling density in 1998 and 1999. Two species are illustrative. The most abundant canopy tree on Barro Colorado Island (BCI), *Trichilia tuberculata*, produced an extraordinary seed crop during the 1997 El Niño year (DeSteven and Wright 2002, Wright 2002). The seeds of *T. tuberculata* germinate quickly, and the 3.8 seedling recruits per m² of this one species comprised 23% of all seedlings in the 1998 census (Wright 2002). The most abundant subcanopy tree on BCI, *Faramaea occidentalis*, also produced an extraordinary seed crop during the 1997 El Niño year (S. J. Wright and O. Calderón, *unpublished data*). The seeds of *F. occidentalis* lie dormant during the dry season so that seedling recruits from the 1997 seed crop were first recorded in the 1999 census, when the 4.5 recruits per m² of this one species comprised 26% of all seedlings. Largely because these two species were not lianas, the proportional contribution of lianas to seedling density fell in 1998 and 1999 (Fig. 3A). It was not possible to evaluate changes in seedling density associated with elevated seed production during the 1992 El Niño year because seedling density was not documented for 1992 and 1993.

Twenty-five liana species and 71 other species fulfilled the criteria to be included in species-level analyses (see *Methods: Seedling Density*). The pulse of

seedlings associated with the 1997 El Niño event contributed to a significant effect of year ($F_{8, 752} = 4.39$, $P < 0.001$) and an insignificant interaction between year and life-form ($F_{8, 752} = 1.18$, $P = 0.32$) in the repeated-measures ANOVA.

DISCUSSION

Leaf litter production by lianas has increased steadily on Barro Colorado Island (BCI) since 1986 (Fig. 1), and the increase has been consistent spatially and among species. The increase of perhaps 55% in the proportional contribution of lianas to leaf litter production on BCI (Fig. 1A) is less than the contemporaneous increase of ~100% in the proportional contribution of large lianas to basal area for sites scattered widely across the Neotropics (Phillips et al. 2002b). Lianas support substantially more leaves per unit basal area than do trees (Putz 1983, Gerwing and Farias 2000). Unless the total leaf area in a forest actually increases, this allometric difference between trees and lianas should magnify the proportional contribution of lianas to leaf litter production relative to their proportional contribution to basal area. Still, the two reported increases are of similar magnitude and are consistent with the hypothesis that lianas are increasing in importance in old growth tropical forests.

In contrast, seed production and seedling density provided no evidence for increasing importance of lianas (Figs. 2 and 3). Elevated seed production during El Niño events contributed to high interannual variation (Wright et al. 1999, DeSteven and Wright 2002). Subsequent elevated seedling recruitment was buffered by older, surviving seedlings, which contributed to intermediate levels of interannual variation in overall seedling density (Fig. 3). As we anticipated, the rapid dynamics and high interannual variation characteristic of seedlings and especially seeds will make it difficult to detect temporal trends in species composition for these life-history stages. Intriguingly, the proportional contribution of lianas was consistently greater for seedling density than for seed and leaf litter production (compare Figs. 1A, 2A, and 3A). We speculate that BCI may record further increases in lianas in the near future.

We conclude that the spatially and interspecifically consistent increase in the proportional contribution of lianas to leaf litter production (Fig. 1A) reflects a real increase in the importance of lianas in old growth forests on BCI. This extends the observation that the biomass of the largest lianas is increasing across Amazonia (Phillips et al. 2002b) by demonstrating that productivity integrated over lianas of all sizes is increasing for a Central American forest. Similar data must be examined for other forests to determine whether the productivity of lianas is increasing elsewhere.

The implications of increases in the importance of lianas are potentially profound (Schnitzer and Bongers 2002). Lianas cross between trees, and, when a tree falls, connecting lianas may pull down neighbors (Putz

1984). Thus, an increase in lianas may contribute to recent increases in Neotropical tree mortality rates (Phillips et al. 2002b). An increase in tree mortality may, in turn, favor more lianas in a positive feedback loop. An increase in lianas may also contribute to recent observations of lianas delaying tree regeneration on BCI (Schnitzer et al. 2000). Within individual canopies, liana leaves displace host tree leaves on a one-to-one mass basis (Kira and Ogawa 1971). Thus, an ecosystem-level increase in leaf area presented by canopy lianas would be expected to cause an ecosystem-level decrease in leaf area presented by other life-forms.

This decrease did not occur on BCI, where leaf litter production by all life-forms other than lianas showed no temporal trend (Fig. 1B). More surprisingly, the basal area of both trees and large lianas increased in Amazon plot enumerations, with the increases averaging 0.34% per year and 4.58% per year for trees and large lianas, respectively (Phillips et al. 1998, 2002b). This presents a quandary. Total canopy leaf area must increase if both trees and lianas increase. An increase in canopy leaf area must reduce light levels in lower strata. Light compensation occurs when photosynthesis exactly balances respiration. Heavily shaded leaves are abscised and heavily shaded individuals die when light availability falls below their respective light compensation points. Assuming many understory plants persist near their light compensation points, an increase in both trees and lianas must be accompanied by a reduction in understory leaf area (fewer herbs, shrubs, saplings and seedlings) or by a reduction in the light compensation points of understory leaves and plants. Shrubs have declined steadily on BCI since 1980 (Condit et al. 1996). This decline is often attributed to drought, but increases in canopy leaf area might also contribute. Rising concentrations of atmospheric CO₂ reduce light compensation points in the very low light levels characteristic of the BCI understory (Würth et al. 1998, Holtum and Winter 2001). Thus, both a reduction in understory leaf area and light compensation points may be underway.

The “changing dynamics of tropical forests” hypothesis attributes recent increases in tree turnover rates, tree basal area, and lianas to rising concentrations of atmospheric CO₂ (Phillips et al. 1998, 2002b). Tropical canopy trees are energy limited (Graham et al. 2003). The effects of CO₂ fertilization on energy budgets may, however, be offset by increasing nighttime temperatures and temperature-dependent respiration (Clark et al. 2003) and by reductions in solar irradiance penetrating the atmosphere, which have averaged 2.7% per decade since the 1950s (Stanhill and Cohen 2001). Diverse anthropogenic influences will interact with forest biota in complex ways. The only obvious prediction is change. The evidence for such change in tropical forests consists almost entirely of controversial stem enumerations. The possible changing dynamics of tropical forests is of central importance, and the search for

its signal in additional independent data sets should be a high priority.

ACKNOWLEDGMENTS

We thank Stefan Schnitzer and Jack Putz for comments and answers to many questions about lianas. The Environmental Sciences Program of the Smithsonian Institution provided financial support.

LITERATURE CITED

- Cavelier, J., S. J. Wright, and J. Santamaria. 1999. Effects of irrigation on fine root biomass and production, litterfall and trunk growth in a semideciduous lowland forest in Panama. *Plant and Soil* **211**:207–213.
- Clark, D. A., S. C. Piper, C. D. Keeling, and D. B. Clark. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences (USA)* **100**:5852–5857.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1996. Changes in tree species abundance in a neotropical forest: impact of climate change. *Journal of Tropical Ecology* **12**:231–256.
- DeSteven, D., and S. J. Wright. 2002. Consequences of variable reproduction for seedling recruitment in three neotropical tree species. *Ecology* **83**:2315–2327.
- Gentry, A. H. 1991. The distribution and evolution of climbing plants. Pages 3–49 *in* F. E. Putz and H. A. Mooney, editors. *The biology of vines*. Cambridge University Press, Cambridge, UK.
- Gerrodette, T. 1991. Models for power of detecting trends—a reply to Link and Hatfield. *Ecology* **72**:1889–1892.
- Gerwing, J. J., and D. L. Farias. 2000. Integrating liana abundance and forest stature into an estimate of total above-ground biomass for an eastern Amazonian forest. *Journal of Tropical Ecology* **16**:327–335.
- Graham, E. A., S. S. Mulkey, K. Kitajima, N. G. Phillips, and S. J. Wright. 2003. Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences (USA)* **100**:572–576.
- Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* **404**:493–495.
- Holtum, J. A. M., and K. Winter. 2001. Are plants growing close to the floors of tropical forests exposed to markedly elevated concentrations of carbon dioxide? *Australian Journal of Botany* **49**:629–636.
- Kira, T., and H. Ogawa. 1971. Assessment of primary production in tropical and equatorial forests. Pages 309–321 *in* P. Duvigneaud, editor. *Productivity of forest ecosystems*. UNESCO, Paris, France.
- Laurance, W. F., D. Pérez-Saliciup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **82**:105–116.
- Leigh, E. G., Jr. 1999. *Tropical forest ecology, a view from Barro Colorado Island*. Oxford University Press, Oxford, UK.
- Malhi, Y., and J. Grace. 2000. Tropical forests and atmospheric carbon dioxide. *Trends in Ecology and Evolution* **15**:332–337.
- Phillips, O. L., and A. H. Gentry. 1994. Increasing turnover through time in tropical forests. *Science* **263**:954–958.
- Phillips, O. L., Y. Malhi, N. Higuchi, W. F. Laurance, P. V. Nunez, R. M. Vasquez, S. G. Laurance, L. V. Ferreira, M. Stern, S. Brown, and J. Grace. 1998. Changes in the carbon balance of tropical forest: evidence from long-term plots. *Science* **282**:439–442.
- Phillips, O. L., Y. Malhi, B. Vinceti, T. Baker, S. L. Lewis, N. Higuchi, W. F. Laurance, P. Nunez Vargas, R. Vasquez Martinez, S. Laurance, L. V. Ferreira, M. Stern, S. Brown, and J. Grace. 2002a. Changes in growth of tropical forests: evaluating potential biases. *Ecological Applications* **12**:576–587.
- Phillips, O. L., R. Vasquez Martinez, L. Arroyo, T. R. Baker, T. Killeen, S. L. Lewis, Y. Malhi, A. M. Mendoza, D. Neill, P. Nunez Vargas, M. Alexiades, C. Ceron, A. Di Fiore, T. Erwin, A. Jardim, W. Palacios, M. Saldias, and B. Vinceti. 2002b. Increasing dominance of large lianas in Amazonian forests. *Nature* **418**:770–774.
- Piperno, D. R. 1990. Fitolitos, arqueología y cambios prehistóricos de la vegetación en un lote de cincuenta hectáreas de la isla de Barro Colorado. Pages 153–156 *in* E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. *Ecología de un bosque tropical*. Smithsonian Institution Press, Washington, D.C., USA.
- 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.
- Schnitzer, S. A., and F. Bongers. 2002. The ecology of lianas and their role in forests. *Trends in Ecology and Evolution* **17**:223–230.
- Schnitzer, S. A., and W. P. Carson. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* **82**:913–919.
- Schnitzer, S. A., J. W. Dalling, and W. P. Carson. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *Journal of Ecology* **88**:655–666.
- Sheil, D. 1996. Species richness, tropical forest dynamics and sampling: questioning cause and effect. *Oikos* **77**:587–509.
- SPSS. 2000. *Systat 10.0*. SPSS, Chicago, Illinois, USA.
- Stanhill, G., and S. Cohen. 2001. Global dimming: a review of the evidence for a widespread and significant reduction in global radiation with discussion of its probable causes and possible agricultural consequences. *Agricultural and Forest Meteorology* **107**:255–278.
- Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**:1–14.
- Wright, S. J., C. Carrasco, O. Calderón, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. *Ecology* **80**:1632–1647.
- Wright, S. J., and F. H. Cornejo. 1990. Seasonal drought and the timing of leaf fall in a tropical forest. *Ecology* **70**:1165–1175.
- Würth, M. K. R., K. Winter, and C. H. Körner. 1998. In situ responses to elevated CO₂ in tropical forest understorey plants. *Functional Ecology* **12**:886–895.