

LIFE HISTORY TRADE-OFFS IN TROPICAL TREES AND LIANAS

BENJAMIN GILBERT,^{1,5} S. JOSEPH WRIGHT,² HELENE C. MULLER-LANDAU,³ KAORU KITAJIMA,⁴
AND ANDRÉS HERNANDEZ²

¹Department of Botany, University of British Columbia, Room #3529, 6270 University Boulevard, Vancouver, British Columbia V6T 1Z4 Canada

²Smithsonian Tropical Research Institute, Apartado 0843*03092, Balboa, Ancón, Republic of Panama

³University of Minnesota, St. Paul, Minnesota 55108 USA

⁴University of Florida, Gainesville, Florida 32611 USA

Abstract. It has been hypothesized that tropical trees partition forest light environments through a life history trade-off between juvenile growth and survival; however, the generality of this trade-off across life stages and functional groups has been questioned. We quantified trade-offs between growth and survival for trees and lianas on Barro Colorado Island (BCI), Panama using first-year seedlings of 22 liana and 31 tree species and saplings (10 mm < dbh < 39 mm) of 30 tree species. Lianas showed trade-offs similar to those of trees, with both groups exhibiting broadly overlapping ranges in survival and relative growth rates as seedlings. Life history strategies at the seedling stage were highly correlated with those at the sapling stage among tree species, with all species showing an increase in survival with size. Only one of 30 tree species demonstrated a statistically significant ontogenetic shift, having a relatively lower survival rate at the sapling stage than expected. Our results indicate that similar life history trade-offs apply across two functional groups (lianas and trees), and that life history strategies are largely conserved across seedling and sapling life-stages for most tropical tree species.

Key words: growth; liana; life history; ontogenetic shift; sapling; seedling; shade tolerance; survival; trade-offs; tropical forest.

INTRODUCTION

Trade-offs in life history strategies structure ecological communities and can contribute to species coexistence and the maintenance of local diversity (Bonsall et al. 2004). Physiological and allocation constraints can enforce trade-offs among traits and limit possible trait combinations, while abiotic and biotic environmental heterogeneity insure that different trait combinations are favored in different places and times, making particular trait values predictive of success in different environments (Crawley 1997). Model communities in which species exhibit life history trade-offs maintain higher species diversity than communities without such trade-offs, and particular features of community dynamics can be traced to particular trade-offs (Pacala et al. 1996, Chave 1999, Chave et al. 2002).

One particularly important life history trade-off among tropical trees is between high survival and rapid growth (Wright 2002, Leigh et al. 2004). Rapid growth and low survival characterize light-demanding pioneer species, while high survival and slow growth characterize the most shade-tolerant species, with most species falling along a continuum between these two extremes (Welden et al. 1991, Condit et al. 1996, Wright et al. 2003). This trade-off becomes important for trees at a very small size, as soon as seed reserves are exhausted (Kitajima

1994, 2002). Kitajima (1994) proposed that this trade-off reflects relative resource allocation to survival-enhancing traits such as large root systems, high wood density, and defenses against herbivores and pathogens. The high survival versus rapid growth trade-off may act as a habitat partitioning mechanism by enabling tree species with high survival rates to persist in the forest understory and thus to have an initial size advantage when a tree fall creates a canopy gap, and by promoting species with high growth rates in larger gaps, where sustained growth rates may be more important than initial size in determining success in reaching the canopy (Poorter 1999, Wright et al. 2003, Leigh et al. 2004).

Although the trade-off between survival and growth is well documented for tropical trees at both the sapling (Welden et al. 1991, Hubbell and Foster 1992, Wright et al. 2003) and seedling (Kitajima 1994, Poorter 1999) stage, it remains unclear whether species occupy the same relative position at different life stages. A number of studies have reported that some tropical tree species shift in growth strategy or shade tolerance as they change in size (Clark and Clark 1992, 1999, Grubb 1996, Poorter et al. 2005), while others report relative consistency (Wright et al. 2003). Ontogenetic shifts in life history strategies are inconsistent with the hypothesis that species consistently occupy distinct niches (i.e., gap or understory) within a forest. Instead, ontogenetic shifts raise the possibility that life history niche differentiation might be higher dimensional. For example, species that grow rapidly as seedlings and survive well as saplings

Manuscript received 25 October; revised 29 August 2005; accepted 8 November 2005. Corresponding Editor: F. He.

⁵ E-mail: bgilbert@zoology.ubc.ca

(but survive poorly as seedlings and grow slowly as saplings) might succeed in sites where light levels are initially high and then deteriorate. Multiple survival-growth tradeoff axes for multiple life stages increase the potential for life history differences to contribute to species coexistence while simultaneously making it much harder to characterize species life history strategies and understand their roles in forest dynamics.

Lianas, or climbing woody plants, comprise 25% of woody plant stem density and diversity in many tropical forests (Schnitzer and Bongers 2002), yet no studies have yet evaluated whether the growth-survival trade-off found among tree species applies to them as well. Although many liana species can persist in the shaded understory of mature forests, the diversity of lianas is often greatest in gaps and disturbed forests (reviewed in Schnitzer and Bongers 2002). For example, surveys of lianas on Barro Colorado Island (BCI), Panama, have shown that liana abundance and diversity are much greater in gaps than in mature forest (Putz 1984, Schnitzer and Carson 2001). These observations have led to the hypothesis that lianas as a group are prone to low establishment and survival in shade but are capable of rapid growth in gaps (Schnitzer and Bongers 2002). In contrast, trees span a wide range of life history trade-offs (e.g., Wright et al. 2003). If lianas and trees do occupy the same growth-survival tradeoff axis but lianas occur over a narrower range of relatively high growth and low survival, this might provide one explanation for why lianas have lower diversity than trees. More generally, any differences in life history strategy distribution between trees and lianas would suggest that the underlying physiological trade-offs differ and would limit the potential for growth-survival trade-offs to contribute to the coexistence of the two life forms.

In this study, we use seedling survival and growth data from BCI in conjunction with data on tree saplings to address the consistency of life history trade-offs in lianas and trees. In particular, we ask (1) whether lianas show the same trade-offs as co-occurring tree species, and (2) whether the relative positions of tree species along the growth-survival trade-off are consistent between the seedling and sapling life stages. For tree seedlings and saplings, we include species that vary widely in maximum height (understory, intermediate height, and canopy trees) to assess the general consistency of trade-offs across the tree community. In our analyses, we use mean growth and survival rates across all individuals within a species and size class; thus, our results reflect the joint influences of the distribution of environments (e.g., light availability; Welden et al. 1991) in which individuals are found, and of their capacity for growth and survival in different environments.

METHODS

Seedling growth and survival are taken from an ongoing study within a 50-ha permanent plot located on Barro Colorado Island (BCI; 9°9' N, 79°51' W). The 50-

ha plot includes 2 ha of young, secondary forest (Condit 1998). The remainder is old growth forest which has been disturbed minimally by humans for at least 1500 yr (Piperno 1990). Detailed descriptions of BCI and the 50-ha plot can be found in Condit (1998), Croat (1978), and Leigh (1999). Nomenclature follows Croat (1978) as updated by Condit et al. (1996).

Seedling survival and relative growth rate were estimated using data from 600 seedling plots located throughout the 50-ha plot. Groups of three 1-m² seedling plots were placed at 2.8 to 4.7 m distance from each other around a central station. Stations were located at 13.5-m intervals along trails and randomly between 4 and 10 m from trails with a mean distance of 18.9 ± 3.6 m (mean \pm SE) between the centers of neighboring stations. All woody plants ≤ 50 cm tall were tagged and identified between January and March 1994. Survivors were remeasured for changes in height and leaf number, and new recruits were tagged and identified between January and March each year from 1995 to 2003 (Wright et al. 2005b). First-year seedling survival was recorded as the number of seedlings recorded for the first time in a particular year (except 1994) to survive to the subsequent year.

Sapling data are from the 1990, 1995, and 2000 censuses of the BCI 50-ha plot for saplings between 10 and 39 mm in diameter at breast height (dbh), and were obtained from the Center for Tropical Forest Science (*data available online*).⁶

STATISTICAL METHODS

First-year seedling survival was estimated using a complementary log–log model with a binomial error distribution, following Allison (1995). A complementary log–log model is appropriate for survival measurements taken at discrete points in time when death of individuals can occur at any point between successive censuses. Species occurring in at least thirty plots were included in the analysis, with seedlings recorded in the initial 1994 census excluded, as these were of unknown age. A total of 22 liana and 31 tree species met these requirements.

Average seedling annual relative growth rates in height ($RGR = \log[\text{height at time } t] - \log[\text{height at time}(t - 1)]$) were determined for all species that entered into the survival analysis. Seedlings under 1 m tall were included, with relative growth rates calculated by averaging RGR within an individual (among years), then within a plot. The number of observations was calculated using each plot as one observation. Numbers of observations per species varied from five to 472 (median of 46) with lower numbers of observations for species that germinated in at least 30 plots, but survived in a limited number of plots. Seedlings that had a negative height growth (due to damage or measurement error) were removed from the calculation of RGR.

⁶ (<http://ctfs.si.edu/datasets/>)

Sapling annual survival was estimated using an exponential survival model and survival rates over the 5-yr census intervals. Annual relative growth rate was estimated using the same formula as for seedlings, but using diameter growth instead of height growth. All values were first averaged within an individual so that each individual acted as one observation. Species with at least 15 individuals were included in the analysis if we also had data for the same species at the seedling stage. A total of 30 sapling species met this requirement. An individual sapling was excluded from the relative growth rate estimation if it had a negative diameter growth, an absolute growth rate over 75 mm dbh/yr (both assumed to be due to measurement error), different heights for diameter measurements between censuses, or had resprouted from a broken stem.

We used a model 2 analysis of covariance (ANCOVA) to test the hypotheses that lianas and trees (1) have different slopes in their survival to growth trade-offs, (2) have different intercepts, and (3) occupy different locations along the trade-off gradient. A model 2 ANCOVA tests for differences among groups (in our case, trees vs. lianas) in the relationship of two variables when neither of the continuous variables (in our case growth and survival) is considered explanatory. It does this by first using a standard major axis (SMA or model 2) regression on each group to determine their slopes; the model 2 regression minimizes the distance of points from the best-fit line along both the x - and y -axis (Sokal and Rohlf 1995, Legendre and Legendre 1998). A permutation test is then used to determine whether the slopes of the two groups differ significantly (Warton and Weber 2002; (S)MATR program, *available online*).⁷ The ability to calculate common slopes allows one to test for intercept differences between individual slopes, as in standard ANCOVA. When significant heterogeneity in group slopes could not be detected, we tested for shifts in elevation and shifts along the common trade-off axis (Wright et al. 2001) by transforming the data such that the common slope was 0, and testing for differences in group means of y' and x' using a one sample ANOVA, where y' and x' are y and x after data is transformed by an amount determined by the common slope β ($y' = y - \beta x$ and $x' = y + \beta x$). The common slope is similar to an average weighted slope from the two groups, with weights determined by sample size and variation explained, and the formula for calculating it can be found in Warton and Weber (2002) and in (S)MATR (see footnote 7).

To test for ontogenetic consistency in tree species' relative positions in the growth to survival trade-off, we first located each species' position on this trade-off axis at the first-year seedling stage and the 10–39 mm dbh sapling stage. Species' positions on the growth-survival trade-off were estimated for each stage using a principal component analysis (PCA) on standardized survival and growth rates, which is equivalent to a standard major

axis (model 2) regression (Legendre and Legendre 1998). The PCA for seedlings included the proportion surviving their first year and the logarithm of RGR. The PCA for saplings included the annual survival rate and the logarithm of RGR. Only species that met sample size requirements as both seedlings and saplings ($n = 30$ species) were used to generate the survival to growth trade-off for each group. The PCA axis 1 score of each species indicates its position along the growth to survival trade-off for the stage (seedling or sapling) tested. We then used a correlation of PCA axis 1 scores for seedlings and conspecific saplings to evaluate the hypothesis that trees show consistent trade-offs versus showing no consistency for these two life stages.

Following the correlation analysis, we determined if any tree species varied significantly from the general trend in life history trade-offs shown by the other tree species. In order to test for changes in individual species, we performed a new PCA using the PCA axis 1 score of each species on the growth to survival trade-off for the seedling and sapling life stages as input. This new PCA measures the best-fit line between seedlings and saplings, with each species counting as an observation. We then evaluated the PCA between seedling and sapling trade-offs for outliers using the axis 2 scores, which indicate the residual distance of each species from the best fit line between seedling and sapling trade-offs. These residuals were analyzed using Grubb's test for outliers (Sokal and Rohlf 1995). Similar analyses were performed directly for survival and growth.

Survival and relative growth rates were calculated with SAS system 8.1 (SAS Institute 1999). PCAs were performed with PCOrd (McCune and Mefford 1999). The model 2 ANCOVA was performed with (S)MATR software (see footnote 7).

RESULTS

Both tree and liana species exhibit a strong trade-off between growth and survival at the seedling stage. Species of both life-forms show similar ranges of survival and growth (Fig. 1; $r = -0.72$ and -0.71 , respectively; $P < 0.001$ for both; full data is available in the Appendix). Tests for differences in slope, relative position along the trade-off gradient and relative position once the covariate was removed, were all insignificant (P values ranging from 0.26 to 0.60). Both life forms are represented by species along the entire trade-off continuum, thus lianas and trees do not show differences in their life history strategies as seedlings.

Tree seedlings and saplings show survival to growth trade-offs (Fig. 2), with these two traits demonstrating a strong negative relationship ($r = -0.72$ and -0.85 , respectively; $P < 0.0001$ for both). The range in survival decreases significantly and shifts from lower to higher survival between the seedling and sapling stage (Fig. 2a and b).

The relative position of each tree species on the survival to growth trade-off was consistent between

⁷ <http://www.bio.mq.edu.au/ecology/SMATR>

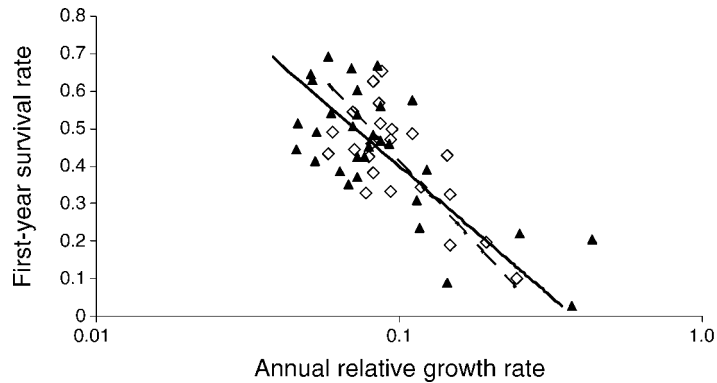


FIG. 1. Relationship between first-year survival and relative growth rate (log scale) for seedlings of trees (solid triangles, solid line; $n = 31$ species) and lianas (open diamonds, dashed line; $n = 22$). Solid and dashed lines are model 2 regression lines for trees and lianas, respectively.

seedling and sapling life stages (Fig. 3a; $r = 0.71$, $P < 0.0001$) with one notable exception—*Inga marginata* did not follow the general trend of most species (Grubb's outlier test, $P < 0.1$). When the trade-off was broken down into its two components, *I. marginata* was typical of other species in its growth trade-offs (Fig. 3b) but showed an inconsistent trend in survival with relatively high seedling survival and relatively low sapling survival (Fig. 3c; Grubb's outlier test, $P < 0.05$). No other species showed inconsistent trends from

the community-wide change in the survival to growth trade-off between the seedling and sapling life stages (tested at $\alpha = 0.1$).

DISCUSSION

Comparing lianas and trees

There is a strong trade-off between growth and survival for both trees and lianas at the seedling stage on BCI, and both life forms include species from the full range of values observed along this tradeoff gradient

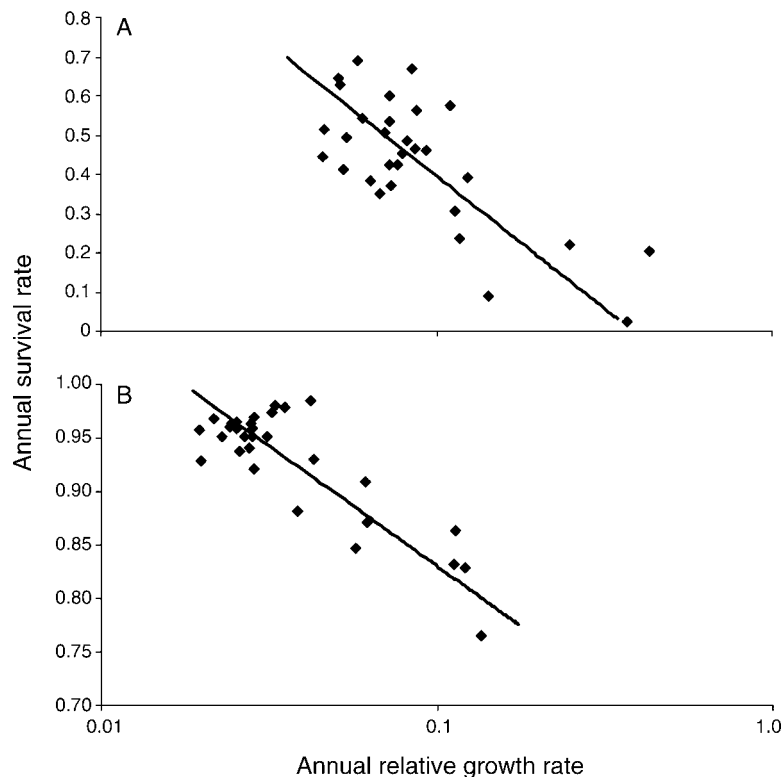


FIG. 2. Relationship between tree survival and relative growth rate (log scale) for (A) seedlings ($n = 31$ species) and (B) saplings from 10 to 39 mm dbh ($n = 30$). Note the difference in the scales of the vertical axes. The x-axis represents relative height growth rates for seedlings and relative diameter growth rates for saplings (see *Methods*).

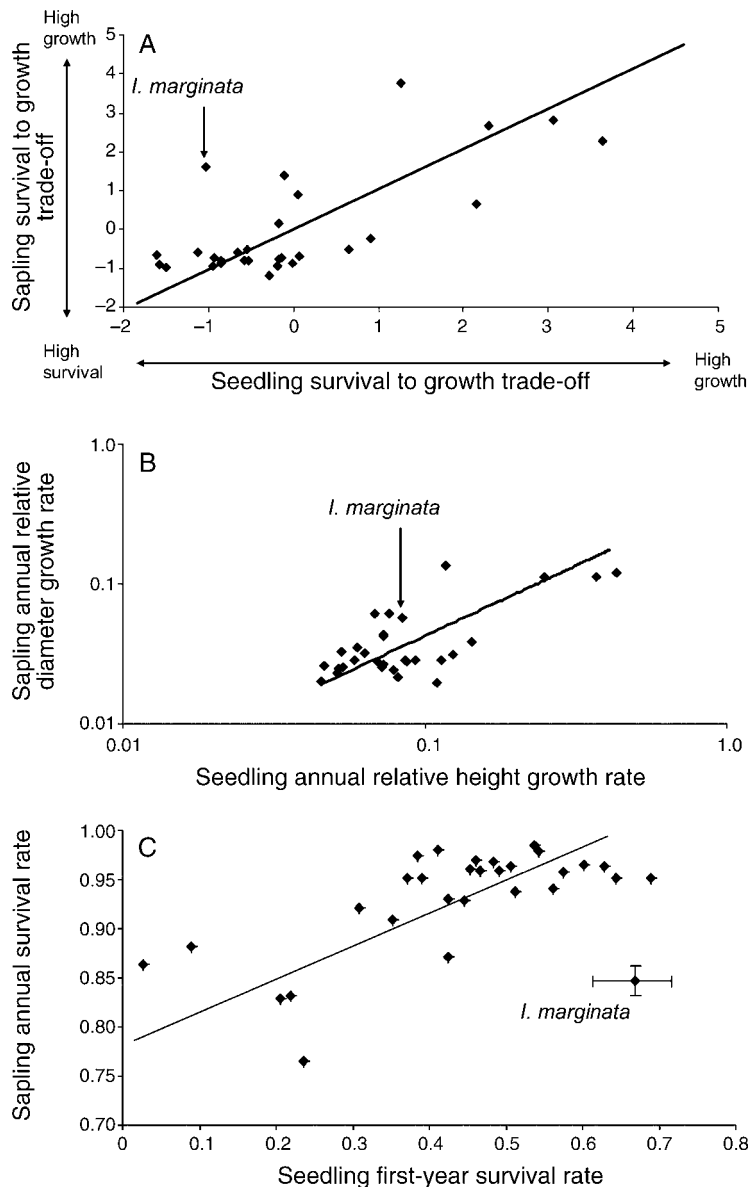


FIG. 3. Relationship between the sapling and seedling stages for trees, with best-fit lines determined using model 2 regressions in (A) survival to growth trade-offs, (B) relative growth rates (log scale), and (C) survival rates. In panel (C), the 95% confidence interval is included for survival of *I. marginata*, the species that showed a significant departure from the rest of the tree community.

(Fig. 1). The species richness of lianas increases in gaps and after disturbance (DeWalt et al. 2000, Laurance et al. 2001, Schnitzer and Carson 2001), which has led to the hypothesis that lianas are mainly light-demanding (Schnitzer and Bongers 2002). We reject this hypothesis because lianas and trees overlap broadly along the growth to survival trade-off as seedlings. Indeed, the overlapping life history strategies of lianas and trees (this study), their competitive interactions (Putz 1984), and liana dependence on the structural support of trees indicate that a simple habitat partitioning model based on life history trade-offs will not capture the complex interactions of these two life forms.

Three other hypotheses have been proposed that explain high liana diversity in gaps. First, adult lianas may have greater survival and a greater potential for vegetative reproduction than do adult trees following a tree fall and the creation of a canopy gap—thus greater persistence of established adults may contribute to the relatively high diversity of lianas in gaps (Putz 1984, Schnitzer and Bongers 2002). A second hypothesis is that lianas have more plastic growth responses than trees, and are thus more able to grow quickly in sunlit conditions even when they are also shade-tolerant (Schnitzer and Bongers 2002). A third possibility is that adult lianas grow into gaps through extension growth from nearby trees and

that established liana seedlings and saplings also grow directionally into newly formed gaps from the nearby understory. All three hypotheses merit further study.

Continuous variation along the trade-off axis

Many studies have placed tropical trees into distinct groups based on gap dependence during regeneration (e.g., Hubbell and Foster 1986, Clark and Clark 1992). Our results do not support this approach, but rather indicate that trees as well as lianas show a continuous range in trade-offs (Fig. 1–3), as has been found in other studies (e.g., Welden et al. 1991, Wright et al. 2003). A comparison of tree species included in our survey vs. all those occurring in BCI (not shown) indicated that our sample is broadly representative of the entire tree community, with only one of our species at the extreme end of the trade-off gradient associated with pioneer species. Our results are not biased by selectively sampling part of the trade-off gradient, although they are restricted to including only relatively abundant species.

Comparing seedlings and saplings

Among tree species, a similar survival to growth trade-off is observed for both first-year seedlings and 10–39 mm dbh saplings (Fig. 2) and, with the exception of a single species, different species have similar relative positions on the trade-off gradient at both the seedling and sapling life stages (Fig. 3). The constancy in trade-off position we observe is consistent with constancy for mortality rates reported by Wright et al. (2003). In contrast, Clark and Clark (1992, 1999) report many ontogenetic shifts in absolute light environments and in maximum growth capacity, and Poorter et al. (2005) find size-dependent changes in relative light environments. Despite the attention that ontogenetic shifts have received over the last 13 years, there is no common system for evaluating shifts in life history strategy or niche position across life stages. Variation in results among studies thus results from variation in methods, including different null hypotheses, different variables compared, different size classes analyzed, and different criteria for choosing species.

One major difference among studies concerns whether ontogenetic shifts are defined by absolute changes with size or by relative changes in the position of a species after accounting for characteristic shifts with size. Clark and Clark (1992) use an absolute definition, and thus conclude that the five species they examine (of nine total) whose light environment changes significantly across different stages of sapling development demonstrate ontogenetic shifts. Such analyses of traits of single species for shifts between seedling and sapling stages will often indicate that ontogenetic shifts are occurring simply because most species show characteristic shifts in growth and survival between life stages (Poorter 1999, Clark and Clark 1992, 2001, Poorter et al. 2005). Our position is that a first level of investigation should therefore examine correlations between life stages for a

large number of species; these correlations would incorporate systematic changes that characterize all species within a community. If ontogenetic shifts dominate in a community, we would expect to see no correlation (or even a negative correlation) between performance at different life stages (see Kitajima and Bolker 2003, Sack and Grubb 2003). When data from Clark and Clark (1992) were re-analyzed in this manner, we found that the proportion of each species present in gaps was highly correlated for three of the tree size classes (r_s ranging from 0.91 to 0.98, $n = 6$, $P < 0.05$), with a single species causing the correlation to be insignificant in a fourth, intermediate size class. Thus, our analysis would have found a much lower level of ontogenetic shifts in the same data because it first examines community level patterns, or consistency among species, and then attempts to identify individual species that do not conform to the community level patterns.

Another important contributor to divergent conclusions across studies is a difference in interpretation of apparent rank reversals in the presence of considerable error in individual data points. Our Fig. 3 shows many species that are off the regression line for all species. Under a null model that all species maintain the same ranks (Sack and Grubb 2003), this might be seen as evidence for many ontogenetic shifts. However, of all the species that fall off the regression line, only one has confidence intervals that exclude the regression line. Thus, we cannot reject the null hypothesis that the remaining species have consistent ranks, and we interpret the overall strong positive correlation as evidence for ontogenetic constancy. It is important to note that we do not have the power to reject the possibility of small ontogenetic shifts in other species. However, given the high level of uncertainty in the locations of individual points, small rank reversals may not be appropriate for detecting shifts in life history trade-offs (Kitajima and Bolker 2003).

Uncertainty in estimating individual species' strategies is high because of small sample sizes, the binomial nature of errors in survival, and environmental heterogeneity. The median tree species in terms of number of plots in which it occurred as a first year seedling (*Hampea appendiculata*, $n = 57$) had a 95% confidence interval for survival that spanned 15–33%. The absolute width of confidence intervals for all tree seedlings ranged from 3 to 30% (Appendix), with smaller intervals occurring for species with large sample sizes (e.g., *Fareamea occidentalis*) or very low survival rates (e.g., *Jacaranda copaia*). An additional source of uncertainty in measured growth and survival is the variability in light levels and other environmental conditions experienced by individuals (Denslow 1987, Engelbrecht and Hertz 2001, Poorter et al. 2005), which influence realized growth and survival rates (e.g., Metcalfe and Grubb 1997, Sack and Grubb 2003, Wright et al. 2003). Especially given the highly skewed distribution of light levels in tropical forests, with few very bright sites at which growth rates are high,

confidence intervals may under-represent true uncertainty and even large random samples may fail to adequately capture species' strategies.

The size classes and species types included in a study also affect the likelihood of observing patterns characteristic of ontogenetic shifts. For example, data from Clark and Clark (1999: Fig. 2) indicate that most species show consistent trends in relative growth until they reach a reproductive size (less than 20 cm dbh for the two *Cecropia* spp. in their figure; Wright et al. 2005a; S. J. Wright, unpublished data). The decrease in relative growth at larger sizes likely reflects a change in resource allocation to reproduction, but not necessarily in a growth to survival trade-off.

Studies on *Alseis blackiana* demonstrate the effect of comparing different life-stages, and also the problems that can arise when systematic shifts in the larger tree community are not used as a null model. Wright et al. (2003) evaluated the consistency in *A. blackiana* seed establishment rate (no. seedlings/no. seeds), seedling mortality and sapling mortality, and reported that it differed from other species due to low seed establishment. Here we confirm the consistency in survival and growth between seedling and sapling stages, suggesting that differences that arise from the high fecundity and small seed size of *A. blackiana* are restricted to the seed establishment phase. In contrast, Dalling et al. (2001) compared establishment requirements, early seedling growth and physiology, and older seedling survival of *A. blackiana* to those of a single known pioneer species and a single shade-tolerant species, and found that *A. blackiana* resembled the pioneer species in its very early life stages while achieving a survival rate higher even than many shade-tolerant species as a larger seedling. This approach did not take into account the continuum of change exhibited by the entire tree community. When the tree community is considered as a whole, *A. blackiana*'s shifts in survival and growth between seedling and sapling life stages are consistent with those of other species.

Of all the species we examine here, *Inga marginata* is the only one that changes strategies from high seedling survival to low sapling survival relative to other species. Previous life history shifts have mainly been reported for species that change from light demanding to shade tolerant with age (e.g., Grubb 1996, Dalling et al. 2001), although two other tropical trees (*Pternandra coerulescens* and *P. echinata*) also switch from shade tolerant at the seedling stage to light-demanding at the sapling stage (Metcalf et al. 1998). Accounts of the life history of *I. marginata* are consistent with our finding of an ontogenetic shift in this species; Roggy and Prevost (1999) list *I. marginata* as partially shade tolerant, based on subadult stage performance and position in the canopy at later stages, and Terborgh et al. (1997) describe it as acting like other pioneer species at sizes above 5 cm dbh. Further investigation of the physiology and evolutionary history of this species could lead to an understanding of how ontogenetic shifts in trade-offs occur.

Conclusions and future directions

Future research should simultaneously examine ontogenetic shifts in regeneration environments (e.g., light levels) and environment-specific performance, and how they interact with realized growth and mortality. Changes in relative regeneration environments with size necessarily result from differential survival at smaller size classes. At larger diameter classes, however, there is also potential for variation among species in light environments encountered due to variation in species architecture and thus in the heights at which crowns are positioned (Poorter et al. 2005). The effects of species vital rates on their distributions in different regeneration environments, and the feedback of these regeneration environments on the realized vital rates, are important for understanding species coexistence in tropical forests.

In summary, life history trade-offs are an important mechanism maintaining species coexistence (e.g., Pacala et al. 1996, Wright 2002). We have explored two aspects of growth-survival trade-offs that increase our understanding of their role in the ecology of tropical forests. We have shown that at the seedling life-stage, lianas and trees have similar survival to growth trade-offs, and that 29 of 30 tree species (97%) display similar relative trade-offs as both first-year seedlings and saplings. These results demonstrate a strong constancy in species vital rates among functional groups and tree sizes. Further research should focus on the interaction between realized vital rates, the environments in which species occur, and their environment-specific performance.

ACKNOWLEDGMENTS

Thank you to Justine Karst, Kathryn Kirby, Jaqueline Ngai, and Roy Turkington for feedback on initial manuscripts. The seedling census has been funded by the Environmental Sciences Program of the Smithsonian Institution. The 50-ha forest dynamics plot has been funded by the National Science Foundation and the Smithsonian Tropical Research Institute under the direction of Drs. Richard Condit and Stephen Hubbell.

LITERATURE CITED

- Allison, P. D. 1995. Survival analysis using SAS: a practical guide. SAS Institute Inc. Cary, North Carolina, USA.
- Bonsall, M. B., V. A. A. Jansen, and M. P. Hassell. 2004. Life history trade-offs assemble ecological guilds. *Science* **306**: 111–114.
- Chave, J. 1999. Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model. *Ecological Modelling* **124**:233–254.
- Chave, J., H. C. Muller-Landau, and S. A. Levin. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *American Naturalist* **159**:1–23.
- Clark, D. A., and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecology* **62**:315–344.
- Clark, D. A., and D. B. Clark. 1999. Assessing the growth of tropical rainforest trees: issues for forest modeling and management. *Ecological Applications* **9**:981–997.
- Clark, D. A., and D. B. Clark. 2001. Getting to the canopy: tree height growth in a neotropical rain forest. *Ecology* **82**:1460–1472.
- Condit, R. 1998. Tropical forest census plots. Springer-Verlag, Berlin, Germany.

- Condit, R., S. P. Hubbell, and R. Foster. 1996. Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science* **7**:405–416.
- Crawley, M. J., editor. 1997. *Plant ecology*. Second edition. Blackwell Science, Oxford, UK.
- Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California, USA.
- Dalling, J. W., K. Winter, J. D. Nason, S. P. Hubbell, D. A. Murawski, and J. L. Hamrick. 2001. The unusual life history of *Alseis blackiana*: a shade tolerant pioneer tree? *Ecology* **82**: 933–945.
- Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* **18**: 431–451.
- Dewalt, S. J., S. A. Schnitzer, and J. S. Denslow. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *Journal of Tropical Ecology* **16**: 1–19.
- Engelbrecht, B. M. J., and H. M. Herz. 2001. Evaluation of different methods to estimate understorey light conditions in tropical forests. *Journal of Tropical Ecology* **17**:207–224.
- Grubb, P. 1996. Rainforest dynamics: the need for new paradigms. Pages 215–233 in D. S. Edwards, S. C. Choy, and W. E. Booth, editors. *Tropical rainforest research: current issues*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Hubbell, S. P., and R. B. Foster. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314–329 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- Hubbell, S. P., and R. B. Foster. 1992. Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management. *Oikos* **63**:48–61.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**:419–428.
- Kitajima, K. 2002. Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. *Functional Ecology* **16**:433–444.
- Kitajima, K., and B. M. Bolker. 2003. Testing performance rank reversals among coexisting species: crossover point irradiance analysis. *Functional Ecology* **17**:276–287.
- Laurance, W. F., D. Perez-Salicrup, 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.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second English edition. Developments in environmental modelling 20. Elsevier Science, Amsterdam, The Netherlands.
- Leigh, E. G., Jr. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, Oxford, UK.
- Leigh, E. G., Jr., P. Davidar, C. W. Dick, J.-P. Puyravaud, J. Terborgh, H. ter Steege, and S. J. Wright. 2004. Why do some tropical forests have so many species of trees? *Biotropica* **36**:447–473.
- McCune, B., and M. J. Mefford. 1999. *Multivariate analysis of ecological data*. Version 4.27. MjM Software, Gleneden Beach, Oregon, USA.
- Metcalfe, D. J., and P. J. Grubb. 1997. The responses to shade of seedlings of very small-seeded tree and shrub species from tropical rain forests in Singapore. *Functional Ecology* **11**: 215–221.
- Metcalfe, D. J., P. J. Grubb, and I. M. Turner. 1998. The ecology of very small-seeded shade-tolerant trees and shrubs in lowland rain forest in Singapore. *Plant Ecology* **134**:131–149.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, Jr., R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecological Monographs* **66**:1–43.
- 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.
- Poorter, L. 1999. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology* **13**:396–410.
- Poorter, L., F. Bongers, F. J. Sterck, and H. Wöll. 2005. Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. *Journal of Ecology* **93**:256–267.
- Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* **6**:1713–1724.
- Roggy, J. C., and M. F. Provost. 1999. Nitrogen-fixing legumes and sivigenesis in a rain forest in French Guiana: a taxonomic and ecological approach. *New Phytologist* **144**: 283–294.
- Sack, L., and P. Grubb. 2003. Testing performance rank reversals among coexisting species: crossover point irradiance analysis by Sack and Grubb (2001) and alternatives. *Functional Ecology* **17**:276–287.
- SAS Institute. 1999. *The SAS system for Windows*, version 8.02. SAS Institute, Inc. Cary, North Carolina, USA.
- 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.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. Freeman, New York, New York, USA.
- Terborgh, J., C. Flores, P. Mueller, and L. Davenport. 1997. Estimating the ages of successional stands of tropical trees from growth increments. *Journal of Tropical Ecology* **13**: 833–856.
- Warton, D. I., and N. C. Weber. 2002. Common slope tests for bivariate structural relationships. *Biometrical Journal* **44**: 161–174.
- Welden, C. W., S. W. Hewett, S. P. Hubbell, and R. B. Foster. 1991. Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology* **72**:35–50.
- Wright, I. J., P. B. Reich, and M. Westoby. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of high- and low-rainfall and high- and low-nutrient habitats. *Functional Ecology* **15**:423–434.
- Wright, S. J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* **130**:1–14.
- Wright, S. J., M. A. Jaramillo, J. Pavon, R. Condit, S. P. Hubbell, and R. B. Foster. 2005a. Reproductive size thresholds in tropical trees: variation among individuals, species and forests. *Journal of Tropical Ecology* **21**:307–315.
- Wright, S. J., H. C. Muller-Landau, O. Calderón, and A. Hernández. 2005b. Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. *Ecology* **86**: 848–860.
- Wright, S. J., H. C. Muller-Landau, R. Condit, and S. P. Hubbell. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* **84**: 3174–3185.

APPENDIX

A table showing survival and relative growth rate of tree and liana seedlings (*Ecological Archives* E087-075-A1).