

Seasonal and spatial variation in water availability drive habitat associations in a tropical forest

LIZA S. COMITA^{1,3} AND BETTINA M. J. ENGELBRECHT^{2,4}

¹*Department of Plant Biology, 2502 Plant Sciences Building, University of Georgia, Athens, Georgia 30606 USA*

²*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama*

Abstract. Associations with topographic units or soil types that vary in water availability are widespread in plant communities and are one of the main structuring aspects for local species distribution patterns, yet the underlying mechanisms are poorly understood. We hypothesized that differential seedling performance across habitats, particularly during the dry season, leads to habitat associations in seasonal tropical forests. We expected this pattern to be most pronounced in particularly dry years, such as those associated with El Niño Southern Oscillation (ENSO) events. We assessed performance of 36 native tree and shrub species in a moist forest in central Panama across the dry and wet seasons in two topographic habitat types during a year in which dry-season precipitation was reduced due to an ENSO event. At the community level, we found lower growth and higher mortality in the dry season relative to the wet season and higher mortality in the drier plateau habitat relative to the wetter slope habitat. There was large variation in species' responses to season and habitat. Species' mortality and growth rates were significantly correlated with experimentally assessed drought sensitivity, but only during the dry season in the plateau habitat. Slope specialists had significantly higher survival, but not growth, in the slope vs. plateau habitat during the dry season. In contrast, plateau specialists showed no performance differences between habitats. The data suggest that associations with plateau habitats result from a numerical advantage of drought-tolerant species in dry habitats in which seedlings of drought-sensitive species are unable to persist. Overall, our results support the idea that seasonal and spatial variation in water availability, particularly in dry years, drive seedling dynamics, which in turn shape local species distributions. Predicted shifts in rainfall patterns caused by global and regional climate change are therefore expected to alter the dynamics, composition, and diversity of seasonal tropical forests.

Key words: Barro Colorado Island, Panama; drought; Forest Dynamics Plot; niche differentiation; species distributions.

INTRODUCTION

Plant population dynamics can vary as a result of both spatial and temporal variation in environmental conditions. Studies of environmental drivers of plant species performance have focused largely on spatiotemporal variation in light availability, particularly in tropical forests (e.g., Denslow et al. 1998, Kobe 1999, Montgomery and Chazdon 2002). However, considerable spatial and temporal variation in water availability also exist in most tropical forests (Becker et al. 1988, Daws et al. 2002, Gibbons and Newbery 2003, Nepstad et al. 2004), and tropical plant species vary widely in their drought sensitivity (Engelbrecht and Kursar 2003, Engelbrecht et al. 2007, Baltzer et al. 2008). Water

availability is therefore likely to differentially influence the spatial and temporal dynamics of tropical plant populations and thus contribute to species distribution patterns and niche differentiation in these diverse communities.

Spatial variation in water availability at local scales is often driven by topography, with higher soil moisture on slopes compared to ridges or plateaus (Whitmore 1984, Becker et al. 1988, Daws et al. 2002, Gibbons and Newbery 2003). We have previously demonstrated that topographic variation in water availability, coupled with species' differential drought sensitivity, directly shapes species distributions in forests in central Panama (Engelbrecht et al. 2007). Species associations with topography have also been reported for a number of other tropical forests (e.g., Webb and Peart 2000, Harms et al. 2001, Balvanera et al. 2002, Palmiotto et al. 2004, Valencia et al. 2004), suggesting that water availability frequently influences tropical tree species distributions, although additional factors, such as nutrient availability (Paoli et al. 2006, John et al. 2007) or pest pressure (Fine et al. 2004), may also be involved. Previous studies

Manuscript received 7 August 2008; revised 18 December 2008; accepted 9 January 2009. Corresponding Editor: F. C. Meinzer.

³ Present address: Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York 10027 USA. E-mail: lsc2125@columbia.edu

⁴ Present address: Department of Biology, San Francisco State University, San Francisco, California 94132 USA.

suggest that such habitat associations typically form after germination and seedling establishment and presumably result from differential survival of seedlings and saplings across habitats (Webb and Peart 2000, Paoli et al. 2006, Comita et al. 2007a).

There is also pronounced temporal variation in water availability in tropical forests, with most experiencing one or two dry seasons annually (Walsh 1996). Additionally, tropical forests, including aseasonal wet forests, occasionally suffer severe droughts associated with El Niño Southern Oscillation (ENSO) events (Condit et al. 1995, Nepstad et al. 2004, Slik 2004). Both regular seasonal changes in water availability and supra-annual cycles of severe drought may have significant effects on population dynamics, with potential long-term consequences for species abundance and distribution (e.g., Condit et al. 1995, Nakagawa et al. 2000, Aiba and Kitayama 2002, Marod et al. 2002, Slik 2004).

Interactions of spatial and temporal variation in water availability are likely to be important for driving plant population dynamics and shaping species distributions across habitats, yet have rarely been examined. During the wet season, soils are typically close to saturation. Soil water potentials decrease in the dry season and can increase plant drought stress, as indicated by visible wilting (Fig. 1), low leaf water potentials, and reduced growth and survival (Becker et al. 1988, Cao 2000, Engelbrecht and Kursar 2003, Gibbons and Newbery 2003). Water availability in the dry season, rather than the wet season, is therefore likely to be important in driving population dynamics and species distributions across moisture gradients in seasonal, non-inundated tropical forests. The effect of the dry season should be especially pronounced in habitats that retain less moisture and for species that are more sensitive to drought. Additionally, this effect is likely to be most evident at the seedling stage, since their small, shallow root systems cannot tap into deeper, moister soil layers (Cao 2000).

A solid understanding of species' reactions to limited water availability is increasingly needed as climate change models predict significant changes in dry-season length and frequency of droughts (Hulme and Viner 1998, Timmermann et al. 1999, IPCC 2007). Here we examine how seasonal and spatial variation in water availability drive seedling dynamics and shape local species distributions in a diverse tree community. To maximize our ability to detect effects of season and habitat on plant performance, we monitored seedlings during a year that experienced a particularly intense dry season due to an ENSO event. We hypothesized that over all species, survival and growth would be lower in the dry season compared to the wet season, due to limited soil water availability. In addition, we hypothesized that species associated with wet habitats and sensitive to drought would exhibit lower survival and growth in drier habitats and that this differential

performance across habitats would only be evident during the dry season.

METHODS

Study site

The study was conducted in the semi-deciduous, lowland moist forest of Barro Colorado Island (BCI), Panama (9°9' N, 79°51' W) (Leigh 1999). Barro Colorado Island has a mean annual rainfall of 2634 ± 456 mm/yr (mean \pm SD for 1925–2005, Smithsonian Tropical Research Institute Terrestrial- Environmental Sciences Program Meteorological data), with a pronounced four-month dry season from mid-December through mid-April. Approximately 10% of tree species on BCI are deciduous during the dry season (Croat 1978). The length and intensity of the dry season vary considerably among years. The study period included an intense dry season associated with the 2002/2003 ENSO event (see Appendix A). The study was carried out in the BCI 50-ha Forest Dynamics Plot (FDP) (Hubbell and Foster 1983, Condit 1998). Previous studies have shown that slopes in the BCI plot remain wetter than plateaus and experience a shorter duration of low water availability during the dry season (Becker et al. 1988, Daws et al. 2002). Midday leaf water potentials taken at the height of the dry season during our study (March 2003) confirm that the maximum drought stress experienced by seedlings was significantly higher in plateau than slope habitats (plateau, mean = -2.13 MPa; slope, mean = -1.80 MPa; $t = 4.04$; plateau, $N = 174$; slope, $N = 84$, $P < 0.001$).

Data collection

We monitored growth and survival of established seedlings of 36 native tree and shrub species (Appendix B) chosen among common species in the BCI FDP to (1) maximize overlap with experimental studies of seedling drought sensitivity (Engelbrecht and Kursar 2003, Engelbrecht et al. 2007) and (2) to cover a wide range of habitat associations within the BCI FDP (Harms et al. 2001). Of the 36 species, four have been reported in the literature to be deciduous during the dry season and one during the wet season at our study site (see Appendix B).

Focal individuals were selected using data on seedlings in 20,000 1-m² seedling plots systematically distributed across the BCI FDP (Comita et al. 2007b). In these plots, free-standing, woody seedlings ≥ 20 cm tall and < 1 cm diameter at breast height (dbh, measured at 1.3 m above the ground surface) were tagged, mapped, measured, and identified to species in 2001. Plots were recensused in January–May 2002. We excluded seedlings located in a 1.5-ha seasonal swamp and a 2-ha patch of secondary forest. In the remaining area, which included dry plateau ($< 7^\circ$ inclination) and wet slope ($\geq 7^\circ$ inclination) habitats, we randomly selected up to 100 seedlings (20–50 cm tall) of each focal species from the 2002 seedling database. Sample



FIG. 1. Wilted seedlings in the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama, during the dry season: clockwise from top left, *Psychotria limonensis* (Rubiaceae), *Nectandra globosa* (Lauraceae), *Hippocratea volubilis* (Hippocrateaceae), *Cydistia aequinoctialis* (Bignoniaceae).

sizes were ultimately determined by seedling abundance in the plot and by number of individuals alive at the start of the study period (Appendix B). Seedlings were censused (1) at the start of the 2002–2003 dry season (census dates, 26 December 2002 through 8 January 2003), (2) shortly after the beginning of the wet season (10–19 May 2003), and (3) again at the end of the 2003 wet season (9–18 December 2003). In each census, we classified seedlings as alive or dead and counted numbers of leaves for individuals with <50 leaves. Given the low seedling growth rates in the understory of tropical forests, leaf number change is typically a more robust measure of growth than height change over short time intervals (Bunker and Carson 2005).

Data analysis

We used a standard exponential growth model to calculate relative growth rates (RGR) during each census interval as $RGR = (\ln[L_{t_2}] - \ln[L_{t_1}]) / (t_2 - t_1)$, where L is the number of leaves and t_1 and t_2 are the beginning and the end of the census interval in months (Evans 1972). To avoid zero values when log-transforming leaf number, we added 0.5 to those individuals with zero leaves. Three species (*Eugenia nesiotica* [deciduous],

Mouriri myrtilloides, *Xylopia macrantha*) frequently had seedlings with >50 leaves and were therefore excluded from growth analyses. We examined the effect of species, habitat, and season on RGR for all individuals alive during the entire study period using a repeated-measures ANOVA with habitat (two levels, dry plateaus and wet slopes) and species (33 species) as main factors and season (two levels, dry and wet) as a repeated factor.

We used generalized linear modeling (GLM) with binomial errors to test for effects of species, season, and habitat on the probability of an individual surviving from one census to the next. Census interval length was included as a covariate. To avoid biased rates of survival over time since weaker individuals are likely to die in the first census interval, we included initial leaf number as a covariate in our survival analysis as a proxy for individual fitness (Zens and Peart 2003). The best model was determined by dropping out each independent variable and testing whether the model fit was significantly reduced when the term was excluded, based on the χ^2 statistic (Crawley 2002). We also calculated instantaneous relative mortality rates for each species as $(\ln[N] - \ln[S]) / (t_2 - t_1)$, where N is the initial number of seedlings, S is the number of survivors, and t_1 and t_2 are

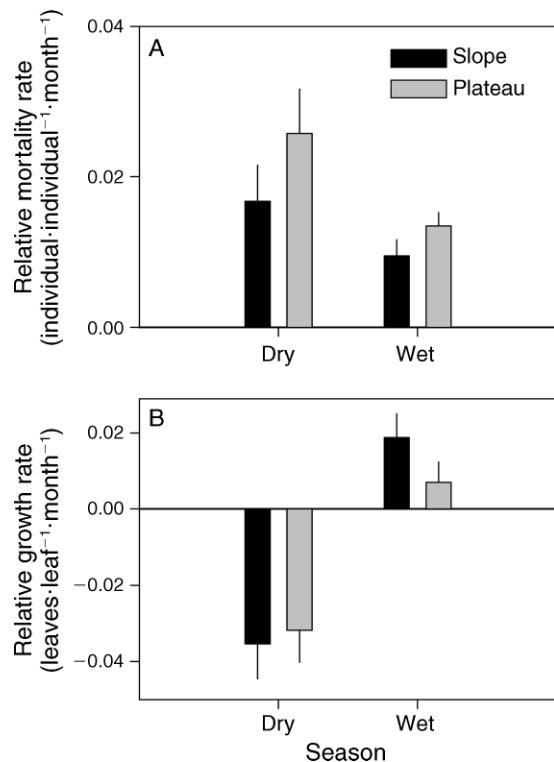


FIG. 2. (A) Relative mortality and (B) relative growth rates of seedlings in the dry and wet season in slope and plateau habitats in the 50-ha Forest Dynamics Plot. Data are means (and SE) over species, with $N = 36$ for mortality and $N = 33$ for growth.

the beginning and end of the census interval in months. Ninety-five percent confidence intervals were calculated based on binomial probabilities (Dixon and Massey 1969).

To examine variation in performance among species, we calculated mortality rates and relative growth rates for each species across the entire year and separately for each habitat and in each season. To adjust for inherent differences among species in annual mortality rates, we also calculated the proportion of deaths that occurred in the dry season (e.g., number of individuals that died in the dry season divided by the total number of individuals that died over the entire year). This was not possible for growth, since growth rates were frequently negative. We then tested whether species performance in each season and habitat was related to species–habitat associations. Species were designated slope or plateau specialists based on results of Harms et al. (2001) for trees ≥ 1 cm dbh (Appendix B). We also tested whether species' mortality and growth rates in each season and habitat correlated with species' drought sensitivity (Appendix B). We used the index of drought sensitivity published in Engelbrecht et al. (2007), which was assessed in the field using irrigation experiments on transplanted first-year seedlings of native tree and shrub

species in the Barro Colorado Nature Monument, including 21 of the focal species in the present study (see Engelbrecht and Kursar [2003] and Engelbrecht et al. [2007] for more details). Species' drought sensitivity (DS) was calculated as the relative difference in survival (S) over the dry season in dry vs. irrigated (irri) experimental plots ($DS = [S_{\text{irri}} - S_{\text{dry}}]/S_{\text{irri}} \times 100$).

RESULTS

Seedling dynamics

Mortality.—The best-fit model for probability of survival included season, habitat, and species, as well as the covariates of census interval length and initial leaf number, but no interaction terms (Appendix C). Overall, the probability of survival was lower in the dry than in the wet season and lower in plateau than in slope sites (Fig. 2A). Seasonal mortality rates varied widely among species. In 23 of the 36 species (64%), there was a trend toward higher mortality rates in the dry season than in the wet season (Fig. 3A). However, only two species showed significantly different mortality between seasons, both having higher mortality in the wet season (Fig. 3A).

Growth.—Relative growth rates were significantly lower in the dry season than in the wet season and varied among species, with a significant species \times season interaction (Fig. 2B; Appendix C). Habitat did not significantly affect RGR. Among species, there was large variation in growth rates (Fig. 3B). For 26 out of 33 species (79%), RGR was lower in the dry season than in the wet season, and for 16 of these species growth rates differed significantly between seasons. A trend for higher RGR in the dry season was only observed in seven species, with four showing significant differences between dry and wet season rates. Overall, plants tended to lose leaves over the dry season (negative leaf number change) and developed new leaves during the wet season (Fig. 2B). In the dry season, only nine species (27%) showed an increase in leaf number, while leaf numbers in the wet season increased for 23 species (70%; Fig. 3B). Interestingly, for all three drought deciduous species analyzed, growth was positive in the dry season. Over the entire census year, however, the average RGR over all species remained negative (-0.07 ± 0.03 leaves·leaves⁻¹·yr⁻¹), and only nine species (27%) showed a net leaf number increase during the study.

Seasonal dynamics, species–habitat associations, and drought sensitivity

Dynamics of habitat specialists.—Comparisons of mortality rates of habitat specialists in the slope vs. plateau habitat revealed that (wet) slope specialists had significantly higher mortality in the (dry) plateau habitat in the dry season, but not in the wet season (Table 1). Conversely, plateau specialists did not exhibit different mortality in the two habitats. However, mortality of slope specialists was considerably higher than plateau

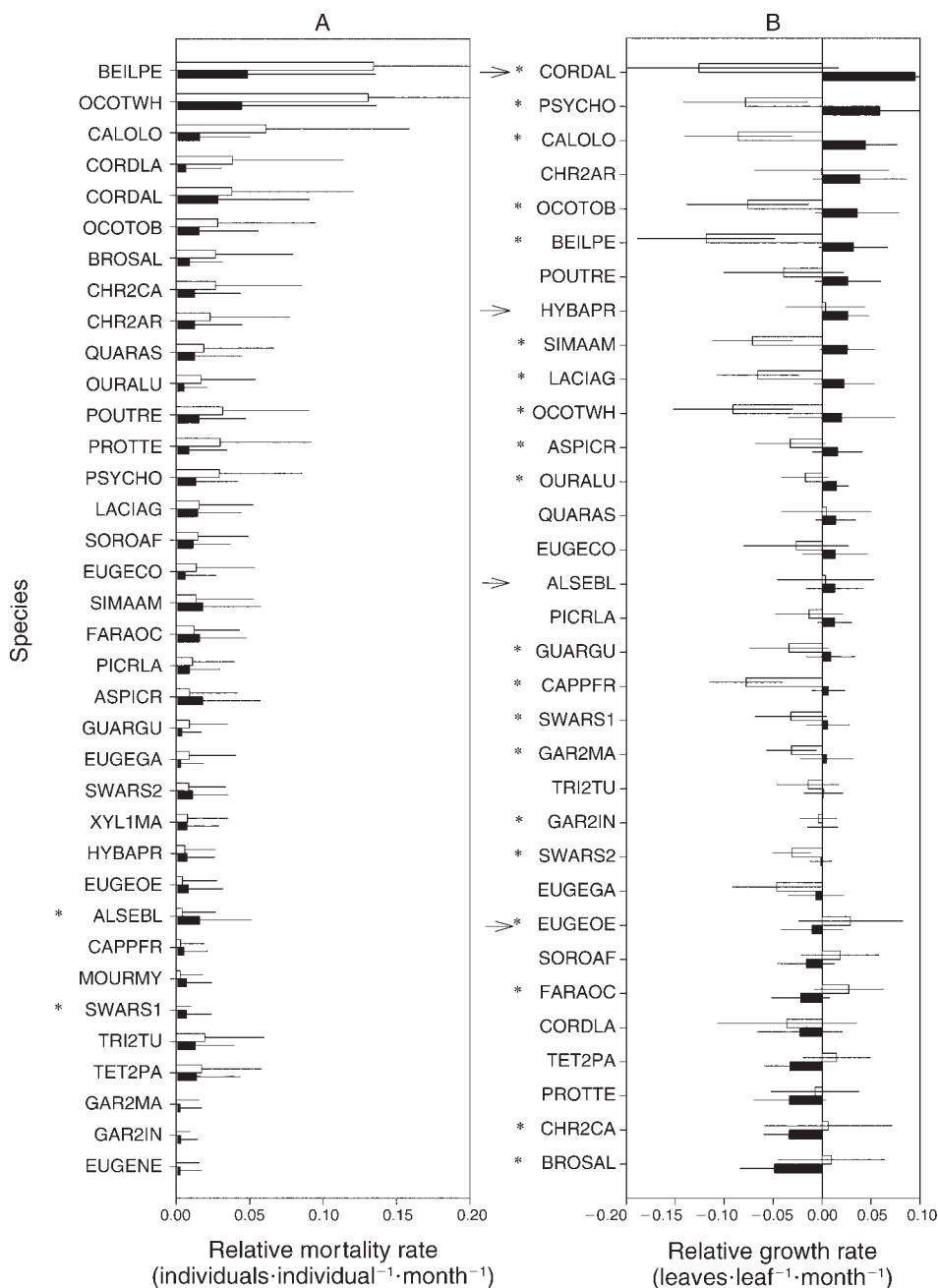


FIG. 3. Relative mortality and relative growth rates of seedlings in the 50-ha Forest Dynamics Plot in the dry season (open bars) and wet season (solid bars) of 2002–2003. (A) Mortality rates of 36 species sorted by descending dry-season mortality rate (see Appendix B for species codes). (B) Growth rates (relative leaf area change per month) for 33 species sorted by decreasing wet-season growth. Data are species' means with 95% confidence limits. Confidence limits of two species exceed the figure in both panels. Species marked with an asterisk are those for which dry- and wet-season rates were significantly different ($P < 0.05$; based on generalized linear model with binomial errors for mortality and Mann-Whitney U tests for growth). In panel (B), species marked with arrows are those reported in the literature to be deciduous.

specialists in both seasons and habitats (Table 1), with the difference most pronounced in the plateau habitat during the dry season ($t = 2.954$, $df = 22.9$, $P = 0.007$). Growth rates were not significantly different in plateau vs. slope habitats for either plateau or slope specialists (Table 1) and did not differ between plateau and slope

specialists in any season or habitat (all $P > 0.10$). Results were similar when excluding deciduous species from growth rate comparisons.

Correlations with drought sensitivity.—Mortality rates over the entire year increased significantly with species' drought sensitivity ($r = 0.45$, $df = 19$, $P = 0.04$). The

TABLE 1. Mortality and growth rates of habitat specialists in the plateau vs. slope habitat during the dry and wet season of 2002–2003 in the Barro Colorado Island 50-ha plot, Panama.

Season	Plateau habitat mean (SD)	Slope habitat mean (SD)	<i>t</i>	df	<i>P</i>
Mortality rate					
Slope specialists					
Dry	0.0390 (0.049)	0.0259 (0.038)	-2.71	15	0.016
Wet	0.0143 (0.013)	0.0139 (0.017)	-0.88	15	0.394
Plateau specialists					
Dry	0.0088 (0.007)	0.0069 (0.014)	-1.33	8	0.221
Wet	0.0097 (0.005)	0.0065 (0.009)	-2.01	8	0.079
Growth rate					
Slope specialists					
Dry	-0.0373 (0.052)	-0.0537 (0.051)	-1.11	14	0.286
Wet	0.0035 (0.032)	0.0152 (0.031)	1.30	14	0.215
Plateau specialists					
Dry	-0.0132 (0.040)	-0.0143 (0.055)	-0.05	7	0.964
Wet	-0.0080 (0.022)	0.0182 (0.025)	2.32	7	0.053

Notes: To meet assumptions of normality and equal variance, species rates were natural log-transformed (after adding 0.01) before carrying out paired *t* tests. Mortality rate was measured as individual-individual⁻¹·month⁻¹; growth rate was measured as leaves-leaf⁻¹·month⁻¹. Boldface type indicates significance at *P* < 0.05.

trend was significant in the dry season (Fig. 4A), but only marginally significant in the wet season (Fig. 4B). Drought sensitivity was also correlated with the proportion of deaths that occurred in the dry season (*r* = 0.51, *df* = 19, *P* = 0.02).

When considering the habitats separately, in the plateau habitat, species' drought sensitivity was significantly correlated with mortality rates in the dry season (Fig. 4C), but not in the wet season (Fig. 4D). Consistent with this, in the plateau habitat, drought sensitivity was positively correlated with the proportion of deaths that occurred in the dry season (Fig. 5A).

On the other hand, in the slope habitat, there was only a marginally significant correlation between drought sensitivity and mortality in the dry season (Fig. 4E), and drought sensitivity was not significantly correlated with mortality rates in the wet season (Fig. 4F) or the proportion of deaths that occurred in the dry season (Fig. 5B).

Species' drought sensitivity was not significantly correlated with growth rate in any season or habitat (all *P* > 0.07, *df* = 17). However, when excluding deciduous species from the analysis, there was a significant trend for drought-sensitive species to have lower growth rates in the plateau habitat during the dry

season (*r* = -0.54, *df* = 15, *P* = 0.02) and overall in the dry season (*r* = -0.49, *df* = 15, *P* = 0.048), consistent with patterns for mortality.

DISCUSSION

By simultaneously assessing seasonal and habitat-specific performance of naturally established seedlings of a large number of species, the current study allows us to evaluate the importance of dry-season performance for population dynamics and species distribution patterns in a community context. We found strong evidence that spatial and temporal variation in water availability drive community-wide patterns of tropical seedling dynamics and that variation among species in dry-season mortality, but not growth, underlies species topographic habitat associations in our study system.

Patterns of dry- and wet-season seedling performance

At the community level, seedling survival and growth rates were lower in the dry season than in the wet season, as we had hypothesized, indicating that dry-season conditions were strongly limiting performance compared to wet-season conditions. Interestingly, the drought deciduous species showed increases in leaf number over the dry season, while leaf number decreased for most evergreen species during the same period. This suggests that deciduous species were able to flush new leaves prior to the census at the start of the wet season. In contrast, the observed leaf loss during the dry season for evergreen species, as well as the overall negative growth across both seasons, likely reflects the harsh conditions during the study year.

Our results are consistent with previous species-level studies on seasonal performance in this and other tropical forests (Turner 1990, Fisher et al. 1991, Gerhardt 1996, Mulkey and Wright 1996, Veenendaal et al. 1996, Lewis and Tanner 2000, Marod et al. 2002, McLaren and McDonald 2003, Bunker and Carson 2005), suggesting that dry-season conditions are an important driver of seedling dynamics throughout the seasonal tropics. Seasonal environmental changes in tropical forests mainly involve rainfall and consequently soil moisture and relative air humidity. However, light conditions are generally higher in the dry compared to the wet season, especially during severe El Niño dry seasons (Appendix A; Barone 1998, Holmgren et al. 2001, Slik 2004, Wright 2005, Huete et al. 2006). In addition, pest pressure may be lower in the dry season (Wolda 1988, Givnish 1999, Van Bael and Brawn 2005). Therefore, positive effects of the dry season on plant performance have also been hypothesized for tropical forest plants (Barone 1998, Slik 2004, Wright 2005). However, the lower seedling survival and growth rates in the dry season observed in our study indicate that the negative effect of water limitation overrides any potential positive effects of increased light availability or reduced pest pressure, at least during severe dry seasons such as the one that occurred during our study.

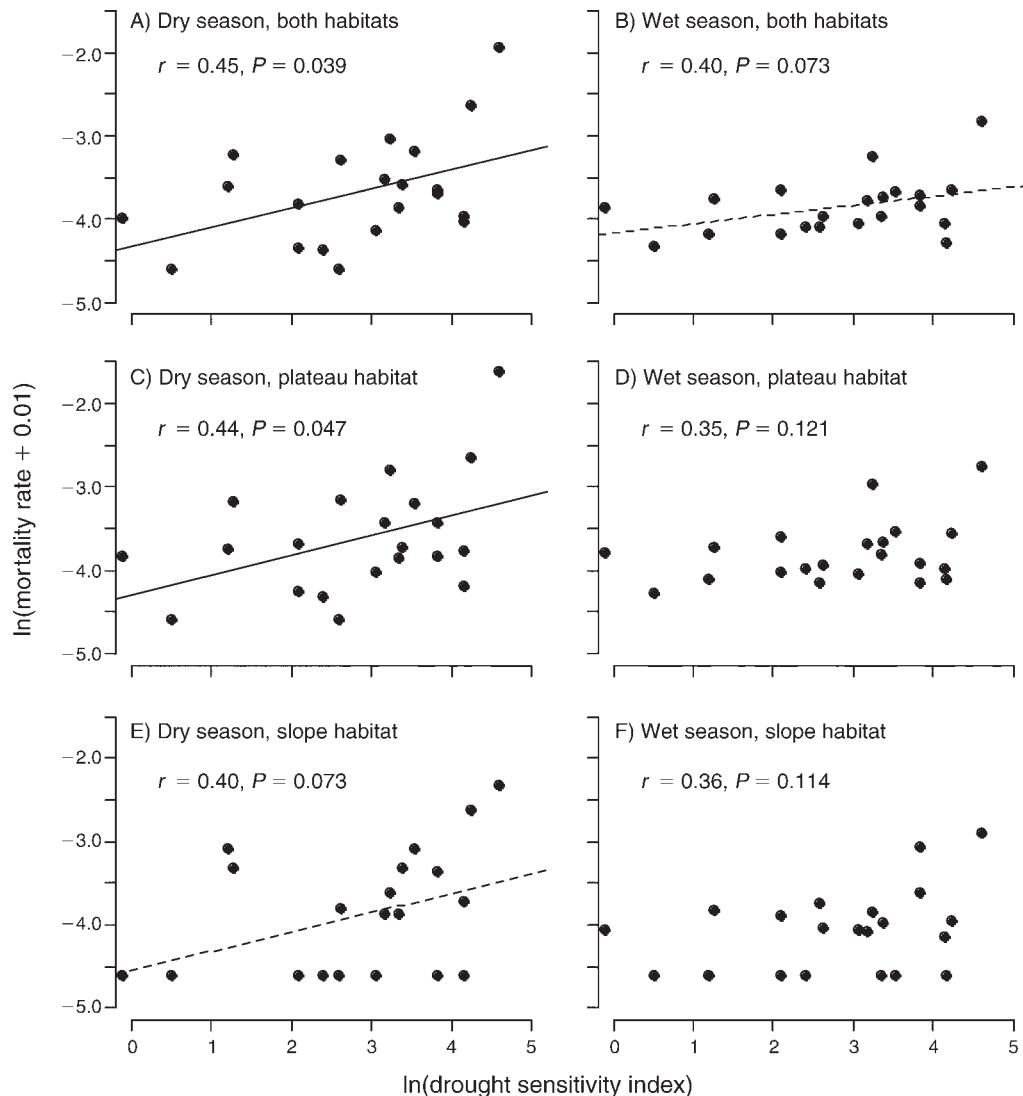


FIG. 4. Relationship between species' drought sensitivity and their dry- and wet-season mortality rates (A, B) in both plateau and slope habitats combined, (C, D) in plateau habitats only, and (E, F) in slope habitats only. Significant correlations ($P < 0.05$) are denoted by solid lines, and marginally significant correlations ($0.05 \leq P < 0.1$) are denoted by dashed lines (all $df = 19$).

The pronounced role of drought in driving observed patterns of seedling dynamics is substantiated by the significant correlations of species' mortality rates and experimentally assessed drought sensitivity (Fig. 4). The importance of drought for seedling performance in our study is also backed by observations of low seedling leaf water potentials (less than -4MPa), widespread wilting and leaf drying, and desiccated seedlings at the height of the dry season (Fig. 1; B. M. J. Engelbrecht and L. S. Comita, unpublished data). Finally, irrigation experiments in the area, as well as in other tropical forests, have typically shown higher survival or growth in irrigated treatments (Fisher et al. 1991, Mulkey and Wright 1996, Engelbrecht and Kursar 2003, Bunker and Carson 2005, Engelbrecht et al. 2007, Tanner and

Barberis 2007, Yavitt and Wright 2008, Paine et al. 2009), further supporting water shortage as the main factor limiting species performance in the dry season. The importance of water availability in other tropical forests likely varies with the length and severity of the dry season, with additional factors, such as nutrient availability and pest pressure, playing an increasingly important role as seasonal water limitation decreases.

Seedling dynamics and species-habitat associations

We found evidence that differential patterns of seedling mortality among species contribute to species topographic habitat associations in the BCI forest community. In contrast, we found no habitat-mediated differences in seedling growth for slope and plateau

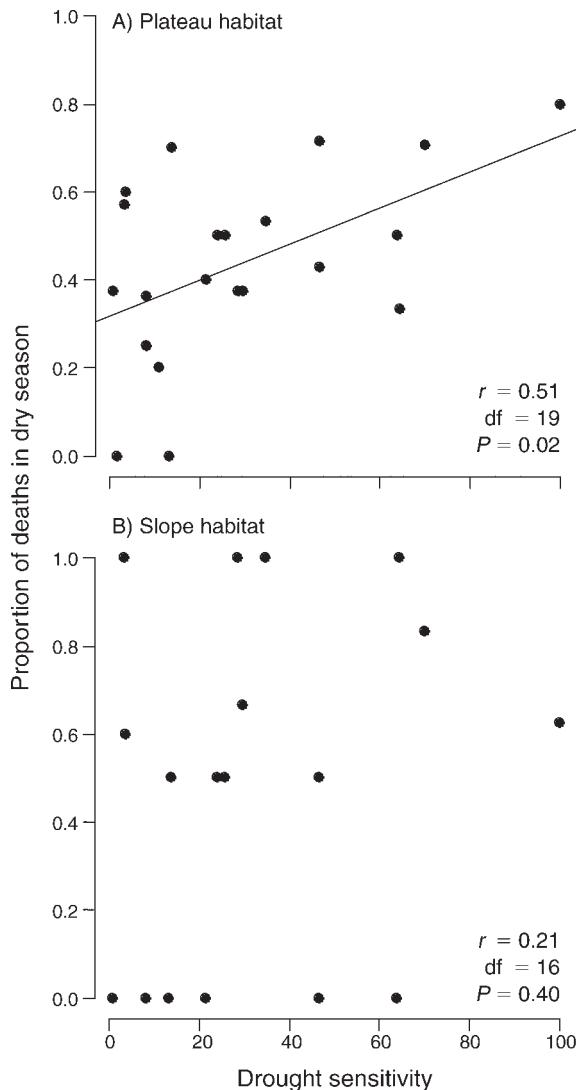


FIG. 5. Correlation between species' drought sensitivity and the proportion of deaths occurring in the dry season in the (A) plateau and (B) slope habitats of the 50-ha Forest Dynamics Plot.

specialists. However, we did find a significant correlation between species' drought sensitivity and growth rates in the dry plateau habitat during the dry season, suggesting that limited growth does play a role in restricting drought-sensitive species to wetter habitats.

Differential performance across topographic or edaphic habitats and differential responses to drought across habitats are common in tropical plants (Ashton et al. 1995, Nakawaga et al. 2000, Aiba and Kitayama 2002, Potts 2003, Palmiotto et al. 2004, Russo et al. 2005, Baltzer et al. 2007). However, in previous studies, differences in performance did not necessarily coincide with a homesite advantage of habitat specialists in their preferred habitat (Baraloto and Goldberg 2004, Russo et al. 2005). In addition, strong habitat associations have

been observed in the absence of large, habitat-specific differences in performance (Yamada et al. 2007).

In our study, however, performance differences between habitats and specialist groups were rather pronounced. Species associated with moist slope habitats had higher survival in their home habitat, and the effect was particularly pronounced in the dry season (Table 1). These results strongly suggest that higher seedling mortality in dry plateau habitats during the dry season shapes species associations with slope sites. Consistent with this, those species that had been experimentally characterized as more sensitive to drought showed higher mortality and lower growth rates in plateau sites during the dry season than more drought-resistant species (Fig. 4). In addition, a higher proportion of the annual mortality occurred in the plateau habitat during the dry season for drought-sensitive vs. drought-resistant species (Fig. 5). This further supports the idea that restricted water availability during the dry season limits drought-sensitive slope specialists to moister habitats. The strength of these results likely reflects the exceptionally dry year in which we chose to assess seedling performance. Continued monitoring of wet- and dry-season seedling survival across multiple years will help evaluate the importance of supra-annual extreme droughts relative to regular dry-season conditions in determining the distribution of drought-sensitive species across habitats.

In contrast to slope specialists, there was no evidence that plateau specialists had higher survival in their dry home habitat than in their non-preferred habitat. In a detailed analysis for one plateau specialist tree species in Malaysia, Yamada et al. (2007) similarly found no habitat-specific performance or demography differences. They suggested that habitat associations do not necessarily require large differences in population dynamics across habitats, but are caused and maintained by relatively higher performance compared to co-occurring species, especially during drought events, which create windows of opportunity for the species tolerant of the dry conditions in plateau sites. Our data showing (1) no significant survival differences for plateau specialists among habitats, (2) higher survival of plateau specialists during an especially dry year relative to slopes specialists, and (3) higher mortality of drought-sensitive species in the dry season, specifically in plateau sites, give strong support to their hypothesis. Alternatively, processes reducing the performance of plateau specialists in wetter habitats may occur during normal or wet years, such as differential pest pressure among habitats (Fine et al. 2004) or lower competitive ability under normal conditions.

Our results suggest that different modes lead to and maintain habitat associations for species associated with high (wet) vs. low (dry) resource habitats. Habitat associations for high-resource specialists are shaped by habitat-specific performance differences (i.e., higher survival in the home, high-resource habitat compared

to lower-resource habitats). The differential habitat performance of these species is due to their inability to tolerate low resource availability, which excludes them from low-resource habitats or reduces their competitive ability there.

Conversely, habitat associations for low-resource habitat specialists are shaped by high tolerance of low resource availability (i.e., little or no habitat-specific performance differences). We propose that this tolerance allows plateau specialists to persist in the seedling layer of the drier habitat, while less drought-tolerant species drop out over time due to seasonal water limitation. While competition between seedlings is generally weak in tropical forests (Paine et al. 2008, Svenning et al. 2008), it is likely to intensify when the seedling layer responds to canopy openings. In the drier plateau habitat, advanced regeneration will largely be composed of drought-tolerant species (i.e., they will be present in greater numbers than less tolerant ones) and will therefore be more likely to win open sites. In other words, drought-sensitive species will be recruitment limited (Clark et al. 1999) in drier habitats, due predominantly to "persistence limitation," rather than seed or establishment limitation. Consistent with this, we have previously shown that habitat specialists on BCI are capable of dispersing seeds and establishing seedlings outside of their preferred habitats (Comita et al. 2007a). In addition, only about one-third of habitat specialists showed evidence of higher seedling establishment in their preferred habitat (Comita et al. 2007a), pointing to an important role for post-establishment seedling survival in shaping species-habitat associations.

In contrast to the plateau habitat, both drought-tolerant and drought-intolerant species can persist in the seedling layer in the wetter slope habitat. As a result, tolerant species will not have a numerical advantage as in the plateau habitat, and a larger number of species will be competing for open sites. Thus, tolerant and intolerant species will have more similar probabilities of winning open sites. This idea is supported by the fact that plateau specialists have significantly higher abundance than slope specialists (at the ≥ 1 cm dbh stage) in the plateau habitat ($t = -2.44$, $df = 17.3$, $P = 0.03$), whereas the two groups have similar abundances in the slope habitat ($t = -0.69$, $df = 16.9$, $P = 0.50$).

Conclusions

Although conducted at only one site in a single year, our study lends strong support to the idea that seasonal and spatial variation in water availability, particularly during drought events, results in differential seedling mortality across habitats, which in turn shapes species' habitat associations in seasonal tropical forests. Differential mortality appears to be most important in the formation of habitat associations for drought-sensitive species. Conversely, drought-tolerant species do not show differential mortality, but instead gain a numerical

advantage in dry habitats in which seedlings of drought-sensitive species are unable to persist. Our results further indicate that the presence of wetter slope habitats allows drought-sensitive species to regenerate in seasonal forests, thereby increasing overall species richness in these communities.

In the tropics, global and regional climate change is predicted to result in significant changes in dry season length and the frequency of El Niño events (Hulme and Viner 1998, Timmermann et al. 1999, IPCC 2007). Our results suggest that such changes will alter the dynamics and distributions of many tropical tree species. In particular, an increase in the intensity or frequency of drought events is likely to cause a decrease and potential loss of drought-sensitive species, resulting in significant shifts in composition and reduced diversity in tropical forests.

ACKNOWLEDGMENTS

We thank Irene Torres de Tejada, Diógenes Ibarra, Oldemar Valdés, David Brassfield, Israel Tejada, Guadalupe Alvarado, Blexein Contreras, Eric Manzané, Johana Balbuena, Didimo Urena, Antonio Aguilar, Rodolfo Rojas, Emilio Sanchez, Alejandro Almanza, and Antonio Cueto for assisting with data collection in the field and Salomón Aguilar for species identifications. This study was funded by a grant from the Center for Tropical Forest Sciences (CTFS) at the Smithsonian Tropical Research Institute. Additional funding was provided by the U.S. National Science Foundation (DEB-0075102). L. S. Comita acknowledges the support of an NSF Graduate Research Fellowship and University of Georgia Presidential Fellowship, and B. M. J. Engelbrecht was supported by the German Research Foundation (DFG). Valuable comments on the manuscript were provided by G. Goldsmith, C. E. T. Paine, and three anonymous reviewers.

LITERATURE CITED

- Aiba, S. I., and K. Kitayama. 2002. Effects of the 1997–98 El Niño drought on rain forests of Mount Kinabalu, Borneo. *Journal of Tropical Ecology* 18:215–230.
- Ashton, P. M. S., C. V. S. Gunatilleke, and I. Gunatilleke. 1995. Seedling survival and growth of 4 *Shorea* species in a Sri Lankan rain forest. *Journal of Tropical Ecology* 11:263–279.
- Baltzer, J. L., S. J. Davies, S. Bunyavejchewin, and N. S. M. Noor. 2008. The role of desiccation tolerance in determining tree species distributions along the Malay-Thai Peninsula. *Functional Ecology* 22:221–231.
- Baltzer, J. L., S. J. Davies, N. S. M. Noor, A. R. Kassim, and J. V. LaFrankie. 2007. Geographical distributions in tropical trees: Can geographical range predict performance and habitat association in co-occurring tree species? *Journal of Biogeography* 34:1916–1926.
- Balvanera, P., E. Lott, G. Segura, C. Siebe, and A. Islas. 2002. Patterns of beta-diversity in a Mexican tropical dry forest. *Journal of Vegetation Science* 13:145–158.
- Baraloto, C., and D. E. Goldberg. 2004. Microhabitat associations and seedling bank dynamics in a neotropical forest. *Oecologia* 141:701–712.
- Barone, J. A. 1998. Effects of light availability and rainfall on leaf production in a moist tropical forest in central Panama. *Journal of Tropical Ecology* 14:309–321.
- Becker, P., P. E. Rabenold, J. R. Idol, and A. P. Smith. 1988. Water potential gradients for gaps and slopes in a Panamanian tropical moist forests dry season. *Journal of Tropical Ecology* 4:173–184.

- Bunker, D. E., and W. P. Carson. 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. *Journal of Ecology* 93:794–806.
- Cao, K. F. 2000. Water relations and gas exchange of tropical saplings during a prolonged drought in a Bornean heath forest, with reference to root architecture. *Journal of Tropical Ecology* 16:101–116.
- Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. HilleRisLambers, J. Lichten, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. Interpreting recruitment limitation in forests. *American Journal of Botany* 86:1–16.
- Comita, L. S., S. Aguilar, R. Perez, S. Lao, and S. P. Hubbell. 2007a. Patterns of woody plant species abundance and diversity in the seedling layer of a tropical forest. *Journal of Vegetation Science* 18:163–174.
- Comita, L. S., R. Condit, and S. P. Hubbell. 2007b. Developmental changes in habitat associations of tropical trees. *Journal of Ecology* 95:482–492.
- Condit, R. 1998. *Tropical forest census plots*. Springer-Verlag, Berlin, Germany.
- Condit, R., S. P. Hubbell, and R. B. Foster. 1995. Mortality rates of 205 Neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65:419–439.
- Crawley, M. J. 2002. *Statistical computing: an introduction to data analysis using S-Plus*. John Wiley and Sons, West Sussex, UK.
- Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California, USA.
- Daws, M. I., C. E. Mullins, D. Burslem, S. R. Paton, and J. W. Dalling. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil* 238:79–90.
- Denslow, J. S., A. M. Ellison, and R. E. Sanford. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. *Journal of Ecology* 86:597–609.
- Dixon, W. J., and F. J. Massey. 1969. *Introduction to statistical analysis*. McGraw-Hill, New York, New York, USA.
- Engelbrecht, B. M. J., L. S. Comita, R. Condit, T. A. Kursar, M. T. Tyree, B. L. Turner, and S. P. Hubbell. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447:80–82.
- Engelbrecht, B. M. J., and T. A. Kursar. 2003. Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia* 136:383–393.
- Evans, G. C. 1972. *The quantitative analysis of plant growth*. University of California Press, Berkeley, California, USA.
- Fine, P. V. A., I. Mesones, and P. D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305:663–665.
- Fisher, B. L., H. F. Howe, and S. J. Wright. 1991. Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understory. *Oecologia* 86:292–297.
- Gerhardt, K. 1996. Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management* 82:33–48.
- Gibbons, J. M., and D. M. Newbery. 2003. Drought avoidance and the effect of local topography on trees in the understory of Bornean lowland rain forest. *Plant Ecology* 164:1–18.
- Givnish, T. J. 1999. On the causes of gradients in tropical tree diversity. *Journal of Ecology* 87:193–210.
- Harms, K. E., R. Condit, S. P. Hubbell, and R. B. Foster. 2001. Habitat associations of trees and shrubs in a 50-ha Neotropical forest plot. *Journal of Ecology* 89:947–959.
- Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutierrez, and G. M. J. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology and Evolution* 16: 89–94.
- Hubbell, S. P., and R. B. Foster. 1983. Diversity of canopy trees in a Neotropical forest and implications for conservation. Pages 25–41 in S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. *Tropical rain forest: ecology and management*. Blackwell Scientific, Oxford, UK.
- Huete, A. R., K. Didan, Y. E. Shimabukuro, P. Ratana, S. R. Saleska, L. R. Hutya, W. Z. Yang, R. R. Nemani, and R. Myneni. 2006. Amazon rainforests green-up with sunlight in dry season. *Geophysical Research Letters* 33:L06405.
- Hulme, M., and D. Viner. 1998. A climate change scenario for the tropics. *Climatic Change* 39:145–176.
- IPCC [Intergovernmental Panel on Climate Change]. 2007. *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- John, R., J. W. Dalling, K. E. Harms, J. B. Yavitt, R. F. Stallard, M. Mirabello, S. P. Hubbell, R. Valencia, H. Navarrete, M. Vallejo, and R. B. Foster. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences (USA)* 104:864–869.
- Kobe, R. K. 1999. Light gradient partitioning among tropical tree species through differential seedling mortality and growth. *Ecology* 80:187–201.
- Leigh, E. G. J. 1999. *Tropical forest ecology: a view from Barro Colorado Island*. Oxford University Press, Oxford, UK.
- Lewis, S. L., and E. V. J. Tanner. 2000. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. *Ecology* 81:2525–2538.
- Marod, D., U. Kutintara, H. Tanaka, and T. Nakashizuka. 2002. The effects of drought and fire on seed and seedling dynamics in a tropical seasonal forest in Thailand. *Plant Ecology* 161:41–57.
- McLaren, K. P., and M. A. McDonald. 2003. Seedling dynamics after different intensities of human disturbance in a tropical dry limestone forest in Jamaica. *Journal of Tropical Ecology* 19:567–578.
- Montgomery, R. A., and R. L. Chazdon. 2002. Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia* 131:165–174.
- Mulkey, S. S., and S. J. Wright. 1996. Influence of seasonal drought on the carbon balance of tropical forest plants. Pages 187–216 in A. P. Smith, S. S. Mulkey, and R. L. Chazdon, editors. *Tropical forest plant ecophysiology*. Chapman and Hall, New York, New York, USA.
- Nakagawa, M., et al. 2000. Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16:355–367.
- Nepstad, D., P. Lefebvre, U. L. Da Silva, J. Tomasella, P. Schlesinger, L. Solorzano, P. Moutinho, D. Ray, and J. G. Benito. 2004. Amazon drought and its implications for forest flammability and tree growth: a basin-wide analysis. *Global Change Biology* 10:704–717.
- Paine, C. E. T., K. E. Harms, and J. Ramos. 2009. Supplemental irrigation increases seedling performance and diversity in a tropical forest. *Journal of Tropical Ecology* 25: 171–180.
- Paine, C. E. T., K. E. Harms, S. A. Schnitzer, and W. P. Carson. 2008. Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica* 40:432–440.
- Palmiotto, P. A., S. J. Davies, K. A. Vogt, M. S. Ashton, D. J. Vogt, and P. S. Ashton. 2004. Soil-related habitat specialization in dipterocarp rain forest tree species in Borneo. *Journal of Ecology* 92:609–623.
- Paoli, G. D., L. M. Curran, and D. R. Zak. 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *Journal of Ecology* 94:157–170.
- Potts, M. D. 2003. Drought in a Bornean everwet rain forest. *Journal of Ecology* 91:467–474.

- Russo, S. E., S. J. Davies, D. A. King, and S. Tan. 2005. Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology* 93: 879–889.
- Slik, J. W. F. 2004. El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia* 141:114–120.
- Svenning, J. C., T. Fabbro, and S. J. Wright. 2008. Seedling interactions in a tropical forest in Panama. *Oecologia* 155: 143–150.
- Tanner, E. V. J., and I. M. Barberis. 2007. Trenching increased growth, and irrigation increased survival of tree seedlings in the understorey of a semi-evergreen rain forest in Panama. *Journal of Tropical Ecology* 23:257–268.
- Timmermann, A., J. Oberhuber, A. Bacher, M. Esch, M. Latif, and E. Roeckner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* 398:694–697.
- Turner, I. M. 1990. The seedling survivorship and growth of 3 Shorea species in a Malaysian tropical rain forest. *Journal of Tropical Ecology* 6:469–478.
- Valencia, R., R. B. Foster, G. Villa, R. Condit, J. C. Svenning, C. Hernandez, K. Romoleroux, E. Losos, E. Magard, and H. Balslev. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92:214–229.
- Van Bael, S. A., and J. D. Brawn. 2005. The direct and indirect effects of insectivory by birds in two contrasting Neotropical forests. *Oecologia* 143:106–116.
- Veenendaal, E. M., M. D. Swaine, V. K. Agyeman, D. Blay, I. K. Abebrese, and C. E. Mullins. 1996. Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology* 84:83–90.
- Walsh, R. P. D. 1996. Climate. Pages 159–205 in P. W. Richards, editor. *The tropical rain forest: an ecological study*. Cambridge University Press, Cambridge, UK.
- Webb, C. O., and D. R. Peart. 2000. Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* 88:464–478.
- Whitmore, T. C. 1984. *Tropical rainforests of the Far East*. Second edition. Clarendon Press, Oxford, UK.
- Wolda, H. 1988. Insect seasonality: Why? *Annual Review of Ecology and Systematics* 19:1–18.
- Wright, S. J. 2005. The El Niño Southern Oscillation influences tree performance in tropical rainforests. Pages 295–312 in E. Bermingham, C. W. Dick, and C. Moritz, editors. *Tropical rainforests: past, present, and future*. University of Chicago Press, Chicago, Illinois, USA.
- Yamada, T., P. A. Zuidema, A. Itoh, T. Yamakura, T. Ohkubo, M. Kanzaki, S. Tan, and P. S. Ashton. 2007. Strong habitat preference of a tropical rain forest tree does not imply large differences in population dynamics across habitats. *Journal of Ecology* 95:332–342.
- Yavitt, J. B., and S. J. Wright. 2008. Seedling growth responses to water and nutrient augmentation in the understorey of a lowland moist forest, Panama. *Journal of Tropical Ecology* 24:19–26.
- Zens, M. S., and D. R. Peart. 2003. Dealing with death data: individual hazards, mortality and bias. *Trends in Ecology and Evolution* 18:366–373.

APPENDIX A

Weather and environmental conditions during the study period (*Ecological Archives* E090-195-A1).

APPENDIX B

Study species, their habitat associations, and experimentally assessed drought sensitivity (*Ecological Archives* E090-195-A2).

APPENDIX C

Results of individual seedling survival and growth analyses (*Ecological Archives* E090-195-A3).