

Drought stress and tropical forest woody seedlings: effect on community structure and composition

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Summary

1 We hypothesized that severe drought affects the structure of tropical forests by favouring seedlings of some species or groups at the expense of others. To test this hypothesis, we irrigated naturally occurring woody seedlings during an El Niño-related drought in seasonal moist tropical forest on Barro Colorado Island, Panama. We predicted that irrigated plots would retain greater species richness than control plots, and that the benefits of irrigation would increase with the abundance of: trees relative to lianas, wet-forest seedlings relative to dry-forest seedlings, and rare species relative to common species. We also hypothesized that the strength of this filter would increase with increased moisture limitation, predicting that the benefits of irrigation would increase with seedling density and light availability, and decrease with mean seedling age.

2 Irrigation did reduce species losses, but not by limiting the loss of drought-sensitive species as predicted. Instead, mortality in irrigated plots was density dependent, whereas species losses in control plots were well predicted by random thinning, suggesting that density dependence weakened as abiotic stress increased.

3 Irrigation increased seedling growth, but did not affect seedling mortality. Contrary to our predictions, irrigation increased growth in plots dominated by dry-forest species relative to those dominated by wet-forest species, suggesting that dry-forest seedlings either occur in moisture-limited microsites or are more able to utilize dry-season precipitation. The strength of the filter did increase with potential moisture limitation, as irrigation increased seedling growth more in higher light environments.

4 Annual precipitation has declined over much of the humid tropics during the 20th century. Our results suggest that this trend may reduce tropical forest diversity by weakening density-dependent mechanisms that maintain diversity. In addition, plots dominated by dry-forest species experienced higher growth in response to irrigation and also far lower dry-season mortality relative to plots dominated by wet-forest species. While we cannot disentangle the effects of microsite from species composition, these results suggest that dry-forest species may benefit from any increase in dry season length or severity.

5 Research conducted during ‘normal’ conditions may overlook the impact of severe events and thus fail to identify critical mechanisms structuring ecological communities.

Key-words: Barro Colorado Island, density dependence, drought, El Niño, irrigation, maintenance of diversity, niche differentiation, rare events, seedling growth and mortality, tropical forest dynamics

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Introduction

The structure and composition of tropical forests change dramatically with increasing precipitation. Overall plant diversity increases with annual precipitation, and liana diversity and abundance decrease (Gentry & Emmons 1987; Gentry 1988; Gentry 1991). However, many have argued that total annual precipitation is not the proximate cause for these relationships, but rather that dry-season duration and severe drought limit species ranges (Gentry & Emmons 1987; Gentry 1988; Wright 1992; Clinebell *et al.* 1995; Condit 1998; Condit *et al.* 2004). Indeed, tropical forest community composition often responds strongly to severe drought (Condit *et al.* 1995, 1996; Nakagawa *et al.* 2000; Laurance & Williamson 2001; Delissio & Primack 2003). Investigations of community dynamics conducted during average conditions may miss these rare but critical extreme events.

Severe drought may act as a filter by eliminating species that are not drought tolerant, and rare species may be more susceptible to severe drought if their rarity is a consequence of narrow environmental niches (Bazzaz 1998). For example, Condit *et al.* (2004) found that two forests at opposite ends of a strong precipitation gradient across the Panamanian isthmus share only 47 of 384 total species, despite being only 55 km apart. This suggests either that many species have clear habitat affinities (Bazzaz 1998; Clark *et al.* 1998) with respect to precipitation or that species are strongly dispersal-limited (Hubbell 2001). Severe drought may also change forest structure by favouring lianas at the expense of trees. Liana abundance peaks in tropical dry forest and declines with increasing precipitation (Gentry 1991; Schnitzer & Bongers 2002). Lianas may be better equipped to tolerate drought because reduced allocation to stems may allow increased allocation to roots (Putz 1983). Lianas strongly influence forest dynamics because they increase the average size of forest gaps, affect slow-growing tree species more than fast-growing pioneers, alter gap-phase succession, and constitute c. 25% of woody species richness in many tropical forests (Croat 1978; Putz 1984; Clark & Clark 1990; Gentry 1991; Appanah *et al.* 1993; Schnitzer & Carson 2000; Schnitzer *et al.* 2000; Schnitzer & Bongers 2002).

While the relationships between precipitation gradients and community structure and composition are well known, the specific mechanisms causing them are not. We argue that severe drought is more likely to stress or kill seedlings, rather than adults, because of their poorly developed root systems (Wright 1992; Coomes & Grubb 2000; Wright 2002). Furthermore, seedling recruitment is often considered the critical stage in forest dynamics, because of the greater susceptibility of seedlings, rather than trees, to the myriad inimical forces acting upon them and because canopies are composed of individuals that have passed through this vulnerable seedling stage (Harper 1977; Wright 1992, 2002). In spite of the importance of seedlings in forest dynamics, most research efforts have focused on the effects of drought on

larger size classes (Condit *et al.* 1995, 1996; Wright *et al.* 1999; Nakagawa *et al.* 2000; Laurance & Williamson 2001), and few have focused on seedlings (Gilbert *et al.* 2001; Engelbrecht *et al.* 2002; Delissio & Primack 2003; Engelbrecht & Kursar 2003). Surprisingly, the community-level effects of drought on tropical woody seedlings have never, to our knowledge, been experimentally tested.

A number of factors including seedling density, seedling age and light availability, are likely to magnify the impact of severe drought on woody seedlings (Fisher *et al.* 1991; Poorter & Hayashida-Oliver 2000; Delissio & Primack 2003). Young seedlings may be more susceptible to drought than older seedlings, which have had more time to develop larger root systems, buffering them against drought. Many studies have shown that mortality is very high for young seedlings and declines with age (Garwood 1983; De Steven 1994; Connell & Green 2000; Gilbert *et al.* 2001; Delissio & Primack 2003). Light is likely to be the most limiting factor at very low light intensities in the understorey, and therefore soil moisture should become relatively more limiting as light availability increases (Bazzaz & Pickett 1980; Coomes & Grubb 2000; but note that soil moisture also increases with light availability, Vitousek & Denslow 1986; Becker *et al.* 1988). Because of the strong asymmetries in size between adults and seedlings, seedlings are likely to compete not with each other, but rather with the overstorey (Coomes & Grubb 2000). Indeed, a lack of competition between seedlings has been suggested as a mechanism for the maintenance of diversity in tropical forests, as competitive exclusion cannot occur without competition (Wright 2002). During severe drought, however, seedlings may compete with each other, and this may intensify with increasing seedling density.

In this study, we capitalized on several factors to test experimentally the community level effects of severe drought, by irrigating naturally occurring woody seedlings during the 1997–98 El Niño-related drought. We addressed two broad hypotheses, each with several specific predictions. First, we hypothesized that severe drought structures the diversity and composition of tropical forests by affecting growth and mortality of some species more than others. We predicted that irrigation would decrease mortality and increase growth: (a) in plots dominated by seedlings of species associated with Panama's wet Atlantic coast more than in plots dominated by seedlings of species associated with the dry Pacific coast; (b) in plots dominated by seedlings of rare species more than in plots dominated by seedlings of common species; and (c) in plots dominated by seedlings of trees more than in plots dominated by seedlings of lianas. We also predicted (d) that irrigation would reduce species losses compared with control plots. Secondly, we hypothesized that the effects of severe drought will increase with factors that exacerbate moisture limitation. Specifically, irrigation will decrease mortality and increase growth: (a) in plots with high

seedling densities more than in plots with low seedling densities; (b) in plots dominated by young seedlings more than in plots dominated by older seedlings; and (c) in plots with higher light availability more than in plots with lower light availability.

Materials and methods

STUDY SITE

We conducted this research in moist tropical forest on Barro Colorado Island (BCI) in the Republic of Panama. Precipitation on BCI averages *c.* 2600 mm y^{-1} , with a pronounced dry season from mid-December through mid-April (Windsor 1990). Detailed descriptions of the study site can be found in Croat (1978) and Leigh *et al.* (1996). We conducted the study on Poacher's peninsula, located on the south side of BCI, which consists of old growth forest that has been relatively undisturbed for more than 500 years (Piperno 1990).

THE 1997–98 EL NIÑO

The El Niño–Southern Oscillation has strong effects on global climate, bringing reduced annual rainfall to much of the humid tropics (Ropelewski & Halpert 1987; Aceituno 1988; Kiladis & Diaz 1989; Dai & Wigley 2000; Diaz *et al.* 2001; New *et al.* 2001; Malhi & Wright 2004). On BCI, El Niño events are associated with reduced precipitation during both the wet season and the early dry season (Kiladis & Diaz 1989; Dai & Wigley 2000; Diaz *et al.* 2001). The 1997–98 El Niño event was one of the strongest on record (Timmermann *et al.* 1999; Fedorov & Philander 2000), and was associated with sharply reduced wet season precipitation and a longer and drier dry season on BCI (Fig. 1), although it was not as long and dry as the 1982–83 event (Windsor 1990; S. Paton, unpublished data). The dry season is defined as the period when precipitation is less than potential evapotranspiration, which is commonly estimated to be *c.* 100 mm $month^{-1}$ for humid tropical forests (Koppen 1931; Shuttleworth 1989; Condit 1998; Hulme & Viner 1998; Malhi *et al.* 2002). By this measure, the 1998 dry season was 19 weeks long, nearly 4 weeks longer than the 1930–2001 average, and one of 11 years during this period with a dry season of 19 or more weeks (Windsor 1990; S. Paton, unpublished data).

EXPERIMENTAL DESIGN

Exclosures

Since 1994, an ongoing exclosure project (W. Carson, unpublished data) has excluded ground-dwelling mammals from eight (30 × 45 m) permanent plots on BCI and nearby Gigante Peninsula. Excluding mammals has caused a twofold increase in mean seedling density inside the two exclosures on Poachers Peninsula relative to the paired control plots (23 vs. 44 individuals m^{-2}).

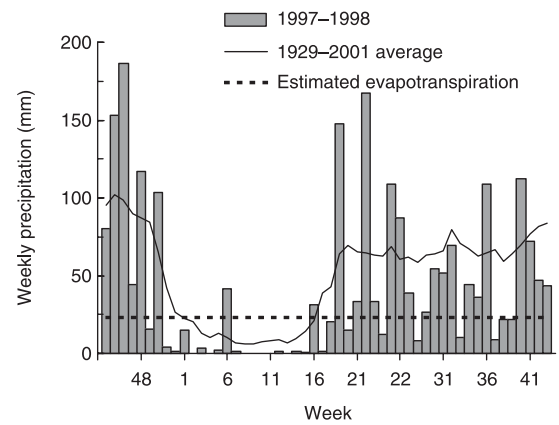


Fig. 1 Weekly precipitation (mm) on Barro Colorado Island, Panama, during the period 15 October 1997 to 14 October 1998 and average weekly precipitation between 1929 and 2001. The 1997–98 El Niño was associated with below average rainfall and an extended dry season, defined as the period when cumulative monthly rainfall does not exceed estimated evapotranspiration (100 mm $month^{-1}$, 23 mm $week^{-1}$, Condit 1998). Data collected by the Terrestrial Environmental Sciences Programme, Smithsonian Tropical Research Institute (Windsor 1990, S. Paton, Unpublished data).

Plot layout

We established 96 (1 m^2) seedling plots, 24 within each of two exclosure plots and two control plots. The seedling plots were randomly placed around the edge of the exclosure or control plot, 2 m from the plot perimeter and at least 2 m from each other. During plot establishment, four plots with fewer than six seedlings were discarded and replaced by additional plots.

Irrigation treatments

We irrigated the seedling plots at three levels (0, 30 and 120 mm $month^{-1}$), designed to mimic severe dry-season conditions (0), typical dry-season precipitation (30), and minimal wet-season precipitation (120) (Windsor 1990; S. Paton, unpublished data). Hereafter we refer to these levels as control, moderate irrigation and high irrigation. Irrigation began in early January 1998 and ceased in early May 1998. Irrigation water was drawn from Gatun Lake, which typically has lower nutrient concentrations than rainwater on BCI (Gonzalez *et al.* 1975; Wright & Cornejo 1990), and gently applied with a low-pressure hose fitted with a watering wand. The irrigated area included the 1 × 1 m seedling plot and a 0.25 m buffer around each plot (2.25 m^2). We irrigated the moderate irrigation plots once each week and the high irrigation plots twice each week. Because our plots were relatively small, the high irrigation treatment probably did not fully mimic true wet-season soil moisture status due to both evaporation and competition for soil moisture from neighbouring overstorey trees. Indeed, while we have no direct observations of soil moisture or plant water status, a similar experiment found that some seedlings wilted even with 193 mm $month^{-1}$ dry season irrigation (Engelbrecht & Kursar 2003).

We assigned the irrigation treatments in a stratified manner with respect to seedling density. Within each main plot, we ranked the 24 seedling plots by density, and randomly assigned one of each of the three irrigation treatments to the three most dense plots, then one of each of the treatments to the three next most dense, until irrigation treatments had been assigned to all plots. One high irrigation plot was mistakenly labelled as a control plot and not irrigated, and thus is included in the analyses as a control plot. One moderate irrigation plot was completely destroyed by a fallen snag and thus was excluded from the analyses, resulting in 33 control plots, 31 moderate irrigation plots and 31 high irrigation plots.

Censuses

We censused the seedlings in December 1997 before irrigation commenced. For every individual less than 1.0 m tall, we recorded its height and number of true leaves, and identified it to species. We censused a total of 3053 individual seedlings and identified more than 96% to species (130 species total), resulting in 2931 individuals with complete data. Only those seedlings with complete data were included in the analyses. We re-censused all seedlings encountered in the first census once after we ceased irrigating at the end of the dry season in May 1998, and again in December 1998 at the end of the following wet season. For the second and third censuses we ignored newly germinated seedlings.

RESPONSE VARIABLES

During the second and third censuses we recorded mortality and counted the number of leaves on each seedling. We used a standard exponential growth model to calculate relative growth rate in number of leaves (RGR, leaves leaf⁻¹ month⁻¹) as: $RGR = (\log_e(L_{t_2}) - \log_e(L_{t_1})) / (t_2 - t_1)$, where L is number of leaves and t_1 and t_2 are the beginning and end, respectively, of the census interval in months (Evans 1972). Number of leaves is considered a reasonable measure of seedling size (Flores 1992; Burslem *et al.* 1996; Poorter & Hayashida-Oliver 2000; Gilbert *et al.* 2001), and thus of growth rate. In contrast, relative change in seedling height is a poor measure of growth rate because change in height is likely to be small relative to measurement error over our relatively short census interval. To avoid zero values when log-transforming leaf number, we added 0.5 leaves to each census for all individuals with zero leaves at either the first or second census, prior to calculating relative growth rate. The vast majority of these individuals were seedlings with only cotyledons but no true leaves, and we assumed that cotyledons were equivalent to 0.5 leaves. As seedlings with true leaves have typically senesced their cotyledons (D. Bunker, personal observation), we added 0.5 only to seedlings with cotyledons but no true leaves. We concluded that individuals were dead if they had lost all true leaves, with the

exception of seven individuals that had no leaves at the end of the dry season but did have leaves at the end of the wet season. We calculated monthly mortality per plot as: $m = 1 - (N_1/N_0)^{1/t}$, where N_1 is the number of surviving seedlings, N_0 is the initial number of seedlings, and t is the census interval in months (30 days) (Sheil *et al.* 1995).

COVARIATES

We included in the analyses six covariates to test the specific predictions outlined above.

Geographic affinity

We measured geographical affinity based on data collected from two permanent plots, one on the wet Atlantic side of Panama at Fort Sherman, and the other on the dry Pacific side at Cocoli. Precipitation at Fort Sherman averages roughly 3030 mm year⁻¹, Cocoli averages 1950 mm year⁻¹, and BCI averages 2616 mm year⁻¹ (Condit *et al.* 2004). Free-standing woody stems > 10 mm diameter at breast height (d.b.h.) were censused in plots of 4 ha at Cocoli and 4.96 ha at Fort Sherman (Condit *et al.* 2004). Lianas > 1 m tall were censused in nine 100-m² plots within each of the above plots at Fort Sherman and Cocoli (S. Schnitzer, unpublished data). Our affinity metric is simply the proportion of total stem density for each species found at Fort Sherman: Affinity = Fort Sherman density / (Fort Sherman density + Cocoli density). Thus species found only at Fort Sherman have an affinity of 1.0 (wet Atlantic affinity), whereas species found only at Cocoli have an affinity of 0.0 (dry Pacific affinity). Species found at neither site, but occurring on BCI, were assigned an affinity of 0.5. Average affinity within seedling plots ranged from 0.10 to 0.93 (mean ± 1 SE: 0.60 ± 0.018, $n = 95$).

Abundance

As a measure of species' commonness or rarity at the landscape level, we used stems > 10 mm d.b.h. per hectare based on 1990 stem density in the BCI 50-ha plot for trees (Condit *et al.* 1996), and stem density in 16 864 m² sampling plots on BCI and nearby Gigante Peninsula for lianas (S. Schnitzer and W. Carson, unpublished data). Average abundance within plots ranged from 12 to 146 (mean ± 1 SE: 45 ± 2.2, $n = 95$).

Growth form

We categorized seedlings into two growth forms: lianas and trees, based on Croat (1978). We included seedlings of all woody species, but excluded all herbaceous seedlings, which were not common. Within seedling plots the average proportion of individual seedlings that were lianas ranged from 0% to 100% (mean ± 1 SE: 23 ± 1.7%, $n = 95$).

Seedling density

Seedling density is the total number of seedlings < 1 m tall in each 1-m² seedling plot, and ranged from 6 to 176 (mean \pm 1 SE: 32 \pm 3.1, n = 95). We log transformed seedling density to normalize the data. We should note here that seedling density and the mammal exclosures are correlated. Because of this collinearity we could not include both effects in the statistical analyses, and any interpretation of the effect of seedling density must include the potential confounding of the exclosure effect. However, we found no effect of increasing seedling density on seedling mortality or growth (see Results).

Seedling age

During the first census we categorized individual seedlings as less than 1 year old vs. seedlings older than 1 year based on seedling condition and our experience re-censusing over 20 000 seedlings of known age on BCI. Within seedling plots the proportion of seedlings that were older than 1 year ranged from 5% to 100% (mean \pm 1 SE: 50 \pm 2.3%, n = 95).

Light availability

In April 1998, during the middle of the dry season, we measured light availability as diffuse non-interceptance of photosynthetically active radiation (Parent & Messier 1996) under homogeneous skies at four evenly spaced locations 25 cm above each seedling plot, using an LAI-2000 canopy analyser (Li-Cor Inc., Lincoln, Nebraska, USA). We then divided each reading by a simultaneously collected above-canopy measurement, and averaged the four measurements for each plot. Light transmission ranged from 0.7% to 5.5% of ambient (mean \pm 1 SE: 2.6 \pm 0.1%, n = 95).

STATISTICAL ANALYSES

To quantify the main effect of irrigation and interactions between the covariates and irrigation we used a maximum likelihood, mixed-model ANCOVA with SAS/STAT Proc Mixed, Version 6.12 (SAS Institute, Cary, North Carolina, USA; Littell *et al.* 1996). Because the individual seedlings within our 1-m² seedling plots are not independent, we used mean mortality (m) and mean RGR for each seedling plot as our response variables. For covariates that vary at the seedling level (age, growth form, geographical affinity and abundance), we used the mean value (for affinity) or the proportion sharing the characteristic (e.g. proportion of seedlings that were older) within each seedling plot for the analysis. We also included the effect of season as a repeated measure.

We analysed relative growth and mortality separately, and included only surviving seedlings in growth analyses. For both models, we used a backwards elimination approach to determine minimally adequate models (Littell *et al.* 1996; Kleinbaum *et al.* 1998; Crawley 2002).

We began with a full model that included the main effects of irrigation, season and the six covariates, as well as all two-way and three-way interactions between each covariate and irrigation and season. Note that we did not include any interactions between the covariates. We also included a random effect for location (the four exclosure and control plots). To account for the repeated measures nature of the design (dry-season and wet-season responses for each seedling plot), we also included a random effect for each seedling plot (Littell *et al.* 1996). We then sequentially removed non-significant ($P > 0.05$) covariates and their interactions, retaining all effects contained within significant higher order terms. We log-transformed abundance and seedling density to normalize the data, and verified the assumptions of normality and homogeneity of variance through visual inspection of normal probability plots and residuals. Percentage mortality for each seedling plot was arcsin-square-root transformed prior to analysis, and adjusted means were back-transformed prior to presentation in figures (Sokal & Rohlf 1995).

This ANCOVA approach allows us to test our hypotheses – that severe drought has the potential to alter community composition and that the effects of drought increase with increasing potential moisture limitation – specifically by identifying significant interactions between irrigation and the covariate in question. A significant interaction demonstrates that the response (growth or mortality) changes disproportionately between irrigation treatments as the covariate changes in value (i.e. the slopes differ between irrigation treatments). For instance, if irrigation increases growth or survivorship more at higher light availability than at low light availability, we can conclude that the relative impact of moisture limitation increases as light availability increases. Where the ANCOVA found significant interactions between irrigation and season and/or a covariate, we used orthogonal contrasts between the control treatment and the moderate and high irrigation treatments at two or more values of the covariate to determine the nature of the interaction (Sokal & Rohlf 1995; Littell *et al.* 1996).

To test the hypothesis that irrigation would increase species richness, we used a randomization test (Sokal & Rohlf 1995) to compare actual loss of species per plot due to mortality with predicted loss based on a random thinning model. Non-random thinning can alter species richness in two ways. First, if individuals of more common species (within a seedling plot) are more likely to die than individuals of less common species, then species loss will be lower than predicted by random thinning. This result would agree with observations of negative density dependence often invoked as a mechanism for the maintenance of diversity in tropical forests (Janzen 1970; Connell 1971; Clark & Clark 1984; Hubbell *et al.* 1990; Condit *et al.* 1992; Wills *et al.* 1997; Harms *et al.* 2000). Alternatively, individuals of particular species or less common species may be more likely to die, which would result in greater species loss

than predicted by random thinning. We calculated mean proportional species loss (dS) as $dS = (\Sigma(S_{i,t_2}/S_{i,t_1}))/n$, where S is the number of species in plot i at the beginning (t_1) or end (t_2) of the dry season, and n is the number of seedling plots in the irrigation treatment. We constructed a null model for the expected distribution of mean proportional species loss for each irrigation treatment by randomly thinning individuals from each plot at the observed mortality rate within each plot, calculating mean dS among plots within each treatment, and repeating this process 10 000 times. By randomizing within plots, this null model incorporates intrinsic differences between plots, such as number of individuals, species richness and evenness. We concluded that treatment effects on species richness were significant when our actual mean dS was beyond 95% of means (two-tailed) calculated from this null model.

COMMUNITY RESPONSES AND THE EFFECT OF COMMON SPECIES

Because we wanted to test the community level response to dry-season soil moisture availability, we irrigated naturally occurring seedlings and thus did not control the abundance of individual species. Thus, our results are not the response of, for instance, the average liana species or average tree species, but rather are the mean of seedling responses within a given seedling plot. Because we did not manipulate initial seedling composition, our results must be interpreted with care: the composition of a given seedling plot and its response to irrigation may be correlated, yet not causally connected.

As in many tropical forests, a few species in our study were common (Table 1), whereas the majority of species were uncommon. Indeed, the relative abundance curve for our study (not shown), closely resembles that of the BCI 50-ha plot (Hubbell 2001). To gauge the effect of common species on our results, we removed the 10 most frequent species and applied the minimally adequate ANCOVA models to seedling plot means calculated using the remaining individuals, and found our results to be robust to the omission of common species (results not shown). We also present growth and mortality for the 10 most frequent species in our study, calculated for each species as the mean and standard error of growth and mortality in the seedling plots where the species occurred (Table 1).

Results

LEAF RELATIVE GROWTH RATE

Irrigation during the dry season significantly increased dry-season relative growth, but had no effect on subsequent wet-season growth after irrigation ceased (Table 2, Fig. 2a). Irrigation significantly increased dry-season growth in plots dominated by seedlings associated with the Pacific coast (dry-forest seedlings), but significantly decreased growth in plots dominated by seedlings asso-

ciated with the Atlantic coast (wet-forest seedlings) (Table 2, Fig. 2c). Plots dominated by wet-forest seedlings always had mean growth rates below 0 during the dry season (Fig. 2c). During the wet season, average growth did not vary significantly with geographical affinity in any of the irrigation treatments (Fig. 2d). Irrigation significantly increased dry-season growth in plots dominated by young seedlings but decreased growth in plots dominated by older seedlings (Table 2, Fig. 2e). Wet-season growth declined as the proportion of older seedlings increased, but did not vary significantly with irrigation treatment (Fig. 2f). Light availability interacted significantly with irrigation and season (Table 2). Dry-season seedling growth increased significantly with light availability in the high irrigation treatment (Table 2, Fig. 2g), while wet-season growth increased significantly with light availability in the moderate irrigation treatment (Fig. 2h). In control plots, seedling growth rate did not increase significantly with increasing light availability during either season (Fig. 2g,h). Growth form did not interact significantly with irrigation but did interact with season (Table 2): dry-season growth rate significantly decreased as the proportion of liana seedlings increased, but wet-season growth did not change significantly (Fig. 2b). Mean abundance and seedling density had no significant effect on seedling RGR, and did not interact significantly with irrigation (Table 2).

MORTALITY

Irrigation did not significantly reduce mean seedling mortality (although the interaction between irrigation and season was marginally significant), nor did any of the covariates interact significantly with irrigation to affect mortality (Table 3, Fig. 3a). However, both light and affinity interacted with season to affect mortality, and age had a direct effect on mortality (Table 3). At the lowest observed light availability (< 1% of ambient), mean seedling mortality did not significantly differ between the dry and wet seasons (Table 3, Fig. 3b). However, dry-season mortality was significantly higher than wet-season mortality at higher light availability (Table 3, Fig. 3b). Mortality decreased sharply as the proportion of older seedlings within a plot increased (Table 3, Fig. 3c). In seedling plots dominated by dry-forest seedlings, mortality was equally low during both the dry and wet seasons (Table 3, Fig. 3d). However, as the proportion of wet-forest seedlings increased, dry-season mortality increased sharply, from less than 1% to more than 6% month⁻¹, while wet-season mortality did not change (Table 3, Fig. 3d). Seedling density, the proportion of seedlings that were lianas, and mean abundance had no effect on seedling mortality (Table 3).

EFFECTS ON SPECIES RICHNESS

Irrigation had a significant positive effect on species richness (Table 4). Species loss per plot under high

Table 1 Characteristics and mean responses of the 10 most frequent species (percentage of plots in which the species occurred). Mean age is the proportion of individuals > 1 year old. See ‘Methods’ for quantification of affinity and abundance. For each species, growth and mortality means for moderate and high irrigation, whose 95% confidence intervals do not overlap their respective control means, are in bold. Specific names follow Croat (1978) and Condit *et al.* (2004)

	Frequency	Growth form	Abundance	Geographic affinity	Mean age	Dry-season growth Leaves leaf ⁻¹ month ⁻¹			Wet-season growth Leaves leaf ⁻¹ month ⁻¹			Dry-season mortality % month ⁻¹			Wet-season mortality % month ⁻¹		
						Control	Dry	Wet	Control	Dry	Wet	Control	Dry	Wet	Control	Dry	Wet
<i>Trichilia tuberculata</i>	77%	Tree	266.0	0.83	0.11 0.005	0.002 0.008 24	0.024 0.009 23	0.034 0.012 20	0.053 0.010 24	0.067 0.014 23	0.058 0.068 20	0.235 0.031 23	0.092 0.052 21	0.093 0.054 20	0.238 0.065 28	0.209 0.043 23	0.149 0.043 21
<i>Prionostemma aspera</i>	66%	Liana	70.9	0.50	0.60	0.013 0.010 19	0.005 0.017 21	0.028 0.009 18	0.038 0.009 18	0.047 0.006 19	0.028 0.012 18	0.148 0.067 21	0.158 0.057 22	0.214 0.073 20	0.137 0.061 19	0.182 0.070 21	0.098 0.054 18
<i>Tetragastris panamensis</i>	58%	Tree	81.7	0.50	0.86	0.002 0.009 19	-0.008 0.007 18	0.009 0.008 17	0.024 0.010 19	0.017 0.008 18	0.027 0.007 17	0.061 0.051 20	0.000 0.000 18	0.083 0.057 17	0.141 0.048 19	0.069 0.039 18	0.132 0.057 17
<i>Faramea occidentalis</i>	44%	Tree	538.2	0.02	0.94	-0.015 0.013 17	-0.026 0.018 12	0.024 0.013 12	0.020 0.017 17	0.028 0.016 12	0.016 0.015 11	0.093 0.059 18	0.000 0.000 12	0.067 0.043 12	0.000 0.000 17	0.000 0.000 12	0.083 0.083 12
<i>Ocotea puberula</i>	44%	Tree	4.4	1.00	0.07	-0.017 0.017 8	-0.037 0.037 6	-0.028 0.015 7	0.082 0.024 3	0.058 0.021 5	0.035 0.050 3	0.639 0.111 15	0.724 0.108 13	0.592 0.121 13	0.625 0.183 8	0.278 0.181 6	0.667 0.178 7
<i>Heisteria concinna</i>	40%	Tree	19.8	0.02	0.11	0.000 0.000 5	0.023 0.017 13	0.052 0.023 14	0.035 0.019 5	0.092 0.027 11	0.102 0.024 14	0.208 0.164 6	0.224 0.101 16	0.166 0.087 16	0.000 0.000 5	0.197 0.106 13	0.045 0.036 14
<i>Pouteria reticulata</i>	38%	Tree	35.3	1.00	0.04	-0.013 0.009 12	-0.004 0.014 12	0.047 0.028 9	0.073 0.014 12	0.115 0.020 11	0.047 0.015 6	0.407 0.093 15	0.112 0.041 12	0.161 0.084 9	0.025 0.015 12	0.168 0.098 12	0.398 0.156 9
<i>Maripa panamensis</i>	32%	Liana	69.4	0.84	0.68	-0.036 0.022 10	-0.027 0.023 9	-0.077 0.051 9	0.038 0.025 8	0.024 0.016 9	0.042 0.026 8	0.107 0.091 11	0.133 0.102 10	0.000 0.000 9	0.244 0.130 10	0.000 0.000 9	0.139 0.111 9
<i>Lacmellea panamensis</i>	29%	Tree	2.0	1.00	0.74	-0.008 0.012 9	-0.005 0.006 9	-0.013 0.021 7	0.046 0.020 8	0.018 0.025 9	0.033 0.017 6	0.100 0.100 10	0.227 0.124 11	0.018 0.018 7	0.111 0.111 9	0.037 0.037 9	0.184 0.142 7
<i>Oenocarpus mapoura</i>	29%	Tree	36.0	0.99	0.61	0.001 0.001 5	0.028 0.014 12	0.030 0.016 9	0.071 0.008 5	0.005 0.016 12	0.050 0.011 9	0.182 0.164 6	0.044 0.024 12	0.117 0.100 10	0.030 0.030 5	0.059 0.042 12	0.000 0.000 9

Table 2 ANCOVA results for retained effects of irrigation, season and covariates on seedling relative growth rate. Error d.f. = 82

Source	d.f.	Type III <i>F</i>	Pr > <i>F</i>
Irrigation	2	1.69	0.1918
Season	1	1.03	0.3121
Irrigation × season	2	10.15	0.0001
Light	1	12.83	0.0006
Light × season	1	3.29	0.0733
Light × irrigation	2	0.2	0.8178
Light × irrigation × season	2	4.64	0.0123
Growth form	1	0.21	0.6464
Growth form × season	1	7.55	0.0074
Age	1	22.24	0.0001
Age × season	1	0.9	0.3451
Age × irrigation	2	1.35	0.2645
Age × irrigation × season	2	6.4	0.0026
Affinity	1	15.27	0.0002
Affinity × season	1	10.67	0.0016
Affinity × irrigation	2	2.07	0.1325
Affinity × irrigation × season	2	10.2	0.0001

irrigation was 22% lower than predicted by random thinning. In contrast, species loss per plot in the control plots was accurately predicted by random thinning. Additionally, total species loss (due to non-random thinning and a non-significant increase in mortality) was 32% lower under high irrigation than in control plots (Table 4).

Discussion

EFFECTS OF IRRIGATION AND DROUGHT ON COMMUNITY COMPOSITION AND STRUCTURE

While the effects of irrigation during severe drought did not change with the relative abundance of rare species or lianas, we did find a sharp difference in growth as the proportion of wet-forest (Atlantic) seedlings increased. We predicted that without irrigation mean seedling growth would decline as the proportion of wet-forest seedlings increased, and that irrigation would mitigate this decline. In fact, we found that without irrigation, growth rate did not change as the proportion of wet-forest seedlings increased ($P = 0.5$), yet when irrigated, growth rate declined in plots dominated by wet-forest seedlings and increased sharply in plots dominated by dry-forest seedlings (Fig. 2c). Two mechanisms may contribute to this result. First, plots dominated by seedlings associated with dry forests are likely to be in dry microsites. However, if this were the sole mechanism, we would predict that dry-season growth rate in the control plots would increase as the relative abundance of wet-forest seedlings increased (and thus moisture limitation decreased), and that irrigation would reduce this difference. Additionally, this pattern could be the result of greater plasticity of water use in dry-forest seedlings, which may be able to respond rapidly to bursts of rainfall during drought (Milnes *et al.* 1998; Silim

Table 3 ANCOVA results for retained effects of irrigation, season and covariates on mean seedling mortality. Error d.f. = 89

Source	d.f.	Type III <i>F</i>	Pr > <i>F</i>
Irrigation	2	0.27	0.7659
Season	1	4.2	0.0434
Irrigation × season	2	2.74	0.0703
Light	1	0.01	0.9360
Light × season	1	5.66	0.0195
Age	1	6.23	0.0144
Affinity	1	5.98	0.0165
Affinity × season	1	4.49	0.0369

et al. 2001; Stratton & Goldstein 2001), while wet-forest seedlings may remain dormant when faced with increased evaporative demands regardless of soil moisture availability (Wright & Cornejo 1990).

Because we did not manipulate species composition, additional experiments will be required to disentangle the effects of microsite from those of species composition. Regardless of the mechanism, our results show that plots dominated by dry-forest seedlings grew well during the dry season when irrigated (Fig. 2c), and also suffered far lower dry-season mortality than plots dominated by wet-forest seedlings (Fig. 3d). Together, these results suggest dry-season length and severity may both play a role in species segregation across precipitation gradients (Gentry & Emmons 1987; Gentry 1988; Wright 1992; Condit 1998; Condit *et al.* 2004).

IMPLICATIONS FOR RESOURCE LIMITATION

We predicted that the effects of irrigation on seedling performance would increase with potential moisture limitation. Our results supported this prediction with higher mean dry-season seedling growth under high irrigation and higher light (Table 2, Fig. 2g). This suggests that our seedlings were not limited by soil moisture in the darkest understorey environments, but that at higher light availability they were moisture limited, in spite of the fact that soil moisture also increases in gaps associated with higher light (Vitousek & Denslow 1986; Becker *et al.* 1988). Similarly, Fisher *et al.* (1991) found that light and irrigation interacted strongly to increase dry-season growth of seedlings of *Virola surinamensis*, a highly drought-sensitive tree that has a strong geographical affinity for wet forests (Howe 1990; Condit *et al.* 1996; Engelbrecht & Kursar 2003; Condit *et al.* 2004), resulting in far higher growth in irrigated gaps than in either irrigated understorey or unirrigated gaps.

Because we did not manipulate mean seedling age and seedling density, our results must be interpreted with care. For instance, while first-year seedlings are likely to experience greater moisture limitation than established seedlings, dry microsites could have fewer first-year seedlings if the prior wet season, which was the driest on record (Windsor 1990; S. Paton, unpublished

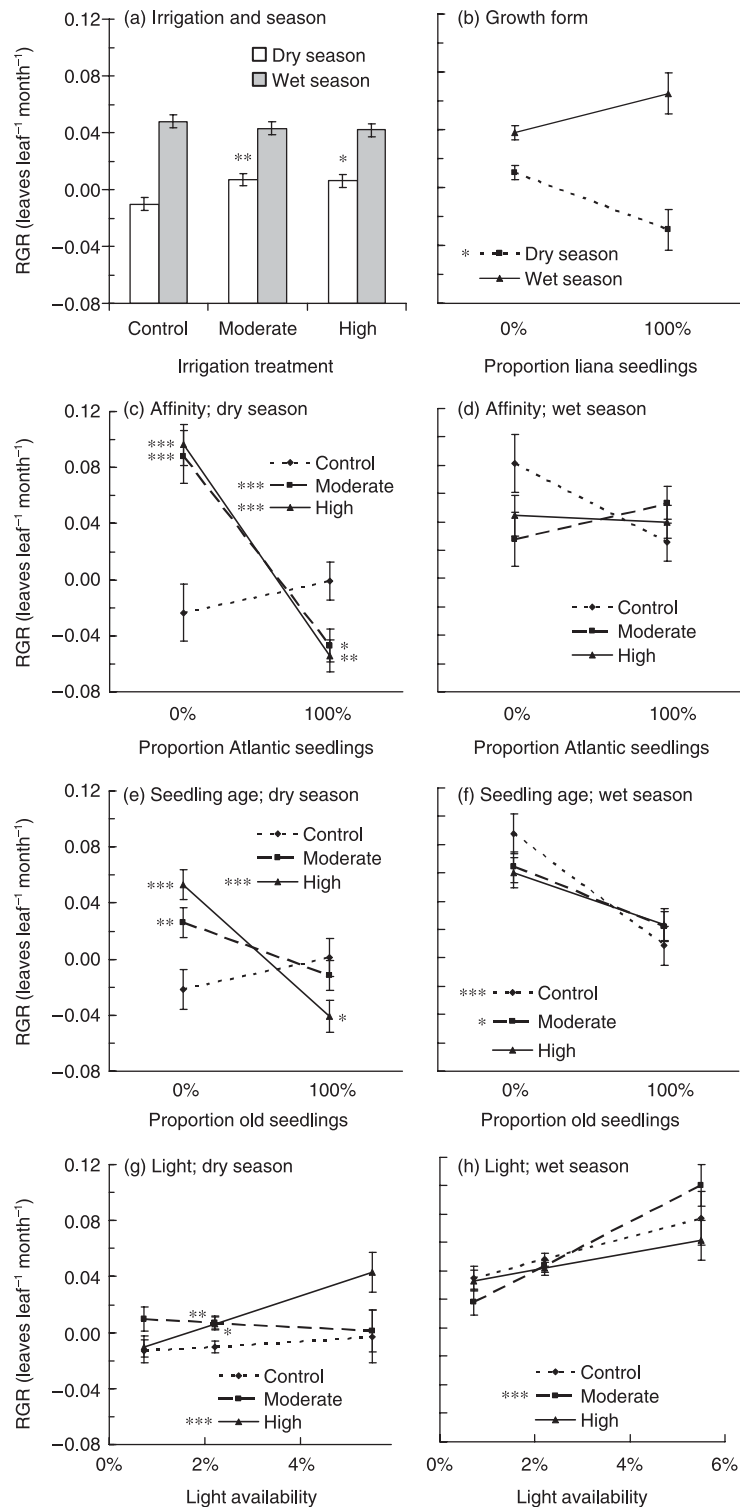


Fig. 2 Effects of irrigation, season and covariates on seedling leaf relative growth rate (adjusted means \pm SE; a, c–h: control, $n = 33$; moderate, $n = 31$; high, $n = 31$; b: $n = 95$). (a) Season and irrigation. (b) Growth form and season. (c) Geographic affinity and irrigation during the dry season. (d) Geographic affinity and irrigation during the wet season. (e) Seedling age and irrigation during the dry season (young ≤ 1 year; old ≥ 1 year). (f) Seedling age and irrigation during the wet-season. (g) Light availability and irrigation during the dry season. (h) Light availability and irrigation during the wet season. Asterisks adjacent to data points denote significant differences between irrigated plots and control plots, whereas asterisks in the key denote significant effects of the covariate within each irrigation treatment; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

data), was dry enough to limit establishment. From either scenario we would predict that seedling performance would increase with increasing mean seedling age in control plots, and that irrigation would allow both

young and old seedlings to grow equally well. In contrast to these predictions, our results show that dry-season seedling growth in control plots did not change with mean seedling age, although growth increased

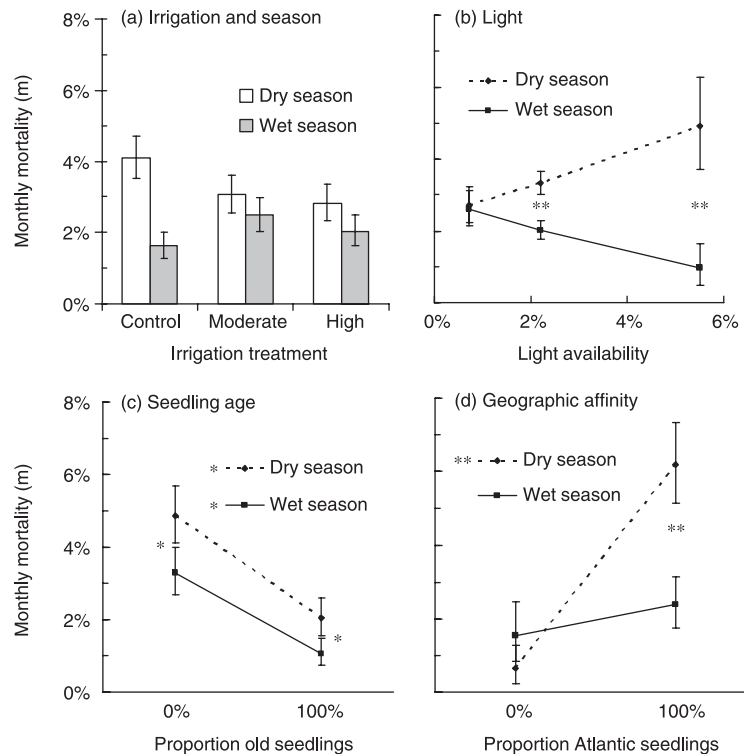


Fig. 3 Effects of irrigation, season and covariates on seedling mortality (adjusted means \pm SE; a: control, $n = 33$; moderate, $n = 31$; high, $n = 31$; b–d: $n = 95$). (a) Season and irrigation. (b) Season and light. (c) Season and seedling age (young ≤ 1 year; old ≥ 1 year). (d) Season and geographical affinity. Asterisks between two data points denote significant differences in mortality between seasons, whereas asterisks in the key denote significant effects of the covariate within season; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

sharply in response to irrigation in plots dominated by young seedlings, while growth declined in plots dominated by older seedlings (Fig. 2e). While we cannot rule out an effect of microsite, these results could be due to intrinsic differences between first-year and older seedlings. For instance, young seedlings may have larger carbon reserves (e.g. cotyledons) that allow them to utilize light and soil resources more effectively during the dry season (Kitajima 1996; Kitajima & Fenner 2000), and older seedlings may have accumulated pathogen loads that become more virulent with increased water supply (Augspurger 1984; Biles *et al.* 1992; Hampson & Coombes 1997).

RELEVANCE TO THEORIES FOR THE MAINTENANCE OF TROPICAL DIVERSITY

Because total species diversity increases with precipitation in the tropics, we predicted that irrigation would have positive effects on overall diversity within our seedling plots by reducing losses of drought-sensitive species (Gentry & Emmons 1987; Gentry 1988; Wright 1992; Condit *et al.* 2004). However, if this were the case, species losses in control plots would be non-random, and higher than predicted, as drought-sensitive species are lost. Instead, species losses were explained by random thinning in control plots, yet plots under high irrigation lost 22% fewer species than predicted by random

Table 4 Observed and expected percent reduction in mean species richness per plot under three irrigation treatments. Expected species loss was estimated from a random thinning model

Irrigation treatment	Observed mean (%)	Expected mean (%)	P
Control	13.5	13.4	0.889
Moderate	10.8	12.4	0.210
High	9.2	11.8	0.031

thinning. In the irrigated plots where the effects of drought were reduced, density-dependent mortality (Janzen 1970; Connell 1971; Clark & Clark 1984; Hubbell *et al.* 1990; Condit *et al.* 1992; Wills *et al.* 1997; Harms *et al.* 2000) appears to have had a positive effect on diversity, yet this mechanism failed to operate in the control plots that experienced severe drought. These results suggest that the strength of density-dependent mortality may decrease as abiotic stress increases.

IMPLICATIONS FOR THE EFFECTS OF GLOBAL CLIMATE CHANGE

Precipitation over tropical land masses has declined during the 20th century (Diaz *et al.* 1989; Kumar *et al.* 2004; Malhi & Wright 2004), and several recent severe

ENSO events suggest a long-term increase in ENSO activity (Trenberth & Hoar 1996, 1997; Fedorov & Philander 2000). Indeed, some global climate models predict an increase in ENSO activity (Timmermann *et al.* 1999) with increasing global temperatures, and longer dry seasons for much of the tropics (Hulme & Viner 1998). While the relationships between global warming, ENSO and precipitation trends remain contentious (Fedorov & Philander 2000; Doherty & Hulme 2002), any reduction in precipitation may affect tropical forest composition by favouring dry-forest species and decreasing overall species diversity.

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References

Aceituno, P. (1988) On the functioning of the Southern Oscillation in the South American sector. Part 1. Surface climate. *Monthly Weather Review*, **116**, 505–524.

Appanah, S., Gentry, A.H. & Lafrankie, J.V. (1993) Liana diversity and species richness of Malaysian rain forests. *Journal of Tropical Forest Science*, **6**, 116–123.

Augsburger, C.K. (1984) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology*, **72**, 777–796.

Bazzaz, F.A. (1998) Tropical forests in a future climate: changes in biological diversity and impact on the global carbon cycle. *Climatic Change*, **39**, 317–336.

Bazzaz, F.A. & Pickett, S.T.A. (1980) Physiological ecology of tropical succession: a comparative review. *Annual Review of Ecology and Systematics*, **11**, 287–310.

Becker, P., Rabenold, P.E., Idol, J.R. & Smith, A.P. (1988) Water potential gradients for gaps and slopes in a Panamanian tropical moist forest's dry season. *Journal of Tropical Ecology*, **4**, 173–184.

Biles, C.L., Lindsey, D.L. & Liddell, C.M. (1992) Control of Phytophthora root rot of chile peppers by irrigation practices and fungicides. *Crop Protection*, **11**, 225–228.

Burslem, D.F.R.P., Grubb, P.J. & Turner, I.M. (1996) Responses to simulated drought and elevated nutrient supply among shade-tolerant tree seedlings of lowland tropical forest in Singapore. *Biotropica*, **28**, 636–648.

Clark, D.A. & Clark, D.B. (1984) Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist*, **124**, 769–788.

Clark, D.B. & Clark, D.A. (1990) Distribution and effects on tree growth of lianas and woody hemiepiphytes in a Costa Rican tropical wet forest. *Journal of Tropical Ecology*, **6**, 321–331.

Clark, D.B., Clark, D.A. & Read, J.M. (1998) Edaphic variation and the mesoscale distribution of tree species in a neotropical rain forest. *Journal of Ecology*, **86**, 101–112.

Clinebell, R.R., Phillips, O.L., Gentry, A.H., Stark, N. & Zuuring, H. (1995) Prediction of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, **4**, 56–90.

Condit, R. (1998) Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climatic Change*, **39**, 413–427.

Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G. *et al.* (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology*, **20**, 51–72.

Condit, R., Hubbell, S.P. & Foster, R.B. (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist*, **140**, 261–286.

Condit, R., Hubbell, S.P. & Foster, R.B. (1995) Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs*, **65**, 419–439.

Condit, R., Hubbell, S.P. & Foster, R.B. (1996) Changes in tree species abundance in a neotropical forest: impact of climate change. *Journal of Tropical Ecology*, **12**, 231–256.

Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations* (eds P.J. den Boer & G.R. Gradwell), pp. 298–312. Center for Agricultural Publication and Documentation, Wageningen, The Netherlands.

Connell, J.H. & Green, P.T. (2000) Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology*, **81**, 568–584.

Coomes, D.A. & Grubb, P.J. (2000) Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs*, **70**, 171–207.

Crawley, M.J. (2002) *Statistical Computing: An Introduction to Data Analysis Using S-Plus*. John Wiley and Sons, Hoboken, New Jersey.

Croat, T.B. (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford.

Dai, A. & Wigley, T.M.L. (2000) Global patterns of ENSO-induced precipitation. *Geophysical Research Letters*, **27**, 1283–1286.

De Steven, D. (1994) Tropical tree seedling dynamics: recruitment patterns and their population consequences for three canopy species in Panama. *Journal of Tropical Ecology*, **10**, 369–383.

Delisio, L.J. & Primack, R.B. (2003) The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest. *Journal of Tropical Ecology*, **19**, 489–500.

Diaz, H.F., Bradley, R.S. & Eischeid, J.K. (1989) Precipitation fluctuations over global land area since the late 1800s. *Journal of Geophysical Research*, **94**, 1195–1210.

Diaz, H.F., Hoerling, M.P. & Eischeid, J.K. (2001) ENSO variability, teleconnections and climate change. *International Journal of Climatology*, **21**, 1845–1862.

Doherty, R. & Hulme, M. (2002) The relationship between the SOI and extended tropical precipitation in simulations of future climate change. *Geophysical Research Letters*, **29**, 113–114.

Engelbrecht, B.M.J. & Kursar, T.A. (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia*, **136**, 383–393.

- Engelbrecht, B.M.J., Wright, S.J. & De Steven, D. (2002) Survival and ecophysiology of tree seedlings during El Niño drought in a tropical moist forest in Panama. *Journal of Tropical Ecology*, **18**, 569–579.
- Evans, G.C. (1972) *The Quantitative Analysis of Plant Growth*. Blackwell, Oxford.
- Fedorov, A.V. & Philander, S.G. (2000) Is El Niño changing? *Science*, **288**, 1997–2002.
- Fisher, B.L., Howe, H.F. & Wright, S.J. (1991) Survival and growth of *Virola surinamensis* yearlings: water augmentation in gap and understorey. *Oecologia*, **86**, 292–297.
- Flores, S. (1992) Growth and seasonality of seedling and juveniles of primary species of a cloud forest in northern Venezuela. *Journal of Tropical Ecology*, **8**, 299–305.
- Garwood, N.C. (1983) Seed germination in a seasonal tropical forest in Panama: a community study. *Ecological Monographs*, **53**, 159–182.
- Gentry, A.H. (1988) Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden*, **75**, 1–34.
- Gentry, A.H. (1991) The distribution and evolution of climbing plants. *The Biology of Vines* (eds F.E. Putz & H.A. Mooney), pp. 3–49. Cambridge University Press, Cambridge.
- Gentry, A.H. & Emmons, L.H. (1987) Geographical variation in fertility, phenology, and composition of the understorey of neotropical forests. *Biotropica*, **19**, 216–227.
- Gilbert, G.S., Harms, K.E., Hamill, D.N. & Hubbell, S.P. (2001) Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panama. *Oecologia*, **127**, 509–516.
- Gonzalez, A., Alvarado-Dufree, G. & Diaz, C.T. (1975) Canal Zone water quality study, final report. Water and Laboratories Branch, Panama Canal Company, Canal Zone, Panama.
- Hampson, M.C. & Coombes, J.W. (1997) Pathogenesis of *Synchytrium endobioticum*. IX. Effect of irrigation regimes and soil mixes on disease incidence with pathotype 2. *Canadian Journal of Plant Pathology*, **19**, 47–51.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, **404**, 493–495.
- Harper, J.L. (1977) *The Population Biology of Plants*. Academic Press, New York.
- Howe, H.F. (1990) Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. *Journal of Tropical Ecology*, **6**, 259–280.
- Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.
- Hubbell, S.P., Condit, R. & Foster, R.B. (1990) Presence and absence of density dependence in a neotropical tree community. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, **330**, 269–282.
- Hulme, M. & Viner, D. (1998) A climate change scenario for the tropics. *Climatic Change*, **39**, 145–176.
- Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *American Naturalist*, **104**, 501–528.
- Kiladis, G.N. & Diaz, H.F. (1989) Global anomalies associated with extremes in the Southern Oscillation. *Journal of Climate*, **2**, 1069–1090.
- Kitajima, K. (1996) Ecophysiology of tropical tree seedlings. *Tropical Forest Plant Ecophysiology* (eds S.S. Mulkey, R.L. Chazdon & A.P. Smith), pp. 559–596. Chapman and Hall, New York.
- Kitajima, K. & Fenner, M. (2000) Ecology of seedling regeneration. *Seeds: the Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 331–359. CABI Publishing, Wallingford.
- Kleinbaum, D.G., Kupper, L.L., Muller, K.E. & Nizam, A. (1998) *Applied Regression Analysis and Multivariable Methods*. Duxbury Press, Pacific Grove, California.
- Koppen, W. (1931) *Grundriss der Klimakunde*. Walter de Gruyter, Berlin.
- Kumar, R., Yang, F., Goddard, L. & Schubert, S. (2004) Differing trends in the tropical surface temperatures and precipitation over land and oceans. *Journal of Climate*, **17**, 653–664.
- Laurance, W.F. & Williamson, G.B. (2001) Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conservation Biology*, **15**, 1529–1535.
- Leigh, E.G., Rand, A.S. & Windsor, D.M. (1996) The ecology of a tropical forest. *Seasonal Rhythms and Long-Term Changes*, 2nd edn. Smithsonian Institution Press, Washington.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute, Cary, North Carolina.
- Malhi, Y., Pegoraro, E., Nobre, A.D., Pereira, M.G.P., Grace, J., Culf, A.D. *et al.* (2002) The water and energy dynamics of a central Amazonian rain forest. *Journal of Geophysical Research – Atmospheres*, **107**, 8061.
- Malhi, Y. & Wright, J. (2004) Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, **359**, 311–329.
- Milnes, K.J., Davies, W.J., Rodwell, J.S. & Francis, B.J. (1998) The responses of *Briza media* and *Koeleria macrantha* to drought and re-watering. *Functional Ecology*, **12**, 665–672.
- Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubo, T., Kato, T., Maeda, T. *et al.* (2000) Impact of severe drought associated with the 1997–98 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology*, **16**, 355–367.
- New, M., Todd, M., Hulme, M. & Jones, P. (2001) Precipitation measurements and trends in the twentieth century. *International Journal of Climatology*, **21**, 1899–1922.
- Parent, S. & Messier, C. (1996) A simple and efficient method to estimate microsite light availability under a forest canopy. *Canadian Journal of Forest Research*, **26**, 151–154.
- Piperno, D.R. (1990) Fitolitos, arqueología y cambios prehistóricos de la vegetación en un lote de cincuenta hectáreas de la isla Barro Colorado. *Ecología de un Bosque Tropical* (eds E.G. Leigh, A.S. Rand & D.M. Windsor), pp. 153–156. Smithsonian Institution Press, Washington.
- Poorter, L. & Hayashida-Oliver, Y. (2000) Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *Journal of Tropical Ecology*, **16**, 481–498.
- 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.
- Ropelewski, C.F. & Halpert, M.S. (1987) Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. *Monthly Weather Review*, **115**, 1606–1626.
- Schnitzer, S.A. & Bongers, F. (2002) The ecology of lianas and their role in forests. *Trends in Ecology and Evolution*, **17**, 223–230.
- Schnitzer, S.A. & Carson, W.P. (2000) Have we forgotten the forest because of the trees? *Trends in Ecology and Evolution*, **15**, 375–376.
- Schnitzer, S.A., Dalling, J.W. & Carson, W.P. (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., Burslem, D.F.R.P. & Alder, D. (1995) The interpretation and misinterpretation of mortality rate measures. *Journal of Ecology*, **83**, 331–333.
- Shuttleworth, W.J. (1989) Micrometeorology of temperate and tropical forest. *Philosophical Transactions of the Royal Society of London B*, **324**, 299–334.

- Silim, S.N., Guy, R.D., Patterson, T.B. & Livingston, N.J. (2001) Plasticity in water-use efficiency of *Picea sitchensis*, *P. glauca* and their natural hybrids. *Oecologia*, **128**, 317–325.
- Sokal, R.R. & Rohlf, F.J. (1995) *Biometry*, 3rd edn. Freeman, New York.
- Stratton, L.C. & Goldstein, G. (2001) Carbon uptake, growth and resource-use efficiency in one invasive and six native Hawaiian dry forest tree species. *Tree Physiology*, **21**, 1327–1334.
- Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. (1999) Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, **398**, 694–697.
- Trenberth, K.E. & Hoar, T.J. (1996) The 1990–95 El Niño Southern Oscillation event: longest on record. *Geophysical Research Letters*, **23**, 57–60.
- Trenberth, K.E. & Hoar, T.J. (1997) El Niño and climate change. *Geophysical Research Letters*, **24**, 3057–3060.
- Vitousek, P.M. & Denslow, J.S. (1986) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. *Journal of Ecology*, **74**, 1167–1178.
- Wills, C., Condit, R., Foster, R.B. & Hubbell, S.P. (1997) Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences of the United States of America*, **94**, 1252–1257.
- Windsor, D.M. (1990) *Climate and Moisture Variability in a Tropical Forest: Long-Term Records from Barro Colorado Island, Panama*. Smithsonian Institution Press, Washington.
- Wright, S.J. (1992) Seasonal drought, soil fertility and the species density of tropical forest plant communities. *Trends in Ecology and Evolution*, **7**, 260–263.
- Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.
- Wright, S.J., Carrasco, C., Calderon, O. & Paton, S. (1999) The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology*, **80**, 1632–1647.
- Wright, S.J. & Cornejo, F.H. (1990) Seasonal drought and leaf fall in a tropical forest. *Ecology*, **71**, 1165–1175.

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