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Pests vs. drought as determinants of plant distribution along a tropical rainfall gradient

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Abstract. Understanding the mechanisms that shape the distribution of organisms can help explain patterns of local and regional biodiversity and predict the susceptibility of communities to environmental change. In the species-rich tropics, a gradient in rainfall between wet evergreen and dry seasonal forests correlates with turnover of plant species. The strength of the dry season has previously been shown to correlate with species composition. Herbivores and pathogens (pests) have also been hypothesized to be important drivers of plant distribution, although empirical evidence is lacking. In this study we experimentally tested the existence of a gradient in pest pressure across a rainfall gradient in the Isthmus of Panama and measured the influence of pests relative to drought on species turnover. We established two common gardens on the dry and wet sides of the Isthmus using seedlings from 24 plant species with contrasting distributions along the Isthmus. By experimentally manipulating water availability and insect herbivore access, we showed that pests are not as strong a determinant of plant distributions as is seasonal drought. Seasonal drought in the dry site excluded wet-distribution species by significantly increasing their seedling mortality. Pathogen mortality and insect herbivore damage were both higher in the wet site, supporting the existence of a gradient in pest pressure. However, contrary to predictions, we found little evidence that dry-distribution species suffered significantly more pest attack than wet-distribution species. Instead, we hypothesize that dry-distribution species are limited from colonizing wetter forests by their inherently slower growth rates imposed by drought adaptations. We conclude that mechanisms limiting the recruitment of dry-distribution species in wet forests are not nearly as strong as those limiting wet-distribution species from dry forests.

Key words: drought tolerance; herbivory; Panama; pathogen attack; rainfall gradient; tree distribution; tropical forests.

INTRODUCTION

Local and regional diversities of plants are exceptionally high in the tropics, with species turnover along environmental gradients being a major component of total diversity (Condit et al. 2002, Chust et al. 2006, Davidar et al. 2007). Neutral processes may contribute to species turnover (Hubbell 2001, Zillio and Condit 2007), but much evidence suggests that habitat associations also determine species distribution (Webb and Peart 2000, Condit et al. 2002, Russo et al. 2008). An important correlate of species turnover in the tropics is a 10-fold change in rainfall between dry and wet tropical forests (Gentry 1988, Clinebell et al. 1995, Pyke et al. 2001). Understanding the mechanisms that determine plant distributions along environmental gradients requires evaluation of habitat specialization with respect to multiple environmental variables. Habitat specialization occurs when selection pressures differ among habitats and plants evolve adaptations to cope with specific environmental stressors. Adaptations can impose trade-offs, such that plant performance differs among habitats, and each species is competitive only in a subset of those habitats. A substantial number of studies that correlate plant distribution with environmental variables have provided valuable hypotheses of why species grow where they do (Swaine 1996, Bongers et al. 1999, Clark et al. 1999, Pyke et al. 2001, Phillips et al. 2003, Davidar et al. 2007), but experimental manipulations are necessary to identify trade-offs. The present study experimentally analyzes the relative impact of two of the principal factors that have been proposed as selective filters determining species distribution along rainfall gradients: drought and pests.

Tropical dry forests receive less annual rainfall and experience longer and more severe dry seasons than wetter forests. The correlation of tree distribution with rainfall or seasonality has been well documented (Bongers et al. 1999, Pyke et al. 2001, Davidar et al. 2007), and a substantial amount of empirical evidence already supports a role for water stress in determining

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species distributions. Even within the humid tropics, species differ considerably in their drought performance (Engelbrecht and Kursar 2003, Engelbrecht et al. 2005), and species distributions along a rainfall gradient correlate with their drought tolerance (Engelbrecht et al. 2007, Baltzer et al. 2008). This suggests that species composition in a dry forest is determined by a difference in performance between susceptible and adapted species during the dry season. To test this hypothesis, we conducted a transplant experiment to determine whether a natural dry season in a dry forest would cause higher mortality for species typically found in wetter forests than for species typically found in drier forests. Also, to demonstrate that any differences in mortality were due to water limitations, we tested whether water supplementation was the main variable needed to eliminate this difference.

Tropical wet forests are hypothesized to suffer greater herbivore and pathogen pressure than drier forests (Marquis and Braker 1994, Givnish 1999, Leigh et al. 2004). Plant–pest interactions are a fundamental aspect of many proposed explanations for plant diversity and dynamics in tropical forests (Janzen 1970, Wright 2002, Leigh et al. 2004), and pests are also thought to be one of the variables determining species distributions along a rainfall gradient. However, unlike seasonality, few empirical studies have characterized how herbivory differs across a rainfall gradient in the tropics (Coley and Aide 1991, Coley and Barone 1996). Furthermore, direct surveys of herbivory and pathogen damage confound the effects of pest pressure and plant defenses, both of which may differ across habitats (Coley and Barone 1996, Brenes-Arguedas et al. 2008*a*). Thus, to demonstrate that a gradient in pest pressure exists, the same species must be transplanted and damage compared between wet and dry sites. If drier forests do experience lower pest pressure, species adapted to these forests would presumably have lower investments in defense (Coley and Aide 1991, Coley and Barone 1996) and might be excluded from wetter forests by excessive herbivore or pathogen damage. Thus, to demonstrate the role of pests in species turnover along a tropical rainfall gradient we must first show the presence of a gradient in pest pressure. Then we must demonstrate that dry-distribution species are more vulnerable to this difference and that herbivore exclusion eliminates this difference.

Across the Isthmus of Panama there is a gradient in rainfall, from drier forests with <2000 mm of rainfall per year near the Pacific Ocean to wetter forests with >3000 mm of rainfall per year on the Atlantic side (Appendix A). While the Isthmus is only 60 km wide, extensive plot data show that there is almost no overlap in the 50 most common tree species in dry and wet sites (Pyke et al. 2001). To compare the role of seasonal drought and pests in species turnover, we established reciprocal transplant gardens on the Pacific and Atlantic sides of the Isthmus. In each site we planted 24 species with contrasting distributions along the rainfall gradient and manipulated water availability during the dry season and exposure to herbivores in a completely crossed design. We measured seedling survival, growth, and leaf damage during 14 months including one dry and two rainy seasons.

If performance trade-offs are important drivers of species turnover, we predicted that under natural conditions of rainfall and herbivory, wet-distribution seedlings should perform best in the wet site and dry-distribution seedlings should perform best in the dry site. If drought limits the establishment of wet-distribution species in the dry site, we predicted that during a dry season wet-distribution species would suffer higher rates of mortality or lower growth than dry-distribution species and that water supplementation would eliminate this difference. Conversely, if higher herbivory limits the establishment of dry-distribution species in the wet site, dry-distribution species would suffer higher rates of pest-induced mortality or lower growth than wet-distribution species and herbivore exclusion would decrease or eliminate this difference.

Materials and Methods

Study sites

We set up our experiment in two contrasting sites in the Isthmus of Panama, along the Panama Canal. On the drier side of the Isthmus, we established gardens at Gunn Hill in Ciudad de Saber (old Fort Clayton). The vegetation is typical of lowland, dry, seasonal forest. Annual rainfall is 1740 mm and elevations are <100 m above sea level. In this site, the dry season is on average four months long. On the wet side, we established gardens at the canopy crane site of the Smithsonian Tropical Research Institute within Parque Nacional San Lorenzo (old Fort Sherman). The vegetation is typical of lowland, evergreen, wet forest. Annual rainfall is 3020 mm and elevations are <150 m above sea level. Here the mean length of the dry season is one month shorter than in the Pacific, and the total dry-season rainfall (from January to April) is higher, averaging 370 mm vs. 200 mm in the dry site. Rainfall and drought conditions throughout the experiment were obtained from the meteorological stations of the Autoridad del Canal de Panama at Miraflores, 3 km from the dry site, and at Gatun West, 6 km from the wet site.

Study species

We collected seedlings in Parque Nacional San Lorenzo (rain forest), Parque Nacional Soberanía (moist forest), Ciudad del Saber, and Parque Natural Metropolitano (dry forests). Using the sources listed in Appendix B, species were classified as wet- or dry-distribution species when their range was limited to the wet or the dry forests or when they were widespread but clearly more abundant in one of the two regions. Overall, we collected seeds and seedlings from 85 species, but we did not use 66 species from our collections due to insufficient sample size (small collections, mortality, or limited germination) or the elimination of species with uncertain or complex distribution patterns. Hence the present study includes 24 species with contrasting distributions along the rainfall gradient (listed in Appendix C). Most species were collected when the seedlings were a few months old, usually indicated by the presence of cotyledons or embryonic leaves. In five cases (ingamu, peripr, pipere, tapigu, and psycgl; see Appendix C for explanations of species abbreviations) seedlings may have been older than one year. Collections were made from June to October 2005, and seedlings were planted in flats or pots in a screened shade house until they were transplanted into the field, usually within one or two months.

Transplant gardens

The transplant gardens were established in a split-split-plot design in the understory at the study sites. There were 10 replicate plots per site scattered along ~1 km. Plots were placed in a variety of understory light environments to allow for some overlap in light level among sites. Each plot was divided into four subplots of 0.5 × 0.5 m with different herbivore–water treatment combinations in a completely crossed design. Two subplots in each plot received supplemental water throughout the dry season (December to April) to alleviate drought stress (watered, W). These were irrigated by hand to complement rainfall such that plants received at least 50 mm each week. The other two subplots experienced a natural dry season. Watered plots were placed 3 m apart and downhill from the control plots to eliminate runoff. One watered and one control subplot within each plot were protected from insect herbivores with mesh cages (exclusion, E), and the other pair had only mesh roofs to allow access by herbivores. Hence, treatment combinations for each subplot were control–control (C–C), control–watered (C–W), exclusion–control (E–C), and exclusion–watered (E–W). In each of the four subplots we planted one individual from each species sufficiently far apart (~20 cm) to avoid shading. Seedlings were planted in the gardens during the rainy season of 2005 between June and November. To compensate for deaths due to transplanting stress, we replaced dead seedlings through December 2005.

Mortality

Censuses started in October 2005. Seedling survival was censused twice monthly until June 2006 and once per month until December 2006. Due to a treefall, one plot at the wet site only includes data for the first five months. When possible, the cause of death (pathogen, herbivores, or drought) was recorded. Because death due to transplant stress was not easy to separate from other causes of death, we included in the analyses only those seedlings that had survived at least 15 days after planting. The start date for each seedling was the first day they were censused alive after they were planted. To compare among species, we calculated an average mortality rate per species using an exponential model: log(percent survival) $= b + a$ (time in months). The percentage mortality per month, $1 - e^{a}$ was estimated for the entire period of the experiment and also for dry, first, and second rainy season separately.

Growth measurements

For each individual seedling we calculated three measures of growth: stem growth, net leaf growth, and leaf production. Once per month we measured height and counted the total number of leaves and the number of new leaves produced since the last census. Because the experiment was relatively short and seedling growth in the understory was very slow, these growth rates were best quantified using a linear regression. Even for the fastest-growing individuals, a linear model fit the data well. While stochastic events such as the loss of multiple leaves or broken stems resulted in short-term variation in growth rates, the slope is still the best measure of mean growth rate for the entire experiment. Thus, mean stem growth was calculated as the slope of the linear regression of height as a function of time in months (in units of millimeters per month). Net leaf growth was the slope of the total number of leaves at each census as a function of time in months, and leaf production was calculated by summing all new leaves produced and dividing by the total number of months the plant was in the experiment. For each species, leaf numbers were converted to leaf area by multiplying by the mean leaf area such that both leaf growth variables are in units of square centimeters per month. Because leaf area per species was smaller in the wet site, we used different values for the species' leaf areas at each site.

Leaf damage measurements

We measured leaf damage in each of the surviving seedlings at the end of the experiment, in November 2006. We measured damage as the percentage of area averaged for the three (or four, for species with opposite leaves) most apical fully expanded leaves. The percentage of area damaged was calculated using a grid and classified as insect or pathogen damage. If any of the three to four apical leaves were completely missing as evidenced by a leaf scar in the stem, we counted it as 100% damage due to unknown causes. Because 70% of the plants produced less than four leaves during the experiment, quantifying only the apical three to four leaves ensures that the leaves were produced after transplantation. A second reason for focusing on the apical leaves is that damage due to 100% leaf loss can be confounded with senescence unless only the youngest leaves are measured.

Data analysis

All data were analyzed using R (R Development Core Team 2005). The experimental design included six fixed effects: forest type (two levels, dry or wet), water treatment (two levels, control or watered), herbivore treatment (two levels, control or exclusion), and species distribution (two levels, wet- or dry-distribution); and two random factors: species (23 levels), and plot (20 levels, 10 plots per site).

Mortality.—Mortality data were analyzed using robust Cox proportional hazards models (original survival package, S by T. Therneau; *available online*).[4] Robust errors were calculated after clustering data by species and by plot. Results are reported in terms of hazard ratios (HR), which are ratios of the event probabilities (death) between two treatments or treatment combinations. For example, W:C HR = 1 represents equal mortality in the watered and control plots and W:C HR < 1 indicates greater mortality in the control plots.

Growth.—The growth variables were analyzed separately and together. To analyze the growth variables together we ran a principal component analysis and used the first principal component (PC1), which correlated positively with all growth variables (weights: leaf production, 0.65; net leaf growth, 0.67; stem height growth, 0.37). We tested the main effects and interactions using linear mixed-effect models (nlme package; Pinheiro and Bates 2004).

Herbivory.—To analyze herbivory data, we collapsed the data into exclusion and control treatments, pooling together watered and unwatered treatments. Because herbivory data are not normal, we could not run a full model with all the variables. Instead we analyzed it by parts using effect sizes and nonparametric Friedman and Kruskal-Wallis tests.

Effect sizes.—To compare the effect of the fixed experimental factors (site, watering, and caging) on growth and leaf damage we used meta-analysis techniques (Hedges 1983, Gurevitch and Hedges 1993). Each species was considered one separate, though not independent, experiment. For each species we calculated the corrected standardized difference due to the treatment as: $d_{1-2} = c(\bar{x}_1 - \bar{x}_2)/sd_{\mathrm{pool}}$, where $\bar{x}_i$ is the mean leaf damage or growth in treatment i, sd_{pool} is the pooled standard deviation, and c is a correction factor. Thus, d_{1-2} is the distance in standard deviations between the two means. We tested for general trends by pooling the effect sizes using weighted averages and calculated 95% confidence intervals (CI) with bootstrap randomizations. Conventionally, values of d_{1-2} of 0.2 are considered small, 0.5 medium, and 0.8 large, and $\mathrm{CI}_{0.95}$ that do not overlap with zero are considered significant.

RESULTS

In control treatments, average monthly mortality per species ranged from 0 to 13% in the dry site, with a median of 2.3%; and from 0 to 19% in the wet site, with a median of 2.5% (Appendix D). There was large variation in average mortality between seasons (Appendix D). Mean leaf production for each species in the dry site ranged from 0.10 to 0.82 leaves/month, with a median of 0.24 leaves/month; and, in the wet site, from 0.04 to 0.43 leaves/month, with a median of 0.12 leaves/month (Appendix E). Growth was very slow such that, overall, 70% of the individual plants (pooling all species and plots) produced four or fewer leaves over the whole experiment. Stem height growth per species ranged from −0.09 to 0.44 mm/month, with a median of 0.15 mm/month in the dry site, and from 0.03 to 0.25 mm/month, with a median of 0.14 mm per month in the wet site (Appendix E).

Performance in relation to site and species distribution

With respect to mortality, seedling performance was best in their typical habitat (see Appendix F for full statistical analysis). Dry-distribution species in the control–control treatment (no cages and no water supplementation) had 41% lower mortality in the dry than in the wet site (dry : wet HR = 0.59, $n = 248$, $P = 0.03$). Wet-distribution species, instead, had 12% lower mortality in the wet than in the dry site, although this difference was not significant (wet : dry HR = 0.88, $n = 228$, $P = 0.57$). This mortality difference resulted in a partial home site recruitment advantage. In the dry site, dry-distribution species had a strong recruitment advantage as they suffered 45% less mortality than wet-distribution species (Fig. 1A; dry : wet HR = 0.55, $n = 231$, $P = 0.02$). While in the wet site, wet-distribution species had only a weak advantage, as they suffered only 10% lower mortality than dry-distribution species, and this difference was not significant (Fig. 1B; wet : dry HR = 0.9, $n = 245$, $P = 0.63$).

With respect to seedling growth, wet-distribution species had a performance advantage over dry-distribution species in both sites. Wet-distribution species grew significantly faster than dry-distribution species in both sites (PC1, wet, df = 1, 22, $F = 7.2$, $P = 0.01$; dry, df = 1, 22, $F = 10.2$, $P = 0.004$; Fig. 2). Also, growth was best in the dry site for all species, but especially for wet-distribution species (Table 1A). The effect of site on the leaf growth variables was significantly stronger for wet- than for dry-distribution species (Table 1A), while the effect of site on the stem height growth was near zero for both groups of species (Table 1A).

Effect of drought and water supplementation on plant performance

The lower survival of the wet-distribution species in the dry site was clearly due to their lack of drought adaptations. The year of the experiment was a wet year, but conditions were within the normal range of long-term interyear variation. Total dry-season rainfall (January to April) at the dry site was 270 mm, 37% higher than the average, and the dry season was four weeks shorter than the average. Only at the beginning of February did rainfall decrease significantly in the dry

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[4] ⟨http://www.r-project.org/⟩

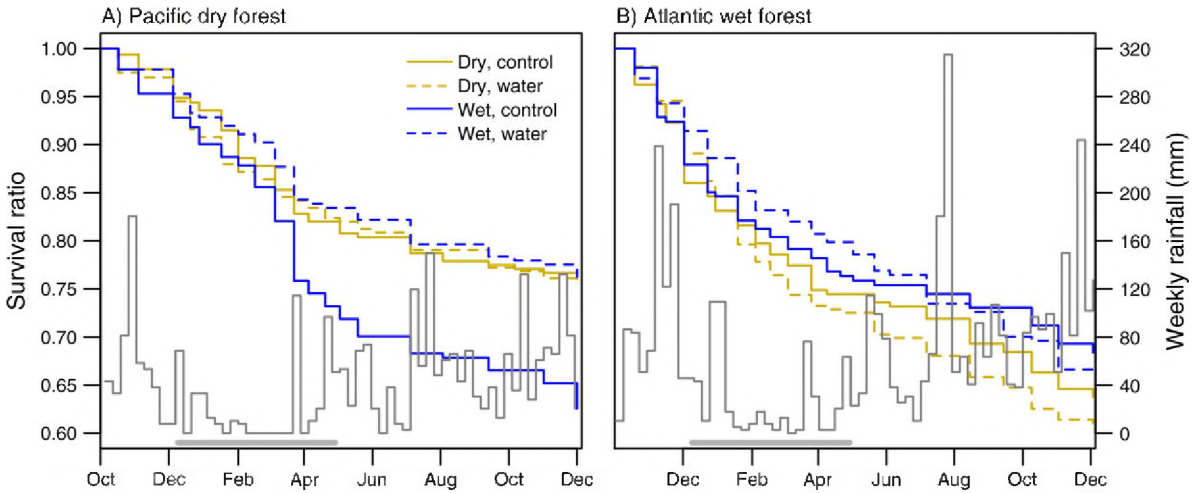

FIG. 1. Seedling survival ratio throughout the study in (A) the dry site (likelihood ratio [LR] = 22.6, df = 4, $P = 0.0002$, $n = 958$) and in (B) the wet site (LR = 7.98, df = 4, $P = 0.09$, $n = 1010$) by month beginning in October 2005. Seedlings are grouped by their distribution (wet, blue; dry, yellow) and the watering treatment (control, solid; water supplementation, dashed). Herbivore treatments are pooled together. Gray lines represent weekly rainfall, and gray horizontal bars along the x-axis indicate the dates when water was supplemented.

site, and by early March soils had reached only moderately dry levels (−1.36 MPa; Appendix G). However, one month after the rains receded, there was a significant increase in the mortality of the wet-distribution species relative to the dry-distribution species (Fig. 1A, solid lines). Between February and March, unwatered wet-distribution species in the dry site suffered twice as much mortality as did dry-distribution species (wet : dry HR = 2.17, $n = 1733$, $P = 0.007$).

The higher mortality of wet-distribution species in the dry site was clearly due to drought effects as it was reversed by dry-season water supplementation to a mortality rate indistinguishable from the dry-distribution species (Fig. 1A, dashed lines). Indeed, water supplementation at the dry site decreased by half the dry-season mortality of wet-distribution species (watered : control [W:C] HR = 0.50, $n = 413$, $P = 0.02$). It also decreased by half the mortality of wet-distribution species during the subsequent rainy season (W:C HR = 0.52, $n = 370$, $P = 0.02$), indicating that drought stress has long-term effects on the performance of sensitive species. While the responses of individual species were very variable, watering reduced mortality for seven of the 11 wet-distribution species (Appendix D). As expected, water supplementation did not have an effect on seedling mortality in the wet site (Fig. 1B; W:C HR = 1.10, $n = 1010$, $P = 0.35$). Our data also suggest that dry-distribution species are better adapted to drought, as, on average, their survival was not affected by water supplementation (Fig. 1A; W:C HR = 1.03, $n = 1035$, $P = 0.88$). Water supplementation in the dry site also had a positive effect on seedling leaf production and net leaf growth (Table 1B, dry site), probably reflecting a decrease in drought-associated leaf loss. In the wet site, this watering effect was much weaker and significant only for the net leaf growth of wet-distribution species (Table 1B, wet site).

The gradient in pest pressure

On average total leaf damage in control treatments at the end of the experiment was 12% in the dry site and 18% in the wet site (Fig. 3). Total leaf damage was greater in the wet site for 17 of the 23 species, and the pooled difference for all species was significantly larger than zero (Table 1A). This between-site difference in leaf damage was the result of higher insect and pathogen attack. Damage assigned to leaf-chewing insect herbivores was 72% higher in the wet than in the dry site (Fig. 3, gray bars; Friedman $\chi^2 = 8.9$, $n = 22$ species, $P = 0.003$), although the pooled effect size of site on leaf-chewing damage was small (Table 1A). Only 27% of the observed leaf damage was assigned to leaf-chewing herbivores (Fig. 3). Most of the remaining leaf damage (69%) was in the form of complete leaf loss (scars) assigned to unidentified causes. Identified pathogen damage in the leaves (spotting) represented only 4% of the visible damage. However, pathogens may have been responsible for most of the complete leaf loss in the wet site, as herbivore exclusion did not influence the total leaf damage to these seedlings (Fig. 3B and Table 1C, wet site). In the dry site, caging did decrease total leaf damage (Fig. 3A and Table 1C, dry site), suggesting that insect herbivory may be relatively more important than pathogens in that site. Probably more important than insect or pathogen damage to the leaves were the lethal effects of systemic pathogens. The mortality in watered-exclusion plots, attributed to attack by systemic pathogens, was 81% higher in the wet than in the dry site (wet : dry HR = 1.81, $n = 507$, $P = 0.005$).

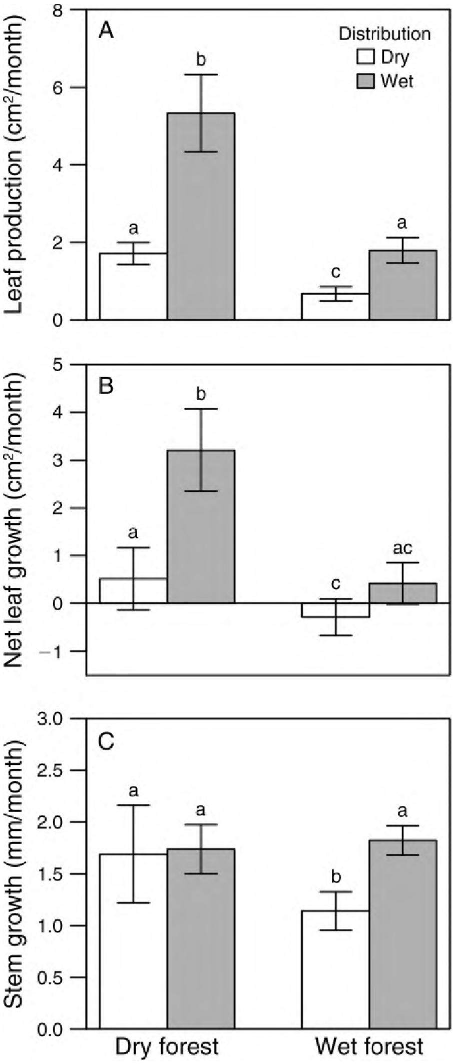

FIG. 2. Growth rates (mean ± SE) in (A) leaf production, (B) net leaf growth, and (C) apical stem growth for the study species, classified by their preferred distribution in the two study sites. All experimental treatments are pooled together. Lowercase letters represent significant differences among bars ($\alpha = 0.05$).

Effect of pests on wet- vs. dry-distribution species

Despite the higher pest pressure in the wet site, we found only weak evidence that wet-distribution species had more effective defensive adaptations. At the wet site, dry-distribution species exposed to herbivores had 22% higher total leaf damage and only 5% higher pathogen mortality than wet-distribution species. None of these comparisons was significant (total damage, Kruskal-Wallis $\chi^2 = 1.8$, $P = 0.17$; pathogens, wet : dry HR = 0.95, $n = 261$, $P = 0.85$), as some of the highest attack rates belonged to wet-distribution species (Appendix H). Leaf-chewing damage in the wet site had a similar nonsignificant pattern ($\chi^2 = 1.4$, $P = 0.23$; Appendix H). In the dry site, there was a greater difference in pest attack between dry- and wet-distribution species, but the effects were still not significant (total damage, $\chi^2 = 2.4$, $P = 0.12$; pathogens, wet : dry HR = 0.57, $n = 246$, $P = 0.12$; Fig. 3A, Appendix D). Five of the 12 dry-distribution species were collected in moist-forest sites (Appendix C) that may have higher pest pressure and hence, selection for higher plant defenses. However, the dry-distribution species collected in moist forests had similar damage rates as those collected from dry forests in both the wet (t test, $P = 0.33$) and the dry site ($P = 0.36$). This indicates that provenance effects did not contribute to the lack of an effect of species distribution on leaf damage.

Effect of herbivore exclusion cages

Herbivore exclusion significantly lowered mortality but did not influence growth of the seedlings. Seedlings in herbivore exclusion cages in the wet site had 21% lower mortality than control seedlings (E:C HR = 0.79, $n = 1010$, $P = 0.01$). This caging effect was 10% stronger in the dry site, but the difference between sites was not significant (dryE:C/wetE:C HR = 0.90, $n = 1968$, $P = 0.51$). Similarly, the caging effect was nonsignificantly stronger for wet- than dry-distribution species (wetE:C/dryE:C HR = 0.85, $n = 1968$, $P = 0.30$). While caging significantly reduced the percentage of leaf damage that could be attributed to leaf-chewing insects in both sites and the total leaf damage in the dry site (Table 1C and Fig. 3), it had no effect on the growth of the seedlings in any of the four growth variables (Table 1C and Appendix I). Also, the effects of caging on leaf damage were not different between dry- and wet-distribution species (Table 1 and Fig. 3).

DISCUSSION

In the wet site, seedling growth was generally lower, partly due to lower soil quality (Brenes-Arguedas et al. 2008*b*) and to lower understory light (T. Brenes-Arguedas, P. D. Coley, and T. A. Kursar, *unpublished data*). Mortality was also higher, mostly due to pathogen attack. Our results support the hypothesis that species' distributions along the Isthmus of Panama are influenced by species' adaptations to the environment, mostly seasonal drought. Dry-distribution species had a home site advantage in survival in their typical habitat, as in the dry site they had significantly lower mortality than wet-distribution species, especially during the dry season (Fig. 1). In the wet site, there was little difference in mortality between dry- and wet-distribution species (Fig. 1), but wet-distribution species had significantly faster growth rates. Indeed, wet-distribution species had faster growth rates than dry-distribution species in both study sites (Fig. 2). This was true even when controlling for light variation (T. Brenes-Arguedas, P. D. Coley, and T. A. Kursar, *unpublished data*) and soil quality (Brenes-Arguedas et al. 2008*b*).

TABLE 1. Pooled effects of garden site (A), water supplementation during the dry season (B), and herbivore exclusion cages (C) on growth and leaf damage (with bootstrap 95% confidence intervals).

	A) Site effect		B) Watering effect				C) Caging effect			
	Dry–wet		Dry site		Wet site		Dry site		Wet site	
Species distribution	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
On leaf production†										
Dry	**1.27**	**0.82–1.59**	**0.24**	**0.12–0.36**	0.03	−0.09–0.15	0.06	−0.16–0.35	0.04	−0.13–0.30
Wet	**2.33**	**1.67–3.12**	0.14	−0.07–0.35	−0.04	−0.25–0.18	0.18	−0.18–0.66	−0.06	−0.24–0.12
All	**1.74**	**1.34–2.17**	**0.19**	**0.06–0.32**	0.00	−0.12–0.11	0.12	−0.12–0.38	−0.01	−0.14–0.14
On net leaf growth†										
Dry	0.60	−0.08–1.20	**0.23**	**0.01–0.45**	−0.03	−0.20–0.17	0.33	−0.02–0.66	−0.05	−0.34–0.45
Wet	**1.64**	**1.17–2.19**	**0.32**	**0.03–0.61**	**0.36**	**0.09–0.61**	0.19	−0.38–0.79	−0.29	−0.57–0.04
All	**1.08**	**0.61–1.56**	**0.27**	**0.12–0.47**	0.15	−0.04–0.33	0.27	−0.08–0.64	−0.17	−0.38–0.11
On stem height growth†										
Dry	0.05	−0.14–0.21	−0.01	−0.10–0.07	−0.11	−0.21–0.01	0.02	−0.09–0.12	−0.02	−0.12–0.06
Wet	−0.01	−0.15–0.13	−0.01	−0.08–0.08	−0.05	−0.17–0.07	−0.07	−0.19–0.02	0.07	−0.04–0.17
All	0.02	−0.09–0.14	−0.01	−0.06–0.05	−0.08	−0.16–0.00	−0.03	−0.10–0.05	0.03	−0.05–0.10
On insect damage‡										
Dry	−0.17	−0.46–0.10	−0.14	−0.44–0.19	0.23	−0.09–0.53	**0.43**	**0.20–0.60**	**0.35**	**0.03–0.67**
Wet	−0.24	−0.47–0.09	0.20	−0.07–0.42	0.19	−0.07–0.46	**0.39**	**0.18–0.55**	0.25	−0.08–0.50
All	**−0.20**	**−0.41–0.01**	0.01	−0.19–0.23	0.21	−0.02–0.42	**0.41**	**0.27–0.53**	**0.30**	**0.09–0.53**
On total leaf damage‡										
Dry	−0.22	−0.48–0.05	**−0.26**	**−0.49–0.04**	0.00	−0.26–0.23	**0.35**	**0.17–0.54**	0.10	−0.16–0.45
Wet	**−0.35**	**−0.72–0.01**	0.05	−0.32–0.31	−0.15	−0.33–0.03	**0.38**	**0.11–0.64**	0.06	−0.34–0.46
All	**−0.28**	**−0.50–0.06**	−0.13	−0.31–0.08	−0.08	−0.23–0.09	**0.36**	**0.18–0.52**	0.08	−0.17–0.31

Notes: The effects are pooled by species distribution (dry or wet) and for all species together (all). Pooled effects that are significantly different from zero appear in boldface.

† Site and dry-site caging effects on growth were calculated for unwatered treatments only.

‡ Site and dry-site water effects on leaf damage were calculated for uncaged treatments only.

What limits the performance of wet-distribution species in dry sites?

Our results agree with a growing body of literature suggesting that seasonal drought is an important determinant of species distribution along a rainfall gradient (Bongers et al. 1999, Baraloto et al. 2007, Davidar et al. 2007, Engelbrecht et al. 2007, Baltzer et al. 2008). In the dry site there was a large difference in mortality between dry- and wet-distribution species and this difference was clearly attributed to different responses to seasonal water limitation. We demonstrated causation with two pieces of evidence: (1) the mortality of wet-distribution species peaked a month

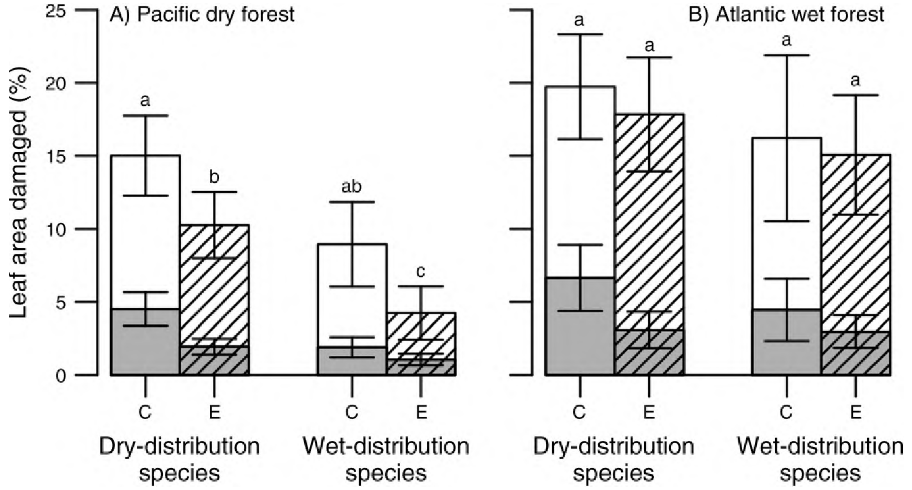

FIG. 3. Percentage of the leaf area damaged (mean ± SE) in (A) the dry site and (B) the wet site, for dry- and wet-distribution species, in control (C, solid) and herbivore exclusion treatments (E, hatched). The gray area represents the fraction of damage attributed to leaf-chewing herbivores. The remainder of the bar represents pathogen damage and unidentified leaf damage in the form of complete leaf loss. Letters represent significant differences in total damage ($\alpha = 0.05$) based on nonparametric comparisons of species means.

after the rains receded and (2) its effect was completely reversed with water supplementation (Fig. 1). Other studies have shown that, on average, dry-distribution species have higher physiological tolerance to drought stress than wet-distribution species (Engelbrecht et al. 2007, Baltzer et al. 2008). Also, a large number of studies have demonstrated the importance of drought tolerance for plant habitat associations along soil-related water gradients at the local scale (Borchert 1994, Palmiotto et al. 2004, Baltzer et al. 2005, Russo et al. 2005, Baraloto et al. 2007). Our results provide experimental support for the conclusions of these previous studies and complement them by showing that physiological differences in drought tolerance can have a strong impact on seedling survival even during a very short dry season.

What limits the performance of dry-distribution species in wetter forests?

Pest pressure is believed to be a relatively more important determinant of plant population dynamics in wetter, less seasonal forests (Coley and Aide 1991, Marquis and Braker 1994, Coley and Barone 1996, Givnish 1999, Wright 2002, Leigh et al. 2004). Analyzing both wet- and dry-distribution species planted in two different locations provides partial control for defensive adaptations of plants that may influence damage rates. Thus we showed that both leaf damage and mortality due to pathogens were higher in the wet site (Fig. 3 and *Results*). The effects of site were highly variable among species (Appendix I), probably reflecting differences among species in anti-pest defenses or herbivore/pathogen specialization. However, only five species had higher leaf damage in the dry site, and of these, only two significantly so, suggesting a clear trend for higher herbivore and pathogen pressure on most species in the wet site. Because plant defenses can depend in complex ways on the precipitation, light, and soils (e.g., Koricheva et al. 1998), a less likely explanation for the herbivory gradient is that plants at the dry site, with higher light and nutrients, had more effective defenses.

While we demonstrated that pest attack was higher in the wet site, evidence suggesting that wet-distribution species were better defended than dry-distribution species was very weak. Wet-distribution species have been reported to have higher leaf toughness and phenolic concentrations than dry-distribution species (Coley and Aide 1991), but our analysis provides the first comparative test of their susceptibility to pests in the field. In the wet site, where we expected larger effects, average leaf damage in the control treatments was very similar for dry- and wet-distribution species (Fig. 3B). Also, wet-distribution species suffered as high pathogen-caused mortality as did dry-distribution species. In the dry site, the differences between wet- and dry-distribution species in leaf damage and in pathogen-caused mortality were larger (Fig. 3A). However, these trends were still not significant and may also represent an escape from specialized pests.

Overall, variation in attack rates among species, regardless of their origin, was larger than the difference in means between wet- vs. dry-distribution species (Appendix H). Thus, while the trend for greater damage to dry-distribution species may become statistically significant over longer time spans or for a larger sample size, it is clear that any effect of adaptations to higher pest pressure is not very large. This may be because plant traits that can influence herbivory can be the result of other selective pressures. For example, severe dry seasons could select for narrow vessels, which could result in denser xylem and lower attack by stem-cutter herbivores. Additionally, most damage to evergreen tropical plants occurs during leaf expansion (Coley and Barone 1996), and the defenses of young leaves and their trade-offs are still poorly understood (Brenes-Arguedas et al. 2006).

We found no evidence that herbivores specifically restrict dry-distribution species from the wet site, as caging did not equalize the performance of dry- and wet-distribution species. When looking at leaf-chewing damage and total leaf damage, wet- and dry-distribution species benefited equally from herbivore exclusion (Table 1C). Indeed, with respect to total leaf damage, herbivore exclusion tended to benefit the wet-distribution species more, although the pooled effect sizes were not significantly different (Table 1C). Furthermore, despite the existence of significant caging effects on leaf damage, herbivore exclusion did not influence the growth rates of the seedlings in either of the two sites (Table 1). This lack of a caging effect suggests that pathogens could have a stronger impact than insects on seedling growth. The most important effect of caging on seedling performance was to reduce the mortality caused by stem-cutter herbivores, which preferentially attacked wet-distribution species in the dry site (Appendix H). These results suggest that, at least at the early seedling stage, herbivores do not exclude dry-distribution species from wetter forests.

What then limits the success of dry-distribution species in wetter forests? Drought-tolerant species could be at a disadvantage due to low soil oxygen in forests with higher rainfall. This seems unlikely, first, because the availability of oxygen in soil during the rainy season in a moist forest was quite high (Kursar et al. 1995). In addition, species may not differ markedly in flooding tolerance (Lopez and Kursar 2003). Notably, mortality rates in the wet site were not significantly different between wet- and dry-distribution species. While the observed 13% difference in mortality between dry- and wet-distribution species in the wet site may become a significant force over longer time spans, this difference was much smaller than the variation in mortality among species (Appendix D). This suggests that neither pests nor other environmental stressors in the wet site have such a selective impact on the mortality or growth of dry-distribution species. While we have not evaluated all possible biotic or abiotic stress factors, our results also suggest another possible mechanism. We hypothesize that dry-distribution species may instead be limited by inherently slow growth rates. In both the dry and the wet site, wet-distribution species had faster growth rates than dry-distribution species (Fig. 2). In a previous study we demonstrated that this difference in growth rates is present even in controlled screened-house conditions with abundant light and water (Brenes-Arguedas et al. 2008*b*).

The slow growth rates of dry-distribution species are probably associated with adaptations for drought tolerance (Grime 1977, Russo et al. 2005, Baltzer et al. 2008). In a study in a rainforest in the Malay-Thai peninsula, species restricted to wetter forests also had faster growth rates than widespread species (found also in drier forests) (Baltzer et al. 2007), suggesting a trade-off between tolerance to abiotic stress and growth rates (Grime 1977, Russo et al. 2005, Baltzer et al. 2008). Similarly, slow growth rates have been observed in species associated with sandy soils, which have lower water and nutrient availability (Baltzer et al. 2005, Russo et al. 2005). Indeed, some of the mechanisms that confer tolerance to drought stress, such as narrow vessels, could also impose a constraint on growth rates (Hacke et al. 2006).

Consequently, mechanisms limiting the recruitment of dry-distribution species in the wetter forests could be related to poor competitive abilities associated with slower growth rates. Relative to dry-distribution species, the fast-growing, wet-distribution species produce more leaf area to intercept light and grow more in height to compete for access to the canopy (Fig. 2). Faster growth rates may also result in a greater capacity to replace leaf area loss despite high pest attack (Coley 1987). Lastly slower growth rates could decrease the probability of survival to adulthood by increasing the time necessary to reach reproductive size.

In conclusion, our mortality and growth patterns suggest that mechanisms limiting the recruitment of dry-distribution species in wetter forests may not be nearly as strong as those limiting wet-distribution species in drier forests. Based on these results, we hypothesize that in wetter forests, competitive interactions may be more important for seedling establishment than environmental stress. Competitive differences alone may not be sufficient to exclude dry-distribution species from wet forests. That competition may be less effective in limiting establishment could explain the higher plant diversity seen in wet sites (Gentry 1988, Givnish 1999, Wright 2002). Also, it could explain the generally broader geographic distribution of species tolerant to abiotic stress (Stevens 1989, Condit et al. 2005, Baltzer et al. 2007) that can often been found, though at low abundance, in wetter forests. Because this mechanism may only be evident in long-term studies of growth, mortality, and reproduction, demonstrating causal effects and teasing apart the relative contribution of environmental factors will be challenging. Furthermore, climate change may alter the seasonality and magnitude of rainfall and the abundance of pests in tropical latitudes (Coley 1998, Christensen et al. 2007). An improved understanding of mechanisms that determine distribution will be vital to predict the future composition of the forest community and to direct biodiversity conservation efforts.

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APPENDIX A

Positions of the study sites along the Isthmus of Panama (*Ecological Archives* E090-124-A1).

APPENDIX B

Sources used to assign the range, distribution, and current names of the study species (*Ecological Archives* E090-124-A2).

APPENDIX C

List of species used in the experiment with information regarding their habit, range, preferred distribution, and site of collection (*Ecological Archives* E090-124-A3).

APPENDIX D

Slope of the mortality function, *a*, for each of the study species during three time periods and due to pathogen and stem-cutter attack (*Ecological Archives* E090-124-A4).

APPENDIX E

Mean monthly growth for each of the study species throughout the experiment (*Ecological Archives* E090-124-A5).

APPENDIX F

Statistical analysis of seedling mortality and growth (*Ecological Archives* E090-124-A6).

APPENDIX G

Weekly summary of environmental variables during the dry season and early rainy season in the two study sites (*Ecological Archives* E090-124-A7).

APPENDIX H

Mean of the percentage of total leaf damage and the percentage of leaf-chewing insect damage present at the end of the experiment for each of the study species (*Ecological Archives* E090-124-A8).

APPENDIX I

Effect size and standard deviation of watering, caging, and site for each of the study species on the growth and leaf damage variables (*Ecological Archives* E090-124-A9).