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The effect of soil on the growth performance of tropical species with contrasting distributions

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Within the tropics, a marked gradient in rainfall between dry and wet forests correlates with a well documented turnover of plant species. While water availability along these gradients is an important determinant of species distributions, other abiotic and biotic factors correlate with rainfall and may also contribute to limit species distribution. One of these is soil fertility, which is often lower in the wetter forests. To test its possible role in species distribution along a rainfall gradient, we performed a screen-house experiment where we measured the growth performance of seedlings of 23 species with contrasting distributions across the Isthmus of Panama. We grew seedlings in soils collected from the drier Pacific side and the wetter Atlantic side. Differences in soil fertility across the Isthmus were large enough to significantly influence the growth performance of the seedlings. However, we found no evidence of home-soil advantage among species with contrasting distributions. Dry-distribution species grew on average slower than wet-distribution species suggesting a cost to drought adaptations. The response to soil differences correlated with the growth rate of the species, such that fast-growing species responded more to changes in soil quality. We hypothesize that inherently slow growth rates of some dry-distribution tropical species may be a more important factor limiting their colonization of wetter sites along the rainfall gradient.

Species turnover along environmental gradients is a key component of tropical regional diversity that is currently receiving considerable attention (Chust et al. 2006, Davidar et al. 2007, Engelbrecht et al. 2007, Baltzer et al. 2008). Among the environmental variables that correlate with the distributions of tree species are rainfall, the length of the dry season, and edaphic characteristics (Swaine 1996, Bongers et al. 1999, Clark et al. 1999, Harms et al. 2001, Phillips et al. 2003). While these associations have long been recognized (Gentry 1988), the specific mechanisms driving species turnover are still poorly understood for two reasons: first, dispersal limitations and neutral processes also can limit species distributions independently of the environment (Phillips et al. 2003, Chust et al. 2006); and second, many of the environmental variables that are thought to contribute to shape species distributions actually are correlated with each other (Swaine 1996, Davidar et al. 2007). Both effects make it difficult to determine whether and how environmental factors determine distribution.

One important environmental gradient in tropical forests is a 10-fold variation in yearly rainfall between dry and wet forests. Along this moisture gradient there is a marked turnover of plant species, with wetter forests harboring much higher diversities than drier forests (Gentry 1988). Water availability along and within these gradients is probably an important determinant of species distributions (Borchert 1994, Engelbrecht et al. 2007, Baltzer et al. 2008), but other covarying biotic and abiotic factors have also been proposed as possible contributors to species distribution. One of those factors is nutrient availability of the soils. In many cases higher rainfall results in increased leaching or lower mineralization rates (Schuur and Matson 2001). Thus wetter forests tend to have lower soil fertility than drier forests (Clinebell II et al. 1995, Swaine 1996, Santiago et al. 2005). Soil nutrients have been found to correlate with species distribution (Swaine 1996, Phillips et al. 2003, John et al. 2007), but soil physical properties, mainly those related to water availability, also correlate with species distribution (Borchert 1994, Sollins 1998). Thus, in the absence of experimental manipulations, the presence of covarying characteristics in the environment make it difficult to specifically isolate the relative contribution of the different soil traits.

One possible mechanism by which soil fertility can limit species distribution along a rainfall gradient is by influencing the competitive ability of adapted vs non-adapted species. Along this gradient, we hypothesize that wet-distribution species may be adapted to poor wet-forest

soils, and may out-compete dry-distribution species in these soils. Conversely dry-distribution species may out-compete wet-distribution species in the richer dry-forest soils. In this study we experimentally evaluated the role of soil fertility on the growth performance of seedlings of 23 woody species with contrasting distributions along a rainfall gradient in the Isthmus of Panama. We used a screen-house experiment to control for other potential covariates, such as water availability, light, and herbivores, and measured the rate of new leaf area production and apical stem growth, as these are important traits in the competition for light in the forest understory. Thus, if soil fertility plays a role in species distribution along this rainfall gradient, we hypothesize that a) between wet and dry forests there are differences in soil quality large enough to influence the growth performance of the seedlings, and b) wet- and dry-distribution species will vary in their response to soil differences such that there will be a home-soil competitive advantage.

Methods

The study was done in the Panama Canal watershed in the Republic of Panama. In central Panama, an extensive protected area of continuous forest stretches between the oceans. The region has a marked gradient in seasonality, from drier forests with less than 2000 mm of rainfall per year near the Pacific Ocean, to wetter forests with more than 3000 mm rainfall per year on the Atlantic side. Although the Isthmus is only 60 km wide, extensive plot data show that there is almost no overlap in the 50 most common tree species at wet and dry sites (Pyke et al. 2001).

Despite large variation in bedrock formations along the Isthmus (Stewart and Stewart 1980), this rainfall gradient correlates with a gradient in soil nutrient concentration, partly influenced by the quality of the vegetation and the leaf litter cycling (Santiago et al. 2005). Extractable PO_4^{-3}, K, Ca and Mg all had higher concentrations in the drier parts of the Isthmus, while nitrogen and carbon showed the opposite trend. Soils in the drier side were also less acidic than in the wetter side. We collected soils from two sites with different seasonality on the Atlantic and Pacific sides of the Isthmus of Panama. On the drier, Pacific side, we collected soils in Gunn Hill, a study site in Fort Clayton that is managed by the Peregrine Foundation (9°0′50″N, 79°35′0″W). The vegetation in this site is typical of a lowland dry deciduous forest. Annual rainfall is 1740 mm, temperatures average 28°C, and elevations are less than 100 m above sea level. The bedrock is La Boca Formation, early Miocene, mudstone, siltstones, sandstone, tuff and limestone (Stewart and Stewart 1980). The soil at a nearby site is an ultisol (Santiago et al. 2005). On the wetter, Atlantic side, we collected soils at the Fort Sherman Canopy Crane site of the Smithsonian Tropical Research Institute (9°17′0″N, 79°58′30″W). The vegetation here is typical of an evergreen, lowland wet forest. Annual rainfall is 3020 mm and elevations are less than 150 m above sea level. The soil is a histosol (Santiago et al. 2005) and the bedrock is Chagres sandstone, late Miocene or early Pliocene, massive, generally fine-grained sandstone (Stewart and Stewart 1980).

In each site, soil for potting was collected from three separate locations about 100 m apart from each other. All locations were well drained areas on flat or gently sloping terrain. At each location, soil was collected from 0 to about 40 cm deep, placed into 75 l bins and transported to the screen-house. Pots were filled with the soil as collected from the field. To the extent possible, we tried to minimize changes in soil structure by avoiding water saturation of soils and by minimizing handling. One year later, additional soil samples from 0–10 cm deep and 10–20 cm deep were collected from the same six locations for nutrient analysis. Soils for analysis were dried at room temperature and the three samples from each site at each depth were combined to yield one pooled sample from each of the Atlantic and Pacific side forests. Analyses were performed by the USU Analytical Laboratories. Soil cation exchange capacity (CEC) was determined after exchangeable cations were displaced from the soil with 1 N ammonium acetate and the solution analyzed for Ca, Mg, K and Na. Total nitrogen was determined by Kjeldhal. Acid-recoverable phosphorus and trace metals were determined after the soil was digested by concentrated HNO_3 and 30% H_2O_2 followed by inductively coupled plasma emission spectroscopy.

We collected recently germinated seedlings from 23 species with contrasting distributions along the rainfall gradient (Table 1). Plants and seeds were collected in Fort Sherman (rain forest), Soberania National Park (moist forest), Fort Clayton and Parque Nacional Metropolitano (seasonal forests). Species were assigned to a distribution using multiple sources described in Appendix 1. Species were classified as wet- or dry-distribution when their range was limited to the Atlantic or the Pacific slope (respectively) or when they were widespread but clearly more abundant in one of the two regions. Eleven species had mostly wet distribution and 12 had mostly dry distribution (Table 1). Four of the dry-distribution species (*Cnestidium rufescens*, *Connarus panamensis*, *Machaerium microphyllum* and *Peritassa pruinosa*) were lianas that may have had faster rates of stem growth due to their habit. However, at the seedling stage, the leaf production and stem height growth were not different between the lianas and the trees and shrubs, so we did not analyze them separately.

Seedlings were planted in individual 1 l pots and grown inside a shaded screen-house in the town of Gamboa, which is approximately intermediate between the two coasts. There were six soil treatments: three sampling points from the wet forest and three from the dry forest. We potted five seedlings of each species in each soil treatment ($n = 690$ seedlings). The pots were randomly placed inside the screen-house, and regularly relocated to avoid potential differences in the light levels in different parts of the house. Because of space limitations, the experiment was carried out in two phases. The first part of the experiment included 12 of the 23 species (from both distributions, Table 1) and ran from November 2005 to April 2006, mostly during the dry season. The second part of the experiment included the last 11 species and ran between April and September 2006, mostly during the rainy season. Light during the experiment was roughly 10% of the full sun. Because of the differences in seasons, light in the screen-house was higher for the first part of the experiment than for the second part

Table 1. List of species used in the experiment with habit, range based on presence/absence, preferred distribution based on abundance (Dist) and seedling collection site (Origin). Collection sites were Clayton (CL), Metropolitano (ME), Soberania (SO) and Sherman (SH). [1]species tested during the first five months of the experiment. [2]alternatively, this could be *M. milleflorum*, also with dry distribution.

Sp-code	Species	Habit	Range	Dist	Origin
chryca	*Chrysophyllum cainito* (Sapotaceae)[1]	tree	wide	dry	CL
cnesru	*Cnestidium rufescens* (Connaraceae)[1]	liana	dry	dry	CL
cojoru	*Cojoba rufescens* (Fab./Mimosoideae)	tree	wide	dry	ME
connpa	*Connarus panamensis* (Connaraceae)[1]	liana	dry	dry	CL
faraoc	*Faramea occidentalis* (Rubiaceae)	shrub	wide	dry	SO
hymeco	*Hymenaea courbaril* (Fab./Caesalpinioideae)[1]	tree	dry	dry	SO
machmi	*Machaerium microphyllum c.f.* (Fab./Papilionoideae)[2]	liana	dry	dry	ME
ormoma	*Ormosia macrocalyx* (Fab./Papilionoideae)[1]	tree	wide	dry	SO
peripr	*Peritassa pruinosa* (Hippocrataceae)	liana	wide	dry	CL
pipere	*Piper reticulatum* (Piperaceae)	shrub	wide	dry	ME
protte	*Protium tenuifolium* (Burseraceae)	tree	dry	dry	SO
tripcu	*Triplaris cumingiana* (Polygonaceae)[1]	tree	wide	dry	SO
brosut	*Brosimum utile* (Moraceae)[1]	tree	wet	wet	SH
ingama	*Inga marginata* (Fab./Mimosoideae)[1]	tree	wet	wet	SH
lacmpa	*Lacmellea panamensis* (Apocynaceae)[1]	tree	wet	wet	SH
licahy	*Licania hypoleuca* (Chrysobalanaceae)	tree	wet	wet	SH
manibi	*Manilkara bidentata* (Sapotaceae)	tree	wet	wet	SH
oxanpa	*Oxandra panamensis* (Annonaceae)[1]	tree	wide	wet	SH
poutre	*Pouteria reticulata* (Sapotaceae)[1]	tree	wet	wet	SH
psycgl	*Psychotria glomerulata* (Rubiaceae)	shrub	wet	wet	SH
pterro	*Pterocarpus rohrii* (Fab./Papilionoideae)[1]	tree	wet	wet	SO
tapigu	*Tapirira guianensis* (Anacardiaceae)	tree	wet	wet	SH
tocopi	*Tocoyena pittieri* (Rubiaceae)	tree	wet	wet	SH

(Nov–Apr: 2.8 ± 0.1, Apr–Sep: 1.30 ± 0.04 mol m^{-2} day^{-1}). However, growth rates did not differ between the two phases of the experiment (less than 2% difference, $p = 0.93$), so the two experiments were analyzed together.

Once a month for five months we censused each seedling, measured stem height (cm), and counted the new leaves produced since the last census. For each individual seedling we calculated stem growth per month, and new leaf production per month. Because the length of the experiment was relatively short (five months for each phase) and because seedlings were small when the experiment started, growth and leaf production were linear for the duration of the experiment. Thus, stem growth was calculated using a linear regression of height as a function of time. The slope of the regression is the stem growth, and units were cm $month^{-1}$. Leaf production was calculated by summing all new leaves produced for each plant during the experiment and dividing by the total number of months the plant was in the experiment. Because there were large among-species differences in the size of the leaves, leaf production was converted to area using the average size of the leaves for each species. Thus leaf production is in units of cm^2 $month^{-1}$.

Data were analyzed using R software. All growth data were log-transformed to normalize for analysis. We tested the interaction of soil origin and species distribution in both seedling growth variables using linear mixed-effect models (nlme package, Pinheiro and Bates 2004). The fixed effects were the soil origin (two levels: wet vs dry forest) and the species distribution (two levels: wet- vs dry-distribution). Random blocking factors were the species (23 levels) and the collection points (three per site), as maximum likelihood analysis indicated that both factors introduced significant variation in the model. To assess among-species variation in the response to soil treatment we used meta-analysis techniques. The effect size was calculated for each species as the log of the response ratio to the two soil treatments (log-ratio = log (growth in dry-origin/growth in wet-origin). Among-species variation was tested as described in Gurevitch and Hedges (1993). The 95% confidence intervals for the pooled effects were calculated using bootstrap randomizations.

Results

Based on both the chemical analysis and the growth rates of the seedlings, the dry site (Pacific) had better soil quality than the wet site (Atlantic). The pooled soil sample from the dry site at 0–10 cm had greater total content of some important macro- and micro-nutrients (Table 2: P, K, Fe, Mn) and slightly higher cation exchange capacities (CEC), all characteristics representing higher nutrient availability. They also had lower content of Al, which at low pH can be toxic. Deeper (10–20 cm) wet-origin soils were considerably more depleted than the dry-origin soils in some of the nutrients (Table 2, N, K, Ca, Mg, Mn). The wet-origin soil also had higher Na concentrations, probably due to its nearness to the coast. Consistent with the soil nutrient results, plants growing in the dry-origin soils performed significantly better in both growth variables. Compared to plants growing in the wet-origin soils, seedlings planted in the dry-origin soils grew on average 37% more new leaf area ($F = 35.5$, $DF = 1/113$, $p < 0.0001$) and 54% more in stem height ($F = 35.7$, $DF = 1/113$, $p < 0.0001$) per month (Fig. 1). Inspection of the growth data showed that five of the collection points are consistent with this pattern, with one dry-site point supporting slightly lower growth than the other two.

While, on average, growth was better in dry-origin soils, the response of individual species to soil treatments was significantly variable (Fig. 2). Four of the 11 wet-distribution

Table 2. Total content and cation exchange capacity (CEC) of soil minerals for the dry, Pacific site and the wet, Atlantic site at two depths.

Depth	Units	Dry-site		Wet-site	
	cm	0–10	10–20	0–10	10–20
N-Kjeldhal	%	0.32	0.20	0.32	0.16
P	%	0.05	0.04	0.03	0.03
CEC	cmol kg^{-1}	26.8	25.9	25.4	24.6
Ca	%	0.18	0.11	0.23	0.04
Mg	%	0.15	0.14	0.13	0.05
K	%	0.022	0.020	0.011	<0.01
Na	mg kg^{-1}	26.1	48.1	165	65.3
Fe	%	7.11	6.49	3.93	4.29
Mn	mg kg^{-1}	1023	570	228	205
Zn	mg kg^{-1}	59.9	47.6	99.5	48.6
Cu	mg kg^{-1}	32.8	32.8	34.3	15.5
Co	mg kg^{-1}	16.8	12.5	<2.0	<2.0
Cr	mg kg^{-1}	7.39	6.72	37.8	29.8
S	%	0.03	0.02	0.04	0.04
B	mg kg^{-1}	<5.0	<5.0	<5.0	<5.0
Al	%	2.95	3.15	3.63	3.99

species had very little response to soil treatment in either leaf area production or stem growth (*Tapirira guianensis, Manilkara bidentata, Licania hypoleuca* and *Brosimum utile*, Fig. 2). Also, two of the dry-distribution species had better growth in the wet-origin soils (*Faramea occidentalis* and *Cojoba rufescens*, Fig. 2). Notably, these two species were also present, though at lower abundance, in the wet forests. Most of those species with zero to negative response to soil origin had also some of the slowest growth rates (Fig. 3). Indeed, using each species as a point, we found that the ratio of the growth rate in dry- vs wet-origin soils showed a positive correlation with the mean growth rate of each species in the dry-origin soils (Fig. 3). In other words, the species that were faster growers had the strongest response to soil origin in both growth variables. This response to soil-origin was not different between dry- and wet-distribution species. The interaction between species distribution and soil origin was not significant for leaf area production ($F = 1.64$, $DF = 1/113$, $p = 0.20$) or for stem height growth ($F = 0.29$, $DF = 1/113$, $p = 0.58$). Also, species rank in growth rate correlated between wet- and dry-origin soils, such that the faster growing species were the same in both soil types (Kendall's rank correlation for leaf area: $\tau = 0.68$, $p < 0.0001$; stem height: $\tau = 0.41$, $p = 0.005$).

Although there were some slow-growers among the wet-distribution species and some fast-growers among the dry-distribution plants (Fig. 3), in general, wet-distribution species had faster growth rates than dry-distribution species. The two growth variables covaried among species ($r^2 = 0.4$, $p = 0.001$). Thus, we joined the two growth variables into one single principal component (pc1) that summarized the main axis of variation in growth (variable loads: leaf area = height growth = 0.71, SD = 1.28). The effect of soil origin using this pc1 was the same as with the analysis of the two variables separately, so we do not report it here. Mean pc1 growth rates were significantly different for species with different distributions ($F = 4.3$, $DF = 1/131$, $p = 0.044$), mostly due to the variation in leaf area production (Fig. 3). Wet-distribution species on average put on 50% more leaf area than dry-distribution species ($F = 3.3$, $DF = 1/21$, $p = 0.085$). They also put on 25% more stem height, but this difference was not significant ($F = 0.71$, $DF = 1/21$, $p = 0.41$).

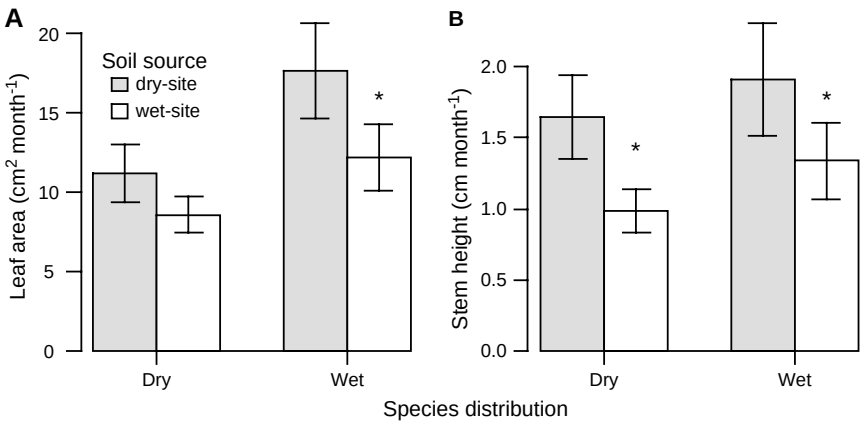

Figure 1. Average growth per month in leaf area (A) and stem height (B) for seedlings with dry and wet distributions planted in dry- and wet-origin soils. Error bars are standard errors and *indicate significant differences between soil sources at $p < 0.05$.

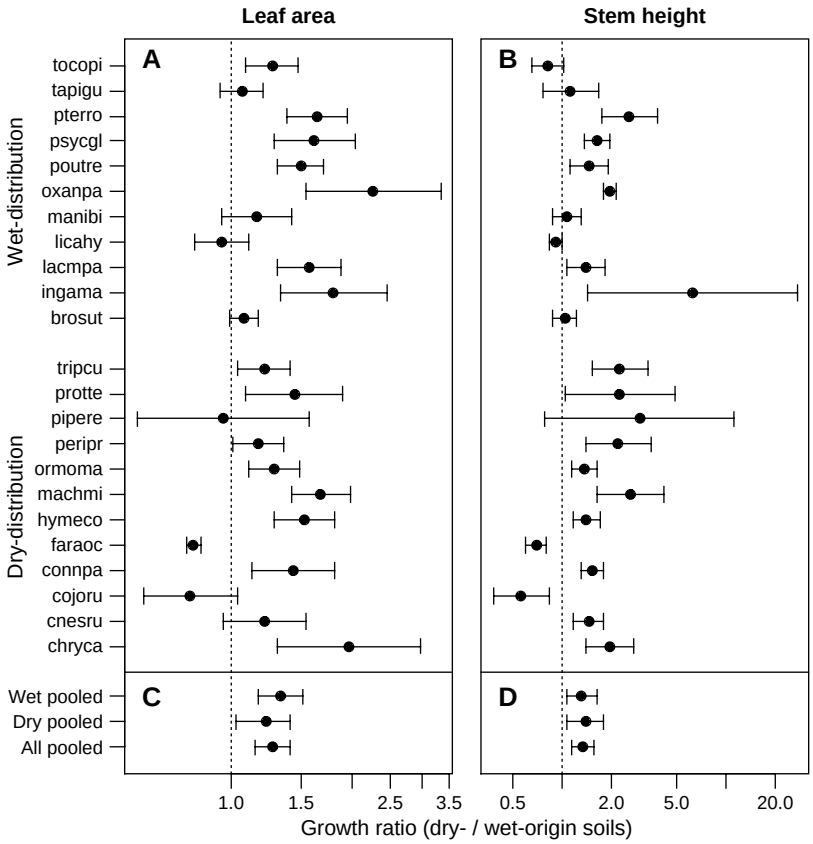

Figure 2. Ratio of growth in the two soil origins for leaf area production in cm^2 $month^{-1}$ (A, C) and for stem height growth in cm $month^{-1}$ (B, D), ratio = 0 represents no difference in growth and ratio > 1 indicates better growth in the dry-origin soils. The responses of individual species (A, B) were significantly variable (leaf area: Q = 100, DF = 22, p < 0.0001, stem height: Q = 81, DF = 22, p < 0.0001); error bars are SE. Pooled values (C, D) were all significantly positive; error bars represent bootstrap 95% CI.

Discussion

The higher overall leaf and stem growth of seedlings planted in the dry-origin soils support the hypothesis that soil fertility correlates inversely with rainfall across the Isthmus of Panama. Our soil chemical analyses also support this hypothesis. Although our soil analyses are only one-point, non-statistical measurements, the change in soil fertility from the wet to the dry sides of central Panama has been well characterized (Pyke et al. 2001, Santiago et al. 2005). Notably, differences in soil quality are present despite complex geological variation in bedrock and soil order, suggesting that other environmental factors determine soil nutrient availability. Leaching may influence the availability of more mobile nutrients (Schuur and Matson 2001). Santiago et al. (2005) also showed that the lower fertility in the wetter side of the Isthmus was partly explained by slower mineralization rates and lower quality of the

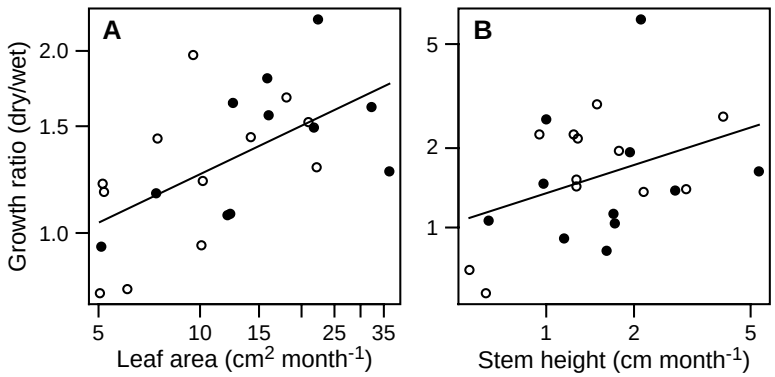

Figure 3. Correlation between the mean growth rate in the fertile, dry-forest soil and the ratio of the growth in the two soils. Each point is a species. (A) New leaf area production in cm^2 $month^{-1}$ (F = 11.26, DF = 21, p = 0.003), and (B) stem height growth in cm $month^{-1}$ (F = 3.6, DF = 21, p = 0.07). Lines represent best fits, and symbols are for wet-distribution species (solid) and dry-distribution species (open).

leaf litter from the most common tree species in those forests. Our results provide added insight by showing that the observed differences in soil fertility across the Isthmus of Panama were relevant to the growth performance of seedlings.

If soil fertility contributes to limit species distribution along this rainfall gradient, we expected wet-distribution species to be better adapted to poor soils and this to result in home-soil advantage. Instead, we found that wet-distribution species outperformed dry-distribution species in both soil types (Fig. 1), suggesting that the richer soils did not provide a growth advantage to dry-distribution species. Also, if wet-distribution species are more adapted to poor soils, they should be less sensitive to decreases in soil quality. Instead, with respect to stem height growth, there was not difference in the sensitivity of wet- and dry-distribution species to decreases soil quality. Further more, with respect to leaf area production, wet-distribution species had a slightly stronger response than dry-distribution species (Fig. 2C). Although, this effect probably results from the faster leaf area production rates of wet-distribution species (Fig. 3A). This suggests that wet-distribution species are not better adapted to poorer soils than dry-distribution species. Thus our results provide little evidence that soil quality contributes to species turnover along the Isthmus of Panama. However, this conclusion is limited to seedling recruitment, as it is still possible that soil fertility may influence mortality or plant performance at other ontogenetic stages, such as the reproductive stage.

While dry- and wet-distribution species differed little in their sensitivity to soil treatment, there was significant variation among individual species (Fig. 2). The species response to soil treatment was more strongly associated with inherent growth rates (Fig. 3) than with species distribution (Fig. 2). Indeed, with respect to leaf area production, the small difference in sensitivity between dry- and wet-distribution species (Fig. 2C) is probably more a reflection of the differences in growth rates between these two groups of species than of any adaptation to soils. Furthermore, with respect to stem height growth, dry- and wet-distribution species did not differ in their responses to soil type (Fig. 1B, 2D) or in mean growth rates (Fig. 1B), but the correlation between growth rates and soil response ratios was marginally significant (Fig. 3B). These correlations suggest that fast-growing species are more able to take advantage of better quality soil, and that slow-growing species are less plastic to differences in resource availability.

Many studies have reported significant soil–plant associations (Borchert 1994, Clark et al. 1998, Harms et al. 2001, Phillips et al. 2003, John et al. 2007), but only some have specifically reported correlations with soil chemical characteristics (Swaine 1996, John et al. 2007). In the absence of experimental manipulations, those studies did not propose a mechanism to explain the associations. Studies that used reciprocal transplant experiments to study the mechanisms of species–soil associations found that manipulation of fertility had little effect on seedling performance (Palmiotto et al. 2004, Baltzer et al. 2005). Instead, species–soil associations were largely explained by soil water availability and species water use efficiency (Baltzer et al. 2005). When studying soil–plant associations, it is important to note that the environmental covariates are different depending on the spatial scale of the associations. At the local scale (same ecosystem), soil characteristics often correlate positively, such that the highest nutrient availability is found in the soils with higher water availability. For example, clay soils have higher nutrient and water availability than sandy soils, and slopes have higher nutrient and water availability than plateaus. Instead, at the regional scale (across ecosystems), as in our experiment, soil fertility can have an inverse relationship with water availability (Schuur and Matson 2001). By using controlled experiments, we showed that, in the absence of water and light limitations to growth, soil differences across the rainfall gradient clearly influenced seedling performance but not in a pattern that could explain observed species turnover.

As wet-distribution species grew on average faster than dry-distribution species, it is possible that our data reflect instead a tradeoff between tolerance to drought stress and growth rates. Ranks of species growth rates were nearly parallel between the two soil types, suggesting that the faster-growing species were the same regardless of the soil resources. This trend was similar for both leaf production and height growth, although it was mostly influenced by the first parameter. It has been hypothesized that there is a tradeoff between tolerance to abiotic stress and growth rates (Grime 1977, Russo et al. 2005, Baltzer et al. 2008), and this pattern is consistent with the more widespread ranges of dry-forest species (Table 1, Baltzer et al. 2007). In a study in a rainforest in the Malay–Thai peninsula, species restricted to wetter forests also had faster growth rates and larger growth responses to different soil types, while widespread species (found also in drier forests) were less sensitive to differences in soil type (Baltzer et al. 2007). In Borneo, species associated with sandy soils, which had lower fertility and water capacity, had the slowest growth and mortality rates (Russo et al. 2005). Baltzer et al. (2005) showed that species specialized to sandstone soils, which have lower water storage capacity, had better water use efficiencies and lower maximum photosynthetic rates. Indeed, some of the mechanisms that confer tolerance to drought or other stresses could also impose a constraint on growth rates. For example, narrow vessels that decrease the vulnerability to cavitation of the xylem may decrease water supply to the photosynthetic tissue (Hacke et al. 2006).

In conclusion, our results are consistent with the hypothesis that the tradeoffs imposed by drought tolerance may be a more important determinant of species competitive ability along a rainfall gradient than soil associations. Currently, there is mounting evidence suggesting that seasonal drought (Baraloto et al. 2007, Engelbrecht et al. 2007, Baltzer et al. 2008), low soil water capacity (Palmiotto et al. 2004, Baltzer et al. 2005, Russo et al. 2005) or isolated drought events (Condit et al. 2004), are important constraints for drought-intolerant species. Thus, drought adaptations, which allow some species to colonize drier forests, may prevent those same species from efficiently competing against fast-growing species in wetter

forests. By experimentally measuring plant responses to natural variation in different environmental variables, we may be able to model how the different stressors interact with each other. Such insights will be important to elucidate the mechanisms that determine species distribution and beta-diversity in tropical forests.

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Appendix 1

Species distribution was established using the following sources:

Tree Atlas of Panama (<http://ctfs.si.edu/webatlas/maintreeatlas.html>) of the Center for Tropical Forest Science. Contains descriptions of species distributions and maps of presence and absence in plots throughout the Isthmus of Panama.

Center for Tropical forest Science datasets (<http://ctfs.si.edu/datasets/>). Contain tables of abundance by species in two forest dynamics plots: the Fort Sherman canopy crane field site, in the Atlantic side of the Isthmus, and in the Cocoli plot in the Pacific side of the Isthmus.

W3 Tropicos database (<http://mobot.mobot.org/W3T/Search/vast.html>). Contains lists and maps with locations of the herbarium specimens located in the

Missouri Botanical Garden. We focused on the Mesoamerican specimens.

INBio plant search (<http://www.inbio.ac.cr/bims/PLANTAE.html>). Contains a list of herbarium specimens and their collection locations for the INBio herbarium in Costa Rica.

STRI database <http://biogeodb.stri.si.edu/bioinformatics/databases/herbarium/collections.php>). Contains specimen records and collection locations from the Smithsonian Tropical Research Institute and the University of Panama herbaria.

Published data in Engelbrecht, B. M. J. et al. Nature 447: 80–83 (2007). Contains data on distribution along the rainfall gradient for some of the focal species.

Field observations by Gonzalo Rivas and Marcos Rios (Rivas & Rios, unpubl.), and expert opinion by Rolando Perez and Salomon Aguilar.

Table A1. Mean growth rates in leaf area production and stem height growth for each of the focal species in the dry- and wet-origin soils. Species six-letter code is formed by the first four letters of the genus and the first two letters of the species. [1]SE and means are estimated based on a sample size of n = 3, representing the mean growth rate for the five seedlings grown in each of the soil collection points from each site.

Distribution	species	Leaf area (cm^2 $month^{-1}$)				Stem height (cm $month^{-1}$)			
		Dry-origin		Wet-origin		Dry-origin		Wet-origin	
		mean	SE[1]	mean	SE	mean	SE	mean	SE
Dry	faraoc	6.1	0.2	7.5	0.1	0.55	0.07	0.80	0.06
Dry	chryca	9.6	1.0	4.9	2.3	1.79	0.18	0.91	0.35
Dry	cnesru	10.2	2.0	8.3	0.9	1.27	0.22	0.88	0.05
Dry	cojoru	5.0	0.3	6.4	1.1	0.62	0.06	1.11	0.25
Dry	connpa	7.5	1.2	5.2	0.8	1.28	0.15	0.84	0.05
Dry	hymeco	21.0	1.6	13.7	0.5	3.01	0.29	2.16	0.37
Dry	machmi	18.1	2.0	10.8	1.1	4.06	0.87	1.54	0.43
Dry	ormoma	22.2	1.3	17.3	2.5	2.16	0.21	1.59	0.23
Dry	peripr	5.2	0.6	4.4	0.4	1.28	0.30	0.59	0.11
Dry	pipere	10.1	3.1	10.5	2.0	1.50	0.55	0.51	0.32
Dry	protte	14.2	1.7	9.9	1.4	0.95	0.33	0.42	0.12
Dry	tripcu	5.2	0.7	4.3	0.2	1.25	0.28	0.55	0.06
Wet	brosut	12.3	0.4	11.4	0.5	1.72	0.09	1.67	0.28
Wet	ingama	15.8	2.9	8.8	1.3	2.11	0.62	0.34	0.09
Wet	lacmpa	16.0	0.8	10.2	2.1	2.77	0.10	2.00	0.58
Wet	licahy	5.1	0.7	5.3	0.4	1.15	0.09	1.27	0.07
Wet	poutre	21.8	1.5	14.5	1.7	0.98	0.20	0.67	0.06
Wet	psycgl	32.2	4.6	19.9	3.0	5.37	0.63	3.27	0.35
Wet	pterro	12.6	1.0	7.7	1.2	1.00	0.19	0.39	0.07
Wet	tapigu	12.1	0.7	11.3	1.2	1.70	0.38	1.52	0.50
Wet	tocopi	36.3	4.4	28.7	1.9	1.62	0.31	1.99	0.22
Wet	manibi	7.4	1.0	6.4	0.7	0.63	0.10	0.60	0.06
Wet	oxanpa	22.4	4.4	9.9	1.9	1.93	0.05	1.00	0.10