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Plant traits in relation to the performance and distribution of woody species in wet and dry tropical forest types in Panama

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Summary

1. Understanding the factors that limit species distributions along environmental gradients is a central question of ecology. Here, we evaluate the hypothesis that the traits that result in performance trade-offs between habitats contribute to the turnover of woody species along a rainfall gradient in the Isthmus of Panama.

2. We studied 24 plant species with contrasting distributions along this rainfall gradient. We measured 18 morphological and physiological traits, and three performance variables in seedlings planted in common garden experiments in two contrasting sites across the Isthmus.

3. We found evidence for a trade-off suggesting that better survival during the dry season corresponded to a lower growth rate in the forest understorey. This trade-off correlated well with the distribution of the species along the rainfall gradient and was explained mostly by variation in photosynthetic capacity.

4. While not all species fit into this trade-off, most dry-distribution species, which we had previously reported to have higher drought survival, were associated with higher stem hydraulic conductance and higher capacity for CO_2 assimilation. Our interpretation is that this combination of traits may be associated mostly with desiccation avoidance (deep roots) or desiccation delay (deciduousness) rather than desiccation tolerance. Despite their higher photosynthetic capacity, these species had lower growth in the low-light understorey, probably because of higher maintenance costs (dark respiration rates).

5. Wet-distribution species, on the other hand, had lower photosynthetic capacity and higher leaf area ratio. This strategy is typical of shade-tolerant species and may explain their higher growth rates in the low-light understorey.

6. In conclusion, our results suggest that habitat associations along the rainfall gradient in the Isthmus of Panama may result in part from a trade-off between traits that are favourable to species that avoid or delay desiccation but that otherwise limit shade tolerance. This trade-off may limit the capacity of some dry-distribution species to colonize wet forests.

Key-words: biomass allocation, defence, drought tolerance, photosynthesis, plasticity, rainfall gradient, shade tolerance, trade-offs, tropical forest

Introduction

Species turnover at the landscape and regional scales is an important component of tropical diversity. For that reason, understanding the factors that limit species distribution is a central question in ecology. At the regional scale, dispersal limitation may constrain species ranges and increase species turnover (Chust *et al.* 2006). However, it has also been shown that along environmental gradients, species turnover is larger than expected solely from dispersal limitation (Swaine 1996; Bongers *et al.* 1999; Clark, Palmer & Clark 1999; Pyke *et al.* 2001; Phillips *et al.* 2003; Davidar *et al.* 2007), suggesting that plant–habitat

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associations also play an important role in species distribution. Plant–habitat associations result from adaptations to environmental conditions that are specific to a site or that differ among sites. Such adaptations or traits can impose trade-offs in performance, such that a trait that results in high performance in one habitat can result in low performance in a different one, resulting in species being competitive only in a subset of environmental conditions. In this study, we use a reciprocal transplant experiment to investigate the mechanisms by which plant traits may explain species performance and distribution in sites with contrasting rainfall in the Isthmus of Panama.

The Isthmus of Panama contains a nearly continuous stretch of forest that spans a gradient in rainfall, from nearly 2000 mm of rainfall per year near the Pacific Ocean to more than 3000 mm of rainfall per year on the Atlantic side. Even though this is a moderate gradient and the Isthmus is only 60 km wide, extensive plot data show considerable turnover of tree species (Pyke *et al.* 2001). Indeed, the correlation of tree distribution with rainfall and seasonality has been well documented in other locations as well (Bongers *et al.* 1999; Davidar *et al.* 2007), and a substantial amount of empirical evidence supports a central role for adaptations that confer drought resistance in determining species distributions (Engelbrecht *et al.* 2007; Baltzer *et al.* 2008; Brenes-Arguedas, Coley & Kursar 2009). While less often considered, pest pressure, light availability in the understorey and soil fertility may also correlate with annual rainfall (Wright & van Schaik 1994; Coley & Barone 1996; Swaine 1996; Givnish 1999; Santiago, Schuur & Silvera 2005). As these variables have also been shown to contribute to species distribution at the local scale (Denslow 1987; Fine, Mesones & Coley 2004; John *et al.* 2007), they may also contribute to species distribution along rainfall gradients.

In our reciprocal transplant experiment, we planted replicated plots in two sites in opposite sides of the Isthmus with contrasting rainfall and seasonality. Plots had seedlings from species with contrasting distributions along the rainfall gradient. We found that water limitations during the dry season were the main factor limiting the performance of wet-distribution species in the drier forest and that dry-season watering treatments eliminated this disadvantage (Brenes-Arguedas, Coley & Kursar 2009). Herbivore damage, low light and poor soils appeared to have little effect on species distribution along this gradient (Brenes-Arguedas *et al.* 2008, 2011; Brenes-Arguedas, Coley & Kursar 2009). However, wet-distribution species had faster growth rates than dry-distribution species and stronger growth responses to better soil and light conditions (Brenes-Arguedas *et al.* 2008, 2011; Brenes-Arguedas, Coley & Kursar 2009). Here, we report how the functional traits of the study species correlate with distribution and the performance differences seen in those experiments.

How traits may influence performance and distribution is complex because multiple, distinct trait combinations or trait syndromes could explain similar performance outcomes (e.g. Poorter & Markesteijn 2008). For example, dry-forest species could exhibit traits associated with desiccation tolerance or desiccation avoidance, two possible strategies to survive prolonged droughts. Desiccation tolerance can be explained by traits such as high stem density, cavitation-resistant xylem, tough, thick tissues and good cell survival at low water content (Kursar *et al.* 2009). Alternatively, dry-forest species may avoid desiccation by having deeper or thicker tap roots that provide water and carbohydrate storage (Borchert 1994; Poorter & Markesteijn 2008; Markesteijn *et al.* 2011). Similarly, species from wetter forests may have adaptations such as longer, thinner roots that increase resource acquisition in poor soils (Paz 2003; Poorter & Markesteijn 2008) or higher leaf area to capture more light in the shady forest understorey. Adaptations to the understorey may also include those that reduce pest pressure and increase leaf persistence, such as tougher and more lignified leaves (Coley 1988; Kitajima 1994; Poorter & Bongers 2006; Alvarez-Clare & Kitajima 2007; Poorter & Kitajima 2007). Species characterized by high understorey survival or conservative water-use strategies may have lower growth rates than resource-demanding species (Kitajima 1994).

Here, we address the following questions: (i) combining all 24 study species of wet and dry distribution, do individual traits or trait combinations correlate with differences in seedling performance, such as drought resistance, growth rate and leaf damage (ii) can wet- and dry-distribution species be distinguished based on their traits or trait combinations? If so, are these traits consistent with adaptations to the environmental conditions at our dry and wet study sites? Based on our previous analyses of this system, we expect that dry-distribution species should have traits that increase drought performance and that some drought-resistant strategies may also impose constraints on growth rate in the understorey of the wet forest (Brenes-Arguedas *et al.* 2008, 2011; Brenes-Arguedas, Coley & Kursar 2009).

Materials and methods

STUDY SPECIES

We measured traits from 24 tree, liana and shrub species with contrasting distributions along the rainfall gradient in the Isthmus of Panama (listed in Table S1 in Supporting Information). All study species were shade-tolerant and commonly found in the forest understorey. The species were classified as wet or dry distribution 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. Species with unclear distributions along the rainfall gradient were not included in this analysis. Seedling collection and classification are described in detail in Brenes-Arguedas, Coley & Kursar (2009).

STUDY SITES

We established 40 common garden plots in each of two forest sites. One forest site was a forest fragment in Ciudad del Saber, Clayton (9°0′50″N, 79°35′W), on the Pacific side of the Isthmus. The area has lowland, semi-deciduous dry forest, with a clearly marked 3–4-month dry season and mean annual rainfall of 2010 mm. The other forest site was at Parque Nacional San Lorenzo (9°17′N, 79°58′W), on the Atlantic side of the Isthmus. The area is characteristic of lowland, evergreen wet forest, with a weak dry season and mean annual rainfall of 3020 mm. The plots were all placed in the shady forest understorey. In each plot, we planted one seedling of each of the study species. Seedlings were planted between July and December 2005 and harvested 1 year later, in December 2006 to January 2007, to measure traits.

The experimental design for the common garden plots in the field also included water supplementation and herbivore exclusion treatments. These experimental manipulations had little effect on the trait expression (see Table S2 in Supporting Information), and their effect on species performance has already been described in detail in Brenes-Arguedas, Coley & Kursar (2009). Hence, for this study, we ignored the experimental treatments for trait measurements and only mention them when necessary to describe the measures of performance.

Because the field seedlings were quite small, four traits that required larger individuals were measured on shade-house-grown plants. Shade-house plants were kept in 1-L pots, well watered and partly shaded in the facilities managed by Smithsonian Tropical Research Institute in Barro Colorado Island, located in the middle of the Isthmus.

TRAITS AND PERFORMANCES

From a previous analysis, we know that plant performance differed significantly between the two experimental sites (Brenes-Arguedas, Coley & Kursar 2009). Preliminary analysis for this paper also showed that the expression of many of the plant traits differed between the dry and the wet sites (Table S2 and Fig. S1, Supporting information). To account for this, whenever possible, we evaluated the traits and performance separately for the two sites.

Growth performance (Gr) was measured as gross leaf production in the common gardens. We calculated the total number of new leaves produced by each seedling for the duration of the experiment and divided by the total number of months the plant was alive in the experiment. Leaf numbers were converted to leaf area by multiplying by the mean leaf area of each species such that leaf growth is in units of $\text{cm}^2\ \text{month}^{-1}$. Gr differed significantly between sites but not due to watering or herbivore exclusion treatments (Brenes-Arguedas, Coley & Kursar 2009). Hence, we pooled all experimental treatments and calculated average Gr for each species in each site. Species ranks in Gr were largely maintained among sites ($r = 0{\cdot}85$, $P < 0{\cdot}0001$; Fig. S2, Supporting information), but the environmental conditions in the drier site yielded the highest Gr.

Leaf damage (Dmg) was measured at the end of the experiment, in November 2006. It is the average percentage of leaf area damaged for the three (or four, for species with opposite leaves) most apical, fully expanded leaves of the seedlings. It included 100% leaf loss when evidenced by scars in the stem. Dmg differed between sites and due to herbivore exclusion treatment but not due to watering (Brenes-Arguedas, Coley & Kursar 2009). Hence, for this analysis, we calculated mean Dmg per species at each site, only using the plots with no herbivore exclusion. Species ranks in Dmg also correlated between the two study sites ($r = 0{\cdot}55$, $P = 0{\cdot}01$; Fig. S2, Supporting information), with plots at the wet site showing the highest Dmg and discrimination among species (Brenes-Arguedas, Coley & Kursar 2009).

Drought performance (Dp) is the ratio of percentage seedling survival in the unwatered relative to the watered plots during the dry season. This is calculated only for the dry site, because there is rarely significant dry-season water stress at the wet site. The index of Dp ranges from zero, for species with the poorest drought performance, to one, for species with the highest drought performance (Engelbrecht & Kursar 2003). However, our experiment occurred in a year with a relatively short dry season in which many seedlings may not have experienced serious water stress and seedling mortality was low. Hence, we did not achieve maximum discrimination among species with respect to Dp. This was especially notable among the more drought-resistant species which, on occasion, had values higher than one, suggesting higher mortality in the watered plots.

Leaf life span (LL) was measured for seedlings without herbivore exclusion or water supplementation in both sites. A total of 190 leaves in both sites were marked upon expansion, and their survival was followed monthly until June 2006. Leaves still alive at the end of the measurements and those that died when the whole plant died were considered censored observations. We report leaf half-life = $\log(0{\cdot}5)/\log(1-e^{a})$, where a is the parameter obtained from fitting the regression log(percentage alive) = $b + a$ (time in years). We pooled the data from the two sites because LL did not significantly differ between them (analysis not shown), and sample size was too small for any given site. However, most of the leaves that we followed were from the dry site. We were able to quantify LL for only 14 species, as not all species produced or lost enough leaves during the experiment.

At the end of the field experiment, we harvested six or more plants per species per site. To ensure that the allocation and tissue properties of the harvested plants reflected local conditions, we harvested only seedlings that had shown positive growth. We used a hand shovel to extract the seedlings from the ground with minimal effects on the roots and carefully separated the soil from the roots by submerging the seedlings in water.

Leaf toughness (Tgh) was measured as the average force needed to perforate a leaf. It was determined in the field immediately upon harvest using a Chatillon pressure gauge with a 3-mm-diameter rod. Due to the small size of the leaves of some species, we measured toughness only on 16 species.

Harvested seedlings were placed in humidified plastic bags upon collection and transported to the Barro Colorado Island Laboratory. For each harvested seedling, we separated leaves (including leafy cotyledons when present), stem and roots within 24 h of collection. We measured the area of one to three, fully expanded, undamaged leaves per seedling using a LI-3000 leaf area meter (LiCor Biosciences, Lincoln NE, USA). The entire root system of half of the harvested seedlings was spread out in a water-filled container and digitized with a flatbed scanner within 24 h of collection. The resulting images were analysed with Delta-T SCAN (Delta-T, Burwell, Cambridge, UK) to estimate total root length (mm). Subsequently, the dry weight to 0·1 mg was obtained for all plant parts (70 °C for at least 48 h). Here, we report Leaf Mass per Area (LMA), the leaf dry weight divided by the leaf fresh area; Specific Root Length (SRL), the root length divided by the root dry mass; Root Length per Plant Mass (RLPM), the root length divided by the whole-plant biomass; the Leaf, Stem and Root Mass Fractions (LMF, SMF and RMF, respectively), the dry weight of each tissue divided by the whole-plant biomass; and Leaf Area Ratio (LAR), the leaf area divided by the whole-plant biomass, here calculated as LMF/LMA.

Dry leaf material from three individuals per species from the unwatered plots of both sites was measured using continuous flow isotope ratio mass spectrometry (SIRFER Lab, University of Utah). We measured nitrogen and carbon content per mass (N_{mass} and C_{mass}: g (g DW of leaf)$^{-1}$) and carbon isotope ratio (δ^{13}C). Nitrogen content per area (N_{area}) was calculated as N_{mass}*LMA. Carbon isotope discrimination ($\Delta^{13}C_{\text{leaf}}$) was calculated as $(\delta_{\text{air}}-\delta^{13}\text{C})/(1 + \delta^{13}\text{C})$, where δ_{air} is the isotopic ratio of ambient air [here assumed to be −11·4 ‰, reported for the understorey of a tropical forest (Farquhar, Ehleringer & Hubick 1989)]. $\Delta^{13}C_{\text{leaf}}$ is always positive, and a high value of $\Delta^{13}C_{\text{leaf}}$ corresponds to a high internal concentration of CO_2 in leaves (high c_i). We analysed only unwatered seedlings because the stable isotope ratio of carbon is very sensitive to plant water status.

Stem density (SD) was measured for 2–10 individuals per species on potted plants grown in the shade house. A piece of stem 3–5 cm long was cut in half longitudinally, the bark and pith were removed, and we determined the volume using Archimedes' principle of water displacement. Stem sections were then dried at 70 °C for at least 48 h or to constant mass, to calculate dry weight per stem volume.

We measured light–response curves on one to two leaves from at least four plants per species grown in the shade house under homogenous light conditions. We used a LI-6400 gas exchange system (LiCor Biosciences, Lincoln NE, USA), recording at 14 light levels between 0 to 1500 mol m^{-2} s^{-1}. We computed maximum assimilation (A_{max}) and dark respiration (R_{dark}) using Photosyn Assistant (Dundee Scientific, Scotland, UK). R_{dark} is reported as a positive value, such that larger numbers represent higher respiration rates.

Whole-stem hydraulic conductance ($k_{ws/la}$) was measured using a vacuum method (Kolb, Sperry & Lamont 1996). After gas exchange measurements, three to six plants per species were submerged in water, while stems were cut at the soil surface and leaves were removed. Total leaf area was determined. The cut stem was placed in 0·10 M KCl solution, and flow rates were measured sequentially at 0, −24, −47, −71, −59, −36, −12 and 0 kPa, using a Sartorius CP2250 balance with an accuracy of 0·05 mg (Precision Weighing Machines, Bradford, MA, USA). $k_{ws/la}$ was calculated from the linear regression of flow as a function of pressure. This measurement was normalized by total leaf area, giving leaf area-specific, whole-stem hydraulic conductance.

For 13 species, we measured desiccation sensitivity (Ψ_{LD50}) as the leaf water potential (Ψ) at which 50% mortality occurs, as described in detail in Kursar *et al.* (2009). At least 20 plants of each species were denied water for several days up to 3 weeks. Each plant was measured once for Ψ and survival. Ψ was measured on two to five leaves at mid-morning with 5·6 mm^2 leaf discs using leaf-cutter psychrometers (Merrill Engineering, Logan, UT, USA) interfaced with a CR7 datalogger (Campbell Instruments, Logan, UT, USA). We included three discs per leaf for well-watered plants and up to nine discs for plants with the lowest water status (Bennett & Cortes 1985). The psychrometers were calibrated with nine NaCl solutions spanning the range of −0·3 to −9 MPa. Water potentials between −9 and −12 MPa were extrapolated using the relationship between the water content per leaf disc and Ψ (Tyree *et al.* 2003). Survival was estimated by rewatering the plants and scoring for mortality beginning 2 weeks after rewatering. The Ψ_{LD50} was estimated as dose–response or by interpolation. These data were incorporated into our analyses as negative values. Hence, a lower (more negative) Ψ_{LD50} represents greater resistance to desiccation, whereas higher or less negative values of Ψ_{LD50} correspond to plants that are more sensitive to desiccation.

DATA ANALYSIS

All data were analysed using R software (R Development Core Team 2011). The list of traits and plant performance variables that we analyse in this paper is summarized in Table 1. Actual values for the traits per species per site are reported in the Supporting Information (Table S3 and Fig. S2, Supporting information). As most performance and trait measurements differed between sites, we ran the same analysis separately for the dry and the wet site. Both analyses had in common those measurements for which we had only one value for a species (those from the shade house, Dp and LL). Reassuringly, analyses from both sites yielded very similar results.

Identification and description of 'trait syndromes' – To take into account that many traits probably covary due to structural or

Table 1. List of performance variables and traits evaluated in this paper. Trait information includes the abbreviations used throughout the text (Abbr.), description, units, the number of species for which we had collected the trait (*N*) and the source of the seedlings used to collect the trait. As most traits showed some levels of plasticity when planted in the dry or wet site, we calculated separate values for each site when possible

	Abbr.	Description	Units	*N*	Source
Performance	Gr	Growth: new leaf area produced per month	cm^2 $month^{-1}$	24	Dry + wet
	Dmg	Leaf damage: percentage of leaf area lost at the end of the experiment in control (uncaged) subplots	%	23	Dry + wet
	Dp	Drought performance: survival in control (unwatered) relative to watered treatments in the dry site	%	23	Dry*
Allocational traits	Tgh	Leaf toughness with pressure gauge	kPa	17	Dry + wet
	LMA	Leaf mass per area	g cm^{-2}	23	Dry + wet
	C_{mass}	Carbon content per leaf dry weight	%	23	Dry + wet
	LL	Leaf life span	years	14	Mixed†
	LAR	Leaf area ratio: leaf area per whole-plant biomass	cm^2 g^{-1}	23	Dry + wet
	LMF	Leaf mass fraction: leaf mass per whole-plant biomass	g g^{-1}	23	Dry + wet
	SMF	Stem mass fraction: stem mass per whole-plant biomass	g g^{-1}	23	Dry + wet
	SD	Stem density	g cm^{-3}	23	Shade house
	RMF	Root mass fraction: root mass per whole-plant biomass	g g^{-1}	23	Dry + wet
	RLPM	Root length per whole-plant biomass	mm g^{-1}	23	Dry + wet
	SRL	Root length per root biomass	mm g^{-1}	23	Dry + wet
Physiological traits	N_{mass}	Nitrogen content per leaf dry weight	%	23	Dry + wet
	N_{area}	Nitrogen content per leaf area	g of N cm^{-2}	23	Dry + wet
	A_{max}	Maximum carbon assimilation rate	μmol m^{-2} s^{-1}	20	Shade house
	R_{dark}	Dark respiration rate	μmol m^{-2} s^{-1}	18	Shade house
	Ψ_{LD50}	Leaf water potential at which 50% mortality occurs	MPa	13	Shade house
	$k_{ws/la}$	Whole-stem hydraulic conductance per leaf area	g s^{-1} MPa^{-1} m^{-2}	21	Shade house
	$\Delta^{13}C_{leaf}$	Leaf carbon isotope enrichment above atmospheric $\delta^{13}C$	‰	23	Dry + wet

*Calculated in the dry site only, because the wet site does not show seasonal drought.

†Obtained one value combining data from both sites because of low sample size.

physiological reasons, we looked for combinations of covarying traits, or ‘trait syndromes’, using principal component analysis (PCA; ‘prcomp’ function). Because PCA is not very reliable when using a small sample size (number of species) relative to the number of variables (traits), we chose to report two separate PCAs based on subsets of the variables. We evaluated a number of possible combinations of traits, but settled for the separation between allocational and physiological traits, because they were relatively natural groupings of related traits, and we had no *a priori* expectation for a correlation between these two groups of traits. We classified as allocational those traits that described the structure or biomass allocation to plant parts (leaves, stems, roots; Table 1). We classified as physiological those traits that are more direct measurements of plant function and the chemical analysis of the leaves (Table 1). We excluded Ψ_{LD50}, Tgh and LL from the PCAs, due to low sample size (Table 1) and used nine allocational and six physiological traits for the analysis. To report the weight of each trait in the PC ordination, we calculated the factor structure correlations, which are the Pearson’s *r* correlation coefficients between each trait and the ordination.

CAN TRAITS EXPLAIN SPECIES PERFORMANCE IN THE FIELD?

To improve normality, Gr was log-transformed and the Dmg was square-root-transformed. Dp was left untransformed. We evaluated how the individual traits or the ‘trait syndromes’ obtained by the multivariate ordination explained these performance variables using simple and multivariate linear regressions. For the multiple regressions, we used stepwise AIC to find the function which best explained performance with a minimum number of predictors.

PERFORMANCE AND TRAIT DIFFERENCES FOR DRY- VS. WET-DISTRIBUTION SPECIES

We evaluated differences in trait expression between dry- and wet-distribution species. We used Wilcoxon’s rank-sum tests on individual traits and linear discriminant analysis (LDA) (‘lda’ function in R package ‘MASS’, Venables & Ripley 2002) on groups of traits. LDA is an ordination technique aimed at finding multivariate differences between grouped samples. We asked for differences between nine dry- and nine wet-distribution species for which we had measured all 15 allocational and physiological plant traits (except Tgh, LL and Ψ_{LD50}).

To further explore trade-offs in performance in the field, we also ran simple correlations, multiple correlations and LDA on the performance variables.

Results

Identification and description of ‘trait syndromes’ – We called syndromes those groups of traits that covary among species possibly due to structural or physiological reasons. We identified those using principal component analysis (PCA). A PCA using only allocational traits from the dry site summarized 71% of the variation among 22 species along two ordination axes (Table 2). This PCA was quite robust to small variations in the analysis (such as excluding a single species or a single trait). The first axis (Allocation-PC1, Table 2) explained 40% of the variance among species and suggested a gradient in tissue persistence. On the one end, species had thicker, more lignified leaves (higher LMA and C_{mass} and lower LAR) and shorter, thicker tap roots (lower SRL and RLPM) (Table 2). On the other end, species had longer, thinner tap roots and lower LMA and lignification. For simplicity, this syndrome will be called ‘robustness’ of the plant.

Table 2. Description of the three plant ‘trait syndromes’ obtained using principal component analysis (PCA) and of the trait combination that differentiates dry- vs. wet-distribution species obtained using linear discriminant analysis (LDA)

	Allocation -PC1 ‘robustness’	Allocation -PC2 Leaf:root allocation	Physiology -PC1 Photosynthetic capacity	LDA
LMA	**0·74****	0·20		−0·08
C_{mass}	**0·77****	−0·02		0·23
LAR	**−0·59****	**0·71****		−0·29
LMF	0·07	**0·97****		−0·38
SMF	0·35	−0·36		0·12
SD	0·38†	−0·34		**0·52***
RMF	−0·41†	**−0·65****		0·24
RLPM	**−0·90****	−0·29		−0·04
SRL	**−0·84****	0·08		−0·14
$k_{ws/la}$			**0·82****	**0·73****
N_{mass}			**0·76****	0·43†
N_{area}			**0·84****	0·44†
A_{max}			**0·60****	0·41†
R_{dark}			**0·66****	**0·51***
$\Delta^{13}C_{leaf}$			−0·45†	−0·12

Values are Pearson’s *r* correlation coefficients between each ordination and the traits, such that higher values (in bold) highlight the traits that define each syndrome. Symbols represent significance († $P < 0{\cdot}1$, * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$). Syndromes and correlations were nearly identical in the wet site (Table S4).

The second axis (Allocation-PC2, Table 2) explained 28% of the variance among species. It suggested a trade-off between allocation to leaves (high LAR and LMF) vs. allocation to roots (higher RMF) (Table 2). For simplicity, this trait syndrome will be called ‘leaf:root allocation’. A PCA analysis using the same allocational traits from the wet site yielded the same syndromes, differing only in that SMF also loaded with RMF in Allocation-PC2 (see Table S4 in Supporting Information).

A second PCA that described variation among species based only on physiological measurements and leaf N content explained 70% of the variation among 18 species along one single axis. This Physiology-PC1 described a gradient in photosynthetic capacity indicated by a positive covariance among all physiological traits except $\Delta^{13}C_{leaf}$ (Table 2). For simplicity, we will call this syndrome ‘photosynthetic capacity’. Physiology-PC1 was nearly identical when using traits from the wet site (see Table S4 in Supporting Information); however, half of the traits in this syndrome were measured in the shade house and not in the field.

CAN TRAITS EXPLAIN SPECIES PERFORMANCE IN THE FIELD?

Growth (Gr) – Gr in the dry site correlated in pairwise comparisons with higher LMF, LAR, lower RMF and, surprisingly, lower $k_{\mathrm{ws/la}}$ and $A_{\max}$ (Table 3). Accordingly, in multiple regressions, higher dry-site Gr was best explained by a simple linear combination of higher LAR and lower $A_{\max}$ (partial correlation coefficients: LAR = 0·65, $A_{\max}$ = −0·52; multiple regression r^2 = 0·62, $P < 0{\cdot}001$). As expected, dry-site Gr also correlated with the two trait syndromes that involved those traits. Hence, higher Gr correlated with higher leaf:root allocation as described by Allocation-PC2 (Table 3 and Fig. 1a) and with lower photosynthetic capacity as described by Physiology-PC1 (Table 3 and Fig. 1b). The syndrome of plant 'robustness' (Allocation-PC1) did not correlate with Gr (Table 3).

Gr in the wet site was explained by similar traits as in the dry site, which lends support to the observed trends. In the multiple regressions, higher wet-site Gr was best explained by higher LAR, and lower $A_{\max}$, $k_{\mathrm{ws/la}}$ and SD (partial correlation coefficients: LAR = 0·58, $k_{\mathrm{ws/la}}$ = −0·57, $A_{\max}$ = −0·49, SD = −0·44; multiple regression r^2 = 0·67, $P < 0{\cdot}001$). However, in pairwise comparisons, higher wet-site Gr correlated only with lower $k_{\mathrm{ws/la}}$, $A_{\max}$, N_{mass} and R_{dark} and greater sensitivity to desiccation (higher Ψ_{LD50}), but not with allocational traits (Table 3). The inconsistency between the multiple regression and the partial correlations indicates that LAR and SD only correlate with wet-site Gr after variation in $A_{\max}$ and $k_{\mathrm{ws/la}}$ is eliminated from the analysis. Consistently, wet-site Gr correlated with the Physiology-PC1 of photosynthetic capacity but not with any of the Allocation-PCs (see Table S4 in Supporting Information). For both sites, we also observed a trend for higher Gr to correspond with lower Dmg (Table 3).

Table 3. Correlates of plant performance in the dry and wet sites

	Dry site			Wet site	
	Gr	Dmg	Dp	Gr	Dmg
A. Pairwise correlations					
Dmg	−0·36†			−0·38†	
Dp	−0·24	0·03		−0·39†	−0·28
LL	0·03	−0·40	0·08	0·14	−0·65*
Tgh	0·23	−0·27	0·00	0·22	−0·43†
LMA	−0·03	−0·38†	0·16	0·03	**−0·63****
C_{mass}	−0·05	−0·14	0·17	−0·14	−0·22
LAR	**0·47***	−0·07	0·03	**0·33**	0·06
LMF	0·53**	−0·44*	0·23	0·28	−0·47*
RMF	−0·44*	**0·50***	−0·28	−0·23	0·35
RLPM	−0·19	0·38†	−0·39†	0·16	0·37†
SRL	0·06	0·15	−0·30	0·29	0·19
SMF	−0·08	−0·07	0·04	−0·12	0·22
SD	−0·15	0·16	0·11	**−0·06**	−0·22
$k_{\mathrm{ws/la}}$	−0·47*	0·27	**0·73****	**−0·58****	0·01
N_{mass}	−0·33	0·32	0·10	−0·45*	0·45*
N_{area}	−0·32	0·00	0·31	−0·35	−0·10
$A_{\max}$	**−0·53***	0·22	0·29	**−0·51***	0·32
R_{dark}	−0·47†	−0·02	0·13	−0·55*	0·06
$\Delta^{13}C_{\mathrm{leaf}}$	0·17	0·14	0·13	0·35†	0·05
Ψ_{LD50}	0·53†	−0·48†	0·02	0·57*	−0·30
B. Correlations with multi-trait syndromes					
'robustness'	−0·12	−0·25	0·30	−0·36	−0·35
Leaf:root allocation	**0·44***	**−0·61****	0·27	0·31	**−0·51***
Photosynthetic capacity	**−0·56***	0·28	**0·54***	**−0·63****	0·14

Values are Pearson's *r* product–moment correlations, with symbols indicating the strength of the correlation (†$P < 0{\cdot}1$, *$P < 0{\cdot}05$, **$P < 0{\cdot}01$). Trait acronyms are described in Table 1, and trait syndromes obtained by PCA are described in Table 2. Bold highlights the traits that are the most important correlates in multiple regressions.

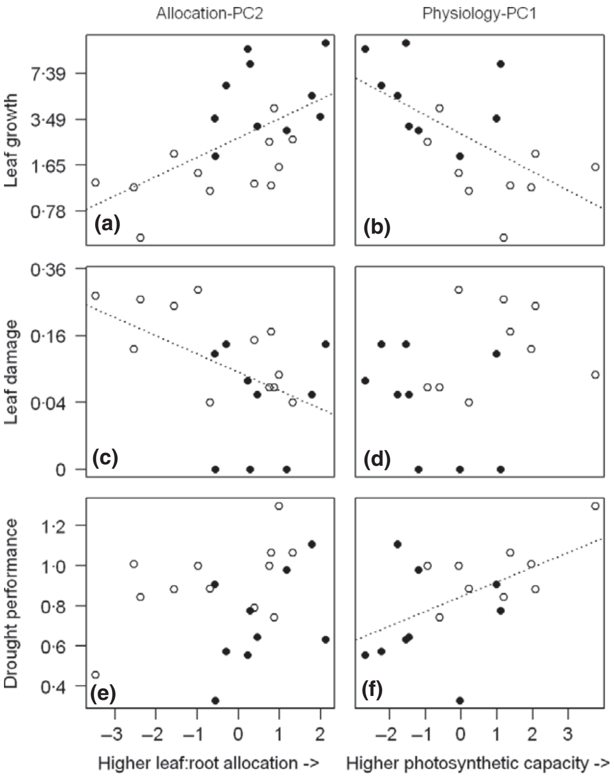

Fig. 1. Scatterplots showing the correlation between trait syndromes and performance in the dry site. Trait syndromes are leaf: root allocation (Allocation-PC2, a, c, e) and photosynthetic capacity (Physiology-PC1, b, d, f), as described in Table 2. Dotted lines show the trend for significant correlations as reported in Table 3. Symbols represent species distributions, such that dry- (open) and wet-distribution (solid) species significantly differed with respect to photosynthetic capacity (P = 0·01), but not with respect to leaf: root allocation (P = 0·06).

Leaf Damage (Dmg) – The correlates of Dmg were quite different between the dry and the wet sites. Higher Dmg in the dry site correlated in the pairwise comparisons only with lower LMF and higher RMF (Table 3), with the single most important predictor in the multiple regressions being higher RMF (r^2 = 0·21, P = 0·02). Consistently, lower dry-site Dmg correlated with higher leaf:root allocation (Table 3, Fig. 1c), but did not correlate with plant 'robustness' or photosynthetic capacity (Table 3, and Fig. 1d). On the other hand, higher wet-site Dmg correlated in pairwise comparisons with lower LL, Tgh, LMA, LMF and higher N_{mass} (Table 3). The single most important predictor using multiple correlations was LMA

($r^2 = 0{\cdot}36$, $P = 0{\cdot}002$). Similar to the dry site, wet-site Dmg correlated with leaf:root allocation but not with 'robustness' (Table 3).

Drought performance (Dp) – Better Dp in the dry site was best explained in the pairwise correlations and in multiple regressions by a single variable, higher $k_{\mathrm{ws/la}}$ ($r^2 = 0{\cdot}45$, $P < 0{\cdot}001$; Table 3). Consistently, Dp correlated well with the syndrome of photosynthetic capacity (Table 2 and Fig. 1f), but not with 'robustness' or leaf: root allocation (Table 3 and Fig. 1e). As Dp is a dry-site measure, we did not evaluate correlations of Dp against wet-site functional traits.

PERFORMANCE AND TRAIT DIFFERENCES FOR DRY- VS. WET-DISTRIBUTION SPECIES

When each trait from the dry site was analysed independently, dry-distribution species had significantly higher $k_{\mathrm{ws/la}}$ and A_{max} (Fig. 2a). There was also a marginally significant trend indicating that some dry-distribution species had higher R_{dark} (Fig. 2a). Multivariate combinations of traits provided a much stronger discrimination between the two groups of species. An LDA combining all allocational and physiological traits from the dry site significantly differentiated dry- and wet-distribution species such that all species were correctly classified. This LDA ordination was similar to the Physiology-PC1 and indicated that most of the discrimination was driven by higher $k_{\mathrm{ws/la}}$, SD and R_{dark} (Table 2). Dry-distribution species had higher values of this LDA than wet-distribution species (Fig. 2b, c), indicating that they had higher photosynthetic capacity and SD. The same LDA using traits from the wet site yielded very similar results (see Table S4 in Supporting Information), which is not surprising because the most important traits in this discrimination were measured in the shade house and not in the field.

Further examination showed that both physiological and allocational traits were important for discriminating dry- from wet-distribution species. Indeed, the power to differentiate the two groups of species with this LDA involving all traits from the dry site (100% correct classifications, $r = 0{\cdot}90$, $P < 0{\cdot}0001$) was larger than the power of an LDA using only physiological traits (88% correct classifications, $r = 0{\cdot}76$, $P = 0{\cdot}0003$; not shown), or of an LDA using only allocational traits (86% correct classifications, $r = 0{\cdot}68$, $P = 0{\cdot}0005$; not shown). The same analysis using wet-site traits was indistinguishable and is not shown here.

Trade-offs – Some evidence suggests the existence of a trade-off between Gr and Dp. Indeed, the LDA that combined all traits and the Physiology-PC1 of photosynthetic capacity both correlated with higher Gr and lower Dp (Fig. 2b, c). Also, an LDA based only on performance variables (Gr, Dp and Dmg, not shown) significantly discriminated dry- vs. wet-distribution species and indicated that wet-distribution species had higher Gr ($r = 0{\cdot}95$, $P < 0{\cdot}001$) and lower Dp ($r = -0{\cdot}47$, $P = 0{\cdot}02$) than dry-distribution species.

While these results all suggest a trade-off between Gr and Dp, a simple correlation between them was not significant in either of the two sites (Table 3). Indeed, some of the species with poor Dp (especially *Triplaris cumingiana* and *Brosimum utile*) also had very slow Gr (see Table S3 in Supporting Information). This changed when we used multiple correlations. Indeed, Gr in the wet site correlated with Dp if we first eliminated among-species variation in Dmg (partial correlation coefficients=-0·56, $P = 0{\cdot}002$). The same was not seen for Gr in the dry site.

Discussion

CAN PLANT TRAITS OR TRAIT SYNDROMES EXPLAIN SPECIES PERFORMANCE?

Growth rate (Gr): When comparing species with contrasting distributions along the rainfall gradient, the determinants of Gr were multiple and complex. However, they were fairly consistent in both sites. Higher Gr was best explained by a combination of high LAR and, surprisingly, low stem hydraulic conductance ($k_{\mathrm{ws/la}}$) and photosynthetic capacity (A_{max}) (Table 3).

The relationship between Gr and LAR is consistent with other studies that measured growth under the low-light conditions of the forest understorey (Kitajima 1994; Reich *et al.* 1998; Poorter 1999). Higher LAR probably increases light interception in the low-light forest understorey. As soils in central Panama are relatively rich in nutrients, it is reasonable that higher growth rates correlate with higher investment in the acquisition of above-ground resources. Consistently, Gr in the dry site also correlated with the trait syndrome that described variation in leaf:root allocation (Fig. 1a). The fact that this relationship was not also significant for growth in the wet site might be due to differences in resources between the sites. The need to access poor soil resources in the wetter site might neutralize any advantage gained by higher light interception.

What was more surprising was the negative correlation between Gr in both sites and the traits that describe photosynthetic capacity (Table 3 and Fig. 1b). To obtain large enough plants for assimilation curves and hydraulic measurements, we had to use shade-house-grown plants, acclimated to higher light levels than our field plants (about 20% vs. 2% of full sun). However, leaf nitrogen content of field-grown plants correlated with assimilation (N_{mass} vs. A_{max}: $r = 0{\cdot}57$, $P = 0{\cdot}01$), suggesting that the species ranks in assimilation measured in the greenhouse were probably similar to those in the field. Hence, we believe that the negative correlation of Gr with photosynthetic capacity is real, and we interpret it to be a consequence of the low light availability. Given that plants in the understorey rarely see high light, maintaining the capacity for high rates of photosynthesis may be inefficient due to consequent higher rates of maintenance respiration. Indeed, other studies have shown that the minimum light level required to gain sufficient carbon for maintenance may not be met for

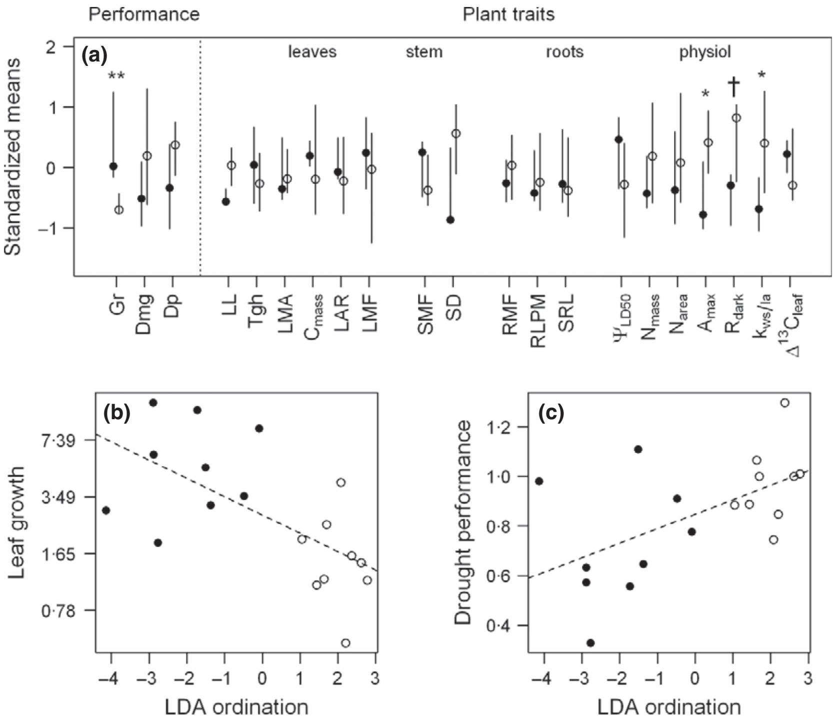

Fig. 2. Differences in performance and traits in the dry site for wet- (solid) vs. dry-distribution (open) species. (a) Median performance and trait values for dry- and wet-distribution species. Vertical lines represent the inter-quartile range. To visualize in the same axis, variables were standardized (mean = 0, SD = 1). Symbols represent the *P*-value for the Wilcoxon's rank-sum test of the difference between dry- and wet-distribution species on each trait independently (**$P < 0{\cdot}01$, *$P < 0{\cdot}05$ and †$P < 0{\cdot}1$). (b) Leaf growth rate (Gr) and (c). Drought performance (Dp) of each species plotted against the LDA ordination that best describes the difference between dry- and wet-distribution species based on plant traits (Table 2). The dotted line represents the best fit regression ($r^2 = 0.30$, $P = 0.02$ and $r^2 = 0.31$, $P = 0.02$, respectively).

many species in the low-light, tropical understorey (Montgomery & Chazdon 2002; Baltzer & Thomas 2007; Janse-ten Klooster, Thomas & Sterck 2007). Hence, species with low photosynthetic capacity and high leaf area (LAR and LMF) grow better in the understorey because they efficiently capture and convert low light into positive carbon gain. Other studies have found that maximum assimilation has little bearing on growth in the understorey (Kitajima 1994; Bonal *et al.* 2007). As those studies compared species at a single site, the discrepancy with our results may reflect our use of species with distinct and contrasting distributions.

Drought performance: Species with higher Dp tended to have higher stem hydraulic conductance ($k_{ws/la}$), which could be seen as less conservative water use. Also, unlike some of our previous work (Kursar *et al.* 2009), we found no correlation between Dp and sensitivity to desiccation (Ψ_{LD50}). It is possible that the correlation between Dp and $k_{ws/la}$ is an artefact of having normalized stem conductance by leaf area, as lower LARs may increase $k_{ws/la}$ for species towards the drier end of a rainfall gradient. However, we found no evidence that LAR differed among our dry- and wet-distribution species (Fig. 2a). Additionally, plants with better drought survival in our study also had a higher photosynthetic capacity (Fig. 1f). Because $k_{ws/la}$ correlated with A_{max} and N_{mass} (A_{max}: $r = 0{\cdot}46$, $P = 0{\cdot}04$; N_{mass}: $r = 0{\cdot}57$, $P = 0{\cdot}01$), this is consistent with a mechanism where a higher rate of water transport to the leaves is necessary to maintain a high assimilation capacity (Brodribb & Feild 2000; Campanello, Gatti & Goldstein 2008).

Indeed, comparison with recent literature suggests that a high capacity for CO_2 assimilation and water transport may be a common trait of species that avoid desiccation (with deep roots and perennial leaves) or that delay desiccation (with shallow roots, stored water and leaf shedding or stomatal closure in response to a small decrease in plant water status). Pineda-García, Paz & Tinoco-Ojanguren (2011) reported that among dry-forest, deciduous species, assimilatory capacity and water transport were higher for dry- vs. wet-habitat specialists, with Reich *et al.* (1999), Maherali, Pockman & Jackson (2004) and Sterck *et al.* (2011) reporting analogous results. We were unable to classify our dry-distribution species as avoiding or delaying desiccation vs. tolerant of desiccation. But, in view of these results, we believe that we probably had a higher representation of desiccation avoiding/delaying species than in our previous study (Kursar *et al.* 2009). Furthermore, we found a weak negative correlation between the photosynthetic capacity and carbon isotope discrimination ($\Delta^{13}C_{leaf}$, Physiology-PC1, Table 2), suggesting that a higher photosynthetic capacity of species that avoid or delay desiccation may result in higher integrated water-use efficiency over the long term.

Leaf damage: Unlike Gr and Dp, the correlates of leaf damage (Dmg) were not consistent among sites. In the wet site, where seedlings experienced higher Dmg and where we could better assess among-species variation in susceptibility to pest attack (Brenes-Arguedas, Coley & Kursar 2009), Dmg correlated with a larger variety of traits than in the dry site (Table 3). Hence, higher wet-site Dmg correlated with lower LMA, high C_{mass}, low leaf nitrogen content (N_{mass}) and longer leaf life span (LL). These have often been reported as key defensive traits (Coley 1983, 1987; Poorter & Bongers 2006; Alvarez-Clare & Kitajima 2007). However, these traits did not contribute to explain Dmg in the dry site, and the syndrome of 'robustness' that involved these traits (Allocation-PC1, Table 2) did not correlate with Dmg in either of the two sites. Instead, Dmg in both sites correlated negatively with the syndrome of leaf:root allocation (Allocation-PC2, Fig. 1c), which may simply indicate that plants that suffer more Dmg end up with less leaf area. While we do not have enough information to satisfactorily interpret these results, we did not find that dry- and wet-distribution species differ with respect to these traits, or to the 'robustness' syndrome. Hence for the purpose of this paper, neither of the traits associated with the observed damage contributed to our understanding of species distributions. This is consistent with our earlier reports that wet- and dry-distribution species did not differ in pathogen mortality or leaf damage (Fig. 2a and Brenes-Arguedas, Coley & Kursar 2009).

PERFORMANCE AND TRAIT DIFFERENCES FOR DRY- VS. WET-DISTRIBUTION SPECIES

Drought performance, growth rates and associated traits (mainly $k_{\mathrm{ws/la}}$) were all significant correlates of species distribution in our experiments. Specifically, our results suggest that there is a trade-off between Gr and Dp, that this trade-off is mediated by stem hydraulic conductance and assimilatory capacity (Figs. 1, 2) and that this accounts for some of the differences between dry- and wet-distribution species. The fact that a direct test for a correlation between Gr vs. Dp showed only weak evidence for a trade-off (Table 3) suggests that this trade-off does not involve all of the study species.

Why would dry-distribution species have higher photosynthetic capacity? A high photosynthetic capacity might permit high carbon gain during periods when both light and soil water availabilities are high (Eamus & Prior 2001). In deciduous or semi-deciduous forests, light and high water availability could both be high during transitions between rainy and dry seasons, one or two times per year. In fact, other studies have shown that a Gr response to increased light can be observed only during the rainy season (Gerhardt 1996). Because the strategy of high photosynthetic capacity may be a liability in conditions of water limitation, it should be associated with strategies of desiccation delay or desiccation avoidance. Additionally, a high assimilatory capacity could result in greater long-term, water-use efficiency and higher biomass accumulation per water used (Farquhar, Ehleringer & Hubick 1989). In wet forests, instead, the forest understorey may be darker, and high-light conditions are normally found only following the formation of light gaps. As these events occur irregularly and after intervals of decades during which seedlings or saplings must survive in very low light, maintaining a high assimilatory capacity during long periods in between light gaps may not be efficient (see discussion of growth rate, above).

This does not explain why dry-distribution species that have a high assimilatory capacity cannot produce leaf area quickly in sites with higher light availability in the dry forests (Brenes-Arguedas, Coley & Kursar 2009), or colonize gaps in wet forests. We speculate that their slower growth may be due to the associated strategies of drought resistance. For example, species may shed more leaves during the dry season to prevent water loss, and this would be reflected in our measure of growth that was based on leaf area production. Also, we found no difference between dry- and wet-distribution species in the morphological traits that might represent the capacity for resource acquisition (Allocation-PC1 or 'robustness'). Hence, the physiological advantages of dry-forest species in high light may not be sufficient to overcome the absence of allocational traits that are advantageous in high light.

Overall, these results can be interpreted as a trade-off between shade tolerance and drought performance (Smith & Huston 1989). Indeed, the conservative assimilatory capacity of some wet-distribution species, combined with higher LAR, may qualify as better shade tolerance, as it permits higher carbon gain and better Gr in low light (Janse-ten Klooster, Thomas & Sterck 2007). Hence, species with strategy of avoiding or delaying desiccation can be considered to be limited in their shade tolerance by their less conservative assimilatory capacity.

We included four lianas among the dry-distribution species. While we acknowledge that this bias may mean that some of our conclusions are the result of the comparison between lianas and trees, it is important to note that lianas compose a larger fraction of the woody species in dry forests relative to the wet forests. Hence, our results still represent a comparison between the two habitats. Also, we found no evidence in our data that our liana seedlings behaved any differently from the tree seedlings in the dry forest. For instance, while lianas might grow faster than trees (Cornelissen, Castro-Díez & Carnelli 1998), our liana growth rates were half those of some of the other dry-distribution species, and their inclusion contributed to the result that Gr was higher for the wet-distribution species. Also, the average $k_{\mathrm{ws/la}}$ for the four lianas equalled that of the five other dry-distribution species for which we have $k_{\mathrm{ws/la}}$ data. Because liana seedlings are self-supporting, they must invest in stem and roots as much as the seedlings of tree species and may not be very different from them at these early developmental stages.

Conclusions

This study was motivated by the hypothesis that traits that result in performance trade-offs between habitats should provide important insights into the mechanisms and the extent to which plant–habitat associations determine the turnover of species along an environmental gradient (Suding, Goldberg & Hartman 2003). Our principal result suggests that for at least some of the study species, a trade-off between poor drought resistance vs. a greater capacity to grow in the low-light forest understorey correlates with the turnover in species composition along the rainfall gradient in the Isthmus of Panama. Interestingly, here we find that relative to the dry-distribution species, wet-distribution species had higher growth rates, as would be expected for more light-demanding species. However, unlike light-demanding species, our wet-distribution species had lower maximum photosynthetic capacities, as would be expected for more shade-tolerant species. On the other hand, dry-distribution, drought-resistant species had a higher capacity for CO_2 assimilation and water transport through the stem. Higher assimilation may be associated with traits for avoiding or delaying desiccation and with limited shade tolerance.

Much recent work has focused on defining functional traits and explaining their correlation with plant performance and habitat distribution (Cavender-Bares, Kitajima & Bazzaz 2004; Poorter & Bongers 2006; Sterck, Poorter & Schieving 2006; Poorter & Markesteijn 2008; Dent & Burslem 2009; Wright *et al.* 2010; Markesteijn *et al.* 2011). Consistent with many other studies, we find that morphological traits were informative; nevertheless, our analysis suggests that physiological traits best explained both the trade-offs and the differences between dry- and wet-distribution species.

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References

Alvarez-Clare, S. & Kitajima, K. (2007) Physical defence traits enhance seedling survival of neotropical tree species. *Functional Ecology*, **21**, 1044–1054.

Baltzer, J.L. & Thomas, S.C. (2007) Determinants of whole-plant light requirements in Bornean rain forest tree saplings. *Journal of Ecology*, **95**, 1208–1221.

Baltzer, J.L., Davies, S.J., Bunyavejchewin, S. & Noor, N.S.M. (2008) The role of desiccation tolerance in determining tree species distributions along the Malay-Thai Peninsula. *Functional Ecology*, **22**, 221–231.

Bennett, J.M. & Cortes, P.M. (1985) Errors in measuring water potentials of small samples resulting from water adsorption by thermocouple psychrometer chambers. *Plant Physiology*, **79**, 184–188.

Bonal, D., Born, C., Brechet, C., Coste, S., Marcon, E., Roggy, J.-C. & Guehl, J.-M. (2007) The successional status of tropical rainforest tree species is associated with differences in leaf carbon isotope discrimination and functional traits. *Annals of Forest Science*, **64**, 169–176.

Bongers, F., Poorter, L., Van Rompaey, R.S.A.R. & Parren, M.P.E. (1999) Distribution of twelve moist forest canopy tree species in Liberia and Côte d'Ivoire: response curves to a climatic gradient. *Journal of Vegetation Science*, **10**, 371–382.

Borchert, R. (1994) Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology*, **75**, 1437–1449.

Brenes-Arguedas, T., Coley, P.D. & Kursar, T.A. (2009) Pests versus drought as determinants of plant distribution along a tropical rainfall gradient. *Ecology*, **90**, 1751–1761.

Brenes-Arguedas, T., Ríos, M., Rivas-Torres, G., Blundo, C., Coley, P.D. & Kursar, T.A. (2008) The effect of soil on the growth performance of tropical species with contrasting distributions. *Oikos*, **117**, 1453–1460.

Brenes-Arguedas, T., Roddy, A.B., Coley, P.D. & Kursar, T.A. (2011) Do differences in understory light contribute to species distributions along a tropical rainfall gradient? *Oecologia*, **166**, 443–456.

Brodribb, T.J. & Feild, T.S. (2000) Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant, Cell and Environment*, **23**, 1381–1388.

Campanello, P.I., Gatti, M.G. & Goldstein, G. (2008) Coordination between water-transport efficiency and photosynthetic capacity in canopy tree species at different growth irradiances. *Tree Physiology*, **28**, 85–94.

Cavender-Bares, J., Kitajima, K. & Bazzaz, F.A. (2004) Multiple trait associations in relation to habitat differentiation among 17 Floridian oak species. *Ecological Monographs*, **74**, 635–662.

Chust, G., Chave, J., Condit, R., Aguilar, S., Lao, S. & Perez, R. (2006) Determinants and spatial modeling of tree β-diversity in a tropical forest landscape in Panama. *Journal of Vegetation Science*, **17**, 83–92.

Clark, D.B., Palmer, M.W. & Clark, D.A. (1999) Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology*, **80**, 2662–2675.

Coley, P.D. (1983) Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs*, **53**, 209–233.

Coley, P.D. (1987) Patterns in plant defenses: why do herbivores prefer certain species. *Revista de Biologia Tropical*, **35**, 151–164.

Coley, P.D. (1988) Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia*, **74**, 531–536.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Reviews of Ecology and Systematics*, **27**, 305–335.

Cornelissen, J.H.C., Castro-Díez, P. & Carnelli, A.L. (1998) Variation in relative growth rate among woody species. *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences* (eds H. Lambers, H. Poorter & M.M.I.V. Vuuren), pp. 363–392. Backhuys Publishers, Leiden.

Davidar, P., Rajagopal, B., Mohandass, D., Puyravaud, J.P., Condit, R., Wright, S.J. & Leigh, E.G. (2007) The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Global Ecology and Biogeography*, **16**, 510–518.

Denslow, J.S. (1987) Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics*, **18**, 431–451.

Dent, D.H. & Burslem, D.F.R.P. (2009) Performance trade-offs driven by morphological plasticity contribute to habitat specialization of Bornean tree species. *Biotropica*, **41**, 424–434.

Eamus, D. & Prior, L. (2001) Ecophysiology of trees of seasonally dry tropics: comparison among phenologies. *Advances in Ecological Research*, **32**, 113–197.

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., Comita, L., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–83.

Farquhar, G.D., Ehleringer, J.R. & Hubick, K.T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Reviews of Plant Physiology and Plant Molecular Biology*, **40**, 503–537.

Fine, P.V.A., Mesones, I. & Coley, P.D. (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, **305**, 663–665.

Gerhardt, K. (1996) Effects of root competition and canopy openness on survival and growth of tree seedlings in a tropical seasonal dry forest. *Forest Ecology and Management*, **82**, 33–48.

Givnish, T.J. (1999) On the causes of gradients in tropical tree diversity. *Journal of Ecology*, **87**, 193–210.

Janse-ten Klooster, S.H., Thomas, E.J.P. & Sterck, F.J. (2007) Explaining interspecific differences in sapling growth and shade tolerance in temperate forests. *Journal of Ecology*, **95**, 1250–1260.

John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M. & Foster, R.B. (2007) Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 864–869.

Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, **98**, 419–428.

Kolb, K.J., Sperry, J.S. & Lamont, B.B. (1996) A method for measuring xylem hydraulic conductance and embolism in entire root and shoot systems. *Journal of Experimental Botany*, **47**, 1805–1810.

Kursar, T.A., Engelbrecht, B.M.J., Burke, A., Tyree, M.T., El Omari, B. & Giraldo, J.P. (2009) Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Functional Ecology*, **23**, 93–102.

Maherali, H., Pockman, W.T. & Jackson, R.B. (2004) Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology*, **85**, 2184–2199.

Markesteijn, L., Poorter, L., Bongers, F., Paz, H. & Sack, L. (2011) Hydraulics and life history of tropical dry forest tree species: coordination of species' drought and shade tolerance. *New Phytologist*, **191**, 480–495.

Montgomery, R.A. & Chazdon, R.L. (2002) Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, **131**, 165–174.

Paz, H. (2003) Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. *Biotropica*, **35**, 318–332.

Phillips, O.L., Vargas, P.N., Monteagudo, A.L., Cruz, A.P., Zans, M.E.C., Sanchez, W.G., Yli-Halla, M. & Rose, S. (2003) Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology*, **91**, 757–775.

Pineda-García, F., Paz, H. & Tinoco-Ojanguren, C. (2011) Morphological and physiological differentiation of seedlings between dry and wet habitats in a tropical dry forest. *Plant, Cell & Environment*, **34**, 1536–1547.

Poorter, L. (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional Ecology*, **13**, 396–410.

Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, **87**, 1733–1743.

Poorter, L. & Kitajima, K. (2007) Carbohydrate storage and light requirements of tropical moist and dry forest tree species. *Ecology*, **88**, 1000–1011.

Poorter, L. & Markesteijn, L. (2008) Seedling traits determine drought tolerance of tropical tree species. *Biotropica*, **40**, 321–331.

Pyke, C.R., Condit, R., Aguilar, S. & Lao, S. (2001) Floristic composition across a climatic gradient in a neotropical lowland forest. *Journal of Vegetation Science*, **12**, 553–566.

Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W. & Buschena, C. (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology*, **12**, 327–338.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Gresham, C., Volin, J.C. & Bowman, W.D. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology*, **80**, 1955–1969.

Santiago, L.S., Schuur, E.A.G. & Silvera, K. (2005) Nutrient cycling and plant-soil feedbacks along a precipitation gradient in lowland Panama. *Journal of Tropical Ecology*, **21**, 461–470.

Smith, T. & Huston, M. (1989) A theory of the spatial and temporal dynamics of plant communities. *Plant Ecology*, **83**, 49–69.

Sterck, F.J., Poorter, L. & Schieving, F. (2006) Leaf traits determine the growth-survival trade-off across rain forest tree species. *American Naturalist*, **167**, 758–765.

Sterck, F., Markesteijn, L., Schieving, F. & Poorter, L. (2011) Functional traits determine trade-offs and niches in a tropical forest community. *Proceedings of the National Academy Sciences USA*, **108**, 20627–20632.

Suding, N.K., Goldberg, D.E. & Hartman, K.M. (2003) Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology*, **84**, 1–16.

Swaine, M.D. (1996) Rainfall and soil fertility as factors limiting forest species distributions in Ghana. *Journal of Ecology*, **84**, 419–428.

R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Tyree, M.T., Engelbrecht, B.M.J., Vargas, G. & Kursar, T.A. (2003) Desiccation tolerance of five tropical seedlings in Panama. Relationship to a field assessment of drought performance. *Plant Physiology*, **132**, 1439–1447.

Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*, 4th edn. Springer, New York.

Wright, S.J. & van Schaik, C.P. (1994) Light and the phenology of tropical trees. *American Naturalist*, **143**, 192–199.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S., Engelbrecht, B.M.J., Harms, K.E., Hubbell, S.P., Marks, C.O., Ruiz-Jaen, M.C., Salvador, C.M. & Zanne, A.E. (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, **91**, 3664–3674.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Site effects for dry- vs. wet-distribution species.
Fig. S2. Rank comparison of traits in the dry and wet sites.
Table S1. List of study species.
Table S2. Evaluation of plasticity in trait expression.
Table S3. Trait values in the two study sites.
Table S4. Multivariate ordinations for wet-site traits.