

Water-use efficiency and whole-plant performance of nine tropical tree species at two sites with contrasting water availability in Panama

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Abstract Across their natural distributions, tropical tree species are regularly exposed to seasonal droughts of varying intensities. Their ability to tolerate drought stress plays a vital role in determining growth and mortality rates, as well as shaping the functional composition of tropical forests. In order to assess the ability of species to acclimate to contrasting levels of drought stress, physiological and structural traits involved in drought adaptation—wood C isotope discrimination ($\delta^{13}\text{C}$), wood specific gravity, and wood C content—of 2-year-old saplings of nine tropical tree species were evaluated in common garden experiments at two study sites in Panama with contrasting seasonality. We assessed co-variation in wood traits with relative growth rates (RGR_{BD}), aboveground biomass, and basal diameter and the plasticity of wood traits across study sites. Overall, species responded to lower water availability by increasing intrinsic water-use efficiency, i.e., less negative wood $\delta^{13}\text{C}$, but did not exhibit a uniform, directional response for wood specific gravity or wood C content. Trait plasticity for all wood traits was independent of RGR_{BD} and tree size. We found that the adaptive value of intrinsic water-use efficiency varied with water availability. Intrinsic water-use efficiency increased with decreasing RGR_{BD}

at the more seasonal site, facilitating higher survival of slower growing species. Conversely, intrinsic water-use efficiency increased with tree size at the less seasonal site, which conferred a competitive advantage to larger individuals at the cost of greater susceptibility to drought-induced mortality. Our results illustrate that acclimation to water availability has negligible impacts on tree growth over short periods, but eventually could favor slow-growing species with conservative water-use strategies in tropical regions experiencing increasingly frequent and severe droughts.

Keywords Carbon isotope · Wood traits · Wood density · WUE · Plasticity · Functional traits · Central America

Introduction

Across tropical regions, global change models predict that droughts will become increasingly frequent and intense (Cox et al. 2008; Williams et al. 2007). Droughts reduce tree growth and increase mortality rates, thereby shifting the competitive advantage toward species with greater drought stress tolerance (Brenes-Arguedas et al. 2011; Engelbrecht and Kursar 2003; Kursar et al. 2009; Phillips et al. 2010). Consequently, changing climatic conditions threaten to alter species' distributions, as well as the functional composition of tropical forests (Condit et al. 2004; Davidar et al. 2007; Phillips et al. 2009, 2010).

Plant water-use efficiency, the amount of water used per carbon gain, explicitly links plant performance with water availability. At the leaf level, intrinsic water-use efficiency is expressed as the balance between photosynthetic C fixation (A) and stomatal conductance (g_s), which is correlated with the ratio of intercellular to ambient CO_2 partial

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pressures (C_i/C_a) in C_3 plants. Therefore, time-integrated, intrinsic water-use efficiency can be inferred using stable carbon isotope ratios ($\delta^{13}C$) of plant tissues given its inverse linear relationship with C_i/C_a , whereby high water-use efficiency is indicated by less negative $\delta^{13}C$ and low C_i/C_a and vice versa (Dawson et al. 2002; Farquhar et al. 1982; Farquhar and Richards 1984). Due to interspecific and temporal variation in mesophyll conductance, intrinsic water-use efficiency (A/g_s) and C_i/C_a can vary independently of plant $\delta^{13}C$ due to interspecific and temporal variation in mesophyll conductance, which is sensitive to shifts in environmental conditions (Bonal et al. 2007; Cernusak et al. 2008, 2009b; Seibt et al. 2008). While foliar $\delta^{13}C$ has been used extensively to investigate plant response to precipitation, seasonal drought, and soil nutrients within and across species and ecosystems (e.g., Ares and Fownes 1999; Cernusak et al. 2007, 2009b; Craven et al. 2007, 2010; Diefendorf et al. 2010; Ramírez-Valiente et al. 2010), there is growing interest in using wood $\delta^{13}C$ to relate patterns of water-use efficiency over multiple years to variation in tree growth, precipitation, ambient CO_2 , and temperature (Brienen et al. 2011; Hietz et al. 2005; Nock et al. 2011; Rozendaal and Zuidema 2011; Schulze et al. 2006) as wood $\delta^{13}C$ records the $\delta^{13}C$ of phloem sap carbon delivered to the vascular cambium during wood formation (Cernusak et al. 2005, 2009a).

The strength and direction of the relationship between water-use efficiency and plant performance can illustrate interspecific differences in drought tolerance strategies, ranging from stress tolerance to stress avoidance (see Aranda et al. 2012; Chaves et al. 2002 and Nicotra et al. 2010 for a more complete discussion of tree responses to drought). Stress tolerance is associated with higher water-use efficiency, lower photosynthetic rates, slower growth, and higher survival, while stress avoidance is associated with lower water-use efficiency, higher photosynthetic rates, faster growth, and lower survival (Chaves et al. 2002). As plant performance underlies variation in life history strategies (Wright et al. 2010), drought tolerance strategies also would be expected to vary in coordination with life history strategies, such that the continuum from pioneer to late-successional species would parallel that of drought tolerance strategies, from stress avoidance to stress tolerance (Llambí et al. 2003).

Wood specific gravity is utilized extensively as a proxy to capture differences in life history strategies, relative growth rates, and survival rates of tropical tree species (Chave et al. 2006, 2009; Kitajima 1994; Wright et al. 2010). These differences in plant performance reflect species-specific responses to myriad abiotic and biotic factors, including water and light availability, soil nutrients, mechanical damage, pathogens, and disturbance (Chave et al. 2006; Fan et al. 2012; Kitajima 1994; Muller-Landau

2004; ter Steege and Hammond 2001). Despite the lack of a consistent, community-level relationship between wood specific gravity and mean annual precipitation across Neotropical forests (Muller-Landau 2004), coordination of wood specific gravity with hydraulic conductivity within tropical forest communities supports the vital role played by wood specific gravity in determining drought tolerance (Markesteyn et al. 2011; Poorter et al. 2010). At the plant level, variation in wood specific gravity represents variation in the arrangement and distribution of wood anatomical traits, principally vessels and fibers, which underlie species' capacity to tolerate the negative pressures in the xylem associated with drought stress (Chave et al. 2009; Fan et al. 2012; Hacke et al. 2001; Poorter et al. 2010; Zanne et al. 2010). The denser spacing of vessels, thicker vessel walls, greater amount of fiber cells, and greater thickness of fiber walls found in tree species with high wood specific gravity suggest a proportionally greater investment in C-rich tissues (Martínez-Cabrera et al. 2009; Swenson and Enquist 2007), although this hypothesized relationship has not been supported empirically for tropical tree species (Martin and Thomas 2011).

The extent to which trees acclimate to their local environment, also known as plasticity (Bradshaw 1965), can confer a competitive advantage to co-occurring individuals as they compete for limiting resources. Plasticity is thought to indicate specialization to a particular environment (Niinemets 2010; Valladares et al. 2007). Hence, plasticity can be used to identify drought tolerance strategies and environments in which different strategies are adaptive (Nicotra et al. 2010; Valladares et al. 2000). Variation in plasticity among leaf traits suggests that different traits are adaptive in different light environments (Hulshof and Swenson 2010; Rozendaal et al. 2006; Valladares et al. 2000). For example, pioneer species (in some cases) have a higher plasticity in leaf traits related to photosynthesis, while shade-tolerant species have higher plasticity in leaf traits related to light interception (Rozendaal et al. 2006). In the context of drought stress, therefore, species with high trait plasticity would be expected to exhibit greater performance where water was not limiting, while species with low trait plasticity would be expected to perform equally well in environments with and without drought stress (Comita and Engelbrecht 2009). The extent to which wood traits acclimate to changes in drought stress remains undetermined for tropical tree species, which could have important implications for the species and functional composition of tropical forests (Baltzer et al. 2009; Phillips et al. 2010).

The principal aims of this study were (a) to evaluate wood $\delta^{13}C$ in relation to whole-plant performance and life history strategies at two study sites with contrasting annual precipitation regimes and dry season lengths and (b) to determine the extent to which saplings of tropical tree

species acclimate wood $\delta^{13}\text{C}$ in response to differences in water availability between study sites. Nine tropical tree species were investigated in a common garden experiment replicated at two study sites with contrasting seasonality, co-variation in wood $\delta^{13}\text{C}$, wood specific gravity (a proxy for life history strategies), and wood C content with whole-plant performance traits (relative growth rates, basal diameter, and aboveground biomass). Specifically, the following three questions were addressed in the present study:

1. To what extent do wood traits vary across species and between sites that have contrasting annual precipitation regimes and dry season lengths?
2. How plastic are wood traits between sites with contrasting annual precipitation regimes and dry season lengths? Is plasticity of wood traits correlated with life history strategies and whole-plant performance?
3. Are wood and tree traits coordinated similarly at sites with contrasting annual precipitation regimes and dry season lengths?

Materials and methods

Study sites

The study was conducted on 2-year-old saplings at two sites in Panama, Rio Hato (Coclé Province) and Las Lajas (Chiriquí Province). The study sites are located in different ecological life zones along the Pacific coast of western Panama: tropical wet (Las Lajas) and tropical dry forest (Rio Hato) (PIDP 1970). Rio Hato receives less annual precipitation and has a longer, more severe dry season than Las Lajas (Table 1; Hijmans et al. 2005). While the study sites have similar mean annual potential evapotranspiration and mean annual temperatures, the lower aridity index at Rio Hato indicates that less precipitation is available for plant uptake relative to Las Lajas (Zomer et al. 2008). The study sites have comparable soil characteristics, as both have similar soil pH and concentrations of total P, total N, and K (Table 1). At both sites, the natural vegetation was converted to agricultural fields and cattle pastures, which were managed actively until the establishment of the experiments. From here on, Las Lajas will be referred to as the less seasonal site and Rio Hato as the more seasonal site.

Species selection

The selected tree species were chosen to represent a range of differing successional statuses and life history strategies

Table 1 Climatic and soil characteristics for the two study sites in Panama

| Study site | Las Lajas | Rio Hato |
|--|--------------------|--------------------|
| Site coordinates | 8°14'N 81° 52'W | 8°22'N 80° 09'W |
| AP (mm yr ⁻¹) | 3375 | 1172 |
| AP ₃ (ffim yr ⁻¹) | 4559.7 (120.6) | 1397.9 (103.3) |
| ET (mm yr ⁻¹) | 1652 | 1564 |
| MAT (°C) | 26.4 | 27.1 |
| Aridity index | 2.048 | 0.755 |
| Dry season length (months yr ⁻¹) | 3.33 (0.67) | 5.00 (0.00) |
| pH(in H ₂ O) | 4.77 (0.5) | 5.38 (0.9) |
| Total N (%) | 0.18 (0.01) | 0.08 (0.00) |
| P (ppm) | 3.12 (0.45) | 2.44 (0.17) |
| Ca (ppm) | 132.00 (24.8) | 440.64 (47.33) |
| K (ppm) | 32.14 (5.41) | 53.92 (7.86) |
| Mg (ppm) | 38.85 (5.51) | 97.94 (7.70) |

Climatic data during the study period (2004–2006) were obtained from weather stations nearby study sites (Empresa de Transmision Electrica Panamena SA, ETESA). The global potential evapotranspiration (Global-PET) and Global Aridity Index (Global-Aridity) datasets (Zomer et al. 2008) are based on a high resolution (1 km²) global climate dataset (WorldClim) (Hijmans et al. 2005). AP is mean annual precipitation (1950–2000, source: WorldClim.), AP₃ is mean annual precipitation during the 3 years of study (2004–2006, adapted from ETESA), ET is mean annual potential evapotranspiration calculated using the Hargreaves method (1950–2000, source: Global-PET), MAT is mean annual temperature (1950–2000, source: WorldClim), Aridity Index is the ratio of mean annual precipitation to mean annual potential evapotranspiration (1950–2000, source: Global-Aridity), and dry season length is number of months per year with less than 100 mm of precipitation during the 3 years of the study (2004–2006, adapted from ETESA)

Soils were sampled from 0–15 cm and analyzed using a Mehlich 1 extraction

Standard errors are in parenthesis

(Table 2). All species occur naturally in Panama and are used locally for their timber and firewood, as well as in silvopastoral systems (Aguilar and Condit 2001; Perez and Condit 2011). Of the studied species, *Dalbergia retusa*, *Ormosia macrocalyx*, and *Zygia longifolia* have been observed to nodulate and likely fix nitrogen (Bryan et al. 1996; de Faria and de Lima 1998; Moreira et al. 1992; Tilki and Fisher 1998).

Experimental design

Two identical common garden experiments were established at both study sites in 2004 (Breugel et al. 2011; Wishnie et al. 2007). Seeds were collected at three sites across Panama and, after germination, were cared for in a nursery for 2–6 months prior to being transplanted. At each study site, tree seedlings were planted in three completely

Table 2 Scientific name, family, successional status, wood specific gravity, N-fixation capacity, and identification code for the nine studied species

| Species | Family | Succession status | Wood specific gravity (g cm ⁻³) | N-fixation capacity | Species code | |
|------------------------------|---------------|-------------------|---|---------------------|--------------|----|
| <i>Hura crepitans</i> | Euphorbiaceae | Early | 0.38 (0.36–0.42) | No | Hc | |
| <i>Byrsonima crassifolia</i> | Malpighiaceae | ↓ | 0.56 (0.54–0.60) | No | Bc | |
| <i>Terminalia amazonia</i> | Combretaceae | | 0.62 (0.57–0.65) | No | Ta | |
| <i>Swietenia macrophylla</i> | Meliaceae | | 0.63 (0.61–0.66) | No | Sm | |
| <i>Ormosia macrocalyx</i> | Fabaceae | | 0.63 (0.59–0.67) | Yes | Om | |
| <i>Zygia longifolia</i> | Fabaceae | | 0.67 (0.64–0.69) | Yes | Zl | |
| <i>Dalbergia retusa</i> | Fabaceae | | 0.70 (0.65–0.73) | Yes | Dr | |
| <i>Tabebuia impetiginosa</i> | Bignoniaceae | | 0.72 (0.68–0.74) | No | Ti | |
| <i>Sapindus saponaria</i> | Sapindaceae | | Late | 0.75 (0.71–0.74) | No | Ss |

Successional status was determined from a literature review (Perez and Condit 2011), wood specific gravity values are taken from the present study (95 % confidence intervals in parenthesis), and N-fixation capacity was determined from a literature review (Moreira et al. 1992; de Faria and de Lima 1998 and Tilki and Fisher 1998)

randomized blocks. Within each block, three replicate plots, each containing 20 trees planted at 3 × 3 m, were established for each species. Plots were cleaned mechanically to reduce competition from grasses, herbaceous plants, and naturally regenerating seedlings.

Whole-plant performance measurements

For measurement of wood traits and aboveground biomass, four to six individuals were selected per species at each site for destructive sampling. Using basal diameter measurements taken at the beginning of the wet season in 2006 (June–August), trees were selected using a stratified random sample of individuals from three diameter size classes, corresponding to the 1–33rd, 34–66th, and 67–100th percentiles (Oelmann et al. 2010).

Basal diameter was measured on seedlings at the time of planting and in subsequent years (2005, 2006). Relative growth (RGR_{BD}) was calculated following Fisher (1921):

$$RGR_{BD} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$$

where W_2 and W_1 are basal diameter at t_2 (2006) and t_1 (2004), respectively. Time period between measurements was calculated in days.

Selected individuals were re-measured for basal diameter at the time of destructive sampling. Fresh weight was determined in the field using either an electronic balance (400 g capacity, 0.1 g precision) or a spring balance (20 kg capacity, 0.1 kg precision). Fresh weights of sub-samples of tree components (leaves, branches, and stem) were also taken and subsequently dried in an oven at 70 °C for 4 days until a constant weight was attained. Total dry weights were estimated by multiplying the wet:dry ratio of the sub-sample by the corresponding total fresh weight (Bastien-Henri et al. 2010).

For determination of oven-dry wood specific gravity of wood, two uncompressed samples were taken using a 2.8 × 1.0 cm borer attached to a power drill from the stems of all destructively sampled individuals. All bark was removed from samples prior to drying. Wood samples were oven dried to a constant weight at 70 °C to avoid binding water to the sample. Samples were weighed to the nearest 0.0001 g using an electronic balance. To prevent rehydration, dried samples were coated thinly with melted paraffin wax and submerged in water to estimate dry volume. A correction factor (0.9982) was applied to oven-dry weights following Muller-Landau (2004), as samples were not dried initially at 100–105 °C. Wood specific gravity was calculated by dividing oven-dry mass (g) by oven-dry volume (cm³) (Fearnside 1997; Williamson and Wiemann 2010). This method was chosen to ensure comparability of wood specific gravity values across sites, as plant water status at the time of sampling can influence green volume.

Isotopic and elemental analysis

For wood $\delta^{13}\text{C}$, two wood samples were taken from all individuals in the manner described for wood specific gravity. All samples were ground using a sample mill with a 40 μm mesh and homogenized and weighed $566.09 \pm 4.59 \mu\text{g}$ (mean \pm standard error). Samples were analyzed using a continuous flow mass spectrometer (ThermoFinnigan DeltaPlus Advantage, Costech Analytical Technologies Inc., Valencia, CA, USA). Carbon isotope ratios were calculated as $^{13}\text{C}/^{12}\text{C}$ ratio relative to PeeDee belemnite with an average precision of 0.14 ‰. At each site, two leaf samples were also collected per species and analyzed for carbon isotope ratios, to enable comparisons between leaf and wood tissue. Relative to leaves, wood tissue is typically more enriched in ^{13}C and we observed a similar pattern for the studied species. On

average, wood was 1.81 ‰ more enriched in ^{13}C than leaves, which is within the range of values reported in other studies (Cernusak et al. 2009a). While there are multiple hypotheses for this pattern (see Cernusak et al. 2009a), we found a high correlation of $\delta^{13}\text{C}$ between wood and leaf tissues for the studied species (ordinary least squares regression, $R^2 = 89.99\%$, p value <0.001), thus indicating that variation in wood $\delta^{13}\text{C}$ accurately reflected leaf-level physiological processes during the 2-year period of this study. Therefore, we use wood $\delta^{13}\text{C}$ as a proxy for time-integrated, whole-plant intrinsic water-use efficiency in the present study (Cernusak et al. 2007).

Using the same wood samples as for wood $\delta^{13}\text{C}$, wood C content was analyzed using a combustion analyzer (Flash EA 1112 Series NC Soil Analyzer, Thermo Electronic Corporation, Waltham, MA, USA). Wood samples weighed 8.26 ± 0.91 mg. Concentrations were calculated directly, using atropine as a standard reference material (70.56 % C).

Wood trait plasticity

For all wood traits, plasticity was calculated to assess species-specific across-site plasticity. Across-site trait plasticity represents the expressed variability of a trait in response to the contrasting seasonality at the two study sites and was calculated in the following manner, for each species:

$$\text{Plasticity}_{\text{Trait}} = \frac{\text{mean trait value}_{\text{DRY}} - \text{mean trait value}_{\text{WET}}}{\text{maximum trait mean}}$$

where ‘dry’ represents the more seasonal site and ‘wet’ represents the less seasonal site (Rozendaal et al. 2006; Valladares et al. 2000). The resulting values for plasticity range from negative to positive one in order to indicate the direction of plasticity, such that positive values denote mean trait values being greater at the more seasonal site and negative values denote mean trait values being greater at the less seasonal site. As wood $\delta^{13}\text{C}$ values are negative, the sign of the plasticity values was switched for comparative purposes.

Statistical analysis

Prior to analysis, all wood traits—wood specific gravity, wood $\delta^{13}\text{C}$, and wood C content—and whole-plant performance traits—basal diameter, aboveground biomass, and RGR_{BD} —were evaluated for normality and homogeneity of variance across groups. All whole-plant performance traits were natural-log transformed and wood C content was arc-sine transformed to meet normality assumptions (Warton and Hui 2011). All variables had homogeneous variance across groups, which were

evaluated with Levene’s test (p value >0.05). For all wood and tree traits, two-way ANOVAs with Type III sum of squares were used to test for differences between species, site, and all interactions. The proportion of the explained variance was calculated by dividing the sum of squares separately of each main factor and the interaction of both main factors by the total sum of squares of the model (Quero et al. 2006). Welch’s two-sample t tests were performed separately for all wood and tree traits for each species. For all wood traits, site-specific averages and 95 % confidence intervals were calculated from 10,000 bootstrapped replicate samples, using the bias-adjusted correction method (Venables and Ripley 2002). Estimates of mean trait plasticity and its corresponding 95 % confidence intervals were calculated for each wood trait in the same manner.

To determine the degree to which species-specific wood trait values at one site correlated with those at the other site, major axis (MA) regression was performed for each wood trait as both variables contained measurement error (Warton et al. 2006). The null expectation of no across-site plasticity was that the slope of the regression would be 1 and the elevation (sample mean of residual scores) would be 0. The null hypothesis was rejected if (a) the trait values were not significantly correlated or if (b) the slope and intercept varied significantly from 1 and 0, respectively. The relationships between plasticity of wood traits and whole-plant performance traits were assessed by Pearson’s correlation coefficients. MA regression analysis was performed using the R package ‘smatr’. Relationships between wood characteristics and tree traits at each study were evaluated using Pearson’s correlation coefficients. As wood $\delta^{13}\text{C}$ values are negative (range 23.5 ‰ to -28.8 ‰), they were natural-log transformed after adding an offset of 30 to make values positive. All analyses were performed with R 2.14.1 (R Development Core Team 2012).

Results

Interspecific variation in whole-plant performance and wood traits across sites

Across the nine studied tree species, differences in growth were strongly determined by species identity (Fig. 1; Table 3). For basal diameter and aboveground biomass, between 34 and 38 % of model variation was explained by species identity, respectively. Although statistically significant, site was practically inconsequential in explaining variation in aboveground biomass and basal diameter. Significant species \times site interactions for both variables showed that species did not respond uniformly to

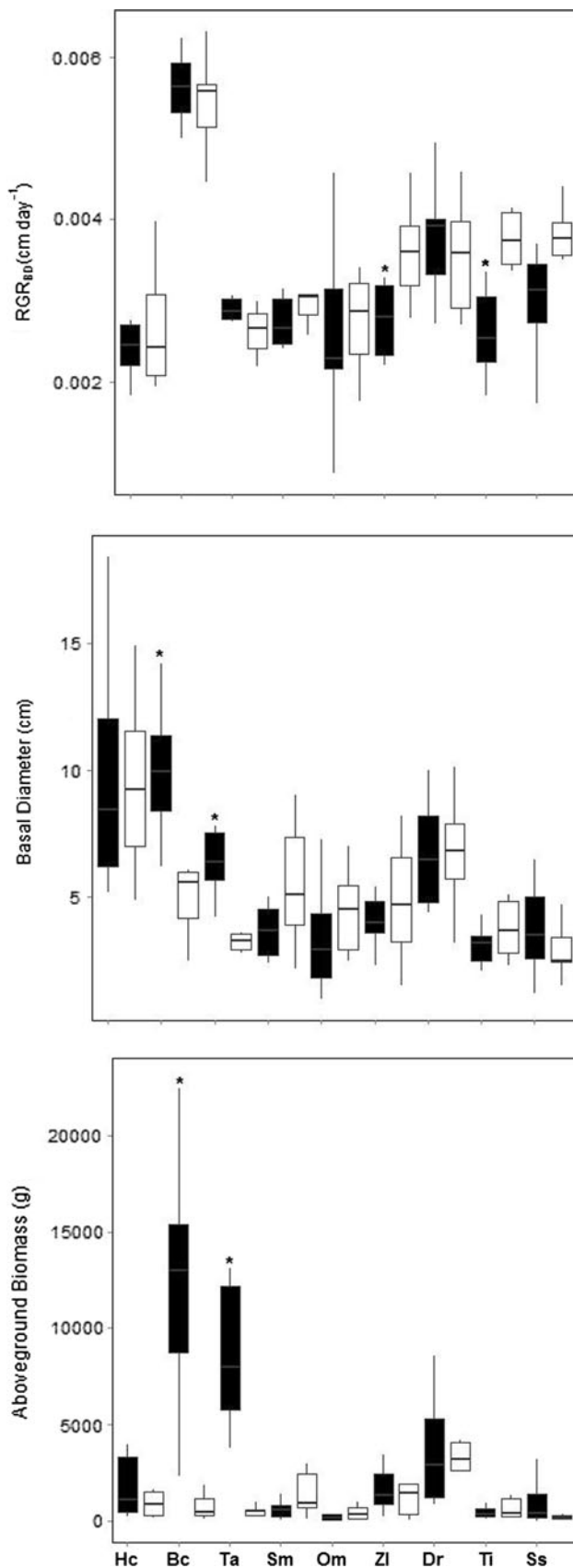


Fig. 1 Whole-plant performance traits of nine tropical tree species in Panama. Asterisks indicate statistically significant differences between sites for each species (Welch's two-sample *T* test, *p* value <0.05). Black-filled bars correspond to the less seasonal site (Las Lajas) and white-filled bars to the more seasonal site (Rio Hato). Whisker bars are standard errors

contrasting environmental conditions at the study sites. Specifically, sampled individuals of *Byrsonima crassifolia* and *Terminalia amazonia* exhibited significantly greater basal diameter (Welch's two-sample *T* test, *p* values <0.05, Fig. 1) and aboveground biomass (Welch's two-sample *T* test, *p* values <0.05, Fig. 1) at the less seasonal site than at the more seasonal site. A high proportion of model variation (47 %) also was explained by species identity for RGR_{BD} , which did not differ at statistically significant levels between sites or for the interaction of species and site (Table 3). While most species grew at similar rates at both study sites (Fig. 1), *Zygia longifolia* and *Tabebuia impetiginosa* had statistically significant higher RGR_{BD} at the more seasonal site than at the less seasonal site (Welch's two-sample *T* test, *p* values <0.05, Fig. 1).

To a greater extent than whole-plant performance traits, variation in all wood traits was concentrated at the species level (Table 3). Interspecific differences in wood traits explained between 35 and 76 % of model variability. Site was not a significant predictor for any of the wood traits and, consequently, explained a low proportion of model variability (0–16 %) (Table 3). Still, average wood $\delta^{13}C$ across all studied species was significantly higher at the more seasonal site (mean -26.10 ‰, 95 % confidence intervals -25.78 , -26.40 ‰) than at the less seasonal site (mean -27.06 ‰, 95 % confidence intervals -26.77 , -27.31 ‰). For wood $\delta^{13}C$, there were significant interactions between species and site, indicating that species responded differently to contrasting site conditions. Four of the studied species, *D. retusa*, *Z. longifolia*, *Sapindus saponaria*, and *T. amazonia*, exhibited significantly higher wood $\delta^{13}C$ at the more seasonal site than at the less seasonal site (Welch's two-sample *T* test, *p* value <0.05; Fig. 2). For wood specific gravity and wood C content, fewer species demonstrated significant differences between sites. Only *T. amazonia* had significantly greater wood C content at the less seasonal site than at the more seasonal site (Welch's two-sample *T* test, *p* value <0.05; Fig. 2) and only one species, *Sapindus saponaria*, had higher wood specific gravity at the more seasonal site than at the less seasonal site (Welch's two-sample *T* test, *p* value = 0.05; Fig. 2).

Wood trait plasticity

The studied species demonstrated a low amount of across-site plasticity for wood traits, with the exception of wood

Table 3 Results of linear models for wood and whole-plant performance traits of nine tree species at two study sites in Panama

| Wood traits | Adjusted R^2 (%) | Species | | Site | | Species \times site | |
|---|--------------------|-------------------|-----------|-------------------|-----------|-----------------------|-----------|
| | | SS_x/SS_{total} | p value | SS_x/SS_{total} | p value | SS_x/SS_{total} | p value |
| Wood $\delta^{13}C$ (‰) | 51.92 | 0.35 | <0.001 | 0.16 | 0.722 | 0.09 | 0.018 |
| Wood specific gravity ($g\ cm^{-3}$) | 75.36 | 0.76 | <0.001 | 0.00 | 0.280 | 0.03 | 0.094 |
| Wood C (%) ^b | 44.04 | 0.47 | <0.001 | 0.00 | 0.732 | 0.06 | 0.226 |
| Whole-plant performance | | | | | | | |
| Aboveground biomass (g) ^a | 42.0 | 0.34 | <0.001 | 0.02 | 0.001 | 0.16 | 0.002 |
| Basal diameter (cm) ^a | 39.8 | 0.38 | <0.001 | 0.00 | 0.012 | 0.11 | 0.021 |
| RGR _{BD} ($cm\ day^{-1}$) ^a | 48.3 | 0.47 | <0.001 | 0.04 | 0.794 | 0.06 | 0.168 |

For all variables, two-way ANOVAs using Type III sum of squares were performed (95 % confidence interval, $\alpha = 0.05$, degrees of freedom for site = 1 and for species = 8) to test for differences across species, sites, and the combination of the main effects. The proportion of explained variance (SS_x/SS_{total}) and the p value are provided for each main effect and the combination of both main effects. All variables had homogeneous variance; all tree traits were natural-log transformed and wood C and wood N were arc-sine transformed to meet normality assumptions. Adjusted R^2 is the proportion of total variance explained by the model, adjusted by the number of terms included in the model

^a Natural-log transformed to meet normality assumptions

^b Arc-sine transformed to meet normality assumptions

$\delta^{13}C$. For wood specific gravity and wood C content, trait values were strongly and significantly correlated between sites (range of R^2 values: 61.5–85.9 %) (Fig. 3). Furthermore, the slopes and elevations of the across-site regressions for the aforementioned wood traits did not vary significantly from 1 or 0, respectively. Wood $\delta^{13}C$ values were not correlated significantly between sites, indicating that across-site plasticity was not uniform across the studied species.

Among wood traits, wood $\delta^{13}C$ was the most plastic wood trait between study sites (mean: 0.037, 95 % confidence intervals: 0.02–0.06), followed by wood specific gravity (mean: 0.0049, 95 % confidence intervals 0.04–0.05) and wood C content (mean 0.001, 95 % confidence intervals 0.007–0.007). Wood $\delta^{13}C$ was the only wood trait whose 95 % confidence intervals did not overlap with zero, which indicates that the acclimation response to the seasonality gradient was negligible for wood specific gravity and wood C content. Across-site plasticity for all wood traits was not correlated significantly with whole-plant performance traits, nor with wood specific gravity (p value >0.05).

Relationships between wood traits and whole-plant performance

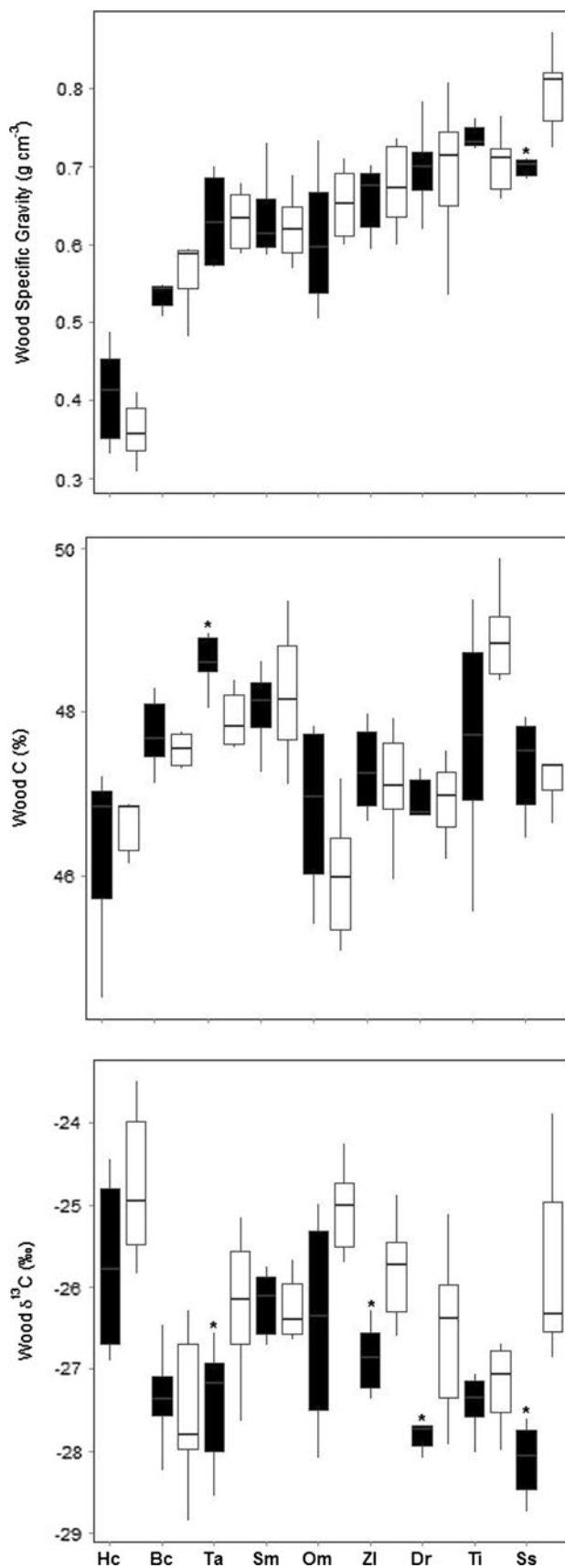
Distinct relationships among wood and whole-plant performance traits were found at each study site (Table 4). At the more seasonal site, wood $\delta^{13}C$ was negatively correlated with RGR_{BD} and wood C content, while at the less seasonal site wood $\delta^{13}C$ only was negatively correlated with wood specific gravity. In contrast, relationships among tree growth traits were largely consistent at both study sites.

Discussion

By assessing young saplings from the same species in replicated common garden experiments located in sites with contrasting seasonality, the current study allows us to evaluate the extent to which water availability modulates relationships between wood $\delta^{13}C$ and whole-plant performance. We found strong evidence that the adaptive value of high intrinsic water-use efficiency (less negative wood $\delta^{13}C$) is restricted to environments with low water availability and that plasticity of wood traits to contrasting levels of water availability was mostly neutral with regard to whole-plant performance.

Interspecific variation in wood traits across seasonality gradient

Overwhelmingly, variation in wood traits was conserved at the species level. The significant interspecific variation in wood $\delta^{13}C$ confirmed expectations that species would exhibit a differential capacity to compete for water. Across the tropical regions, interspecific differences in wood and foliar $\delta^{13}C$ have been reported extensively (Bonal et al. 2000, 2007; Cernusak et al. 2007; Craven et al. 2007; Guehl et al. 1998; Huc et al. 1994; Jackson et al. 1996) and are determined largely by variation in g_s and hydraulic conductivity, not A , related to differences in successional status, shade tolerance, and leaf phenology. For example, evergreen species in a tropical dry forest in Mexico compensated for low intrinsic water-use efficiency by using water from deeper in the soil to avoid seasonal drought stress, while deciduous species tolerated drought stress by reducing g_s , which increased intrinsic water-use efficiency (Hasselquist et al. 2010). In the French Guiana, similar



◀ **Fig. 2** Wood traits of nine tropical tree species in Panama. Asterisks indicate statistically significant differences between sites for each species (Welch's two-sample T test, p value <0.05). Black-filled bars correspond to the less seasonal site (Las Lajas) and white-filled bars to the more seasonal site (Rio Hato). Whisker bars are standard errors

differences were observed for shade-tolerant and intolerant species, where contrasting hydraulic conductance between the two functional groups determined variation in $\delta^{13}\text{C}$ (Bonal et al. 2000). The observed differences in wood $\delta^{13}\text{C}$ of the studied species likely correspond to different drought tolerance strategies, whose impacts on whole-plant performance will be discussed below.

Across-site variation of wood $\delta^{13}\text{C}$ was moderate relative to interspecific variation, yet revealed the capacity for the studied species to acclimate long-term intrinsic water-use efficiency to changes in water availability. Average wood $\delta^{13}\text{C}$ was significantly lower at the more seasonal site, indicating that the studied species—except for *B. crassifolia* and *S. macrophylla*—acclimated to lower annual precipitation and a longer dry season by increasing water-use efficiency. The aridity index, which integrates annual precipitation and potential evapotranspiration, is 2.7 times higher at the less seasonal site than at the more seasonal site and, thus, further supports the idea that the sampled individuals responded to lower water availability by increasing water-use efficiency (Diefendorf et al. 2010; Donovan et al. 2007; Gouveia and Freitas 2009; Ramírez-Valiente et al. 2010). In general, our results corroborate previous studies along water availability gradients in tropical, temperate, and Mediterranean ecosystems, which have found increasing water-use efficiency with decreasing water availability (e.g., Ares and Fownes 1999; Damesin et al. 1997; Keitel et al. 2006; Ramírez-Valiente et al. 2010; Schulze et al. 2006; Sobrado 2010). At the species level, the response of wood $\delta^{13}\text{C}$ to contrasting seasonality varied considerably as evidenced by the significant interaction of species and site, where four of the nine studied species (*D. retusa*, *S. saponaria*, *T. amazonia*, and *Z. longifolia*) exhibited significant differences between sites for wood $\delta^{13}\text{C}$. These results suggest that changes in water availability altered which species competed most effectively for water.

Whereas previous research on inter- and intra-specific variation of wood specific gravity of tropical tree species has focused on micro-habitat variation within the same forest community (Sungpalee et al. 2009) or across large geographical regions (Chave et al. 2006; Martínez-Cabrera et al. 2009; Muller-Landau 2004); the present study is unique in that we compared wood specific gravity of the same nine tree species across a seasonality gradient under the same management and using the same seed sources, while controlling for soil fertility and land-use history. Variation of wood specific gravity was strongly conserved at the species level,

Fig. 3 Mean wood traits at two sites of nine tropical tree species in Panama. Mean values for each wood trait per species at each site are plotted against one another. On the X and Y axes, ‘wet’ and ‘dry’ correspond to the less seasonal and more seasonal sites, respectively. The *solid black line* is the major axis (MA) regression line (*p* value <0.05). The *dotted gray line* represents a 1:1 relationship; species that occur along this line have equivalent trait values at both study sites. Species codes correspond to Table 2

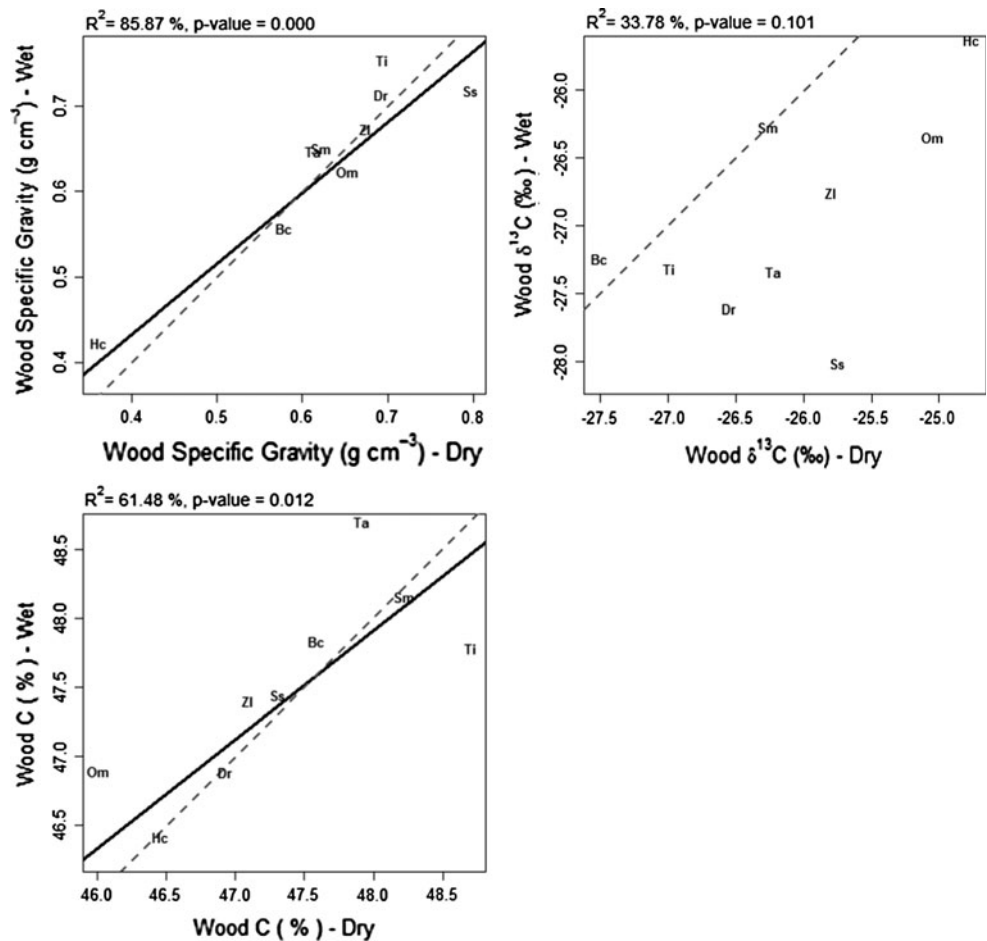


Table 4 Results of correlation analysis of wood and whole-plant performance traits of nine tree species in Panama at each study site

| Dry (Rio Hato) | Basal diameter (cm) | RGR _{BD} (cm day ⁻¹) | Aboveground Biomass (g) | Wood specific Gravity (g cm ⁻³) | Wood C (%) | Wood δ ¹³ C (‰) |
|---|---------------------|---|-------------------------|---|------------|----------------------------|
| Basal diameter (cm) | | | | | | |
| RGR _{BD} (cm day ⁻¹) | -0.10 | | | | | |
| Aboveground biomass (g) | 0.70 | 0.08 | | | | |
| Wood specific gravity (g cm ⁻³) | -0.76 | 0.33 | -0.20 | | | |
| Wood C (%) | -0.35 | 0.34 | 0.09 | 0.31 | | |
| Wood δ ¹³ C (‰) | 0.12 | -0.80 | -0.17 | -0.31 | -0.67 | |
| Wet (Las Lajas) | Basal diameter (cm) | RGR _{BD} (cm day ⁻¹) | Aboveground biomass (g) | Wood specific gravity (g cm ⁻³) | Wood C (%) | Wood δ ¹³ C (‰) |
| Basal diameter (cm) | | | | | | |
| RGR _{BD} (cm day ⁻¹) | 0.58 | | | | | |
| Aboveground biomass (g) | 0.87 | 0.68 | | | | |
| Wood specific gravity (g cm ⁻³) | -0.70 | -0.06 | -0.32 | | | |
| Wood C (%) | -0.13 | 0.08 | 0.25 | 0.42 | | |
| Wood δ ¹³ C (‰) | 0.11 | -0.40 | -0.22 | -0.68 | -0.31 | |

Pearson correlation coefficients were calculated using natural-log transformed values for all variables. As wood δ¹³C values are negative, they were natural-log transformed after adding an offset of 30 to make values positive. In the lower left corner, Pearson correlation coefficients are presented; values in bold are statistically significant at α = 0.05

as 76 % of its variation was attributable to interspecific differences. This value compares favorably with values reported by Chave et al. (2006) of 74 % for 2,456 species in Central and South America and by Sungpalee et al. (2009) of 80 % for 72 species in Thailand. Despite expectations that wood specific gravity would be higher at the drier site due to slower growth and preferential allocation to wood structural traits associated with drought tolerance (Hacke et al. 2001; Swenson and Enquist 2007), wood specific gravity of the studied species, except *S. saponaria*, did not vary significantly between sites. Our results support findings from previous studies, in which differences in species composition, as well as soil fertility, were identified as being the principal drivers of variation in wood specific gravity in neotropical forests (Baker et al. 2004; Muller-Landau 2004; ter Steege and Hammond 2001).

Similar to wood specific gravity and wood $\delta^{13}\text{C}$, wood C content also varied significantly across species. Average non-volatile wood C content for all species was 47.4 %, which is very similar to the global value of non-volatile wood C content (47.5 %) and is considerably below the expected value of 50 % (Martin and Thomas 2011; Thomas and Malczewski 2007). This result illustrates the importance of using actual wood C content values when estimating tropical forest C storage, which can result in significant overestimations when using the assumed value of 50 % to scale up C storage estimates at large spatial scales (Martin and Thomas 2011).

Acclimation to variation in water availability: plasticity in wood traits

We found that the plastic response of three wood traits to contrasting levels of water availability varied across wood traits. Wood $\delta^{13}\text{C}$ exhibited the most plasticity, while the plastic responses of wood specific gravity and wood C content were effectively neutral. Our results are consistent with previous studies on leaf trait plasticity in tropical forests, which reported greater plasticity for physiological traits than for morphological traits (Valladares et al. 2000). The differences in plasticity across wood traits possibly reflect the relative costs of acclimation to changes in water availability for particular traits. The energetic costs of increasing intrinsic water-use efficiency are minimal as no additional structures are needed to regulate stomatal movement. The costs of plasticity of wood specific gravity and wood C content to environmental variation are relatively high, as species would have to allocate proportionally greater amounts of C to increase cell wall thickness and fiber density (Martínez-Cabrera et al. 2009). Furthermore, structural investments to increase drought stress tolerance are not reversible and have long-term consequences that could decrease the competitive advantage of structural adaptations

in the future (Nicotra and Davidson 2010). Therefore, the low plasticity of wood specific gravity and wood C content points to genetic constraints, not variation in water availability, as being the principal determinants of variation for these traits (Baltzer et al. 2007; Chave et al. 2009).

We expected that plasticity in wood traits would be associated with life history strategies and whole-plant performance traits. As early successional species experience more stressful and variable environmental conditions in recently cleared areas and young secondary forests (Duff et al. 1997; Holl 1999; Lebrija-Trejos et al. 2011), we anticipated that these species would exhibit lower plasticity in wood traits than late-successional species. Counter to expectations, trait plasticity for all wood traits was statistically independent of life history strategies, which suggests that the ability to acclimate to changes in water availability is equally adaptive in both younger and older tropical forests (Engelbrecht et al. 2006; Slot and Poorter 2007).

In general, plasticity of all wood traits was neutral as the studied species achieved similar levels of whole-plant performance across sites despite variation in their physiological response to contrasting seasonality. These results conform with other studies that have found neutral or maladaptive plasticity of drought tolerance traits in response to water limitation for annual and tree species in desert and arid ecosystems (Donovan et al. 2007; Pohlman et al. 2005; Ramírez-Valiente et al. 2010). However, we encountered an exception to the overall pattern of neutral plasticity in *T. amazonia*, which exhibited an adaptive plastic response to the seasonality gradient. At the more seasonal site, the significant decreases in aboveground biomass and basal diameter of *T. amazonia* were matched by increases in water-use efficiency and wood C content. The adaptive plastic response of *T. amazonia* is consistent with the performance of habitat specialists, which exhibit better performance in more favorable environments, thus indicating that this species could be limited to areas with shorter, less intense dry seasons within the geographical range of its distribution (Comita and Engelbrecht 2009). This finding is further substantiated by the significant higher mortality rates of *T. amazonia* saplings at the more seasonal site reported by Breugel et al. (2011). Conversely, the neutral plastic response of the other studied species is comparable to the performance of habitat generalists (no differences across environments), which suggests that the habitat preferences of these species are not strongly influenced by water availability (Baltzer et al. 2009; Comita and Engelbrecht 2009).

Relationships of wood- and whole-plant performance traits in contrasting environments

We also explored relationships among wood and whole-plant performance traits to evaluate the adaptive value of

wood traits in sites with contrasting seasonality and found support for the prediction of Nicotra et al. (2010) that the adaptive value of wood $\delta^{13}\text{C}$ is context specific. At the more seasonal site, the studied species demonstrated a trade-off between water-use efficiency and growth, where wood $\delta^{13}\text{C}$ was significantly and negatively correlated with RGR_{BD} . The coordination of wood $\delta^{13}\text{C}$ with RGR_{BD} illustrates the consequences of water-use efficiency for species with contrasting drought tolerance strategies where water availability is limiting; fast-growing species had low intrinsic water-use efficiency, which is consistent with the stress avoidance strategy, while slow-growing species had high intrinsic water-use efficiency, which is associated with the stress tolerance strategy (Bonal et al. 2007; Chaves et al. 2002). While high intrinsic water-use efficiency did not enhance whole-plant performance in terms of greater tree size at the more seasonal site, the slower growth of species was adaptive given its well-established association with higher survival (King et al. 2006; Wright et al. 2010). However, high intrinsic water-use efficiency was not similarly coordinated with wood traits related to hydraulic function. Rather, the inverse relationship between wood $\delta^{13}\text{C}$ and wood C content at the more seasonal site suggests that species with low intrinsic water-use efficiency increased hydraulic safety by allocating more resources to C-rich structures (Hacke et al. 2001; Martínez-Cabrera et al. 2009; Swenson and Enquist 2007).

The relatively favorable growing conditions at the less seasonal site substantively altered the relationship of wood $\delta^{13}\text{C}$ to whole-plant performance traits. At the less seasonal site, we found that wood $\delta^{13}\text{C}$, through its inverse relationship with wood specific gravity, decreased with tree size at the less seasonal site. Despite having focused on saplings, the relationship between wood $\delta^{13}\text{C}$ and tree size found in the present study broadly coincides with previous studies on adult-sized trees in tropical forests, where increasing physiological efficiency with tree size also has been reported (Martinelli et al. 1998; Nock et al. 2011; Rijkers et al. 2000). With increasing tree stature, which is highly correlated with tree diameter (see King et al. 2005), trees adjust to the greater hydraulic resistance to water flow in the xylem by closing stomata and increasing leaf mass area to limit water loss (Rijkers et al. 2000; Thomas and Winner 2002). The greater drought-induced mortality suffered by large trees with low wood specific gravity in Amazonian forests suggests that, despite being more conservative in their water use, species with larger individuals and low wood specific gravity in the present study are more susceptible to drought stress (Nepstad et al. 2007; Phillips et al. 2010). While able to buffer against water stress because of greater stem water storage capacity, species with low wood specific gravity have a lower resistance to drought-induced embolism than species with higher wood

specific gravity due to larger diameter vessels and fibers (Borchert and Pockman 2005; Hacke et al. 2001; McCulloh et al. 2012). Thus, the adaptive value of intrinsic high water-use efficiency at the less seasonal site is conditional upon water availability; species with large-statured individuals would have a competitive advantage during periods of abundant precipitation (Coomes and Allen 2007; Potvin and Dutilleul 2009), but would likely experience disproportionately higher mortality following droughts.

Conclusions

To our knowledge, this is one of the few studies where the adaptive value of traits that underlie drought tolerance strategies in areas with contrasting levels of water availability have been explicitly tested in the tropics. Variation in wood traits of tree saplings was strongly determined by species identity, greatly exceeding variation attributable to differences in water availability between study sites. This variation in wood traits suggests that the response of tropical forests to severe droughts will depend greatly upon species composition. Perhaps due to genetic constraints, plasticity of wood traits to water availability was largely neutral, indicating that most species at younger life stages are able to maintain similar levels of growth across habitats that vary in water availability. Relationships of water-use efficiency with whole-plant performance and other wood traits also revealed that the adaptive value of water-use efficiency changed with water availability. While lower water availability can induce acclimation responses of physiological processes, our results suggest that—absent direct competition from other individuals—the effects of increased drought stress on growth of 2-year-old saplings were negligible for a majority of the studied species. Over longer periods of time, the prolonged impact of longer, more intense dry seasons might favor slow-growing species with conservative water-use strategies, as they might suffer less drought-induced mortality than less water-use efficient species.

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References

- Aguilar S, Condit R (2001) Use of native tree species by an Hispanic community in Panama. *Econ Bot* 55:223–235
- Aranda I, Gil-Pelegrín E, Gascó A, Guevara M, Cano J, Miguel M, Ramírez-Valiente J, Peguero-Pina J, Perdiguero P, Soto A (2012) Drought Response in forest trees: from the species to the gene. *Plant Responses to Drought Stress*: 293–333
- Ares A, Fownes JH (1999) Water supply regulates structure, productivity, and water use efficiency of *Acacia koa* forest in Hawaii. *Oecologia* 121:458–466
- Baker TR, Phillips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, Erwin T, Killeen TJ, Laurance SG, Laurance WF, Lewis SL, Lloyd J, Monteagudo A, Neill DA, Patino S, Pitman NCA, Silva MJN, Vasquez Martinez R (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Glob Change Biol* 10:545–562
- Baltzer JL, Davies SJ, Noor NSM, Kassim AR, Lafrankie JV (2007) Geographical distributions in tropical trees: can geographical range predict performance and habitat association in co-occurring tree species? *J Biogeogr*: 1–11
- Baltzer JL, Gregoire DM, Bunyavejchewin S (2009) Coordination of foliar and wood anatomical traits contributes to tropical tree distributions and productivity along the Malay-Thai Peninsula. *Am J Bot* 96:2214–2223
- Bastien-Henri S, Park A, Ashton M, Messier C (2010) Biomass distribution among tropical tree species grown under differing regional climates. *For Ecol Manage* 260:403–410
- Bonal D, Sabatier D, Montpied P, Tremeaux D, Guehl J (2000) Interspecific variability of $\delta^{13}\text{C}$ among trees in rainforests of French Guiana: functional groups and canopy integration. *Oecologia* 124:454–468
- 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. *Ann For Sci* 64:169–176
- Borchert R, Pockman WT (2005) Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. *Tree Physiol* 25:457–466
- Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. In: Caspari EW, Thoday JM (eds) *Advances in genetics*, vol 13. Academic Press, London pp 115–155
- Brenes-Arguedas T, Roddy A, Coley P, Kursar T (2011) Do differences in understory light contribute to species distributions along a tropical rainfall gradient? *Oecologia* 166:443–456
- Brienen R, Wanek W, Hietz P (2011) Stable carbon isotopes in tree rings indicate improved water use efficiency and drought responses of a tropical dry forest tree species. *Trees-Str Funct* 25:103–113
- Bryan JA, Berlyn GP, Gordon JC (1996) Toward a new concept of the evolution of symbiotic nitrogen fixation in the Leguminosae. *Plant Soil* 186:151–159
- Cernusak LA, Farquhar GD, Pate JS (2005) Environmental and physiological controls over oxygen and carbon isotope composition of Tasmanian blue gum, *Eucalyptus globulus*. *Tree Physiol* 25:129–146
- Cernusak LA, Aranda J, Marshall JD, Winter K (2007) Large variation in whole-plant water-use efficiency among tropical tree species. *New Phytol* 173:294–305
- Cernusak LA, Winter K, Aranda J, Turner BL (2008) Conifers, angiosperm trees, and lianas: growth, whole-plant water and nitrogen use efficiency, and stable isotope composition ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) of seedlings grown in a tropical environment. *Plant Physiol* 148:642–659
- Cernusak LA, Tcherkez G, Keitel C, Cornwell WK, Santiago LS, Knohl A, Barbour MM, Williams DG, Reich PB, Ellsworth DS, Dawson TE, Griffiths HG, Farquhar GD, Wright IJ (2009a) Why are non-photosynthetic tissues generally ^{13}C enriched compared with leaves in C_3 plants? Review and synthesis of current hypotheses. *Funct Plant Biol* 36:199–213
- Cernusak LA, Winter K, Turner BL (2009b) Physiological and isotopic ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) responses of three tropical tree species to water and nutrient availability. *Plant, Cell Environ*, pp 1441–1455
- Chave J, Muller-Landau HC, Baker TR, Easdale TA, Steege HT, Webb CO (2006) Regional and phylogenetic variation of wood density across 2,456 Neotropical tree species. *Ecol Appl* 16:2356–2367
- Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. *Ecol Lett* 12:351–366
- Chaves MM, Pereira JS, Maroco J, Rodrigues ML, Ricardo CPP, Osorio ML, Carvalho I, Faria T, Pinheiro C (2002) How plants cope with water stress in the field? Photosynthesis and growth. *Ann Bot* 89:907–916
- Comita LS, Engelbrecht BMJ (2009) Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology* 90:2755–2765
- Condit R, Aguilar S, Hernandez A, Pérez R, Lao S, Angher G, Hubbell SP, Foster RB (2004) Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J Trop Ecol* 20:51–72
- Coomes DA, Allen RB (2007) Mortality and tree-size distributions in natural mixed-age forests. *J Ecol* 95:27–40
- Cox PM, Harris PP, Huntingford C, Betts RA, Collins M, Jones CD, Jupp TE, Marengo JA, Nobre CA (2008) Increasing risk of Amazonian drought due to decreasing aerosol pollution. *Nature* 453:212–215
- Craven D, Braden D, Ashton MS, Berlyn GP, Wishnie M, Dent D (2007) Between and within-site comparisons of structural and physiological characteristics and foliar nutrient content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama. *For Ecol Manage* 238:335–346
- Craven D, Gulamhussein S, Berlyn GP (2010) Physiological and anatomical responses of *Acacia koa* (Gray) seedlings to varying light and drought conditions. *Environ Exp Bot* 69:205–213
- Damesin C, Rambal S, Joffre R (1997) Between-tree variations in leaf $\delta^{13}\text{C}$ of *Quercus pubescens* and *Quercus ilex* among Mediterranean habitats with different water availability. *Oecologia* 111:26–35
- Davidar P, Rajagopal B, Mohandass D, Puyravaud JP, Condit R, Wright SJ, Leigh EG (2007) The effect of climatic gradients, topographic variation and species traits on the beta diversity of rain forest trees. *Glob Ecol Biogeogr* 16:510–518
- Dawson TE, Mambelli S, Plamboeck AH, Templer PH, Tu KP (2002) Stable isotopes in plant ecology. *Annu Rev Ecol Syst* 33:507
- de Faria SM, de Lima HC (1998) Additional studies of the nodulation status of legume species in Brazil. *Plant Soil* 200:185–192
- Diefendorf AF, Mueller KE, Wing SL, Koch PL, Freeman KH (2010) Global patterns in leaf ^{13}C discrimination and implications for studies of past and future climate. *Proc Natl Acad Sci* 107:5738
- Donovan LA, Dudley SA, Rosenthal DM, Ludwig F (2007) Phenotypic selection on leaf water use efficiency and related

- ecophysiological traits for natural populations of desert sunflowers. *Oecologia* 152:13–25
- Duff GA, Myers BA, Williams RJ, Eamus D, O'Grady A, Fordyce IR (1997) Seasonal patterns in soil moisture, vapour pressure deficit, tree canopy cover and pre-dawn water potential in a Northern Australian Savanna. *Aust J Bot* 45:211–224
- Engelbrecht BMJ, Kursar TA (2003) Comparative drought-resistance of seedlings of 28 species of co-occurring tropical woody plants. *Oecologia* 136:383–393
- Engelbrecht BMJ, Dalling JW, Pearson TRH, Wolf RL, Gálvez DA, Koehler T, Tyree MT, Kursar TA (2006) Short dry spells in the wet season increase mortality of tropical pioneer seedlings. *Oecologia* 148:258–269
- Fan Z-X, Zhang S-B, Hao G-Y, Ferry Slik JW, Cao K-F (2012) Hydraulic conductivity traits predict growth rates and adult stature of 40 Asian tropical tree species better than wood density. *J Ecol* 100:732–741
- Farquhar GD, Richards RA (1984) Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes 11:539–552
- Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Funct Plant Biol* 9:121–137
- Fearnside PM (1997) Wood density for estimating forest biomass in Brazilian Amazonia. *For Ecol Manage* 90:59–87
- Fisher RA (1921) Some remarks on the methods formulated in a recent article on “the quantitative analysis of plant growth”. *Ann Appl Biol* 7:367–372
- Gouveia A, Freitas H (2009) Modulation of leaf attributes and water use efficiency in *Quercus suber* along a rainfall gradient. *Trees-Str Funct* 23:267–275
- Guehl J, Domenach A, Bereau M, Barigah T, Casabianca H, Ferhi A, Garbaye J (1998) Functional diversity in an Amazonian rainforest of French Guyana: a dual isotope approach ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). *Oecologia* 116:316–330
- Hacke UG, Sperry JS, Pockman WT, Davis SD, McCulloh (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461
- Hasselquist N, Allen M, Santiago L (2010) Water relations of evergreen and drought-deciduous trees along a seasonally dry tropical forest chronosequence. *Oecologia* 164:881–890
- Hietz P, Wanek W, Dünisch O (2005) Long-term trends in cellulose $\delta^{13}\text{C}$ and water-use efficiency of tropical *Cedrela* and *Swietenia* from Brazil. *Tree Physiol* 25:745–752
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978
- Holl KD (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica* 31:229–242
- Huc R, Ferhi A, Guehl JM (1994) Pioneer and late stage tropical rainforest tree species (French Guiana) growing under common conditions differ in leaf gas exchange regulation, carbon isotope discrimination and leaf water potential. *Oecologia* 99:297–305
- Hulshof CM, Swenson NG (2010) Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. *Funct Ecol* 24:217–223
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411
- Keitel C, Matzarakis A, Rennenberg H, Gessler A (2006) Carbon isotopic composition and oxygen isotopic enrichment in phloem and total leaf organic matter of European beech (*Fagus sylvatica* L.) along a climate gradient. *Plant, Cell Environ* 29:1492–1507
- King DA, Davies SJ, Supardi Noor MN, Tan S (2005) Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct Ecol* 19:445–453
- King DA, Davies SJ, Noor NSM (2006) Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. *For Ecol Manage* 223:152–158
- 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
- Kursar TA, Engelbrecht BMJ, Burke A, Tyree MT, Ei Omari B, Giraldo JP (2009) Tolerance to low leaf water status of tropical tree seedlings is related to drought performance and distribution. *Funct Ecol* 23:93–102
- Lebrija-Trejos E, Pérez-García EA, Meave JA, Poorter L, Bongers F (2011) Environmental changes during secondary succession in a tropical dry forest in Mexico. *J Trop Ecol* 27:477–489
- Llambí LD, Fontaine M, Rada F, Saugier B, Sarmiento L (2003) Ecophysiology of dominant plant species during old-field succession in a high tropical Andean ecosystem. *Arct Antarct Alp Res* 35:447–453
- Markestijn 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 Phytol* 191:480–495
- Martin AR, Thomas SC (2011) A reassessment of carbon content in tropical trees. *PLoS ONE* 6:e23533
- Martinelli L, Almeida S, Brown I, Moreira M, Victoria R, Sternberg L, Ferreira C, Thomas W (1998) Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondonia, Brazil. *Oecologia* 114:170–179
- Martínez-Cabrera HI, Jones CS, Espino S, Schenk HJ (2009) Wood anatomy and wood density in shrubs: responses to varying aridity along transcontinental transects. *Am J Bot* 96:1388–1398
- McCulloh KA, Johnson DM, Meinzer FC, Voelker SL, Lachenbruch B, Domec J-C (2012) Hydraulic architecture of two species differing in wood density: opposing strategies in co-occurring tropical pioneer trees. *Plant, Cell Environ* 35:116–125
- Moreira FMDS, Silva MFD, Faria SMD (1992) Occurrence of nodulation in legume species in the Amazon region of Brazil. *New Phytol* 121:563–570
- Muller-Landau HC (2004) Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36:20–32
- Mv Breugel, Hall JS, Craven DJ, Gregoire TG, Park A, Dent DH, Wishnie MH, Mariscal E, Deago J, Ibarra D, Cedeño N, Ashton MS (2011) Early growth and survival of 49 tropical tree species across sites differing in soil fertility and rainfall in Panama. *For Ecol Manage* 261:1580–1589
- Nepstad DC, Tohver IM, Ray D, Moutinho P, Cardinot G (2007) Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* 88:2259–2269
- Nicotra AB, Davidson A (2010) Adaptive phenotypic plasticity and plant water use. *Funct Plant Biol* 37:117–127
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. *Trends Plant Sci* 15:684–692
- Niinemets Ü (2010) Responses of forest trees to single and multiple environmental stresses from seedlings to mature plants: past stress history, stress interactions, tolerance and acclimation. *For Ecol Manage* 260:1623–1639
- Nock CA, Baker PJ, Wanek W, Leis A, Grabner M, Bunyavejchewin S, Hietz P (2011) Long-term increases in intrinsic water-use efficiency do not lead to increased stem growth in a tropical monsoon forest in western Thailand. *Glob Change Biol* 17:1049–1063

- Oelmann Y, Potvin C, Mark T, Werther L, Tapernon S, Wilcke W (2010) Tree mixture effects on aboveground nutrient pools of trees in an experimental plantation in Panama. *Plant Soil* 326:199–212
- Perez R, Condit R (2011) Tree atlas of Panama. <http://ctfs.arnarb.harvard.edu/webatlas/maintreeatlas.php>. January 23, 2011
- Phillips OL, Aragao LE, Lewis SL, Fisher JB, Lloyd J, Lopez-Gonzalez G, Malhi Y, Monteagudo A, Peacock J, Quesada CA, van der Heijden G, Almeida S, Amaral I, Arroyo L, Aymard G, Baker TR, Banki O, Blanc L, Bonal D, Brando P, Chave J, de Oliveira AC, Cardozo ND, Czimczik CI, Feldpausch TR, Freitas MA, Gloor E, Higuchi N, Jimenez E, Lloyd G, Meir P, Mendoza C, Morel A, Neill DA, Nepstad D, Patino S, Penuela MC, Prieto A, Ramirez F, Schwarz M, Silva J, Silveira M, Thomas AS, Steege HT, Stropp J, Vasquez R, Zelazowski P, Alvarez Davila E, Andelman S, Andrade A, Chao KJ, Erwin T, Di Fiore A, Honorio CE, Keeling H, Killeen TJ, Laurance WF, Pena Cruz A, Pitman NC, Nunez Vargas P, Ramirez-Angulo H, Rudas A, Salamao R, Silva N, Terborgh J, Torres-Lezama A (2009) Drought sensitivity of the Amazon rainforest. *Science* 323:1344–1347
- Phillips OL, van der Heijden G, Lewis SL, López-González G, Aragão LEOC, Lloyd J, Malhi Y, Monteagudo A, Almeida S, Dávila EA, Amaral I, Andelman S, Andrade A, Arroyo L, Aymard G, Baker TR, Blanc L, Bonal D, de Oliveira ÁCA, Chao K-J, Cardozo ND, da Costa L, Feldpausch TR, Fisher JB, Fyllas NM, Freitas MA, Galbraith D, Gloor E, Higuchi N, Honorio E, Jiménez E, Keeling H, Killeen TJ, Lovett JC, Meir P, Mendoza C, Morel A, Vargas PN, Patiño S, Peh KSH, Cruz AP, Prieto A, Quesada CA, Ramírez F, Ramírez H, Rudas A, Salamao R, Schwarz M, Silva J, Silveira M, Ferry Slik JW, Sonké B, Thomas AS, Stropp J, Taplin JRD, Vásquez R, Vilanova E (2010) Drought-mortality relationships for tropical forests. *New Phytol* 187:631–646
- Pohlman CL, Nicotra AB, Murray BR (2005) Geographic range size, seedling ecophysiology and phenotypic plasticity in Australian *Acacia* species. *J Biogeogr* 32:341–351
- Poorter L, McDonald I, Alarcón A, Fichtler E, Licona J-C, Peña-Claros M, Sterck F, Villegas Z, Sass-Klaassen U (2010) The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytol* 185:481–492
- Potvin C, Dutilleul P (2009) Neighborhood effects and size-asymmetric competition in a tree plantation varying in diversity. *Ecology* 90:321–327
- Proyecto de Inventario y Demostraciones Forestales (PIDP) (1970) Mapa ecológico de Panamá. El Proyecto, Panamá
- Quero JL, Villar R, Marañón T, Zamora R (2006) Interactions of drought and shade effects on seedlings of four *Quercus* species: physiological and structural leaf responses. *New Phytol* 170:819–834
- Ramírez-Valiente JA, Sánchez-Gómez D, Aranda I, Valladares F (2010) Phenotypic plasticity and local adaptation in leaf ecophysiological traits of 13 contrasting cork oak populations under different water availabilities. *Tree Physiol* 30:618–627
- R Development Core Team (2011) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org/>
- Rijkers T, Pons TL, Bongers F (2000) The effect of tree height and light availability on photosynthetic leaf traits of four Neotropical species differing in shade tolerance. *Funct Ecol* 14:77–86
- Rozendaal D, Zuidema P (2011) Dendroecology in the tropics: a review. *Trees-Str Funct* 25:3–16
- Rozendaal DMA, Hurtado VH, Poorter L (2006) Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Funct Ecol* 20:207–216
- Schulze E-D, Turner NC, Nicolle D, Schumacher J (2006) Leaf and wood carbon isotope ratios, specific leaf areas and wood growth of Eucalyptus species across a rainfall gradient in Australia. *Tree Physiol* 26:479–492
- Seibt U, Rajabi A, Griffiths H, Berry JA (2008) Carbon isotopes and water use efficiency: sense and sensitivity. *Oecologia* 155:441–454
- Slot M, Poorter L (2007) Diversity of tropical tree seedling responses to drought. *Biotropica* 39:683–690
- Sobrado MA (2010) Leaf characteristics, wood anatomy and hydraulic properties in tree species from contrasting habitats within upper Rio Negro forests in the Amazon region. *J Trop Ecol* 26:215–226
- Sungpalee W, Itoh A, Kanzaki M, Sri-ngernyuan K, Noguchi H, Mizuno T, Teejuntuk S, Hara M, Chai-udom K, Ohkubo T, Sahunalu P, Dhanmmanonda P, Nanami S, Yamakura T, Sornngai A (2009) Intra- and interspecific variation in wood density and fine-scale spatial distribution of stand-level wood density in a northern Thai tropical montane forest. *J Trop Ecol* 25:359–370
- Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *Am J Bot* 94:451–459
- ter Steege H, Hammond DS (2001) Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology* 82:3197–3212
- Thomas SC, Malczewski G (2007) Wood carbon content of tree species in Eastern China: interspecific variability and the importance of the volatile fraction. *J Environ Manage* 85:659–662
- Thomas SC, Winner WE (2002) Photosynthetic differences between saplings and adult trees: an integration of field results by meta-analysis. *Tree Physiol* 22:117–127
- Tilki F, Fisher RF (1998) Tropical leguminous species for acid soils: studies on plant form and growth in Costa Rica. *For Ecol Manage* 108:175–192
- Valladares F, Wright SJ, Lasso E, Kitajima K, Pearcy RW (2000) Plastic phenotypic response to light of 16 congeneric shrubs from a Panamanian rainforest. *Ecology* 81:1925–1936
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. *New Phytol* 176:749–763
- Venables WN, Ripley BD (2002) Modern applied statistics with S. Springer, Verlag
- Warton DI, Hui FKC (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology* 92:3–10
- Warton DI, Wright IJ, Falster DS, Westoby M (2006) Bivariate line-fitting methods for allometry. *Biol Rev* 81:259–291
- Williams JW, Jackson ST, Kutzbach JE (2007) Projected distributions of novel and disappearing climates by 2100 AD. *Proc Natl Acad Sci* 104:5738
- Williamson GB, Wiemann MC (2010) Measuring wood specific gravity...correctly. *Am J Bot* 97:519–524
- Wishnie MH, Dent DH, Mariscal E, Deago J, Cedenó N, Ibarra D, Condit R, Ashton PMS (2007) Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama. *For Ecol Manage* 243:39–49
- Wright SJ, Kitajima K, Kraft NJB, Reich PB, Wright IJ, Bunker DE, Condit R, Dalling JW, Davies SJ, Diaz S, Engelbrecht BMJ, Harms KE, Hubbell SP, Marks CO, Ruiz-Jaen MC, Salvador CM, Zanne AE (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* 91:3664–3674

- Zanne AE, Westoby M, Falster DS, Ackerly DD, Loarie SR, Arnold SE, Coomes DA (2010) Angiosperm wood structure: global patterns in vessel anatomy and their relation to wood density and potential conductivity. *Am J Bot* 97:207–215
- Zomer RJ, Trabucco A, Bossio DA, Verchot LV (2008) Climate change mitigation: a spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agric Ecosyst Environ* 126:67–80