

Functional traits shape size-dependent growth and mortality rates of dry forest tree species

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Abstract

Aims

Functional traits have emerged as an important tool to evaluate plant performance. However, the environmental conditions and ecological pressures that plants face change with their size, and the relationship between traits and plant performance should therefore be size-dependent, which has rarely been tested.

Methods

Here, we evaluated over a broad range of tree sizes the interspecific relationship between tree growth and mortality and eight functional stem, leaf and seed traits. We did so across 59 tree species in Brazilian dry forests and evaluated whether the relationships found for wet forest types in the literature also hold for dry forests, where water rather than light might limit tree performance.

Important Findings

We indeed found a strong size-dependent relationship between demographic rates and functional traits. At small sizes, when trees are in the shaded understory, species with functional trait values

that enhance light capture or shade tolerance (i.e. higher maximum adult stature, taller heights, wider crowns, higher seed mass) have higher growth and/or lower mortality rates (MR). This relationship disappears at larger sizes when trees attain better light conditions in the canopy. Drought adaptations play only a role at larger tree sizes; once trees are in the dry and exposed canopy, species with higher wood density (an indicator of cavitation resistance) have lower MRs. Our study shows that both drought and shade adaptations are important in this dry forest, and that the relationships between functional traits and plant performance changes with plant size. Plant size should therefore explicitly be included as an axis of variation in functional analyses, to better understand the relationship between functional traits and demographic rates.

Keywords: demographic rates, leaf traits, seed mass, tree architecture, wood density

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INTRODUCTION

The influence of plant functional traits on interspecific demographic rates (growth and mortality) has received an increasing attention because it allows us for an understanding of the underlying determinants of species' success (Reich 2014; Westoby and Wright 2006). Trait-driven variation in species growth and survival promotes species coexistence through differential exploitation of resources (Violle and Jiang 2009),

and affects ecosystem functioning, altering communities productivity and resilience to disturbances (Lebrija-Trejos *et al.* 2008; Prado-Junior *et al.* 2016).

Most community-level studies that indicate how functional traits affect growth and mortality rates (MRs) were conducted in tropical wet forests, where light is a strongly limiting resource in the forest understory (Hérault *et al.* 2011; Iida *et al.* 2014a; Poorter *et al.* 2008; Wright *et al.* 2010). Among these studies, there is a general consensus that adult stature,

plant architecture (i.e. dimensions of the tree's stem and crown), wood density (WD), leaf traits and seed mass (SM) are good predictors of the growth and survival trade-offs (Liu *et al.* 2013; Reich *et al.* 2003; Rüger *et al.* 2012; Westoby 1998). Our current knowledge for wet forests indicates that (i) higher adult stature species grow faster because they experience on average brighter light conditions throughout most ontogenetic stages (Poorter 2007), and can shift allocation from reproduction to growth to reach the highest strata at which they start to reproduce (Iida *et al.* 2014a; Poorter 2008; Thomas 2011), whereas small statured species exhibit higher survival rates that allow them to persist in the forest understory (Iida *et al.* 2014a; Thomas 2011); (ii) species with taller and wider crowns have higher growth as they intercept a higher amount of light and overtop competing neighbours (Poorter and Bongers 2006; Poorter 2008), while they have a higher mortality because they are more sensitive to mechanical damage by falling branches and wind forces (Iida *et al.* 2014b; Sterck and Bongers 1998), (iii) species with dense wood have lower growth because of higher construction costs per wood volume, and lower mortality because of enhanced resistance to stem breakage and to fungal and pathogen attack (Chave *et al.* 2009; King *et al.* 2006; Poorter *et al.* 2006); (iv) species with larger leaf area (LA) and specific leaf area (SLA) have faster growth because of a higher interception of light, photosynthesis and carbon net gain, whereas they have a higher mortality because of higher respiratory rates, leaf turnover and vulnerability to herbivory and pathogen attack (Iida *et al.* 2014a; Kitajima and Poorter 2010; Liu *et al.* 2013) and (v) species with higher SM have slower growth because they have a higher biomass investment in long-lived leaves than in stem or roots as their higher seed resources enable them to become autotrophic later (Paz *et al.* 2005), while they have lower mortality because the large seed reserves allow them to make large, robust seedlings that can escape size-dependent mortality caused by defoliation, drought and shading by neighbours, and recover after damage (Harms and Dalling 1997; Leishman *et al.* 2000). Although this trade-off is found for seedlings, in wet forests SM is also related to the growth and MRS of trees. This is not because of mechanistic reasons, but because SM is an important life-history trait and correlated to a suite of morphological and physiological traits of small-seeded fast-growing pioneer species and large-seeded slow growing shade-tolerant species (Leishman *et al.* 2000; Poorter and Rose 2005).

The trait–demography relationships are mainly based on the growth and survival trade-off, driven by the contrasts between slow-growing shade-tolerant species that survive very well in the shade versus light-demanding pioneer species that grow very fast in high light but die very fast (Poorter and Bongers 2006; Poorter *et al.* 2006; Wright *et al.* 2010). However, trait–demography relationships may be fundamentally different in other forest types where other resources limit plant performance (Prado-Junior *et al.* 2016). For example in Mediterranean forests, strongly limited by seasonal

variation in water availability and temperature, demographic rates were closely associated to changes in temperature and rainfall (Ibáñez *et al.* 2014). Other studies in temperate and Mediterranean forests also find that the classical trade-off between growth and survival based on high-light demanding species and shade tolerant species is weaker (or absent) compared to them commonly in wet forests (Kunstler *et al.* 2009; Martínez-Vilalta *et al.* 2010). Few comparative studies have been carried out in tropical dry forests. In dry forests, light should not be a major limiting resource, due their lower and more open forest canopy (Lebrija-Trejos *et al.* 2008; Lohbeck *et al.* 2013). Traits that are associated to light capture may therefore be weakly correlated with demographic rates. Instead water availability may become limiting in dry forests, because of the strong seasonal variation in rainfall in dry forest regions. Dry forests species possess a suite of traits such as a deciduousness, higher WD and SLA (Borchert 1994; Reich *et al.* 2003) that are associated to drought avoidance and/or resistance (Barajas-Morales 1987; Tripathi and Raghubanshi 2014). These traits could therefore also be more closely related to species variation in demographic rates.

A central but yet understudied question in functional ecology is whether in natural communities functional traits really affect demographic rates and hence, what traits are ecologically relevant. Moreover, the environmental conditions and ecological pressures that plants face change with their size, and the relationship between traits and plant performance should therefore be size-dependent, especially for plants that can attain large sizes, such as trees. Very few studies showed how these trait–demography relationships change over tree size from saplings to large trees (Iida *et al.* 2014a; Iida *et al.* 2014b), and such a size-dependent approach is needed, if we better want to understand species- and community dynamics (Wright *et al.* 2010). The effects of these functional traits on demographic rates should especially be strongly size-dependent in forest communities, as in forests species are exposed to a strong vertical gradient in abiotic conditions. From the understory to the canopy, there is an increase in irradiance, temperature, wind exposure and atmospheric water stress (Niinemets and Valladares 2004). Thus, functional trait values that increase light capture, photosynthetic carbon gain and shade tolerance (e.g. wider crowns and higher SLA) should increase demographic rates mainly at small sizes when trees are in the shaded understory (Iida *et al.* 2014a; Sterck *et al.* 2003), whereas functional traits that increase species' resistance to water stress and wind exposure (e.g. higher WD) should enhance demographic rates mainly at larger sizes when trees are in the exposed canopy (Koch *et al.* 2004). Dry forests are among the most fragmented and threatened ecosystems in the world (Miles *et al.* 2006). Insight in their functioning, and how functional traits affects species dynamics can help to improve their management and conservation.

The aim of this study is to evaluate (1) which functional traits are associated to demographic rates (i.e. growth and mortality) of dry forests tree species, (2) how this relationships

change with tree size and (3) to what extent the classical trade-off between growth and survival reported for moist and wet forests also hold for dry forests. If dry forests show similar trait–demography relationships as in wet forests, then we would expect that (1) growth and MRs will be higher for species with higher maximum diameter, taller heights, larger crown area and first branch height, larger (specific) LA and lower WD and SM; (2a) the relationships between demographic rates and functional traits that affect species light capture and shade tolerance (e.g. tree architecture, leaf traits and SM) will be strong at small sizes in the light-limited understory, and will be weaker at larger sizes when trees attain the canopy; (2b) the relationships between demographic rates and functional traits that affect species' resistance to water stress and wind exposure (e.g. WD) should influence demographic rates mainly at larger sizes when trees are in the dry and exposed canopy. These hypotheses were tested by evaluating the relationship between size-dependent growth and mortality and eight functional stem, leaf and seed traits of 59 common tree species (~6000 trees) in Brazilian dry forests.

METHODS

Study sites and species sampling

This study was conducted in eight seasonal dry forests (18°29' to 19°40' S and 47°30' to 48°24' W), at extreme west of Minas Gerais state, Southeastern Brazil (Prado-Junior *et al.* 2016). The distance among forests ranges from 20 to 180 km. The region experiences a tropical savanna climate (Aw Megathermic climate of Köppen), characterized by rainy summers (October–March) and dry winters (April–September). Annual rainfall ranges from 1123 to 1547 mm, the dry season length from 4 to 6 months (<100 mm in the whole dry season) and mean annual temperature of 21–22°C (Prado-Junior *et al.* 2016). The study areas are considered mature forests (Prado-Junior *et al.* 2016), located in conservation units or legal reserves and are surrounded by an agricultural or urban matrix (Lopes *et al.* 2012). Soil type in studied areas is primarily red latosols that vary from moderately to strongly acidic (Dos Santos *et al.* 2013). The canopy height of the forests is around 17–20 m, and trees attain a position in the canopy when they have a diameter at breast height (DBH) of 25 cm. Unfortunately we could not evaluate how differences in abiotic variables among forests could affect our results, but because our study forests experience homogeneous climate, soil type and disturbance, we expect that the abiotic variables had minimal effects on our results.

In each forest, a 1-ha permanent sample plot was established. In the first census (2006–2009), all trees with stem (DBH, 1.30 m) ≥ 5 cm were tagged, their diameter was measured, height estimated and identified to species. In the second census, after 5 years (2011–2014), all trees were re-measured and growth and MRs were evaluated. A total of 7868 individuals were measured, belonging to 237 species, 161 genera and 58 families. For this study, we used the 59 species most

abundant species (comprising 76% of all individuals) that had at least 25 individuals and sufficient information about their functional traits (Supplementary Table 1). From the 59 selected species, traits were measured from random adult trees across forests (when a species occurred in more than one area). Traits were measured during the second census.

Functional traits

Adult stature

To quantify species-specific adult stature, we used potential maximum stem diameter rather than tree height because stem diameter was measured more precisely, and height estimations are especially difficult in tropical forests, where there is a large error for large trees. Maximum stem diameter (D_{\max}) scales closely with maximum tree height of the species (King *et al.* 2006), so it is a proper indicator of the potential adult stature of the species (Iida *et al.* 2014a). D_{\max} was calculated for each species as the upper 95-percentile stem diameter for those trees whose diameter was equal to or greater than 10% of the observed maximum diameter of a population (King *et al.* 2006). This method minimizes the effect of the shape of the population structure on the maximum stem diameter estimate and reduces the probability of underestimating the potential maximum size for a specific population with a large proportion of small individuals (King *et al.* 2006). We used the DBH dataset of the first census to determine species D_{\max} . Maximum diameter across the selected species ranged from 8.9 to 169.7 cm, with an average of 33.7 cm (Supplementary Table S1). We acknowledge that thicker individuals may be found, but this is the best quantitative estimate of D_{\max} that we have, and reflects the size potential of the species given the local environmental conditions.

Tree architecture

Tree architectural variables as tree height (H), first branch height (FBH) and the average of two perpendicular projected crown widths (CW) were collected from 5 to 10 (average 7.8) adult trees (with DBH near to D_{\max}) for each species, totalling 464 trees. DBH and CW were measured with a tape measure, and H and FBH with a clinometer (Haglof HEC, Langsele, Sweden). As the aim of this study was to link demographic rates to absolute values of tree architecture at different reference diameters, and FBH and CW vary with tree height we used a three-step approach. First, we calculated for each species a relative measure of tree architecture by calculating the median crown length ratio (FBH/H) and crown width ratio (CW/H). The coefficients of variation within species for FBH were on average 23% and for CW was 25%. Trees of the same species tend to attain a characteristic crown shape (Poorter *et al.* 2006; Valladares and Niinemets 2007) and several models to estimate crown area are based on tree height (Valladares and Niinemets 2007). By doing so we assumed that the relative architecture changes little or not with size (Supplementary Table 1). Secondly, we used this relative measure to calculate the absolute FBH and CW for the 5988

individuals for which DBH and H values were available from the census. Third, we used the absolute data of these 5988 individuals to make species-specific allometric regressions relating absolute H, FBH and CW to DBH. The explained variation (r^2) of these species-specific regressions was for H–DBH was 52% (range 23–83%), for FBH–DBH 46% (range 17–77%) and for CW–DBH 41% (range 9–68%). We used the species-specific logarithmic regressions to predict H, FBH and CW at each reference stem diameter at 1 cm interval from 5 cm to 40 cm (see below; Supplementary Table 1).

Wood density

Species-specific WD data were obtained from a global WD database (Zanne *et al.* 2009; Global Wood Density Database, available online). WD data were selected from the South America tropical region in the database to reduce region-specific differences as much as possible. When species-level WD values were not available, then genus-level WD values were used, because WD is a trait that is phylogenetically conserved (Chave *et al.* 2006). WD across the selected species ranged from 0.46 to 0.93 g cm⁻³, with an average of 0.70 g cm⁻³ (Supplementary Table S1).

Leaf traits

We collected fully expanded leaves with no obvious symptoms of pathogen or herbivore damage from the same adult trees for which tree architecture was measured (DBH near to D_{\max} , between 7 and 18 m). For species that occur under sun and shade conditions, we collected leaves from both condition and then used the average values between sun and shade leaves. We collected sun and shade leaves. Ten leaves were collected from 5 to 10 individuals for each species (average 7.8 individuals). Leaves were sealed in plastic bags to remain turgid until leaf traits were measured in the laboratory. Leaves including the petiole were scanned with a metric reference scale and the total LA of an individual leaf (LA in cm²) was calculated using the program ImageJ (version 1.34, National Institutes of Health, <http://imagej.nih.gov/ij/>). Leaves were placed in an oven at 60°C for 72 h before measurement of leaf dry mass (LDM in mg). SLA (mm² mg⁻¹) was calculated as LA divided by leaf dry mass. For species with compound leaves, leaf traits were calculated for the whole leaf, including the rachis. LA across species ranged from 9.4 to 460.6 cm², with an average of 89.4 cm²; and SLA ranged from 7.4 to 22.8 mm² mg⁻¹, with an average of 13.5 mm² mg⁻¹ and across species, the average coefficient of variation for LA was 32% and for SLA was 18% (Supplementary Table 1).

Seed mass

Species-specific fresh SM data were obtained from literature (Lorenzi 1992, 1998) for 49 of the 59 studied species. SM across the selected species ranged from 3.4 to 3225.8 mg, with an average of 474.6 mg (Supplementary Table 1).

Size-dependent growth and MR

We estimated the size-dependent relative diameter growth rate (RGR) and MR following Iida *et al.* (2014b). First, we calculated the RGR of each tree that survived during the census

interval as $RGR = (\ln DBH_2 - \ln DBH_1) \cdot (t_2 - t_1)^{-1}$. We then estimated the RGR of i th individual tree, RGR_i , as a linear function of the natural logarithm of the initial stem diameter DBH_{1i} of individual tree i of the species j :

$$RGR_{ij} = r_{1j} + r_{2j} \ln(DBH_{1i}) \quad (1)$$

The parameter r_{1j} is the equation's intercept and r_{2j} show the effect of increased DBH on growth. We calculated growth rates for 5282 individual trees belonging to 59 species (average number of trees per species is 89.5, range 26–302 trees; Supplementary Table 2). The mean explained variation (r^2) of these species-specific regressions was 18% (range 2–41%),

Our mortality model is based on the observation of a individual tree i and whether it died through the census period ($M_i = 1$) or not ($M_i = 0$). Mortality probability (M_i) of the i th individual tree and species j was predicted as a binary logistic regression based on the stem diameter of individual i at the first census, DBH_{1i} :

$$\text{logit}(MR_{ij}) = m_{1j} + m_{2j} \ln(DBH_{1i}) \quad (2)$$

Parameter m_{1j} is the equation's intercept and m_{2j} show the effect of increased DBH on it mortality probability. After that, the MR was divided by the census length (5 years) to have annual MRs. We calculated MRs for 5988 individual trees belonging to 59 species (average number of trees per species is 101.5, range 28–388 trees; Supplementary Table 2). The explained variation (r^2) of these species-specific regressions was 12% (range 2–23%).

Interspecific relationships between demographic rates and functional traits

We related demographic rates to the average functional traits of the species, rather than measuring functional traits at each size, which would logistically be very challenging. We acknowledge that all species and traits do show plastic trait responses to environmental conditions (Poorter 2012; Sendall 2013; Siefert 2015), and that traits vary with plant size. Yet, the intraspecific trait variation in our study was smaller (11%, range 4–18%) compared to interspecific trait variation (89%, range 82–96%) (Supplementary Table 4), and across species, seedling trait values and adult trait values are strongly positively correlated (Poorter 2008), indicating that species ranking in interspecific comparisons will not change. Besides, the relative amount of intraspecific variation compared to interspecific variation decreases with increasing species richness (lower in tropical forests), and lower for morphological traits (which we measured) compared to chemical traits (Siefert *et al.* 2015), indicating that plastic trait changes will confound our results only to a limited extent.

Using the species-specific regression equations, we calculated for each species its demographic rate (RGR and MR) using Equations 1 and 2, and tree architecture (H, FBH and CW) at several standardized reference stem diameters from 5 to 40 cm, using 1 cm intervals. We did so to obtain the best estimates of

the values of demographic rates and functional traits at a range of reference sizes, to be able to detect at what stem diameter trait–demographic rate relationships appear, are strongest, or disappear. We then calculated for each reference stem diameter Kendall's rank correlation coefficient (τ) between species demographic rates and functional traits. Kendall's τ is used to measure the association between two non-parametric variables (i.e. species demographic rates and functional traits of this study), as Spearman's correlation coefficient (ρ). Although Kendall's τ is less popular than Spearman's ρ , it is a better estimator of non-parametric correlations because it provides much tighter confidence intervals and less biased estimation of the true correlation than Spearman's ρ and allow for more accurate generalizations (Monjardet 1998).

D_{\max} and WD are the main predictors of growth and mortality (Héroult et al. 2011; Iida et al. 2014a; King et al. 2006; Poorter and Markesteijn 2008; Poorter et al. 2008; Wright et al. 2010), but they can also be correlated with our other functional predictor traits. We therefore first examined the correlations between D_{\max} and WD versus the other functional traits (H, FBH, CW, LA, SLA and SM) (Supplementary Table 4). As tree architecture varies with stem diameter, we examined these correlations at different reference diameters (5, 10, 15, 20 and 25 cm), where most of species were included. D_{\max} was positively correlated with tree architecture (H, FBH, CW) for most of reference diameters, negatively with SLA and not significantly correlated with LA or SM. WD was not related to any other functional traits (Supplementary Table 4). Thus, to evaluate the interspecific relationships between growth and MRs and H, FBH, CW and SLA, we used Kendall's partial rank correlation, thus eliminating the confounding effect of D_{\max} on these relationships (Siegel and Castellan 1988). To relate demographic rates to LA and SM, we used the normal Kendall's tau correlation, because these two predictor traits were not related to D_{\max} or WD. Kendall's correlation was considered to be significant if probability value was smaller than 5% ($P < 0.05$). Species were included in the correlation analysis for each reference stem diameter smaller than their D_{\max} . The number of species used in the correlation analysis decreased with reference stem diameter due to the dropout of small-statured species from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm). To evaluate whether the observed size-dependent patterns of correlations were due to decreasing sample size, dropout of species with smaller D_{\max} or size-dependent changes in demographic rates, we repeated the analysis for the largest 25 species only (D_{\max} from (range from 27.6 to 169.6 cm). All statistical analyses were conducted using the statistical program R 3.1.2 (R Developing Core Team 2014).

RESULTS

Interspecific relationships between RGR and functional traits

Relative growth rate (RGR) declined with increasing stem diameter for most species (Fig. 1a). Across species, RGR was

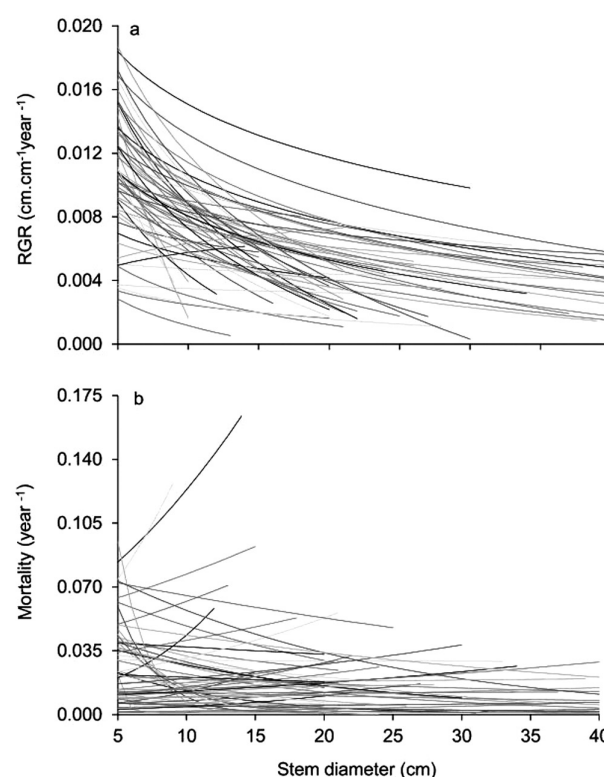


Figure 1: size-dependent changes in relative stem diameter growth rate (RGR) and MR across 59 dry-forest tree species. Lines show changes in RGR (a) and mortality (b) with increasing stem diameter (cm) by applying medians of probability distributions of RGR and MR for 59 tree species.

positively correlated with maximum diameter (D_{\max}) for small trees (reference stem diameters up to 25 cm) (Fig. 2a) indicating that, at small sizes, larger species tend to grow faster in stem diameter than small species. RGR was not related to WD for any of the reference stem diameters (Fig. 2c).

At small sizes, RGR was positively correlated with H and FBH (most of reference diameters up to 22–25 cm) (Fig. 3a and c) and with CW and LA (up to 8–13 cm) (Fig. 3e and g). RGR was negatively correlated with SLA from 16 to 18 cm stem diameter (Fig. 3i) and not correlated with SM (Fig. 3k). These results indicate that, at small sizes, species with taller heights, higher FBH, wider crowns, larger LA and lower SLA tend to grow faster in stem diameter, independently of their maximum diameter.

To determine whether size-dependent growth rate changes were due to the dropout of species with small maximum diameter from interspecific comparisons, we repeated the same analyses for the 25 largest species. Similar relationships between RGR-H and RGR-FBH were found as in the analysis in which all species were included (Supplementary Figure 5) whereas the relationships between RGR and the other traits (CW, LA and SLA) became non-significant. These results confirm that relationships between RGR-H and RGR-FBH across species are size-dependent, are stronger and significant at

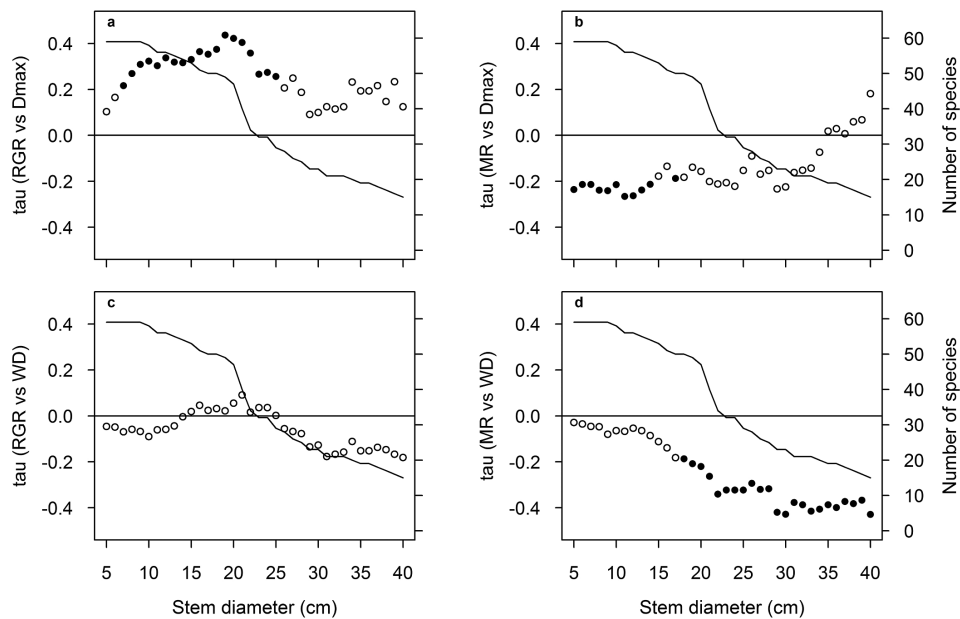


Figure 2: size-dependent changes in correlation coefficients (Kendall's tau) between demographic rates (RGR and MR) and maximum diameter (**a, b**) and WD (**c, d**) across dry forest tree species at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations ($P < 0.05$), and open symbols indicate non-significant correlations ($P > 0.05$). Solid gray lines show a decline in the number of species with increasing stem diameter from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm).

small sizes and become weaker at larger sizes, and that they were not due to a decrease in species number or the dropout of small species from the comparison.

Interspecific relationships between MR and functional traits

Species differed largely in their size-dependent changes in MR; some species decreased mortality with increasing stem diameter and others increased their mortality with stem diameter (Fig. 1b). MR was negatively correlated with maximum diameter (D_{\max}) across species for most of reference diameters up to 17 cm (Fig. 2b), and with WD for the reference stem diameters larger than 18 cm (Fig. 2d). These results indicate that, at small sizes, larger species have lower MRs, whereas at large sizes, species with higher WD have lower MRs.

Kendall's partial rank correlation across species was negative between MR-CW and MR-SM for small trees (for reference stem diameters up to 23 and 8 cm, respectively) (Fig. 3f and i). MR was not related with the other tree architecture variables (H and FBH) or leaf traits (LA and SLA) (Fig. 3b,d,h and j). These results indicate that, at small sizes, species with wider crowns and higher SM tend to have lower MRs. For the 25 largest species, similar relationships were found between MR-CW, but not for MR-SM (Supplementary Figure 5).

Relationship between RGR and MR

RGR and MR showed a significant negative correlation for small trees (reference diameters up to 15 cm), indicating that, at small sizes, species with higher growth rates have lower

MRs (Fig. 4). However, this relationship disappeared when we used a Kendall's partial rank correlation (controlled by D_{\max}) or when this analysis was applied to the 25 largest species only (Supplementary Figure 6).

DISCUSSION

The aim of this study was to evaluate to what extent demographic rates (growth and mortality) are shaped by functional traits and how this changes with tree size. We indeed found that the effect of functional traits on growth and mortality is strongly size-dependent. At small sizes, species with functional trait values that enhance light capture (i.e. large maximum adult stature and CW) have higher growth and lower MRs, whereas only at larger sizes, species with functional trait values that enhance drought tolerance (i.e. higher WD) have lower MRs.

Species growth and mortality are size-dependent

We predicted that most species would show a decrease in RGR with an increase in stem diameter because they (1) change their morphology (larger trees suffer more from self-shading, they have a relative lower light capturing LA per unit living biomass, and more stem respiration costs; (King 1988; Reich *et al.* 2003), (2) face more water stress because taller trees have longer hydraulic pathways (Koch *et al.* 2004), (3) shift allocation from growth towards reproduction (Thomas 2011) or (4) become senescent (Thomas 2011). The results confirmed our hypothesis and are supported by many other wet, temperate and Mediterranean forests studies (Iida *et al.* 2014a,

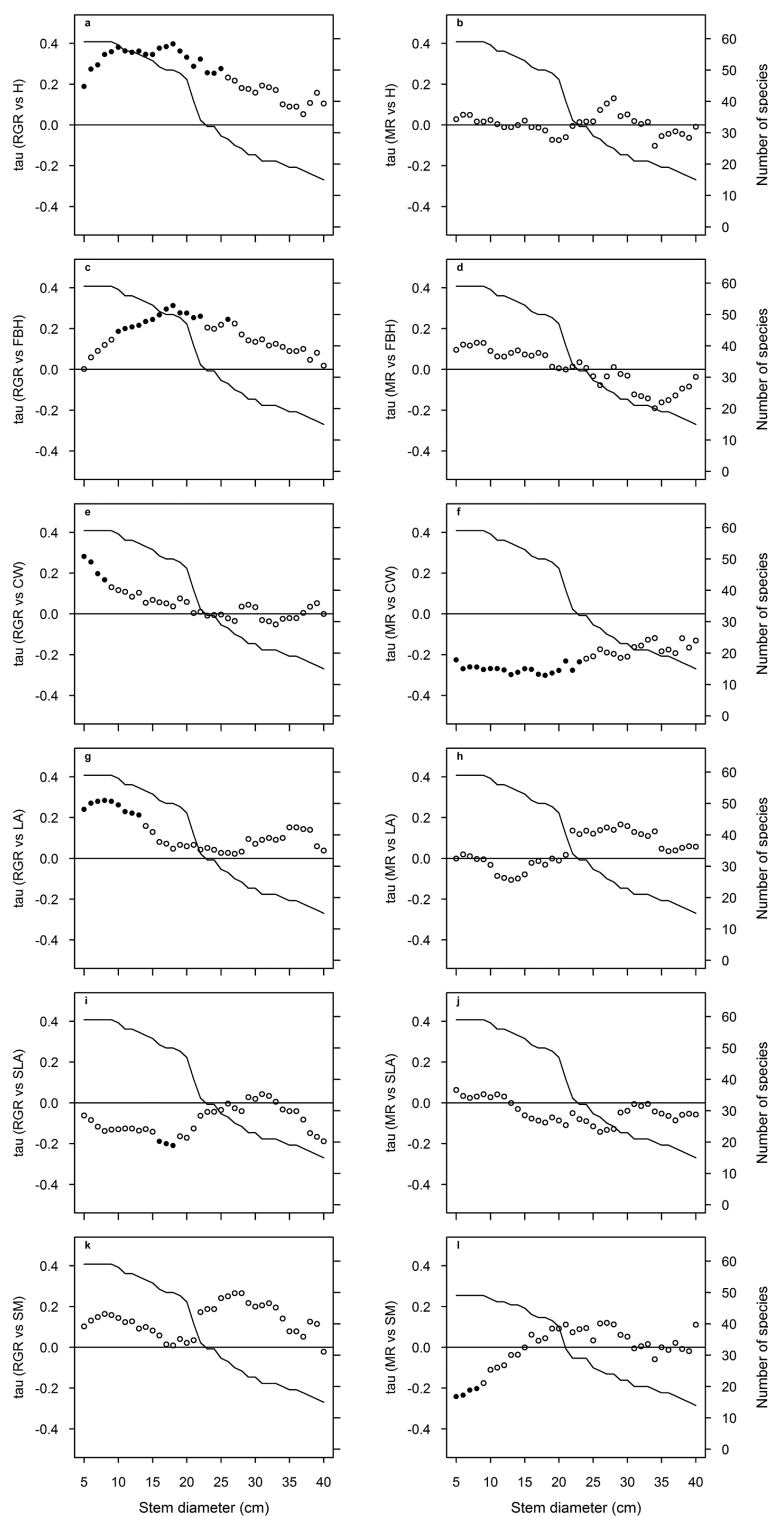


Figure 3: size-dependent changes in partial correlation coefficients (Kendall's tau) between demographic rates (RGR in left panels, and MR in right panels) and species functional traits: height, H (**a, b**); FBH (**c, d**); crown wide, CW (**e, f**); LA (**g, h**); SLA (**i, j**) and SM (**k, l**), controlling for the effect of maximum diameter (D_{\max}) for H, FBH, CW and SLA. Symbols show Kendall's partial correlation coefficients between probability distributions of RGR (left panels) and MR (right panels) versus tree architectural variables and leaf traits at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations ($P < 0.05$), and open symbols indicate non-significant correlations ($P > 0.05$). Solid gray lines show a decline in the number of species with increasing stem diameter from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm).

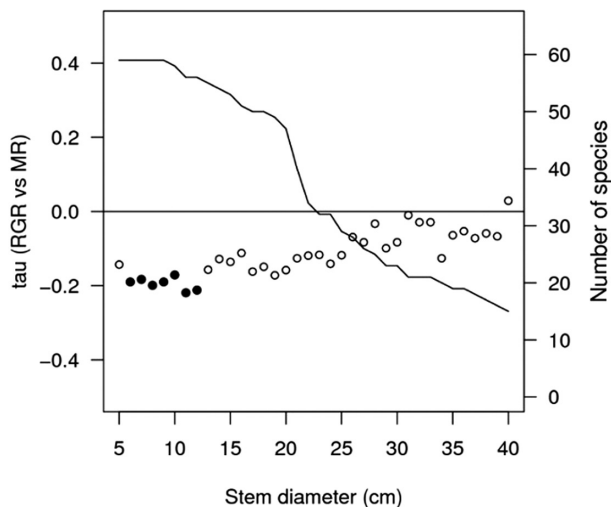


Figure 4: size-dependent changes in correlation coefficients between RGR and MR across 59 species. Symbols show medians of distributions of Kendall's correlation coefficients between probability distributions of RGR versus MR at different reference stem diameters, from 5 to 40 cm. Solid symbols indicate significant correlations ($P < 0.05$) and open symbols indicate non-significant correlations ($P > 0.05$). Solid gray line shows a decline in the number of species with increasing stem diameter, from 59 species at the smallest reference diameter (5 cm) to 15 species at the largest reference diameter (40 cm).

2014b; King *et al.* 2006; Martínez-Vilalta *et al.* 2010; Poorter *et al.* 2008).

Species MRs decreased or increased with increasing stem diameter, which can reflect differences in species life histories based and their capacity to either survive well in the understory or to survive well in the exposed conditions of the forest canopy. Small trees may have a higher MR because of the low carbon gain in the shaded understory (Poorter and Bongers 2006), or because they face higher risks of mechanical damage by falling debris (Sterck and Bongers 1998). Alternatively, larger trees may have higher MRs due to increased water limitation with height in combination with sudden droughts (Carnicer *et al.* 2011), physical damage by strong winds (Sterck *et al.* 2003) or because of senescence (King *et al.* 2006; Mencuccini *et al.* 2005; Thomas 2011).

Species with larger adult stature have higher RGR and lower MR

Species differences in growth and MRs are likely driven by interspecific differences in functional traits. We predicted that, in the sapling stage, larger species would grow faster than small species to rapidly attain higher light conditions in the canopy at which can become reproductive (Thomas 2011). Conversely, small species may grow slowly because they allocate resources to early reproduction rather than growth (Mencuccini *et al.* 2005; Thomas 2011). We indeed found that larger species grew faster, especially at small stem diameters (7–25 cm dbh), which has also been found in many others comparative studies (Iida *et al.* 2014a; King *et al.* 2006; Poorter *et al.* 2008; Wright *et al.* 2010).

Small statured species exhibit higher survival rates that allow them to persist in the forest understory (Iida *et al.* 2014a; Thomas 2011). Thus, we predicted that larger species should have higher MRs than small species (Poorter *et al.* 2008). Small species might have inherent higher MRs because, for the minimum diameter considered in this study (5 cm), they are closer to their maximal size (near to senescence) (Kohyama *et al.* 2003; Poorter *et al.* 2008). Our results confirmed our hypothesis for small reference diameters, but at larger stem diameters (DBH > 15 cm), when most understory species have dropped out of the comparison, MR was not related to maximum diameter. Previous studies also found negative relationships between mortality and adult stature over different diameter classes (Iida *et al.* 2014a, 2014b) whereas others found non-significant relationships (Martínez-Vilalta *et al.* 2010; Wright *et al.* 2010) between mortality and adult stature, probably because they only used average MRs.

Dense wood enhances drought survival of larger trees

We predicted that WD would have a negative effect on stem diameter growth rates because of the higher construction costs per unit stem wood volume. Surprisingly, our results showed that WD was not related with RGR for any of the reference stem diameters, in contrast with the findings of wet, temperate, Mediterranean and subtropical forest studies (Chave *et al.* 2009; Martínez-Vilalta *et al.* 2010; Poorter *et al.* 2008; Shen *et al.* 2014). A possible explanation for the absence of a WD effect on growth is that, although higher WD implies in higher wood cost production, dense wood species are capable to sustain growth under reduced water availability (Mendivelso *et al.* 2013), and then, can have a longer growing period over the year in dry forests. Thus, the relationship between RGR and WD for dry forest species should be weaker (or absent) compared to that of others forest types species because it is more related to enhance species' drought avoidance and/or resistance.

We predicted that species with high WD would have lower MR because they are more resistant to hydraulic failures. In wet forest, there is especially a close negative relationship between WD and MR at small reference sizes and a weaker relationship at larger sizes (Chave *et al.* 2009; Poorter *et al.* 2008; Wright *et al.* 2010) whereas for our dry forest trees we only found a strong and negative relationship at larger sizes. The long periods of drought in dry forests can lead species to reduced hydraulic conductivity and potentially to cavitation, hydraulic failure and tree death (Wheeler *et al.* 2005). This water stress become stronger with increasing tree height because of longer hydraulic pathways (Koch *et al.* 2004) and more exposed tree crowns that experience larger vapour pressure deficits. Higher WD enhances the cavitation resistance of dry forest and Mediterranean tree species (Martínez-Vilalta *et al.* 2010; Markesteijn *et al.* 2011; Pineda-García *et al.* 2013) and reduces their sensitivity to dry-season water stress (Mendivelso *et al.* 2013). Our results suggest that WD plays a fundamentally different role in wet and dry forests. Where in

wet forest WD is closely associated with shade tolerance (Van Gelder *et al.* 2006) and the protection of small trees against the abundant pathogens and physical damage, in dry forest it is closely associated with drought tolerance (Markesteijn *et al.* 2011) and the protection of large, exposed, trees to drought-induced hydraulic failure.

Tree architecture affects the light capture and performance of small trees

We predicted that species with taller heights and higher FBH at a given stem diameter, should have higher growth rates. Light increases exponentially with height in forest and thus, taller trees may intercept a higher amount of light compared to smaller trees (Poorter *et al.* 2006). Furthermore, by postponing the FBH or by investing in cheap, throw-away branches (resulting in a shallower crown) species may invest more biomass in height expansion, thus rapidly getting access to better light conditions higher up in the canopy. Beyond, lower FBH species suffer more from self-shading by the tree (King 1988; Poorter *et al.* 2006). We indeed found that RGR was positively related to H and FBH at small sizes (<25 cm DBH) when many understory species are still in the comparisons, and light should be a strong limiting resource (Iida *et al.* 2014b; Sterck *et al.* 2003). We also predicted that species with a wider crown at a given stem diameter should have higher growth rates, because although their investment in horizontal crown expansion implies less available carbon for horizontal stem expansion (Iida *et al.* 2014b; Sterck *et al.* 2003), wider crowns imply a larger area for light capture (alternatively species could make deeper crowns but that would increase self-shading by the tree). The relationship between RGR and CW was positive at small sizes, which means that in the shaded understory the benefits of a larger capacity for light capture through wider crowns exceed the disadvantage of reduced vertical growth.

We predicted that species with taller heights, deeper (lower FBH) and wider crowns (higher CW) would have higher MRs because they are more sensitive to dynamic loading due to wind or falling debris (Iida *et al.* 2014b; Sterck and Bongers 1998). However, mortality was not related to height or FBH, whereas at small sizes, species with wider crowns had actually lower MRs (Poorter *et al.* 2006; Sterck *et al.* 2003) probably because wider crowns enhance light capture, and hence, carbon gain and tree persistence in the shaded understory (Poorter *et al.* 2006). Although it is often suggested that light is not a major limiting resource for dry forests understories, due their lower and (seasonally) more open canopy (Lebrija-Trejos *et al.* 2008; Lohbeck *et al.* 2013), our results contradict these studies and show that light availability is also an important driver for growth in the dry forest understory, and that tree architecture is especially important for light capture when trees are young.

Leaf traits have little or even negative effects on tree growth in dry forest

We predicted that species with higher LA and SLA have higher growth rate because they intercept a higher amount of light

(Falster and Westoby 2003; Reich *et al.* 2003). We indeed found a positive correlation between RGR and LA at small sizes (when all species were included). At larger sizes this relationship became weaker, possibly because larger leaves suffer more from overheating, especially when they are in the canopy, which can reduce the photosynthetic net gain of large-leaved species (King 1988). Rather than a positive relation between RGR and SLA, we found no relationship, or at some reference diameters even a significant negative relationship between RGR and SLA (when all species were included). An explanation for absence (or also a weak negative correlation in small sizes) is that species with lower SLA have an improved water balance since they transpire less water (Poorter and Bongers 2006). Species with low SLA also produce leaves with smaller cells and thicker cell walls, thus decreasing cell elasticity and allowing plants to reduce leaf water potential and continue plant functioning during the onset of the dry period (Baltzer *et al.* 2008).

For the MRs, no correlations were found for the leaf traits. Positive relationships between MRs and LA and SLA have often been found for small seedlings (Kitajima 1994; Poorter and Bongers 2006), but this relationship is weak or absent for large trees growing in the field (Poorter *et al.* 2008; Martínez-Vilalta *et al.* 2010; Shen *et al.* 2014; Wright *et al.* 2010), consistent with our results. For larger trees other leaf-related functional traits could become important; the amount of biomass allocated to leaves (leaf mass fraction) and biomass growth per unit LA (net assimilation rate) should be more related to RGR and mortality (Reich *et al.* 2003; Tomlinson *et al.* 2014).

Species with higher SM have lower MR

We predicted that species with lower SM have higher growth rates, not because of mechanistic reasons, but because small seed size is a typical life-history trait of fast-growing pioneer species. However, our results showed that RGR was not related with SM for any of the reference stem diameters, which is in agreement with other studies showing that correlations between RGR and SM are especially high for seedlings, just after germination (Poorter and Rose 2005; Martínez-Vilalta *et al.* 2010; Wright *et al.* 2010). We predicted that species with lower SM should have higher MRs (when all species were included), because they produce less robust seedlings that suffer more from stress and disturbance (Harms and Dalling 1997; Leishman *et al.* 2000) and because low SM is typical for pioneer species that have high inherent MRs. We indeed found that MR was higher for small-seeded species at small sizes. This relationship may disappear at larger sizes because other traits become more important for big trees (such as WD), or because most species have very low MRs and mortality becomes more stochastic (Poorter *et al.* 2008).

The absence of a growth versus survival trade-off in dry forests

We predicted that species with faster growth have higher mortality, especially at small sizes. The growth-survival

trade-off is mainly driven by the contrast between slow-growing shade-tolerant species that survive very well in the shade versus light-demanding pioneer species that grow very fast in high light but die very fast as well (Poorter and Bongers 2006; Poorter *et al.* 2006; Wright *et al.* 2010). This relationship tends to become weaker with increasing stem diameter when trees escape shade suppression and both shade-tolerant and pioneer species gradually attain more similar exposed conditions in the canopy (Iida *et al.* 2014a, 2014b; Wright *et al.* 2010). However, we found that growth and mortality were *negatively* correlated at small sizes (when all species were included). This absence of a trade-off between growth and mortality was also reported in temperate and Mediterranean forests (Kunstler *et al.* 2009; Martínez-Vilalta *et al.* 2010). At small sizes, species with higher growth should have higher light availability and thus, can survive better. When this analysis was repeated by including only the largest species or by controlling for the effect of D_{\max} , then the growth–mortality relationship became non-significant. These results indicate that in our dry forest, the negative relation between RGR and MR was mainly driven by life histories between canopy and understory species with higher growth and lower mortality of large canopy species compared to small understory species.

The (size-dependent) trade-off between growth and survival is thought to contribute to species coexistence and, therefore, to the maintenance of forest diversity in wet forests (Poorter *et al.* 2008; Wright *et al.* 2010). Our results are in agreement with other studies in dry forest systems that there is no growth–survival trade-off (Kunstler *et al.* 2009; Martínez-Vilalta *et al.* 2010). If any, there is a positive relationship between growth and survival, indicating that, from a demographic point of view, there are superperformers species that combine high growth with high survival (e.g. large statured and wider crown species), thus outcompeting other species and potentially leading to reduced species diversity (which is also observed to be lower in dry compared to wet forests).

CONCLUDING REMARKS

We reported size-dependent correlations between functional traits and demographic rates. While we have shown the potential of these size-dependent changes, our study has the limitation that we only used WD and leaf traits of adult trees. We acknowledge that WD changes to some extent with an increase in tree size, whereas leaf traits can be fairly plastic. Yet, intraspecific variation is relatively small compared to interspecific variation (Siefert *et al.* 2015), and across species the trait values of saplings are positively correlated with the trait values of adults (Poorter 2007, 2008), indicating that species ranking in trait values will be maintained. We therefore feel that our results are robust, although we may have underestimated the strength of trait–demographic rate relationship in the sapling stage. We recommend that future studies will also measure trait values at all different size stages.

Our study can be summarized in four main results. First, the effect of functional traits on growth and mortality is strongly size-dependent; at small sizes, functional traits that enhance light capture lead to higher growth and lower MRs, whereas at larger sizes functional traits that enhance drought tolerance lead to lower MRs. Second, we found that, despite the high light levels in dry forest understories, light can still be an important factor for plant adaptations and performance in dry forest. Third, from a functional point of view, dry forests show different trait–demography relationships than wet forests. Whereas in wet forest WD and SLA are tightly linked to shade tolerance, growth and survival, in dry forest WD is related to drought tolerance and survival. Moreover, one of the most frequently measured traits, SLA, was not related to plant performance at all. Finally, we observed for small tree sizes a positive relationship between growth and survival, rather than a trade-off, which could potentially lead to species dominance and a reduced diversity. Environmental conditions and ecological pressures that plants face change with their size, and our study shows that the relationships between functional traits and plant performance changes with plant size. Plant size should therefore explicitly be included as an axis of variation in functional analyses, to better understand the relationship between functional traits and demographic rates.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology* online.

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