Research paper

Size-dependent changes in leaf and wood chemical traits in two Caribbean rainforest trees

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Tree functional traits and their link to patterns of growth and demography are central to informing trait-based analyses of forest communities, and mechanistic models of forest dynamics. However, few data are available on how functional traits in trees vary through ontogeny, particularly in tropical species; and less is known about how patterns of size-dependent changes in traits may differ across species of contrasting life-history strategies. Here we describe size-dependent variation in seven leaf functional traits and four wood chemical traits, in two Dominican rainforest tree species (*Dacryodes excelsa* Vahl. and *Miconia mirabilis* (Aubl.) L.O. Williams), ranging from small saplings to the largest canopy trees. With one exception, all traits showed pronounced variation with tree size (diameter at breast height, DBH). Leaf mass per area (LMA), thickness and tissue density increased monotonically with DBH in both species. Leaf area, leaf nitrogen (N) and carbon (C) : nitrogen (N) ratios also varied significantly with DBH; however, these patterns were unimodal, with peak trait values preceding the DBH at reproductive onset in both species. Size-dependent changes in leaf structural traits (LMA and leaf thickness) were generally similar in both species, while traits associated with leaf-level investment in C gain (leaf area, leaf C : N ratio) showed contrasting ontogenetic trends between species. Wood starch concentration varied with DBH in both species, also showing unimodal patterns with peaks preceding size at reproductive onset. Wood C concentration increased linearly with DBH in both species, though significantly only in *M. mirabilis*. Size-dependent patterns in wood chemical traits were similar between both species. Our data demonstrate pronounced variation in functional traits through tree ontogeny, probably due to a combination of environmental factors and shifts in resource allocation. Such ontogenetic variation is comparable in magnitude with interspecific variation, and so should be accounted for in trait-based studies of forest dynamics, structure and function.

Keywords: carbon, functional traits, leaf economics, non-structural carbohydrates, size-dependence, tree ontogeny, tropical forest, wood economics.

Introduction

In recent years, ecologists have made significant progress in understanding how species functional traits influence forest community structure and ecosystem function. Particular attention has been given to morphological and physiological traits of leaf and wood tissues, particularly traits associated with the 'leaf economics spectrum' (Wright et al. 2004) and wood density (Chave et al. 2009). These traits have specifically been linked to patterns in tree demography (e.g., Poorter et al. 2008, Wright et al. 2010), tree community assembly (e.g.,

Kraft et al. 2008), tree species distributions (e.g., Diaz et al. 2004, Baltzer and Thomas 2010), decomposition rates (e.g., Weedon et al. 2009), carbon (C) dynamics (e.g., Baker et al. 2004) and forest recovery following disturbance (e.g., Curran et al. 2008). Understanding how leaf and wood traits contribute to these patterns and processes is becoming more tractable, due to the availability of large trait datasets (e.g., Kattge et al. 2011), standardized methodologies for trait collection (e.g., Cornelissen et al. 2003) and comparative analytical methods for understanding trait evolution (e.g., Harvey and Pagel 1991).

Using functional traits as proxies for species life-history strategies has been particularly appealing for tropical forest ecologists, as the presence of hundreds of co-occurring tree species makes collection of site- and species-specific growth and mortality data a difficult or even insurmountable task (Wright et al. 2003, Herault et al. 2011). At the same time, there is uncertainty over how well individual leaf or wood traits or suites of traits predict vital rates of tropical tree species (sensu Wright et al. 2003) across all ontogenetic stages. For example, studies in multiple forest sites have found that specific leaf area (SLA, or its inverse leaf mass per area, LMA) is correlated with growth, mortality and shade tolerance of tropical seedlings or saplings (e.g., Poorter and Bongers 2006, Baltzer and Thomas 2007); however, when larger tree sizes are analysed, these relationships becomes notably weaker (Poorter et al. 2008) or non-existent (Wright et al. 2010).

There are several possible explanations for a decoupling of traits from tree performance measures through tree ontogeny. First, it is likely that some traits become less important determinants of growth as trees develop (Herault et al. 2011). For example, while growth rate may be strongly related to SLA in saplings, growth in larger trees is likely to be more strongly related to total leaf number (Poorter et al. 2009), or leaf and branch extension patterns that determine leaf display efficiency (Sterck and Bongers 2001). A second explanation for non-significant trait–demography relationships is that 'soft traits' (i.e., SLA, LMA) are not as tightly linked to tree growth and mortality (either biologically or statistically) as 'hard traits' such as photosynthetic capacity and dark respiration rates (Wright et al. 2010). A third potential explanation is that weak trait–demography relationships are due to size-dependent variation in functional traits. If traits vary strongly with tree size, it would not be surprising that trait values collected on smaller stems do not correlate with growth rates of large canopy trees (Poorter et al. 2008, Wright et al. 2010). However, while some studies have acknowledged that ontogenetic variation in traits is important in predicting long-term forest dynamics (Niinemets 2006), we know surprisingly little about how leaf or wood chemical traits vary with size in tropical trees.

With few exceptions, our understanding of ontogenetic variation in leaf traits comes from comparisons of saplings or seedlings with large canopy trees (e.g., Thomas and Bazzaz 1999, Ishida et al. 2005, Wright et al. 2010), or from studies quantifying traits over a truncated range of tree sizes (Rijkers et al. 2000, Coopman et al. 2008, 2011, Sendall and Reich 2013). Some authors have quantified leaf trait variation as a function of tree height (H) using datasets pooled across species (Kenzo et al. 2006, 2012, Cavaleri et al. 2010), but this approach has important limitations. Methodologically, using H as a measure of tree size may not capture complete ontogenetic trends in trait change for species exhibiting asymptotic H–diameter allometry (Thomas 1996a, 2010).

From a comparative biology perspective, species-pooled analyses are likely to obscure differences in patterns of ontogenetic trait change among species of contrasting life-history strategies. Tree species differing in life-history strategy may show different size-dependent patterns of trait change due to: (i) differences in size-dependent changes in light exposure (Poorter et al. 2005); (ii) variation in leaf plastic responses to changing light availability (Rozendaal et al. 2006); and/or (iii) differences in size at reproductive onset that may affect size-dependent patterns in leaf traits (Thomas and Ickes 1995, Thomas 2010). Quantifying size-dependent patterns of trait change across species of contrasting life-history strategies could inform an understanding of the evolutionary causes and consequences of ontogenetic changes in tree functional biology (cf. Thomas and Bazzaz 1999).

The few studies documenting species-specific trait variation across complete diameter continua convey very different conclusions: not only do different traits show different ontogenetic patterns (i.e., linear vs. non-linear), but different traits also vary in response to multiple biotic or abiotic cues. For example, in three temperate deciduous species, Thomas (2010) found that leaf structural traits (LMA, leaf tissue density, leaf thickness) showed linear allometric increases with tree size. However, traits associated with C gain (photosynthetic rates, stomatal conductance, leaf nitrogen (N) and leaf area) all showed unimodal or 'hump-shaped' patterns, with trait maxima preceding or near reproductive size thresholds. This pattern is generally consistent with declines late in ontogeny being driven at least in part by reproductive allocation effects (Thomas 2011). Unimodal relationships between leaf size and tree size have also been found in several tropical tree species (Alvarez-Buylla and Martinez-Ramos 1992, Thomas and Ickes 1995). However, because so few species-specific data documenting size-dependent variation in leaf traits of tropical trees exist, it is unclear if (i) larger suites of traits show different size-dependent patterns of change or (ii) patterns of trait variation differ across trees from different successional guilds.

In tropical trees, we also have few data or theories as to how wood chemical traits may vary as a function of tree size. Available data on size-dependent variation in wood chemistry is primarily based on comparisons of seedlings or saplings and canopy trees (Martin et al. 2013), or studies documenting within-stem variation (i.e., variation occurring from pith to bark; e.g., Hoch et al. 2003, Wurth et al. 2005, Lamlom and Savidge 2006). One wood trait likely to show size-dependent variation is the concentration of non-structural carbohydrates (NSCs, referring to starches and simple sugars). As a species-level trait, at least in saplings, NSC concentration is an important correlate of life-history strategies in trees (Kobe 1997, Poorter and Kitajima 2007) but is also regarded as a proxy for tree C status: NSC accumulation suggests that assimilated C exceeds requirements for growth (i.e., C storage), while NSC depletion suggests

a C deficit (Körner 2003). In tropical trees, this view has been supported by studies finding significant reductions in NSC concentrations occurring in concert with seasonal leaf flushing (Newell et al. 2002, Wurth et al. 2005). Analogously, it can be hypothesized that NSC pools in tropical evergreen trees will show 'hump-shaped' patterns with respect to tree size: accumulation of C stores prior to reproductive onset, followed by NSC decline post-reproduction as C is allocated to fruits and flowers. Studies to date of deciduous tropical or temperate species have not found evidence for any size-related decline in NSCs in large trees (Bullock 1992, Körner 2003, Genet et al. 2010); however, seasonal fluctuations in NSCs due to leaf phenology are strongly pronounced in deciduous species (Körner 2003), increasing uncertainty in patterns (Sala et al. 2011). The limited data on tropical and temperate species also have pooled trees from a range of sizes (e.g., trees with DBH >10 cm in Bullock 1992), and may therefore mask continuous size-dependent variation in NSCs (Sala and Hoch 2009, Sala et al. 2011). Wood C concentration (%C on a mass basis) may also vary ontogenetically and have important implications for forest C accounting (Lamlom and Savidge 2006, Martin et al. 2013), but to our knowledge no data are available on patterns across a wide range of tree sizes in any tropical species.

In the present study, we quantify variation in leaf and wood traits in two evergreen neotropical tree species, across a wide range of tree sizes. Our study was designed to address the following questions: (i) What are the patterns of size-dependent variation in leaf and wood chemical traits in tropical trees? (ii) Do patterns of size-dependent trait change differ among species of contrasting life-history strategies? (iii) Do traits related to carbon economy, specifically leaf N and wood NSC concentrations, show a peak at intermediate tree sizes? (iv) Are any observed peaks in leaf or wood chemical traits related to size at reproductive onset?

Materials and methods

Study site and species

Our study was conducted in Dominica, Lesser Antilles (15°25′N, 61°20′W), a small island situated between the islands of Guadeloupe to the north and Martinique to the south. Sampling was conducted in tropical rainforest in Morne Trois Pitons (MTP) National Park (650 m above sea level (a.s.l.)). Forests in MTP receive an average annual rainfall of ~4400 mm, with a wet period occurring between June and October, and a less-wet period from November through May (Nicolson et al. 1991). The rainforest canopy in MTP reaches ~30–35 m, and is dominated by *Dacryodes excelsa* Vahl. (Burseraceae), *Amanoa caribaea* Krug & Urb. (Euphorbiaceae), *Sloanea caribaea* Krug & Urb. ex Duss and *Sloanea dentata* L. (Elaeocarpaceae) (Nicolson et al. 1991).

Within MTP, we chose two of the most common rainforest tree species for study: *Miconia mirabilis* (Aubl.) L.O. Williams (Melastomataceae), a short-lived, light-demanding pioneer species, and *D. excelsa*, a canopy-dominant, long-lived late-successional species. *Miconia mirabilis* is a common, strict forest-gap colonizer in MTP whose presence and abundance is positively correlated with hurricane damage, owing to high light requirements for survival (Nicolson et al. 1991). *Dacryodes excelsa* is qualitatively classified as a shade-tolerant and late-successional species (Nicolson et al. 1991).

In May of 2010, we selected 57 *D. excelsa* and 65 *M. mirabilis* individuals across a range of tree sizes (0.56–91.3 cm DBH and 0.56–32.7 cm DBH, respectively) for collection and analysis of leaf and wood chemical traits, and whole-tree measurements. All sample trees were selected within MTP, and were a minimum distance of 10 m from one another. Although we did not use a strict randomization procedure, trees were selected so as to spatially intersperse individuals of differing size. To ensure that elevational gradients in functional traits did not confound analysis of size-dependent patterns (e.g., Hoch et al. 2002), we restricted all study trees to those located within MTP at approximately the same elevation (~650 m a.s.l.). We also excluded trees showing visible signs of crown (major branch falls, highly pronounced crown asymmetries or defoliation) or bole damage (open stem wounds) owing to hurricane winds, or those showing signs of dieback due to physiological stress.

Functional trait sampling

For leaf traits, we collected three individual leaves per tree that were fully developed and free of herbivore damage or heavy epiphyll cover, and taken from the upper- and outermost branches (Cornelissen et al. 2003). Leaves from trees ≤12 m in H were collected using a telescoping pole pruner. For trees >12 m H, a tree climber was employed to collect leaves; for all trees accessible only via tree climbing, once the climber was situated in the crown, the telescoping pole pruner was then hoisted into the canopy to ensure collection of the upper- and outermost branches of all trees in our dataset.

For each leaf, we measured the leaf area of fresh leaves (cm²) using digital photographs analysed in ImageJ software (Abramoff et al. 2004). Leaf lamina thickness (mm) for fresh leaves was determined using a low-force micrometer (No. 227-101, Mitutoyo Co., Mississauga, Canada), calculated as the mean value of three replicate measurements taken across the lamina while avoiding major veins. Following these measurements, all leaves were oven-dried at 60 °C to constant mass and weighed. We then calculated the LMA as leaf dry mass/area (g m⁻²) and computed leaf tissue density (g cm⁻³) as LMA/leaf thickness.

Following leaf morphology measurements, leaves were transported to the University of Toronto, Canada where they were analysed for leaf N and C concentration (both on a mass/

mass basis) using an ECS4010 CHNS elemental analyser (Costech Analytical Technologies, Inc., Valencia, CA, USA), which was calibrated between each sample run using an ethylenediaminetetraacetic acid standard. In total, leaf morphological and chemical traits were taken on 57 *D. excelsa* and 65 *M. mirabilis* trees, with one minor exception: leaf thickness and tissue density were not measured for one *M. mirabilis* tree due to an unusually high density of major veins.

To assess size-dependent changes in wood chemistry, we focused on the outermost 6 cm of trunk wood. This was done in order to: (i) focus on the tree tissue that is least seasonally variable with respect to NSC concentrations (Hoch et al. 2003, Wurth et al. 2005); and (ii) ensure our analysis captures size-dependent variation in NSCs within the portion of xylem that is most active in NSC transport (Newell et al. 2002, Genet et al. 2010) and maintains the highest NSC concentrations within-stem cross sections (Barbaroux and Breda 2002, Newell et al. 2002, Hoch et al. 2003, Wurth et al. 2005). Utilizing the outermost 6 cm also ensures that our analysis of size-dependent variation in wood C focuses explicitly on newly formed wood, and is therefore not confounded with potential radial variation in wood C (e.g., Lamlom and Savidge 2006).

We collected wood samples from a large subset of sampled trees of each species, including 48 *D. excelsa* and 49 *M. mirabilis*. For smaller stems (≤5 cm DBH), we clipped the main stem and collected the woody tissue at 50–130 cm aboveground. For trees >5 cm DBH, we collected wood cores at breast height (1.3 m aboveground) using a 5.15 mm increment borer. Once collected, all samples were oven-dried to constant mass at 110 °C. After drying, we used utility knives to pare away the outer edges of samples that may have been contaminated by the surface of the core borer, and removed all bark and pith from smaller samples. We then measured and removed the outermost 6 cm of sapwood, and pulverized each sample into a homogeneous powder using a Wiley mill (no. 40 mesh).

Following sample preparation, analysis of wood C concentration (% C mass/mass basis—not accounting for volatile C, Martin and Thomas 2011) was performed on a portion of the powdered core with the same elemental analyser used for leaf analysis. We then used 10 mg of each powdered sample for analysis of NSC concentration by analysing simple sugars (glucose, fructose and sucrose) and starch separately. Sugar concentration was determined using the phenol–sulfuric acid method. Starch and other complex sugars were then extracted from the pellet of wood remaining with 1 ml of 10 N NaOH in a boiling bath for 5 min. Following extraction, supernatants were neutralized with 1 ml of 10 M H_3PO_4, and each sample was centrifuged for 2 min at 10,000g. Starch in the supernatant was then hydrolysed to glucose for 12 h at room temperature with amyloglucosidase (ab83393, Abcam, Cambridge, MA, USA), and the carbohydrate concentration in glucose equivalents for the hydrolysed starch samples was determined colorimetrically

at 570 nm. For starch and sugar analyses, values are presented on a percentage dry mass basis, and are the means of two replicate measurements per sample.

Reproductive surveys and whole-tree measurements

For each tree in our dataset we measured the DBH, H, reproductive status and crown exposure. We measured H to the nearest meter using a laser rangefinder (Laser Technology, Inc., Centennial, CO, USA), as the mean of five measurements from tree base to the uppermost crown. To ensure consistency, all tree height measurements were taken by a single observer (A.R.M.) and trees in which the uppermost reaches of the crown were not visible were excluded from the dataset. Reproductive status was quantified as a binary response (reproductive (1) or non-reproductive (0)), determined by two independent observers (A.R.M. and E.S. Stedman) who extensively searched tree crowns to determine the presence/absence of reproductive structures (i.e., fruits, flowers or pedicels).

Crown exposure for each tree was measured as a semi-quantitative assessment following Clark and Clark (1992) as modified by Thomas (2010). All crown exposure assessments were made by a single observer (A.R.M.). To provide adequate sample sizes for size at reproductive onset (S_{crit}) and maximum tree height (H_{max}), we supplemented our dataset with identical whole-tree measurements (i.e., DBH, H, reproductive status, crown exposure) on additional *D. excelsa* and *M. mirabilis* trees. All additional trees surveyed were randomly sampled within MTP, and provided sample sizes of 161 *M. mirabilis* and 171 *D. excelsa* used for S_{crit} and H_{max} estimates (Table 1).

Analysis of reproductive size thresholds and H_{max}

To estimate species-specific S_{crit}, we used a modified logistic regression model with binomial error distributions, fit using maximum likelihood methods. Our methods follow Thomas (1996*b*), whereby the probability of a tree being reproductive (P_{rep}) was estimated as a function of DBH such that

$$P_{rep} = \frac{e^{a+b\ln DBH}}{1 + e^{a+b\ln DBH}}, \qquad (1)$$

where e is the base of the natural logarithm, and both a and b are fitted constants. The inflection point of this function then represents a statistical estimate of S_{crit} calculated as

$$S_{crit} = e^{b^{-1}[\ln((b-1)/(b+1))-a]}. \qquad (2)$$

We then estimated H_{max} following Thomas (1996*a*) based on the non-linear allometric equation

$$H = H_{max}(1 - e^{(-a DBH^b)}), \qquad (3)$$

Table 1. Parameters for whole-tree trait analysis of two Dominican tree species. Sample sizes and estimates of size at reproductive onset (S_{crit} (cm)) and maximum tree height (H_{max}, $H_{max-obs}$ (m)) for *D. excelsa* and *M. mirabilis*. Parameters *a* and *b* for reproductive onset and maximum tree height estimates are as in Eqs. (2) and (3), respectively.

Trait	Parameter	D. excelsa	M. mirabilis
	n_{total}	171	161
	n_{rep}	39	91
Reproductive onset	S_{crit} (95% CI)	18.2 (11.2, 30.0)	12.2 (8.1, 18.5)
	a (95% CI)	−16.76 (−26.23, −10.69)	−11.37 (−16.71, −7.72)
	b (95% CI)	10.57 (6.84, 16.3)	12.21 (8.51, 17.66)
Maximum tree height	H_{max} (±SE)	31.0 ± 2.0	35.0 ± 14.7
	a (±SE)	−0.075 ± 0.005	−0.064 ± 0.021
	b (±SE)	0.736 ± 0.038	0.726 ± 0.092
	$H_{max-obs}$ (±SE)	30.1 ± 6.4	21.8 ± 2.5

where H_{max} is the asymptotic maximum tree height, and *a* and *b* are fitted constants (Thomas 1996*a*). Preliminary analysis suggested that the DBH–*H* relationships for *M. mirabilis* was non-asymptotic (data not shown), indicating that Eq. (3) may overestimate H_{max}. Therefore, we also calculated the H_{max} as the mean observed *H* of the three largest trees by the DBH from our expanded whole-tree measurement dataset ($H_{max-obs}$).

Analysis of size-dependent variation in traits

Preliminary analyses suggested that size-dependent trait variation was well described by an allometric relationship of the form $Y = a\text{DBH}^b$, where *Y* represents a given trait, DBH represents tree diameter, and both *a* and *b* are fitted constants. Therefore, all analyses of size–trait relationships were based on log–log transformed data to improve normality and reduce heteroscedasticity. Analyses followed a two-step procedure: we first tested for significant non-linearity in patterns of trait variation as a function of DBH, by pooling both species' data for a given trait and testing for a significant second-order polynomial term (DBH^2) in a linear regression model of the form

$$\log Y = \beta_0 + \beta_1(\log \text{DBH}) + \beta_2(\log \text{DBH}^2) + \beta_3(\text{sp}) + \beta_4(\text{sp} \times \log \text{DBH}), \quad (4)$$

where *Y* represents a given trait, β_0 represents the intercept, β_1 and β_2 are the regression model coefficients for DBH and DBH^2, respectively, β_3 is a coefficient for species ('sp') coded as a binary 'dummy variable' and β_4 is a coefficient for a species-by-DBH interaction.

We used results of pooled analysis to inform species-specific analysis: where β_2 in Eq. (4) was significant, a linear model including a second-order polynomial term was used to describe patterns of size-dependent trait variation in *D. excelsa* and *M. mirabilis* individually as

$$\log Y = \beta_0 + \beta_1(\log \text{DBH}) + \beta_2(\log \text{DBH}^2), \quad (5)$$

where model terms and coefficients are as in Eq. (4). When β_2 was not significant in pooled analysis, traits for each species were analysed with linear regression models of the form

$$\log Y = \beta_0 + \beta_1(\log \text{DBH}), \quad (6)$$

where model terms and coefficients are as in Eq. (4). Analyses were also performed with *H* as a measure of size in Eqs (4–6). Since DBH was generally a stronger predictor of ontogenetic changes (Data S1 available as Supplementary Data at *Tree Physiology* Online), we do not discuss these results at length.

For all non-linear trait–DBH relationships, 95% confidence limits for tree DBH corresponding to trait peaks were calculated by bootstrapping the polynomial regression of the log–log transformed data, with 1000 bootstrap samples used. For this analysis, the reciprocals of traits showing 'U-shaped patterns' were analysed. As a final analysis step, we tested for the effects of DBH and light exposure on traits simultaneously, by including DBH and DBH^2 (as determined above) and crown exposure as explanatory variables in a multiple regression model. All statistical analyses were conducted using R v. 2.10.1 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Size at reproductive onset and H_{max}

Both species showed size-dependent patterns of reproduction consistent with a threshold, where *b* in Eq. (1) was >1 (Thomas 1996*b*; Table 1). Estimated S_{crit} for *D. excelsa* was 18.2 cm (95% CI = 11.2–30.0 cm), and that for *M. mirabilis* was 12.2 cm (95% CI = 8.1–18.5 cm; Table 1). Relationships between DBH and *H* in *D. excelsa* were consistent with an asymptotic pattern, with H_{max} and $H_{max-obs}$ being comparable with overlapping confidence limits (Table 1; see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Specifically H_{max} for *D. excelsa* was estimated as 31.0 ± 2.0 m (95% CI), while $H_{max-obs}$ was

30.1 m, but displayed much wider 95% confidence limits (±6.4 m; Table 1; see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Conversely, *M. mirabilis* did not show asymptotic patterns in its DBH–*H* relationship, whereby *H* tended to increase monotonically through the range of measured DBH; this led to drastically different maximum heights for *M. mirabilis* depending on whether it was estimated (through Eq. (3)) or measured. Specifically, H_{max} estimates were very high with wide confidence limits (35.0 ± 14.7 m, 95% CI), while $H_{max-obs}$ yielded an estimate of 21.8 ± 2.5 m (95% CI), which was ~30% lower than H_{max} (Table 1; see Figure S1 available as Supplementary Data at *Tree Physiology* Online).

Leaf traits

In the pooled analysis, LMA, leaf thickness and leaf tissue density all increased monotonically with tree size (Table 2), with linear allometric models explaining 89.7 and 81.9% of the variation in LMA for *D. excelsa* and *M. mirabilis*, respectively (Figure 1). Similarly, leaf thickness and leaf tissue density were both well explained by linear allometric models ($P < 0.0001$, adj. $r^2 = 0.533$–0.842 in all cases; Table 2; Figure 1; Data S2 available as Supplementary Data at *Tree Physiology* Online). In comparing size-dependent patterns between *D. excelsa* and *M. mirabilis*, pooled analysis of leaf structural traits only found significant differences in the slope of the DBH–leaf tissue density relationship (slope = 0.064 and 0.139 for *D. excelsa* and *M. mirabilis*, respectively, species-by-size interaction term $P = 0.001$; Table 2; Data S2 available as Supplementary Data at *Tree Physiology* Online). The slopes of the DBH–LMA (0.238 and 0.272 for *D. excelsa* and *M. mirabilis*, respectively) and the DBH–thickness relationships (0.175 and 0.137 for *D. excelsa* and *M. mirabilis*, respectively) were not statistically different between the two species (Table 2; Data S2 available as Supplementary Data at *Tree Physiology* Online).

Pooled analyses of leaf chemical traits (N, C and C : N) and leaf size (area per leaf) found that all four of these traits showed deviations from linear allometry with tree size, as indicated by highly significant second-order polynomial terms in the species-pooled analysis ($P \leq 0.0002$; Table 2). In *D. excelsa*, quadratic models were highly significant ($P < 0.0001$) and explained a high proportion of the variance in leaf area (adj. $r^2 = 0.693$), leaf N (adj. $r^2 = 0.557$) and leaf C : N (adj. $r^2 = 0.506$; Figures 2 and 3; Data S2 available as Supplementary Data at *Tree Physiology* Online). Area per leaf and leaf N concentrations showed pronounced unimodal or 'hump-shaped patterns', while leaf C : N ratio showed a pronounced 'U-shaped' pattern (Figures 2 and 3). In *D. excelsa*, leaf C concentration was also well explained by a quadratic model ($P < 0.0001$), but the relationship was weaker (adj. $r^2 = 0.291$) and the unimodality less pronounced (Figure 3).

Miconia mirabilis leaf area and chemical traits all varied significantly as a function of tree size, with patterns well explained by quadratic models (Table 2). Leaf area was significantly related to tree size (adj. $r^2 = 0.589$; $P < 0.0001$), as was leaf N (adj. $r^2 = 0.187$; $P = 0.001$), leaf C (adj. $r^2 = 0.21$; $P = 0.0003$) and leaf C : N (adj. $r^2 = 0.374$; $P < 0.0001$; Figures 2 and 3; Data S2 available as Supplementary Data at *Tree Physiology* Online). However, in *M. mirabilis*, these traits did not show pronounced unimodal patterns, and instead generally declined (leaf area, leaf N) or increased (leaf C, leaf C : N) monotonically with tree size (Figures 2 and 3).

Size-dependent patterns in leaf area, leaf C and leaf C : N ratios differed significantly between species, with *D. excelsa* showing much more pronounced unimodal patterns in these traits when compared with *M. mirabilis* (Figures 2 and 3; Table 2). While size-dependent patterns in leaf N did not differ statistically between species, there were pronounced qualitative differences in DBH–leaf N patterns (Figures 2 and 3; Table 2).

Wood chemical traits

In pooled analysis, wood C concentration (% mass basis) varied significantly as a function of tree size, with patterns being

Table 2. Sample sizes and results (*P* values) from species-pooled analysis of size-dependent changes in 11 leaf and wood traits, in two Dominican tree species (*D. excelsa* and *M. mirabilis*). Significant terms in the regression analysis ($P < 0.05$) are in bold, and all results are based on analysis of log–log transformed values.

| Trait	N	DBH	DBH²	Species	Species × DBH
LMA (g m⁻²)	122	**<0.0001**	0.2869	0.6414	0.1773
Leaf thickness (μm)	121	**<0.0001**	0.9834	**<0.0001**	0.1857
Leaf tissue density (g cm⁻³)	121	**<0.0001**	0.1535	**<0.0001**	**0.0012**
Leaf area (cm²)	122	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Leaf N (% dry mass)	122	**<0.0001**	**<0.0001**	**<0.0001**	0.3096
Leaf C (% dry mass)	122	**0.0158**	**0.0002**	**<0.0001**	**0.0001**
Leaf C: N ratio	122	**<0.0001**	**<0.0001**	**<0.0001**	**0.0106**
Wood C (% dry mass)	97	**0.0089**	0.8757	0.1314	0.4608
Starch (% dry mass)	97	0.1164	**0.0008**	0.5944	0.2298
Sugar (% dry mass)	97	**0.0222**	**0.0256**	**0.0001**	0.3795
Sugar: starch ratio	97	**0.0066**	**0.0014**	**<0.0001**	0.2182
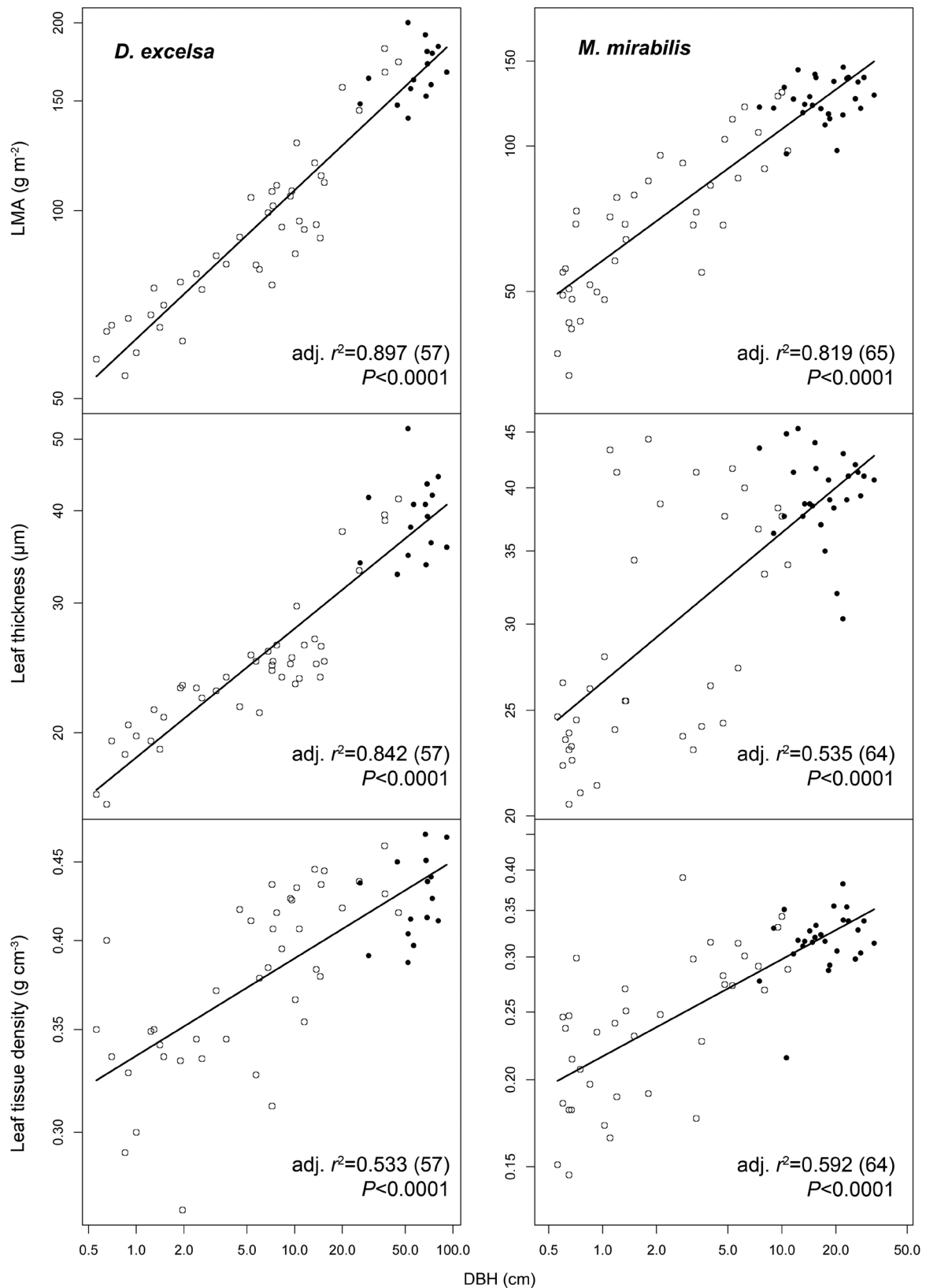
Figure 1. Leaf structural traits as a function of tree size (DBH) for *D. excelsa* (left panels) and *M. mirabilis* (right panels). Leaf structural traits include LMA (upper panels), leaf thickness (middle panels) and leaf tissue density (lower panels). Open and closed circles represent non-reproductive and reproductive individuals, respectively. Trend lines represent leaf structural trait–DBH relationships based on regression analysis performed on log–log transformed data. Adjusted r^2 values, sample sizes (in brackets) and P values are given for species-specific model fits for each trait (see Data S2 available as Supplementary Data at *Tree Physiology* Online for model parameters).
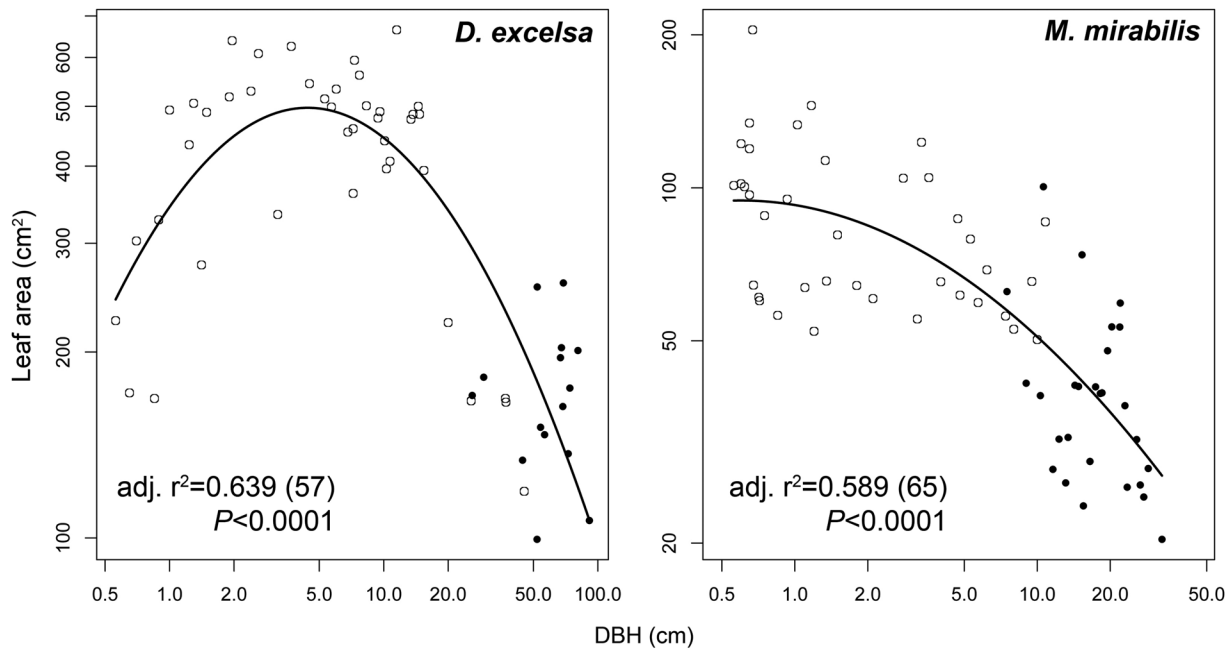
Figure 2. Leaf area as a function of tree size (DBH) for *D. excelsa* and *M. mirabilis*. Open and close circles represent non-reproductive and reproductive individuals, respectively. Trend lines indicate leaf area–DBH relationships based on regression analysis performed on log–log transformed data. Adjusted r^2 values, sample sizes (in brackets) and P values are given for species-specific model fits for each trait (see Data S2 available as Supplementary Data at *Tree Physiology* Online for model parameters).

well described by a linear model (Table 2, Figure 4). Increases in wood C with DBH in *D. excelsa* were weak and not statistically significant ($P = 0.128$; adj. $r^2 = 0.029$). However, in *M. mirabilis*, wood C increased significantly with tree size ($P = 0.002$; adj. $r^2 = 0.165$; Figure 4). Patterns of size-dependent changes in wood C concentration did not differ significantly between species (Figure 4, Table 2).

Size-dependent variation in wood starch concentration was well explained by a quadratic model in the pooled analysis (Table 2), with size-dependent patterns not differing significantly between species (Figure 5, Table 2). When analysed individually, starch concentration was significantly related to DBH in both *D. excelsa* ($P = 0.024$; adj. $r^2 = 0.115$) and *M. mirabilis* ($P = 0.026$; adj. $r^2 = 0.109$; Figure 5; Data S2 available as Supplementary Data at *Tree Physiology* Online). Patterns of size-dependent variation in starch concentrations were unimodal in both species, with modelled and observed peak starch concentration occurring at intermediate tree sizes (Figure 5). Analysis of size-dependent variation in sugar concentration also indicated a significant second-order polynomial term in the pooled analysis (Table 2). At the species level, sugar concentration varied significantly with size only in *D. excelsa* ($P = 0.009$; adj. $r^2 = 0.155$), showing a pronounced 'U-shaped' pattern with minimum concentrations occurring at intermediate tree sizes; sugar concentration was unrelated to tree size in *M. mirabilis* ($P = 0.728$, adj. $r^2 = 0$; Figure 5). Sugar : starch ratios were unrelated to tree size in *M. mirabilis*

($P = 0.389$; adj. $r^2 = 0$), but varied significantly with tree size in *D. excelsa* ($P = 0.0003$; adj. $r^2 = 0.27$), showing a pronounced 'U-shaped' pattern with the lowest sugar concentration relative to starch occurring at intermediate tree sizes (Figure 5; Data S2 available as Supplementary Data at *Tree Physiology* Online).

Location of peak trait values

With one exception (leaf C concentration in *M. mirabilis*), in all traits that showed significant second-order polynomial terms (Table 2), the estimated maximum values (or minimum in the case of C : N ratios and sugar concentration, and sugar : starch ratio in *D. excelsa*) occurred prior to the size at reproductive onset (Figure 6). In *M. mirabilis*, leaf N, the reciprocal of leaf C : N ratio and leaf area peaked in the smallest tree sizes (~0.56 cm DBH), while peak starch concentration was observed in trees that were slightly larger (4.6 cm DBH) but still below the lower 95% confidence bound for reproduction (Figure 6).

In *D. excelsa*, all traits showing a significant second-order polynomial term peaked or showed minimum values (in the case of leaf C : N, sugar concentration and sugar : starch ratios) prior to reproductive onset (18.2 cm DBH; Figure 6). Specifically, peak leaf area occurred at 4.5 cm DBH, leaf N peaked at 3.5 cm DBH and leaf C : N was lowest at 3.9 cm DBH. Maximum values for leaf C concentration occurred in smaller trees that were 1.6 cm DBH. Maximum starch concentration was detected in larger trees (6.6 cm DBH), as was
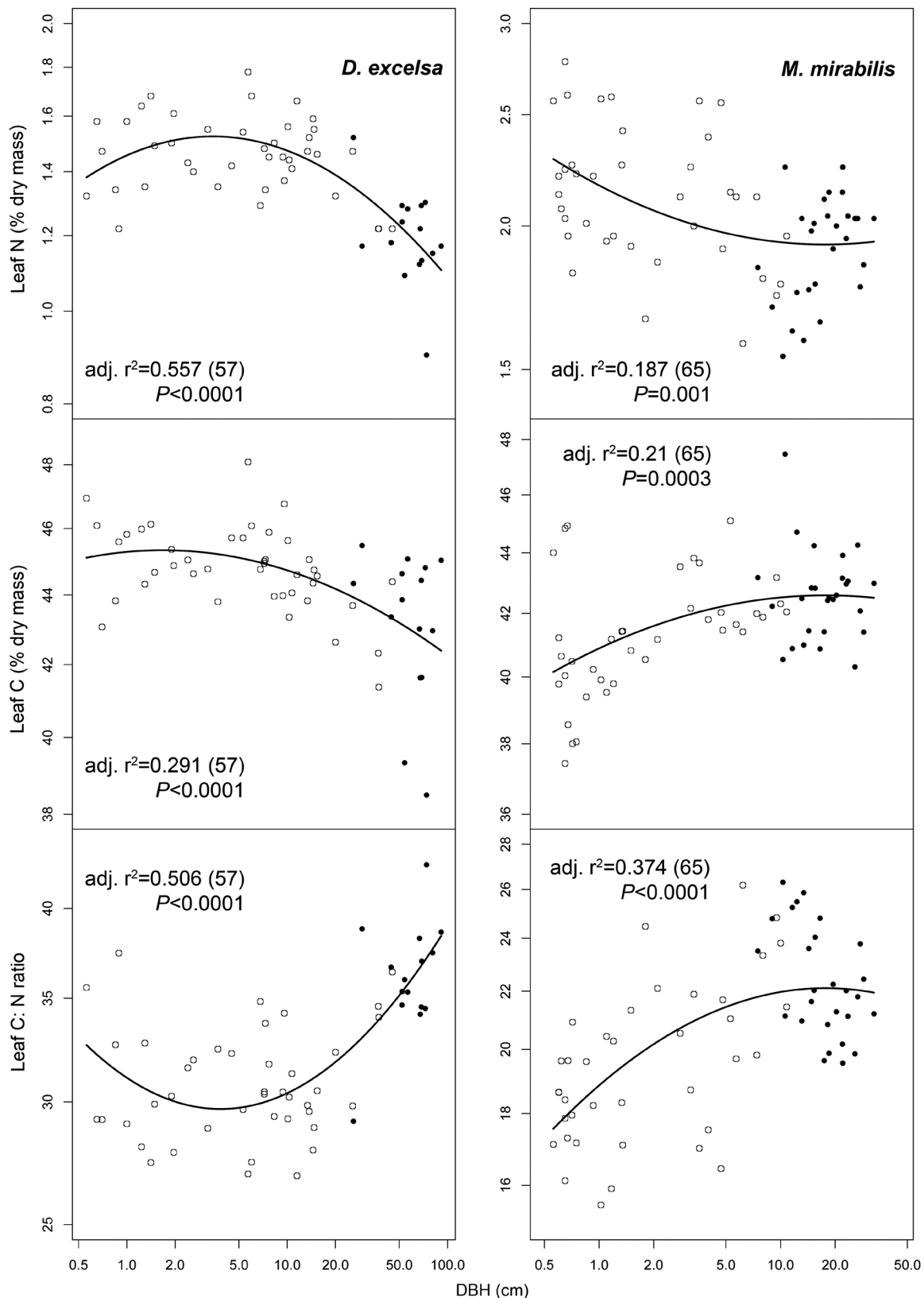
Figure 3. Leaf chemical traits as a function of tree size (DBH) for *D. excelsa* (left panels) and *M. mirabilis* (right panels). Leaf chemical traits include leaf N concentration (upper panels), leaf C concentration (middle panels) and leaf C : N ratio (lower panels). Open and closed circles represent non-reproductive and reproductive individuals, respectively. Trend lines represent leaf chemical trait–DBH relationships based on regression analysis performed on log–log transformed data. Adjusted r^2 values, sample sizes (in brackets) and P values are given for species-specific model fits for each trait (see Data S2 available as Supplementary Data at *Tree Physiology* Online for model parameters).
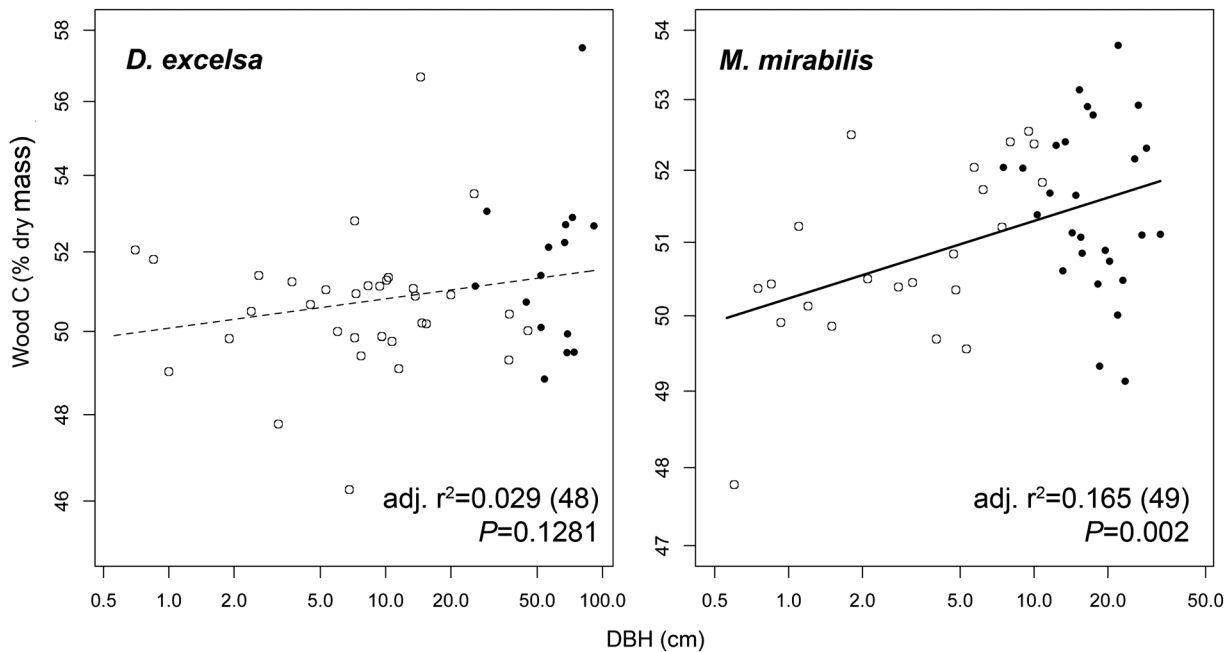
Figure 4. Wood C concentration as a function of tree size (DBH) for *D. excelsa* and *M. mirabilis*. Open and closed circles represent non-reproductive and reproductive individuals, respectively. A solid trend line indicates a significant wood C–DBH relationship, and dashed line represents a non-significant relationship, based on regression analysis performed on log–log transformed data. Adjusted r^2 values, sample sizes (in brackets) and P values are given for species-specific model fits for each trait (see Data S2 available as Supplementary Data at *Tree Physiology* Online for model parameters).

minimum sugar concentration and sugar : starch ratios (6.9 cm DBH for both traits); upper confidence bounds for peak starch and minimum sugar concentrations narrowly overlapped lower confidence bounds for reproductive onset (Figure 6).

Influence of crown exposure

The effect of tree size on trait variation was largely robust when controlling for crown exposure. Only three leaf traits in *D. excelsa* (LMA, thickness, leaf area) varied significantly as a function of crown exposure while holding tree size constant (Table 3). All other leaf and wood traits in *D. excelsa*, and all traits in *M. mirabilis* did not vary with crown exposure when controlling for tree size (Table 3). Conversely, virtually all traits initially found to vary with tree size also varied with DBH when controlling for crown exposure (Table 3). When controlling for crown exposure, the influence of DBH in driving trait variation was non-significant in three traits in *M. mirabilis* (leaf area, leaf N, wood C), and only leaf C in *D. excelsa* (Table 3).

Discussion

Essentially all leaf and wood functional traits examined showed pronounced trends with tree size (DBH) in both species. Also, with only four minor exceptions of weak relationships (where differences in adj. $r^2 \leq 0.012$), size-dependent patterns were more strongly predicted by DBH than tree *H* (Data S1 available as Supplementary Data at *Tree Physiology* Online). Traits

reflecting investment in leaf structure (LMA, leaf thickness, leaf tissue density) showed a strong positive allometric relationship to tree size, with patterns being largely similar between species (Figure 1, Table 2); this positive relationship also persisted when crown exposure was included as a covariate (Table 3). In contrast, leaf traits associated with C-gain, including leaf size and leaf C : N ratios, differed considerably between species, most notably showing 'hump-shaped' patterns with a peak at intermediate tree sizes in the late-successional species *D. excelsa*. These patterns are remarkably similar to those observed in mid- to late-successional temperate species (Thomas 2010, Sendall and Reich 2013), and are consistent with available data on ontogenetic trends in leaf size in tropical trees (Alvarez-Buylla and Martinez-Ramos 1992, Thomas and Ickes 1995). Our findings extend this body of work to indicate that certain wood functional traits show similar patterns: specifically, wood C concentration increased monotonically with tree size, whereas wood starch concentration reached a maximum at intermediate tree sizes. Similar to leaf structural traits, patterns of size-dependent changes in wood chemical traits did not differ between species of contrasting life-history strategies.

Patterns and causes of ontogenetic trait variation

Size-dependent trends in leaf structural traits (LMA, leaf thickness, leaf tissue density) have often been explained as an acclimation response to light availability (reviewed by Lusk et al.
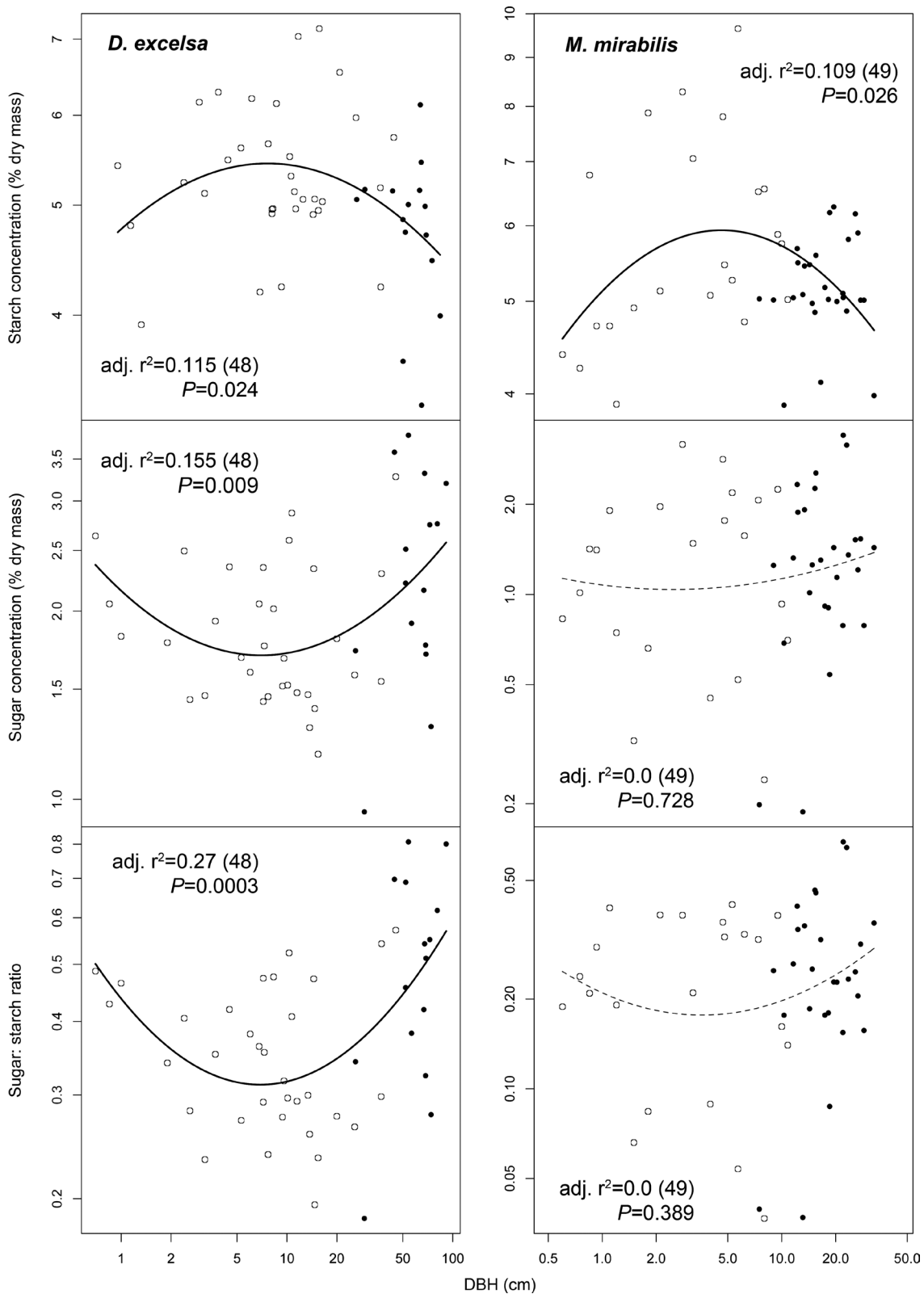
Figure 5. Size-dependent changes in NSC concentration for *D. excelsa* (left panels) and *M. mirabilis* (right panels). Traits include wood starch concentration (upper panels), wood sugar concentration (middle panels) and wood sugar: starch ratio (lower panels). Open circles represent non-reproductive individuals and filled circles represent reproductive individuals. Solid trend lines indicate significant NSC trait–DBH relationships and dashed lines represent non-significant relationships ($P \geq 0.389$), based on regression analysis performed on log–log transformed data. Adjusted r^2 values, sample sizes (in brackets) and P values are given for species-specific model fits for each trait (see Data S2 available as Supplementary Data at *Tree Physiology* Online for model parameters).
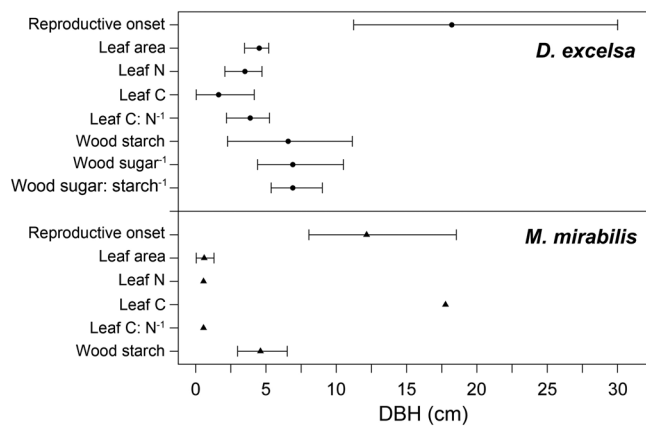
Figure 6. Location of trait peaks relative to size at reproductive onset for *D. excelsa* (upper panel, filled circles) and *M. mirabilis* (lower panel, filled triangles). Trait peaks were calculated from equations based on regression analysis of log–log transformed data (Table 3, Figures 2, 3 and 5). Error bars represent 95% confidence limits determined through bootstrapping for reproductive size thresholds (Table 1) and location of peaks for traits showing unimodal patterns.

2008), though studies also point to tree size as an independent driver of variation in these traits (e.g., Niinemets and Kull 1995, Thomas 2010). For example, studies on Norway spruce (*Picea abies*) have found that leaf thickness varies in response to light availability, leaf tissue density tracks closely with tree size, and LMA covaries with both light availability and size (Niinemets and Kull 1995, Niinemets 1997). It is challenging to disentangle the relative influences of size vs. light in driving ontogenetic changes in functional traits, particularly in field studies such as ours that include large trees where light levels are categorically estimated. In our study, leaf structural traits all varied significantly with tree size when crown exposure was included as a covariate (Table 3), a finding consistent with several previous studies on temperate and tropical hardwood species (e.g., Poorter et al. 1995, Rijkers et al. 2000, Cavaleri et al. 2010, Thomas 2010, Sendall and Reich 2013). Collectively, these results indicate that leaf structural traits respond to factors associated with tree size, but independent of light. Previous studies have pointed to increasing hydraulic path length as an important size-related factor driving monotonic increases in leaf structural traits through ontogeny (Rijkers et al. 2000, Poorter et al. 2005, Cavaleri et al. 2010). Invoking this single causal mechanism experienced by all trees as they grow larger is particularly appealing, considering that patterns of size-dependent change in leaf structural traits are generally similar (i.e., monotonically increasing) among species of contrasting life-history strategies (Figure 1; Thomas 2010) and across plant functional types (Cavaleri et al. 2010). However, prior research also points to additional factors that could be responsible for size-dependent changes in traits associated with leaf-level C gain. Specifically, declines in leaf N and photosynthetic capacity with size among large canopy trees include increased mechanical

perturbation due to herbivory and/or wind exposure (Patankar et al. 2011), and increased reproductive allocation (Thomas 2010, 2011). These factors cannot, however, explain the increase in leaf size, leaf N and related traits seen early in tree development observed in the present and related studies (Ishida et al. 2005, Kenzo et al. 2006, 2012, Coopman et al. 2008, 2011).

In terms of ultimate evolutionary causation, it has been hypothesized that due to predictable vertical gradients in light and a high 'costs of acclimation', mid- and late-successional tree species have evolved a deterministic developmental program in which seedling leaves show shade-plant traits, but progressively exhibit sun-plant traits with increasing tree size (Thomas 2010). Such a pattern is not expected in the case of extreme early-successional species (such as *M. mirabilis*) where regeneration predictably occurs under high light conditions similar to those experienced by adult trees. In the present study, we found differences between the late-successional *D. excelsa* compared with the early-successional *M. mirabilis* that are broadly consistent with this hypothesis. In *D. excelsa*, leaf area, leaf N and C : N ratios showed a distinct increasing phase (decreasing in C : N), followed by a declining trend (increasing in C : N) that begins prior to reproductive onset (Figures 2, 3 and 6). In contrast, *M. mirabilis* showed monotonic declines in leaf area and leaf N, and a monotonic increase in leaf C : N; patterns that occur in concert with a smaller size threshold for reproduction (Table 1; Figures 2, 3 and 6).

Our data on NSC concentrations (Figure 5) closely parallel patterns observed for leaf size and leaf N, and suggest that resource source–sink dynamics associated with reproduction influence the pools of C stored in trees. Hump-shaped patterns in wood starch concentration, with peaks approximating size at reproductive onset (Figures 5 and 6), are consistent with the expectation that reproductive allocation acts as a C sink in trees. This finding corroborates studies that have found that tree reproduction is to some degree reliant on NSCs stored in main stems or other woody tissues (Stephenson et al. 1989, Newell 1991, Miyazaki et al. 2002, Ichie et al. 2005). However, other studies have not found this pattern (Körner 2003, Hoch 2005, Genet et al. 2010, Sala et al. 2011), and there is also recent evidence that nutrients in woody tissues (i.e., N and P) are more important in limiting tree reproductive output (Sala et al. 2012). Differences across studies could well be attributable to species differences in limiting factors, and in the site(s) of storage of labile C and nutrients.

Although size-dependent patterns for wood C were generally 'noisy' and only significant in *M. mirabilis*, we also observed an increasing trend in wood C concentration with size in both species (Figure 4). This pattern is consistent with previous observations of increasing wood C concentration from pith to bark in large *Acer saccharum* Marsh. individuals (Lamlom and Savidge 2006). However, because our analysis focused on

Table 3. Parameter estimates and results (*P* values) from multiple regression analysis of trait variation as a function of tree size (DBH) and crown exposure, in *D. excelsa* and *M. mirabilis*. Second-order polynomial terms were included in the analysis of traits exhibiting significant DBH^2 in the-species-pooled analysis (see Table 2). Significant terms (*P* < 0.05) are in bold.

Variable	Term	*D. excelsa*		*M. mirabilis*	
		Parameter	*P*-value	Parameter	*P*-value
LMA (g m^{-2})	DBH	0.161	**<0.001**	0.251	**<0.001**
	Exposure	0.087	**0.015**	0.024	0.597
Leaf thickness (µm)	DBH	0.074	**0.012**	0.105	**0.016**
	Exposure	0.113	**<0.001**	0.037	0.407
Leaf tissue density (g cm^{-3})	DBH	0.086	**0.001**	0.153	**<0.001**
	Exposure	−0.026	0.337	−0.015	0.711
Leaf area (cm^2)	DBH	0.538	**<0.001**	−0.015	0.885
	DBH^2	−0.152	**<0.001**	−0.057	0.117
	Exposure	−0.118	**<0.001**	−0.138	0.141
Leaf N (% dry mass)	DBH	0.088	**0.002**	−0.062	0.101
	DBH^2	−0.025	**0.001**	0.021	0.109
	Exposure	−0.042	0.216	−0.043	0.204
Leaf C (% dry mass)	DBH	0.007	0.502	0.031	**0.015**
	DBH^2	−0.003	0.227	−0.004	0.326
	Exposure	−0.007	0.558	−0.005	0.662
Leaf C : N	DBH	−0.0674	**0.024**	0.101	**0.032**
	DBH^2	0.01847	**0.007**	−0.033	**0.019**
	Exposure	0.0324	0.2426	0.043	0.147
Wood C (% dry mass)	DBH	0.002	0.871	0.012	0.078
	Exposure	0.005	0.704	−0.003	0.672
Starch (% dry mass)	DBH	0.117	**0.056**	0.192	**0.022**
	DBH^2	−0.022	0.112	−0.063	**0.011**
	Exposure	−0.039	0.492	0.002	0.968
Sugar (% dry mass)	DBH	−0.192	0.1031	−0.2444	0.433
	DBH^2	0.0835	**0.0028**	0.0012	0.99
	Exposure	−0.157	0.1589	0.3035	0.128
Sugar : starch ratio	DBH	−0.309	**0.0171**	−0.4352	0.167
	DBH^2	0.1056	**0.0006**	0.0644	0.483
	Exposure	−0.1177	0.3255	0.3008	0.132

only newly formed wood, our results suggest that size-dependent increases in wood C are due to tree size, rather than ambient environmental conditions (cf. Lamlom and Savidge 2006). We speculate that our results may be explained in part by greater formation of tension wood in larger trees, in response to increasing wind- or crown-loading in larger individuals (O'Brien et al. 1995, Du and Yamamoto 2007). In Dominica high wind loading seems likely to be especially important in driving size-dependent changes in wood C: winds of 9.5 m s^{-1} have been documented in MTP (Smith et al. 2009), leading to highly dynamic canopies and reduced tree height (Martin et al. 2011; S.C. Thomas, unpublished data).

Implications of high ontogenetic variation in functional traits

Our data point to the importance of accounting for ontogenetic variation in trait-based studies of forest community assembly. Comparative studies often implicitly assume that species' trait values are size-invariant (Cornwell et al. 2006, Ackerly and Cornwell 2007, Kraft et al. 2008), or that intraspecific variation is manifest as trait plasticity among comparably sized conspecifics (Clark et al. 2003, Lichstein et al. 2007, Kraft and Ackerley 2009). Both assumptions imply that interspecific trait variation is more pronounced (and hence important to take into account) than size-dependent variation. If this were the case, species identity should explain the majority of trait variation in our pooled trait dataset, when tree size is included as a model covariate (i.e., Table 2, Eq. (4)). For *D. excelsa* and *M. mirabilis*, this should be particularly marked since they were chosen to represent opposing ends of the shade tolerance/leaf economics spectrum. However, in our dataset species identity explains 0% of the variation in LMA while DBH explains 85.9%. In the case of leaf N, species identity does explain 48.8% of the variation in leaf N, but DBH explains an additional 23.8%; for leaf size, species explains 6.4% of the variation while tree size explains 38.0%. Although more data are clearly needed, these results suggest that accounting for size-dependent trait variation is essential to understanding niche-based processes structuring tree communities (Kraft et al. 2008, Kraft and Ackerly 2010).

Differences in intraspecific size-dependent patterns of trait change may also influence our understanding of the generality of leaf trait syndromes and/or trait correlations. The 'leaf economics spectrum' (LES) of Wright et al. (2004) describes a suite of leaf functional traits (including leaf N and LMA) that form distinctive linear tradeoffs. Studies have shown very strong evidence that LES relationships are robust across large numbers of species (e.g., Reich et al. 1999, Wright et al. 2004), but studies to date have not accounted for size-dependent trait variation. Our data, and related work (Thomas 2010, Sendall and Reich 2013), suggest that leaf economics tradeoffs may deviate from a linear relationship during ontogeny. For example LMA and leaf N are negatively related when compared across large groups of species (Wright et al. 2004). However, in *D. excelsa* LMA and leaf N show contrasting linear and hump-shaped patterns with size, respectively, implying that a negative linear relationship may not describe how these traits are correlated over the whole course of ontogeny (Figures 2 and 4, respectively). Similarly, in three temperate deciduous species, Thomas (2010) found LMA increased linearly with size, while two other LES traits (leaf N and mass-based leaf photosynthetic capacity) showed pronounced unimodal patterns.

Our data on size-dependent changes in wood C (Figure 4) are perhaps of greatest relevance to forest C accounting protocols. Currently, the Intergovernmental Panel on Climate Change (IPCC 2006) suggests wood in small tropical trees (<10 cm DBH) contain 46% C, while larger tropical trees (≥10 cm DBH) contain 49% C, but these values are not based on empirical studies providing explicit size comparisons within species (Hughes et al. 2000). When averaged across the same size categories, our data agree with their overall assumption of increasing wood C with size, but our differences are much smaller than 3%. In *D. excelsa*, larger trees (<10 cm DBH) averaged 51.4% wood C (±0.3 SE), while small trees (≥10 cm DBH) averaged 50.4% wood C (±2.0 SE). Similarly, in *M. mirabilis* smaller trees averaged 50.8% wood C (±0.3 SE), while larger trees averaged 51.5% wood C (±0.2 SE). However, the generality of these patterns is uncertain, given that we have found pronounced decreases in wood C concentration in comparisons of saplings and canopy trees in some Panamanian species (Martin et al. 2013).

Conclusion

To our knowledge, this study is the first to quantify species-specific leaf and wood functional trait variation across the entire spectrum of sizes in any tropical tree species. We found that all but one trait varied strongly with tree size (DBH) in both species, following predictable linear and non-linear patterns. Moreover, although patterns of size-dependent variation are quantitatively different among traits and between species that differ in life-history strategy, similarities across broad forest types are compelling (cf. Thomas 2010). Further efforts

to quantify size-dependent variation in traits across full size spectrums for greater numbers of species would contribute significantly to our understanding of the functional ecology and comparative biology of tropical and temperate trees.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Conflict of interest

None declared.

References

Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with ImageJ. Biophotonics Int 11:36–42.

Ackerly DD, Cornwell WK (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. Ecol Lett 10:135–145.

Alvarez-Buylla ER, Martinez-Ramos M (1992) Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree—an evaluation of the climax pioneer paradigm for tropical rainforests. J Ecol 80:275–290.

Baker TR, Phillips OL, Malhi Y et al. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. Glob Change Biol 10:545–562.

Baltzer JL, Thomas SC (2007) Determinants of whole-plant light requirements in Bornean rain forest tree saplings. J Ecol 95:1208–1221.

Baltzer JL, Thomas SC (2010) A second dimension to the leaf economics spectrum predicts edaphic habitat association in a tropical forest. PLoS One 5:e13163.

Barbaroux C, Breda N (2002) Contrasting distribution and seasonal dynamics of carbohydrate reserves in stem wood of adult ring-porous sessile oak and diffuse-porous beech trees. Tree Physiol 22:1201–1210.

Bullock SH (1992) Seasonal differences in nonstructural carbohydrates in two dioecious monsoon-climate trees. Biotropica 24:140–145.

Cavaleri MA, Oberbauer SF, Clark DB, Clark DA, Ryan MG (2010) Height is more important than light in determining leaf morphology in a tropical forest. Ecology 91:1730–1739.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE (2009) Towards a worldwide wood economics spectrum. Ecol Lett 12:351–366.

Clark DA, Clark DB (1992) Life-history diversity of canopy and emergent trees in a neotropical rainforest. Ecol Monogr 62:315–344.

Clark JS, Mohan J, Dietze M, Ibanez I (2003) Coexistence: how to identify trophic trade-offs. Ecology 84:17–31.

Coopman RE, Reyes-Diaz M, Briceno VF, Corcuera LJ, Cabrera HM, Bravo LA (2008) Changes during early development in photosynthetic light acclimation capacity explain the shade to sun transition in *Nothofagus nitida*. Tree Physiol 28:1561–1571.

Coopman RE, Briceno VF, Corcuera LJ, Reyes-Diaz M, Alvarez D, Saez K, Garcia-Plazaola JI, Alberdi M, Bravo LA (2011) Tree size and light availability increase photochemical instead of non-photochemical capacities of *Nothofagus nitida* trees growing in an evergreen temperate rain forest. Tree Physiol 31:1128–1141.

Cornelissen JHC, Lavorel S, Garnier E et al. (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51:335–380.

Cornwell WK, Schwilk DW, Ackerly DD (2006) A trait-based test for habitat filtering: convex hull volume. Ecology 87:1465–1471.

Curran TJ, Gersbach LN, Edwards W, Krockenberger AK (2008) Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of north Queensland, Australia. Austral Ecol 33:442–450.

Diaz S, Hodgson JG, Thompson K et al. (2004) The plant traits that drive ecosystems: evidence from three continents. J Veg Sci 15:295–304.

Du S, Yamamoto F (2007) An overview of the biology of reaction wood formation. J Integr Plant Biol 49:131–143.

Genet H, Breda N, Dufrene E (2010) Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. Tree Physiol 30:177–192.

Harvey PH, Pagel MD (1991) The comparative method in evolutionary biology. Oxford series in ecology and evolution. Oxford University Press, New York, NY, 239 p.

Herault B, Bachelot B, Poorter L, Rossi V, Bongers F, Chave J, Paine CET, Wagner F, Baraloto C (2011) Functional traits shape ontogenetic growth trajectories of rainforest tree species. J Ecol 99:1431–1440.

Hoch G (2005) Fruit-bearing branchlets are carbon autonomous in mature broad-leaved temperate forest trees. Plant Cell Environ 28:651–659.

Hoch G, Popp M, Korner C (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. Oikos 98:361–374.

Hoch G, Richter A, Korner C (2003) Non-structural carbon compounds in temperate forest trees. Plant Cell Environ 26:1067–1081.

Hughes RF, Kauffman JB, Jaramillo VJ (2000) Ecosystem-scale impacts of deforestation and land use in a humid tropical region of Mexico. Ecol Appl 10:515–527.

Ichie T, Kenzo T, Kitahashi Y, Koike T, Nakashizuka T (2005) How does *Dryobalanops aromatica* supply carbohydrate resources for reproduction in a masting year? Trees-Struct Funct 19:703–710.

IPCC (2006) Intergovernmental panel on climate change guidelines for national greenhouse gas inventories. Chapter 4: Forest lands. In: Eggleston HS, Buendia L, Miwa K, Ngara T, Tanabe K (eds) National Greenhouse Gas Inventories Programme, Hayama, Japan, 83 p.

Ishida A, Yazaki K, Hoe AL (2005) Ontogenetic transition of leaf physiology and anatomy from seedlings to mature trees of a rainforest pioneer tree, *Macaranga gigantea*. Tree Physiol 25:513–522.

Kattge J, Diaz S, Lavorel S et al. (2011) TRY—a global database of plant traits. Global Change Biol 17:2905–2935.

Kenzo T, Ichie T, Watanabe Y, Yoneda R, Ninomiya I, Koike T (2006) Changes in photosynthesis and leaf characteristics with tree height in five dipterocarp species in a tropical rain forest. Tree Physiol 26:865–873.

Kenzo T, Yoneda R, Sano M, Araki M, Shimizu A, Tanaka-Oda A, Chann S (2012) Variations in leaf photosynthetic and morphological traits with tree height in various tree species in a Cambodian tropical dry evergreen forest. JARQ-Jpn Agr Res Q 46:167–180.

Kobe RK (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos 80:226–233.

Körner C (2003) Carbon limitation in trees. J Ecol 91:4–17.

Kraft NJB, Ackerly DD (2009) Response to comment on Functional traits and niche-based tree community assembly in an Amazonian forest. Science 324:1015.

Kraft NJB, Ackerly DD (2010) Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. Ecol Monogr 80:401–422.

Kraft NJB, Valencia R, Ackerly DD (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. Science 322:580–582.

Lamlom SH, Savidge RA (2006) Carbon content variation in boles of mature sugar maple and giant sequoia. Tree Physiol 26:459–468.

Lichstein JW, Dushoff J, Levin SA, Pacala SW (2007) Intraspecific variation and species coexistence. Am Nat 170:807–818.

Lusk CH, Reich PB, Montgomery RA, Ackerly DD, Cavender-Bares J (2008) Why are evergreen leaves so contrary about shade? Trends Ecol Evol 23:299–303.

Martin AR, Thomas SC (2011) A reassessment of carbon content in tropical trees. PLoS One 6:e23533.

Martin AR, Thomas SC, Stedman ER (2011) Size-dependent changes in light requirements of tropical trees: weak light – growth relationships in seven Caribbean rainforest species preclude testing a general hypothesis. JNR EEB 8:6–17.

Martin AR, Thomas SC, Zhao Y (2013) Size-dependent changes in wood chemical traits: a comparison of neotropical saplings and large trees. AoB Plants 5: plt039; doi:10.1093/aobpla/plt039.

Miyazaki Y, Hiura T, Kato E, Funada R (2002) Allocation of resources to reproduction in *Styrax obassia* in a masting year. Ann Bot 89:767–772.

Newell EA (1991) Direct and delayed costs of reproduction in *Aesculus californica*. J Ecol 79:365–378.

Newell EA, Mulkey SS, Wright SJ (2002) Seasonal patterns of carbohydrate storage in four tropical tree species. Oecologia 131:333–342.

Nicolson DH, DeFilipps RA, Nicolson AC (1991) Flora of dominica, Part 2: Dicotyledoneae. Smithsonian contributions to botany number 77. Smithsonian Institution Press, Washington, DC, 274 p.

Niinemets U (1997) Distribution patterns of foliar carbon and nitrogen as affected by tree dimensions and relative light conditions in the canopy of *Picea abies*. Trees Struct Funct 11:144–154.

Niinemets U (2006) The controversy over traits conferring shade-tolerance in trees: ontogenetic changes revisited. J Ecol 94:464–470.

Niinemets U, Kull O (1995) Effects of light availability and tree size on the architecture of assimilative surface in the canopy of *Picea abies*—variation in needle morphology. Tree Physiol 15:307–315.

O'Brien ST, Hubbell SP, Spiro P, Condit R, Foster RB (1995) Diameter, height, crown, and age relationships in eight neotropical tree species. Ecology 76:1926–1939.

Patankar R, Thomas SC, Smith SM (2011) A gall-inducing arthropod drives declines in canopy tree photosynthesis. Oecologia 167:701–709.

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

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

Poorter L, Oberbauer SF, Clark DB (1995) Leaf optical properties along a vertical gradient in a tropical rainforest canopy in Costa Rica. Am J Bot 82:1257–1263.

Poorter L, Bongers F, Sterck FJ, Woll H (2005) Beyond the regeneration phase: differentiation of height-light trajectories among tropical tree species. J Ecol 93:256–267.

Poorter L, Wright SJ, Paz H et al. (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. Ecology 89:1908–1920.

Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. New Phytol 182:565–588.

Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: a test across six biomes. Ecology 80:1955–1969.

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 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.

Sala A, Hoch G (2009) Height-related growth declines in ponderosa pine are not due to carbon limitation. Plant Cell Environ 32:22–30.

Sala A, Fouts W, Hoch G (2011) Carbon storage in trees: does relative carbon supply decrease with tree size? In: Meinzer FC, Dawson T, Lachenbruch BJ (eds) Size- and age-related changes in tree structure and function. Springer, New York, Heidelberg, pp 287–306.

Sala A, Hopping K, McIntire EJB, Delzon S, Crone EE (2012) Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. New Phytol 196:189–199.

Sendall KM, Reich PB (2013) Variation in leaf and twig CO_2 flux as a function of plant size: a comparison of seedlings, saplings and trees. Tree Physiol 33:713–729.

Smith RB, Schafer P, Kirshbaum DJ, Regina E (2009) Orographic precipitation in the tropics: experiments in Dominica. J Atmos Sci 66:1698–1716.

Stephenson RA, Gallagher EC, Rasmussen TS (1989) Effects of growth manipulation on carbohydrate reserves of macadamia trees. Sci Hort 40:227–235.

Sterck FJ, Bongers F (2001) Crown development in tropical rain forest trees: patterns with tree height and light availability. J Ecol 89:1–13.

Thomas SC (1996a) Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. Am J Bot 83:556–566.

Thomas SC (1996b) Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. Oikos 76:145–154.

Thomas SC (2010) Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. Tree Physiol 30:555–573.

Thomas SC (2011) Age-related changes in tree growth and functional biology: the role of reproduction. In: Meinzer FC, Dawson T, Lachenbruch BJ (eds) Size- and age-related changes in tree structure and function. Springer, New York, Heidelberg, pp 33–64.

Thomas SC, Bazzaz FA (1999) Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology 80:1607–1622.

Thomas SC, Ickes K (1995) Ontogenetic changes in leaf size in Malaysian rainforest trees. Biotropica 27:427–434.

Weedon JT, Cornwell WK, Cornelissen JHC, Zanne AE, Wirth C, Coomes DA (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol Lett 12:45–56.

Wright IJ, Reich PB, Westoby M et al. (2004) The worldwide leaf economics spectrum. Nature 428:821–827.

Wright SJ, Muller-Landau HC, Condit R, Hubbell SP (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology 84:3174–3185.

Wright SJ, Kitajima K, Kraft NJB et al. (2010) Functional traits and the growth-mortality trade-off in tropical trees. Ecology 91:3664–3674.

Wurth MKR, Pelaez-Riedl S, Wright SJ, Korner C (2005) Non-structural carbohydrate pools in a tropical forest. Oecologia 143:11–24.