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Global patterns of biomass allocation in woody species with different tolerances of shade and drought: evidence for multiple strategies

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Summary

- The optimal partitioning theory predicts that plants of a given species acclimate to different environments by allocating a larger proportion of biomass to the organs acquiring the most limiting resource. Are similar patterns found across species adapted to environments with contrasting levels of abiotic stress?
- We tested the optimal partitioning theory by analysing how fractional biomass allocation to leaves, stems and roots differed between woody species with different tolerances of shade and drought in plants of different age and size (seedlings to mature trees) using a global dataset including 604 species.
- No overarching biomass allocation patterns at different tolerance values across species were found. Biomass allocation varied among functional types as a result of phenological (deciduous vs evergreen broad-leaved species) and broad phylogenetical (angiosperms vs gymnosperms) differences. Furthermore, the direction of biomass allocation responses between tolerant and intolerant species was often opposite to that predicted by the optimal partitioning theory.
- We conclude that plant functional type is the major determinant of biomass allocation in woody species. We propose that interactions between plant functional type, ontogeny and species-specific stress tolerance adaptations allow woody species with different shade and drought tolerances to display multiple biomass partitioning strategies.

Introduction

Plants in nature are exposed to vastly varying environmental conditions and strong competition by neighbours. Modification of biomass allocation is one of the major means of maximizing plant growth rate, survival and fitness under different biotic and abiotic pressures (Poorter *et al.*, 2015; Veresoglou & Peñuelas, 2019). An appropriate biomass allocation that maximizes plant growth rate and survival is particularly critical for long-living woody species that continuously increase in size and need to balance carbon allocation among above- and below-ground parts to satisfy the requirements for efficient resource use as well as plant mechanical stability; thus, biomass allocation has an important and prolonged influence on woody species morphology and functioning (Veresoglou & Peñuelas, 2019). Despite the relatively large body of literature on species biomass allocation in relation to environmental conditions, there is still little information of differences in biomass allocation patterns among woody species with different environmental preferences (Reich, 2002).

The most common approach for comparing patterns of biomass allocation across resource gradients, both within and between species, is the use of standing biomass fractions (e.g. leaf mass fraction; Poorter & Sack, 2012). This 'clasmometric' approach has been widely used to analyse the responses of biomass allocation to different environmental conditions; ontogenetic trends in biomass partitioning over time; and differences in biomass partitioning among species (Poorter *et al.*, 2015). Responses of leaf, stem and root mass fractions (LMF, SMF and RMF, respectively; Table 1) to availability of different resources have often been interpreted in terms of an optimal partitioning theory (or a functional equilibrium model) (Poorter *et al.*, 2015). According to this theory, plants modify their LMF, SMF and RMF according to the relative limitations of light, CO_2, water and nutrient supply (Brouwer, 1963; Bloom *et al.*, 1985; Hilbert & Reynolds, 1991; Shipley & Meziane, 2002; Poorter *et al.*, 2012). The optimal partitioning theory predicts that plant growth will be maximized by allocating a relatively larger proportion of biomass to the organs responsible for the acquisition of the most limiting resource for growth (Bloom *et al.*, 1985). Although the optimal partitioning theory is typically used to predict phenotypic responses (i.e. acclimation) of plants to resource supply (Reich, 2002), it is widely assumed that the same

Table 1 List of abbreviations used in this study.

	Abbreviation	Name	Unit
Traits used	LMF	Leaf mass fraction	g g^{-1}
	SMF	Stem mass fraction	g g^{-1}
	RMF	Root mass fraction	g g^{-1}
	Log$_{10}$TDM	Log$_{10}$-transformed total plant dry mass	Log (g)
Classification	PFT	Plant functional type	–
	DBL	Deciduous broadleaf species	–
	EBL	Evergreen broadleaf species	–
	ENL	Evergreen needleleaf species	–
Other abbreviations	LMA	Leaf dry mass per unit area	g m^{-2}
	LAI	Leaf area index	m^2 m^{-2}
	LAR	Leaf area ratio	m^2 g^{-1}

principles hold for adaptive responses of biomass allocation between species that colonize environments that differ in resource supply (Grime, 1977; Chapin, 1980; Tilman, 1988; Gleeson & Tilman, 1990).

Shade and drought are two key environmental drivers that, to a large degree, determine forest composition, with mesic dense forests typically dominated by shade-tolerant and drought-intolerant species, and open dry forests by drought-tolerant and shade-intolerant species (Niinemets & Valladares, 2006; Zhang *et al.*, 2018). Part of this differentiation has been attributed to species differences in biomass allocation (Smith & Huston, 1989). In particular, when light limits plant growth, the optimal partitioning theory predicts that more biomass should be allocated to above- than to below-ground plant parts, whereas when water is limiting, more biomass should be allocated to those below ground (Givnish, 1988; Smith & Huston, 1989). The debate on how plants gain shade-tolerance is centred on two main hypotheses (Poorter *et al.*, 2019). The carbon gain hypothesis (Givnish, 1988) predicts that shade-tolerant species enhance net energy capture in low light mainly by allocating carbon to leaf production to maximize leaf area. The second hypothesis assumes high stress tolerance in shade and lower carbon losses (Kitajima, 1994), and predicts that shade-tolerant species construct more robust leaves with greater dry mass per unit leaf area (LMA). Such more robust leaves have a greater longevity as a result of a lower vulnerability to mechanical damage, and better resistance to herbivore and pathogen pressures under shade. According to the carbon gain hypothesis, an enhanced allocation to leaves might result in a greater LMF when comparing shade-tolerant and shade-intolerant species under similar light conditions. The same can also be true for the stress tolerance hypothesis, as a higher LMA would mean a slower leaf turnover and greater leaf biomass accumulation in the canopy (Lusk, 2004; Lusk *et al.*, 2008b; Niinemets, 2010). Accumulation of leaves should positively scale with the investment in branches and stems required for leaf support (Niinemets, 2010), and thus SMF should increase together with LMF. This suggests that SMF and LMF are expected to be greater, and, accordingly, RMF to be smaller for shade-tolerant species than for shade-intolerant species. These predictions are indeed consistent with the optimal partitioning theory.

However, interspecific comparisons of biomass allocation between shade-tolerant and shade-intolerant species have yielded contrasting results in woody (Reich, 2002) and herbaceous species grown at both low and high light intensities (Pons & Poorter, 2014). For instance, Walters & Reich (1999) found that shade-tolerant winter-deciduous broadleaf species are characterized by lower LMF and higher RMF than shade-intolerant species, while evergreen broadleaf species display limited differences in both LMF and RMF between shade-tolerant and shade-intolerant species. A similar pattern has been found for tropical woody species (Veneklaas & Poorter, 1998).

Trait changes throughout plant ontogeny can modify the relationship between biomass allocation and shade-tolerance (Sack & Grubb, 2001; Niinemets, 2006). For instance, Lusk (2004) found that shade-tolerant evergreens invested less biomass in leaves and more in roots compared with shade-intolerant species at common light intensities during the early stages of development; however, the trend was reversed as the plants grew in size. Also, young individuals of shade-tolerant species typically have a more monolayered canopy that maximizes light interception and minimizes self-shading (Horn, 1971; but see Lusk *et al.*, 2011). As the plants gain in height and reach the canopy, they generate more layers (Horn, 1971; Brown & Parker, 1994; Frazer *et al.*, 2000; King, 2003; Niinemets, 2010). Such architectural changes during ontogeny can affect species' biomass allocation without altering their relative shade tolerance rank compared with neighbouring competitors. For example, if allocating more biomass to leaf layers at the top of the canopy makes trees more vulnerable to elastic buckling, toppling and uprooting (McMahon, 1975), the development of a monolayer canopy may necessitate greater investment in stem wood and possibly even in root mass for more secure anchorage. Thus, ultimately, the tradeoff between different functions (light harvesting vs mechanical stability) might determine how biomass allocation scales with shade-tolerance.

If water is the most limiting resource, the optimal partitioning theory predicts an increase in RMF at the expense of SMF and LMF. Such acclimation responses have often been observed in experiments, but generally only at more severe drought levels (Poorter *et al.*, 2012). In terms of adaptation, the expected increase in RMF in species from habitats with lower water availability has been reported in several cases (e.g. Markesteijn & Poorter, 2009), but inconsistent differences have been observed in local species comparisons (e.g. Schall *et al.*, 2012) and in global-scale analyses (McCarthy & Enquist, 2007; Reich *et al.*, 2014). Changes in root functional traits (e.g. root surface area per unit root mass) rather than changes in biomass allocation (Reich, 2002; McCarthy & Enquist, 2007), and fluctuations in water availability over shorter timescales than those necessary to accommodate changes in biomass allocation strategies (e.g. seasonal water fluctuations; Poorter *et al.*, 2012; Reich *et al.*, 2014) have been proposed as possible explanations for the deviation of biomass allocation patterns from the optimal partitioning theory.

The aim of the present study was to examine and compare patterns of biomass allocation in woody species with different ecological tolerances (Niinemets & Valladares, 2006) to shade and drought at a global scale. The global biomass allocation dataset (Poorter *et al.*, 2015) combined with estimates of species' ecological potentials consisted of > 7000 observations of LMF, SMF and RMF for *c.* 600 woody species from tropical to boreal climates.

We tested two broad hypotheses based on the predictions of the optimal partitioning theory: first, that shade-tolerant species will consistently allocate a greater proportion of their biomass to leaves and stems, and less in roots compared with shade-intolerant species; and second, that drought-tolerant species will consistently allocate a greater fraction of biomass to roots, and a lower fraction to stems and leaves compared with drought-intolerant species. Biomass fractions, especially LMF and SMF, inherently vary with plant size (total plant biomass) and among plant functional types (PFTs; Niinemets, 2010; Poorter *et al.*, 2015). However, we expected that 'optimality' in biomass allocation is reflected in systematic differences between tolerant and intolerant species, independent of PFT, after correction for plant size effect on biomass allocation.

Materials and Methods

Dataset

Biomass allocation fractions in leaves (LMF), stems (SMF), roots (RMF) and total plant dry mass (TDM) for woody species were taken from Poorter *et al.* (2015). This dataset has been compiled using published and unpublished studies in which biomass values for the three biomass components were concurrently measured. Data were obtained from plants growing under a wide range of conditions including growth chambers, glasshouses, open-top chambers and natural field conditions. The data for plants from natural field conditions were taken from large data compilations based on Western scientific literature (Cannell, 1982), Eastern European literature (Usoltsev, 2013) and Chinese papers and reports (Luo *et al.*, 2014), supplemented with original data collected from various sources (see Poorter *et al.*, 2015 for further details). Data from genetically modified organisms and plants treated with herbicides, hormones, and/or heavy metals were excluded, as they may have provided atypical patterns of biomass distribution.

Species-specific rankings for tolerance of shade and drought were obtained from Poorter *et al.* (2010, 2012, 2019). These datasets include tolerance estimates based on a three-level scale (1, intolerant; 2, intermediate tolerant; 3, tolerant) for 430 woody species also present in Poorter *et al.* (2015). Additional species-specific estimates of shade and drought tolerance were obtained from Niinemets & Valladares (2006). In the latter, stress tolerance scales for each stress factor range from 1 (very intolerant) to 5 (very tolerant). In the present study, drought tolerance scores from Niinemets & Valladares (2006) were updated following Zhang *et al.* (2018). Additional five-level scores of shade and drought tolerances were added from Hallik *et al.* (2009) and Harrison *et al.* (2013) using relevant case studies and authors' knowledge of species biology, following the methodology of Niinemets & Valladares (2006).

The five-level scores for shade and drought tolerances were converted to a three-point scale, following Hallik *et al.* (2009). The following thresholds were adopted: (1) drought tolerance < 2; (2) drought tolerance ≤ 3.5 and ≥ 2; (3) drought tolerance > 3.5; (1) shade tolerance < 1.5; (2) shade tolerance ≤ 3 and ≥ 1.5; and (3) shade tolerance > 3. The final dataset of tolerance scores and biomass allocation data included 7377 observations for 604 woody species worldwide.

Species were broadly classified into three functional types: deciduous broadleaf (DBL, 207 species), evergreen broadleaf (EBL, 269 species), and evergreen needleleaf (ENL, 84 species) species. PFT classification was made using the Global Leaf Phenology (Zanne *et al.*, 2014; Wright *et al.*, 2019) and Glopnet (Wright *et al.*, 2004) databases, databases of Hallik *et al.* (2009) and Niinemets (2010), some web databases (http://davesgarden.com/; http://tropical.theferns.info/; https://pfaf.org/) and the authors' knowledge of species biology.

The complete list of species in the database, their stress tolerance scores and PFT classification are provided in Table S1. Main descriptive statistics of biomass allocation and $\log_{10}$-transformed TDM, $\log_{10}$TDM data, number of species and observations at each stress tolerance level and PFT combination are shown in Table S2.

Data analyses

In the original Poorter *et al.* (2015) dataset, differences in TDM spanned more than 10 orders of magnitude, from 0.0001 g to 15 000 kg, and $\log_{10}$TDM explained 78%, 87% and 21% of LMF, SMF and RMF variation across individuals, respectively. TDM relationships with biomass fractions were best described by nonlinear functions. To analyse differences in biomass allocation among stress tolerance groups while accounting for changes in biomass allocation as a result of differences in $\log_{10}$TDM, we employed the following approach:

(**1**) We first identified the best nonlinear function describing the relationship between biomass fractions and $\log_{10}$TDM for all data pooled using the 'Curve Finder' tool of CURVEEXPERT 1.4 (Hyams Development, Chattanooga, TN, USA). This tool employs a large number of regression models and each fit is ranked according to its standard error and correlation coefficient. High-degree (> 3) polynomials were excluded to avoid overfitting. The relationship between $\log_{10}$TDM and mass fractions (MFs, either LMF, SMF or RMF) was best described by a Gaussian model in the form:

$$\mathrm{MF} = ae^{-(b-\log_{10}\mathrm{TDM})^2/(2c^2)}$$

The model fits for all data pooled are shown in Supporting Information Fig. S1. For comparative purposes, we assumed that the same model (with different values for the parameters) could describe the relationship between biomass fractions and $\log_{10}$TDM for each of the considered stress tolerance groups within each PFT.

(**2**) After selection of the best model describing the target relationship within each stress tolerance group, we cross-validated the model using 50 random subsets of the original dataset stratified per tolerance group. At each run, the model was calibrated with 70% of the input data and its predictive accuracy evaluated using the remaining 30% of data by simple linear regression (i.e. examining the correlation coefficient between predicted vs observed values). Model parameters were separately estimated at each run for each tolerance group using the 'nlsList' function (NLME package in R; Pinheiro *et al.*, 2020). This operation was applied separately to each PFT. The cross-validation procedure is summarized in Fig. S2. Means and standard deviations for model parameters and the correlation coefficients for predicted vs observed values are summarized in Tables S3 and S4. Cross-validation curves for each biomass fraction within PFTs are shown in Figs S3 and S4.

(**3**) Finally, we used the cross-validated models to evaluate differences in LMF, SMF or RMF among stress tolerance groups at three TDM values representative of seedlings (TDM = 1 g), small trees (TDM = 10 kg), and big trees (TDM = 10^3 kg).

This procedure resulted in 50 estimates for each biomass fraction at three given plant size classes per stress tolerance group and PFT. Given that such numbers were generated using cross-validation and their variance artificially constrained, we did not apply any *P*-value-based statistics to evaluate differences among stress tolerance groups at the selected TDMs. Instead we analysed the dissimilarity among trait probability distributions (TPDs) of the generated predictions across stress tolerance groups (Carmona *et al.*, 2016) using the functions included in the TPD R package (Carmona *et al.*, 2019). To reduce TPD sensitivity to eventual outliers, TPDs were always constructed such that the proportion of the probability density function of each tolerance group was 0.95. TPDs define the probability of a trait value within a given stress tolerance group and are calculated over the entire range of trait values. TPDs are therefore equivalent to the trait space of a given stress tolerance group.

Trait probability distribution-based dissimilarity can be decomposed into two underlying components that represent the proportion of the trait space: shared by the stress tolerance groups; and occupied by one group but not by the others. By analysing how the components influenced the overall dissimilarity among groups (Notes S1; Fig. S5) the differences in biomass allocation among stress tolerance groups were defined as:

(**1**) Overlapped – if stress tolerance groups exactly occupied the same trait space (i.e. no difference).

(**2**) Divergent – if stress tolerance groups were partially overlapping while tending to diverge. The divergence threshold is determined by the defined dissimilarity value (Notes S1). A dissimilarity ≥ 0.70 was arbitrarily chosen as the threshold.

(**3**) Nested – if tolerance groups shared only a portion of the trait space but one group was entirely included in the trait space of the other. This difference was considered as not absolute (Notes S1).

(**4**) Dissimilar – if there was no overlap among stress tolerance groups.

Only results for differences between tolerant and intolerant species are presented, as the behaviour of 'intermediately tolerant' (tolerance = 2) species was similar to either intolerant or tolerant species depending on the comparison. All pairwise comparisons of the dissimilarity decomposition analysis, including all tolerance groups, are included in Tables S5 and S6.

To further widen the scope of our analysis, we also compared the magnitude of the observed adaptive responses of biomass allocation for the considered stress factors with the magnitude of acclimation responses obtained by Poorter *et al.* (2012). Using the data of our study, we summarized adaptive responses as the difference between tolerant and intolerant species using the averages obtained from model predictions for each PFT ($\Delta_{\text{adaptation}}$). Using the data of Poorter *et al.* (2012), acclimation responses were expressed as the differences between the values of biomass fractions at the minimum value of an environmental factor (either light or water availability) and those measured at a reference value in the dose–response curve (i.e. at 8 mol photons $\text{m}^{-2}\ \text{d}^{-1}$ for light availability; 1 for water availability, expressing the maximum water availability in a relative scale) ($\Delta_{\text{acclimation}}$). Both $\Delta_{\text{adaptation}}$ and $\Delta_{\text{acclimation}}$ could not be calculated for the exact same species set, but many of the species in our study were also included in Poorter *et al.* (2012). Also, the dose–response curves of Poorter *et al.* (2012) display acclimation responses for small plants and they are averaged across species. Therefore, we only used $\Delta_{\text{adaptation}}$ values obtained for seedlings and averaged the values across PFTs to make the comparisons more reliable.

Finally we want to emphasize two key assumptions of the present study:

(**1**) For many species in Poorter *et al.* (2015) biomass allocation was measured in plants grown under a wide variety of conditions. We assumed that the data available for different species with different shade and drought tolerances had been obtained, on average, from a similar range of environmental conditions.

(**2**) We assumed that the relative tolerance scores used here do not change through plant ontogeny, despite the fact that plant species can change their absolute tolerance to abiotic stress factors during ontogeny (e.g. Lusk *et al.*, 2008a; Sendall *et al.*, 2015). Nevertheless, relative rankings at different stages of ontogeny are remarkably conservative (Niinemets & Valladares, 2006), and the information of rank changes through ontogeny is very limited, making the fine-tuning of tolerance indices across ontogenetic stages currently impossible at the global scale.

Results

Biomass allocation and shade tolerance

Contrary to our hypothesis, LMF was lower for shade-tolerant than for shade-intolerant DBL species. This difference was independent of size (Fig. 1a–c), and tolerant and intolerant species never overlapped in the trait space (i.e. dissimilar; Table 2). SMF was greater for shade-tolerant than for shade-intolerant seedlings (Fig. 1d) and the tolerance groups were dissimilar (Table 2). SMF was greater for shade-tolerant than for shade-intolerant small trees (Fig. 1e), and the tolerance groups were divergent with a dissimilarity value of 0.81, implying that they only shared a small portion of the trait space (Table 2). Conversely, shade-

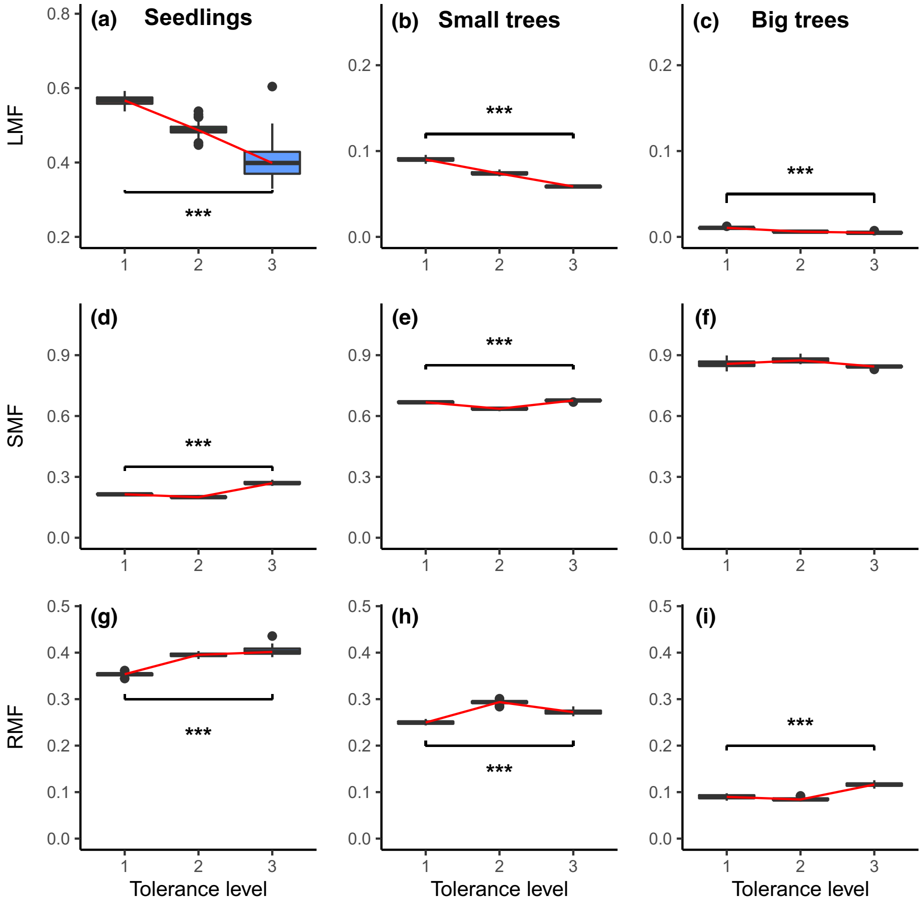

Fig. 1 Biomass allocation fractions at different shade tolerances in deciduous broadleaf species. (a–i) Boxplots summarizing medians (linked by solid red lines), interquartile range (25^{th} and 75^{th} percentile, box limits) and values greater than interquartile range (whisker limits) for estimates of biomass allocation fractions to leaves (LMF) (a–c), stems (SMF) (d–f) and roots (RMF) (g–i) at different shade tolerances (1, intolerant; 2, intermediate; 3, tolerant). Differences among stress tolerance groups were evaluated at three fixed values of total plant dry mass (TDM) (seedlings, 1 g; small trees, 10 kg; big trees, 10^3 kg). Biomass allocation fraction estimates were obtained from cross-validated models, $n = 50$. *** indicates that tolerant and intolerant species occupy a different portion of the trait space corresponding to dissimilar (dissimilarity = 1; no overlap) or divergent (dissimilarity value ≥ 0.70 and little overlap) difference category. Details on categories are reported in the Materials and Methods section and Supporting Information Notes S1. More information on differences between tolerant and intolerant species are summarized in Table 2. All pairwise comparisons are reported in Table S5. Units are as in Table 1. Points indicate values exceeding interquartile range, but they are not used in dissimilarity calculations (see the Materials and Methods section).

tolerant and shade-intolerant big trees were nested according to their SMF values (Table 2), and the difference was not absolute (Fig. 1f). Also contrary to our hypothesis, RMF was consistently greater for shade-tolerant than for shade-intolerant species, independent of size (Fig. 1g–i) and tolerance groups were always dissimilar (Table 2).

Similar to the variation in DBL species, LMF was lower (Fig. 2a–c) and SMF greater (Fig. 2d–f), independent of size, for shade-tolerant than for shade-intolerant EBL species, and tolerant and intolerant species were always dissimilar (Table 2). Shade-tolerant and -intolerant seedlings were nested according to their RMF values (Table 2), so differences between them were not absolute (Fig. 2g). Contrary to DBL species but in agreement with our hypothesis, in EBL species, RMF was lower for small and big trees of shade-tolerant species compared with shade-intolerant species (Fig. 2h,i) and the groups were dissimilar (Table 2).

In agreement with our hypothesis, LMF in ENL species was always greater for shade-tolerant than for shade-intolerant species. These differences were independent of size (Fig. 3a–c), although shade-tolerant and shade-intolerant seedling trait spaces were nested (Fig. 3a; Table 2). Concerning SMF, tolerant and intolerant ENL species were always dissimilar (Table 2), but the difference depended on size, as SMF was greater for seedlings and big trees of shade-tolerant species (Fig. 3d,f), but lower for small trees of shade-tolerant species (Fig. 3e). RMF variation also depended on size and, contrary to our hypothesis, it was lower for shade-tolerant than for shade-intolerant seedlings (Fig. 3g), but the difference was reversed when comparing shade-tolerant and shade-intolerant small and big trees (Fig. 3h,i). For RMF, the tolerance groups were always dissimilar (Table 2).

Biomass allocation and drought tolerance

Among DBL species, LMF tended to be greater for drought-tolerant than for drought-intolerant species, independent of size (Fig. 4a–c), but the trait spaces of tolerant and intolerant species were always nested and differences were not absolute (Table 2).

Table 2 Dissimilarity-based differences in biomass allocation fractions between tolerant and intolerant species.

		Seedlings			Small trees			Big trees		
Tolerance		LMF Tolerant	SMF Tolerant	RMF Tolerant	LMF Tolerant	SMF Tolerant	RMF Tolerant	LMF Tolerant	SMF Tolerant	RMF Tolerant
Shade										
DBL	Intolerant	$1^{n.o.}$ (dissimilar)	1* (dissimilar)	$1^{n.o.}$ (dissimilar)	$1^{n.o.}$ (dissimilar)	0.81* (divergent)	$1^{n.o.}$ (dissimilar)	$1^{n.o.}$ (dissimilar)	0.71 (nested)	$1^{n.o.}$ (dissimilar)
EBL	Intolerant	$1^{n.o.}$ (dissimilar)	1* (dissimilar)	0.33 (nested)	$1^{n.o.}$ (dissimilar)	1* (dissimilar)	1* (dissimilar)	$1^{n.o.}$ (dissimilar)	1* (dissimilar)	1* (dissimilar)
ENL	Intolerant	0.73 (nested)	1* (dissimilar)	1* (dissimilar)	1* (dissimilar)	$1^{n.o.}$ (dissimilar)	$1^{n.o.}$ (dissimilar)	1* (dissimilar)	1* (dissimilar)	$1^{n.o.}$ (dissimilar)
Drought										
DBL	Intolerant	0.41 (nested)	1* (dissimilar)	1* (dissimilar)	0.55 (nested)	1* (dissimilar)	1* (dissimilar)	0.59 (nested)	0.59 (nested)	0.97* (divergent)
EBL	Intolerant	0.94 (nested)	1* (dissimilar)	1* (dissimilar)	1* (dissimilar)	0.79 (nested)	1* (dissimilar)	1* (dissimilar)	$1^{n.o.}$ (dissimilar)	0.95* (divergent)
ENL	Intolerant	0.36 (nested)	1* (dissimilar)	1* (dissimilar)	1* (dissimilar)	$1^{n.o.}$ (dissimilar)	$1^{n.o.}$ (dissimilar)	1* (dissimilar)	1* (dissimilar)	$1^{n.o.}$ (dissimilar)

Dissimilarity values obtained from trait probability density (TPD)-based dissimilarity analysis (Carmona *et al.*, 2016, 2019) for biomass allocation fractions to leaves (LMF, $g\,g^{-1}$), stems (SMF, $g\,g^{-1}$) and roots ($g\,g^{-1}$) between tolerant and intolerant seedlings, small trees and big trees for deciduous broadleaf (DBL), evergreen broadleaf (EBL) and evergreen needleleaf (ENL) species. All contrasts are provided separately for shade and drought tolerances. * and 'n.o.' indicate when the direction of the observed response did or did not follow predictions of the optimal partitioning theory. Descriptions in italics correspond to the categories summarizing differences between intolerant and tolerant species based on the dissimilarity decomposition analysis (Carmona *et al.*, 2016, 2019; Supporting Information Notes S1). Dissimilar: complete lack of an overlap among stress tolerance groups; divergent: stress tolerance groups were only partially overlapped in the trait space, whereas the divergence threshold is set by an arbitrarily chosen dissimilarity value (≥ 0.70); nested: tolerance groups share only a portion of the trait space, but one group is entirely comprised in the probabilistic distribution of the other. More details on the classification are given in Materials and Methods section and Notes S1.

SMF was lower for drought-tolerant than for drought-intolerant seedlings and small trees (Fig. 4d,e), and the groups were dissimilar (Table 2). No absolute differences in SMF (nested variation) were observed between drought-tolerant and drought-intolerant big trees (Fig. 4f; Table 2). In agreement with our hypothesis, RMF was consistently greater for drought-tolerant than for drought-intolerant species, independent of size (Fig. 4g–i). The tolerance groups were dissimilar for seedlings and small trees and highly divergent (dissimilarity = 0.97; Table 2) for big trees, but the differences between the groups were still consistent (Fig. 4i).

In EBL species, LMF difference among drought-tolerant and drought-intolerant species was the opposite of that in DBL species. Although the variation was nested (not absolute difference) when comparing drought-tolerant and drought-intolerant seedlings (Fig. 5a; Table 2), LMF was lower for drought-tolerant than for drought-intolerant small and big trees (Fig. 5e,f), and the groups were always dissimilar (Table 2), in agreement with our hypothesis. The direction of SMF differences between tolerant and intolerant species depended on plant size. SMF was at its lowest for drought-tolerant seedlings (Fig. 5d), and at its highest for drought-tolerant big trees (Fig. 5f). In both cases, tolerant and intolerant species were dissimilar (Table 2). SMF differences between drought-tolerant and drought-intolerant species of small trees were nested (Fig. 5e; Table 2). Similarly to DBL species, and in agreement with our hypothesis, RMF was always greater for drought-tolerant than for drought-intolerant EBL species independent of size (Fig. 5g–i), and the tolerance groups were always dissimilar (Table 2).

In the case of ENL seedlings, LMF displayed nested variation, similarly to DBL and EBL seedlings (Table 2; Fig. 6a), so the differences between drought-tolerant and drought-intolerant seedlings were not absolute. LMF was lower for drought-tolerant small and big trees, compared with drought-intolerant ones (Fig. 6b,c), and the groups were always dissimilar (Table 2). SMF was lower for drought-tolerant than for drought-intolerant seedlings and big trees (Fig. 6d,f), and greater for drought-tolerant than for drought-intolerant small trees (Fig. 6e). The tolerance groups were always dissimilar for SMF values (Table 2). RMF was greater for drought-tolerant seedlings than for drought-intolerant ones (Fig. 6g), while, contrary to our hypothesis, it was lower in drought-tolerant than drought-intolerant species of small and big trees (Fig. 6h,i). For RMF, the tolerance groups were always dissimilar (Table 2).

Biomass allocation: adaptive vs acclimation responses

The differences in magnitude and direction of acclimation ($\Delta_{acclimation}$) and adaptive responses ($\Delta_{adaptation}$) of biomass allocation depended on the considered biomass fraction and PFT (Table 3). $\Delta_{acclimation}$ and $\Delta_{adaptation}$ sometimes ran in opposite directions. Averaged across seedlings of the three PFTs, $\Delta_{adaptation}$ values for LMF and RMF calculated between shade-tolerant and shade-intolerant species were -0.08 and 0.00, respectively, while $\Delta_{acclimation}$ values were 0.05 and -0.07 (Table 3). Conversely, the direction of $\Delta_{adaptation}$ calculated for RMF between drought-tolerant and drought-intolerant species

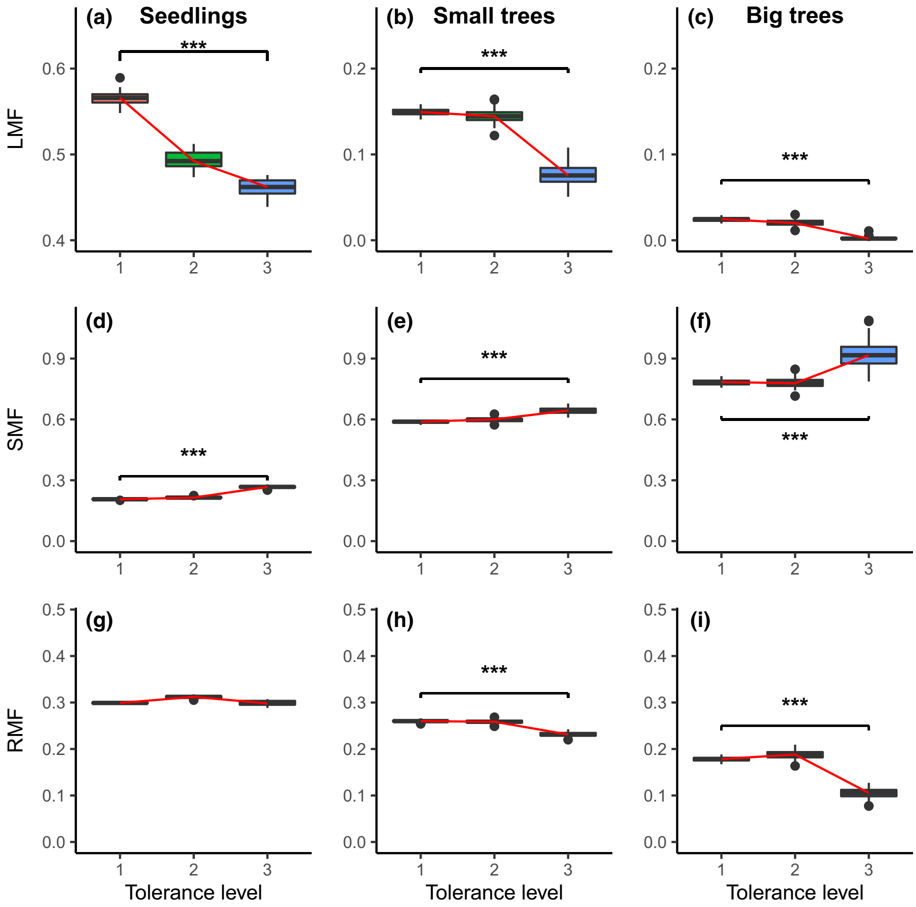

Fig. 2 Biomass allocation fractions at different shade tolerances in evergreen broadleaf species. (a–i) Boxplots summarizing medians (linked by solid red lines), interquartile range (25th and 75th percentile, box limits) and values greater than interquartile range (whisker limits) for estimates of biomass allocation fractions to leaves (LMF) (a–c), stems (SMF) (d–f) and roots (RMF) (g–i) at different shade tolerances (1, intolerant; 2, intermediate; 3, tolerant). Differences among stress tolerance groups were evaluated at three fixed values of total plant dry mass (TDM) (seedlings = 1 g; small trees = 10 kg; big trees = 10^3 kg). Biomass allocation fraction estimates were obtained from cross-validated models, n = 50. *** Indicates that tolerant and intolerant species occupy a different portion of the trait space corresponding to dissimilar (dissimilarity = 1; no overlap) or divergent (dissimilarity value ≥ 0.70 and little overlap) difference category. Details on categories are reported in the Materials and Methods section and Supporting Information Notes S1. More information on differences between tolerant and intolerant species are summarized in Table 2. All pairwise comparisons are reported in Table S5. Units are as in Table 1. Points indicate values exceeding interquartile range, but they are not used in dissimilarity calculations (see the Materials and Methods section).

coincided with that of $\Delta_{\text{acclimation}}$, but $\Delta_{\text{adaptation}}$ was smaller in magnitude (0.04) compared with $\Delta_{\text{acclimation}}$ (0.09) (Table 3).

Discussion

Our results show that – corrected for size and independent of the stress factor considered – tolerant and intolerant species occupy a different part of the trait space in terms of biomass allocation (Figs 1–6; Table 2). Despite the different position in the trait space, the direction of adaptive responses of biomass allocation often differs from predictions based on optimal partitioning theory (Tables 2, 3). Overall, the differences between tolerant and intolerant species were small compared with ontogenetic shifts (Figs 1–6). Nevertheless, the lack of trait space overlap suggests that the tolerance groups can deviate from a common size-dependent allocation pattern. These differences between tolerance groups can still be relevant from an adaptive point of view, despite the moderate magnitude. In the following, we propose three main causes for the observed patterns in biomass allocation among species with different shade and drought tolerances.

Differences between PFTs

Plant functional type was the major factor determining differences in biomass allocation patterns between tolerant and intolerant species. At PFT level, we found that biomass allocation patterns did not always agree with the predictions of the optimal partitioning theory, and, furthermore, that they often ran in opposite directions (Figs 1–6; Tables 2, 3). Species with different phylogenies (angiosperms vs gymnosperms) (Niklas & Enquist, 2002) and PFTs (Niinemets, 2010; Poorter *et al.*, 2012, 2015) inherently differ in their biomass allocation, possibly constraining

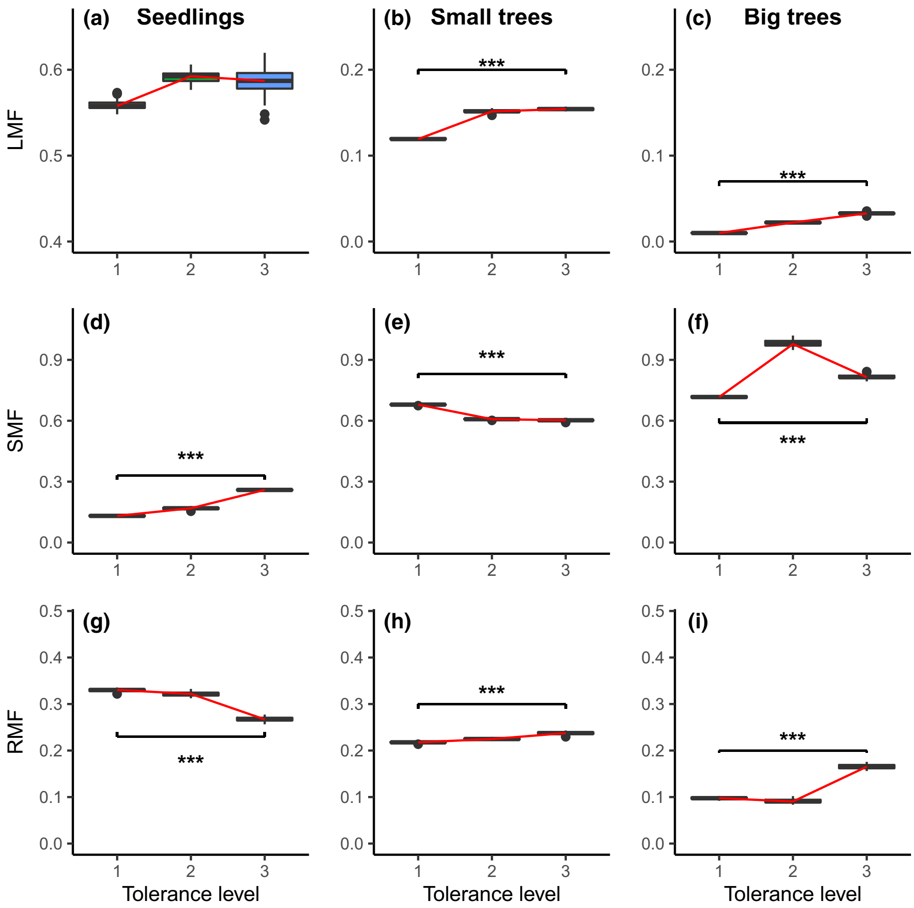

Fig. 3 Biomass allocation fractions at different shade tolerances for evergreen needleleaf species. (a–i) Boxplots summarizing medians (linked by solid red lines), interquartile range (25th and 75th percentile, box limits) and values greater than interquartile range (whisker limits) for estimates of biomass allocation fractions to leaves (LMF) (a–c), stems (SMF) (d–f) and roots (RMF) (g–i) at different shade tolerances (1, intolerant; 2, intermediate; 3, tolerant). Differences among stress tolerance groups were evaluated at three fixed values of total plant dry mass (TDM) (seedlings = 1 g; small trees = 10 kg; big trees = 10^3 kg). Biomass allocation fraction estimates were obtained from cross-validated models, n = 50. *** Indicates that tolerant and intolerant species occupy a different portion of the trait space corresponding to dissimilar (dissimilarity = 1; no overlap) or divergent (dissimilarity value ≥ 0.70 and little overlap) difference category. Details on categories are reported in the Materials and Methods section and Supporting Information Notes S1. More information on differences between tolerant and intolerant species are summarized in Table 2. All pairwise comparisons are reported in Table S5. Units are as in Table 1. Points indicate values exceeding interquartile range, but they are not used in dissimilarity calculations (see the Materials and Methods section).

the emergence of a single response pattern across PFTs. Similar to our results, Hallik *et al.* (2009) found that leaf trait covariation in species with different shade and drought tolerances strongly depend on the considered PFT. Analogously, Lusk *et al.* (2008b) found that the adaptive shade response of LMA, a trait which may codetermine LMF, was different between deciduous and evergreen angiosperms.

The differences between DBL and EBL species observed here (Figs 1, 2, 4, 5) might be mainly attributed to seasonal leaf flushing for new canopy formation for DBL species. This represents a major allocation constraint that might lead to a greater allocation to storage in DBL than in EBL species (Tomlinson *et al.*, 2013a, b). Increased allocation to storage in the roots has been suggested as a key strategy for DBL species to enhance either shade (Kobe, 1997; DeLucia *et al.*, 1998; Canham *et al.*, 1999; Piper *et al.*, 2009) or drought tolerance (Tomlinson *et al.*, 2013a,b). For example, increased allocation to storage in the roots has been proposed as a possible explanation for differences in root to shoot partitioning between communities dominated by evergreen and deciduous species (Jackson *et al.*, 1996; Tomlinson *et al.*, 2013a, b). Also, survival under shade may require a certain minimum biomass allocation to roots in DBL species (DeLucia *et al.*, 1998) providing an explanation for a greater RMF in shade-tolerant than in shade-intolerant DBL (Fig. 1g–i), while the opposite is observed for EBL species (Fig. 2g–i). The higher RMF in shade-tolerant DBL species comes at the expense of LMF (Fig. 1a–c). All these differences run counter to predictions of the optimal partitioning theory.

Analogous tradeoffs can be responsible for the observed patterns in biomass allocation among species with different drought tolerance. LMF did not vary with drought-tolerance for DBL species (Fig. 4a–c), but a greater allocation to storage in the roots

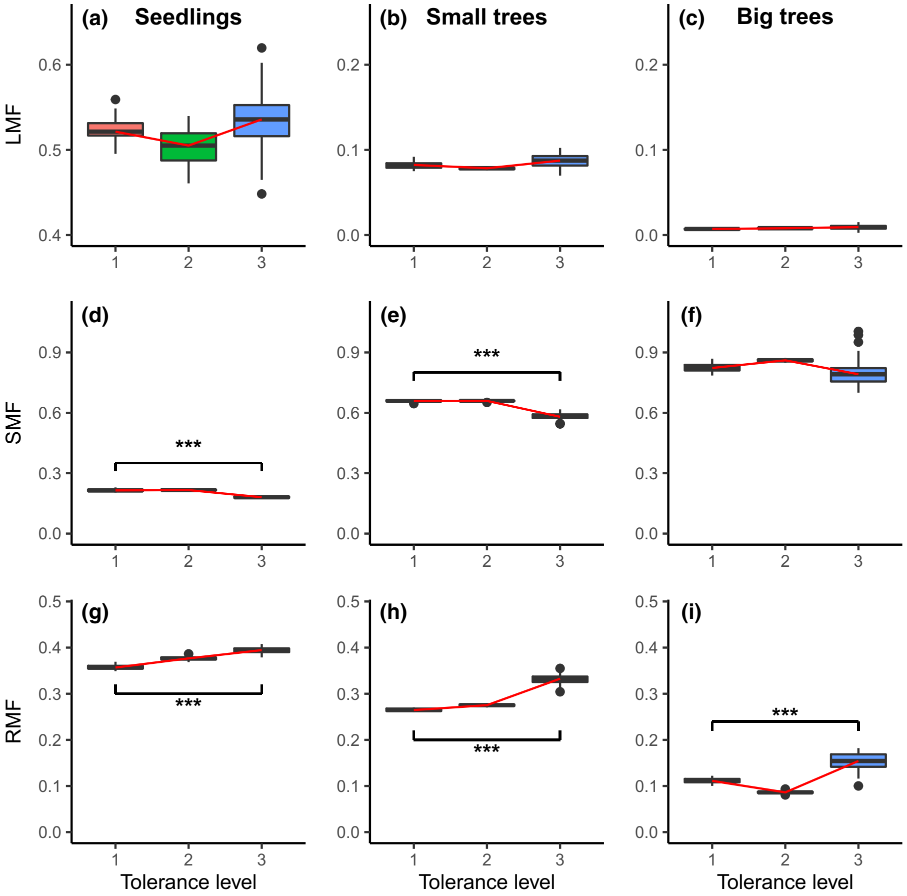

Fig. 4 Biomass allocation fractions at different drought tolerances in deciduous broad-leaved species. (a–i) Boxplots summarizing medians (linked by solid red lines), interquartile range (25th and 75th percentile, box limits) and values greater than interquartile range (whisker limits) for estimates of biomass allocation fractions to leaves (LMF) (a–c), stems (SMF) (d–f) and roots (RMF) (g–i) at different drought tolerances (1, intolerant; 2, intermediate; 3, tolerant). Differences among stress tolerance groups were evaluated at three fixed values of total plant dry mass (TDM) (seedlings = 1 g; small trees = 10 kg; big trees = 10^3 kg). Biomass allocation fraction estimates were obtained from cross-validated models, *n* = 50. *** Indicates that tolerant and intolerant species occupy a different portion of the trait space corresponding to dissimilar (dissimilarity = 1; no overlap) or divergent (dissimilarity value ≥ 0.70 and little overlap) difference category. Details on categories are reported in the Materials and Methods section and Supporting Information Notes S1. More information on differences between tolerant and intolerant species are summarized in Table 2. All pairwise comparisons are reported in Table S6. Units are as in Table 1. Points indicate values exceeding interquartile range, but they are not used in dissimilarity calculations (see the Materials and Methods section).

can partly drive the greater RMF in drought-tolerant compared with drought-intolerant DBL species (Fig. 4g–i), at the expense of SMF (Fig. 4d–f). Leaf shedding during the dry season might remain the main mechanism to enhance drought survival for DBL (Poorter & Markesteijn, 2008), rendering LMF changes unnecessary at different drought tolerances.

Conservative use of carbon resources (i.e. greater longevity of tissues) both in the shaded understorey (Walters & Reich, 1999; Lusk, 2004; Poorter, 2009; Maharjan *et al*., 2011) and in dry sites (Tomlinson *et al*., 2012) probably constitutes the dominant strategy in EBL species. Shade-tolerant EBL species are characterized by greater LMA and leaf longevity compared with shade-intolerant species (Lusk, 2004; Lusk *et al*., 2008b), and this should increase leaf retention time in the canopy (low leaf turnover rate). A greater LMF is therefore expected for shade-tolerant EBL species than for shade-intolerant EBL species. However, a greater LMA without an increase in LMF results in a reduced leaf area index at a common plant mass (LAI, Niinemets, 2010), making EBL species less competitive in shaded environments. In order for EBL species to increase LAI and be competitive in shade, LMF should increase together with LMA (Poorter *et al*., 2015). Independent of the mechanism by which EBL species are expected to increase LMF under shade, this increase was not observed here (Fig. 2a–c). This suggests that the balance between leaf production and leaf turnover rate, and maximization of LAI are are not necessarily the mechanisms determining LMF differences between shade-tolerant and shade-intolerant EBL species. It has also been suggested that differences in the proportion of leaf area exposed per unit plant dry mass (i.e. leaf area ratio, LAR = LMF/LMA) might determine the observed behaviour of shade-tolerant and shade-intolerant EBL species (e.g. Lusk, 2004), but our results also do not support this suggestion.

With regard to species differences in drought tolerance, RMF was greater for drought-tolerant EBL species than for drought-

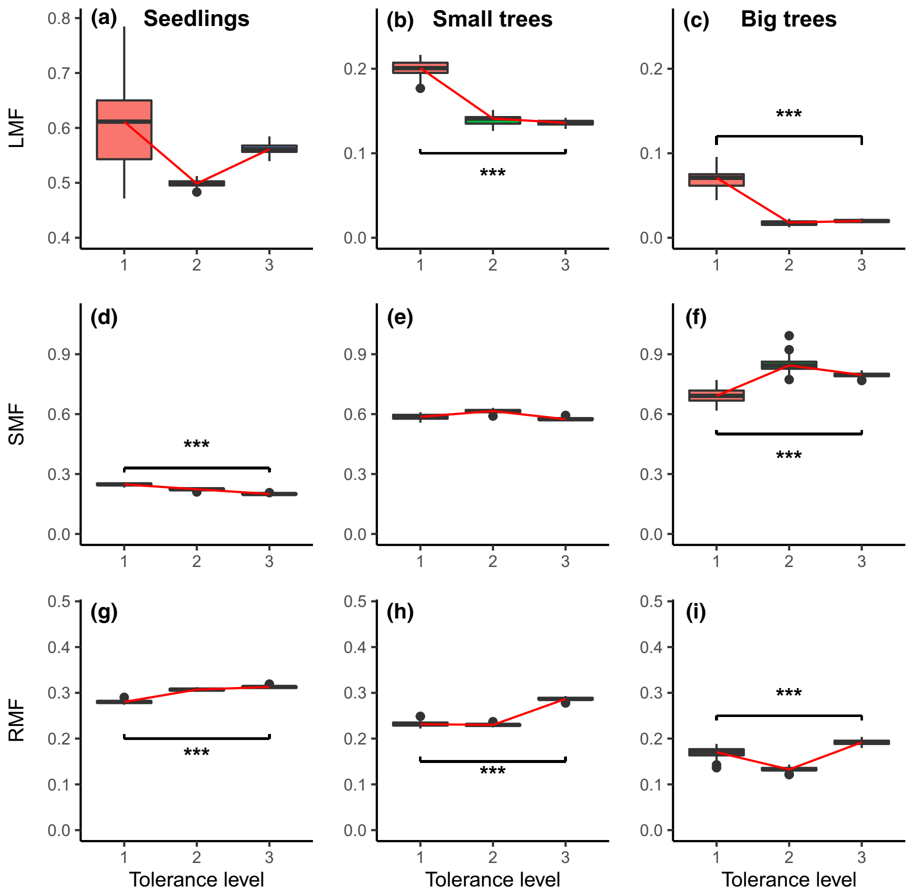

Fig. 5 Biomass allocation fractions at different drought tolerances in evergreen broad-leaved species. (a–i) Boxplots summarizing medians (linked by solid red lines), interquartile range (25th and 75th percentile, box limits) and values greater than interquartile range (whisker limits) for estimates of biomass allocation fractions to leaves (LMF) (a–c), stems (SMF) (d–f) and roots (RMF) (g–i) at different drought tolerances (1, intolerant; 2, intermediate; 3, tolerant). Differences among stress tolerance groups were evaluated at three fixed values of total plant dry mass (TDM) (seedlings = 1 g; small trees = 10 kg; big trees = 10^3 kg). Biomass allocation fraction estimates were obtained from cross-validated models, n = 50. *** Indicates that tolerant and intolerant species occupy a different portion of the trait space corresponding to dissimilar (dissimilarity = 1; no overlap) or divergent (dissimilarity value ≥ 0.70 and little overlap) difference category. Details on categories are reported in the Materials and Methods section and Supporting Information Notes S1. More information on differences between tolerant and intolerant species are summarized in Table 2. All pairwise comparisons are reported in Table S6. Units are as in Table 1. Points indicate values exceeding interquartile range, but they are not used in dissimilarity calculations (see the Materials and Methods section).

intolerant EBL species (Fig. 5g–i), in agreement with the optimal partitioning theory. At the same time, LMF (Fig. 5a–c) and SMF (Fig. 5d–f) differences depended on plant size. Architectural rearrangements during ontogeny, such as enhanced leaf clumping at shoot and canopy levels that can strongly reduce radiation interception and transpirational water losses (Valladares & Niinemets, 2008), might be a crucial factor contributing to drought-dependent biomass allocation patterns in EBL species.

Biomass allocation patterns in ENL species (Figs 3, 6) were always different from DBL and EBL species, and never in full agreement with predictions of the optimal partitioning theory. SMF difference between tolerant and intolerant ENL species always depended on plant size, regardless of the stress factor (Figs 3d–f, 6d–f). This might account for major architectural rearrangements during ontogeny in ENL species. The way ENL species differ from both DBL and EBL species might also reflect characteristic canopy and shoot architectural differences (monopodial vs sympodial, high leaf clumping vs moderate clumping) and leaf anatomical differences between gymnosperms and angiosperms (Niklas & Enquist, 2002; Niinemets, 2010; Poorter *et al.*, 2015). For instance, a high shoot silhouette : shoot total needle area ratio allows shade-tolerant ENL species to form flat shoots with lower foliage clumping. This is an important trait conferring shade-tolerance in ENL species compared with angiosperms (Niinemets, 1997, 2010; Stenberg *et al.*, 1998; Cescatti & Zorer, 2003). It is therefore reasonable to expect differences in biomass allocation patterns between ENL species on the one hand, and both DBL and EBL species on the other.

Based on the provided evidence, we argue that the differences in biomass allocation between needle- and broadleaf species run at a higher phylogenetic level (angiosperms vs gymnosperms). We also claim that the differences between DBL and EBL species might be related to the differential allocation of resources to

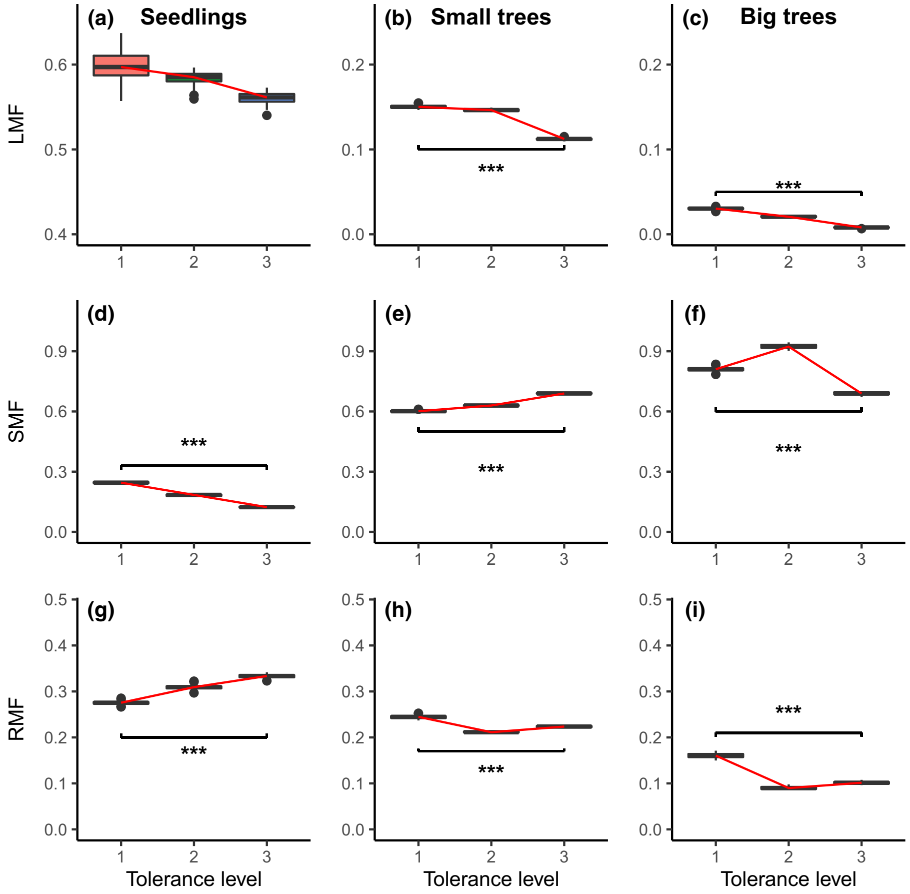

Fig. 6 Biomass allocation fractions at different drought tolerances for evergreen needle-leaved species. (a–i) Boxplots summarizing medians (linked by solid red lines), interquartile range (25th and 75th percentile, box limits) and values greater than interquartile range (whisker limits) for estimates of biomass allocation fractions to leaves (LMF) (a–c), stems (SMF) (d–f) and roots (RMF) (g–i) at different drought tolerances (1, intolerant; 2, intermediate; 3, tolerant). Differences among stress tolerance groups were evaluated at three fixed values of total plant dry mass (TDM) (seedlings = 1 g; small trees = 10 kg; big trees = 10^3 kg). Biomass allocation fraction estimates were obtained from cross-validated models, n = 50. *** Indicates that tolerant and intolerant species occupy a different portion of the trait space corresponding to dissimilar (dissimilarity = 1; no overlap) or divergent (dissimilarity value ≥ 0.70 and little overlap) difference category. Details on categories are reported in the Materials and Methods section and Supporting Information Notes S1. More information on differences between tolerant and intolerant species are summarized in Table 2. All pairwise comparisons are reported in Table S6. Units as in Table 1. Points indicate values exceeding interquartile range, but they are not used in dissimilarity calculations (see the Materials and Methods section).

storage in the roots and to the PFT-dependent suite of leaf functional traits (i.e. fast vs slow return strategy, *sensu* Wright *et al.*, 2004).

Adaptive differences vs acclimation responses

Possible presence or lack of consistent differences in biomass allocation between stress-tolerant and stress-intolerant species as predicted by the optimal partitioning theory is a long-standing debate in plant ecology (Reich, 2002). So far, the results have been contrasting, with some studies supporting the optimal partitioning theory, and others showing differences that are the opposite of the predictions or no contrast at all (Veneklaas & Poorter, 1998; Walters & Reich, 1999; Ryser & Eek, 2000; Sánchez-Gómez *et al.*, 2006; Pons & Poorter, 2014; Körner, 2018). Similarly, a recent meta-analysis of growth light responses for 70 plant traits (Poorter *et al.*, 2019) could not identify a clear shade-tolerance syndrome. Thus, at the interspecific level there is a wide spectrum of strategies that can prevent the emergence of an adaptive 'optimal' allocation pattern.

It is often assumed that interspecific adaptations, for instance to light, should parallel intraspecific phenotypic adjustments as in both cases plants have to cope with a shortage of the same resource (Givnish, 1988; Reich, 2002; Poorter & Rozendaal, 2008; Reich *et al.*, 2014). Reponses of biomass allocation at the intraspecific level (i.e. acclimation) (Table 3; see Poorter *et al.*, 2012) are more often in agreement with the optimal partitioning theory, and they can be similar between stress-tolerant and stress-intolerant species in some cases (Poorter *et al.*, 2012). Phenotypic shifts of biomass allocation along resource gradients, or at different levels of a given environmental factor, can therefore provide a limitation in defining clear adaptive responses across species at broad scale (McCarthy & Enquist, 2007), as single data points might

Table 3 Magnitude of the adaptive and acclimation responses in biomass allocation between seedlings of stress-tolerant and -intolerant species.

	Adaptive response ($\Delta_{adaptation}$)				Acclimation response ($\Delta_{acclimation}$)			
	Plant functional type	ΔLMF	ΔSMF	ΔRMF	Environmental factor	ΔLMF	ΔSMF	ΔRMF
Shade tolerance	DBL	−0.16	0.06	0.05				
	EBL	−0.10	0.06	0.00				
	ENL	0.03	0.13	−0.06				
	Mean	−0.08	0.08	0.00	Light availability	0.05	0.02	−0.07
Drought tolerance	DBL	0.01	−0.04	0.04				
	EBL	−0.05	−0.05	0.03				
	ENL	−0.03	−0.12	0.06				
	Mean	−0.03	−0.07	0.04	Water availability	−0.03	−0.06	0.09

Difference in biomass allocation fractions (Δ) to leaves (LMF, g g^{-1}), stems (SMF, g g^{-1}) and roots (RMF, g g^{-1}) between tolerant and intolerant species (adaptive response, $\Delta_{adaptation}$) for each of the three considered plant functional types (PFTs), deciduous broadleaf species (DBL), evergreen broadleaf species (EBL) and evergreen needleleaf species (ENL), and their mean values compared with the average acclimation responses ($\Delta_{acclimation}$) calculated from Poorter *et al*. (2012). Acclimation response is expressed as the difference between the value of biomass fractions measured at the lowest level of the considered resource and that measured at reference levels derived from corresponding dose--response curves (see Poorter *et al*., 2012 for further details of this methodology).

depend on the specific habitat conditions in which the given specimen was sampled.

In addition, at the intraspecific level, organ anatomy and morphology seem to be more plastic than allocation (Reich, 2002; Poorter *et al.*, 2012). This is also valid at the interspecific level, where differences between stress-tolerant and stress-intolerant species in tissue morphology and physiology are well demarcated (Reich, 2002, 2014; Wright *et al.*, 2004; Hallik *et al.*, 2009; Díaz *et al.*, 2016). Multiple compensatory morphological adaptations (e.g. changes in specific root length), that plants can recruit to overcome changes in environmental conditions, can blur differences in biomass allocation between tolerant and intolerant species (Ryser & Eek, 2000). Organ-level adaptations can be found without any differences in biomass allocation between species (McCarthy & Enquist, 2007), further underscoring the inherent limitation of applying optimal partitioning theory across species. Differences in allocation among species may also reflect opposite effects of simultaneous environmental stresses (e.g. shade vs drought) and morphological integration among plant traits that constrains trait changeability (Milla & Reich, 2011; Price *et al.*, 2014).

Plant architecture and biomass allocation

Plant architectural traits and biomechanical properties are a function of plant size (Read & Stokes, 2006) and environmental conditions (Lusk, 2002; Houter & Pons, 2012; Prado-Junior *et al.*, 2017). Inherent differences in architecture and biomechanical characteristics *per se* can limit species-specific differences in biomass allocation independently of species-specific ability to tolerate a given abiotic stress factor. This is especially true when trees grow in size and it becomes increasingly costly to add additional leaf layers at the top of the canopy or to expand laterally (Honda *et al.*, 1982; Tomlinson & Anderson, 1998). Increases in size also lead to changes in plant exposure to environmental factors within the canopy (e.g. light, wind) with major consequences for biomass allocation (Normand *et al.*, 2008). LMF differences between species can be entirely driven by changes in the vertical stratification of the canopy as plants grow in size (Niklas & Cobb, 2008; Sendall & Reich, 2013; Sendall *et al.*, 2015). Furthermore, turnover rates of leaves vs woody tissues can shape plant architecture and alter biomass allocation patterns during ontogeny for both EBL (Lusk, 2004) and DBL species (Delagrange *et al.*, 2004) under similar environmental conditions. To further complicate the matters, the turnover rates and biomass allocation patterns also depend on environmental conditions (Reich *et al.*, 2014).

Changes in size also modify plant hydraulic resistance by altering hydraulic path length and gravitational component of water potential (Wen *et al.*, 2008). A mechanism to reduce the hydraulic resistance is to lower the leaf area : sapwood area ratio (McDowell *et al.*, 2002). This can lead to alterations in species' biomass allocation, as lower leaf area : sapwood area ratio can be associated with increased biomass allocation to sapwood, and lower biomass allocation to leaves (DeLucia *et al.*, 2000). Interactions between hydraulic limitations and plant size can also occur when shade-tolerant species grow and reach the canopy and start competing for light (Ryan *et al.*, 2006).

Overall, ontogeny and environmental conditions can separately or simultaneously lead to a huge number of alternative architectural solutions that in turn shape biomass allocation patterns in woody plants, potentially uncoupling allocation from species' stress tolerance. Thus, a similar LMF-SMF-RMF combination in different species can reflect a similar architecture, rather than a similar stress tolerance.

Conclusions

Woody plant species with different shade and drought tolerance did not overlap in the trait space defined by biomass allocation fractions. However, the differences often ran in opposite directions to the acclimation responses, and thus did not always agree with predictions of the optimal partitioning theory.

We propose three main determinants for the observed differences in biomass allocation between tolerant and intolerant species at the global scale:

- Plant functional type is the main determinant of biomass allocation patterns. We found two main contrasts: differences between deciduous and evergreen angiosperms, and, at a higher phylogenetic level, between gymnosperms and angiosperms;
- Phenotypic plasticity and species-specific adaptations to tolerate stress, such as changes in organ dry mass per unit organ area, can alter differences in biomass allocation when contrasting tolerant and intolerant species. Changes in organ dry mass per unit area can happen without differences in biomass allocation;
- Convergence in plant architecture can blur biomass allocation differences, as comparable architectural features can result in similar combinations of biomass allocation fractions, independent of species' stress tolerance.

Altogether, the proposed effects allow for a variety of biomass allocation solutions across species, allowing for multiple biomass allocation strategies between shade- and drought-tolerant and -intolerant species at the global scale.

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Author Contributions

GP, LL and ÜN designed the study; HP provided the biomass data; ÜN provided the tolerance data; GP and HP planned the data analysis procedures; GP performed data analyses and wrote the first draft of the manuscript; all authors contributed to the critical revision of the manuscript to produce the final version.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Model fit for the for the relationship between biomass allocation fractions and log10-transformed total plant dry mass across all data.

Fig. S2 Summary of the cross-validation procedure.

Fig. S3 Cross-validation curves for the relationship between biomass allocation fractions and log10-transformed total plant dry mass across shade tolerance groups.

Fig. S4 Cross-validation curves for the relationship between biomass allocation fractions and log10-transformed total plant dry mass across drought tolerance groups.

Fig. S5 Examples of TPD-based dissimilarity decomposition.

Notes S1 Differences among stress tolerance groups expressed on the basis of TPD-based dissimilarity decomposition.

Table S1 List of the 604 species included in the study, their stress tolerance ranking and plant functional type classification.

Table S2 Main features of the dataset.

Table S3 Model parameters for the relationship between biomass allocation fractions and log10-transformed total plant dry mass for shade tolerance groups.

Table S4 Model parameters for the relationship between biomass allocation fractions and log10-transformed total plant dry mass for drought tolerance groups.

Table S5 Pairwise TPD-based dissimilarity decomposition among shade tolerance groups.

Table S6 Pairwise TPD-based dissimilarity decomposition among drought tolerance groups.