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Research

Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora?

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Summary

- Leaf-level determinants of species environmental stress tolerance are still poorly understood. Here, we explored dependencies of species shade (T_{shade}) and drought (T_{drought}) tolerance scores on key leaf structural and functional traits in 339 Northern Hemisphere temperate woody species.
- In general, T_{shade} was positively associated with leaf life-span (L_L), and negatively with leaf dry mass (M_A), nitrogen content (N_A), and photosynthetic capacity (A_A) per area, while opposite relationships were observed with drought tolerance. Different trait combinations responsible for T_{shade} and T_{drought} were observed among the key plant functional types: deciduous and evergreen broadleaves and evergreen conifers.
- According to principal component analysis, resource-conserving species with low N content and photosynthetic capacity, and high L_L and M_A, had higher T_{drought}, consistent with the general stress tolerance strategy, whereas variation in T_{shade} did not concur with the postulated stress tolerance strategy.
- As drought and shade often interact in natural communities, reverse effects of foliar traits on these key environmental stress tolerances demonstrate that species niche differentiation is inherently constrained in temperate woody species. Different combinations of traits among key plant functional types further explain the contrasting bivariate correlations often observed in studies seeking functional explanation of variation in species environmental tolerances.

Introduction

Plants differ widely in the tolerance of environmental stresses and resource harvesting and use (Tilman, 1988; Grime *et al.*, 1997). Such species variations in tolerance to various stresses constitute a key determinant of species segregation across environmental gradients (Bugmann, 1997; Bigelow & Canham, 2002; Cavender-Bares *et al.*, 2004). Limited light availability is a key environmental stress in temperate forests (Reich & Bolstad, 2001), and there is continuous interest in traits determining species shade tolerance (Janse-Ten Klooster *et al.*, 2007; Lusk & Warton, 2007; Valladares & Niinemets, 2008).

Stress tolerance is commonly associated with a suite of traits improving persistence and longevity, such as extended leaf life-span (L_L), large leaf dry mass per unit area (M_A), low foliage nitrogen (N) concentration (N_M), and photosynthetic capacity and low growth rates both in stressed and nonstressed conditions (Lambers & Poorter, 1992; Westoby *et al.*, 2002). Although the correlations between species shade tolerance and leaf traits have been found to confirm the general stress tolerance strategy in some studies (Kitajima, 1994; Walters & Reich, 1999; Lusk, 2004), contrasting patterns have been found in other studies, in particular, in temperate woody species (Niinemets, 2006; Janse-Ten Klooster *et al.*, 2007). Further, it is unclear how the entire suite of M_A-associated traits varies with species shade tolerance. While there is a broad consensus that shade-tolerant species have low photosynthetic capacities (Bazzaz, 1979), and negative scaling of photosynthetic capacity with shade tolerance is implemented in most forest succession models (Bugmann, 1997), this suggestion has not been tested for a broad dataset. Comparisons of photosynthetic capacity in mixed-species forest stands have failed to find a strong consistent relationship between photosynthetic capacity and shade tolerance (Bassow & Bazzaz, 1997; Niinemets *et al.*, 1998; Kazda *et al.*, 2000; Leuzinger *et al.*, 2005).

In addition to shade, multiple stresses in different combinations and severities can occur in temperate forests. Drought spells of various duration constitute a major stress operating in temperate forests (Abrams, 1994; Reich & Bolstad, 2001). Such drought episodes are traditionally considered to affect plant performance more under high irradiance, but prolonged water limitations can also be more severe for plants growing under shade (Valladares & Pearcy, 2002; Valladares *et al.*, 2008). Although the same suite of traits enhancing persistence and longevity is expected to enhance plant tolerance to low water potentials, and thus, plant drought tolerance (Abrams, 1996; Niinemets, 2001), species shade and drought tolerances have been found to be inversely associated in the Northern Hemisphere temperate woody flora (Niinemets & Valladares, 2006). Given the departure of leaf trait relations in shade-tolerant species from general stress patterns in temperate trees, it is tempting to speculate that conflicting leaf-level structural and physiological limitations are partly responsible for the trade-off between species shade and drought tolerances. For example, large leaf area common in saplings and mature trees of shade tolerant species (Niinemets, 1998; Lusk, 2004) can be achieved by increasing leaf longevity or by decreasing M_A, or by both mechanisms. While enhanced longevity can be adaptive under drought, larger evaporative surface and less robust leaves (lower M_A) are not. In a like manner, high photosynthetic capacity can maximize carbon gain during the periods intervening drought spells, and thus whole-plant carbon gain. Yet, enhanced investment of resources into proteins responsible for CO_2 fixation may jeopardize effective light harvesting and carbon gain under low light, because both high CO_2-fixation capacity and enhanced light-harvesting potential are expensive in terms of nitrogen (Evans, 1989).

There is strong convergence of leaf functioning, (i.e. occurrence of limited combinations of traits across plant kingdom defined as the global 'leaf economics spectrum'; Wright *et al.*, 2004) from fast-return strategy with leaves having intrinsically short L_L, low M_A, high N_M and high photosynthetic capacity to slow-return strategy with opposite trait values. Inherently constrained leaf structure/function variation may be ultimately responsible for different suites of traits in drought- and shade-tolerant species. At the same time, there is some space for ecological variation within the fundamental trait spectrum (Wright *et al.*, 2005a), but the effects of species ecological requirements on the trait relationships have not been analysed in detail. Filling this gap is of major significance for development of a general theory of plant functional differentiation in relation to stress tolerance.

Temperate forests consist of a complex mixture of species belonging to several plant functional types. In cool temperate forests, key plant functional types are winter-deciduous broadleaved species and evergreen conifers, while warmer temperate forests gradually become dominated by evergreen broadleaved species. Evergreen and deciduous species have fundamentally different options for coping with stress conditions. Evergreens can minimize biomass loss through longer leaf life-spans, but variation in leaf longevity among winter-deciduous species is limited by growing season length. In fact, the relationships of foliage traits with shade tolerance have been suggested to depend on plant functional type. In particular, evergreens, but not deciduous species, fit the general stress tolerance strategy (i.e. larger M_A in shade tolerators) (Lusk & Warton, 2007; Lusk *et al.*, 2008b). However, the conclusions of Lusk & Warton (2007) are based on tropical and Southern Hemisphere temperate evergreens as no studies from Northern Hemisphere temperate evergreens were included in their analysis. Given that the growing season of temperate biome is shorter than that in wet tropics, and the growing season of more continental Northern Hemisphere temperate forests is also shorter than that of more oceanic temperate forests of the Southern Hemisphere, the role of longevity and associated traits in shade tolerance can be different.

In the current study, we constructed an extensive database combining tolerances to shade and drought and key foliage functional traits for temperate Northern Hemisphere woody species, and addressed the following main questions. (1) How do species shade and drought tolerance of Northern Hemisphere temperate species depend on foliage traits? (2) Are different traits responsible for species shade and drought tolerance? (3) Are the combinations of foliar traits of different temperate plant functional types different? (4) Finally, we asked whether the variation in species drought and shade tolerance is reflected in ecological differentiation within the 'leaf economics spectrum' (i.e. whether species shade and drought tolerance can alter the bivariate leaf/structure function correlations). These are the crucial questions to ask to understand how species differing in tolerance to various environmental stresses and belonging to different plant functional types vary in light-harvesting and carbon-gain strategy. These questions are also important to gain insight into the potential variation limits of the trait relationships within the general 'leaf economics spectrum' (Reich, 1993; Diemer, 1998; Wright *et al.*, 2005a). We initially suggested simple scaling of species shade tolerance with traits improving foliar area accumulation (higher longevity, lower M_A) and drought tolerance with traits enhancing resistance to low leaf water potentials (larger M_A). We further hypothesized that drought tolerance scales with traits improving tolerance of sustained drought periods (higher longevity) and efficient use of resources during periods of high water availability (higher N content and photosynthetic capacity). The modifications in longevity were expected to play a more important role in evergreen species. The results of current study do demonstrate important correlations of species shade and drought tolerance with leaf-level traits, but also that the strength and direction of these correlations can differ between different plant functional types. The results of this study also demonstrate significant variation in trait relationships driven by species shade and drought tolerances.

Materials and Methods

Combined database of species shade and drought tolerance and leaf traits for Northern Hemisphere temperate woody species

Three primary databases were used for construction of the combined database of species tolerances and leaf traits. Species shade and drought tolerance scores (i.e. the relative values characterizing species potential to grow under given environmental limitations relative to other species) were obtained from Niinemets & Valladares (2006). Data on foliage structural and physiological traits were obtained from the databases of Niinemets (1999, 597 tree and shrub species from 182 sites) and Wright *et al.*, (2004; Glopnet database, 1978 species from 175 sites). A combined leaf structure/function database of 339 species belonging to three key plant functional types – broadleaved deciduous (DB), broadleaved evergreens (EB) and evergreen conifers (EC) – was constructed (see Appendix A1 for further details of the merged database construction). For leaf longevity, these two databases and 42 additional studies (Appendix A1, *Leaf life-span data* section) providing information for a total of 248 species were used. For the remaining 91 species, leaf longevity was estimated for deciduous species (73 species) on the basis of growing season length and the number of leaf flushes during the growing season in species' native habitats and for evergreens (5 conifers, 13 broadleaved species) by counting the average number of leaf cohorts with at least 50% foliage remaining, as detailed in Appendix A1. All statistical relationships presented in this study were qualitatively identical using the full database and the subset of data with only literature-derived estimates of leaf longevity.

As the two primary databases provided information mainly only for leaves exposed to high light levels, data for high-light leaves are included in this analysis and the effects of plasticity were not studied.

Data analyses

As L_L and M_A and the residuals of most bivariate relationships were log-normally distributed (Kolmogorov–Smirnov test), all leaf traits were $\log_{10}$-transformed to satisfy the criteria of linear statistical methods. Apart from improved normality of trait and residual distributions, log-transformation reduces the effect of observations positioned far from the mean, and is therefore a common procedure for large datasets, where trait values vary over several orders of magnitude (Wright *et al.*, 2004; Reich *et al.*, 2006; Niklas *et al.*, 2007). In our study, transformation *per se* did not alter any of our conclusions with respect to the statistical significance of the relationships.

Bivariate relationships between the traits were analysed using Pearson pairwise correlation coefficients that provide information on the strength of the statistical correlation and the sign of the relationship using the *R* statistical package (R Development Core Team, 2005). Bivariate relationships between tolerance estimates and leaf traits were studied separately for the key plant functional types (DB, EB and EC). In addition, differences among the slopes of bivariate correlations were compared by standardized major axis regressions (SMA) using the common slope test with the interaction term (SMATR for R, Warton *et al.*, 2006). Because a SMA fit is the line along the longest axis of a bivariate data cloud found by minimizing sums of squares in the *X* and *Y* dimensions simultaneously, the SMA slope describes the slope of the first component from a principal component analysis (PCA). It has been demonstrated that the probability for Type I error (i.e. rejecting the hypothesis of no difference) when comparing SMA slopes among datasets with different sample size is close to the nominal level (Warton *et al.*, 2006).

Because leaf life-span and key structural and physiological traits are correlated with each other (Wright *et al.*, 2004; Supporting Information, Notes S1 for representative relationships in this study), bivariate relationships alone provide limited information of the causal relations within the correlative network. Path analysis using the *R* statistical package (R Development Core Team, 2005) was further used to investigate the complex correlation network of tolerance, leaf longevity and leaf structural and physiological traits for the entire dataset. As area- and mass-based relationships are connected through M_A (see Hallik *et al.*, 2009 for the ways M_A can alter the correlation network between the leaf traits), we used L_L, M_A, nitrogen content per dry mass (N_M), and photosynthetic capacity per dry mass (A_M) together with the tolerance scores in the path analysis. Path analysis involves definition of a series of hypothetical causal relationships between the measured variables combined to form a directed graph, the path model (Shipley, 2000). Path models provide a useful tool to explore the comparative strength of relationships and investigate the mediating pathways, i.e. direct and indirect relationships among the variables. Initially, all physiologically possible paths (for example, M_A can drive A_M not vice versa) were allowed in the model, and this initial complex path model was further simplified by removing nonsignificant paths between leaf traits and tolerance scores. Path models represent the hypotheses about the relationships, and cannot be statistically tested for directionality (Everitt & Dunn, 2001). As there is still a debate of the cause–effect relationships in 'leaf economics spectrum'

Table 1 Comparison of tolerance estimates and leaf traits between the key plant functional types in the Northern Hemisphere temperate woody flora

	Average ± SD (sample size)[1]		
Trait	Deciduous broadleaved	Evergreen broadleaved	Evergreen conifers
Shade tolerance	2.5 ± 1.0a (244)	2.8 ± 1.0a (50)	2.8 ± 1.4a (35)
Drought tolerance	2.7 ± 1.0a (244)	3.1 ± 1.3a (50)	3.2 ± 1.3a (35)
Leaf life-span (months)	5.2 ± 1.1a (244)	24 ± 10b (50)	55 ± 26c (35)
Leaf dry mass per area (g m^{-2})	79 ± 19a (206)	144 ± 33b (42)	247 ± 80.7c (32)
Nitrogen content per leaf dry mass (%)	2.2 ± 0.5a (148)	1.33 ± 0.31b (38)	1.22 ± 0.34b (29)
Nitrogen content per leaf area (g m^{-2})	1.7 ± 0.5a (139)	1.9 ± 0.5a (37)	3.1 ± 1.0b (28)
Photosynthetic capacity per leaf dry mass (nmol g^{-1} s^{-1})	121 ± 33a (100)	64 ± 18b (24)	31 ± 9c (22)
Photosynthetic capacity per leaf area (μmol m^{-2} s^{-1})	9.6 ± 3.1a (99)	8.7 ± 2.5ab (24)	7.8 ± 2.3b (21)
Photosynthetic nitrogen use efficiency (μmol g^{-1} s^{-1})	6.1 ± 1.6a (77)	5.0 ± 1.4b (23)	2.6 ± 0.6c (22)

[1] Means with the same letter are not significantly different among the plant functional types according to ANOVA ($P > 0.05$). Multiple comparisons among the plant functional types were made with the Games–Howell test if the variance was heterogeneous, and with Tukey's test if the variance was nonheterogeneous.

(Shipley *et al.*, 2006), in particular, whether M_A drives L_L or vice versa, we use a bidirectional line for this relationship to denote the equivalent models corresponding to different hypotheses.

To analyse the correlations between species shade and drought tolerance with species position in the 'leaf economics spectrum' (the slow-return end, characterized by high leaf life-span and M_A, low N_M and photosynthetic capacity, vs the fast-return end, characterized by short leaf life-span and low M_A, high N_M and photosynthetic capacity) in simplified manner, we used PCA to reduce the multi-dimensional leaf structure/function data-set to one-dimensional principal component. The first principal component is a linear combination of the traits describing the maximum variance in the dataset, as described by Wright *et al.* (2004). As with the path analysis, four log-transformed traits, L_L, M_A, N_M and A_M, were included in the analysis. The resulting first principal component described 83% of total variance. We further used the Rubin–Anderson method to determine the standardized factor score for each species. The resulting factor score that has a mean of 0 and standard deviation of 1 describes the position of given species along this PCA axis. This factor score was further used as a variable in subsequent correlation analyses with shade and drought tolerance ranks. As our goal was to estimate the species positions along the broad spectrum, PCA was conducted only on pooled data. The PCA was performed using SPSS ver. 8.0 (SPSS Inc., Chicago, IL, USA). In addition, to evaluate the effect of varying tolerance on specific relationships, bivariate correlations describing 'leaf economics spectrum' (e.g. L_L vs M_A, L_L vs A_M) were fitted separately with standardized major axis regressions for species with given tolerance score > 3.5 (high tolerance) and < 2 (low tolerance), and the slopes and intercepts of these regressions were compared among these groups by SMATR for R (Warton *et al.*, 2006). All statistical tests were considered significant at $P < 0.05$.

Results

General characteristics of the dataset

As in the full tolerance dataset of more than 800 Northern Hemisphere temperate species (Niinemets & Valladares, 2006), in our combined tolerance and traits database including 339 species (Appendix A1), T_{shade} and $T_{drought}$ were negatively correlated ($r = -0.19$, $P < 0.001$). The average L_L varied 42-fold, M_A varied 10-fold, N_M varied 5-fold and A_M varied 15-fold (Appendix A1, Table S1). For the entire dataset, all relationships among foliage structural and functional traits were as expected, confirming the global 'leaf economics spectrum' (Wright *et al.*, 2004) (i.e. negative scaling of Log A_M and Log N_M with Log M_A and Log L_L, and a positive scaling between Log L_L and Log M_A; Notes S1). The correlation coefficients of bivariate leaf trait relationships in our dataset were very similar to those observed in the Glopnet database (Wright *et al.*, 2004; Notes S1).

The key plant functional types – decideous broadleaved (DB), evergreen broadleaved (EB) and evergreen conifers (EC) – did not differ in average shade tolerance score, but species in EC group were, on average, more drought tolerant than the species in the DB group (Table 1). However, the span of drought tolerance scores was similar among the functional groups (Fig. 1). Group ranking according to L_L and M_A was DB < EB < EC, while the ranking was reversed, although less clear-cut, for mass-based chemical and physiological traits (Table 1). The key plant functional types were clearly separated in bivariate leaf structure/function relationships (Notes S1). The DB species had high N_M and A_M, short L_L and low M_A (fast-return end of the 'leaf economics spectrum'), and EC species had low N_M and A_M, long L_L and high M_A (slow-return end of the 'leaf economics spectrum', while EB species had intermediate values (Notes S1). The differences in M_A among the functional types were sufficiently large to completely reverse

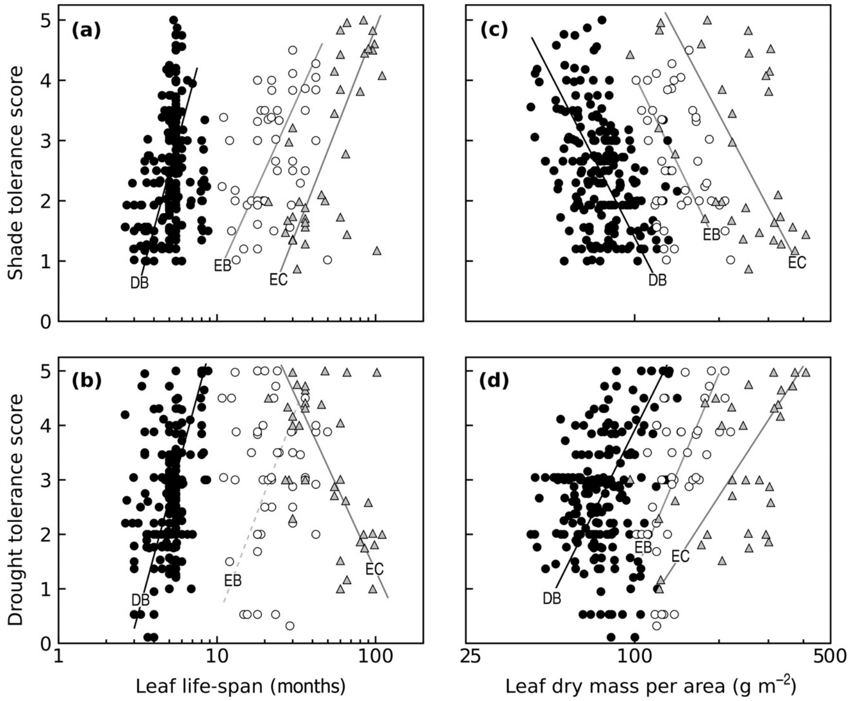

Fig. 1 Bivariate correlations of plant shade (T_{shade}, a,c) and drought (T_{drought}, b,d) tolerance scores with average leaf life-span (L_L, a,b) and leaf dry mass per area (M_A, c,d) in Northern Hemisphere temperate woody species. The combined dataset consisting of 339 species (see Appendix A1) is based on the database of Niinemets & Valladares (2006) for shade and drought tolerance and mainly on databases of Niinemets (1999) and Wright *et al*. (2004; Glopnet database) for leaf traits. Data were separately fitted by standardized major axis regressions for key plant functional types: broadleaved deciduous (DB, closed circles), broadleaved evergreen (EB, open circles) angiosperms and evergreen conifers (EC, triangles). L_L and M_A were log-transformed. Sample sizes for each plant functional type are provided in Table 1, and pairwise correlation coefficients and corresponding regression slopes for the relationships depicted are provided in Table 2 (T_{shade}) and in Table 3 (T_{drought}). A nonsignificant relationship in (b) is shown by a dashed line.

the group rankings according to mass-based and area-based nitrogen contents ($N_A = M_A N_M$). For area-based photosynthetic capacity ($A_A = M_A A_M$), group differences observed for A_M almost vanished (Table 1). The bivariate correlations among leaf traits within plant functional types were much weaker than for the pooled data (Notes S1).

Bivariate relationships with shade tolerance rankings

For all data pooled, species shade tolerance (T_{shade}) score was positively correlated to L_L and negatively to M_A (Fig. 1a,c; Table 2). The correlations of T_{shade} with N_M and A_M were nonsignificant (Fig. 2a, Table 2). Owing to the negative scaling of T_{shade} with M_A, N_A and A_A were both negatively associated with T_{shade} (Fig. 2c, Table 2).

There were broad similarities among the three plant functional types in the correlative networks of T_{shade} vs leaf traits, but also several important differences. In the DB group, leaf nitrogen content per area (Table 2) and photosynthetic capacity both per mass and area (Fig. 2a,c, Table 2) were negatively related to T_{shade}. By contrast, in the EB group, neither nitrogen contents nor photosynthetic capacities per area and mass were associated with T_{shade}. In the EC group, A_M was positively correlated with T_{shade} (Table 2, Fig. 2a). Despite these nonsignificant patterns for these plant functional types, the scaling slopes did not differ significantly among the groups for M_A, N_A, and A_A vs T_{shade} relationships (Figs 1c, 2c, Table 2). By contrast, the scaling slopes of L_L, A_M, and photosynthetic nitrogen use efficiency (A_M/N_M) vs T_{shade} differed among the groups (Fig. 1a, Table 2). In particular, the correlation of A_M vs T_{shade} had opposite signs for DB and EC groups (Fig. 2a, Table 2).

Bivariate relationships with drought tolerance rankings

For all data pooled, species drought tolerance (T_{drought}) score scaled positively with L_L, M_A, N_A and A_A, and negatively with N_M and A_M (Figs 1b,d, 2b,d, Table 3). Thus, the variation in M_A was stronger than in N_M and A_M, resulting in positive scaling of T_{drought} with A_A and N_A.

Within the key plant functional groups, only M_A was positively correlated to T_{drought} within each functional group (Fig. 1d, Table 3) and the scaling slopes were not significantly different among the functional groups (Table 3). By contrast, the relationship of L_L vs T_{drought} was positive in the DB group, not significant in the EB group, and negative in the EC group (Fig. 1b, Table 3), such that the scaling slopes of L_L vs T_{drought} differed among the plant functional types (Table 3). In the DB group, leaf nitrogen content per area (Table 3) and photosynthetic capacity both per mass and area (Fig. 2b,d) were positively related to T_{drought} (Table 3). In both the EB and EC groups, A_M scaled negatively with T_{drought} (Fig. 2b, Table 3). Despite the nonsignificant relationships for some plant functional types, the scaling slopes of N_M, N_A, and A_A relationships did not differ significantly between the groups (Fig. 2d, Table 3). By contrast, the relationships of T_{drought} with A_M and A_M/N_M had different scaling slopes (Fig. 2b, Table 3).

Path analysis

The results of the path analysis with pooled data of 339 species showed that among the four key leaf traits L_L, M_A, N_M and A_M, mainly L_L and M_A influenced the species tolerance to shade and drought. The direct effect of L_L was to increase

Table 2 Pearson correlation coefficients (*r*) and standardized major axis regression slopes (η) of leaf traits (all traits log-transformed) vs shade tolerance, and sample size (*n*) for all data pooled and for major plant functional types in Northern Hemisphere temperate woody flora[1]

Shade tolerance	All data pooled			Deciduous broadleaved			Evergreen broadleaved			Evergreen conifers		
vs log-transformed leaf trait	*r*	η	*n*	*r*	η	*n*	*r*	η	*n*	*r*	η	*n*
Leaf life-span (months)	**0.21*****	8.57	339	**0.30*****	9.82a	244	**0.33***	5.82b	50	**0.68*****	6.74b	35
Dry mass per area (g m^{-2})	**–0.12***	–9.01	289	**–0.39*****	–9.05a	206	**–0.36***	–9.56a	42	**–0.49****	–8.80a	32
N content per dry mass (%)	–0.07ns	–9.48	224	–0.16ns	–9.25a	148	0.01ns	10.16b	38	0.31ns	12.73b	29
N content per area (g m^{-2})	**–0.26*****	–7.94	212	**–0.47*****	–8.03a	139	–0.25ns	–7.64a	37	–0.25ns	–8.86a	28
Photosynthetic capacity per leaf dry mass (nmol g^{-1} s^{-1})	–0.04ns	–8.70	149	**–0.47*****	–8.67a	100	0.21ns	7.56b	24	**0.56****	9.38b	22
Photosynthetic capacity per leaf area (μmol m^{-2} s^{-1})	**–0.42*****	–7.27	149	**–0.61*****	–6.95a	99	–0.20ns	–6.96a	24	–0.05ns	–9.56a	21
Photosynthetic nitrogen use efficiency (μmol g^{-1} s^{-1})	0.04ns	8.57	125	–0.19ns	–7.97a	77	0.13ns	7.50b	23	**0.50***	12.65b	22

[1] Statistical significance as: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant. Bold font denotes statistically significant η values. Slopes with the same letter are not significantly different ($P > 0.05$).

Table 3 Pearson correlation coefficients (*r*) and standardized major axis regression slopes (η) of leaf traits (all traits log-transformed) vs drought tolerance for pooled data and for key plant functional types in the Northern Hemisphere temperate woody species[1]

Drought tolerance	All data pooled		Deciduous broadleaved		Evergreen broadleaved		Evergreen conifers	
vs log-transformed leaf trait	*r*	η	*r*	η	*r*	η	*r*	η
Leaf life-span (months)	**0.18*****	9.91	**0.40*****	10.73a	0.04ns	7.78a	**–0.56*****	–6.34b
Dry mass per area (g m^{-2})	**0.30*****	10.33	**0.23*****	10.34a	**0.53*****	12.21a	**0.53****	7.93a
Nitrogen (N) content per dry mass (%)	**–0.21****	–9.77	**–0.17***	–9.32a	–0.15ns	–12.38a	–0.23ns	–11.88a
N content per area (g m^{-2})	**0.28*****	8.30	**0.20***	8.29a	0.29ns	9.35a	0.37ns	8.05a
Photosynthetic capacity per leaf dry mass (nmol g^{-1} s^{-1})	**–0.24****	–9.53	**0.21***	9.10a	**–0.46***	–11.00b	**–0.55****	–9.24b
Photosynthetic capacity per leaf area (μmol m^{-2} s^{-1})	**0.22****	8.07	**0.35*****	7.28a	0.004ns	10.12a	0.29ns	9.11a
Photosynthetic nitrogen use efficiency (μmol g^{-1} s^{-1})	–0.14ns	9.47	**0.29***	8.44a	–0.31ns	–10.91b	**–0.52***	–12.45b

[1] Sample sizes and statistical significance as in Table 2.

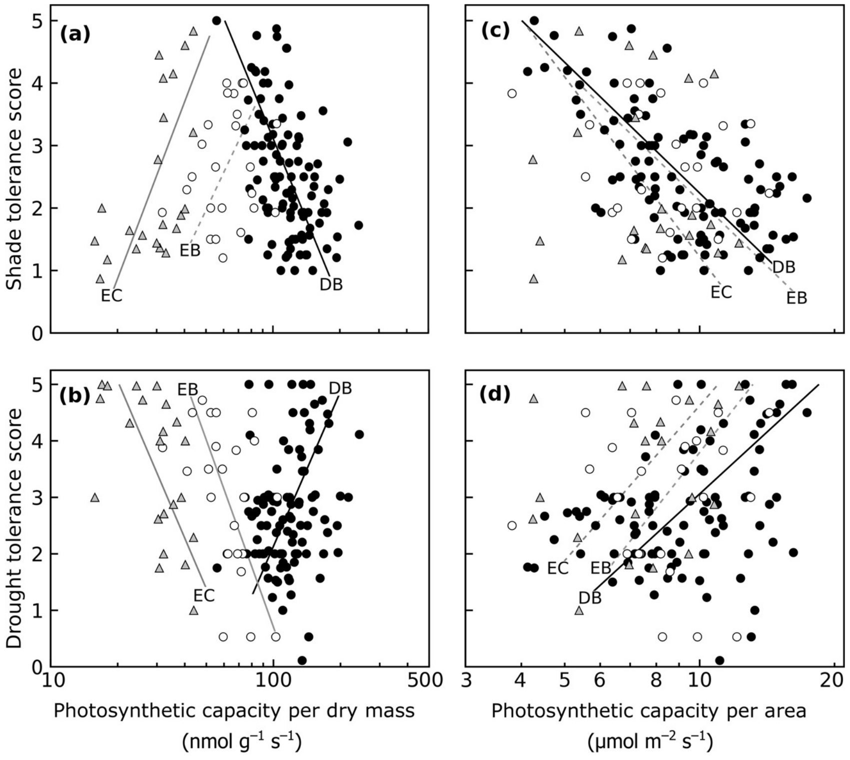

Fig. 2 Relationships of plant shade (T_{shade}, a,c) and drought ($T_{drought}$, b,d) tolerance scores with photosynthetic capacity per unit dry mass (A_M, a,b) and per unit area (A_A, c,d) in the Northern Hemisphere temperate woody species (the same dataset as in Fig. 1). As in Fig. 1, the data are separately fitted by major axis regressions for broadleaved deciduous (DB, closed circles), broadleaved evergreen (EB, open circles) angiosperms and evergreen conifers (EC, triangles). Both A_M and A_A were log-transformed. Pairwise correlation coefficients and the major axis regression slopes for the relationships are given in Tables 2 (T_{shade}) and 3 ($T_{drought}$). Nonsignificant relationships are shown by a dashed line.

T_{shade} and to reduce $T_{drought}$, while M_A was negatively associated with T_{shade} and positively with $T_{drought}$. At the same time, L_L and M_A were positively related to each other (Fig. 3). These results illustrate the controversial relationships between M_A and T_{shade} reported in literature, as the positive association between L_L and M_A combined with the positive effect of L_L on T_{shade} can weaken (as in our data) or completely overshadow the negative relationship between species-specific M_A and T_{shade}. While species-specific shade and drought tolerances were governed by the opposite effects of L_L and M_A in the path analysis, the effects of L_L and M_A on the other traits forming the 'leaf economics spectrum', N_M and A_M, were similar (Fig. 3).

These results further complement the bivariate analyses, in particular, underscoring the circumstance that the correlations between tolerance scores and N_M and A_M are indirect, and the relationships between tolerances and area-based nitrogen content and photosynthetic capacity are driven by variation in M_A rather than by variation in N_M and A_M (Tables 2, 3, Fig. 3).

'Leaf economics spectrum' in relation to the tolerance scores

'Leaf economics spectrum' is defined as the coordinated variation among leaf traits running from a slow-return suite of traits (high M_A and L_L and low N_M and A_M) to a fast-return suite of traits (low M_A and L_L and high N_M and A_M) (Wright *et al.*, 2004). To evaluate the extent to which species shade tolerance scores can alter the bivariate correlations between leaf traits, the pooled dataset of 339 species was divided into three tolerance classes: high tolerance with a tolerance score > 3.5, low tolerance with a tolerance score < 2, and intermediate tolerance class with tolerance values between these two classes. Species with high and low T_{shade} had similar standardized major axis slopes of M_A vs L_L, but more shade-tolerant species had lower M_A at given L_L (Fig. 4a), while the slope of L_L vs A_M was significantly deeper for species with lower T_{shade} (Fig. 4b). The scaling slopes of these relationships (Fig. 4c,d) were significantly deeper for species with high $T_{drought}$ relative to species with low $T_{drought}$. The patterns outlined were intermediate for the mid-tolerance class (data not shown). These data collectively indicate that species variation in tolerance does affect the bivariate scaling relationships between foliage structural and functional traits.

Principal component analysis (PCA) was conducted with the pooled data using the key log-transformed leaf traits L_L, M_A, N_M and A_M. The first principal component described 83% of total variance and factor scores along the first axis were further used to assess the correlations with individual leaf traits. Correlations between leaf characteristics and factor scores demonstrated that the individual leaf traits were generally related to 'leaf economics spectrum' similarly in pooled data and within each functional type, although the relationships were weaker within the functional types (Table 4). The comparison of species tolerance rankings with factor scores from the first PCA axis showed that species shade-tolerance ranking was not significantly related to its position along the 'leaf economics spectrum' (Fig. 5a, Table 5), reflecting the essentially equal, but opposite effects of L_L and M_A on T_{shade} (Fig. 3).

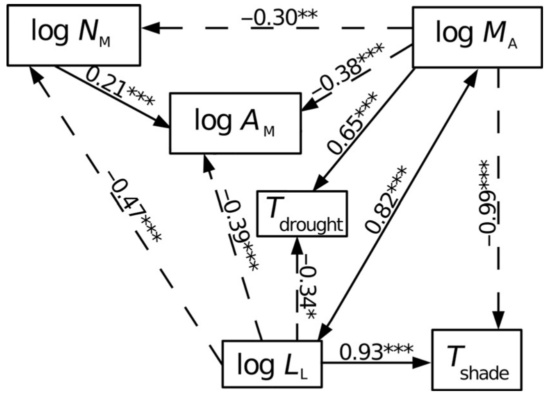

Fig. 3 Path diagram to assess how leaf life-span (L_L), leaf dry mass per area (M_A), nitrogen content per leaf dry mass (N_M) and photosynthetic capacity per leaf dry mass (A_M) influence species shade (T_{shade}) and drought ($T_{drought}$) tolerances in Northern Hemisphere temperate woody species (the same dataset as in Fig. 1; see Appendix A1 for species and key traits). Leaf traits were log-transformed. The model was tested with likelihood ratio χ^2 test: $\chi^2 = 5.60$ (df = 5), $P = 0.35$ (probability that the covariance matrix implied by the model differs from the observed covariance matrix), goodness-of-fit index = 0.985. Path coefficients were calculated based on standardized values, and negative paths are marked by dashed lines. Asterisks denote significance: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. Nonsignificant ($P > 0.05$) paths ($T_{shade} \leftrightarrow T_{drought}$; $N_M \rightarrow T_{drought}$; $N_M \rightarrow T_{shade}$; $A_M \rightarrow T_{drought}$ and $A_M \rightarrow T_{shade}$) were excluded from the model.

Drought tolerance showed a tendency to run parallel with variation in 'leaf economics spectrum', but this covariation was more apparent within the functional types than for the entire dataset (Fig. 5b, Table 5).

Discussion

Plant shade tolerance is dependent on foliage traits

Understanding the suites of traits responsible for species tolerance to environmental stresses is of key significance for quantitative prediction of ecosystem functioning (Lavorel & Garnier, 2002). Correlations of temperate species shade tolerance with foliage structure have long been postulated (Jackson, 1967). Although the literature on the subject is huge, the patterns reported are contrasting. For example, leaf dry mass per area (M_A) has been observed to be positively or negatively associated with species shade tolerance (T_{shade}), partly as the result of modification of M_A ranking during species ontogeny from seedlings to mature plants (Niinemets, 2006; Valladares & Niinemets, 2008).

Correlations among the traits further complicate the patterns, especially for species sets with widely varying longevity, as is common in the Northern Hemisphere temperate forests where evergreen and deciduous species coexist. In our study, the bivariate relationships with T_{shade} were generally weak for the pooled dataset (Table 2). Bivariate relationships highlighted a positive broad correlation of T_{shade} with foliage longevity (Fig. 1a), agreeing with previous observations from temperate and tropical ecosystems (Kitajima, 1994; Lusk & Warton, 2007). By contrast, foliage photosynthetic capacity and nitrogen content per area decreased with T_{shade} (Table 2, Fig. 2c), again concurring with the evidence from temperate and tropical ecosystems (Kitajima, 1994; Reich *et al.*, 2003). However, as the path analysis demonstrated (Fig. 3), these correlations within the pooled dataset were the result of a complex

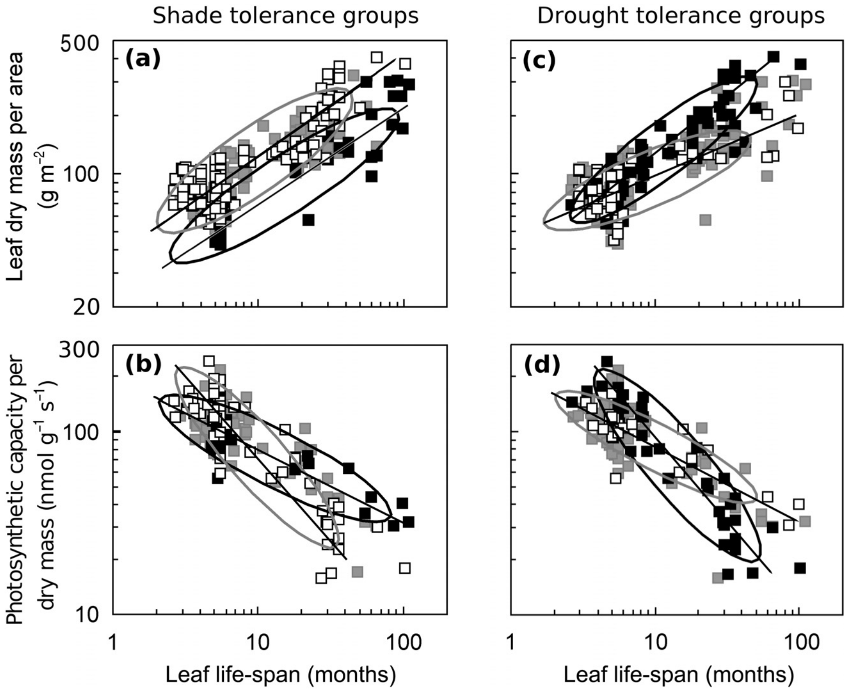

Fig. 4 Relationships of leaf dry mass per area (a,c) and photosynthetic capacity (b,d) with leaf life-span for Northern Hemisphere temperate woody species (the same dataset as in Fig. 1; see Appendix A1 for species). Data were distributed between three groups: high tolerance (tolerance > 3.5, closed squares), low tolerance (tolerance < 2, open squares) and intermediate tolerance (2 ≥ tolerance ≤ 3.5, tinted squares). Separate major axis regressions are shown for the high and low tolerance groups. Ellipses denote the 68% confidence intervals (± SD) (Sokal & Rohlf, 1995 for calculating the confidence intervals for major axis regressions). All plant functional types were fitted simultaneously. (Notes S1 demonstrates the separate relationships for different plant functional types (Fig. S1).)

Table 4 Pearson correlation coefficients between key leaf traits (all log-transformed) and Anderson–Rubin factor scores from the first axis of principal component analysis (PCA)[1] for pooled data, and for key plant functional types in Northern Hemisphere temperate woody species

Log-transformed leaf trait	All data pooled	Deciduous broadleaved	Evergreen broadleaved	Evergreen conifers
Leaf life-span (L_L, months)	0.93***[2]	0.59***	0.52*	0.30ns
Dry mass per area (M_A, g m^{-2})	0.92***	0.66***	0.61**	0.70***
Nitrogen (N) content per dry mass (N_M, %)	–0.86***	–0.84***	–0.60**	–0.72***
Photosynthetic capacity per leaf dry mass (A_M, nmol g^{-1} s^{-1})	–0.94***	–0.62***	–0.84***	–0.82***

[1] PCA for all data pooled was conducted using the four key log-transformed leaf traits (L_L, M_A, N_M, A_M). The first axis explained 83% of the variation in the total data set and it has been traditionally interpreted as 'leaf economics spectrum' (Wright *et al.*, 2004). For different plant functional types, separate PCAs were not performed, but the correlation coefficients were calculated between leaf traits within functional types and the factor scores from PCA conducted with pooled data.

[2] Statistical significance: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, not significant.

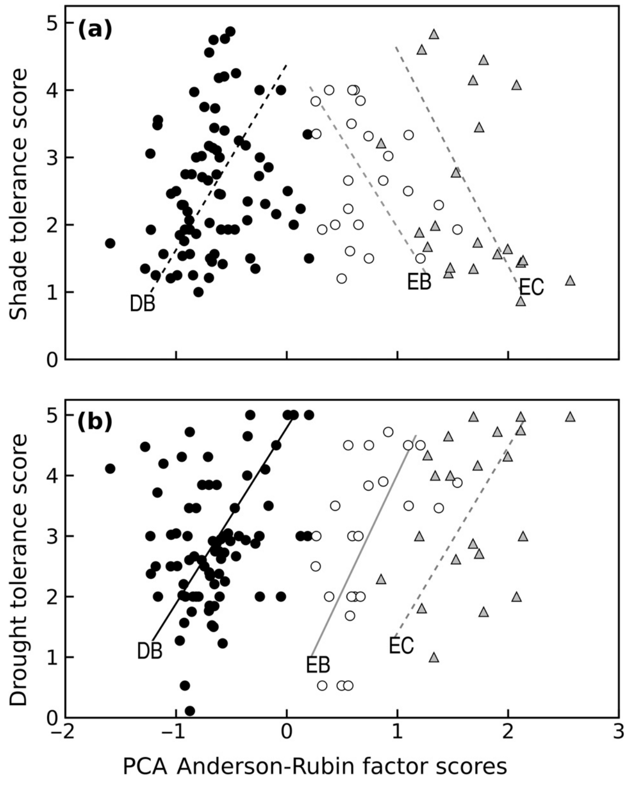

Fig. 5 Relationships of plant shade (T_{shade}) and drought ($T_{drought}$) tolerance scores of Northern Hemisphere temperate woody species (see Appendix A1, all plant functional types pooled) with the first principal component factor score of 'leaf economics spectrum' (covariation among leaf traits, Supporting Information, Notes S1) calculated according to Anderson–Rubin method. The principal component analysis (PCA) was conducted with four log-transformed leaf traits: leaf life-span, leaf dry mass per area, leaf nitrogen content per dry mass and photosynthetic capacity per dry mass. Data were fitted separately by standardized major axis regressions for key temperate plant functional types: broadleaved deciduous (DB, closed circles), broadleaved evergreen (EB, open circles) and angiosperms and evergreen conifers (EC, triangles). Table 4 provides the pairwise correlation coefficients and the major axis regression slopes for the relationships depicted. Nonsignificant relationships ($P > 0.05$) are shown by a dashed line.

correlation network within the trait space. These correlations between foliar traits masked some of the effects of leaf traits on tolerance and affected the strength of correlations within the pooled set of data. For example, bivariate correlations suggested a minor effect of M_A on T_{shade}, but a strong negative direct effect of M_A was evident when the other factors were controlled by path analysis (Fig. 3).

Lack of some relevant traits in our analysis owing to low data coverage can affect the conclusions on the importance of foliage traits in species tolerance of key environmental stresses. In particular, respiration rate has been implicated as a major driver of shade tolerance (Walters & Reich, 2000b), although other studies demonstrate that dark respiration is not always strongly associated with tolerance (Walters & Reich, 1999; Lusk & Reich, 2000). Furthermore, correlations of respiration rate with other plant traits, such as nitrogen and photosynthetic capacity, complicate the patterns and may partly explain the study-to-study differences. According to the path analysis, respiration rate was not a significant predictor of shade tolerance for 14 temperate species (Janse-Ten Klooster *et al.*, 2007).

Shade tolerance vs leaf traits in different plant functional types

Within the general patterns of longer L_L, lower M_A, lower N_A and lower A_A in more shade-tolerant species, different plant functional types had specific trait combinations (Table 1). As a result, the strength, and in some cases the sign of bivariate correlations varied among the plant functional types (Table 2). Lower M_A in shade-tolerant species has been postulated to be an important adaptive trait allowing the species to construct a larger foliar area with a given fraction of plant mass in leaves (Givnish, 1988). Previously, a negative relationship of leaf thickness and M_A with shade tolerance has been observed for saplings and mature trees of winter-deciduous temperate species (Jackson, 1967; Niinemets & Kull, 1994; Janse-Ten Klooster *et al.*, 2007; for a meta-analysis see Lusk & Warton, 2007). However, as shade tolerance is also driven by L_L that in turn is positively associated with M_A (Wright *et al.*, 2004), the

Table 5 Pearson correlation coefficients (*r*) and standardized major axis regression slopes (η) of the relationships between the numerical tolerance scores and the Anderson–Rubin factor scores of the first axis of the principal component analysis (PCA)[1] for pooled data and for the major plant functional types of Northern Hemisphere temperate species

PCA factor score	All data pooled		Deciduous broadleaved		Evergreen broadleaved		Evergreen conifers	
vs	*r*	η	*r*	η	*r*	η	*r*	η
Shade tolerance	–0.02ns[2]	2.81	0.19ns	2.75a	–0.27ns	–2.64b	–0.33ns	–3.20b
Drought tolerance	**0.29****	3.13	**0.27***	2.90a	**0.56****	3.87a	0.42ns	3.07a

[1] Principal component analysis was conducted on four log-transformed leaf traits (leaf life-span, leaf dry mass per area, leaf nitrogen per dry mass and photosynthetic capacity per leaf dry mass) with the pooled data (see the Supporting Information, Notes S1, for the bivariate correlations). The first axis explained 83% of the variation in the total data set and it has been traditionally interpreted as 'leaf economics spectrum' with slow-return species having high dry mass per area (M_A) and leaf life-span (L_L) and low photosynthetic capacity per leaf dry mass (A_M) and nitrogen content per dry mass (N_M), and fast-return species having the opposite suite of traits (Wright *et al*., 2004). See also Table 4 for more information on PCA.

[2] Statistical significance: **, $P < 0.01$; *, $P < 0.05$; ns, not significant. Significant *r* values are shown in bold font. Slopes with the same letter are not significantly different between the functional types ($P > 0.05$).

relationship of M_A vs shade tolerance has been suggested to be positive in evergreen species (Lusk *et al.*, 2008b). According to the global meta-analysis, M_A did scale positively with shade tolerance in the Southern Hemisphere evergreens (Lusk & Warton, 2007), but this analysis did not include the Northern Hemisphere temperate evergreens. We found that M_A of both the Northern Hemisphere temperate broadleaved evergreen angiosperms and evergreen conifers was lower in more shade-tolerant species (Table 2). Given that the growing season length of cool temperate conifers and winter-deciduous species may be similar (Schulze *et al.*, 1977; Schulze, 1981), the cost of producing leaves with high M_A in cool temperate evergreens may be too high to be compatible with enhanced shade tolerance. However, broadleaved evergreen angiosperms from warm temperate Northern Hemisphere commonly sustain a significant drought period during the growing season (Mooney, 1983). Drought with cold winters on continental sites reduces the effective growing season length and can make the cost of leaves with high M_A prohibitively expensive under shade.

The strength of bivariate correlations between L_L and shade tolerance score varied with the mean L_L of the functional group, being strongest in evergreen conifers with the longest leaf life-span (Table 1; see also Wright *et al.*, 2005b for the overview of the variations in leaf traits within the functional groups in the Glopnet database), and the weakest in deciduous broadleaved species. Winter-deciduous species obviously cannot markedly enhance leaf life-span, and are bound to use other ways to cope with resource limitation. Within the DB group in our data, shade tolerance was negatively correlated with leaf nitrogen content and photosynthetic capacity (both mass- and area-based). Such relationships did not occur among evergreen groups with longer leaf life-spans and lower photosynthetic capacities. This evidence suggests that deciduous broadleaved species, which generally have high photosynthetic capacities, but limited variation in L_L, achieve shade tolerance by reducing the cost of production of a unit of leaf tissue with given investment of nitrogen in leaves. While this modification, together with lower M_A, results in larger foliar area, it results in reduced leaf assimilation capacity. In addition, to reduce damage by herbivores that may be particularly devastating under low light where carbon is in short supply, leaves must have low palatability. In addition to structural toughness achieved by enhanced M_A and 'high cost' defense chemicals such as condensed phenolics, leaf palatability scales positively with leaf nitrogen content (Matsuki & Koike, 2006). Hence, lower leaf nitrogen content of shade-tolerant deciduous species that likely have lower structural protection, owing to lower M_A, can be an important adaptive feature reducing the risk of herbivore attack. In addition, protein turnover constitutes a significant carbohydrate cost for the plants (Noguchi *et al.*, 2001). Thus, low nitrogen content may also be an important part of the suite of traits reducing foliage respiration rate and light compensation point in the shade tolerators (Walters & Reich, 2000b; Craine & Reich, 2005). Overall, such simultaneous reductions in M_A, nitrogen and photosynthetic capacity in broadleaved winter-deciduous species are contrary to broad-scale patterns (Wright *et al.*, 2004) and suggest that there is more room for different strategies within the broad relationships than has been previously thought (Wright *et al.*, 2005a, see below).

Drought tolerance vs leaf traits

Correlations between leaf drought tolerance and foliage structural and physiological traits have frequently been reported (Abrams, 1994; Abrams *et al.*, 1994; Niinemets, 2001). Larger M_A, as often observed in species from drier environments (Niinemets, 2001; Wright & Westoby, 2002), was confirmed for the entire dataset in our study (Table 3, Fig. 1d). Such a larger M_A implies more robust leaf structure, allowing drought-tolerant species to sustain lower water potentials before leaf structural collapse and xylem cavitation, and extract water from dry soil with lower leaf water loss (for a discussion see Niinemets, 2001).

Larger M_A is in agreement with the general suite of traits characterizing stress-tolerant plants (see the Introduction), but the variation in other leaf traits with drought tolerance score partly contrasted the widespread views on the traits in stress-tolerant plants. While the plants in stressful habitats are expected to have low photosynthetic capacity both per unit mass and area, in our study for all species pooled, only leaf photosynthetic capacity per mass scaled negatively with T_{drought}, and the capacity per unit area was positively associated with T_{drought} (Fig. 2d, Table 3). Although it might seem controversial, such a higher capacity allows the plants to achieve high photosynthesis during periods when water availability is high. This can contribute to overall high water-use efficiency (WUE: photosynthesis per unit water use) and plant survival of drought-tolerant species in environments with extensive reductions of growing season because of drought (Xu & Baldocchi, 2003).

As with shade tolerance, bivariate correlations differed among plant functional types. Leaf life-span and M_A were positively correlated with drought tolerance in deciduous species, reflecting lower leaf turnover. Contrary to the world-scale relationships where longer leaf life-span and higher M_A are, in general, associated with lower photosynthetic capacity (Wright *et al.*, 2004), drought-tolerant deciduous species in our dataset also had higher photosynthetic capacity (both area and dry mass based) and higher photosynthetic nitrogen use efficiency. This pattern may reflect the overall difference among temperate deciduous and evergreen species. Temperate deciduous species must generally resist a single drought cycle during the growing season, and the longer the leaf life-span, the longer the 'drought-free' period for photosynthesis. By contrast, evergreens must sustain multiple drought cycles and the period of active photosynthesis during a given growing season is less directly associated with overall leaf longevity. At the same time, drought-tolerant evergreen species possessed lower photosynthetic capacity, mainly as the result of larger M_A and lower photosynthetic nitrogen use efficiency (Table 3). Although these differences from deciduous species may seem puzzling, absolute values of M_A and longevity were much larger in evergreens, especially in conifers (Table 1), and M_A also changed more strongly with drought tolerance. Thus, enhancement of foliage photosynthetic capacity against the burden of increasing M_A simply may not be possible in evergreens.

'Leaf economics spectrum' vs shade and drought tolerance

Global-scale quantification shows strong coordination of leaf traits forming 'leaf economics spectrum' (Wright *et al.*, 2004). Long L_L, which means prolonged return from investment into leaf biomass, is generally associated with high M_A. This is because greater structural toughness of leaves is needed for extended survival. In addition, high L_L and greater investments into cell walls in structurally more robust leaves brings about low N_M and A_M. These broad relationships were also observed within our data (Notes S1). The key question is to which extent such broad relationships among leaf traits constrain the variation of foliage structure and function in contrasting environments. For example, survival under shade would benefit from a large light-harvesting surface that can be achieved by low M_A and high L_L. In our study, species with higher T_{shade} had lower M_A at a given L_L (Fig. 4a). In addition, foliage photosynthetic potentials decreased, with a slower rate with increasing L_L in more shade-tolerant species (Fig. 4b). By contrast, M_A increased more with increasing L_L, resulting in a steeper decline in A_M in more drought-tolerant species (Fig. 4c,d). These relationships demonstrate that species ecological potential (degree of shade and drought tolerance) can importantly alter the 'general' bivariate trait relationships.

The other key question is whether the variation in shade and drought tolerance is compatible with the general strategies postulated for stress-tolerant and intolerant species (Grime, 1977; Grime *et al.*, 1997). Four key leaf traits, L_L, M_A, A_M and N_M were combined as the first PCA axis, which describes the 'leaf economics spectrum' with fast-return species with low L_L and M_A and high N_M and A_M at one end (postulated to be a suite of traits for stress-intolerant species) and slow-return species at the other end (postulated as stress-tolerant strategy). Because L_L and M_A dominate the patterns within the leaf economics and are positively related to each other in the 'leaf economics spectrum', T_{shade} was always simultaneously increasing with L_L and decreasing with M_A. Thus, the expected result was that T_{shade} was not significantly related to species position along the 'leaf economics spectrum', hence also suggesting that variation in species shade tolerance with leaf traits does not confirm the postulated stress-tolerance strategy.

Drought tolerance score scaled positively with the species position along the 'leaf economics spectrum', but this relationship was more apparent within the functional types (Fig. 5b). Three functional types (DB, EB and EC) were clearly separated along the leaf trait space forming the 'leaf economics spectrum' (Fig. S1, Notes S1), while the entire range of drought (and shade) tolerance scores were present within each plant functional type. This resulted in functional type-specific correlations of drought tolerance score with the PCA axis factor score (Table 5, Fig. 5). These contrasting correlations reflect the varying suites of traits responsible for drought tolerance in different plant functional types. Deciduous broadleaved species, which were positioned at the fast-return end of the general 'leaf economics spectrum' (Notes S1), achieved greater drought tolerance by increasing A_M and A_M/N_M, while evergreen conifers at the other end of the economics spectrum achieved drought tolerance by reduced A_M and nitrogen use efficiency and increased M_A (Table 3).

Inverse correlations of foliage traits with shade and drought tolerance: evidence of a trade-off

These data collectively do not support a general suite of traits characteristic to stress-tolerant plants. In general, leaf traits that increased T_{shade} in one functional group, were negatively related to T_{drought} in the same group and vice versa, the only exception being positive scaling of both T_{shade} and T_{drought} with L_{L} in deciduous broadleaved species. Thus, the trade-off between species shade and drought tolerance in Northern Hemisphere woody flora (Niinemets & Valladares, 2006) was also reflected in contrasting variation patterns in leaf structural and physiological traits. However, as revealed by the differences between the functional groups, the contribution of a single leaf trait to species tolerance to shade and/or drought was strongly modified by the combination of other traits. Nevertheless, all data together suggest that the inverse correlation between species T_{shade} and T_{drought} can partly be explained by constrained viable trait combinations.

Our study focused on leaf-level traits, but whole-plant factors can also play a role in the trade-off between shade and drought tolerance. For example, there can be conflicting requirements for biomass allocation with drought conditions favoring the biomass investment in roots, and shade that favors greater allocation in leaves (Smith & Huston, 1989). In addition, stronger foliage aggregation reduces energy absorption and water loss and thus is expected to enhance tolerance to drought, while the opposite is needed for improved light capture in shade. Further studies are needed to test the relative importance of leaf-level traits versus whole-plant factors on species shade and drought tolerances.

Conclusions

These results provide encouraging evidence of correlations between leaf structure and species tolerance to environmental factors and suggest that within the broad continuum of structural and physiological traits ('leaf economics spectrum', Wright *et al.*, 2004) there is room for ecological differentiation of structure–function relationships. This study further demonstrates that there are structural limitations that can prevent species from achieving polytolerance to simultaneous drought and shade stresses such that the concept of 'stress suite of traits' fails at least for two common stresses in temperate ecosystems.

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Appendix A1

Combined tolerance and leaf traits database

Construction of the combined tolerance and leaf trait database for the Northern Hemisphere temperate woody species

Three main databases were used for generation of the combined database of species tolerances and leaf traits. The database of Niinemets & Valladares (2006) provided information of shade, drought and waterlogging tolerance scores (numerical rankings) for 806 temperate species. Species tolerance estimates are relative values that characterize the species capacity to grow under given environmental conditions relative to other species. Plant absolute stress resistance can depend on many factors, for instance the absolute plant light requirement depends on plant age (Niinemets, 2006; Lusk *et al.*, 2008a), and site fertility (Kobe *et al.*, 1995; Walters & Reich, 2000a). By contrast, species tolerance rankings are considerably more conservative (see Valladares & Niinemets, 2008 for discussion), although rank changes may sometimes occur (Latham, 1992). The tolerance estimates for the Northern Hemisphere species were based on 26 individual rankings for shade, 14 rankings for drought and 20 ranking for waterlogging tolerance and a large number of individual studies (Niinemets & Valladares, 2006). In deriving these tolerance rankings, continent-specific tolerance scales were all first cross-calibrated using the species scored in several datasets simultaneously and consensus tolerance estimates were derived. Finally tolerance ranks for Europe, East-Asia and North America were cross-calibrated using species studied in several continents, resulting in common tolerance scales for the entire temperate Northern Hemisphere (Niinemets & Valladares, 2006). The tolerance database covers *c.* 40% of native temperate Northern Hemisphere woody vegetation (*c.* 73% of North American, 69% of European, and 23% of East-Asian woody species (Qian & Ricklefs, 1999, 2000; Ricklefs *et al.*, 2004).

While there is ample information of correlations between drought and shade tolerance with foliage traits (e.g. Abrams & Mostoller, 1995; Lusk & Warton, 2007; Valladares & Niinemets, 2008), waterlogging tolerance is generally believed to be linked to whole plant traits (see Blom, 1999 for discussion). Therefore, we did not expect a priori correlations of leaf structure and physiology with waterlogging tolerance. As the correlations with waterlogging tolerance within this dataset were in most cases missing or very weak, waterlogging tolerance was left out from this analysis.

The information of leaf structural and physiological traits was obtained from the databases of Niinemets (1999; 597 tree and shrub species from 182 sites) and Wright *et al.* (Glopnet database, Wright *et al.*, 2004; 1978 species from 175 sites). In these two databases of foliage traits, there were 339 temperate woody species for which tolerance estimates were available from the study of Niinemets & Valladares (2006). Out of these species, 179 were unique to Wright *et al.* (2004) database, 45 to Niinemets (1999) databases and 115 were present in both databases. Out of these 115 overlapping species, only for 31 species, the same studies had been used for foliage structural and physiological data in both the databases of Niinemets (1999) and Wright *et al.* (2004): 29 species from the study of Koike (1988) and two species from the study of Niinemets & Kull (1994). Thus, the two databases were largely complementary.

In Wright *et al.* (2004) database, 1–8 observations per species (average ± SE = 1.74 ± 0.07) and in Niinemets (1999), 1–29 observations per species (3.30 ± 0.32) were available. Only the data for high light exposed leaves were used in all cases, and averages per species were calculated. In calculation of the averages, each individual literature observation was only used once. In the analyses of Niinemets (1999) and Wright *et al.* (2004), each literature observation was considered as an independent data point, such that multiple entries per species were sometimes included in the statistical relationships. Our study differs from the previous analyses by using only individual species as experimental units, i.e. by more conservative statistical treatment. As different data sources had gaps in trait coverage, species-specific structural and physiological traits in the combined database often came from different data sources. While this induces additional error variance in the dataset, it randomizes the effect of any specific study on the general patterns. Although largely independent studies were used for construction of the databases of Niinemets (1999) and Wright *et al.* (2004), the key foliage traits derived from different studies (84 overlapping species from different data sources) were strongly correlated among these two databases. For instance, $r^2 = 0.72$ for leaf dry mass per unit area, and $r^2 = 0.78$ for photosynthetic capacity per leaf dry mass ($P < 0.001$ for both correlations). These strong correlations for the datasets based on independent data sources suggest that a robust database was generated that is not strongly affected by study-to-study variation in foliage traits.

Leaf life-span data

Leaf life-span (L_L) as commonly used in studies on foliage structure and function is not the maximum possible leaf longevity (e.g. Niinemets & Lukjanova, 2003), but average leaf life-span (Wright & Westoby, 2003). Exact estimation of L_L requires determination of leaf survivorship functions (e.g. Wright & Westoby, 2002; Reich *et al.*, 2004), but this information is not routinely available. Thus, L_L is commonly estimated as the oldest leaf age-class with at least 50% of leaves remaining (Cordell *et al.*, 2001; Kayama *et al.*, 2002; Prior *et al.*, 2003). In the combined dataset, the data for L_L were initially available for 148 species. For the species lacking L_L values in the two main databases used, average L_L estimates were obtained from additional literature sources (Smith, 1972; Bell & Johnson, 1975; Ewers & Schmid, 1981; Maillette, 1982; Whitney, 1982; Kikuzawa, 1983; Shaver, 1983; Kikuzawa, 1984; Lechowicz, 1984; Matyssek, 1986; Aerts, 1989; Jonasson, 1989; Murray *et al.*, 1989; Schoettle, 1990; Everett & Thran, 1992; Karlsson, 1992; Wang *et al.*, 1992; Gower *et al.*, 1993; Kramer, 1994; Ceulemans *et al.*, 1995; Hunter, 1997; Chuine & Cour, 1999; Kramer *et al.*, 2000; Rönnberg-Wästljung, 2001; Kollmann & Grubb, 2002; Augspurger & Bartlett, 2003; Hall & Simms, 2003; Mediavilla & Escudero, 2003; Niva *et al.*, 2003; Santini *et al.*, 2004; Augspurger *et al.*, 2005; Masin *et al.*, 2005; Niinemets & Tamm, 2005; Uemura *et al.*, 2005; Matsuki & Koike, 2006; Wesołowski & Rowinski, 2006; Black *et al.*, 2007; Henderson & Havens, 2008; Lopez *et al.*, 2008; Thomas *et al.*, 2008; Davi *et al.*, 2009) providing altogether information of L_L or information to derive L_L (data on phenology of deciduous species) for 100 species in the combined database. As leaf life-span can vary in dependence on site altitude and nutrient availability (Reich *et al.*, 1995b for a review), in all cases, only data for lowland populations and from control treatments were used to match the sampling conditions for the other leaf traits in the combined trait/tolerance database. For the remaining 91 species, L_L was estimated in representative field-grown individuals (e.g. Niinemets & Kull, 1994; Niinemets *et al.*, 2003). For evergreens (5 conifers and 13 broadleaved species), L_L was determined by counting the average number of leaf cohorts with at least 50% of leaves remaining (see Wright & Westoby, 2003 for discussion). The repeatability of this procedure was ± 3–5 months for species with shorter L_L (12–30 months) to ± 12–24 months for species with longer L_L (80–100 months). This is similar to the precision that can be commonly achieved from leaf survivorship curves determined for multiple individuals of given species (Whitney, 1982; Holder, 2000; Niinemets & Lukjanova, 2003; Reich *et al.*, 2004). For the deciduous species, L_L was estimated based on growing-season length and species phenology in the native locations. For the species with several leaf flushes and leaf abscission throughout the growing season (18 species), a value of L_L between 3–4 months was assigned depending on the date of spring bud-burst, while for the species with only one leaf flush in the beginning of the growing season (47 species), a value of L_L between 5–6 months was assigned, again depending on the onset of growing season and timing of leaf fall. For the four semi-deciduous species, a value of L_L of 8 months was assigned. As the timings of bud-burst and leaf fall may vary depending on climatic conditions in the specific year, average site climate and genotype (e.g. Murray *et al.*, 1989; Ovaska *et al.*, 2005), the precision of our estimations for the deciduous species is *c.* ± 0.5–1 months, being similar to the bulk of the deciduous species leaf longevity estimates in the Glopnet database.

Overall, L_L data derived this way from independent observations are similar to the data on structural and physiological leaf traits that were often averaged using different independent studies for specific traits in a given species. In our study, all statistical relationships were qualitatively identical using only a subset of species for which literature data of L_L were available (73% of total) compared with the whole dataset including both literature data and L_L data derived here.

Structural and physiological traits selected for detailed analyses

Both the databases of Niinemets (1999) and Wright *et al.* (2004) contained information of a large number of foliage structural and physiological traits. However, for many traits, limited number of observations was available. For instance, in the Glopnet database, foliage phosphorus concentration was available for 30% of species, and stomatal conductance and dark respiration rate for 10% of species. Given these limitations, we selected key and most complete chemical (nitrogen content per area, N_A, and dry mass, N_M), structural (leaf dry mass per unit area, M_A) and physiological (foliage photosynthetic capacity per area, A_A, and dry mass A_M) characteristics for detailed analyses. Because of the potential importance of respiration rate as a determinant of foliage and whole plant light compensation points and plant shade tolerance (Walters & Reich, 2000b; Craine & Reich, 2005; Baltzer & Thomas, 2007), lack of respiration data may limit our conclusions. However, there were high correlations between the physiological traits, for instance, for the entire dataset, $r^2 = 0.67$, $P < 0.001$ for the correlation between A_M and the respiration rate per dry mass. Thus, at least the available data for the traits not included in the current analysis suggest that lack of these data did not bias our main conclusions on the scaling of shade and drought tolerance rankings with leaf traits.

Area- and mass-based relationships are connected through M_A, $N_A = M_A N_M$ and $A_A = M_A A_M$. Thus, comparison of both area- and mass-based photosynthesis relationships allowed us to separate between structural (M_A) and physiological (average photosynthetic potential of individual leaf cells, A_M) sources of variation in area-based relations. In addition, A_M/N_M (photosynthetic nitrogen use efficiency) was also calculated. Photosynthetic nitrogen use efficiency primarily reflects the fractional investment of foliage nitrogen in photosynthetic apparatus (Niinemets & Tenhunen, 1997), and thus provides important additional information to understand differences in foliage photosynthetic capacity of leaves with given N_M.

In needleleaved species, the traits can be expressed per unit total or projected area (Poorter *et al.*, 2009 for a discussion). In our study, all area-based characteristics are expressed per unit projected area in needleleaved species.

Functional group contrasts

The final dataset of 339 woody species contained 244 deciduous broadleaved species (DB), 50 evergreen broadleaved species (EB), 35 evergreen conifers (EC), 7 evergreen needleleaved angiosperms (e.g. *Genista* spp.), and 3 deciduous conifers (Supporting Information Table S1 for the list of species included in the analysis). Due to small sample size for needleleaved angiosperms and deciduous conifers, we analyzed separately only deciduous and evergreen broadleaved species and evergreen conifers (Table 1 for comparison of tolerance estimates and key leaf traits among these main plant functional types). The data for the two smallest groups were included in the analyses with the entire dataset. Evergreen needleleaved angiosperms had similar L_L (average ± SD = 22.9 ± 2.8 months) as broadleaved evergreen angiosperms, and deciduous conifers (5.8 ± 0.6 months) had similar L_L as deciduous broadleaved species (Table 1). Furthermore, as the structural and physiological traits were also similar between the minor and corresponding major groups (data not shown), these minor species groups were not outliers in any of the broad relationships. Although in our dataset, EB and EC groups are smaller than DB group, this difference in group size reflects the overall species proportions in the temperate Northern Hemisphere (Qian & Ricklefs, 1999, 2000; Ricklefs *et al.*, 2004). Worldwide, the number of angiosperm species hugely exceeds the number of gymnosperm species (Stebbins, 1981). For instance, for North America, the number of gymnosperm genera is *c.* 100-fold less than the number of angiosperm genera (Qian, 1998). In the Northern Hemisphere, the distribution of evergreen broadleaved ecosystems and species number is also much lower than that of broadleaved deciduous forests (Box, 2002). In Niinemets & Valladares (2006) database, gymnosperms constituted 14% of total species number, compared with 11% in the current database, while broadleaved evergreen angiosperms constituted 17%, compared with 15% in the current database. Thus, we conclude that a fair percentage of different plant functional types was included in our combined tolerance/foliage structure database. Previously, important information on functional type differences in structure/function scaling relationships has been obtained using smaller datasets (e.g. 22 broadleaved vs 9 evergreen conifers in Reich *et al.*, 1995a), suggesting that species numbers available in our study are not driving the reported statistical relationships among the data.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Bivariate relationships between leaf life-span (L_L), leaf dry mass per area (M_A), leaf nitrogen content per unit dry mass (N_M) and leaf photosynthetic capacity per unit dry mass (A_M) in Northern Hemisphere temperate woody species.

Table S1 List of 339 Northern Hemisphere temperate woody plant species included in the analysis

Table S2 Comparison of the Pearson's pairwise correlation coefficients (r) among leaf life-span (L_L), dry mass per unit area (M_A), nitrogen content per dry mass (N_M), and photosynthetic capacity per dry mass (A_M) between the current (see Appendix A1) and the Glopnet database (Wright *et al*., 2004)

Notes S1 Visualization of 'leaf economics spectrum' for Northern Hemisphere temperate woody flora

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