

Whole-plant trait spectra of North American woody plant species reflect fundamental ecological strategies

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Abstract. The adaptation of plant species to their biotic and abiotic environment is manifested in their traits. Suites of correlated functional traits may reflect fundamental tradeoffs and general plant strategies and hence represent trait spectra along which plant species can vary according to their respective strategies. However, the functional interpretation of these trait spectra requires the inspection of their relation to plant performance. We employed principle coordinate analysis (PCoA) to quantify fundamental whole-plant trait spectra based on 23 traits for 305 North American woody species that span boreal to subtropical climates. We related the major axes of PCoA to five measures of plant performance (i.e., growth rate, and tolerance to drought, shade, water-logging and fire) for all species and separately for gymnosperms and angiosperms. Across all species a unified gymnosperm-angiosperm trait spectrum (wood density, seed mass, rooting habit) is identified, which is correlated with drought tolerance. Apart from this, leaf type and specific leaf area (SLA) strongly separate gymnosperms from angiosperms. For gymnosperms, one trait spectrum emerges (seed mass, rooting habit), which is positively correlated with drought tolerance and inversely with shade tolerance, reflecting a tradeoff between these two strategies due to opposing trait characteristics. Angiosperms are functionally more diverse. The trait spectra related to drought tolerance and shade tolerance are decoupled and three distinct strategies emerge: high drought tolerance (low SLA, dense wood, heavy seeds, taproot), high shade tolerance (high SLA, shallow roots, high toxicity, opposite arranged leaves), and fast growth/stress intolerance (large maximum heights, soft wood, light seeds, high seed spread rate). In summary, our approach reveals that complex suits of traits and potential tradeoffs underlie fundamental performance strategies in forests. Studies relying on small sets of plant traits may not be able to reveal such underlying strategies.

Key words: drought tolerance; forests; ordinal-scaled traits; plant performance; plant strategies; principle coordinate analysis; shade tolerance; trait tradeoffs; vital rates.

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INTRODUCTION

Plant functional traits reflect adaptations to the environment and affect ecosystem functioning. They are thus the key inferring plant strategies and for predicting ecosystem properties (Cornelissen et al. 2003, McGill et al. 2006, Lavorel et al. 2007). Plant strategies are manifested in a suite of whole-plant performances including e.g., reproduction, growth and survival, each governed by a particular set of morphological, anatomical or physiological traits. Characterizing plant strategies therefore requires the knowledge of many traits. However, we typically lack the complete information on multiple important traits, because plant trait datasets are often biased towards a few traits that are easily measured (e.g., characteristics of leaves, seed weight, plant maximum height), while other traits may only be available for a small subset of plant species (e.g., potential allelopathy, bark thickness) (Kattge et al. 2011).

Functional traits are often grouped as sets of co-varying traits that reflect evolutionary or biophysical tradeoffs and hence jointly represent an axis of trait variation (trait spectrum) along which plant species can vary according to their respective strategies (Reich et al. 2003, Lavorel et al. 2007). Such trait spectra are typically identified with dimension reduction methods that extract lower-dimensional information (orthogonal principle components) from multidimensional trait data sets (Grime et al. 1997, Wright et al. 2007). Two prominent examples are the leaf and the wood economic spectrum (Wright et al. 2004, Chave et al. 2009) each of which described by a characteristic set of co-varying traits. The two spectra appear to be orthogonal to one another (Baraloto et al. 2010). This implies that the number and types of traits that vary independently of each other (i.e., not necessarily the total number of traits) determine unique strategy axes. However, proving the existence of trait spectra per se does not necessarily tell us anything about their relevance for whole-plant performance and for vital rates such as growth, stress tolerance or reproduction. Thus additional information on plant performance must be considered to fully understand their implications. This is challenging because comparative field data on species-specific performances controlled for the biotic and abiotic environment are scarce. Hence, studies

relating traits to performances are typically conducted in controlled settings, often with short-lived herbaceous species (Poorter and Van der Werf 1998, Useche and Shipley 2010). Such ‘rates and traits’ studies for trees are typically restricted to growth and mortality and conducted on well-studied small forest plots with homogeneous environmental conditions (Rüger et al. 2012). Biome-scale studies are lacking. Moreover, there are hardly any studies focusing on more holistic performance measures such as niche preferences or stress tolerances—integrating growth, survival and recruitment—despite the fact that these are critical for understanding vegetation composition and dynamics under global change.

In forest communities, light and water availability are critical drivers of temporal and spatial processes such as succession and zonation (Smith and Huston 1989, Pacala et al. 1996, Poorter and Markesteijn 2008). Species-specific shade and drought tolerances are typically inferred as ordinal indices (‘scores’) from occurrences and vitality along gradients of light and water availability and are viewed as suitable measures of performance. Niinemets and Valladares (2006) found an inverse relationship between shade and drought tolerance indices among woody species of different plant functional types for all continents that aligns with Smith and Huston’s (1989) cost-benefit tradeoff model. This model predicts (1) no viable strategies should exist under both low light and low water due to conflicts between allocation to roots versus shoots, (2) under abundant light and water, the highest growth rates are expected in species deemed intolerant of both stresses, and (3) a tradeoff between high growth under favorable conditions versus low growth under more stressful conditions (Craine 2009). The first two predictions suggest a tight tradeoff between shade and drought tolerance, implying a highly constrained trait space (i.e., limited niche differentiation) for traits underlying these tolerance indices. Independence between these two tolerance indices would indicate a more flexible trait space (Sack 2004). Trait-based analyses, however, have yielded ambiguous results. For instance, Hallik et al. (2009) identified leaf traits underlying the inverse relationship between shade and drought tolerance of temperate tree species, while Markesteijn and Poorter

(2009) found different trait spectra associated with shade and drought tolerance of tropical tree seedlings based on leaf, stem and root traits.

Disturbance events that lead to significant biomass loss can interact with stress tolerance strategies to affect whole-plant performance. This implies the existence of other strategies related to the ability to tolerate or recover from disturbances such as fires, wind-throw, or snow-break. For instance, Loehle (2000) described a tree strategy scheme with four independent axes (shade tolerance, tree height, seed dispersal, capacity to resprout) that was incorporated into a fitness-based model to predict species richness under different disturbance regimes in North American forests. According to Bond and Midgley (2001), three of these four axes align with the traits and tradeoffs defined in Westoby's (1998) LHS scheme (L = specific leaf area [SLA] relates to shade tolerance; H = maximum tree height; S = seed mass relates to seed dispersal). Loehle's fourth axis (capacity to resprout) reflects adaptations to disturbance (Pausas and Lavorel 2003).

In summary, the linkage between plant functional traits and tolerance indices which reflect whole-plant performance as a function of growth, reproduction and survival along environmental and disturbance gradients has yet to be quantified. This quantification requires species-specific information for a potentially large number of traits (Grime et al. 1997, Diaz et al. 2004, Wright et al. 2007) that reflect adaptations to key environmental factors (Cornelissen et al. 2003, Lavorel et al. 2007) and influence whole-plant performance (Violle et al. 2007) ideally for a large number of species.

In this study, we developed a database that contains information on 23 traits for 305 North American woody species that span boreal to subtropical climates. We conducted principle coordinate analyses (PCoA) to identify dominant trait spectra, and we evaluated how these spectra are related to whole-plant performance indices. In doing so, we addressed three sets of questions: (1) What are the dominant trait spectra, what are the traits underlying each spectrum, and how do they relate to whole-plant performance measures, i.e., growth rate and tolerance to shade, drought, water-logging, and fire? (2) Do the relationships between trait spectra and performances differ between major phylogenetic

clades, such as gymnosperms versus angiosperms? (3) To what degree do these trait spectra agree with existing plant strategy schemes proposed by Westoby (1998) and Loehle (2000)?

MATERIAL AND METHODS

Selection of species and traits

The primary literature and various existing databases (USDA, NRCS, National Plant Data Team 2007, Kattge et al. 2011) were mined for data on functional traits for the 305 North American woody species (103 gymnosperms, 202 angiosperms) identified by the US Forest Service's Forest Inventory and Analysis (FIA) program (Miles et al. 2001) (see Appendix A: Table A1 for a complete list). The species span a range of habitat types (semi-arid woodlands, mesic temperate, boreal, to sub-tropical forests), and are classified mostly as trees (only 16 shrubs are included, of which 7 are chaparral species). The 305 species are phylogenetically dispersed across 79 genera, 36 families, 16 orders, and the two major clades.

To identify traits that most likely reflect adaptation to key environmental factors and that are likely to be related to whole-plant performance we used the following criteria: (1) traits are causally related to fitness components, i.e., growth, reproduction and survival (Violle et al. 2007), (2) they reflect adaptation to constraints by water and light, (3) they are related to the ability to resist or recover from disturbances, and/or adaptation to competition stress (Lavorel et al. 2007), (4) they reflect relevant functions (storage, defense, resource acquisition, dispersal) carried out by different plant organs (leaf, stem, root, seed) and (5) they are quantifiable for many species spanning a range of resource, climatic, and disturbance gradients. To minimize trait redundancy, we avoided selection of multiple, correlated traits related to the same tradeoff; e.g., only one trait (SLA) was chosen from the leaf economics spectrum (Wright et al. 2004). We focused on 23 traits that fulfilled these criteria (Table 1 and Appendix A: Table A2 for a detailed description).

In case of multiple values per species we averaged across the individual values to obtain one species-specific trait value. All traits were available for at least 70% of the species, except for

Table 1. Traits with their respective units or categorical levels and performance measures compiled including their main sources.

Trait/performance	Data type	Trait levels or units	Abbr.†	Source
Leaf traits				
Leaf composition	nominal	composite vs simple	lcomp	1
Leaf arrangement	nominal	alternate whorled opposite spirally shoots	alt lwhorl lopp lspir lshoot	1
Leaf type	nominal	evergreen needle leaved deciduous needle leaved evergreen scaled evergreen broad leaved deciduous broad leaved evergreen/deciduous broad leaved	evnd dcnd evsc evbr dcb evdcb	1
Leaf margin	ordinal	0 = entire, 1 = toothed and/or entire, 2 = toothed, 3 = lobed	lmar	2‡
Specific leaf area	continuous	cm ² /g	sla	3
Reproduction traits				
Dispersal syndrome	multi-choice nominal	dispersal via animals dispersal unassisted dispersal via water dispersal via wind	animal unass water wind	(4, 5, 6)§
Seed mass	continuous	mg	seed	(4,5)§
Seed spread rate	ordinal	0 = none, 1 = slow, 2 = moderate, 3 = rapid	sspr	7
Vegetative spread rate	ordinal	0 = none, 1 = slow, 2 = moderate, 3 = rapid	vspr	7
Resprout ability	binary	able to resprout vs not able to resprout	sprout	7
Root and stem traits				
Rooting habit	nominal	taproot shallow root variable root habit	taproot sha.root var.root	8
Bark surface	ordinal	1 = smooth, 2 = between smooth and medium, 3 = medium, 4 = between medium and rugged, 5 = rugged	barksu	1
Bark thickness	continuous	cm	barkth	8
Wood density	continuous	g/cm ³	wood	9, 10
Maximum height	continuous	m	height	8
Conduit type and arrangement (porosity)	multi-choice nominal	vessels ring porous vessels diffuse porous vessels semi ring porous tracheids	rp dp sr tr	8, 11, 12
Plant level traits				
Lifespan	continuous	years	age	7, 12‡
C:N ratio (% carbon/ % nitrogen)	continuous	unitless	CN	7‡
Nitrogen fixation	ordinal	0 = none, 1 = low < 85 lb N/acre/year, 2 = medium = 85-160, 3 = high > 160	Nfix	7
Toxicity	ordinal	0 = none, 1 = slight, 2 = moderate, 3 = severe	tox	7
Potential allelopathy	ordinal	0 = none, 1 = slight, 2 = moderate, 3 = strong	allelo	13
Growth form	nominal	tree shrub tree/shrub	tree shrub tree/shrub	1
Fire resistance (flammability)	binary	fire resistant vs not fire resistant	fireres	7
Performance measures				
Growth rate	ordinal	1 = slow, 2 = moderate, 3 = rapid	GROWTH	7
Shade tolerance	continuous	scores from 1 = low to 5 = high	SHADE	14
Drought tolerance	continuous	scores from 1 = low to 5 = high	DROUGHT	14
Water-logging tolerance	continuous	scores from 1 = low to 5 = high	WATER	14
Fire tolerance	ordinal	0 = none, 1 = low, 2 = medium, 3 = high	FIRE	7

Notes: Sources are 1, Flora of North America Editorial Committee (1993); 2, Adams et al. (2008); 3, Ogle et al. (2012); 4, Moles et al. (2005); 5, Royal Botanical Garden KEW (2008); 6, Paula et al. (2009); 7, USDA, NRCS, National Plant Data Team (2007); 8, Appendix B; 9, Zanne et al. (2009); 10, Jenkins et al. (2004); 11, Inside Wood (2004); 12, Dallwitz et al. (1993); 13, Coder (1999); 14, Niinemets and Valladares (2006). For detailed description of traits and their ecological function see Appendix A: Table A2.

† Abbreviations used in Figs. 1-4.

‡ For details regarding how trait scales were adapted see Appendix B.

§ Data were provided via the TRY initiative (Kattge et al. 2011), which includes data from different sources given in brackets.

'dispersal mode', which we included despite that it was only available for 54% of the species (see Appendix A: Table A3). The species-trait matrix that we compiled was 85% complete (15% missing data). The fraction of missing information was further reduced to 4% by replacing missing continuous and ordinal traits with the mean values of the respective genera. The 23 traits included nine nominal traits (e.g., leaf type, root habit), seven ordinal traits (e.g., bark surface, seed spread rate, nitrogen fixation), and seven continuous traits (e.g., SLA, seed mass); see Table 1 for the complete list. Because we are interested in broad patterns across species, variability within a species was not incorporated into the analysis.

Selection of performance measures

We selected five species-specific performance measures: growth rate (USDA, NRCS, National Plant Data Team 2007), shade, drought, water-logging tolerances (Niinemets and Valladares 2006), and fire tolerance (USDA, NRCS, National Plant Data Team 2007). These indices represent whole-plant behavior that affects plant performance along resource or disturbance gradients and are expected to result from the coordination of multiple functional traits (Reich et al. 2003, Violle et al. 2007, Webb et al. 2010). Shade, drought, and water-logging tolerance are ordinal variables ranging from 1 (intolerant) to 5 (tolerant). These species-specific tolerance indices are based on (1) site characteristics (e.g., annual precipitation and duration of the dry period for drought tolerance) representative for each species' range, (2) the physiological potential that a species can survive long periods of exposure to the associated stress (e.g., 50% of foliage damage for drought tolerance), but to a certain degree also on expert knowledge about morphological and life history traits (Niinemets and Valladares 2006). To reduce the risk of circularity we validated the shade and drought tolerance indices. To validate the shade tolerance classifications of Niinemets and Valladares (2006), we correlated these with the shade tolerance estimates of Lichstein et al. (2010), which are only derived from individual growth versus light-level measurements. Both shade tolerances were significantly correlated ($r = 0.56$, $P < 0.001$, see Appendix A: Fig. A1), and thus, we used one of

the indices (Niinemets and Valladares 2006). To validate the drought tolerance classifications, we correlated these with species-specific scores of humidity (annual P minus potential evapotranspiration derived from species' geographic distribution; see Appendix A: Fig. A2) and found a significant correlation ($r = 0.40$, $P < 0.001$). Fire tolerance is also an ordinal variable that ranges from 0 (intolerant) to 3 (high tolerant) and describes the relative ability of a species to resprout, regrow, or reestablish from seeds after a fire. Growth rate is represented on an ordinal scale from 1 (slow) to 3 (fast) and describes the growth potential of a species relative to other species after successful establishment. The imputation of missing values for the performance measures was done in the same manner as for the functional traits (see Appendix A: Table A3).

Data analysis

The data analysis was performed in two steps. First, we quantified trait spectra (sets of co-varying traits) as composite variables by extracting dominant axes of trait variation running a principle coordinate analysis (PCoA) (Gower 1971). We chose PCoA over principal components analysis (PCA) or correspondence analysis (CA) because it is flexible in the choice of distance measures, which was more appropriate for our analysis given the different data types (i.e., nominal, continuous, ordinal, multi-choice nominal); Euclidean (PCA) or chi-square (CA) distances are not appropriate in our setting. PCoA provides a Euclidean representation (i.e., a graphical representation in a Cartesian coordinate system) of the distance relationships between species based on their trait values. Thus, the major PCoA axes extracted from our data represent dominant variation in the traits, i.e., the axes are explained by certain sets of traits (trait spectra). To understand the attributes of the respective trait spectra, we correlated the PCoA axes with the trait values. Second, we explored relationships between the main trait spectra (i.e., major PCoA axes) and the plant performance indices.

PCoA was conducted on a general extension of Gower's distance coefficient (Gower 1971) developed by Pavoine et al. (2009), which accounts for different trait data types by assigning appropriate metrics for the specific data types, has Euclidean properties, and accounts for missing

values. Due to missing data (4%), the distance matrix was unbalanced, and thus, the PCoA yielded some negative eigenvalues. We did not correct for these because the largest negative eigenvalues were smaller in absolute magnitude than any of the first three positive eigenvalues of interest, i.e., their interpretation was still meaningful following the rules provided by Legendre and Legendre (1998).

To account for differences between gymnosperms and angiosperms, we repeated the analysis three times: once for all 305 species and 23 traits followed by two analyses that considered gymnosperms and angiosperms separately. The gymnosperm analysis was based on 19 traits (conduit type/arrangement, leaf composition, leaf margin, and nitrogen fixation were excluded because they did not vary within this group). The angiosperm analysis was based on 22 traits (dispersal mode was excluded because of missing values for 46%). If necessary traits were square-root- or log-transformed to approximate normality and to reduce the influence of extremely high values. All continuous-valued traits (original or transformed) were standardized to z-scores by subtracting the mean trait value across species from each species-specific value and by dividing this difference by the standard deviation across species.

To assess the relative contribution of each trait to the trait spectra, we computed linear correlation coefficients (Pearson's r) between all traits and the first three PCoA axes of the species-trait matrix, representing the main trait spectra. To explore the relationship between the main trait spectra and the plant performance indices, we computed linear correlations between the first three PCoA axes and the growth rate and tolerance indices. All statistical analyses were conducted in R (R Development Core Team 2010).

RESULTS

For each of the three analyses (all species, gymnosperms, angiosperms), the first three PCoA axes explain a significant amount of variation (total ~40%) in trait values (Table 2). Each additional axis explains <6 % of the total variation, and we do not include these axes in subsequent analyses.

All 305 woody species

When considering all 305 species, the first axis explains 26% of trait variation (Table 2; Fig. 1). This axis is mainly correlated with leaf traits (leaf type, SLA, leaf margin), resprouting capacity and conduit type (vessel vs tracheids) (Fig. 1A and B, Table 2) and separates angiosperms and gymnosperms. Water-logging tolerance, fire tolerance, and growth rate are the performance indices that are most strongly correlated with this axis (Fig. 1B, Table 2). The second axis explains 9% of trait variation, and is mainly driven by traits representing responses to water availability and reproduction (wood density, root habit, seed mass). Drought tolerance and growth rate are correlated with this axis, but in opposite directions. Drought tolerant, slow growing species are located at the positive end of this axis and are characterized by a growth form intermediate between trees and shrubs (see Appendix A: Table A2 for definition) with heavy seeds, slow seed spread rate, slow vegetative spread rate, dense wood, and a taproot (Fig. 1B, Table 2). Conversely, drought intolerant, fast growing species are located at the negative end of the axis. They exhibit a tree-like growth form and support the opposite trait configuration. The third axis explains 6.9% of the trait variation and is mainly driven by leaf composition, potential for allelopathy and bark surface; it is not significantly correlated with any of the performance measures (Table 2).

Gymnosperms

For the gymnosperm-only analysis, the first axis explains 22% of trait variation and separates species in the Cupressaceae family, characterized by opposite arranged evergreen scale-like leaves, from Pinaceae, Taxaceae, and Taxodiaceae with spirally arranged evergreen needles (Fig. 2A and B, Table 2). Growth rate and drought tolerance indices are correlated with the first axis (Fig. 2B, Table 2). The second axis explains 13% of trait variation and is driven by traits related to water acquisition and reproduction. Drought tolerance and shade tolerance are inversely correlated with this axis (Fig. 2B, Table 2), reflecting the negative relationship between these tolerance strategies. The drought tolerant and shade intolerant species located at the positive end of the second axis exhibit tree/shrub growth forms, animal-

Table 2. Pearson's correlation coefficient (r) between traits and performance indices versus the first three PCoA axes (A1, A2, A3) obtained by analyzing all species, only gymnosperms and only angiosperms.

Trait/performance	All species			Gymnosperms			Angiosperms		
	A1 26.1%	A2 9.1%	A3 6.9%	A1 21.6%	A2 12.6%	A3 11.2%	A1 13.7%	A2 12.0%	A3 8.7%
Leaf traits									
Leaf composition	0.33***	n.s.	-0.65***	n.s.	0.76***	0.27***
Leaves alternate	0.77***	0.27***	0.26***	n.s.	n.s.	0.44***	0.37***	-0.25***	-0.58***
Leaves whorled	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Leaves opposite	n.s.	-0.23***	-0.33***	0.92***	n.s.	n.s.	-0.41***	0.28***	0.57***
Leaves spirally	-0.78***	n.s.	n.s.	-0.8***	0.2*	n.s.	n.s.	n.s.	n.s.
Leaves in shoots	-0.17**	n.s.	n.s.	n.s.	n.s.	n.s.
Evergreen needle leaved	-0.84***	n.s.	n.s.	-0.9***	n.s.	n.s.
Deciduous needle leaved	n.s.	n.s.	n.s.	n.s.	n.s.	0.25*
Evergreen scaled	-0.28***	n.s.	n.s.	0.91***	n.s.	n.s.
Evergreen broad leaved	n.s.	0.32***	0.3***	0.43***	-0.4***	0.32***
Deciduous broad leaved	0.85***	-0.17**	-0.19**	-0.47***	0.44***	-0.32***
Evergreen/deciduous broad leaved	n.s.	0.13*	0.13*	0.16*	-0.15*	n.s.
Leaf margin	0.74***	-0.19**	-0.13**	-0.36***	0.26***	-0.3***
Specific leaf area	0.83***	-0.13***	n.s.	n.s.	-0.21*	0.09	-0.44***	n.s.	0.34***
Reproduction traits									
Dispersal via animals	n.s.	0.52***	n.s.	0.48***	0.54***	-0.28*
Dispersal unassisted	0.22**	n.s.	-0.29***
Dispersal via water	n.s.	n.s.	0.29***	n.s.	n.s.	0.36**
Dispersal via wind	-0.26**	-0.58***	n.s.	-0.74***	-0.44***	n.s.
Seed mass	0.22***	0.55***	-0.38***	n.s.	0.56***	n.s.	0.55***	0.43***	n.s.
Seed spread rate	n.s.	-0.43***	0.13*	0.28**	-0.5***	0.23*	-0.48***	-0.16*	n.s.
Vegetative spread rate	0.19**	-0.39***	n.s.	n.s.	-0.46***	-0.25*	-0.37***	n.s.	-0.17*
Resprout ability	0.83***	n.s.	0.06	n.s.	-0.43***	0.51***	n.s.	n.s.	-0.24**
Root and stem traits									
Taproot	n.s.	0.79***	n.s.	n.s.	0.67***	0.7***	0.71***	0.2*	-0.36***
Shallow root	n.s.	-0.76***	n.s.	n.s.	-0.69***	-0.69***	-0.7***	n.s.	0.37***
Variable root	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Bark surface	-0.35***	0.21***	-0.44***	n.s.	-0.22*	n.s.	0.34***	0.34***	n.s.
Bark thickness	-0.14*	0.15*	n.s.	-0.34***	-0.2*	0.41***	0.31***	n.s.	-0.26***
Wood density	0.4***	0.48***	n.s.	0.23*	0.34**	n.s.	0.58***	n.s.	n.s.
Maximum height	-0.25***	-0.22***	-0.13*	-0.43***	-0.45***	0.34**	-0.22**	0.27***	-0.42***
Ring porous	0.48***	0.34***	-0.38***	0.49***	0.49***	-0.29***
Diffuse porous	0.43***	-0.4***	0.38***	-0.61***	-0.48***	0.21**
Semi ring porous	0.36***	0.16**	n.s.	0.17*	n.s.	n.s.
Tracheids	-0.95***	n.s.	n.s.
Plant level traits									
Lifespan	-0.49***	0.17**	n.s.	0.22*	n.s.	n.s.	0.34***	n.s.	n.s.
C:N ratio	-0.2**	n.s.	-0.18**	n.s.	n.s.	n.s.	n.s.	0.16*	n.s.
Nitrogen fixation	0.14*	n.s.	n.s.	n.s.	n.s.	n.s.
Toxicity	0.16**	n.s.	-0.18**	n.s.	n.s.	n.s.	n.s.	0.16*	0.43***
Potential allelopathy	n.s.	-0.34***	-0.52***	n.s.	n.s.	n.s.	-0.35***	0.5***	n.s.
Tree	n.s.	-0.36***	n.s.	-0.48***	-0.4***	n.s.	-0.38***	0.2**	-0.56***
Shrub	0.16**	n.s.	n.s.	n.s.	-0.16*	0.33***
Tree/shrub	n.s.	0.39***	n.s.	0.48***	0.4***	n.s.	0.39***	n.s.	0.41***
Fire resistance	0.2**	-0.12*	n.s.	0.23*	n.s.	-0.54***	n.s.	n.s.	n.s.
Performance measures									
Growth rate	0.27***	-0.22***	n.s.	-0.38***	n.s.	0.39***	-0.33***	n.s.	n.s.
Shade tolerance	n.s.	-0.15*	n.s.	-0.3**	-0.38***	n.s.	n.s.	n.s.	0.22**
Drought tolerance	-0.12*	0.44***	n.s.	0.44***	0.45***	n.s.	0.49***	n.s.	n.s.
Water-logging tolerance	0.28***	-0.17**	n.s.	n.s.	n.s.	n.s.	-0.22**	n.s.	n.s.
Fire tolerance	0.34***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Notes: r with p < 0.001***, p < 0.01** and p < 0.05*, p > 0.05 n.s. (not significant). The explained variance per axis is given in %; in case of no data entry the trait did not occur or did not vary in the specific group or was excluded from the analysis (see Appendix A: Table A3 and *Material and Methods*).

dispersed seeds, heavy seeds, a taproot, low seed spread rate, low vegetative spread rates, and small maximum heights (Fig. 2A and B, Table 2). Drought intolerant and shade tolerant species are

located at the negative end of the second axis. They exhibit the opposite trait configuration and a tree-like growth form. The third axis explains 11% of the trait variation, and growth rate is

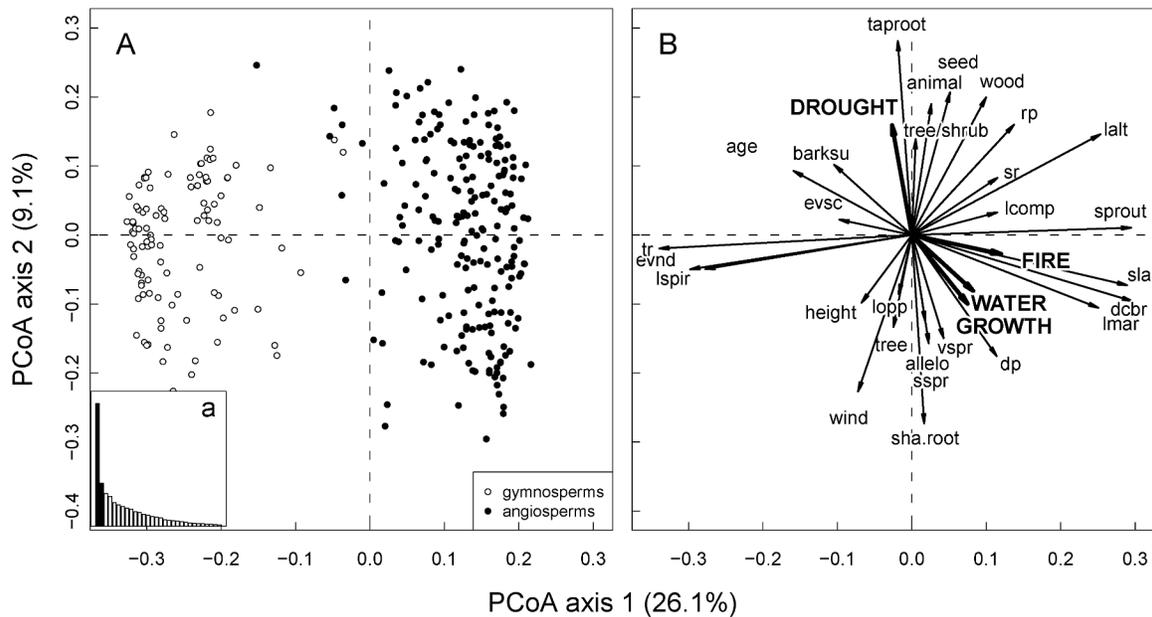


Fig. 1. PCoA ordination plot showing distances among 305 North American woody species based on 23 traits for the first two axes (A) with a histogram (a) showing the first 30 eigenvalues. In (B) significant correlations ($p < 0.001$) of both traits and performance measures (capitals) with the first two PCoA axes are represented as arrows (see Table 1 for abbreviations and Table 2 for respective correlation coefficients); the lengths of the arrows are proportional to their correlation coefficient, and they point in the direction of most rapid change; nominal traits were dummy coded before correlation.

correlated with this axis (Fig. 2C and D, Table 2). Fast growing species are located at the positive end of this axis and tend to have alternate-arranged leaves, a taproot, thick bark, high resprouting capacity, and low fire resistance, compared to the opposite trait configuration for slow growing species at the negative end of this axis. Several genera such as *Pinus*, *Larix*, and *Abies* cover the full range of traits spanned by the third axis.

Angiosperms

In the angiosperm-only analysis, the first axis explains 14% of trait variation and is driven by traits related to water availability and reproduction (Fig. 3A and B and Table 2). This axis is positively correlated with drought tolerance and negatively with growth rate and water-logging tolerance. The second axis explains 12% of the trait variation and is driven by leaf composition and potential for allelopathy; this axis is not notably correlated with any performance measure used (Fig. 3A and B, Table 2). The third axis

explains 9% of trait variation and is driven by maximum height and leaf arrangement. This axis is correlated with shade tolerance (Fig. 3C and D, Table 2).

The first and third axes reveal differences between species possessing three different strategies forming a plant strategy triangle with respect to combinations of shade, drought, water-logging tolerance and growth rate (Fig. 3C and D). The corners of this triangle are depicted by (1) species intolerant to shade and drought but with high growth rate and high water-logging tolerance, (2) species tolerant to shade but intolerant to drought and water-logging and no correlation with growth rate, (3) species tolerant to drought but intolerant to shade and water-logging and exhibiting low growth rate (Fig. 3C and D, Table 2). The first strategy is represented by species of the genera *Populus* and *Betula*, which are characterized by low wood density, light seeds, large maximum heights, deciduous leaves, tree-like growth form, short lifespan, low toxicity, high seed spread,

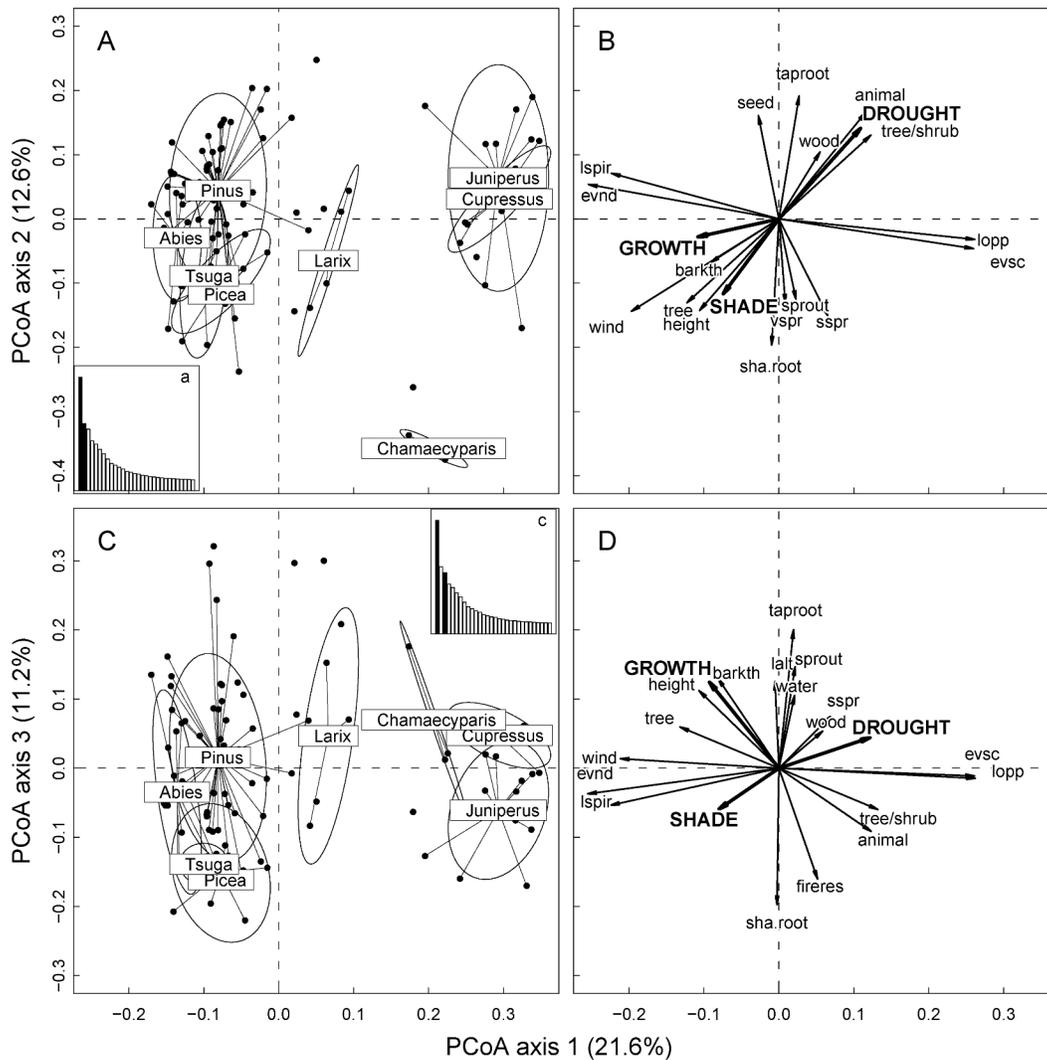


Fig. 2. PCoA ordination plot showing distances among 103 North American woody gymnosperm species based on 19 traits for the first two axes (A) and for the first and third axis (C) with histograms (a and c) of the first 30 eigenvalues, respectively. The dispersion of important genera (containing many species or largely explain the axes) are shown as ellipses using standard deviation of the point scores with a confidence limit of 0.7 while the lines connect the species to the genus centroid, respectively. In (B) and (D) significant correlations ($p < 0.01$) of both traits and performances (capitals) with the respective PCoA axes are represented as arrows, see Fig. 1 for detailed description.

high vegetative spread rate, and dissected leaf margins (Fig. 3C and D, Table 2). The second strategy is mainly represented by species of the genera *Acer*, *Aesculus* and *Cercocarpus*, which are characterized by high SLA, opposite-arranged leaves, shallow roots, small maximum heights, diffuse-porous wood, high toxicity, thin bark,

and a shrub-like growth form. The third strategy type is mainly represented by species of the genus *Quercus*, which is characterized by low SLA, dense wood, heavy seeds, taproot, thick bark with a rough surface, long lifespan, ring-porous wood, and alternately arranged leaves (Fig. 3C and D, Table 2).

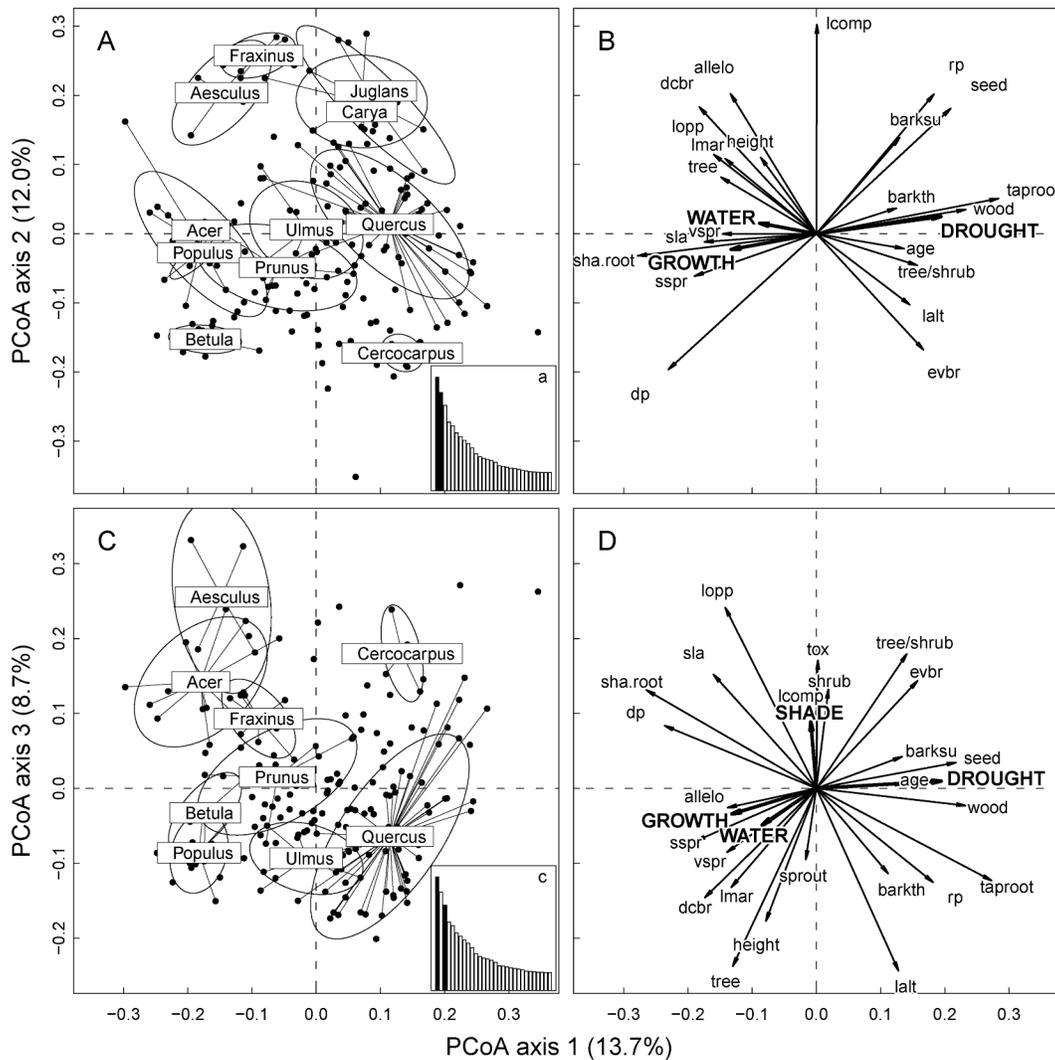


Fig. 3. PCoA ordination plot showing distances among 202 North American woody angiosperm species based on 22 traits for the first two axes (A) and for the first and third axis (C) with histograms of the first 30 eigenvalues (a and c), respectively. The dispersion of important genera are shown as ellipses, see Fig. 2 for detailed description. In (B) and (D) significant correlations ($p < 0.01$) of both traits and performance measures (capitals) with the respective PCoA axes are represented as arrows, see Fig. 1 for detailed description.

Comparison of gymnosperms and angiosperms

Here we compare the PCoA axes obtained from the gymnosperm- and angiosperm-only analyses that are most strongly correlated with shade and drought tolerance (Fig. 4). The axes that are primarily related to drought tolerance (second axis for gymnosperms, first axis for angiosperms, see Table 2) are explained by the same set of traits, which are correlated with

each axis in the same direction. That is, regardless of clade association, drought tolerant species tend to have tree/shrub like growth form with a taproot, dense wood, high seed mass, and both low vegetative and low seed spread rates (Fig. 4A, upper right corner); drought intolerant species are characterized by the opposite trait configuration (Fig. 4A, lower left corner). Conversely, the set of traits that are correlated with the axes related to

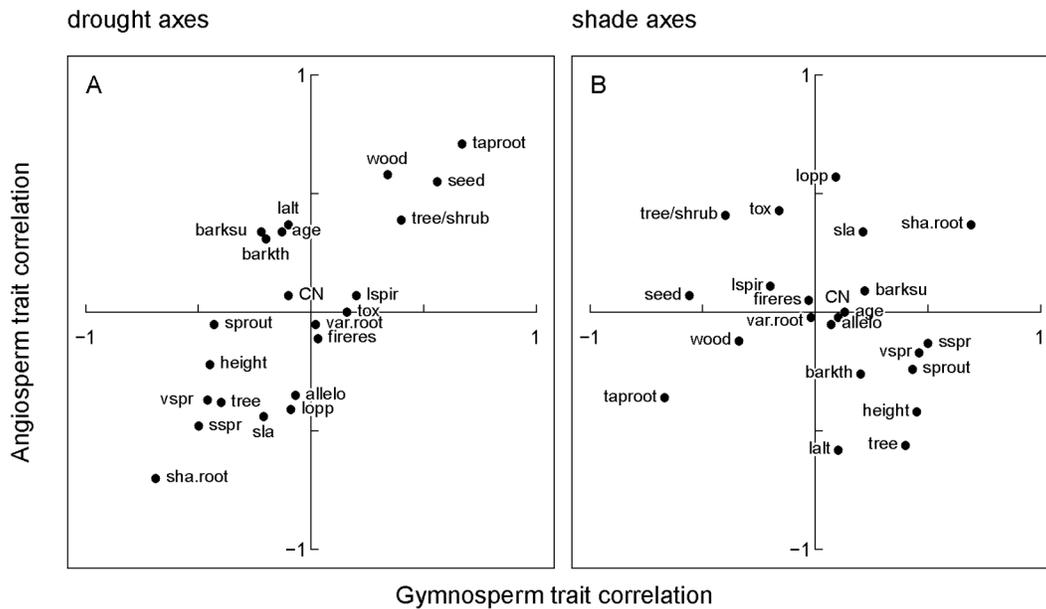


Fig. 4. Comparison of trait spectra reflecting drought (A) and shade tolerance (B) between gymnosperms and angiosperms. Pearson's correlation (r) between traits and those PCoA axes that correlated best with drought tolerance = "drought axes" (A) and best with shade tolerance = "shade axes" (B) in gymnosperm and angiosperm only analysis, respectively (see Table 2 for correlation coefficients and explained variance). If the respective trait spectra of the two clades are similar (i.e., the same traits vary in the same manner) the Pearson's r values show a linear arrangement along the 1 to 1 line.

shade tolerance (second axis for gymnosperms, third axis for angiosperms) differ between clades (Fig. 4B). These differences occur in two aspects: (1) different traits are correlated with shade tolerance (e.g., leaf arrangement in angiosperms vs. seed mass in gymnosperms), or (2) the same traits are correlated with shade tolerance, but in the opposite direction (e.g., maximum height increased with shade tolerance in gymnosperms but decreased in angiosperms). These clade-level differences in the trait versus shade tolerance associations explain the lack of significant trait correlations with shade tolerance when all species are analyzed together.

DISCUSSION

In this study we quantified major whole-plant spectra for morphological, anatomical and demographic traits for North American woody species and analyzed their relationship to whole-plant performance measures, i.e., growth

rate and tolerance to shade, drought, water-logging and fire (see *Material and Methods* for definition). The results of these analyses confirm that these holistic whole-plant performance measures reflect integrated processes of growth, reproduction and survival involving multiple traits (Reich et al. 2003, Violle et al. 2007, Webb et al. 2010). Furthermore, they support that the major whole-plant trait spectra reflect adaptations to key environmental drivers in temperate forests corroborating the prevalence of fundamental functional tradeoffs defining fundamental plant strategies (Smith and Huston 1989, Pacala et al. 1996, Poorter and Markesteijn 2008) but with substantial differences between gymnosperms and angiosperms. However, we also identified trait spectra which are not related to any of the performance measures used or which reflect clearly the differences between the major clades suggesting that there are also other factors (e.g., evolutionary history) explaining major trait variation.

Whole-plant trait spectra reflect fundamental strategies and differences between basal phylogenetic groups

When all 305 species are considered together, the difference between gymnosperms and angiosperms is captured by the first major PCoA axis. This strong phylogenetic signal essentially reflects the two dominant plant functional types that differ in leaf traits such as SLA, leaf type (evergreen needle-leaved versus deciduous broad-leaved), conduit type (tracheids versus vessels) and resprouting capacity. The strong correlation between SLA and the first major axis highlights its importance as a lineage separating trait in addition to reflecting ecological strategies (Diaz et al. 2004). We also found a weak but significant correlation between growth rate and the first major axis. Overall, this supports the notion that SLA could be used as a weak proxy for growth rate in adult trees (Wright et al. 2010). The correlation of water-logging and fire tolerance with the first axis supports the difference in functionality between the two major clades and indicates phylogenetic conservatism.

In contrast to the first axis, the traits associated with the second major axis are consistent for both clades and are positively correlated with drought tolerance and negatively with growth rate. In our study, the drought tolerant species have a lower growth rate and are characterized by a tree/shrub like growth form with high seed mass, high wood density and a taproot. High seed mass enables the rapid development of a taproot, which allows seedlings to escape dry surface soil conditions and enhances survival rates (Leishman and Westoby 1994). High wood density tends to be associated with low minimum leaf water potentials, deep rooting ability (Brodribb and Feild 2000, Bucci et al. 2004) and increases resistance to drought-induced xylem embolism (Hacke et al. 2001). Thus a complex spectrum of traits involving demographic traits (seed mass), anatomical (wood density) and morphological (taproot) is governing drought tolerance. The fact that the same set of traits governs drought tolerance in the otherwise contrasting gymno- and angiosperms emphasizes their ecological relevance. Our results also suggest that water availability is a key driver of tree growth in North American forests and that the growth rate is low in species adapted to drought. The high

wood density associated with drought tolerance could be one indirect factor leading to reduced growth rate—a relationship frequently reported for tropical tree species (Muller-Landau 2004).

Fundamental relationships between drought, shade tolerance, and growth rate are reflected by whole-plant trait spectra within gymnosperms and angiosperms

Shade and drought tolerance are inversely related, but the strength of this relationship differs between gymnosperms (strong correlation) and angiosperms (weak correlation) (Niinemets and Valladares 2006). Our results reveal that different trait spectra underlie the shade versus drought tolerance relationship for gymnosperms and angiosperms, reflecting different trait tradeoffs between these two major clades.

In the gymnosperms, the negative correlation between shade and drought tolerance was reflected by one trait spectrum (large maximum height and shallow roots in shade tolerant species versus small maximum height and taproots in drought tolerant species). This reflects a tradeoff between allocation to roots versus shoots (Fig. 2B). Traits reflecting growth rate are unrelated to the trait spectrum reflecting shade/drought tolerance. This could reflect a true independence, or it may be masking a non-linear, hump-shaped relationship between growth rate and the drought-shade tolerance axis (Smith and Huston 1989, Craine 2009) because the linear methods used here are not suited to identify such non-linearity. However, the very nature of the trait spectrum reflecting high growth rates suggests independent strategies. For example, gymnosperms with high growth rate tend to be trees with large maximum heights and with thick bark that possess the ability to resprout, suggesting a relationship to disturbance strategies, which are expected to be independent of drought/shade tolerance strategies (Loehle 2000).

In the angiosperms, two independent trait spectra imply a difference between the three strategies with respect to shade, drought, and water-logging tolerance (Fig. 3C and D) suggesting different tradeoffs. Shade and drought intolerant angiosperms (e.g., species in *Betula* and *Populus*) are tolerant to water-logging and represent a resource use strategy suited to quickly exploit suitable habitats (tall stature,

small wind dispersed seeds, high vegetative spread rates) at the cost of protection and maintenance structures (soft wood)—a typical pioneer trait association. In agreement with Smith and Huston (1989), these species tend to have higher growth rates compared to species that are tolerant to either shade or drought stress. Furthermore, our study agrees with Niinemets and Valladares (2006) in that the deciduous broad-leaved habit is a feature of shade and drought intolerance in North American forests, while evergreen broad-leaved habit tends to be a feature of species able to tolerate these stresses. Shade tolerant species (e.g., species of *Acer*) attain a relatively small stature, and light interception is enhanced by oppositely arranged leaves with a high SLA; these species also support shallow roots and produce toxic defense chemicals. High SLA is typical of winter-deciduous, shade tolerant trees growing in the understory (Lusk and Warton 2007), while the production of toxic defense chemicals might enhance their resistance to herbivores, making such species strong competitors (Kitajima 1994). Drought tolerant angiosperms (e.g., evergreen species of *Quercus*) exhibit a conservative resource use strategy with trait associations aligning with those reported by Markesteijn and Poorter (2009): slow nutrient turnover and long residence times (low SLA), high investment in protection and survival structures (dense wood, thick bark, heavy seeds), combined with features favored under low water availability (taproot and ring-porous wood).

Whole-plant trait spectra independent of growth rate, shade, and drought tolerance

In the angiosperm-only analysis, leaf composition and allelopathy co-vary (composite leaves paired with high potential for allelopathy versus simple leaves paired with low potential for allelopathy) and explain the second major axis. This axis is strongly determined by phylogeny as it separates species in the genera *Fraxinus* (Oleaceae), *Carya*, *Juglans* (Juglandaceae), and *Aesculus* (Sapindaceae) with composite leaves from those with single leaves (Fig. 3A and B); this axis is also independent of growth rate and drought or shade tolerance (Table 2). The fact that leaf composition is not related to shade tolerance has been observed in different deciduous woody floras (Stowe and Brown 1981, Niinemets 1998, Malhado et al. 2010).

Species with composite leaves tend to have low branching costs that allow rapid vertical growth during favorable light conditions, which is equally relevant for shade intolerant early successional (Givnish 1978) and shade tolerant late successional (Niinemets 1998). Stowe and Brown (1981) and Malhado et al. (2010) showed that leaf composition was related to climatic variables (e.g., spring and summer temperatures and variation in rainfall and water deficits), in such a way that seasonal drought favors composite leaves. Adaptations to episodic drought events are expected to differ from adaptations to persistent drought (Craine 2009), which may explain why we found leaf composition to be independent to trait associations reflecting high drought tolerance. High allelopathic interference more commonly occurs in stressful environments (Blanco 2007), such as under extremes in water and temperature and rapid successional changes. Thus, the co-variation of allelopathy and composite leaves seems to be an indirect relationship that merely emerges from phylogenetic relatedness.

Significance of the results in terms of data and methodological limitations

The results reported in this study could be influenced by the uncertainty caused by intra-specific variability, the choice of traits and by assignment errors in categorical traits and performance indices and the methods used. Our approach to filling-in missing species-level trait data with genus means had little influence on the results (data not shown).

The influence of intra-specific variability is likely to be negligible because we quantified tradeoffs based on 23 traits, with many traits describing morphological features (e.g., leaf arrangement) that are expected to be largely fixed for a given species; however, some traits (e.g., SLA) are likely to vary within a species (Ogle et al. 2012). However, Albert et al. (2010) found that the PCoA solution based on continuous traits exhibiting considerable intra-specific variability remains stable irrespective of whether an analysis was conducted at the species, population, or individual level. Furthermore, in our analysis, species are distributed across large environmental gradients, which is likely to lead to greater inter-species compared to intra-species trait variability (Kattge et al. 2011).

The incorporation of other potentially important traits, such as leaf area, mycorrhiza-associations, fine root diameter, serotiny or twig thickness might have the potential to detect novel tradeoffs (e.g., tradeoffs related to fire tolerance which we could not identify within the major clades), sharpen or slightly modify tradeoffs and strategies found. However, weak correlation between performance measures and the first three major axes might also depend on the resolution and information the indices are based on. Thus, fire tolerance and growth rate should rather be viewed as coarse approximations because they are primarily based on field observations, expert knowledge and estimates from the literature and not on precise measurements or experiments. However, drought tolerance and shade tolerance values used are reliable because they either are directly based on specific plant survival and site condition measurements or correlated well with species-specific values based on such measurements (see *Material and Methods* for details). Thus, the weak correlation of shade tolerance with the third axis analyzing the angiosperms might rather be caused by the complex interactions of functional traits. Moreover, we found a significant strong correlation of shade tolerance with the fifth PCoA axis (data not shown) suggesting that there are several different trait solutions for being shade tolerant (Valladares and Niinemets 2008).

Generally, our analysis is meant to be exploratory and aims to reveal the most important trait spectra in the first part and explores in the second part whether they reflect whole-plant performances describing fundamental ecological strategies or not. In this way it allows the exploration of novel trait spectra (e.g., the second axis in the angiosperm-only analysis) and hypothesis about underlying factors (e.g., adaptation to seasonal drought or phylogenetic constraints), which could be tested in a second step using appropriate designs (e.g., permutations and null-models). However, constrained analyses, e.g., distance-based Redundancy Analysis revealing the trait spectra which are best explained by the performance measures, yielded nearly identical results (analyses not shown), and thus underpins that adaptation to light and water availability are indeed important factors explaining major trait variation in North American

woody species.

Phylogenetic signal

An explicit quantification of the phylogenetic signal is challenging in this study because we imputed missing species-specific traits with genus means, which could artificially inflate the phylogenetic signal. The analysis involving the complete species pool suggests a trivial phylogenetic signal related to differences in trait strategies between gymnosperms and angiosperms. Thus, performing the separate analyses for these two major clades resulted in a coarse phylogenetic correction (Diaz et al. 2004). Comparison of these three analyses enabled us to identify important trait-performance relationships that differed between these two groups, representing potential adaptations that arose early in the evolution of these two major clades. Niinemets and Valladares (2006) found a significant phylogenetic signal in shade and drought tolerances, which pointed to trait conservatism operating between species within genera. Thus, the trait associations uncovered in this study are potentially not phylogenetically independent at, for example, the genus level. For instance, trait spectra related to drought and shade tolerance often grouped species by genera (Fig. 3); conversely, species are widely spread along the trait spectrum reflecting growth rate, and their position appears to be independent of their genus affiliation (Fig. 2).

Whole-plant trait spectra support plant strategies schemes

Comparing our whole-plant trait spectra with strategy axes of existing plant strategy schemes we found consensus but also insufficiency. For example, the widely used LHS scheme of Westoby (1998) was not sufficient to describe the main axes of trait variation of temperate woody species. The LHS scheme was moderately useful for understanding the trait spectra of angiosperms; for example, SLA (L), maximum tree height (H), and seed mass (S) were independent and contribute to complex spectra reflecting adaptation to shade and drought stress. However, among gymnosperms, SLA was irrelevant for describing inverse adaptations to drought and shade. The differential importance of SLA reflects the contrasting relationship between SLA and

leaf life span for evergreen needle-leaved (little variation in SLA and large variation in leaf life span) versus deciduous broad-leaved species (large variation in SLA and little variation in life span, which reflects growing season length). The differential importance of maximum tree height with respect to plant performance indices might reflect different strategies that are controlled by different tradeoffs (Falster and Westoby 2005). In angiosperms, tall stature and fast growth correlate with a stress intolerant strategy, which might trade off with lower productivity (e.g., small stature and slow growth) when shade or drought tolerance increases. Conversely, in gymnosperms, the tall stature of shade tolerant species might be the result of competition for light.

Resprouting and leaf composition might represent additional dimensions reflecting responses to disturbance or periodic stresses that are not captured by the LHS scheme. Thus, the extension to four axes that includes resprouting capacity (Loehle 2000) seems justified for North American forests, but this may still be insufficient. The inclusion of additional traits related to adaptations dealing with disturbance and/or reflecting competitive strength would likely improve upon these existing schemata.

Conclusion

Our study shows that major whole-plant trait spectra of North American woody species are related to performance indices of growth and tolerance to shade, drought and water-logging that reflect whole-plant strategies with respect to growth, reproduction, and survival along environmental gradients in forests (light, water and disturbance). The whole-plant trait spectra related to performance measures are compound of morphological, anatomical and demographic traits and interact with each other, corroborating the assumption of fundamental functional tradeoffs between stress tolerances and growth. Ideal measures of plant performance would include direct observations of vital rates in response to environmental drivers, and a growing number of studies use repeated forest inventories to estimate these rates and relate them to local trait databases (Poorter et al. 2008, Martínez Vilalta et al. 2010, Poorter et al. 2010, Wright et al. 2010). However, this has not been accomplished for a complete continental flora encompassing a wide

range of long-lived species and contrasting environments. In this sense, our approach represents a macro-ecological complement to the growing field of the ‘rates and traits’ research. Moreover, it might be an appropriate way to associate the principles of fundamental conceptual strategy schemes (Grime 1977, Smith and Huston 1989, Grubb 1998, Craine 2009) with information on traits to refine current trait-based schemes and to identify underlying tradeoffs.

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LITERATURE CITED

- Adams, J. M., W. A. Green, and Y. Zhang. 2008. Leaf margins and temperature in the North American flora: Recalibrating the paleoclimatic thermometer. *Global and Planetary Change* 60:523–534.
- Albert, C. H., W. Thuiller, N. G. Yoccoz, R. Douzet, S. Aubert, and S. Lavorel. 2010. A multi trait approach reveals the structure and the relative importance of intra vs. interspecific variability in plant traits. *Functional Ecology* 24:1192–1201.
- Baraloto, C., C. E. T. Paine, L. Poorter, J. Beauchene, D. Bonal, A. M. Domenach, B. Herault, S. Patino, J. C. Roggy, and J. Chave. 2010. Decoupled leaf and stem economics in rain forest trees. *Ecology Letters* 13:1338–1347.
- Blanco, J. A. 2007. The representation of allelopathy in ecosystem-level forest models. *Ecological Modelling* 209:65–77.
- Bond, W. J., and J. J. Midgley. 2001. Ecology of sprouting in woody plants: the persistence niche.

- Trends in Ecology & Evolution 16:45–51.
- Brodribb, T. J., and T. S. Feild. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: evidence from New Caledonian and Tasmanian rainforests. *Plant, Cell & Environment* 23:1381–1388.
- Bucci, S. J., G. Goldstein, F. C. Meinzer, F. G. Scholz, A. C. Franco, and M. Bustamante. 2004. Functional convergence in hydraulic architecture and water relations of tropical savanna trees: from leaf to whole plant. *Tree Physiology* 24:891.
- Burns, R. M., and B. H. Honkala, tech. coords. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654. U.S. Department of Agriculture. Forest Service, Washington, D.C., USA.
- Chave, J., D. Coomes, S. Jansen, S. L. Lewis, N. G. Swenson, and A. E. Zanne. 2009. Towards a worldwide wood economics spectrum. *Ecology Letters* 12:351–366.
- Coder, K. D. 1999. Potential allelopathy in different tree species. University of Georgia, Daniel B. Warnell School of Forest Resources Extension publication FOR99-003.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Diaz, N. Buchmann, D. E. Gurvich, P. B. Reich, H. ter Steege, H. D. Morgan, M. G. A. van der Heijden, J. G. Pausas, and H. Poorter. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51:335–380.
- Craine, J. M. 2009. *Resource strategies of wild plants*. Princeton University Press, Princeton, New Jersey, USA.
- Dallwitz, M. J., T. A. Paine, and E. J. Zurcher. 1993. User's guide to the DELTA system: a general system for processing taxonomic descriptions. <http://delta-intkey.com>
- Diaz, S., J. G. Hodgson, K. Thompson, M. Cabido, J. H. C. Cornelissen, A. Jalili, G. Montserrat-Marti, J. P. Grime, F. Zarrinkamar, Y. Asri, S. R. Band, S. Basconcelo, P. Castro-Diez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Perez-Harguindeguy, M. C. Perez-Rontome, F. A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martinez, A. Romo-Diez, S. Shaw, B. Siavash, P. Villar-Salvador, and M. R. Zak. 2004. The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science* 15:295–304.
- Falster, D. S., and M. Westoby. 2005. Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology* 93:521–535.
- Flora of North America Editorial Committee. 1993. *Flora of North America North of Mexico*. 16+volumes. Flora of North America Association, New York, New York, USA. <http://floranorthamerica.org/>
- Givnish, T. J. 1978. On the adaptive significance of compound leaves, with particular reference to tropical trees. Pages 351–380 in P. Tomlinson, B. and M. H. Zimmerman, editors. *Tropical trees as living systems*. Cambridge University Press, Cambridge, UK.
- Gower, J. C. 1971. General coefficient of similarity and some of its properties. *Biometrics* 27:857–871.
- Grime, J. P. 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:1169–1194.
- Grime, J. P., K. Thompson, R. Hunt, J. G. Hodgson, J. H. C. Cornelissen, I. H. Rorison, G. A. F. Hendry, T. W. Ashenden, A. P. Askew, S. R. Band, R. E. Booth, C. C. Bossard, B. D. Campbell, J. E. L. Cooper, A. W. Davison, P. L. Gupta, W. Hall, D. W. Hand, M. A. Hannah, S. H. Hillier, D. J. Hodgkinson, A. Jalili, Z. Liu, J. M. L. Mackey, N. Matthews, M. A. Mowforth, A. M. Neal, R. J. Reader, K. Reiling, W. Ross-Fraser, R. E. Spencer, F. Sutton, D. E. Tasker, P. C. Thorpe, and J. Whitehouse. 1997. Integrated screening validates primary axes of specialisation in plants. *Oikos* 79:259–281.
- Grubb, P. J. 1998. A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics* 1:3–31.
- Hacke, U. G., J. S. Sperry, W. T. Pockman, S. D. Davis, and K. A. McCulloh. 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126:457–461.
- Hallik, L., U. Niinemets, and I. J. Wright. 2009. Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in Northern Hemisphere temperate woody flora? *New Phytologist* 184:257–274.
- Inside Wood. 2004. <http://insidewood.lib.ncsu.edu/search>
- Jenkins, J. C., D. C. Chojnacky, L. S. Heath, and R. A. Birdsey. 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. General Technical Report NE-319. USDA Forest Service, Northeastern Research Station, Newtown Square, Pennsylvania, USA.
- Kattge, J., S. Diaz, S. Lavorel, I. C. Prentice, P. Leadley, G. Bönisch, E. Garnier, M. Westoby, P. B. Reich, I. J. Wright, J. H. C. Cornelissen, C. Violle, S. P. Harrison, P. M. van Bodegom, M. Reichstein, B. J. Enquist, N. A. Soudzilovskaia, D. D. Ackerly, M. Anand, O. Atkin, M. Bahn, T. R. Baker, D. Baldocchi, R. Bekker, C. C. Blanco, B. Blonder,

- W. J. Bond, R. Bradstock, D. E. Bunker, F. Casanoves, J. Cavender-Bares, J. Q. Chambers, F. S. Chapin, J. Chave, D. Coomes, W. K. Cornwell, J. M. Craine, B. H. Dobrin, L. Duarte, W. Durka, J. Elser, G. Esser, M. Estiarte, W. F. Fagan, J. Fang, F. Fernández-Méndez, A. Fidelis, B. Finegan, O. Flores, H. Ford, D. Frank, G. T. Freschet, N. M. Fyllas, R. V. Gallagher, W. A. Green, A. G. Gutierrez, T. Hickler, S. Higgins, J. G. Hodgson, A. Jalili, S. Jansen, C. Joly, A. J. Kerkhoff, D. O. N. Kirkup, K. Kitajima, M. Kleyer, S. Klotz, J. M. H. Knops, K. Kramer, I. Kühn, H. Kurokawa, D. Laughlin, T. D. Lee, M. Leishman, F. Lens, T. Lenz, S. L. Lewis, J. O. N. Lloyd, J. Llusia, F. Louault, S. Ma, M. D. Mahecha, P. Manning, T. Massad, B. Medlyn, J. Messier, A. T. Moles, S. C. Müller, K. Nadrowski, S. Naeem, Ü. Niinemets, S. Nöllert, A. Nüske, R. Ogaya, J. Oleksyn, V. G. Onipchenko, Y. Onoda, J. Ordoñez, G. Overbeck, W. A. Ozinga, S. Patino, S. Paula, J. G. Pausas, J. Peñuelas, O. L. Phillips, V. Pillar, H. Poorter, L. Poorter, P. Poschlod, A. Prinzing, R. Proulx, A. Rammig, S. Reinsch, B. Reu, L. Sack, B. Salgado-Negret, J. Sardans, S. Shiodera, B. Shipley, A. Siefert, E. Sosinski, J.-F. Soussana, E. Swaine, N. Swenson, K. E. N. Thompson, P. Thornton, M. Waldram, E. Weiher, M. White, S. White, S. J. Wright, B. Yguel, S. Zaehle, A. E. Zanne, and C. Wirth. 2011. TRY—a global database of plant traits. *Global Change Biology* 17:2905–2935.
- Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428.
- Lavorel, S., S. Díaz, J. Cornelissen, E. Garnier, S. Harrison, S. McIntyre, J. Pausas, N. Pérez-Harguindeguy, C. Roumet, and C. Urceley. 2007. Plant functional types: are we getting any closer to the Holy Grail? Pages 149–164 in J. G. Canadell, D. E. Pataki, and L. Pitelka, editors. *Terrestrial ecosystems in a changing world*. Springer, Berlin, Germany.
- Legendre, P., and L. Legendre. 1998. *Numerical ecology*. Second English edition. Elsevier Science, Amsterdam, The Netherlands.
- Leishman, M. R., and M. Westoby. 1994. The role of seed size in seedling establishment in dry soil conditions—experimental evidence from semi-arid species. *Journal of Ecology* 82:249–258.
- Lichstein, J. W., J. Dushoff, K. Ogle, A. Chen, D. W. Purves, J. P. Caspersen, and S. W. Pacala. 2010. Unlocking the forest inventory data: relating individual tree performance to unmeasured environmental factors. *Ecological Applications* 20:684–699.
- Loehle, C. 2000. Strategy space and the disturbance spectrum: A life-history model for tree species coexistence. *American Naturalist* 156:14–33.
- Lusk, C. H., and D. I. Warton. 2007. Global meta-analysis shows that relationships of leaf mass per area with species shade tolerance depend on leaf habit and ontogeny. *New Phytologist* 176:764–774.
- Malhado, A. C. M., R. J. Whittaker, Y. Malhi, R. J. Ladle, H. ter Steege, O. Phillips, L. Aragao, T. R. Baker, L. Arroyo, S. Almeida, N. Higuchi, T. J. Killeen, A. Monteagudo, N. C. A. Pitman, A. Prieto, R. P. Salomao, R. Vasquez-Martinez, W. F. Laurance, and H. Ramirez-Angulo. 2010. Are compound leaves an adaptation to seasonal drought or to rapid growth? Evidence from the Amazon rain forest. *Global Ecology and Biogeography* 19:852–862.
- Markestijn, L., and L. Poorter. 2009. Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology* 97:311–325.
- Martínez Vilalta, J., M. Mencuccini, J. Vayreda, and J. Retana. 2010. Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *Journal of Ecology* 98:1462–1475.
- McGill, B. J., B. J. Enquist, E. Weiher, and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21:178–185.
- Miles, P. D., G. J. Brand, C. L. Alerich, L. F. Bednar, S. W. Woudenberg, J. F. Glover, and E. N. Ezell. 2001. *The Forest Inventory and Analysis Database: description and users manual*. Version 1.0. USDA Forest Service, North Central Forest Experiment Station, Washington, D.C., USA.
- Moles, A. T., D. D. Ackerly, C. O. Webb, J. C. Tweddle, J. B. Dickie, and M. Westoby. 2005. A brief history of seed size. *Science* 307:576–580.
- Muller-Landau, H. C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36:20–32.
- Niinemets, U. 1998. Are compound-leaved woody species inherently shade-intolerant? An analysis of species ecological requirements and foliar support costs. *Plant Ecology* 134:1–11.
- Niinemets, U., and F. Valladares. 2006. Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* 76:521–547.
- Ogle, K., J. Barber, and K. Sartor. 2012. Feedback and modularization in a Bayesian meta-analysis of tree traits affecting forest dynamics. *Bayesian Analysis* 7:771–806.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs*

- 66:1–43.
- Paula, S., M. Arianoutsou, D. Kazanis, Ā. Tavsanoğlu, F. Lloret, C. Buhk, F. Ojeda, B. Luna, J. M. Moreno, and A. Rodrigo. 2009. Fire-related traits for plant species of the Mediterranean Basin. *Ecology* 90:1420–1420.
- Pausas, J. G., and S. Lavorel. 2003. A hierarchical deductive approach for functional types in disturbed ecosystems. *Journal of Vegetation Science* 14:409–416.
- Pavoine, S., J. Vallet, A. B. Dufour, S. Gachet, and H. Daniel. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118:391–402.
- Poorter, H., and A. Van der Werf. 1998. Is inherent variation in RGR determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. Pages 309–336 *in* H. Lambers, H. Poorter, and M. M. I. Van Vuuren, editors. *Inherent variation in plant growth: physiological mechanisms and ecological consequences*. Backhuys, Leiden, The Netherlands.
- Poorter, L., and L. Markesteijn. 2008. Seedling traits determine drought tolerance of tropical tree species. *Biotropica* 40:321–331.
- Poorter, L., I. McDonald, A. Alarcon, E. Fichtler, J. C. Licona, M. Pena-Claros, F. Sterck, Z. Villegas, and U. Sass-Klaassen. 2010. The importance of wood traits and hydraulic conductance for the performance and life history strategies of 42 rainforest tree species. *New Phytologist* 185:481–492.
- Poorter, L., S. J. Wright, H. Paz, D. D. Ackerly, R. Condit, G. Ibarra-Manríquez, K. E. Harms, J. C. Licona, M. Martínez-Ramos, S. J. Mazer, H. C. Müller-Landau, M. Pena-Claros, C. O. Webb, and I. J. Wright. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. *Ecology* 89:1908–1920.
- R Development Core Team. 2010. R: a language and environment for statistical computing. Version 2.11.0. R Foundation for Statistical Computing, Vienna, Austria.
- Reich, P. B., I. J. Wright, J. Cavender-Bares, J. M. Craine, J. Oleksyn, M. Westoby, and M. B. Walters. 2003. The evolution of plant functional variation: Traits, spectra, and strategies. *International Journal of Plant Sciences* 164:S143–S164.
- Royal Botanical Garden KEW. 2008. Seed information database. Version 7.1. <http://data.kew.org/sid/>
- Rüger, N., C. Wirth, S. J. Wright, and R. Condit. 2012. Functional traits explain light and size response of growth rates in tropical tree species. *Ecology* 93:2626–2636.
- Sack, L. 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos* 107:110–127.
- Smith, T., and M. Huston. 1989. A theory of the spatial and temporal dynamics of plant-communities. *Vegetatio* 83:49–69.
- Stowe, L. G., and J. L. Brown. 1981. A geographic perspective on the ecology of compound leaves. *Evolution* 35:818–821.
- The Plant List. 2010. <http://www.theplantlist.org/>
- USDA, NRCS, National Plant Data Team. 2007. The PLANTS Database. <http://plants.usda.gov/java/>
- U.S. Geological Survey. 1999. Digital representation of “Atlas of United States Trees” by Elbert L. Little, Jr. U.S. Geological Survey Professional Paper 1650. <http://pubs.usgs.gov/pp/p1650-a/>
- Useche, A., and B. Shipley. 2010. Interspecific correlates of plasticity in relative growth rate following a decrease in nitrogen availability. *Annals of Botany* 105:333.
- Valladares, F., and U. Niinemets. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology Evolution and Systematics* 39:237–257.
- Violle, C., M. L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel, and E. Garnier. 2007. Let the concept of trait be functional! *Oikos* 116:882–892.
- Webb, C. T., J. A. Hoeting, G. M. Ames, M. I. Pyne, and N. L. Poff. 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology Letters* 13:267–283.
- Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199:213–227.
- Wirth, C., and J. W. Lichstein. 2009. The imprint of succession on old-growth forest carbon balances: insights from a trait-based model of forest dynamics. Pages 81–113 *in* C. Wirth, G. Gleixner, and M. Heimann, editors. *Old-growth forests: function, fate and value*. Springer Verlag, New York, New York, USA.
- Willmott, C. J., and K. Matsuura. 2007. Terrestrial water budget data archive: monthly time series (1950–1999). http://climate.geog.udel.edu/~climate/html_pages/README.wb_ts2.html
- Wright, I. J., D. D. Ackerly, F. Bongers, K. E. Harms, G. Ibarra-Manríquez, M. Martínez-Ramos, S. J. Mazer, H. C. Müller-Landau, H. Paz, N. C. A. Pitman, L. Poorter, M. R. Silman, C. F. Vriesendorp, C. O. Webb, M. Westoby, and S. J. Wright. 2007. Relationships among ecologically important dimensions of plant trait variation in seven Neotropical forests. *Annals of Botany* 99:1003–1015.
- Wright, I. J., P. B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares, T. Chapin, J. H. C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias, K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.-L. Navas, U. Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. Prior, V. I. Pyankov, C. Roumet,

- S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, and R. Villar. 2004. The worldwide leaf economics spectrum. *Nature* 428:821–827.
- Wright, S. J., K. Kitajima, N. J. B. Kraft, P. B. Reich, I. J. Wright, D. E. Bunker, R. Condit, J. W. Dalling, S. J. Davies, S. Diaz, B. M. J. Engelbrecht, K. E. Harms, S. P. Hubbell, C. O. Marks, M. C. Ruiz-Jaen, C. M. Salvador, and A. E. Zanne. 2010. Functional traits and the growth-mortality trade-off in tropical trees. *Ecology* 91:3664–3674.
- Zanne, A. E., G. Lopez-Gonzalez, D. A. Coomes, J. Ilic, S. Jansen, S. L. Lewis, R. B. Miller, N. G. Swenson, M. C. Wiemann, and J. Chave. 2009. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository doi: 10.5061/dryad.234

SUPPLEMENTAL MATERIAL APPENDIX A

Table A1. List of taxa names used for the analyses and accepted names after name-checking.

Taxa names used for analyses	Comments	Accepted taxa names†
<i>Abies amabilis</i>		<i>Abies amabilis</i> (Douglas ex Loudon) J.Forbes
<i>Abies balsamea</i>		<i>Abies balsamea</i> (L.) Mill.
<i>Abies bracteata</i>		<i>Abies bracteata</i> (D.Don) Poit.
<i>Abies concolor</i>		<i>Abies concolor</i> (Gordon) Lindl. ex Hildebr.
<i>Abies fraseri</i>		<i>Abies fraseri</i> (Pursh) Poir.
<i>Abies grandis</i>		<i>Abies grandis</i> (Douglas ex D.Don) Lindl.
<i>Abies lasiocarpa</i>		<i>Abies lasiocarpa</i> (Hook.) Nutt.
<i>Abies lasiocarpa</i> var. <i>arizonica</i>		<i>Abies lasiocarpa</i> var. <i>arizonica</i> (Merriam) Lemmon
<i>Abies magnifica</i>		<i>Abies magnifica</i> A.Murray bis
<i>Abies magnifica</i> var. <i>shastensis</i>		<i>Abies magnifica</i> var. <i>shastensis</i> Lemmon
<i>Abies procera</i>		<i>Abies procera</i> Rehder
<i>Acer barbatum</i>	synonymy not resolvable without specific authority	<i>Acer</i> (<i>barbatum</i>)
<i>Acer glabrum</i>		<i>Acer glabrum</i> Torr.
<i>Acer grandidentatum</i>	synonym	<i>Acer saccharum</i> subsp. <i>grandidentatum</i> (Torr. & A.Gray) Desmarais
<i>Acer leucoderme</i>	synonym	<i>Acer saccharum</i> subsp. <i>leucoderme</i> (Small) Desmarais
<i>Acer macrophyllum</i>		<i>Acer macrophyllum</i> Pursh
<i>Acer negundo</i>		<i>Acer negundo</i> L.
<i>Acer nigrum</i>	synonym	<i>Acer saccharum</i> subsp. <i>nigrum</i> (F.Michx.) Desmarais
<i>Acer pensylvanicum</i>		<i>Acer pensylvanicum</i> L.
<i>Acer platanoides</i>		<i>Acer platanoides</i> L.
<i>Acer rubrum</i>		<i>Acer rubrum</i> L.
<i>Acer saccharinum</i>		<i>Acer saccharinum</i> L.
<i>Acer saccharum</i>		<i>Acer saccharum</i> Marshall
<i>Acer spicatum</i>		<i>Acer spicatum</i> Lam.
<i>Aesculus californica</i>		<i>Aesculus californica</i> (Spach) Nutt.
<i>Aesculus glabra</i>		<i>Aesculus glabra</i> Willd.
<i>Aesculus glabra</i> var. <i>arguta</i>		<i>Aesculus glabra</i> var. <i>arguta</i> (Buckley) Rob.
<i>Aesculus octandra</i>	synonym	<i>Aesculus flava</i> Sol.
<i>Ailanthus altissima</i>		<i>Ailanthus altissima</i> (Mill.) Swingle
<i>Albizia julibrissin</i>		<i>Albizia julibrissin</i> Durazz.
<i>Alnus glutinosa</i>		<i>Alnus glutinosa</i> (L.) Gaertn.
<i>Alnus rhombifolia</i>		<i>Alnus rhombifolia</i> Nutt.
<i>Alnus rubra</i>		<i>Alnus rubra</i> Bong.
<i>Arbutus menziesii</i>		<i>Arbutus menziesii</i> Pursh
<i>Asimina triloba</i>		<i>Asimina triloba</i> (L.) Dunal
<i>Betula alleghaniensis</i>		<i>Betula alleghaniensis</i>
<i>Betula lenta</i>		<i>Betula lenta</i> L.
<i>Betula nigra</i>		<i>Betula nigra</i> L.
<i>Betula occidentalis</i>		<i>Betula occidentalis</i> Hook.
<i>Betula papyrifera</i>		<i>Betula papyrifera</i> Marshall
<i>Betula papyrifera</i> var. <i>commutata</i>	synonym	<i>Betula papyrifera</i> Marshall var. <i>papyrifera</i>
<i>Betula papyrifera</i> var. <i>subcordata</i>	synonym	<i>Betula papyrifera</i> Marshall var. <i>papyrifera</i>
<i>Betula populifolia</i>		<i>Betula populifolia</i> Marshall
<i>Bumelia lanuginosa</i>	synonym	<i>Sideroxylon lanuginosum</i> Michx.
<i>Calocedrus decurrens</i>		<i>Calocedrus decurrens</i> (Torr.) Florin

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
<i>Carpinus caroliniana</i>		<i>Carpinus caroliniana</i> Walter
<i>Carya aquatica</i>		<i>Carya aquatica</i> (F.Michx.) Nutt. ex Elliott
<i>Carya cordiformis</i>		<i>Carya cordiformis</i> (Wangenh.) K.Koch
<i>Carya glabra</i>		<i>Carya glabra</i> (Mill.) Sweet
<i>Carya illinoensis</i>		<i>Carya illinoensis</i> (Wangenh.) K.Koch
<i>Carya laciniata</i>		<i>Carya laciniata</i> (F.Michx.) G.Don
<i>Carya myristiciformis</i>		<i>Carya myristiciformis</i> (F.Michx.) Nutt. ex Elliott
<i>Carya ovata</i>		<i>Carya ovata</i> (Mill.) K.Koch
<i>Carya pallida</i>		<i>Carya pallida</i> (Ashe) Engelm. & Graebn.
<i>Carya texana</i>		<i>Carya texana</i> Buckley
<i>Carya tomentosa</i>	synonym	<i>Carya alba</i> (L.) Nutt. ex Elliott
<i>Castanea dentata</i>		<i>Castanea dentata</i> (Marshall) Borkh.
<i>Castanea ozarkensis</i>		<i>Castanea ozarkensis</i> Ashe
<i>Castanea pumila</i>		<i>Castanea pumila</i> (L.) Mill.
<i>Catalpa bignonioides</i>		<i>Catalpa bignonioides</i> Walter
<i>Catalpa speciosa</i>		<i>Catalpa speciosa</i> (Warder ex Barney) Warder ex Engelm.
<i>Celtis laevigata</i>		<i>Celtis laevigata</i> Willd.
<i>Celtis occidentalis</i>		<i>Celtis occidentalis</i> L.
<i>Celtis reticulata</i>	synonym	<i>Celtis laevigata</i> var. <i>reticulata</i> (Torr.) Benson
<i>Cercis canadensis</i>		<i>Cercis canadensis</i> L.
<i>Cercocarpus ledifolius</i>	unresolved name	<i>Cercocarpus</i> (<i>ledifolius</i>)
<i>Cercocarpus ledifolius</i> var. <i>intricatus</i>	synonym	<i>Cercocarpus intricatus</i> S. Watson
<i>Cercocarpus montanus</i>		<i>Cercocarpus montanus</i> Raf.
<i>Cercocarpus montanus</i> var. <i>glaber</i>		<i>Cercocarpus montanus</i> var. <i>glaber</i> (S. Watson) F.L. Martin
<i>Cercocarpus montanus</i> var. <i>paucidentatus</i>		<i>Cercocarpus montanus</i> var. <i>paucidentatus</i> (S. Watson) F.L. Martin
<i>Chamaecyparis lawsoniana</i>		<i>Chamaecyparis lawsoniana</i> (A.Murray bis) Parl.
<i>Chamaecyparis nootkatensis</i>	synonym	<i>Xanthocyparis nootkatensis</i> (D.Don) Farjon & D.K.Harder
<i>Chamaecyparis thyoides</i>		<i>Chamaecyparis thyoides</i> (L.) Britton, Sterns & Poggenb.
<i>Chrysolepis chrysophylla</i>		<i>Chrysolepis chrysophylla</i> (Douglas ex Hook.) Hjelmq.
<i>Cladrastis kentukea</i>		<i>Cladrastis kentukea</i> (Dum.Cours.) Rudd
<i>Cornus florida</i>		<i>Cornus florida</i> L.
<i>Cornus nuttallii</i>		<i>Cornus nuttallii</i> Audubon ex Torr. & A.Gray
<i>Cotinus obovatus</i>		<i>Cotinus obovatus</i> Raf.
<i>Crataegus crus-galli</i>		<i>Crataegus crus-galli</i> L.
<i>Crataegus mollis</i>	synonym	<i>Oxyacantha mollis</i> (Scheele) Lunell
<i>Cupressus arizonica</i>		<i>Cupressus arizonica</i> Greene
<i>Cupressus bakeri</i>		<i>Cupressus bakeri</i> Jeps.
<i>Cupressus guadalupensis</i> var. <i>forbesii</i>		<i>Cupressus guadalupensis</i> var. <i>forbesii</i> (Jeps.) Little
<i>Cupressus macrocarpa</i>		<i>Cupressus macrocarpa</i> Hartw.
<i>Cupressus sargentii</i>		<i>Cupressus sargentii</i> Jeps.
<i>Diospyros virginiana</i>		<i>Diospyros virginiana</i> L.
<i>Elaeagnus angustifolia</i>		<i>Elaeagnus angustifolia</i> L.
<i>Fagus grandifolia</i>		<i>Fagus grandifolia</i> Ehrh.
<i>Fraxinus americana</i>		<i>Fraxinus americana</i> L.
<i>Fraxinus caroliniana</i>		<i>Fraxinus caroliniana</i> Mill.
<i>Fraxinus latifolia</i>		<i>Fraxinus latifolia</i> Benth.
<i>Fraxinus nigra</i>		<i>Fraxinus nigra</i> Marshall
<i>Fraxinus pennsylvanica</i>		<i>Fraxinus pennsylvanica</i> Marshall
<i>Fraxinus profunda</i>		<i>Fraxinus profunda</i> (Bush) Bush
<i>Fraxinus quadrangulata</i>		<i>Fraxinus quadrangulata</i> Michx.
<i>Fraxinus velutina</i>		<i>Fraxinus velutina</i> Torr.
<i>Gleditsia aquatica</i>		<i>Gleditsia aquatica</i> Marshall
<i>Gleditsia triacanthos</i>		<i>Gleditsia triacanthos</i> L.
<i>Gordonia lasianthus</i>		<i>Gordonia lasianthus</i> (L.) Ellis
<i>Gymnocladus dioicus</i>	synonym (spelling variant)	<i>Gymnocladus dioica</i> (L.) K.Koch
<i>Ilex opaca</i>	unresolved name	<i>Ilex</i> (<i>opaca</i>)
<i>Juglans californica</i>	unresolved name	<i>Juglans</i> (<i>californica</i>)
<i>Juglans cinerea</i>		<i>Juglans cinerea</i> L.
<i>Juglans hindsii</i>		<i>Juglans hindsii</i> Jeps. ex R.E. Sm.
<i>Juglans microcarpa</i>		<i>Juglans microcarpa</i> Berland.
<i>Juglans nigra</i>		<i>Juglans nigra</i> L.
<i>Juniperus ashei</i>		<i>Juniperus ashei</i> J.Buchholz

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
<i>Juniperus californica</i>		<i>Juniperus californica</i> Carrière
<i>Juniperus coahuilensis</i>		<i>Juniperus coahuilensis</i> (Martínez) Gausson ex R.P.Adams
<i>Juniperus communis</i>		<i>Juniperus communis</i> L.
<i>Juniperus deppeana</i>		<i>Juniperus deppeana</i> Steud.
<i>Juniperus monosperma</i>		<i>Juniperus monosperma</i> (Engelm.) Sarg.
<i>Juniperus occidentalis</i>		<i>Juniperus occidentalis</i> Hook.
<i>Juniperus osteosperma</i>		<i>Juniperus osteosperma</i> (Torr.) Little
<i>Juniperus pinchotii</i>		<i>Juniperus pinchotii</i> Sudw.
<i>Juniperus scopulorum</i>		<i>Juniperus scopulorum</i> Sarg.
<i>Juniperus silicicola</i>	synonym	<i>Juniperus virginiana</i> var. <i>silicicola</i> (Small) A.E.Murray
<i>Juniperus virginiana</i>		<i>Juniperus virginiana</i> L.
<i>Larix laricina</i>		<i>Larix laricina</i> (Du Roi) K.Koch
<i>Larix lyallii</i>		<i>Larix lyallii</i> Parl.
<i>Larix occidentalis</i>		<i>Larix occidentalis</i> Nutt.
<i>Liquidambar styraciflua</i>		<i>Liquidambar styraciflua</i> L.
<i>Liriodendron tulipifera</i>		<i>Liriodendron tulipifera</i> L.
<i>Lithocarpus densiflorus</i>		<i>Lithocarpus densiflorus</i> (Hook. & Arn.) Rehder
<i>Maclura pomifera</i>		<i>Maclura pomifera</i> (Raf.) C.K.Schneid.
<i>Magnolia acuminata</i>		<i>Magnolia acuminata</i> (L.) L.
<i>Magnolia fraseri</i>		<i>Magnolia fraseri</i> Walter
<i>Magnolia grandiflora</i>		<i>Magnolia grandiflora</i> L.
<i>Magnolia macrophylla</i>		<i>Magnolia macrophylla</i> Michx.
<i>Magnolia virginiana</i>		<i>Magnolia virginiana</i> L.
<i>Malus fusca</i>		<i>Malus fusca</i> (Raf.) C.K. Schneid.
<i>Melaleuca quinquenervia</i>		<i>Melaleuca quinquenervia</i> (Cav.) S.T.Blake
<i>Melia azedarach</i>		<i>Melia azedarach</i> L.
<i>Morus alba</i>		<i>Morus alba</i> L.
<i>Morus rubra</i>		<i>Morus rubra</i> L.
<i>Nyssa aquatica</i>		<i>Nyssa aquatica</i> L.
<i>Nyssa ogeche</i>		<i>Nyssa ogeche</i> Bartram ex Marshall
<i>Nyssa sylvatica</i>		<i>Nyssa sylvatica</i> Marshall
<i>Nyssa sylvatica</i> var. <i>biflora</i>		<i>Nyssa sylvatica</i> var. <i>biflora</i> (Walter) Sarg.
<i>Olneya tesota</i>		<i>Olneya tesota</i> A.Gray
<i>Ostrya virginiana</i>		<i>Ostrya virginiana</i> (Mill.) K.Koch
<i>Oxydendrum arboreum</i>		<i>Oxydendrum arboreum</i> (L.) DC.
<i>Paulownia tomentosa</i>		<i>Paulownia tomentosa</i> Steud.
<i>Persea borbonia</i>		<i>Persea borbonia</i> (L.) Spreng.
<i>Picea abies</i>		<i>Picea abies</i> (L.) H.Karst.
<i>Picea breweriana</i>		<i>Picea breweriana</i> S.Watson
<i>Picea engelmannii</i>		<i>Picea engelmannii</i> Parry ex Engelm.
<i>Picea glauca</i>		<i>Picea glauca</i> (Moench) Voss
<i>Picea mariana</i>		<i>Picea mariana</i> (Mill.) Britton, Sterns & Poggenb.
<i>Picea pungens</i>		<i>Picea pungens</i> Engelm.
<i>Picea rubens</i>		<i>Picea rubens</i> Sarg.
<i>Picea sitchensis</i>		<i>Picea sitchensis</i> (Bong.) Carrière
<i>Pinus albicaulis</i>		<i>Pinus albicaulis</i> Engelm.
<i>Pinus aristata</i>		<i>Pinus aristata</i> Engelm.
<i>Pinus attenuata</i>		<i>Pinus attenuata</i> Lemmon
<i>Pinus balfouriana</i>		<i>Pinus balfouriana</i> Balf.
<i>Pinus banksiana</i>		<i>Pinus banksiana</i> Lamb.
<i>Pinus cembroides</i>		<i>Pinus cembroides</i> Zucc.
<i>Pinus clausa</i>		<i>Pinus clausa</i> (Chapm. ex Engelm.) Vasey ex Sarg.
<i>Pinus contorta</i> var. <i>contorta</i>		<i>Pinus contorta</i> Douglas ex Loudon var. <i>contorta</i>
<i>Pinus contorta</i> var. <i>latifolia</i>		<i>Pinus contorta</i> var. <i>latifolia</i> Engelm.
<i>Pinus contorta</i> var. <i>murrayana</i>		<i>Pinus contorta</i> var. <i>murrayana</i> (Balf.) S.Watson
<i>Pinus coulteri</i>		<i>Pinus coulteri</i> D.Don
<i>Pinus discolor</i>	synonym	<i>Pinus cembroides</i> var. <i>bicolor</i> Little
<i>Pinus echinata</i>		<i>Pinus echinata</i> Mill.
<i>Pinus edulis</i>		<i>Pinus edulis</i> Engelm.
<i>Pinus elliottii</i>		<i>Pinus elliottii</i> Engelm.
<i>Pinus engelmannii</i>		<i>Pinus engelmannii</i> Carrière
<i>Pinus flexilis</i>		<i>Pinus flexilis</i> E.James
<i>Pinus glabra</i>		<i>Pinus glabra</i> Walter
<i>Pinus jeffreyi</i>		<i>Pinus jeffreyi</i> A.Murray bis
<i>Pinus lambertiana</i>		<i>Pinus lambertiana</i> Douglas
<i>Pinus leiophylla</i> var. <i>chihuahuana</i>		<i>Pinus leiophylla</i> var. <i>chihuahuana</i> (Engelm.) Shaw

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
<i>Pinus longaeva</i>		<i>Pinus longaeva</i> D.K.Bailey
<i>Pinus monophylla</i>		<i>Pinus monophylla</i> Torr. & Frém.
<i>Pinus monophylla</i> var. <i>fallax</i>	synonym	<i>Pinus monophylla</i> Torr. & Frém.
<i>Pinus monticola</i>		<i>Pinus monticola</i> Douglas ex D.Don
<i>Pinus muricata</i>		<i>Pinus muricata</i> D.Don
<i>Pinus nigra</i>		<i>Pinus nigra</i> J.F.Arnold
<i>Pinus palustris</i>		<i>Pinus palustris</i> Mill.
<i>Pinus ponderosa</i>		<i>Pinus ponderosa</i> Douglas ex C.Lawson
<i>Pinus ponderosa</i> var. <i>arizonica</i>	synonym	<i>Pinus arizonica</i> Engelm.
<i>Pinus pungens</i>		<i>Pinus pungens</i> Lamb.
<i>Pinus quadrifolia</i>		<i>Pinus quadrifolia</i> Parl. ex Sudw.
<i>Pinus radiata</i>		<i>Pinus radiata</i> D.Don
<i>Pinus resinosa</i>		<i>Pinus resinosa</i> Aiton
<i>Pinus rigida</i>		<i>Pinus rigida</i> Mill.
<i>Pinus sabiniana</i>		<i>Pinus sabiniana</i> Douglas
<i>Pinus serotina</i>		<i>Pinus serotina</i> Michx.
<i>Pinus strobiformis</i>		<i>Pinus strobiformis</i> Engelm.
<i>Pinus strobus</i>		<i>Pinus strobus</i> L.
<i>Pinus sylvestris</i>		<i>Pinus sylvestris</i> L.
<i>Pinus taeda</i>		<i>Pinus taeda</i> L.
<i>Pinus torreyana</i>		<i>Pinus torreyana</i> Parry ex Carrière
<i>Pinus virginiana</i>		<i>Pinus virginiana</i> Mill.
<i>Pinus washoensis</i>	synonym	<i>Pinus ponderosa</i> Douglas ex C.Lawson
<i>Planera aquatica</i>		<i>Planera aquatica</i> J.F.Gmel.
<i>Platanus occidentalis</i>		<i>Platanus occidentalis</i> L.
<i>Platanus racemosa</i>		<i>Platanus racemosa</i> Nutt.
<i>Populus alba</i>		<i>Populus alba</i> L.
<i>Populus angustifolia</i>		<i>Populus angustifolia</i> E. James
<i>Populus balsamifera</i>		<i>Populus balsamifera</i> L.
<i>Populus deltoides</i>		<i>Populus deltoides</i> W. Bartram ex Marshall
<i>Populus deltoides</i> var. <i>monilifera</i>	synonym	<i>Populus deltoides</i> var. <i>occidentalis</i> Rydb.
<i>Populus fremontii</i>		<i>Populus fremontii</i> S. Watson
<i>Populus grandidentata</i>	synonym	<i>Populus tremula</i> subsp. <i>grandidentata</i> (Michx.) Á. Löve & D. Löve
<i>Populus heterophylla</i>	unresolved name	<i>Populus</i> (<i>heterophylla</i>)
<i>Populus tremuloides</i>		<i>Populus tremuloides</i> Michx.
<i>Populus trichocarpa</i>		<i>Populus trichocarpa</i> Torr. & A. Gray
<i>Prosopis glandulosa</i> var. <i>torreyana</i>		<i>Prosopis glandulosa</i> var. <i>torreyana</i> (L.D.Benson) M.C.Johnst.
<i>Prosopis pubescens</i>		<i>Prosopis pubescens</i> Benth.
<i>Prosopis velutina</i>		<i>Prosopis velutina</i> Wooton
<i>Prunus americana</i>	synonymy not resolvable without specific variety	<i>Prunus</i> (<i>americana</i>)
<i>Prunus emarginata</i>		<i>Prunus emarginata</i> (Douglas) Walp.
<i>Prunus nigra</i>	synonym	<i>Armeniaca dasycarpa</i> (Ehrh.) Borkh.
<i>Prunus pensylvanica</i>	unresolved name	<i>Prunus</i> (<i>pensylvanica</i>)
<i>Prunus serotina</i>		<i>Prunus serotina</i> Ehrh.
<i>Prunus virginiana</i>	synonym	<i>Padus virginiana</i> (L.) M. Roem.
<i>Pseudotsuga macrocarpa</i>		<i>Pseudotsuga macrocarpa</i> (Vasey) Mayr
<i>Pseudotsuga menziesii</i> var. <i>menziesii</i>		<i>Pseudotsuga menziesii</i> (Mirb.) Franco var. <i>menziesii</i> ‡
<i>Pseudotsuga menziesii</i> var. <i>glauca</i>		<i>Pseudotsuga menziesii</i> var. <i>glauca</i> (Beissn.) Franco
<i>Quercus agrifolia</i>		<i>Quercus agrifolia</i> Née
<i>Quercus alba</i>		<i>Quercus alba</i> L.
<i>Quercus arizonica</i>		<i>Quercus arizonica</i> Sarg.
<i>Quercus bicolor</i>		<i>Quercus bicolor</i> Willd.
<i>Quercus chrysolepis</i>		<i>Quercus chrysolepis</i> Liebm.
<i>Quercus coccinea</i>		<i>Quercus coccinea</i> Münchh.
<i>Quercus douglasii</i>		<i>Quercus douglasii</i> Hook. & Arn.
<i>Quercus durandii</i>	synonym	<i>Quercus sinuata</i> Walter var. <i>sinuata</i>
<i>Quercus ellipsoidalis</i>		<i>Quercus ellipsoidalis</i> E.J.Hill
<i>Quercus emoryi</i>		<i>Quercus emoryi</i> Torr.
<i>Quercus engelmannii</i>		<i>Quercus engelmannii</i> Greene
<i>Quercus falcata</i> var. <i>falcata</i>		<i>Quercus falcata</i> Michx. var. <i>falcata</i> ‡
<i>Quercus falcata</i> var. <i>pagodifolia</i>	synonym	<i>Quercus pagoda</i> Raf.
<i>Quercus gambelii</i>		<i>Quercus gambelii</i> Nutt.
<i>Quercus garryana</i>		<i>Quercus garryana</i> Douglas ex Hook.

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
<i>Quercus grisea</i>		<i>Quercus grisea</i> Liebm.
<i>Quercus hypoleucoides</i>		<i>Quercus hypoleucoides</i> A.Camus
<i>Quercus ilicifolia</i>		<i>Quercus ilicifolia</i> Wangenh.
<i>Quercus imbricaria</i>		<i>Quercus imbricaria</i> Michx.
<i>Quercus incana</i>		<i>Quercus incana</i> Bartram
<i>Quercus kelloggii</i>		<i>Quercus kelloggii</i> Newb.
<i>Quercus laevis</i>		<i>Quercus laevis</i> Walter
<i>Quercus laurifolia</i>		<i>Quercus laurifolia</i> Michx.
<i>Quercus lobata</i>		<i>Quercus lobata</i> Née
<i>Quercus lyrata</i>		<i>Quercus lyrata</i> Walter
<i>Quercus macrocarpa</i>		<i>Quercus macrocarpa</i> Michx.
<i>Quercus marilandica</i>		<i>Quercus marilandica</i> (L.) Münchh.
<i>Quercus michauxii</i>		<i>Quercus michauxii</i> Nutt.
<i>Quercus minima</i>		<i>Quercus minima</i> (Sarg.) Small
<i>Quercus muehlenbergii</i>		<i>Quercus muehlenbergii</i> Engelm.
<i>Quercus nigra</i>		<i>Quercus nigra</i> L.
<i>Quercus nuttallii</i>	synonym	<i>Quercus texana</i> Buckley
<i>Quercus oblongifolia</i>		<i>Quercus oblongifolia</i> Torr.
<i>Quercus oglethorpensis</i>		<i>Quercus oglethorpensis</i> W.H.Duncan
<i>Quercus palustris</i>		<i>Quercus palustris</i> Münchh.
<i>Quercus phellos</i>		<i>Quercus phellos</i> L.
<i>Quercus prinoides</i>		<i>Quercus prinoides</i> Willd.
<i>Quercus prinus</i>	synonym	<i>Quercus michauxii</i> Nutt.
<i>Quercus rubra</i>		<i>Quercus rubra</i> L.
<i>Quercus shumardii</i>		<i>Quercus shumardii</i> Buckley
<i>Quercus stellata</i>		<i>Quercus stellata</i> Wangenh.
<i>Quercus stellata</i> var. <i>margarettae</i>	synonym	<i>Quercus margarettiae</i> (Ashe) Small
<i>Quercus stellata</i> var. <i>mississippiensis</i>		<i>Quercus similis</i> Ashe
<i>Quercus velutina</i>		<i>Quercus velutina</i> Lam.
<i>Quercus virginiana</i>		<i>Quercus virginiana</i> Mill.
<i>Quercus wislizeni</i>	synonym	<i>Quercus wislizeni</i> A.DC.
<i>Rhizophora mangle</i>		<i>Rhizophora mangle</i> L.
<i>Robinia neomexicana</i>		<i>Robinia neomexicana</i> A.Gray
<i>Robinia pseudoacacia</i>		<i>Robinia pseudoacacia</i> L.
<i>Salix alba</i>		<i>Salix alba</i> L.
<i>Salix amygdaloides</i>		<i>Salix amygdaloides</i> Andersson
<i>Salix discolor</i> var. <i>eriocephala</i>	synonym which itself is unresolved	<i>Salix</i> (<i>eriocephala</i> var. <i>eriocephala</i>)
<i>Salix nigra</i>		<i>Salix nigra</i> Marshall ‡
<i>Sapindus drummondii</i>		<i>Sapindus drummondii</i> Hook. & Arn.
<i>Sapium sebiferum</i>	synonym	<i>Triadica sebifera</i> (L.) Small
<i>Sassafras albidum</i>		<i>Sassafras albidum</i> (Nutt.) Nees
<i>Sequoia sempervirens</i>		<i>Sequoia sempervirens</i> (D.Don) Endl.
<i>Sequoiadendron giganteum</i>		<i>Sequoiadendron giganteum</i> (Lindl.) J.Buchholz
<i>Sorbus americana</i>	synonym	<i>Aucuparia americana</i> (Marshall) Nieuwl.
<i>Sorbus aucuparia</i>		<i>Sorbus aucuparia</i> L.
<i>Taxodium distichum</i>		<i>Taxodium distichum</i> (L.) Rich.
<i>Taxodium distichum</i> var. <i>nutans</i>	synonym not resolvable without specific authority	<i>Taxodium</i> (<i>distichum</i> var. <i>nutans</i>)
<i>Taxus brevifolia</i>		<i>Taxus brevifolia</i> Nutt.
<i>Thuja occidentalis</i>		<i>Thuja occidentalis</i> L.
<i>Thuja plicata</i>		<i>Thuja plicata</i> Donn ex D.Don
<i>Tilia americana</i>		<i>Tilia americana</i> L.
<i>Tilia americana</i> var. <i>caroliniana</i>		<i>Tilia americana</i> var. <i>caroliniana</i> (Mill.) Castigl.
<i>Tilia heterophylla</i>	synonym	<i>Tilia americana</i> var. <i>heterophylla</i> (Vent.) Loudon
<i>Torreya californica</i>		<i>Torreya californica</i> Torr.
<i>Torreya taxifolia</i>		<i>Torreya taxifolia</i> Arn.
<i>Tsuga canadensis</i>		<i>Tsuga canadensis</i> (L.) Carrière
<i>Tsuga caroliniana</i>		<i>Tsuga caroliniana</i> Engelm.
<i>Tsuga heterophylla</i>		<i>Tsuga heterophylla</i> (Raf.) Sarg.
<i>Tsuga mertensiana</i>		<i>Tsuga mertensiana</i> (Bong.) Carrière
<i>Ulmus alata</i>		<i>Ulmus alata</i> Michx.
<i>Ulmus americana</i>		<i>Ulmus americana</i> L.
<i>Ulmus crassifolia</i>		<i>Ulmus crassifolia</i> Nutt.
<i>Ulmus pumila</i>		<i>Ulmus pumila</i> L.
<i>Ulmus rubra</i>		<i>Ulmus rubra</i> Muhl.
<i>Ulmus serotina</i>		<i>Ulmus serotina</i> Sarg.

Table A1. Continued.

Taxa names used for analyses	Comments	Accepted taxa names†
Ulmus thomasii		Ulmus thomasii Sarg.
Umbellularia californica		Umbellularia californica (Hook. & Arn.) Nutt.
Vaccinium arboreum	synonym which itself is unresolved	Batodendron (arboretum)
Vernicia fordii		Vernicia fordii (Hemsl.) Airy Shaw

Notes: All analyses and gap-filling (see *Material and Methods*) were based on the original list of taxa names for which all the traits were collected. In order to identify authority, synonyms and accepted names for the used taxa names we checked them against The Plant List (2010). After name-checking we found two taxa which were synonymous to two other taxa of the list.

† Resolved accepted names are given with authority; for unresolved names the original name is in parentheses with no authority attached to it.

‡ Accepted names are taken from following sources: USDA, NRCS, National Plant Data Team (2007) and Burns and Honkala (1990).

Table A2. Description of traits used for ordination analyses with their main ecological function/proxy.

Trait	Description	Function or proxy for
Leaf traits		
Leaf composition	describes whether a leaf is compound consisting of several leaflets on a rachis or whether it is single-leaved with one leaf on a petiole	branching costs
Leaf arrangement	describes how leaves are arranged at their nodes	light interception
Leaf type	the shape of a leaf in combination whether it is deciduous or evergreen	photosynthetic rate, nutrient turnover time
Leaf margin	the shape of the leaf margin	conductive boundary layer, distributary network, initiation of photosynthesis
Specific leaf area	leaf area per leaf weight	photosynthetic rate, potential relative growth, structural leaf defenses
Reproduction traits		
Dispersal syndrome	the way how the plant disperses its seeds	colonization strategy
Seed mass	seed dry weight	recruitment survival and dispersal
Seed spread rate	the capability of a species to spread through its seed production compared to other tree species	colonization strategy
Vegetative spread rate	the capability of a species to spread compared to other tree species	reproduction strategy, disturbance response
Resprout ability	the ability of a species to resprout after aboveground biomass removal	persisting strategy after major disturbance
Root and stem traits		
Rooting habit	root habit with respect to rooting depth	water and nutrient uptake, fixation in ground
Bark surface	roughness of the bark	stem flow, soil moisture replenishment
Bark thickness	thickness of the bark	protection (e.g. against fire)
Wood density	oven dry mass per fresh volume	durability, mechanic strength, water transport
Maximum height	maximum height observed at a given site	competitive vigor, disturbance frequency
Conduit type and arrangement (porosity)	the arrangement of the vessels (exclusively angiosperms) throughout a growing season or whether there are tracheids (exclusively gymnosperms) instead	water transport, growth period, risk of cavitation and embolism
Plant level traits		
Lifespan	the expected lifespan of a tree species relative to other tree species	general plant strategy
C:N ratio (%carbon/%nitrogen)	the percentage of organic carbon divided by the percentage of total nitrogen in organic material; organic material is specified as the above ground herbaceous material of a woody plant.	general plant strategy, ontogenetic stage
Nitrogen fixation	the amount of nitrogen which is fixed by a species in monoculture	N availability in soil

Table A2. Continued.

Trait	Description	Function or proxy for
Toxicity	the relative toxicity of the plant to either humans or livestock	defense against herbivores
Potential allelopathy	the chemical potential of a species to be considered allelopathic; the relative ranking of species are based upon the completeness of the allelopathic literature, of species' growth strategies, successional position, and conjecture of the author.	direct competition, disturbance /stress response
Growth form	defines a tree as a perennial upright woody plant able to reach at least 6 m in height, a shrub as a woody plant with multiple stems and lower height, usually less than 5–6 m (15–20 ft) tall and intermediate between tree and shrub when both growth forms are combined or even likely.	climate factors, land use, general plant strategy, multi stem vs single stem growth behavior
Fire resistance (flammability)	to the ability of a species to resist burning or alternatively to carry a fire; fire resistant means low flammable	contributor to fire regimes

Table A3. Traits and performances filled for 305 species, 103 gymnosperms and 202 angiosperms, respectively before and after imputing missing values.

Trait	Percentage filled								
	For all species			For gymnosperms			For angiosperms		
	Before	After	Filled	Before	After	Filled	Before	After	Filled
Leaf traits									
Leaf composition	100.0	100.0	0.0	100.0	100.0	0.0
Leaf arrangement	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Leaf type	99.7	99.7	0.0	100.0	100.0	0.0	99.5	99.5	0.0
Leaf margin	100.0	100.0	0.0	100.0	100.0	0.0
Specific leaf area	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Reproduction traits									
Dispersal syndrome	54.1	54.1	0.0	69.9	69.9	0.0	46.0	46.0	46.0
Seed mass	83.9	97.4	13.4	95.1	100.0	4.9	78.2	96.0	17.8
Seed spread rate	76.1	97.7	21.6	72.8	100.0	27.2	77.7	96.5	18.8
Vegetative spread rate	74.1	96.7	22.6	70.9	100.0	29.1	75.7	95.0	19.3
Resprout ability	76.1	97.7	21.6	72.8	100.0	27.2	77.7	96.5	18.8
Root and stem traits									
Rooting habit	72.5	72.5	0.0	77.7	77.7	0.0	69.8	69.8	0.0
Bark surface	88.9	98.7	9.8	92.2	100.0	7.8	87.1	98.0	10.9
Bark thickness	70.8	93.8	23.0	79.6	100.0	20.4	66.3	90.6	24.3
Wood density	70.5	92.5	22.0	60.2	94.2	34.0	75.7	91.6	15.8
Maximum height	93.4	99.3	5.9	95.1	100.0	4.9	92.6	99.0	6.4
Conduit type and arrangement (porosity)	92.8	92.8	0.0	89.1	89.1	0.0
Plant level traits									
Lifespan	83.6	97.7	14.1	86.4	100.0	13.6	82.2	96.5	14.4
C:N ratio	73.8	96.7	23.0	72.8	100.0	27.2	74.3	95.0	20.8
Nitrogen fixation	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Toxicity	75.7	97.4	21.6	72.8	100.0	27.2	77.2	96.0	18.8
Potential allelopathy	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Growth form	100.0	100.0	0.0	100.0	100.0	0.0	100.0	100.0	0.0
Fire resistance (flammability)	76.1	97.7	21.6	72.8	100.0	27.2	77.7	96.5	18.8
Performances									
Growth rate	75.4	97.7	22.3	71.8	100.0	28.2	77.2	96.5	19.3
Shade tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Drought tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Shade tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Water tolerance	73.8	96.1	22.3	73.8	100.0	26.2	73.8	94.1	20.3
Fire tolerance	74.4	97.0	22.6	72.8	100.0	27.2	75.2	95.5	20.3

Note: In case of no data entry the trait did not occur or did not vary in the specific group.

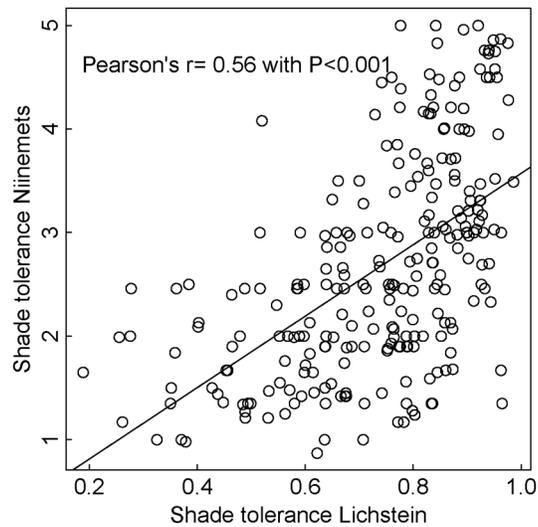


Fig. A1. Relationship between shade tolerance estimates of Lichstein et al. (2010) and shade tolerance values of Niinemets and Valladares (2006) for 261 North American woody species.

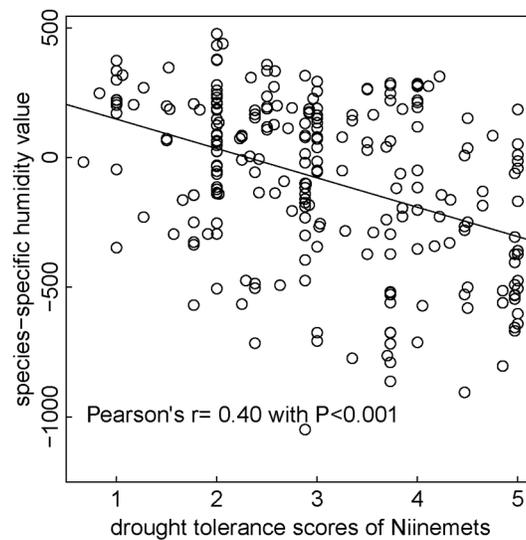


Fig. A2. Relationship between drought tolerance scores of Niinemets and Valladares (2006) and measures of humidity (annual P minus potential evapotranspiration [Willmott and Matsuura 2007]) derived from geographic distribution maps for 247 North American woody species (U.S. Geological Survey 1999) on 0.5 degree resolution. To obtain species-specific measures reflecting species' drought tolerance we used the lower limit (5th quantile) of the humidity measures covering a species range. We used quantiles instead of extreme values (i.e., minimum and maximum values) to minimize the effect of outliers caused by potential mismatches intersecting species range maps with climate.

APPENDIX B

*Literature sources of trait entries
for maximum height, bark thickness,
and rooting habit*

- Alabama Forestry Commission. 2007. <http://www.forestry.state.al.us>
- Brown, J. K., and N. V. Debye. 1987. Fire damage, mortality, and suckering in aspen. *Canadian Journal of Forest Research* 17:1100–1109.
- Burns, R. M., and B. H. Honkala, technical coordinators. 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654. USDA Forest Service, Washington, D.C., USA.
- Dengler, A. 1992. *Waldbau1: Der Wald als Vegetationsform und seine Bedeutung für den Menschen*. Paul Parey, Hamburg, Germany.
- Fernandes, P. M., J. A. Vega, E. Jimenez, and E. Rigolot. 2008. Fire resistance of European pines. *Forest Ecology and Management* 256:246–255.
- Grosser, D. 1998. *Loseblattsammlung: Einheimische Nutzhölzer. Vorkommen, Baum- und Stammform, Holzbeschreibung, Eigenschaften, Verwendung*. Holzabsatzfonds Bonn, Centrale Marketinggesellschaft der deutschen Agrarwirtschaft mbH, Bonn, Germany.
- Hengst, G. E., and J. O. Dawson. 1994. Bark properties and fire resistance of selected tree species from the central hardwood region of North America. *Canadian Journal of Forest Research* 24:688–696.
- Hepp, C., and C. Gurk, 2004. *Baumkunde, Einheimische und exotische Baumarten und Sträucher in einer Gehölze-Datenbank*. <http://www.baumkunde.de>
- Kling, G., C. P. Lindsey, and M. E. Zempardo, University of Illinois. 2009. *UI Plants* <http://woodyplants.nres.uiuc.edu/>
- Lickey, E. B., F. D. Watson, and G. L. Walker. 2002. Differences in bark thickness among populations of baldcypress [*Taxodium distichum* (L.) Rich. var. *distichum*] and pondcypress [*T. distichum* var. *imbricarium* (Nuttall) Croom]. *Castanea* 67:33–41.
- McCune, B. 1988. Ecological diversity in North American pines. *American Journal of Botany* 75:353–368.
- Montana State Stat Library's Natural Resource Information System, University of Montana. 2007. *Montana National Heritage Program*. <http://mtnhp.org/>
- Missouri Botanical Garden and Harvard University Herbaria. 2008. *eFloras*. <http://www.efloras.org>
- North Carolina State University, College of Agriculture and Life Science. 2000–2005. *Plant fact sheets*. <http://www.ces.ncsu.edu/depts/hort/consumer/factsheets/>
- Perry, Jr., J. P. 1991. *The pines of Mexico and Central America*. Timber Press, Portland, Oregon, USA.
- Roloff, A., and A. Bärtels. 2006. *Flora der Gehölze*. Eugen Ulmer KG, Stuttgart, Germany.
- Sargent, C. S. 1965. *Manual of the trees of North America*. Volumes 1 and 2. Dover, New York, New York, USA.
- Scheper, J. 1996–2011. *Floridata*. <http://www.floridata.com/index.cfm>
- Schütt, P., H. J. Schuck and B. Stimm. 2002. *Lexikon der Baum- und Straucharten*. Nikol Verlagsgesellschaft, Hamburg, Germany.
- Schütt, P., H. Weisgerber, H. J. Schuck, U. Lang, B. Stimm, and A. Roloff. 2004. *Lexikon der Nadelbäume*. Nikol Verlagsgesellschaft, Hamburg, Germany.
- Seiler, J., and J. Peterson. 2007. *Tree identification fact sheets*. Virginia Tech, Department of Forest Resources and Environmental Conservation. <http://dendro.cnre.vt.edu/dendrology/factsheets.cfm>
- Sidoroff, K., T. Kuuluvainen, H. Tanskanen, and I. Vanha-Majamaa. 2007. Tree mortality after low-intensity prescribed fires in managed *Pinus sylvestris* stands in southern Finland. *Scandinavian Journal of Forest Research* 22:2–12.
- Simpson, B. 2007. *Native trees of Texas*. Texas Agricultural Experiment Program. <http://aggie-horticulture.tamu.edu/ornamentals/natives/>
- Smith, J. H. G., and A. Kozak. 1971. Thickness, moisture content, and specific gravity of inner and outer bark of some Pacific Northwest trees. *Forest Products Journal* 21:38–40.
- Stayton, C. L., and M. Hoffman. 1970. Estimating sugar maple bark thickness and volume. *Research Paper NC-38*. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, USA.
- Stephens, S. L., and W. J. Libby. 2006. Anthropogenic fire and bark thickness in coastal and island pine populations from Alta and Baja California. *Journal of Biogeography* 33:648–652.
- Stinglwagner, G. K. F., I. E. Haseder, and R. Erlbeck. 2005. *Das Kosmos Wald- und Forst Lexikon*. Kosmos Verlag, Stuttgart, Germany.
- Sudworth, G. B. 1917. The pine trees of the Rocky Mountain region. *Bulletin* (1915–23) 460. USDA, Washington, D.C., USA.
- Tutin, T., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters, D. A. Webb, editors. 1964–1993. *Flora Europaea*. Cambridge University Press, Cambridge, UK.
- USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. 2008. *Fire effects information system*. <http://www.fs.fed.us/database/feis>
- USDA, NRCS, National Plant Data Team. 2007. *The*

PLANTS database. <http://plants.usda.gov/java/>
 Van Mantgem, P., and M. Schwartz. 2004. An experimental demonstration of stem damage as a predictor of fire-caused mortality for ponderosa pine. *Canadian Journal of Forest Research* 34:1343–1347.

Documentation of the final trait scale for leaf margin, C:N ratio, life span, leaf type and standardization of SLA

For leaf margin we extended the original scale (Adams et al. 2008) of 3 levels (1 = entire, 0.5 = toothed and/or entire, 0 = toothed) to 4 levels (0 = entire, 1 = toothed and/or entire, 2 = toothed, 3 = lobed) to account for species with a pronounced lobed leaf margin. For the C:N ratio we changed the original class based scale (low < 23, medium = 23–59, high > 59) by taking class means instead of class borders (low = 15, medium = 40, high = 65) to account for a realistic upper limit. For life

span we combined classed based data (USDA, NRCS, National Plant Data Team 2007) and continuous data (Wirth and Lichstein 2009) as follows: (1) in cases of multiple entries per species continuous data were given priority and (2) first class (short < 100 years), second class (moderate = 100–250 years) and third class (long > 250 years) were converted to 80, 175 and 300 years, respectively. The two traits leaf type with 3 levels (needle-leaved, scale-like, broadleaved) and leaf deciduousness with 3 levels (evergreen, deciduous, evergreen/deciduous) were combined to one nominal trait with 6 levels (called leaf type) to reduce the strong separating effects of the traits with a low number of levels. SLA was a standardized species specific estimate based on a comprehensive meta-analysis for North America which accounts for phylogeny and intra-specific variability (Ogle et al. 2012).