TOLERANCE TO SHADE, DROUGHT, AND WATERLOGGING OF TEMPERATE NORTHERN HEMISPHERE TREES AND SHRUBS

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Abstract. Lack of information on ecological characteristics of species across different continents hinders development of general world-scale quantitative vegetation dynamic models. We constructed common scales of shade, drought, and waterlogging tolerance for 806 North American, European/West Asian, and East Asian temperate shrubs and trees representing about 40% of the extant natural Northern Hemisphere species pool. These scales were used to test the hypotheses that shade tolerance is negatively related to drought and waterlogging tolerances, and that these correlations vary among continents and plant functional types. We observed significant negative correlations among shade and drought tolerance rankings for all data pooled, and separately for every continent and plant functional type, except for evergreen angiosperms. Another significant trade-off was found for drought and waterlogging tolerance for all continents, and for evergreen and deciduous angiosperms, but not for gymnosperms. For all data pooled, for Europe and East Asia, and for evergreen and deciduous angiosperms, shade tolerance was also negatively associated with waterlogging tolerance. Quantile regressions revealed that the negative relationship between shade and drought tolerance was significant for species growing in deep to moderate shade and that the negative relationship between shade and waterlogging tolerance was significant for species growing in moderate shade to high light, explaining why all relationships between different tolerances were negative according to general regression analyses. Phylogenetic signal in the tolerance to any one of the three environmental factors studied was significant but low, with only 21–24% of cladogram nodes exhibiting significant conservatism. The inverse relationships between different tolerances were significant in phylogenetically independent analyses both for the overall pool of species and for two multispecies genera (*Pinus* and *Quercus*) for which reliable molecular phylogenies were available. Only 2.6–10.3% of the species were relatively tolerant to two environmental stresses simultaneously (tolerance value ≥3), and only three species were tolerant to all three stresses, supporting the existence of functional trade-offs in adjusting to multiple environmental limitations. These trade-offs represent a constraint for niche differentiation, reducing the diversity of plant responses to the many combinations of irradiance and water supply that are found in natural ecosystems.

Key words: drought tolerance; functional plant type; intercontinental comparisons; phylogeny; shade tolerance; trade-offs; waterlogging tolerance.

INTRODUCTION

Differential tolerance to environmental stress among plants is a crucial aspect underlying geographic patterns of vegetation and a central concept to understanding the structure and dynamics of terrestrial ecosystems (Mooney et al. 2002). Tolerance to a given stress has a physiological basis but it is strongly affected by many environmental factors, which has led to the distinction between physiological and ecological tolerances. The tolerance to a given stress is typically reduced by other co-occurring stresses or by biotic factors such as herbivores, pests, and competition from neighbor plants. For example shade tolerance is reduced by mildew in

many temperate forest species such as oaks (Rackham 2003), and by drought in woody seedlings (Battaglia et al. 2000, Sánchez-Gómez et al. 2006b). However, knowledge of the tolerance to the primary abiotic stresses is still scant for many important wild plants and tolerance to simultaneous stresses is poorly understood despite the ubiquitous coexistence of multiple stresses in nature (Hall and Harcombe 1998, Battaglia et al. 2000, Niinemets and Valladares 2004). Due at least in part to these knowledge gaps, few attempts have been made to develop a general theory of succession and dynamics for main vegetation types across the globe, and the existing diversity of theories on vegetation dynamics is associated with the lack of a common intercontinental stress tolerance scale (Bugmann and Solomon 1995, Bugmann and Cramer 1998, Peng 2000, Glenz 2005).

Since multiple stresses co-occur, the many combinations of different severities for different stresses generate many potential niches and provide a larger framework for an advanced understanding of species coexistence than species segregation according tolerance to one single stress (Sack 2004, Sánchez-Gómez et al. 2006a). However, not all the possible combinations of environmental drivers are frequent in natural conditions. In fact, shaded sites tend to be moist, and plants from waterlogged sites do not usually experience root zone drought and low air humidity. We argue that even though the frequency is not the same for all the possible combinations of stress intensity, significant interactions of three important and widespread stress factors for vegetation (i.e., shade, drought, and waterlogging) do occur in nature. For instance, drought not only occurs under high light but also, and with potentially severe effects, in the shade (Tschaplinski et al. 1998, Valladares and Pearcy 2002, Hastwell and Facelli 2003, Sack et al. 2003); waterlogging occurs both under high light and in the shade, many flooded areas include drier microsites, and in certain areas waterlogging alternates with severe drought (Streng et al. 1989, Hall and Harcombe 1998, Silvertown et al. 2001, Glenz 2005). Thus, selection could favor most if not all polytolerance strategies since there are niches available. Consequently, the main limitation for these polytolerance strategies would be physiological and morphological trade-offs that prevent species from achieving simultaneous tolerance to more than one stress. Although some of these compromises have been shown in certain experimental studies dealing with a limited number of species (Sack 2004, Sánchez-Gómez et al. 2006a), the extent and generality of these trade-offs is poorly known despite many theoretical considerations (Tilman 1988, Smith and Huston 1989).

General occurrence of inverse gradients of water and light availabilities has led to suggestions that species' shade and drought tolerances are negatively associated (Smith and Huston 1989, Abrams 1994, Kubiske et al. 1996, Niinemets and Kull 1998, Niinemets and Valladares 2004). Existence of inverse correlations between ecological requirements of species involves the ad hoc hypothesis that being tolerant to a certain environmental factor involves a cost such that the plant cannot adjust simultaneously to multiple environmental stresses. In fact, shade and drought tolerance involve conflicting requirements for biomass investment in foliage and branches for efficient light capture vs. biomass investment in roots for efficient water uptake, and reductions in total foliage area and enhanced leaf clumping to reduce evaporation (Valladares 2003, Cescatti and Niinemets 2004). This hypothesis has been supported by some experimental studies (e.g., Kubiske et al. 1996, Niinemets and Kull 1998, Sánchez-Gómez et al. 2006a, b) but not others (e.g., Coomes and Grubb 2000, Sack and Grubb 2002, Sack 2004). Conclusive testing of this hypothesis is of paramount significance to understanding species dispersal along natural water and light availability gradients. A trade-off between shade tolerance and drought tolerance would imply a constraint on niche differentiation in coexisting species, while no trade-off would indicate greater scope for niche differentiation (Sack 2004).

Depending on site topography and soil texture, certain habitats are significantly influenced by waterlogging, which results in low oxygen concentration in the soil. An excess of water in the soil may paradoxically cause water stress symptoms in plants (Lambers et al. 1998). Flooding and waterlogging can alternate with drought and they may differentially affect open and understory habitats. This means that the relationship between shade and drought tolerance for a given set of plant species can be modified by their differential waterlogging tolerance. Overall, there are few woody plant species that can tolerate long-term low soil oxygen availabilities, and even these species form a sparse canopy in heavy stress conditions (Talbot and Etherington 1987, Kozlowski et al. 1991). There are many potential conflicts in developing functional strategies to cope simultaneously with waterlogging and other stresses such as shade or drought. Tolerance to waterlogging can be achieved by an overall enhanced root turnover and by the maintenance of numerous metabolically costly meristematic cells in stems and roots for adventitious root formation (Kozlowski 1997, Eissenstat and Volder 2005), which is not compatible with survival and growth under low light. In fact, teasing apart the interactions between light and waterlogging in a study of seedlings and saplings growing in river floodplains in Texas, USA, proved complex because waterlogging tolerance interacted with many life history traits and stress tolerance capacities of the plants (Streng et al. 1989, Hall and Harcombe 1998). Compromises between plant traits that augment waterlogging tolerance and those that increase shade or drought tolerance, though, predict a negative correlation between waterlogging and these other stresses.

The aim of this study was to explore the tolerance to three important stresses (shade, drought, and waterlogging) in an ample number of species sharing a general growth form (self-supporting trees and shrubs) and occurring over a wide geographical area (temperate zone of the Northern Hemisphere). An extensive review of studies, syntheses, and databases was carried out with this aim in mind, and information on the tolerance to these stresses of several hundreds of woody species was compiled. This information was then critically inspected to remove unreliable values and cross-calibrated to generate homogeneous rankings of species' tolerances according to a uniform five-level scale. An initial critical task in our study was to construct common scales of species' shade, drought, and waterlogging tolerance for dominant species in European/West Asian, North American, and East Asian temperate forest ecosystems. Using these intercontinental shade, waterlogging, and drought tolerance rankings, we then tested the hypoth-

eses of an inverse correlation between species' shade and drought tolerance, and the modification of this correlation by species' waterlogging tolerance. These inverse correlations would indicate that polytolerance was not favored over evolutionary time due to functional trade-offs that prevent maximal tolerance to more than one stress factor. The influence of leaf habit (evergreen vs. deciduous) on these correlations was also explored because leaf habit has been shown to be a key element in the adaptation of plants to cope with limiting factors (Press 1999).

The ranking of species according to their tolerance for these three stress factors led to the identification of general functional groups among coexisting plant species. A functional group is a nonphylogenetic classification resulting in a grouping of organisms that respond in a similar way to environmental factors (Gitay and Noble 1994). But phylogenetic signal (i.e., the tendency for related species to resemble each other) is ubiquitous (Blomberg et al. 2003), and ultimately all the species of a given community or region share a common ancestor at some point in their phylogeny. Thus, we argue that there is always a phylogenetic signal that can be found in the traits of any group of species. The phylogenetic signal is thus a continuous characteristic and neither of the extremes (0% or 100% of phylogenetic signal) is likely (Blomberg et al. 2003). We explored the phylogenetic signal in our data set taking into account that phylogeny is a source of historical information that can be used to generalize functional relationships across the species more efficiently (Westoby 1999).

It must be recognized that there are inherent limitations in a study like the present one, primarily deriving from the lack of information on many potentially interesting species and from the heterogeneity across both continents and authors in approaches to scoring stress tolerance. Another limitation is imposed by the fact that most research on the stress tolerance of woody plants has been focused on juveniles, and the age of the plant can affect many functional aspects of a given species, including its stress tolerance (Battaglia and Reid 1993, Cavender-Bares and Bazzaz 2000). For instance, shade tolerance has been shown to decrease with age in certain species (Condit et al. 1999, Lusk 2004), while drought tolerance is usually larger in saplings and adults than in seedlings (Cavender-Bares and Bazzaz 2000, Castro et al. 2004, Mediavilla and Escudero 2004). Even though the empirical knowledge on the ontogenetic changes in stress tolerance is fragmentary, there are theoretical bases to support some of these changes (Grubb 1998). Nevertheless, these ontogenetic effects are expected to play a marginal role in comparative rankings of stress tolerance of large numbers of species such as the present one, since stress tolerance of adults is broadly correlated with that of seedlings, as has been well-documented for the shade tolerance of temperate trees (Ellenberg 1996, Reich et al. 2003).

MATERIALS AND METHODS

The data set of species ecological requirements

An extensive data set of species' shade, drought, and waterlogging tolerance estimates was constructed to include important trees and shrubs with different foliage physiognomy (conifers, deciduous and evergreen broadleaf species) on all three continents. The entire data set consists of 806 temperate Northern Hemisphere woody taxa and species nomenclature follows the latest version of the W_3TROPICOS database (Missouri Botanical Garden 2005) along with the Flora of China Checklist (available online).[5]

We tried to keep the scope of the experimental unit, "species," comparable for all cases. Due to infraspecific taxa and microspecies, the initial data set included ~5% more taxa. Several data sources provided estimates of ecological potentials of subspecies or species varieties (Ellenberg 1991). The estimates of ecological potentials for species varieties and subspecies were in most cases averaged. Infraspecific taxa were used only for species populations widely separated geographically that also exhibited significant differentiation in ecological potentials (Alnus incana and A. viridis from Europe vs. A. incana ssp. rugosa, A. incana ssp. tenuifolia, and A. viridis ssp. sinuata from North America; Betula pubescens from the northern and central part of Europe vs. B. pubsecens ssp. carpatica from the southeastern part of Europe), and for the two Pinus contorta subspecies contorta and latifolia that have different site preference and important divergence in crown form, and foliage and cone morphology (Burns and Honkala 1990).

Due to apomixis and/or hybridization and polyploidization, the taxonomy and genetic origin of several woody species genera such as Acer, Crataegus, Rosa, Rubus, Sorbus, and Ulmus is complex and species definition differs among authors (Richens 1980, Timmermann 1992, Armstrong and Sell 1996, Carrión Vilches et al. 2000, King and Ferris 2002, Whitley et al. 2003, Collada et al. 2004, Robertson et al. 2004). A number of studies reported estimates of ecological potentials of endemic polyploid hybrid species or microspecies (e.g., Hill et al. [1999] reports ecological potentials for 14 endemic British Sorbus species), while other data sources reported estimates for corresponding aggregated species. Given that microspecies have limited range of dispersal (Pilgrim et al. 2004), and there is often a continuum in traits among hybrid species due to multiple hybridization events (King and Ferris 2002, Whitley et al. 2003, Robertson et al. 2004), microspecies were grouped together as corresponding aggregate species or species hybrids on the basis of recent genetic studies (Armstrong and Sell 1996, Whitley et al. 2003, Robertson et al. 2004). The values of the ecological potentials of grouped microspecies were averaged.

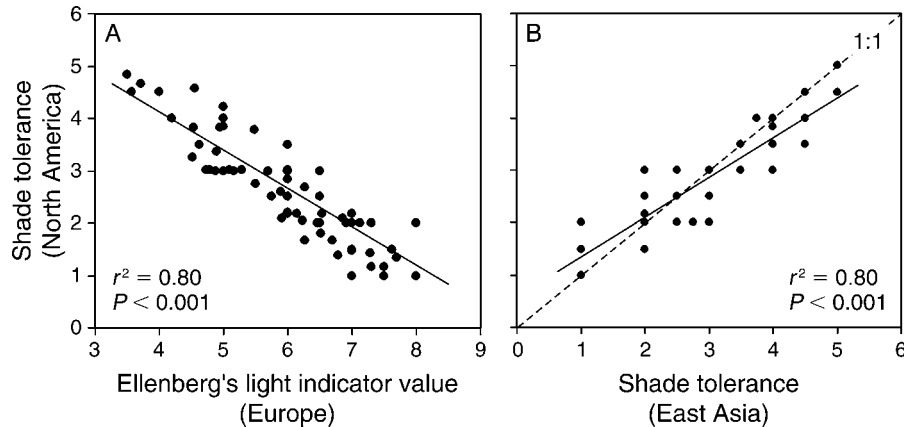[5] ⟨http://mobot.mobot.org/W3T/Search/foc.html⟩

FIG. 1. (A) Relationships between the shade tolerance scoring developed for temperate species in North America and the species light requirement developed in Europe (Ellenberg's light indicator value; Ellenberg 1991), and (B) relationships between the North American shade tolerance ranking and the species scoring developed in East Asia. Data points in (A) correspond to native, naturalized, or widely occurring species in both North America and Europe. In (B), the shade tolerance estimates derived for introduced East Asian species in North America and Europe are regressed against the shade tolerance estimates determined for the same species growing in the native habitats in East Asia. The dashed line in (B) denotes the 1:1 relationship. The correlation in (A) was employed to convert the shade tolerance estimates of North American and European species to a common scale, while the regression in (B) was employed to calibrate the East Asian species rankings.

Out of the 806 species in the final data set, 566 were winter deciduous and 240 were evergreen. The data set included 118 gymnosperms of which 11 species and interspecific hybrids from the genera *Gingko*, *Larix*, *Metasequoia*, and *Taxodium* are winter deciduous. In terms of origins, 364 species were native to North America, 262 to Europe/West Asia, and 211 to East Asia (Appendix A). The data set included five interspecific hybrids between North American and European species: *Aesculus × carnea* (*A. hippocastanum × A. pavia*), *Crataegus × lavallei* (*C. stipulacea × C. crus-galli*), *Laburnum × watereri* (*L. alpinum × L. anagyroides*), *Platanus × acerifolia* (*P. orientalis × P. occidentalis*), and *Populus × canadensis* (*P. nigra × P. deltoides*). The data set also included an interspecific hybrid *Larix × eurolepis* (*L. decidua × L. kaempferi*) of European/East Asian origin. In addition to these intercontinental hybrids, 25 species were native to both North America and Europe (Appendix A). Overall, the data set covers ~40% of extant native Northern Hemisphere woody vegetation (~73% of North American, 69% of European/West Asian, and 23% of East Asian woody species; Qian and Ricklefs 1999, 2000, Ricklefs et al. 2004).

Construction of uniform tolerance rankings for Northern Hemisphere

Shade, drought, and waterlogging tolerance rankings of species were first developed separately for every continent using an extensive selection of published tolerance rankings, and cross-calibrating every tolerance ranking using species present in several tolerance rankings. The continent-specific rankings were further converted to word-scale shade, drought, and water-logging rankings using tolerance estimates for more than a hundred native and introduced widespread species that

were available for two or more continents (Figs. 1, 2). Data from different sources and different environmental conditions led to different rankings of tolerance for a given species. Here we use the average, always after detailed cross-calibration of the different data sets using common species. The standard error, which is given for species with rankings available from two or more studies (Appendix A), reflects this dispersion. To control for erroneous data, estimates of the species requirement in any single data set that differed by more than two levels from the general species mean were removed, and the corrected species mean value was calculated. Basic steps followed for the cross-calibration among different sources are given in the following section; a more detailed description of the process followed to get a common scale of tolerance and a list of the original sources of information are provided in Appendix B.

Derivation of shade tolerance scales

From the many possible definitions of shade tolerance (survival, growth, completion of life cycle, optimal physiological performance, etc.; e.g., Grime 1979, Smith and Huston 1989, Woodward 1990, Grubb 1998, Reich et al. 2003, Valladares et al. 2005a), shade tolerance is taken here as the capacity for growth in the shade. Since shade comprises a range of light availabilities from very dark to rather bright environments, shade tolerance is ideally defined by the minimum light at which a given species is able to grow. Shade tolerance of woody plants is most frequently provided for the juveniles of each species and thus the values obtained here apply primarily to seedlings and saplings. Even though many species have been shown to change their shade tolerance during their lifetime, with a tendency for a decreasing tolerance with age, in most cases the relative rankings of
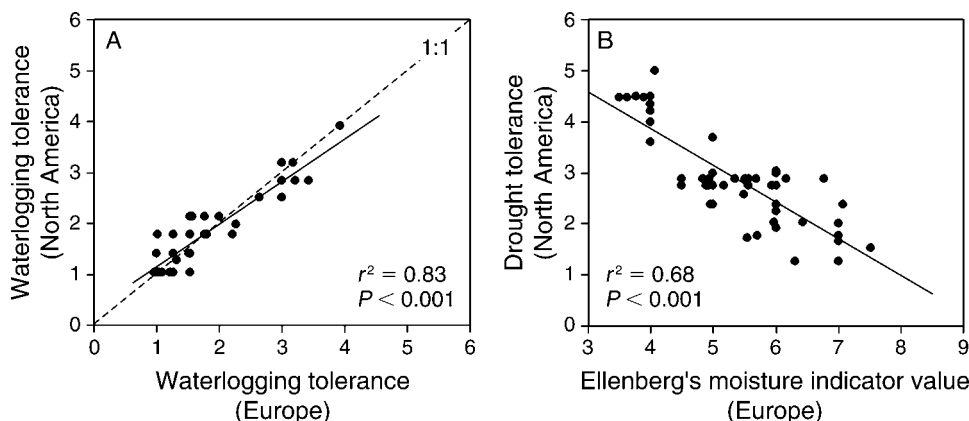
Fig. 2. (A) Correlations between the waterlogging tolerance rankings of temperate species developed in North America and Europe, and (B) correlations between the drought tolerance ranking developed in North America and species moisture indicator value developed in Europe. Data points are as described for Fig. 1A. The dashed line in (A) is for the 1:1 relationship. The regressions in (A) and (B) were used to obtain common waterlogging and drought tolerance scales for North American and European species.

coexisting species do not change from seedlings to adults (Yevstigneyev 1990, Grubb 1998, Kitajima and Bolker 2003). The five-level scale used for shade tolerance (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant) corresponds approximately to the following light availabilities expressed as percentage of full sunlight: 1, >50%; 2, 25–50%; 3, 10–25%; 4, 5–10%; 5, 2–5%.

We used the five-level shade tolerance scale of Baker (1949) as the starting point for the North American species. This shade tolerance ranking is based on actual measurements of minimum light availability of species location (Wiesner 1907, Zon and Graves 1911), further modified to include a wide range of foresters' opinions on species biology. Because it includes a large number of important species, it is commonly used in classifying tree light requirements in comparative studies of life history traits in North American tree species (Kobe et al. 1995, Coomes and Grubb 2000, Walters and Reich 2000). Data for nine additional data sets covering more species and providing additional data for the species included by Baker were used to construct a more complete and robust data set for North America (Tables 1, 2; see Appendix B for details).

For European species, we used the species ranking of Ellenberg (1991), which is commonly employed to characterize species' potential to grow in the understory (Niinemets and Kull 1994, Coomes and Grubb 2000, Cornwell and Grubb 2003). Ellenberg's ecological indicator values for light characterize species' natural dispersal along the habitats of varying light availability, and vary for woody species from values of three to nine, giving a seven-level scale (Ellenberg 1991, Hill et al. 1999, 2000). These values are derived from actual measurements of light availability in a species' habitat. To improve the shade tolerance estimates of important European trees and increase the scope of the data set, 11

additional shade tolerance scorings were included and cross-calibrated as detailed in Appendix B and Tables 1, 2.

For East Asian species, we used the study of Kikuzawa (1984) augmented by the assessments of species successional position in Koike (1988) and Maruyama (1978) and from various comparative studies reporting species' successional sequence and species; tolerance of understory shade (e.g., Kohyama 1984, Ohsawa et al. 1986, Kikuzawa 1988, Peters 1992, 1997, Kamijo and Okutomi 1995a, b, Ozaki and Ohsawa 1995, Peters et al. 1995, Sumida 1995, Tanouchi and Yamamoto 1995, Nakashizuka and Iida 1996, Tanouchi 1996, Ohsawa and Nitta 1997, Suzuki 1997, Hiroki and Ichino 1998, Lei et al. 1998, Ke and Werger 1999, Masaki 2002, Hiroki 2003, Ishii et al. 2003, Nanami et al. 2004; Table 1; see Appendix B for details). The greater woody species richness in East Asia relative to Europe and North America, which prevents the development of straightforward rankings of the species, and the lack of a standard classification of shade tolerance on this continent imposed obvious limitations to the reliable inclusion of many Asian species in our data set.

To derive a common shade tolerance scale for North American and European species, we used the species present in both data sets and derived a linear regression between the shade tolerance and the light requirement scorings (Fig. 1A). This regression equation was employed to convert the estimates of light requirement of European species to the common five-level shade tolerance scale (1, very intolerant; 5, very tolerant). Ultimately, the different shade tolerance estimates of species common in both data sets were averaged.

For 149 East Asian native species we obtained corresponding shade tolerance estimates for the same species introduced to North America and/or Europe (Table 1). We employed linear regression analysis to test

TABLE 1. Studies that provided the estimates of shade tolerance for native and introduced plants on different continents.

	Number of species			
References	North America	Europe	East Asia	Total
Shade tolerance rankings developed in North America for native and introduced species				
Baker (1949)	148			148
Fowells (1965)	117			117
Graham (1954)	20			20
Hicks and Chabot (1985)	14			14
Kuhns and Rupp (2000)	117	37	57	212
Minore (1979)	24			24
Online databases and documents†	194	53	120	232
White (1983)	48			48
Wiesner (1907)	15	2		17
Zon and Graves (1911)	85			85
Shade tolerance scales developed in Europe for native and introduced species				
Brzeziecki and Kienast (1994)	1	36		36
Ellenberg (1996)		42		42
Ellenberg (1991)	32	208	4	218
Gayer (1898)	1	20		21
Hill et al. (1999)	28	146	10	166
Ivanov (1932)		8	2	10
Jahn (1991)		44		44
Morozov (1903)		14		14
Otto (1994)		33		33
Wiesner (1907)	4	16	1	21
Walter (1968)		12		12
Warming (1909)		16		16
Yevstigneyev (1990)		11		11
Shade tolerance estimates for Japanese native species				
Kikuzawa (1984)				28
Koike (1988)				30
Maruyama (1978)				13

† These include Stange et al. (2002), Smith (2004), Dirr (2005), Morris (2005), and USDA NRCS (2005).

whether the five-level scale of shade tolerance developed in the native habitat of the species corresponds to the five-level scale developed previously for the North American and European species. This analysis demonstrates that both the shade tolerance scorings obtained in species' native and foreign locations were strongly related with minor deviations from the 1:1 line (Fig. 1B). The final shade tolerance ranking for the East Asian species was obtained as the mean of the shade tolerance estimates determined in the native habitats and for these species growing on other continents. This ranking was critically revised further by Professors Kihachiro Kikuzawa, Tohru Nakashizuka, Masahiko Ohsawa, and Tsutom Hiura (see *Acknowledgments*), and we believe that the best possible shade tolerance scale for East Asian species was obtained.

Comparative waterlogging tolerance estimates

The definitions of species' waterlogging tolerance (i.e., tolerance of reduced root-zone soil oxygen availabilities) vary strongly from study to study (Bell and Johnson 1974, Whitlow and Harris 1979, Bratkovich et al. 1993, Kuhns and Rupp 2000). This large variation in definitions is partly associated with inherent differences in response of temperate species to waterlogging depending on whether the waterlogging is during winter or during the growing season, whether the water is flowing or standing, and the degree to which soil oxygen contents decrease and soil redox potential is altered (Bratkovich et al. 1993, Crawford 1996, Pezeshki et al. 1996, 1997). We adopt the qualitative waterlogging tolerance scale of Whitlow and Harris (1979): 5, very tolerant (survives deep, prolonged waterlogging for more than one year); 4, tolerant (survives deep waterlogging for one growing season); 3, moderately tolerant (survives waterlogging or saturated soils for 30 consecutive days during the growing season); 2, intolerant (tolerates one to two weeks of waterlogging during the growing season); 1, very intolerant (does not tolerate water-saturated soils for more than a few days during the growing season). Although waterlogging tolerance is often considered synonymous with flooding tolerance, we note that flooding impact in riparian ecosystems also involves, in addition, sand/gravel depositions around the tree base and various mechanical stresses (Naiman et al. 1998, Bendix and Hupp 2000).

Waterlogging tolerance rankings for the North American species were obtained from Bell and Johnson (1974), Minore (1979), Whitlow and Harris (1979) revised using the data from White (1973), Barnes (1991), Tesche (1992), Bratkovich et al. (1993), Iles and Gleason (1994), USDA NRCS (1996), Kuhns and

TABLE 2. Comparison of various shade-tolerance scorings.

Reference†	North American shade-tolerance rankings								
	1	2	3	4	5	6	7	8	9
1) Baker (1949)	1.000								
2) Fowells (1965)	0.907	1.000							
3) Graham (1954)	0.955	0.897	1.000						
4) Hicks and Chabot (1985)	0.802	0.794	0.949	1.000					
5) Kuhns and Rupp (2000)	0.875	0.877	0.927	0.932	1.000				
6) Minore (1979)	0.910	0.887	···	···	0.970	1.000			
7) Online databases and documents‡	0.832	0.786	0.818	0.970	0.735	0.845	1.000		
8) White (1983)	0.834	0.820	0.775	0.927	0.920	···	0.801	1.000	
9) Wiesner (1907)	−0.927	−0.564	···	···	−0.832	···	−0.674	···	1.000
10) Zon and Graves (1911)	0.870	0.830	0.948	0.841	0.882	0.707	0.887	0.710	0.896

Reference†	European shade-tolerance rankings											
	11	12	13	14	15	16	17	18	19	20	21	22
11) Brzeziecki and Kienast (1994)	1.000											
12) Ellenberg (1996)	0.817	1.000										
13) Ellenberg (1991)	−0.816	−0.897	1.000									
14) Gayer (1898)	0.846	0.952	−0.866	1.000								
15) Hill et al. (1999)	−0.762	−0.811	0.864	0.811	1.000							
16) Ivanov (1932)	−0.883	−0.767	0.898	−0.600	0.867	1.000						
17) Jahn (1991)	−0.778	−0.874	0.897	−0.870	0.866	0.833	1.000					
18) Morozov (1903)	0.907	−0.937	−0.884	0.975	−0.911	···	−0.961	1.000				
19) Otto (1994)	0.807	−0.824	−0.821	0.778	−0.733	−0.638	−0.756	0.775	1.000			
20) Walter (1968)	0.694	−0.789	−0.778	0.916	−0.789	−0.700	−0.840	0.991	0.657	1.000		
21) Warming (1909)	0.949	0.895	−0.901	0.939	−0.853	−0.700	−0.922	0.963	0.882	0.949	1.000	
22) Wiesner (1907)	−0.843	−0.793	0.860	−0.882	0.698	0.800	0.839	−0.974	−0.752	−0.979	−0.964	1.000
23) Yevstigneyev (1990)	0.850	−0.710	−0.826	0.886	−0.762	···	−0.741	0.900	0.735	0.759	0.886	0.771

Note: Data are presented as Spearman rank correlation coefficients significant at $P < 0.05$ or better. Ellipses (···) indicate that fewer than five common species were available.

† The number of species for every data set is given in Table 1. All rankings increase with increasing species' shade tolerance except for Wiesner (minimum light at species growth location), Jahn (light requirement), both Ellenberg and Hill et al. (light indicator value), and Ivanov (photosynthetic compensation point); these are negatively related to shade-tolerance.

‡ Stange et al. (2002), Smith (2004), Dirr (2005), Morris (2005), USDA NRCS (2005).

Rupp (2000), and from the online USDA Plants database Version 3.5 (USDA NRCS 2005). All data sets were cross-calibrated as detailed in Appendix B. The refinement of final rankings of species with similar waterlogging tolerance according to large data sets was achieved by using the studies on dispersal of species along wetland–upland continua as well as ecophysiological common garden investigations (Hosner 1958, Harms et al. 1980, Jones and Sharitz 1989, Jones et al. 1994, Ranney 1994, Ranney and Bir 1994, Yin et al. 1994, Hoagland et al. 1996, Naiman et al. 1998, Bendix and Hupp 2000, Dale and Ware 2004).

For the European species, waterlogging tolerance estimates were obtained from Prentice and Helmisaari (1991), Tesche (1992), Merritt (1994), Schaffrath (2000), Glenz (2005), the Biological Flora of British Isles review series published regularly by the Journal of Ecology (1941–2005), from studies of comparative waterlogging tolerance (Frye and Grosse 1992, Tapper 1993, 1996, Ranney 1994, Ranney and Bir 1994, van Splunder et al. 1995, Anonymous 1996, Siebel and Blom 1998, Siebel et al. 1998, van Splunder 1998, Burkart 2001, Karrenberg et al. 2002, Kreuzwieser et al. 2002), and country-specific floras (e.g., Vaga et al. 1960, Oberdorfer et al. 1994).

Linear regressions were employed to cross-calibrate the data sets. Details of number of species from each source and cross-calibration statistics are given in Appendix B. The obtained scale was further converted to the five-level scale derived for North American species using the species common in both North American and European waterlogging tolerance assessments (Fig. 2A).

Among the North American and European data sets, cross-calibrated waterlogging tolerance estimates were available for 90 East Asian species. Further data of species waterlogging tolerance were obtained from Nikolov and Helmisaari (1992; comparative data for nine European and East Asian species), from the online databases Virtual Plant Tags (Dirr 2005) and Plants for a Future (Morris 2005), and from comparative ecophysiological studies (Tsukahara 1985, Takahashi et al. 1988, Ranney 1994, Ranney and Bir 1994, Terazawa and Kikuzawa 1994, Yamamoto et al. 1995, Sakio 2003). Ecophysiological comparative studies were also employed to revise the initial estimates obtained from online databases. Using the cross-calibrated values, all waterlogging estimates were converted to a common scale, and a mean waterlogging tolerance estimate was calculated for every species. The final ranking of East

Asian species was critically reviewed by Professors Kihachiro Kikuzawa, Tohru Nakashizuka , Masahiko Ohsawa, and Tsutom Hiura (see *Acknowledgments*), and the tolerance rankings were adjusted by ±0.25–1.0 tolerance units for a total of 26% of species in response to their expert suggestions.

Determination of drought tolerance rankings

Drought tolerance can be achieved by a diverse array of structural and physiological traits, and plant rankings according to drought tolerance are often based on different combinations of traits and evidence. The three major bases for species rankings are physiological tolerance to water stress, morphological and life cycle strategies to cope with scant water, and the water availability estimated on the sites where the species more frequently occur (Hsiao 1973, Ludlow 1989, Ellenberg 1996, Chaves et al. 2002, Sack 2004, Valladares et al. 2005b). For this reason, our drought tolerance rankings (1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant) are based on site characteristics of species dispersal and physiological potentials of species. The relevant site features considered are total annual precipitation, ratio of precipitation to potential evapotranspiration (P:PET ratio), and duration of the dry period. Plant physiological potentials are characterized by minimum soil water potential that can be tolerated over the long term with <50% of foliage damage or dieback (Larcher 1994). The five-level scale used for drought tolerance approximately corresponded with the following values for each category rank: 1, >600 mm precipitation with little variation during growing season, P:PET ratio of >3.0, few days of drought, and greater than −0.3 MPa soil water potential; 2, 500–600 mm precipitation, variation of precipitation distribution during growing season characterized by coefficient of variation <10%, P:PET ratio of 1.5:3 , few weeks of drought, and from −0.3 to −0.8 MPa soil water potential; 3, 400–500 mm precipitation with a growing season coefficient of variation of 10–15%, P:PET ratio of 0.8:1.5, up to one month of drought, and from −0.8 to −1.5 MPa soil water potential; 4, 300–400 mm precipitation with a growing season coefficient of variation of 20–25%, P:PET ratio of 0.5:0.8, two to three months of drought, and from −1.5 to −3 MPa soil water potential; 5, <300 mm precipitation with a growing season coefficient of variation >25%, P:PET ratio of <0.5, more than three months of drought, and less than −3 MPa soil water potential. Since plants found in a dry area can be on locally wet soils and vice versa, and plants previously exposed to a dry period can tolerate lower soil water potential than those not exposed to it (Kozlowski et al. 1991, Larcher 1995, Valladares and Pearcy 1997), the rank assigned to a given species is the one corresponding to the lowest score (lowest tolerance) for each of these four categories. This yields a more conservative estimate of the real drought tolerance of the species. As with shade and waterlogging tolerance, different drought tolerance scales were cross-calibrated using the species common in specific data sets, and a mean drought tolerance score was determined for each species.

For the North American species, the drought tolerance rankings were derived from Minore (1979), Meerow and Norcini (1997), Kuhns and Rupp (2000), Cerny et al. (2002), the online USDA Plants database (USDA NRCS 2005), and from comparative studies on species' drought tolerance (e.g., Abrams 1990, Ni and Pallardy 1991, Ranney et al. 1991, Tyree and Alexander 1993, Abrams et al. 1994, Kubiske and Abrams 1994, Sperry et al. 1994, Kubiske et al. 1996, Linton et al. 1998, Loewenstein and Pallardy 1998). The drought tolerance scales were cross-calibrated in a similar manner as shade and waterlogging tolerance scales. Appendix B provides the details of cross-calibration and data sources.

For the European species, data on species' drought tolerance were obtained from species rankings provided by Ellenberg (1991, 1996), Jahn (1991), Brzeziecki and Kienast (1994), Otto (1994), Brzeziecki (1995), and Hill et al. (1999), and from comparative ecophysiological studies (e.g., Ranney et al. 1991, Acherar and Rambal 1992, Epron et al. 1993, Epron 1997, Aasamaa and Sõber 2001, Aasamaa et al. 2004, Cochard et al. 2004). Details of data sets used and homogenization of data sets are reported in Appendix B. The European and North American species were converted to a common scale by a linear regression based on the species scored on both continents (Fig. 2B).

As with the waterlogging tolerance ranks, cross-calibrated estimates of species' drought tolerance were available for 90 East Asian species in the North American and European data sets. Drought tolerance assessments of East Asian species relative to European species were also provided for 30 species by Percival and Sheriffs (2002) and for nine species by Nikolov and Helmisaari (1992). Additional data of species' drought tolerance were obtained from studies comparing species biology (Maruyama and Toyama 1987, Ranney et al. 1991, Liang et al. 1995) and from the online databases Plant Virtual Tags (Dirr 2005) and Plants for a Future (Morris 2005). Using the cross-calibrated values, all drought tolerance assessments were converted to a common scale, and averages were calculated. On the basis of critical assessment of the East Asian drought tolerance scale by Professors Kihachiro Kikuzawa, Tohru Nakashizuka, Masahiko Ohsawa, and Tsutom Hiura (see *Acknowledgments*), the tolerance rankings were adjusted by ±0.25–1.0 tolerance units for a total of 17% of the species.

Phylogenetic signal and phylogenetically independent contrasts

We tested for the presence of phylogenetic signal in the comparative data set of species' tolerance to shade, drought, and waterlogging. The term "phylogenetic

signal" refers to the tendency of related species to resemble each other (Blomberg and Garland 2002). Since different methods frequently yield different results, phylogenetic signal was estimated by two complementary approaches: (1) by the correlation between the phylogenetic and the tolerance matrices of distances among the species, and (2) by calculating the average magnitude of phylogenetically independent contrasts over the phylogenetic tree using the analysis of traits module in the PHYLOCOM software (Ackerly 2004). Trait conservatism was estimated using the mean values of the contrasts (see Garland [1991] in Blomberg and Garland [2002]) also using PHYLOCOM. For quantification of association between the phylogenetic distance matrix and each of the tolerance distance matrices a Mantel test (Sokal and Rohlf 1995) was carried out with the software Mantel Nonparametric Test Calculator 2.0 (Adam Liedloff, Queensland University of Technology, Australia). The values of Z (Mantel coefficient), g (standard normal variate) and r (correlation coefficient) were calculated from the two matrices specified. The obtained values of g were then compared with critical values for the most common levels of significance ($P = 0.01$, $P = 0.025$, and $P = 0.05$). The program also generated a user-specified number of random permutations of the first matrix to determine the possible variation within the data. In our case, 1000 random iterations were calculated for each distance (or dissimilarity) matrix and the values of g and Z were obtained in each case from the randomized distribution. Euclidean distances were used for the matrices and the zeros of the diagonal were excluded from the analyses as recommended by Legendre and Legendre (1983).

The phylogenetic signal was estimated for both the whole set of species where reliable phylogenetic information was available up to the level of genera, and separately for two genera (Quercus and Pinus) for which reliable phylogenetic information could be found down to species level. These two genera were selected to have one representative of each of the two main groups of woody plants (gymnosperms and angiosperms), and because both Quercus, with over 500 extant species, and Pinus, with over 100 extant species, are ecologically important as major components of many temperate forests.

The ANALYSIS OF TRAITS (AOT, Version 3.0) module of PHYLOCOM (Ackerly 2004) was used to explore the phylogenetic signal and to carry out node-level analyses of trait means and diversification. Phylomatic, a tool associated with PHYLOCOM (Ackerly 2004) was used to generate the initial tree in the Newick format; the obtained tree was checked and corrected manually for species not yet included in the web database. Phylogenetic signal was estimated in AOT by the average divergence deviation relative to the null hypothesis (randomizations of trait values across the tips of the tree). If closely related species are highly divergent, there will be many large contrasts near the tips of the tree, while if the trait evolution is conserved, the divergence will be small. To handle polytomies, AOT used standard deviation of the descendent trait means. Significance testing for the patterns of traits conservatism was conducted by randomization of trait values across the tips of the phylogeny; 10 000 randomizations were carried out for the results presented here. For the tolerance to each of the three stresses studied here, the percentage of nodes exhibiting significant conservatism and divergence, and the mean divergence and age of these nodes, were calculated. Conservatism was taken as significant when standard deviation was significant in the low tail of the null distribution, and divergence was significant when standard deviation was significant in the high tail of the null distribution. Mean divergence was expressed as standard deviation of values at daughter nodes and age was expressed as percentage of relative age across the tree, with 100% being the root and 0% being the tips of the tree.

Quantitative information to build the phylogenetic tree and the phylogenetic distance matrix was obtained from Soltis et al. (2000) for angiosperm plants, from Schmidt and Schneider-Poetsch (2002) for gymnosperms, from Manos et al. (1999) for the genus Quercus, and from Liston et al (1999) for the genus Pinus. The concurrent species of our data set and those phylogenetic studies were, for the genus Quercus, Q. acutissima, Q. agrifolia, Q. alba, Q. cerris, Q. chrysolepis, Q. ilex, Q. palustris, Q. robur, Q. rubra, Q. turbinella, and Q. virginiana, and for the genus Pinus, P. albicaulis, P. aristata, P. attenuata, P. bungeana, P. cembra, P. contorta, P. coulteri, P. echinata, P. halepensis, P. lambertiana, P. parviflora, P. ponderosa, P. resinosa, P. strobus, P. sylvestris, P. thunbergii, P. virginiana, and P. wallichiana.

With the phylogenetic information of these species of Quercus and Pinus, phylogenetic independent contrasts (Felsenstein 1985) were carried out to remove the influence of phylogeny on the relationships between the tolerances to shade, drought, and waterlogging. The software PDAP (Phenotypic Diversity Analysis Programs, Version 6.0, by T. Garland, Jr., P. E. Midford, J. A. Jones, A. W. Dickerman, and R. Diaz-Uriarte), which is described in Garland et al. (1993), was used. The independent contrasts were carried out with the module PDTREE (Garland et al. 1999). PDTREE allows the user to enter and edit a phylogenetic tree and associated phenotypic data for the species at its tips, which in our case were the values of tolerance to shade, drought, and waterlogging. Since only two phenotypic values can be entered at each tip and node, three trees per genus were used to estimate pairwise correlations between the tolerances to the three environmental factors. Branch lengths from the molecular phylogenies of the species of Quercus and Pinus were directly taken from the bibliography (Liston et al. 1999, Manos et al. 1999). A Brownian motion model of evolution was assumed. Multifurcations (polytomies) were only found for the Pinus tree and these were handled as described in

Purvis and Garland (1993). Felsenstein's pairwise independent differences (contrasts) were standardized by dividing each contrast by the standard deviation of the contrast (i.e., square root of the sum of the lengths of the branches of the phylogenetic tree). Correlations between traits were also estimated in phylogenetically independent contrasts using the AOT module of PHYLOCOM. The significance was obtained using $n − 2$ degrees of freedom in a table R, where n is the number of internal nodes providing contrasts, because randomization of tip values breaks down patterns of trait conservatism (Lapointe and Garland 2001). This approach was used for both the whole data set of species and the species of *Quercus* and *Pinus* listed above.

Data analysis

All tolerance scales were derived from independent observations on species' ecological potentials and thus satisfy the primary criterion of the statistical analysis. The bivariate relationships between shade, drought, and waterlogging tolerance estimates were explored by standardized major axis regressions using the program (S)MATR 1.0 (Falster et al. 2003). Standardized major axis (SMA) regression estimates the residuals from the line in both x and y dimensions (Warton and Weber 2002); SMA regression is an appropriate method for fitting the data if the functional relationships between the variables is not known a priori, and if both x and y variables are measured with a certain degree of error. In addition, SMA regressions are particularly pertinent for comparison of bivariate relationships among groups of data, because SMA fitting avoids flattening of the slope as the correlation between the variables decreases (Wright and Cannon 2001, Warton and Weber 2002).

The SMA regressions between species groups were compared by (S)MATR 1.0 (Falster et al. 2003). This program first uses a maximum-likelihood ratio developed by Warton and Weber (2002) to test for the slope differences of SMA regressions. (The equivalent test in ordinary ANCOVA is the separate slope model.) Whenever slopes are found not to be different, the analysis is continued according to standard ANCOVA (common slope model) to test for difference among the intercepts. All relationships were considered significant at $P < 0.05$.

Quantile regression, a powerful technique to examine ecological patterns (Cade and Noon 2003), was used to explore the relationships between tolerances over the entire surface of the scatter diagrams. Quantile regression is based on least absolute values and the model is fit by minimizing the sum of the absolute values of the residuals; the technique is very resistant to outliers and allows for the exploration of relationships from the edges of the diagrams by estimating quantiles of the dependent variable ranging from 0% to 100% (Scharf et al. 1998). Quantile regression was carried out with the software Blossom, Version 2005.05.26 (Cade and Richards 2005).

RESULTS

Tolerance scales

Ten species rankings were employed to derive the final mean shade tolerance estimate for North American species, while 13 shade tolerance rankings were used for European species, and three major rankings along with a series of detailed succession and ecophysiological studies were used for East Asian species (Table 1). For all sets of data, various shade tolerance scorings were strongly correlated (Table 2 for North American and European data sets; $r = 0.91$ for Kikuzawa [1984] vs. East Asian mean ranking; $r = 0.89$ for Koike [1988] vs. mean; and $r = 0.92$ for Maruyama [1978] vs. mean; $P < 0.001$ for all), demonstrating a strong convergence of different species' shade tolerance rankings and the reliability of the derived mean species value.

In addition, cross-calibration of shade tolerance scales among different continents and available data of shade tolerance of naturalized species on specific continents further enhanced the reliability and extension of the data set. Certainly, including shade tolerance estimates for species naturalized in foreign habitats introduces some uncertainty. In particular, exotic species may become more tolerant in foreign habitats due to hybridization with native species and following gene flow by introgression into exotic species populations (Milne and Abbott 2000), as well as due to selection of more tolerant varieties by gardeners. However, we compared the shade tolerance estimates of species in natural and introduced habitat using paired t tests and found that the shade tolerance in the introduced habitat did not differ significantly from that in native habitat. For instance, $P > 0.7$, for comparison of shade tolerance estimates of North American species growing in native habitat and in Europe.

We obtained reliable drought and waterlogging tolerance scales for North American and European/ East Asian species using a series of revised assessments of species' performance (13 extensive data sets for North America and 13 for Europe along with a series of case studies). All data sets were strongly correlated, and these correlations were employed to cross-calibrate the data sets and calculate the mean tolerance estimates (see Appendix B for the statistics). Using the mean values effectively reduces the study-to-study bias in species' scorings, thereby enhancing the reliability of final tolerance estimates. Further using these cross-calibrated mean values for species in every continent, we used species native on several continents as well as introduced species to develop global waterlogging and drought tolerance scales (Fig. 2). As with shade tolerance, we did not observe any statistical difference among the drought and waterlogging tolerance estimates of the species in their native and introduced habitat ($P > 0.5$), suggesting that we have obtained general and unbiased intercontinental drought and waterlogging tolerance scales.

TABLE 3. Bivariate relationships between shade, drought, and waterlogging tolerance estimates for 806 temperate shrub and tree species: standardized major axis regressions.

| Group | Tolerance | | Intercept | Slope | r^2 | P |
	y variable	x variable				
A) Species from all functional types pooled ($n = 806$)						
Pooled	Shade	Drought	5.24	−0.956	0.082	0.001
Pooled	Shade	Drought†	5.92	−1.06	0.303	0.001
Pooled	Shade	Waterlogging	4.42	−1.02	0.015	0.001
Pooled	Drought	Waterlogging	4.90	−1.07	0.246	0.001
B) Comparison among gymnosperm ($n = 118$) and angiosperm (mostly broad-leaved, $n = 688$) species‡						
Gymnosperms	Shade	Drought	6.20	−1.14a	0.466	0.001
Angiosperms	Shade	Drought	5.04	−0.909b	0.035	0.001
Gymnosperms	Shade	Waterlogging	5.45	−1.89a	0.000	0.97
Angiosperms	Shade	Waterlogging	4.28	−0.929b	0.018	0.001
Gymnosperms	Drought	Waterlogging	5.50	−1.66a	0.023	0.10
Angiosperms	Drought	Waterlogging	4.85	−1.02b	0.298	0.001
C) Comparison among evergreen ($n = 134$) and deciduous ($n = 554$) broad-leaved species						
Evergreen	Shade	Drought	5.22a	−0.889a	0.022	0.08
Deciduous	Shade	Drought	5.01b	−0.918a	0.042	0.001
Evergreen	Shade	Waterlogging	4.49a	−1.039a	0.041	0.02
Deciduous	Shade	Waterlogging	4.22a	−0.904a	0.013	0.007
Evergreen	Drought	Waterlogging	5.22	−1.168a	0.337	0.001
Deciduous	Drought	Waterlogging	4.76	−0.985b	0.289	0.001

† Species with moderate to very high waterlogging tolerance (>2.5) were removed ($n = 612$).
‡ Standardized major axis (SMA) regression slopes and intercepts among different functional types were compared using the computer program (S)MATR 1.0 (Falster et al. 2003). To compare the slopes, this software uses a maximum-likelihood ratio developed by Warton and Weber (2002). When the slopes are not statistically different, the analysis is continued using standard ANCOVA techniques (common slope model) to test for the difference among the intercepts (Falster et al. 2003).

Correlations between species' shade, drought, and waterlogging tolerances

Pooling all data, we observed negative correlations between species' shade and drought tolerance, shade and waterlogging tolerance, and drought and waterlogging tolerance (Table 3A, Figs. 3–5). The negative correlations between shade and drought tolerance (Figs. 3A–C, 4A) and drought and waterlogging tolerance (Figs. 3G–I, 4C) were significant for all continents, and a negative correlation was also found between species' shade and waterlogging tolerance for the European (Fig. 3E) and East Asian (Fig. 3F) data sets.

Due to the simultaneous negative correlations between species' shade and waterlogging tolerance (Fig. 3E) and drought and waterlogging tolerance (Fig. 3H), in particular for the European data set, several species were apparently outliers in Fig. 3B. These shade intolerant species with high waterlogging tolerance had low drought tolerance, and interestingly, most of them belonged to the family Ericaceae, which contains many dominant species in raised bogs. The negative correlation between species' shade and drought tolerance was improved when species with waterlogging tolerance >2.5 were removed from the data set (inset in Fig. 3B for European data set; for all data pooled, $r^2 = 0.303$ for the truncated vs. $r^2 = 0.082$ for the entire data set; Table 3A). The role of waterlogging tolerance in the relationship between shade and drought tolerance was further assessed by linear multiple regression with all data. In this regression, both drought ($P < 0.001$) and water-logging tolerance ($P < 0.001$) were negatively associated with shade tolerance ($r^2 = 0.176$).

Comparisons of the standardized major axis (SMA) regression slopes for the relationships between shade and drought tolerance ranked the continents according to the slope as East Asia < North America < Europe (Fig. 4A; $P < 0.005$ for comparisons between East Asian data set with other two, and $P = 0.051$ for the comparison between European and North American data sets). The East Asian data set also had significantly more negative slope for the shade vs. waterlogging tolerance relationship ($P < 0.001$). The slopes were not different among the continents for the drought vs. waterlogging tolerance relationship (Fig. 4C; $P > 0.8$), but the elevation of the regression line was significantly lower for the East Asian than for the North American and European data sets (Fig. 4C; $P < 0.001$).

In these comparisons, the species native to both Europe and North America (mostly species from Ericaceae and Salicaceae families) and intercontinental hybrids of European and North American origin, and European and East Asian origin ($n = 30$) were considered as part of the European data set. When these species with wide distribution and the intercontinental hybrids were considered as part of the flora of other continents, the negative correlation between species' shade and waterlogging tolerance was significant both for European ($r^2 = 0.022$, $P = 0.023$) and North American ($r^2 = 0.012$, $P = 0.039$) data sets, further
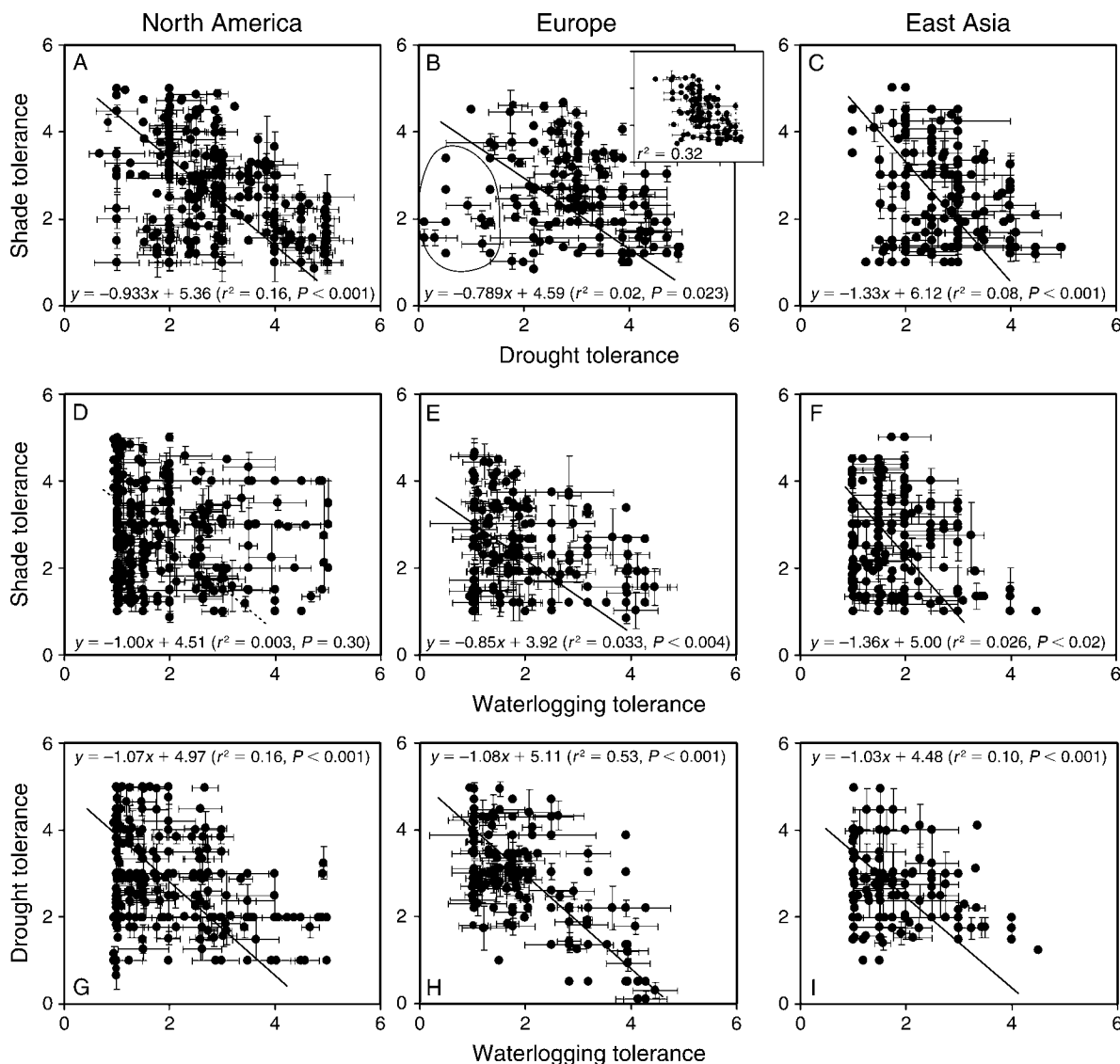
Fig. 3. Correlations between species' shade tolerance and drought tolerance (A–C) and waterlogging tolerance (D–F), and between species' drought and waterlogging tolerance (G–I) for 806 temperate woody species from North America (A, D, G; $n = 339$), Europe/West Asia (B, E, H; $n = 256$), and East Asia (C, F; $n = 211$). Data were fitted by standardized major axis (SMA) regressions (see Table 3 for pooled regressions) using the program (S)MATR 1.0 (Falster et al. 2003), and the regressions for all continents are shown in Fig. 4. The statistically nonsignificant regression in (D) is shown by a dotted line. Data encircled in (B) correspond to species with high waterlogging tolerance and low drought tolerance, and the inset demonstrates the correlation for a truncated data set containing only species with waterlogging tolerance estimate <2.5 ($P < 0.001$). Error bars show ±SE of separate independent assessments for the same species. A full species list with tolerance values is provided in Appendix A.

demonstrating the importance of wide distribution Ericaceae with specific physiological potentials.

Quantile regression revealed that these negative relationships were not always significant across the entire scatter diagram (Fig. 5). High light species exhibited a wide range of drought tolerances, so the negative relationship between shade and drought tolerance was significant only for species growing in moderate to deep shade (Fig. 5A, D). The relationship between shade and waterlogging tolerances was weak, being significant only for the lowest quantiles (i.e., for

species growing in moderate shade to high light). By contrast, the negative relationship between drought and waterlogging tolerances was significant for all quantiles, except for the 99% (i.e., for some exceptional species tolerating extreme drought; Fig. 5C, F).

Functional type and tolerance to shade, drought, and waterlogging

To determine the extent to which the correlations between species' ecological potentials are modified by various functional types, we quantified the relationships

among tolerance estimates separately for gymnosperms (mostly needle-leaved species in our data set, except for *Ginkgo biloba*, which is a broad-leaved species) and angiosperms (mostly broad-leaved species with the exception of some needle-leaved species such as *Erica* and *Calluna* from Ericaceae). These relationships were also explored separately for evergreen and deciduous angiosperms (mostly broad-leaved species).

Species' shade and drought tolerance was correlated both for gymnosperms and angiosperms (Fig. 6A, Table 3B). The slope of this relationship was significantly greater for gymnosperms than for angiosperms (Table 3B). However, the correlations between species' shade and waterlogging tolerance (Fig. 6B, Table 3B) and drought and waterlogging tolerance (Fig. 6B, Table 3B) were significant only for angiosperms. Due to the lack of simultaneous correlations between shade and waterlogging and drought and waterlogging tolerance, the explained variance of shade vs. drought tolerance was much larger for gymnosperms ($r^2 = 0.466$) than for angiosperms ($r^2 = 0.035$).

Among the angiosperms, the slope of the shade vs. drought tolerance relationship was not significantly different between deciduous and evergreen broad-leaved species, but evergreens had significantly larger shade tolerance at a common drought tolerance (Fig. 6D, Table 3C): For shade tolerance vs. waterlogging tolerance, the correlations were not significantly different among evergreen and deciduous species (Fig. 6E, Table 3C). The slope of drought vs. waterlogging tolerance was more negative in evergreen species (Fig. 6F, Table 3C). When the species with relatively high waterlogging tolerance (>2.5) were removed from the data set (mostly Ericaceae), the correlation between shade and drought tolerance was significantly stronger for both evergreen ($n = 101$, $r^2 = 0.337$, $P < 0.001$) and deciduous species ($n = 403$, $r^2 = 0.227$, $P < 0.001$). Again, evergreens had a larger intercept than deciduous species ($P < 0.001$), while the SMA slopes did not differ among the groups ($P > 0.8$).

Simultaneous tolerance to several environmental factors

There were only a few species that were tolerant to more than one limiting factor (tolerance index for two variables ≥ 3). Eighty-three species (10.3% of total species number) were both shade and drought tolerant (e.g., *Aucuba japonica*, *Buxus sempervirens*, *Quercus ilex*, *Ostrya* spp., some *Sorbus* spp., *Taxus baccata*), 32 species (4% of total) both shade and waterlogging tolerant (e.g., *Acer rubrum*, *A. saccharinum*, *Aesculus turbinata*, *Chamaecyparis thyoides*, *Clethra alnifolia*, several *Fraxinus* spp., several *Ilex* spp., *Persea borbonia*, *Pinus glabra*, *Planera aquatica*, *Ulmus davidiana*), and 21 species (2.6% of total; e.g., *Amelanchier laevis*, *Pinus serotina*, *Rhus copallina*, *Tamarix ramosissima*, *Taxodium distichum*, *Vaccinium vitis-idaea*) were both drought and waterlogging tolerant. There were only three species that were tolerant to all three environ-
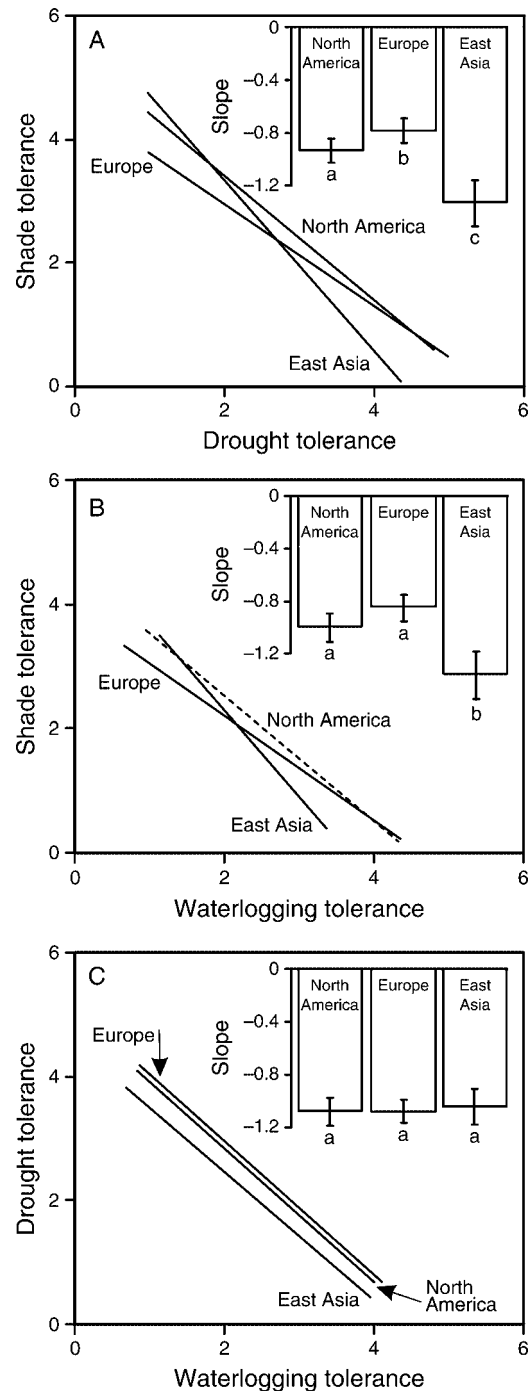

Fig. 4. Regressions for the correlations of (A) shade tolerance with drought tolerance, (B) shade tolerance with waterlogging tolerance, and (C) drought tolerance with waterlogging tolerance shown in Fig. 3. Insets provide the slopes of the standardized major axis (SMA) regressions with 95% confidence intervals (Falster et al. 2003). Slopes with the same letter are not significantly different ($P > 0.05$) according to the maximum-likelihood ratio test of Warton and Weber (2002; see also Falster et al. 2003).
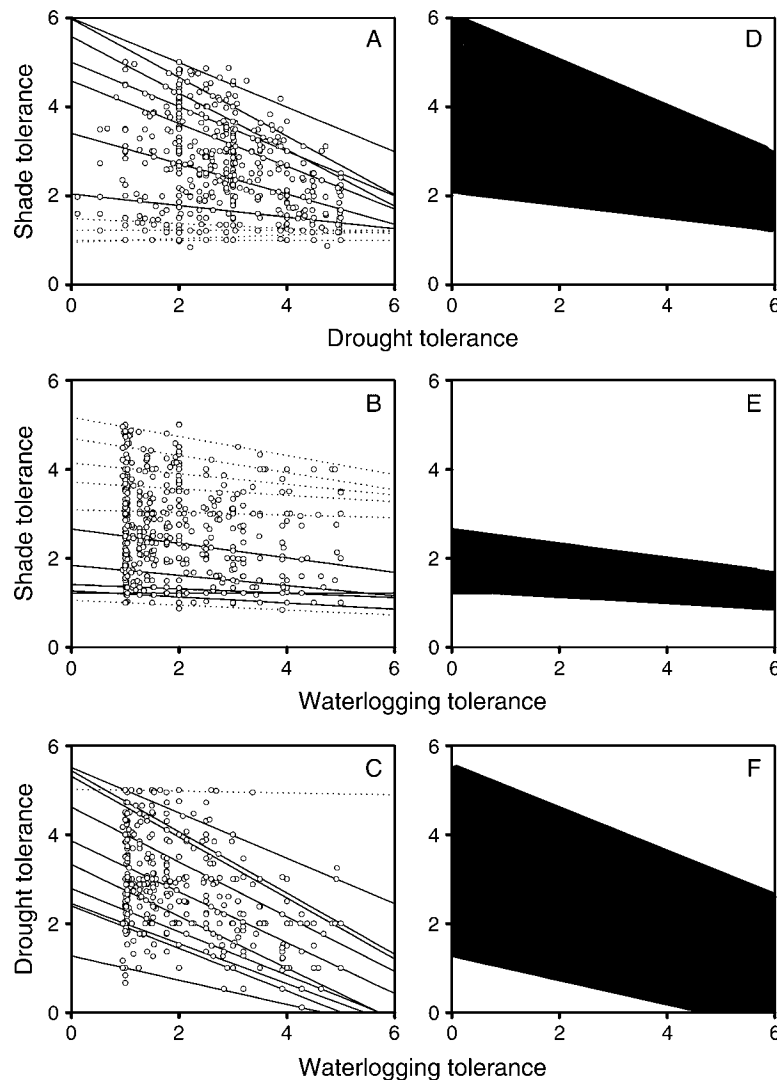
FIG. 5. Quantile regressions for (A) shade tolerance vs. drought tolerance, (B) shade tolerance vs. waterlogging tolerance, and (C) drought tolerance vs. waterlogging tolerance. Lines are estimates based on least absolute values for 12 quantiles (from top to bottom: 99%, 95%, 90%, 85%, 75%, 50%, 25%, 20%, 15%, 10%, 5%, and 1%). Solid lines indicate significant regressions ($P < 0.001$); dotted lines indicate nonsignificant regressions. Panels D–F illustrate, in a simplified way, the corresponding polygonal pattern of each relationship.

mental limitations (tolerance index for all variables ≥3): *Amelanchier laevis, Rhododendron periclymenoides, Rhododendron viscosum.* Yet, the mean tolerance value (shade, waterlogging, drought) was 3.0–3.5 for these species, suggesting that polytolerant plants were not very tolerant to any of these limitations.

We calculated the overall tolerance (sum of all three indices), and the coefficients of variation (standard deviation per sample mean) for all the tolerance estimates and overall tolerance to further characterize the extent of polytolerance within the entire data set. The coefficients of variation were 0.407 for shade, 0.367 for drought, and 0.524 for waterlogging tolerance, while the coefficient for variation for the sum of all three tolerance indices was 0.152. This low variation in overall

tolerance further underscores the inherent trade-offs between species' adaptation to interacting environmental limitations and low degree of polytolerance. "Polyintolerance" was also rare, with only some genera like *Betula* and *Larix* including species that were tolerant neither to shade nor drought nor waterlogging.

Phylogenetic signal and influence of phylogeny on correlations among tolerances

Phylogenetic signal, estimated as the correlation between the phylogenetic and the tolerance matrices of distances among species, was significant for the tolerance of any of the three environmental factors studied (Table 4). Between 22% and 24% of the nodes of the phylogenetic tree exhibited trait conservatism (i.e., stress
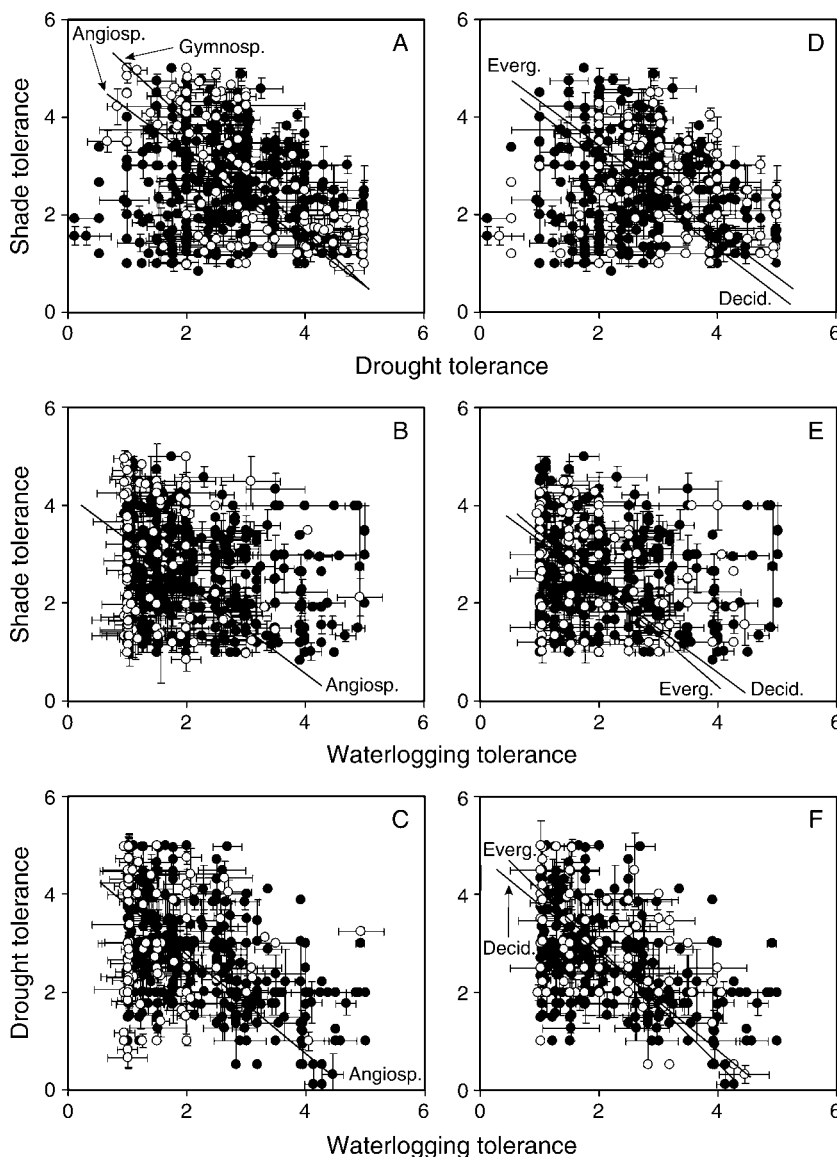
FIG. 6. Comparison of the relationships between (A, D) shade and drought tolerance, (B, E) shade and waterlogging tolerance, and (C, F) drought and waterlogging tolerance. In panels A–C, gymnosperms (open circles) and angiosperms (solid circles) are compared, and in panels D–F, deciduous (open circles) and evergreen (solid circles) angiosperms are compared. Data were fitted by standardized major axis (SMA) regressions (Falster et al. 2003). The regression statistics are provided in Table 3B and C. Nonsignificant regression lines ($P > 0.05$) for gymnosperms in B and C are not shown. Error bars represent $\pm$SE. Gymnosperm species are mostly conifers, while angiosperm species are mainly broad-leaved (Appendix A).

tolerance was more similar among related species than expected by chance) and only 6–8% of the nodes exhibited significant divergence (Table 5). Divergence occurred at branches closer to the root of the phylogenetic tree than conservatism, which was observed in bifurcations nearer the tips (Table 5). Phylogenetic signal was significant for the whole data set of species, and for the 18 species of *Pinus* for which we could obtain reliable phylogenetic information, but not for the 11 species of *Quercus* with available phylogenetic information. This phylogenetic signal was generally low with the correlation coefficients (Pearson's

r) of 0.026–0.147. The exception was shade tolerance in *Pinus* species ($r = 0.404$).

The inverse relationships between stress tolerance estimates were significant in phylogenetically independent contrasts carried out with the whole set of species (AOT module of PHYLOCOM). The correlations ranged from -0.1 (drought vs. waterlogging tolerance) to -0.37 (shade vs. drought tolerance; $P < 0.01$ for all). The strongest relationship was between shade and drought, and this relationship was also significant in species-level phylogenetically independent contrasts in both *Pinus* and *Quercus* (Figs. 7, 8). Among the rest of

TABLE 4. Phylogenetic signal estimated by the correlation between the phylogenetic and the tolerance matrices of distances among species in shade, drought, and waterlogging tolerances in the whole species data set, and in the genera *Quercus* and *Pinus*.

Tolerance	r	g†	P
Whole species data set			
Shade tolerance	0.082	18.211	<0.005
Drought	0.059	13.297	<0.005
Waterlogging	0.026	5.131	<0.005
Quercus species			
Shade	0.069	0.540	>0.05
Drought	0.147	1.181	>0.05
Waterlogging	0.098	0.817	>0.05
Pinus species			
Shade	0.404	5.572	<0.005
Drought	0.195	2.685	<0.005
Waterlogging	0.053	0.731	>0.05

† Standard normal variate from Mantel test.

the pairwise inverse relationships between tolerance estimates, only drought and waterlogging tolerance were significantly correlated in *Pinus*. While significant divergences and convergences in stress tolerance in *Quercus* occurred near the tips (i.e., within sections and subgenera), an interesting significant divergence in drought tolerance was found in *Pinus*, with species of the subgenus *Pinus* being more drought tolerant than species of the subgenus *Strobus* (Figs. 7, 8).

DISCUSSION

Plant shade tolerance rankings

Any stress factor that decreases the ability of plants to use available light will increase the minimum daily light dose that the plant requires to survive under given conditions. Therefore, there is no single minimum light level that an individual of a particular species tolerates; "shade tolerance" is not an absolute but rather a relative term (Spurr and Barnes 1980). Nutrient and water availabilities, and air and soil temperature are potentially capable of affecting shade tolerance (Tilman 1993, Bazzaz and Wayne 1994), and they vary in gradients of irradiance across gap–understory continuum. Thus, species' dispersal across light gradients is determined by a complex interplay of various edaphic and climatic factors. Due to this interplay of species' minimum light

requirements with other environmental factors, reliable relative rankings of species' shade tolerance potentials are invaluable in trying to understand forest development and diversity.

We revised an extensive set of published shade tolerance scorings, and constructed a common intercontinental scale of shade tolerance. Surprisingly, the shade tolerance rankings of woody species, most of which are based on foresters' and ecologists' knowledge of species behavior, and only very few on some quantitative work on species dispersal across understory habitats, have remained remarkably constant for more than a century (Table 2). This general agreement of species classification further corroborates the suggestion that the relative light requirements of species vary considerably less than the absolute ones.

Very few studies have tried to develop comparative shade tolerance rankings for different continents (Peters 1997), and even these rankings are limited to a few dominant species. For construction of the intercontinental shade tolerance scale, we used shade tolerance rankings for species native on several continents (North America/Europe) and the data of shade tolerance of introduced species (North America/Europe/East Asia) to cross-calibrate the shade tolerance rankings developed on different continents. Statistical tests suggested that the shade tolerance of species did not differ significantly in foreign and native habitats, possibly because most species have been introduced during a relatively short time period of 50–200 years. Further detailed studies suggest that European introduced species that have escaped from cultivation (such as the tolerant to very tolerant species *Acer platanoides*, tolerant to medium tolerant species *Acer pseudoplatanus*, and intolerant species *Rhamnus cathartica*) appear to occur in similar habitats and canopy positions as in their respective native habitats (Webb and Kaunzinger 1993, Kloeppel and Abrams 1995, Hoffman and Kearns 1997, Mehrhoff et al. 2003). The same appears to be valid for North American species such as *Picea sitchensis* and *Pseudotsuga menziesii* widely cultivated in Europe or *Robinia pseudacacia* and *Symphoricarpus albus* naturalized in Europe (Hermann 1987). A series of widespread Asian species such as *Ailanthus altissima* or *Lonicera japonica* also occur in similar habitats across the globe (Hoffman and Kearns 1997, Mehrhoff et al. 2003).

TABLE 5. Percentage of cladogram nodes exhibiting significant conservatism and divergence, mean divergence, and mean age for the nodes for shade, drought, and waterlogging tolerances in the whole data set.

Tolerance	Nodes with conservatism			Nodes with divergence		
	Number (%)	Divergence (SD)	Mean age† (%)	Number (%)	Divergence (SD)	Mean age (%)
Shade	21.5	0.30	35.0	5.7	1.50	45.0
Drought	24.3	0.35	37.5	6.2	1.58	48.1
Waterlogging	22.6	0.17	39.4	7.9	1.43	40.6

† Mean age is expressed as a percentage of maximal age, with zero representing the tips and 100% representing the root of the cladogram.
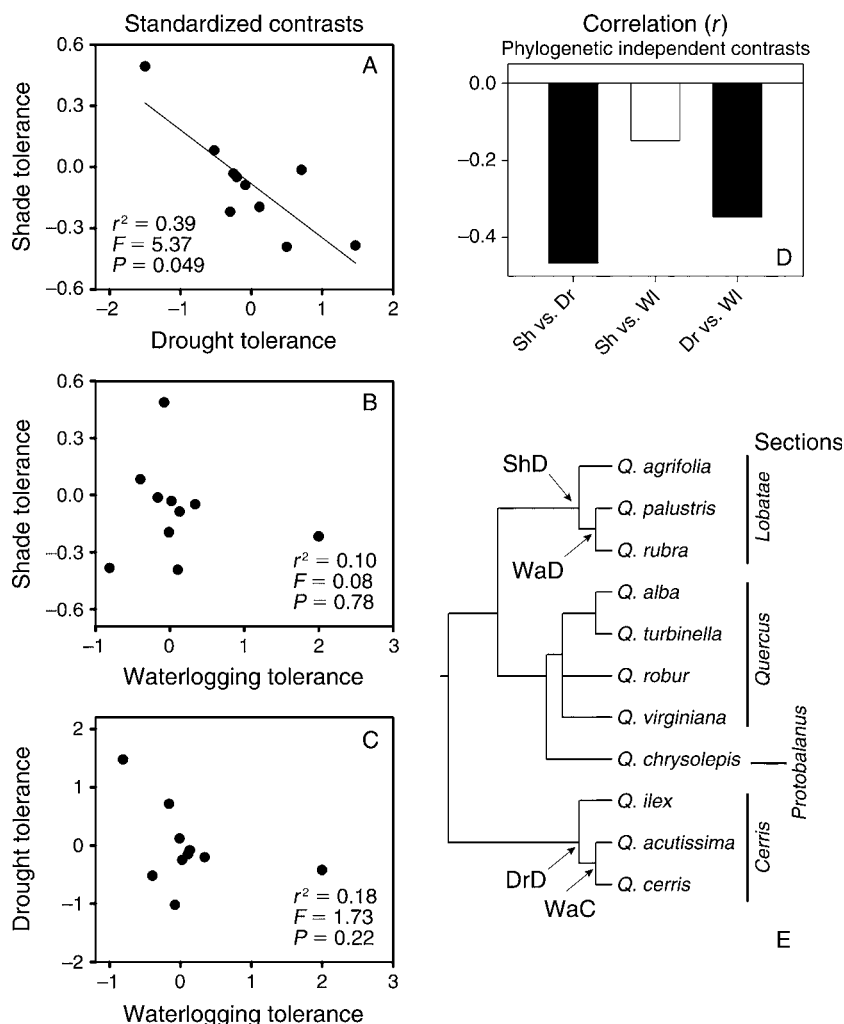
Fig. 7. (A) Phylogenetically independent relationships between shade and drought tolerance, (B) shade and waterlogging tolerance, and (C) drought and waterlogging tolerance for the species of the genus *Quercus* represented in panel E. The data points are the Felsenstein's pairwise independent contrasts (Felsenstein 1985) standardized with respect to the standard deviation of the contrast. Nonsignificant ($P > 0.05$) regression lines are not shown. (D) Phylogenetically independent correlation coefficients (Pearson's *r*) obtained with the PHYLOCOM analysis of trait routine (see *Materials and Methods: Phylogenetic signal and phylogenetically independent contrasts*). Key to abbreviations: Sh, shade; Dr, drought; Wl; waterlogging. Solid bars indicate significant correlations. (E) The *Quercus* phylogenetic tree is derived from the data in Manos et al. (1999). Arrows indicate nodes at which significant divergence (D) or conservatism (C) was obtained for the three tolerances.

The obtained shade tolerance scale further agrees with global distribution patterns of species at the extremes of the shade tolerance rankings as illustrated by *Alnus*, *Betula*, and *Salix* species being in the majority of forests among the most intolerant species, and *Acer* and *Fagus* species typically among the most tolerant woody components. In fact, minimum light availabilities in late successional temperate *Fagus* forests are very similar across the globe (Peters 1997), further corroborating that *F. crenata*, *F. grandifolia*, and *F. sylvatica* should be classified as very shade tolerant. These data collectively suggest that the global shade tolerance scale we have derived is robust.

Plant waterlogging and drought tolerance rankings

Significant negative correlation exists between air humidity and the distance from streams and wetlands (Chen et al. 1999), implying that the way the species respond to gradual changes from excess to limiting water availabilities may significantly modify forest succession along these gradients, and in interaction with shade tolerance determine the forest chronosequence in any specific site with given water availability. Therefore, extended forest gap models also use estimates of species' drought and waterlogging tolerance to predict forest succession (Bugmann and Cramer 1998). Reliable estimates of species' drought and waterlogging tolerance
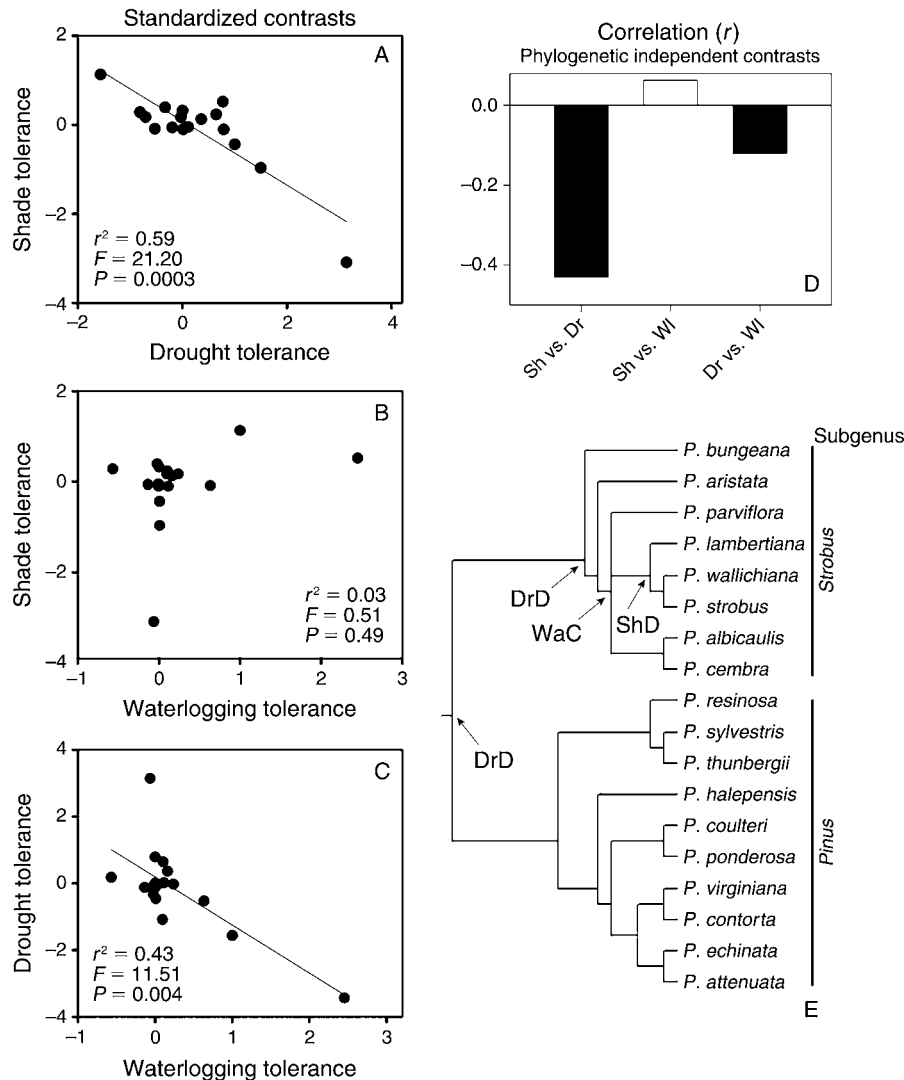
Fig. 8. (A) Phylogenetically independent relationships between shade and drought tolerance, (B) shade and waterlogging tolerance, and (C) drought and waterlogging tolerance for the species of the genus *Pinus* represented in panel E; data points are as described in Fig. 7. Nonsignificant ($P > 0.05$) regressions are not shown. (D) Phylogenetically independent correlation coefficients (Pearson's r) obtained with PHYLOCOM analysis of trait routine, as described in Fig. 7. (E) The *Pinus* phylogenetic tree was obtained from the data of Liston et al (1999). Arrows indicate nodes at which significant divergence (D) or conservatism (C) was observed for the three tolerances.

have been noted as primary limitations to further development of these models (Bugmann and Solomon 1995, Bugmann and Cramer 1998). Species' potentials to cope with drought and waterlogging stress are often characterized in succession models using a coarse scale of tolerant/intolerant or by adding the gradation intermediate (Prentice and Helmisaari 1991). Such coarse scale assessments may be adequate for understanding the performance of species assemblages during moderate stress events. More refined species rankings may be needed to predict species' survival during extreme stress periods that occur only infrequently, but that greatly influence community composition.

In this context, the assessment of stress tolerance at the extremes becomes especially important. Even in our detailed and uniform classification, many species tended to aggregate at the lowest extreme of waterlogging tolerance (e.g., Fig. 3D, G), partly because not many species are tolerant, but also suggesting that the resolution of the tolerance scale could be improved at the lower range (tolerance = 1, very intolerant). At the higher end of our waterlogging tolerance scale, the North American data set stands out as having more species than European or East Asian data set. While waterlogging tolerance scales specifically developed for Europe include several species with waterlogging ranked as 5, very tolerant (Glenz 2005), these values are

diminished when the data sets are cross-calibrated to a common scale for the entire Northern Hemisphere. The most waterlogging-tolerant trees in swamp forests in the lowlands of cool temperate and warm temperate Europe are *Alnus glutinosa*, and *Populus* and *Salix* species, while Japanese wet forests are characterized by *Alnus japonica*, *Fraxinus mandshurica*, *Ulmus davidiana*, and *Salix* species. None of these forests are comparable, however, to the extreme swamp forests of *Taxodium* in the southeast United States that can be flooded all year (Shidei 1974). Thus, the lack of very waterlogging-tolerant species in Europe and East Asia in the cross-calibrated rankings corresponds to reality.

As with waterlogging tolerance, many species tended to cluster at the lower end of the cross-calibrated drought tolerance scale (see Fig. 3A, G, for sample graphs). Given that the climatic change scenarios predict increasing shortage of water in certain geographic locations, and more frequent waterlogging in other locations (Albritton et al. 2001), it is important to improve the resolution of this data set in the extremes. Comparative ecophysiological studies like those of van Splunder et al. (van Splunder et al. 1995, 1996, van Splunder 1998) on European Salicaceae species, and common garden experiments of Ranney and colleagues on waterlogging tolerance of a series of North American, European, and East Asian *Betula* and *Prunus* species (Ranney 1994, Ranney and Bir 1994) and drought tolerance of *Betula* species (Ranney et al. 1991) provide invaluable means to fine-tune the tolerance rankings of closely related species and develop reliable succession models for communities such as riparian forests. We conclude that future comparative ecophysiological studies are needed to refine the resolution of drought and waterlogging scales for species at the upper and lower limits of tolerance.

Inverse correlations between species' ecological potentials

An inverse correlation between species' shade and drought tolerance has been hypothesized in several studies (Smith and Huston 1989, Abrams 1994, Kubiske et al. 1996), but tests of this hypothesis are conflicting. Kubiske et al. (1996) investigated gas-exchange physiology in six species of varying shade and drought tolerance and found a stronger effect of drought on leaf physiology in shade tolerant than in intolerant species. In contrast, Sack (2004) found a similar effect of drought on growth in 12 species of varying shade and drought tolerance.

We observed an inverse correlation between species' shade and drought tolerance for 806 species covering the major dominants in North American, European/West Asian, and East Asian temperate woody ecosystems (Table 3A), as well as separately for every continent (Figs. 3A–C, 4A), and plant functional type (Fig. 6A, D, Table 3B, C), except for the evergreen angiosperms (Fig. 6D, Table 3C). This relationship had wide scatter with significant variation of drought tolerance at a given

shade tolerance, and thus confirmed the suggestion that the correlation between drought and shade tolerance is not absolute (Sack 2004).

However, the large variability for all data pooled was also associated with correlations between shade and waterlogging tolerance (Figs. 3E, 6B, E, Table 3), and drought and waterlogging tolerance (Figs. 3G–I, 4C, 6C, F, Table 3). The latter correlation agrees with previous observations for tropical species (ter Steege 1994). These negative correlations essentially mean that certain shade intolerant species, instead of being drought tolerant were waterlogging tolerant (see Fig. 3B, E, H), further underscoring the importance of trade-offs among species in terms of their ecological potentials. When species from the family Ericaceae were removed from the global data set, the correlations were improved significantly.

Among the different plant functional types, the strongest correlation between shade and drought tolerance was for gymnosperms (Fig. 6A, Table 3B), which did not exhibit a correlation between shade and waterlogging (Fig. 6B) and drought and waterlogging (Fig. 6C) tolerance. In fact, only *Taxodium distichum* was characterized by a high degree of waterlogging tolerance, while *Chamaecyparis thyoides*, *Larix gmelinii*, *Pinus contorta* ssp. *contorta*, *P. elliotti*, *P. glabra*, *P. serotina*, *P. sibirica*, and *P. sylvestris* were moderately tolerant of waterlogging. This low number of waterlogging-tolerant species in gymnosperms demonstrates that not only the ecological and physiological trade-offs, but also phylogeny and historical factors may constrain the viable combinations of ecological potentials in species.

It is striking that the correlations among species' shade and drought tolerance and waterlogging and drought tolerance were observed for all continents (Figs. 3, 4), and among most plant functional types. It is further remarkable that the standardized major axis regressions fitted to the data (Fig. 4A–C, Table 3) differed only to a minor extent among the continents and functional types. Part of these intercontinental and functional type differences were associated with the existence of a negative relationship between shade and waterlogging tolerance in a specific subset of data, primarily the species of Ericaceae. Despite the significant phylogenetic signal found in the tolerance to each environmental limitation (Table 4), the negative correlations were also significant in phylogenetic independent contrasts for species in the genera *Pinus* and *Quercus*, particularly for the shade–drought tolerance relationship (Fig. 5). All these findings support the generality of the trade-offs in the tolerances to different limiting factors.

Simultaneous tolerance to shade and drought

Certain species appeared to be tolerant of both drought and shade (Appendix A), a simultaneous tolerance that is difficult to understand given the
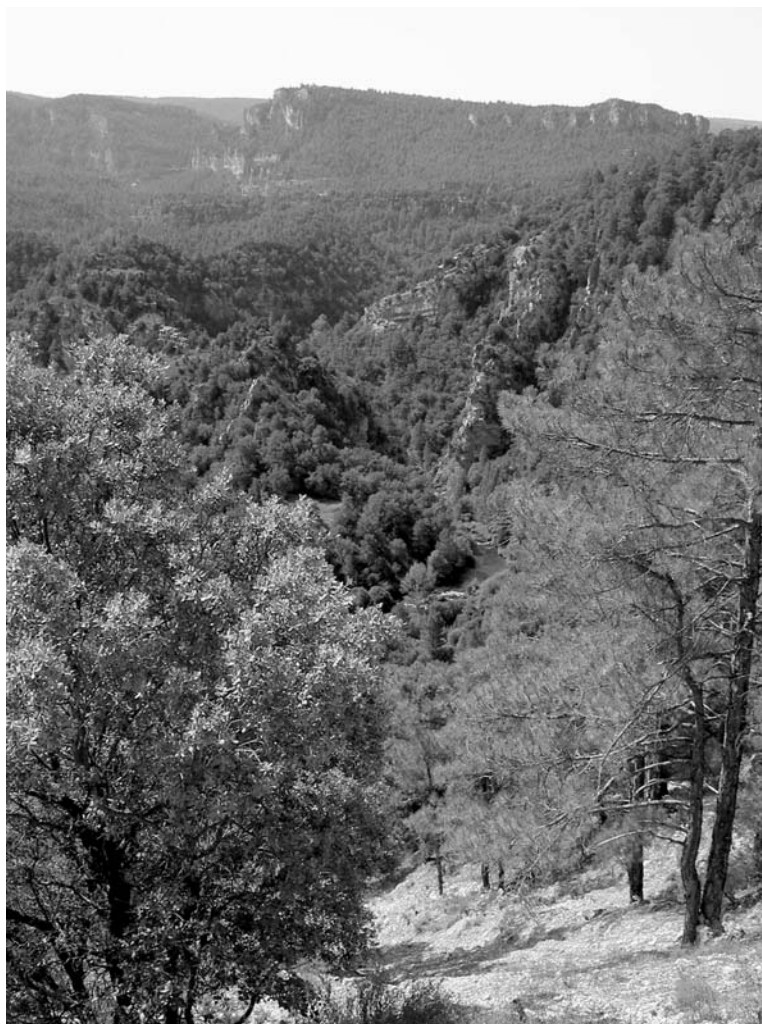
PLATE 1.   Many dry, Mediterranean forests such as this one in Alto Tajo Natural Park (central Spain) exhibit a remarkably poor understory due, at least in part, to the combination of drought and shade coupled with a short growth period imposed by extreme temperatures. Dominant canopy species are *Quercus ilex* and *Pinus nigra,* and the woody flora in shaded and dry sites is represented only by scattered individuals of *Arctostaphylos uva-ursi* and *Buxus sempervirens.* Photo credit: F. Valladares.

conflicting requirements for efficient light capture (large leaf area, enhanced biomass investment aboveground) and drought avoidance (low leaf area, enhanced biomass investment in roots). However, none of the species tolerant of both shade and drought were very tolerant to either of these limitations, which indicates that this trade-off inevitably shaped the observed patterns to at least some degree. Interestingly, essentially all of the species tolerant of both shade and drought were those colonizing relatively warm habitats (minimum winter $T > -15°C$) extending from the temperate deciduous forests to warm temperate forests at the transition to Mediterranean habitats (see Plate 1). This suggests that the species tolerant of both shade and drought may require extended growing periods to construct a canopy that can support high leaf area, even though this leaf area may be drought stressed during a significant part of

the year. For several East Asian shade-tolerant broad-leaved evergreens colonizing the understories of decid-uous canopy trees, daily winter photosynthesis when the overstory is leafless has been estimated to occasionally exceed the daily photosynthesis in summer when the overstory is fully active (Miyazawa and Kikuzawa 2005), further underscoring the importance of extended growing season in broad-leaved shade-tolerant ever-greens. Our data set contained 23 broad-leaved ever-green species such as *Arbutus menziesii, Aucuba japonica, Lithocarpus densiflorus,* and *Quercus acuta, Q. glauca,* and *Q. ilex* that were both shade and drought tolerant. In Sack (2004), the shade-tolerant species included were broad-leaved evergreens (*Buxus sempervirens, Hedera helix,* and *Ruscus aculeatus*) that are also drought tolerant, but competitive only in habitats with an extended growing season. Thus, the noncorrelation

between shade tolerance and drought tolerance observed in this study (Sack 2004) relies on the presence of evergreen broad-leaved species of warmer habitats.

Interestingly, only four gymnosperms, *Abies firma*, *Calocedrus decurrens*, *Taxus baccata*, and *Tsuga sieboldii*, are both shade and drought tolerant; but again, these gymnosperms are characteristic of warm temperate or oceanic temperate forests with extended growing season. In contrast, other shade-tolerant *Abies*, *Picea*, or *Tsuga* species that dominate cool temperate forests, where the length of growing season is similar for deciduous and evergreen species, are not drought tolerant. This evidence further underscores the importance of extended growing season in simultaneous tolerance to shade and drought. It also confirms the infrequency of polytolerance; none of the species in our data set was simultaneously tolerant to drought, shade, and low winter temperatures.

Polytolerance: rarity and possible implications

Several species that were moderately tolerant (tolerance value ≥3.0) simultaneously to several environmental factors such as *Acer negundo* (shade/drought), *Lonicera xylosteum* (shade/drought), *Prunus padus* (shade/waterlogging), *Rhododendron ponticum* (shade/drought), and *Tamarix ramosissima* (waterlogging/drought), have been reported as invasive outside their natural areas (Randall and Marinelli 1996, Mooney and Hobbs 2000). However, the three plant species in our study that were simultaneously tolerant to all three environmental limitations (*Amelanchier laevis*, *Rhododendron periclymenoides*, and *Rhododendron viscosum*, with tolerance value for all characteristics ≥3.0) are species with very limited invasive potential, suggesting that polytolerance is not associated with invasiveness. Besides, the mean tolerance value was 3.0–3.5 for these species suggesting that polytolerant plants were not very tolerant to any of these environmental limitations. Being simultaneously tolerant to several environmental limitations could imply a lack of full adaptation to each particular limitation.

CONCLUSIONS

Limited and often biased information on species' ecological potentials and scarcity of comparative information on species' ecological potentials on different continents has hampered the development of general world-scale vegetation dynamic models. All temperate forests in the Northern Hemisphere are physiognomically similar, often sharing species from the same genera at various stages of succession (*Alnus*, *Betula*, *Pinus*, and *Populus* in early-successional forests and *Abies*, *Acer*, *Fagus*, and *Picea* in late-successional forests), suggesting similar performance of temperate forests on different continents and possibilities for common general patterns at broad geographical scales.

With a few exceptions, the negative correlations among shade, drought, and waterlogging tolerance were significant for our global data set as well as within each functional or phylogenetic group considered. These negative correlations indicate that the number of possible combinations of ecological potentials in a species is limited by trade-offs between tolerance to differing environmental limitations. In fact, and as the data demonstrate, few species are characterized by simultaneous tolerance to two environmental factors, and even fewer are moderately tolerant to three environmental factors. Although most species commonly cope with multiple environmental limitations, polytolerance has not been frequently achieved during the evolution of trees and shrubs of the Northern Hemisphere. The trade-offs among the tolerances to different limiting factors found here represent a constraint for niche differentiation of coexisting species since they reduce the diversity of plant responses to the many combinations of irradiance and water supply that are found in natural ecosystems.

LITERATURE CITED

Aasamaa, K., and A. Sõber. 2001. Hydraulic conductance and stomatal sensitivity to changes of leaf water status in six deciduous tree species. Biologia Plantarum **44**:65–73.

Aasamaa, K., A. Sõber, W. Hartung, and Ü. Niinemets. 2004. Drought acclimation of two deciduous tree species of different layers in a temperate forest canopy. Trees: Structure and Function **18**:93–101.

Abrams, M. D. 1990. Adaptations and responses to drought in *Quercus* species of North America. Tree Physiology **7**:227–238.

Abrams, M. D. 1994. Genotypic and phenotypic variation as stress adaptations in temperate tree species: a review of several case studies. Tree Physiology **14**:833–842.

Abrams, M. D., M. E. Kubiske, and S. A. Mostoller. 1994. Relating wet and dry year ecophysiology to leaf structure in contrasting temperate tree species. Ecology **75**:123–133.

Acherar, M., and S. Rambal. 1992. Comparative water relations of four Mediterranean oak species. Vegetatio **99–100**:177–184.

Ackerly, D. D. 2004. ANALYSIS OF TRAITS (AOT), Version 3.0: a module of PHYLOCOM, and Version 3.21 by C. O. Webb, S. Kempel, D. D. Ackerly, and S. W. Kempel. ⟨http://www.phylodiversity.net/phylocom⟩

Albritton, D. L., et al. 2001. Technical summary. Pages 21–83 *in* IPCC third assessment report: contributions of IPCC working groups. Summaries for policymakers and technical summaries from the three working group reports. Geneva, Switzerland. ⟨http://www.epa.gov/oppeoee1/globalwarming/publications/reference/index.html⟩

Anonymous. 1996. Auwälder in Südbayern. Standörtliche Grundlagen und Bestockungsverhältnisse im Staatswald. LWF Bericht, 9. Bayerische Landesanstalt für Wald und Forstwirtschaft, Freising.

Armstrong, J. V., and P. D. Sell. 1996. A revision of the British elms (*Ulmus* L., Ulmaceae): the historical background. Botanical Journal of the Linnean Society 120:39–50.

Baker, F. S. 1949. A revised tolerance table. Journal of Forestry 47:179–181.

Barnes, B. V. 1991. Deciduous forests of North America. Pages 219–344 *in* E. Röhrig and B. Ulrich, editors. Temperate deciduous forests. Ecosystems of the world, 7. Elsevier, Amsterdam, The Netherlands.

Battaglia, L. L., S. A. Fore, and R. R. Sharitz. 2000. Seedling emergence, survival and size in relation to light and water availability in two bottomland hardwood species. Journal of Ecology 88:1041–1050.

Battaglia, M., and J. B. Reid. 1993. Ontogenetic variation in frost resistance of *Eucalyptus delegatensis* R. T. Baker. Australian Journal of Botany 41:137–141.

Bazzaz, F. A., and P. M. Wayne. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap–understory continuum. Pages 349–390 *in* M. M. Caldwell and R. W. Pearcy, editors Exploitation of environmental heterogeneity by plants. Ecophysiological processes above- and belowground. Physiological ecology. A series of monographs, texts, and treatises. Academic Press, San Diego, California, USA.

Bell, D. T., and E. L. Johnson. 1974. Flood-caused tree mortality around Illinois reservoirs. Transactions of the Illinois State Academy of Science 67:28–37.

Bendix, J., and C. R. Hupp. 2000. Hydrological and geomorphological impacts on riparian plant communities. Hydrological Processes 14:2977–2990.

Blomberg, S. P., and T. Garland, Jr. 2002. Tempo and mode in evolution: phylogenetic inertia, adaptation and comparative methods. Journal of Evolutionary Biology 15:899–910.

Blomberg, S. P., T. Garland, Jr., and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. International Journal of Organic Evolution 57:717–745.

Bratkovich, S., L. Burban, S. Katovich, C. Locey, J. Pokorny, and R. Wiest. 1993. Flooding and its effect on trees: information packet. Forest Resources Management and Forest Health Protection, USDA Forest Service, Northeastern Area State and Private Forestry, St. Paul, Minnesota, USA. ⟨http://www.na.fs.fed.us/spfo/pubs/nresource/flood/cover.html⟩

Brzeziecki, B. 1995. Skale nominalne wymagan klimatycznych gatunków drzew lesnych. (Nominal scales for climatic requirements of forest tree species). Sylwan 139:53–65.

Brzeziecki, B., and F. Kienast. 1994. Classifying the life-history strategies of trees on the basis of the Grimian model. Forest Ecology and Management 69:167–187.

Bugmann, H., and W. Cramer. 1998. Improving the behaviour of forest gap models along drought gradients. Forest Ecology and Management 103:247–263.

Bugmann, H. K. M., and A. M. Solomon. 1995. The use of a European forest model in North America: a study of ecosystem response to climate gradients. Journal of Biogeography 22:477–484.

Burkart, M. 2001. River corridor plants (Stromtalpflanzen) in Central European lowland: a review of a poorly understood plant distribution pattern. Global Ecology and Biogeography 10:449–468.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America. Agricultural Handbook 654. USDA Forest Service, Washington, D.C., USA.

Cade, B. S., and B. R. Noon. 2003. A gentle introduction to quantile regression for ecologists. Frontiers in Ecology and the Environment 1:412–420.

Cade, B. S., and J. D. Richards. 2005. User manual for Blossum statistical software. U.S. Department of Interior, U.S. Geological Survey, Reston, Virginia, USA.

Carrión Vilches, M. A., P. Sánchez Gómez, and J. Güemes Heras. 2000. Primera aproximación al significado taxonómico de la variabilidad foliar de Acer opalus gr. en la Península Ibérica (First approach to the taxonomic meaning of the foliar variability of Acer opalus gr. in Iberian Peninsula). Portugaliae Acta Biologica, Series A. 19:239–248.

Castro, J., R. Zamora, J. A. Hodar, J. M. Gomez, and L. Gomez-Aparicio. 2004. Benefits of using shrubs as nurse plants for reforestation in Mediterranean mountains: a 4-year study. Restoration Ecology 12:352–358.

Cavender-Bares, J., and F. A. Bazzaz. 2000. Changes in drought response strategies with ontogeny in *Quercus rubra*: implications for scaling from seedlings to mature trees. Oecologia 124:8–18.

Cerny, T. A., M. Kuhns, K. L. Kopp, and M. Johnson. 2002. Efficient irrigation of trees and shrubs. Utah State University Extension, Logan, Utah, USA. Electronic Publishing, HG-523. ⟨http://extension.usu.edu/files/gardpubs/hg523.html⟩

Cescatti, A., and Ü. Niinemets. 2004. Sunlight capture. Leaf to landscape. Pages 42–85 *in* W. K. Smith, T. C. Vogelmann, and C. Chritchley, editors. Photosynthetic adaptation. Chloroplast to landscape. Ecological Studies, 178. Springer Verlag, Berlin, Germany.

Chaves, M. M., J. S. Pereira, J. Maroco, M. L. Rodrigues, C. P. P. Ricardo, M. L. Osorio, I. Carvalho, T. Faria, and C. Pinheiro. 2002. How plants cope with water stress in the field: photosynthesis and growth. Annals of Botany 89:907–916.

Chen, J., S. Saunders, T. Crow, R. J. Naiman, K. Brosofske, G. Mroz, B. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. BioScience 49:288–297.

Cochard, H., F. Froux, S. Mayr, and C. Coutand. 2004. Xylem wall collapse in water-stressed pine needles. Plant Physiology 134:401–408.

Collada, C., P. Fuentes-Utrilla, L. Gil, and M. T. Cervera. 2004. Characterization of microsatellite loci in *Ulmus minor* Miller and cross-amplification in *U. glabra* Hudson and *U. laevis* Pall. Molecular Ecology Notes 4:731–732.

Condit, R., P. S. Ashton, N. Manokaran, J. V. LaFrankie, S. P. Hubbell, and R. B. Foster. 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 354:1739–1748.

Coomes, D. A., and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecological Monographs 70:171–207.

Cornwell, W. K., and P. J. Grubb. 2003. Regional and local patterns in plant species richness with respect to resource availability. Oikos 100:417–428.

Crawford, R. M. M. 1996. Whole plant adaptations to fluctuating water tables. Folia Geobotanica et Phytotaxonomica 31:7–24.

Dale, E. E., Jr., and S. Ware. 2004. Distribution of wetland tree species in relation to a flooding gradient and backwater vs. streamside location in Arkansas, USA. Journal of the Torrey Botanical Society 131:177–186.

Dirr, M. 2005. Virtual plant tags. Steve Cissel, Green Industry Yellow Pages, Inc. ⟨http://www.virtualplanttags.com⟩

Eissenstat, D. M., and A. Volder. 2005. The efficiency of nutrient acquisition over the life of a root. Pages 185–220 *in* H. BassiriRad, editor. Nutrient acquisition by plants: an

ecological perspective. Ecological Studies, 181. Springer Verlag, Berlin, Germany.

Ellenberg, H. 1991. Zeigerwerte der Gefäßpflanzen (ohne *Rubus*). Pages 9–166 *in* H. Ellenberg, R. Düll, V. Wirth, W. Werner, and D. Paulißen, editors. Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica, 18. Erich Goltze KG, Göttingen, Germany.

Ellenberg, H. 1996. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. Fifth edition. Verlag Eugen Ulmer, Stuttgart, Germany.

Epron, D. 1997. Effects of drought on photosynthesis and on the thermotolerance of photosystem II in seedlings of cedar (*Cedrus atlantica* and *C. libani*). Journal of Experimental Botany **48**:1835–1841.

Epron, D., E. Dreyer, and G. Aussenac. 1993. A comparison of photosynthetic responses to water stress in seedlings from 3 oak species: *Quercus petraea* (Matt.) Liebl., *Q. rubra* L. and *Q. cerris* L. Annales des Sciences Forestieres **50**:48–60.

Falster, D. S., D. I. Warton, and I. J. Wright. 2003. (S)MATR: standardized major axis tests and routines. Version 1.0. Department of Biological Sciences, Macquarie University, Sydney, Australia. ⟨http://www.bio.mq.edu.au/SMATR⟩

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist **125**:1–15.

Fowells, H. A. 1965. Silvics of forest trees of the United States. Agriculture handbook, No. 271. U.S. Department of Agriculture Forest Service, Washington, D.C., USA.

Frye, J., and W. Grosse. 1992. Growth responses to flooding and recovery of deciduous trees. Zeitschrift für Naturforschung, Section C. Journal of Biosciences **47c**:683–689.

Garland, T., Jr., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. Systematic Biology **42**:265–292.

Garland, T., Jr., P. E. Midford, and A. R. Ives. 1999. An introduction to phylogenetically based statistical methods, with a new method for confidence intervals on ancestral states. American Zoologist **39**:374–388.

Gayer, K. 1898. Der Waldbau. vierte, verbesserte Auflage edition. Verlagsbuchhandlung Paul Parey, Berlin, Germany.

Gitay, H., and I. R. Noble. 1994. What are functional types and how should we seek them? Pages 3–19 *in* T. M. Smith, H. H. Shugart, and F. I. Woodward, editors. Plant functional types. Their relevance to ecosystem properties and global change. International Geosphere–Biosphere Programme book series, 1. Cambridge University Press, Cambridge, UK.

Glenz, C. 2005. Process-based, spatially-explicit modelling of riparian forest dynamics in Central Europe—tool for decisionmaking in river restoration. École Polytechnique Fédérale de Lausanne, Lausanne, France.

Graham, S. A. 1954. Scoring tolerance of forest trees. University of Michigan Research Note 4. School of Natural Resources, University of Michigan, Ann Arbor, Michigan, USA.

Grime, J. P. 1979. Plant strategies and vegetation processes. Wiley, New York, New York, USA.

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.

Hall, R. B. W., and P. A. Harcombe. 1998. Flooding alters apparent position of floodplain saplings on a light gradient. Ecology **79**:847–855.

Harms, W. R., H. T. Schreuder, D. D. Hook, and C. L. Brown. 1980. The effects of flooding on the swamp forest in Lake Ocklawaha, Florida. Ecology **61**:1412–1421.

Hastwell, G. T., and J. M. Facelli. 2003. Differing effects of shade-induced facilitation on growth and survival during the establishment of a chenopod shrub. Journal of Ecology **91**: 941–950.

Hermann, R. K. 1987. North American tree species in Europe. Journal of Forestry **85**:27–32.

Hicks, D. J., and B. F. Chabot. 1985. Deciduous forest. Pages 257–277 *in* B. F. Chabot and H. A. Mooney, editors. Physiological ecology of North American plant communities. Chapman and Hall, New York, New York, USA.

Hill, M. O., J. O. Mountford, D. B. Roy, and R. G. H. Bunce. 1999. Ellenberg's indicator values for British plants. Centre for Ecology and Hydrology, Huntingdon, Cambs, UK.

Hill, M. O., D. B. Roy, J. O. Mountford, and R. G. H. Bunce. 2000. Extending Ellenberg's indicator values to a new area: an algorithmic approach. Journal of Applied Ecology **37**:3–15.

Hiroki, S. 2003. Early life history stage and segregative distribution of Fagaceae in Japan. Pages 14–14 *in* Integration of silviculture and genetics in creating and sustaining oak forests. Joint meeting of IUFRO working groups. Genetics of *Quercus* and improvement and silviculture of oaks. OAK 2003, Tsukuba, Japan.

Hiroki, S., and K. Ichino. 1998. Comparison of growth habits under various light conditions between two climax species, *Castanopsis sieboldii* and *Castanopsis cuspidata*, with special reference to their shade tolerance. Ecological Research **13**: 65–72.

Hoagland, B. W., L. R. Sorrels, and S. M. Glenn. 1996. Woody species composition of floodplain forests of the Little River, McCurtain and LeFlore Counties, Oklahoma. Proceedings of the Oklahoma Academy of Science **76**:23–29.

Hoffman, R., and K. Kearns. 1997. Wisconsin manual of control recommendations for ecologically invasive plants. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

Hosner, J. F. 1958. The effects of complete inundation upon seedlings of six bottomland tree species. Ecology **39**:371–373.

Hsiao, T. C. 1973. Plant responses to water stress. Annual Review of Plant Physiology **24**:519–570.

Iles, J., and M. Gleason. 1994. Understanding the effects of flooding on trees. Sustainable urban landscapes, 1. Iowa State University Extension, Urbandale, Iowa, USA. ⟨www.extension.iastate.edu/Publications/SUL1.pdf⟩

Ishii, H., M. Ooishi, Y. Maruyama, and T. Koike. 2003. Acclimation of shoot and needle morphology and photosynthesis of two *Picea* species to differences in soil nutrient availability. Tree Physiology **23**:453–461.

Ivanov, L. A., and N. L. Kossovich. 1932. O rabote assimilyatsionnovo apparata drevesnyh porod. II. Botanicheskii Zhurnal **17**:3–71.

Jahn, G. 1991. Temperate deciduous forests of Europe. Pages 377–502 *in* E. Röhrig and B. Ulrich, editors. Temperate deciduous forests. Ecosystems of the world, 7. Elsevier, Amsterdam, The Netherlands.

Jones, R. H., and R. R. Sharitz. 1989. Potential advantages and disadvantages of germinating early for trees in floodplain forests. Oecologia **81**:443–449.

Jones, R. H., R. R. Sharitz, P. M. Dixon, D. S. Segal, and R. L. Schneider. 1994. Woody plant regeneration in four floodplain forests. Ecological Monographs **64**:345–367.

Journal of Ecology. 1941–2005. The biological flora. British Ecological Society, London, UK. ⟨http://www.open.ac.uk/OU/Academic/Biology/JEcolol/Bflora.htm⟩

Kamijo, T., and K. Okutomi. 1995a. Distribution of *Castanopsis* forest and *Persea* forest and its causal factors on the southern part of Izu Islands. Journal of Phytogeography and Taxonomy **43**:67–73.

Kamijo, T., and K. Okutomi. 1995b. Seedling establishment of *Castanopsis cuspidata* var. *sieboldii* and *Persea thunbergii* on lava and scoria of the 1962 eruption on Miyake-jima Island, the Izu Islands. Ecological Research **10**:235–242.

Karrenberg, S., P. J. Edwards, and J. Kollmann. 2002. The life history of Salicaceace living in the active zone of floodplains. Freshwater Biology **47**:733–748.

Ke, G., and M. J. A. Werger. 1999. Different responses to shade of evergreen and deciduous oak seedlings and the effect of acorn size. Acta Oecologica **20**:579–586.

Kikuzawa, K. 1984. Leaf survival of woody plants in deciduous broad-leaved forests. 2. Small trees and shrubs. Canadian Journal of Botany 62:2551–2556.

Kikuzawa, K. 1988. Leaf survivals of tree species in deciduous broad-leaved forests. Plant Species Biology 3:67–76.

King, R. A., and C. Ferris. 2002. A variable minisatellite sequence in the chloroplast genome of Sorbus L. (Rosaceae: Maloideae). Genome 45:570–576.

Kitajima, K., and B. M. Bolker. 2003. Testing performance and rank reversals among coexisting species: crossover point irradiance analysis by Sack and Grubb (2001) and alternatives. Functional Ecology 17:276–281.

Kloeppel, B. D., and M. D. Abrams. 1995. Ecophysiological attributes of the native Acer saccharum and the exotic Acer platanoides in urban oak forests in Pennsylvania, USA. Tree Physiology 15:739–746.

Kobe, R. K., S. W. Pacala, J. A. Silander, Jr., and C. D. Canham. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5:517–532.

Kohyama, T. 1984. Regeneration and coexistence of two Abies species dominating subalpine forests in central Japan. Oecologia 62:156–161.

Koike, T. 1988. Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. Plant Species Biology 3:77–87.

Kozlowski, T. T. 1997. Responses of woody plants to flooding and salinity. Tree physiology monograph, No. 1. Heron Publishing, Victoria, British Columbia, Canada.

Kozlowski, T. T., P. J. Kramer, and S. G. Pallardy. 1991. The physiological ecology of woody plants. Physiological ecology. A series of monographs, texts, and treatises. Academic Press, San Diego, California, USA.

Kreuzwieser, J., S. Fürniss, and H. Rennenberg. 2002. Impact of waterlogging on the N-metabolism of flood tolerant and nontolerant tree species. Plant, Cell and Environment 25:1039–1049.

Kubiske, M. E., and M. D. Abrams. 1994. Ecophysiological analysis of woody species in contrasting temperate communities during wet and dry years. Oecologia 98:303–312.

Kubiske, M. E., M. D. Abrams, and S. A. Mostoller. 1996. Stomatal and nonstomatal limitations of photosynthesis in relation to the drought and shade tolerance of tree species in open and understory environments. Trees: Structure and Function 11:76–82.

Kuhns, M., and L. Rupp. 2000. Selecting and planting landscape trees. Electronic Publishing, NR-460. Utah State University Extension, Logan, Utah, USA. ⟨http://extension.usu.edu/files/natrpubs/nr460.html⟩

Lambers, H., F. S. Chapin, III, and T. L. Pons. 1998. Plant physiological ecology. Springer Verlag, New York, New York, USA.

Lapointe, F. J., and T. Garland, Jr. 2001. A generalized permutation model for the analysis of cross-species data. Journal of Classification 18:109–127.

Larcher, W. 1994. Ökophysiologie der Pflanzen. Leben, Leistung und Streßbewältigung der Pflanzen in ihrer Umwelt. UTB für Wissenschaft: Große Reihe, Fifth edition. Verlag Eugen Ulmer, Stuttgart, Germany.

Larcher, W. 1995. Physiological plant ecology. Ecophysiology and stress physiology of functional groups. Springer Verlag, Berlin, Germany.

Legendre, P., and L. Legendre. 1983. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Lei, T. T., R. Tabuchi, M. Kitao, K. Takahashi, and T. Koike. 1998. Effects of season, weather and vertical position on the variation in light quantity and quality in a Japanese deciduous broadleaf forest. Journal of Sustainable Forestry 6:35–55.

Liang, N., K. Maruyama, and Y. Huang. 1995. Interactions of elevated CO_2 and drought stress in gas exchange and water-use efficiency in three temperate deciduous tree species. Photosynthetica 31:529–539.

Linton, M. J., J. S. Sperry, and D. G. Williams. 1998. Limits to water transport in Juniperus osteosperma and Pinus edulis: implications for drought tolerance and regulation of transpiration. Functional Ecology 12:906–911.

Liston, A., W. A. Robinso, D. Piñero, and E. R. Alvarez-Buylla. 1999. Phylogenetics of Pinus (Pinaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. Molecular Phylogenetics and Evolution 11:95–109.

Loewenstein, N. J., and S. G. Pallardy. 1998. Drought tolerance, xylem sap abscisic acid and stomatal conductance during soil drying: a comparison of young plants of four temperate deciduous angiosperms. Tree Physiology 18:421–430.

Ludlow, M. M. 1989. Strategies of response to water stress. Pages 269–281 in K. H. Kreeb, H. Richter, and T. M. Hinckley, editors. Structural and functional responses to environmental stresses: water shortage. SPB Academic Publishers, The Hague, The Netherlands.

Lusk, C. H. 2004. Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. Functional Ecology 18:820–828.

Manos, P. S., J. J. Doyle, and K. C. Nixon. 1999. Phylogeny, biogeography, and processes of molecular differentiation in Quercus subgenus Quercus (Fagaceae). Molecular Phylogenetics and Evolution 12:333–349.

Maruyama, K. 1978. Ecological studies on natural beech forest. 32. Shoot elongation characteristics and phenological behavior of forest trees in natural beech forest. Bulletin of the Niigata University Forests 11:1–30.

Maruyama, K., and Y. Toyama. 1987. Effect of water stress on photosynthesis and transpiration in three tall deciduous trees. Journal of the Japanese Forest Society 69:165–170.

Masaki, T. 2002. Structure and dynamics. Pages 53–65 in T. Nakashizuka and Y. Matsumoto, editors. Diversity and interaction in a temperate forest community—Ogawa Forest Reserve of Japan. Ecological Studies, 158. Springer Verlag, Berlin, Germany.

Mediavilla, S., and A. Escudero. 2004. Stomatal responses to drought of mature trees and seedlings of two co-occurring Mediterranean oaks. Forest Ecology and Management 187:281–294.

Meerow, A. W., and J. G. Norcini. 1997. Native trees for North Florida. Date first printed September 1989; reviewed June 1997 and October 2003. Department of Environmental Horticulture, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida, Gainesville, Florida, USA. ⟨http://edis.ifas.ufl.edu/⟩

Mehrhoff, L. J., K. J. Metzler, and E. E. Corrigan. 2003. Nonnative and potentially invasive vascular plants in Conneticut. Center for Conservation and Biodiversity, University of Conneticut, Storrs, Connecticut, USA.

Merritt, A. 1994. Wetlands, industry and wildlife. A manual of principles and practices. The Wildfowl and Wetlands Trust, Slimbridge, Gloucester, UK.

Milne, R. I., and R. J. Abbott. 2000. Origin and evolution of invasive naturalized material of Rhododendron ponticum L. in the British Isles. Molecular Ecology 9:541–556.

Minore, D. 1979. Comparative autecological characteristics of northwestern tree species: a literature review. USDA Forest Service Technical Report, PNW-87. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, USA.

Missouri Botanical Garden. 2005. W_3TROPICOS: Missouri Botanical Garden's VAST (VAScular Tropicos) nomenclatural database revision 1.5. Missouri Botanical Garden, St. Louis, Missouri, USA. ⟨http://mobot.mobot.org/W3T/Search/vast.html⟩

Miyazawa, Y., and K. Kikuzawa. 2005. Winter photosynthesis by saplings of evergreen broadleaved trees in a deciduous temperate forest. New Phytologist 165:857–866.

Mooney, H. A., F. S. Chapin, III, and P. A. Matson. 2002. Principles of terrestrial ecosystem ecology. Springer Verlag, New York, New York, USA.

Mooney, H. A., and R. J. Hobbs. 2000. Invasive species in a changing world. Island Press, Washington, D.C., USA.

Morozov, G. F. 1903. Forest dendrology. Attitude of tree species to light. On the types of of tree stands. A conspectus of lectures. Lesnoi Institute, St. Peterburg, Russia.

Morris, R., editor. 2005. Plants for a future. Edible medicinal and useful plants for a healthier world. Plants for a Future Foundation. Charity No. 1057719, Lerryn, Lostwithiel, Cornwall, PL22 0QJ. ⟨http://pfaf.org/⟩

Naiman, R. J., K. L. Fetherston, S. McKay, and J. Chen. 1998. Riparian forests. Pages 289–323 in R. J. Naiman and E. Bilby, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer Verlag, New York, New York, USA.

Nakashizuka, T., and S. Iida. 1996. Composition, dynamics and disturbance regime of temperate deciduous forests in monsoon Asia. Pages 23–30 in T. Hirose, B. H. Walker, H. A. Mooney, and A. Kratochwil, editors Global change and terrestrial ecosystems in monsoon Asia. Tasks for vegetation science. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Nanami, S., H. Kawaguchi, R. Tateno, C. Li, and S. Katagiri. 2004. Sprouting traits and population structure of co-occurring Castanopsis species in an evergreen broad-leaved forest in southern China. Ecological Research 19:341–348.

Ni, B.-R., and S. G. Pallardy. 1991. Response of gas exchange to water stress in seedlings of woody angiosperms. Tree Physiology 8:1–9.

Niinemets, Ü., and K. Kull. 1994. Leaf weight per area and leaf size of 85 Estonian woody species in relation to shade tolerance and light availability. Forest Ecology and Management 70:1–10.

Niinemets, Ü., and O. Kull. 1998. Stoichiometry of foliar carbon constituents varies along light gradients in temperate woody canopies: implications for foliage morphological plasticity. Tree Physiology 18:467–479.

Niinemets, Ü., and F. Valladares. 2004. Photosynthetic acclimation to simultaneous and interacting environmental stresses along natural light gradients: optimality and constraints. Plant Biology 6:254–268.

Nikolov, N., and H. Helmisaari. 1992. Silvics of the circum-polar boreal forest tree species. Pages 13–84 in H. H. Shugart, R. Leemans, and G. B. Bonan, editors. A system analysis of the global boreal forest. Cambridge University Press, Cambridge, UK.

Oberdorfer, E., T. Müller, D. Korneck, W. Lippert, E. Patzke, and H. E. Weber. 1994. Pflanzensoziologische Exkursions-flora. UTB für Wissenschaft: Uni-Taschenbücher, 1828, Seventh edition. Verlag Eugen Ulmer, Stuttgart, Germany.

Ohsawa, M., and I. Nitta. 1997. Patterning of subtropical/warm-temperate evergreen broad-leaved forests in East Asian mountains with special reference to shoot phenology. Tropics 6:317–334.

Ohsawa, M., P. R. Shakya, and M. Numata. 1986. Distribution and succession of west Himalaya forest types in the eastern part of the Nepal Himalaya. Mountain Research and Development 6:143–157.

Otto, H.-J. 1994. Waldökologie. Verlag Eugen Ulmer, Stuttgart, Germany.

Ozaki, K., and M. Ohsawa. 1995. Successional change of forest pattern along topographical gradients in warm-temperate mixed forests in Mt. Kiyosumi, central Japan. Ecological Research 10:223–234.

Peng, C. H. 2000. From static biogeographical model to dynamic global vegetation model: a global perspective on modelling vegetation dynamics. Ecological Modelling 135:33–54.

Percival, G. C., and C. N. Sheriffs. 2002. Identification of drought-tolerant woody perennials using chlorophyll fluorescence. Journal of Arboriculture 28:215–222.

Peters, R. 1992. Ecology of beech forests in the Northern Hemisphere. Dissertation. Landbouwuniversiteit Wageningen, The Netherlands.

Peters, R. 1997. Beech forests. Geobotany. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Peters, R., H. Tanaka, M. Shibata, and T. Nakashizuka. 1995. Light climate and growth in shade-tolerant Fagus crenata, Acer mono and Carpinus cordata. Ecoscience 2:67–74.

Pezeshki, S. R., R. D. DeLaune, and J. F. Meeder. 1997. Carbon assimilation and biomass partitioning in Avicennia germinans and Rhizophora mangle seedlings in response to soil redox conditions. Environmental and Experimental Botany 37:161–171.

Pezeshki, S. R., J. H. Pardue, and R. D. DeLaune. 1996. Leaf gas exchange and growth of flood-tolerant and flood-sensitive tree species under low soil redox conditions. Tree Physiology 16:453–458.

Pilgrim, E. S., M. J. Crawley, and K. Dolphin. 2004. Patterns of rarity in the native British flora. Biological Conservation 120:165–174.

Prentice, I. C., and H. Helmisaari. 1991. Silvics of North-European trees: compilation, comparisons and implications for forest succession modelling. Forest Ecology and Management 42:79–93.

Press, M. C. 1999. Research review. The functional significance of leaf structure: a search for generalizations. New Phytologist 143:213–219.

Purvis, A., and T. Garland, Jr. 1993. Polytomies in comparative analyses of continuous data. Systematic Biology 42:569–575.

Qian, H., and R. E. Ricklefs. 1999. A comparison of the taxonomic richness of vascular plants in China and the United States. American Naturalist 154:160–181.

Qian, H., and R. E. Ricklefs. 2000. Large-scale processes and the Asian bias in species diversity of temperate plants. Nature 407:180–182.

Rackham, O. 2003. Ancient woodland: its history, vegetation and uses in England. Second edition. Castlepoint Press, Dalbeattie, UK.

Randall, J. M., and J. Marinelli. 1996. Invasive plants, weeds of the global garden. Brooklyn Botanical Garden, New York, New York, USA.

Ranney, T. G. 1994. Differential tolerance of eleven Prunus taxa to root zone flooding. Journal of Environmental Horticulture 12:138–141.

Ranney, T. G., and R. E. Bir. 1994. Comparative flood tolerance of birch rootstocks. Journal of the American Society for Horticultural Science 119:43–48.

Ranney, T. G., R. E. Bir, and W. A. Skroch. 1991. Comparative drought resistance among six species of birch (Betula): influence of mild water stress on water relations and leaf gas exchange. Tree Physiology 8:351–360.

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:s143–164.

Richens, R. 1980. On fine distinctions in Ulmus L. Taxon 29:305–312.

Ricklefs, R. E., H. Qian, and P. S. White. 2004. The region effect on mesoscale plant species richness between eastern Asia and eastern North America. Ecography 27:129–136.

Robertson, A., A. C. Newton, and R. A. Ennos. 2004. Multiple hybrid origins, genetic diversity and population genetic structure of two endemic Sorbus taxa on the Isle of Arran, Scotland. Molecular Ecology 13:123–134.

Sack, L. 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? Oikos 107:107–127.

Sack, L., and P. J. Grubb. 2002. The combined impacts of deep shade and drought on the growth and biomass allocation of shade tolerant woody seedlings. Oecologia **131**:175–185.

Sack, L., P. J. Grubb, and T. Marañón. 2003. The functional morphology of juvenile plants tolerant of strong summer drought in shaded forest understories in southern Spain. Plant Ecology **168**:139–163.

Sakio, H. 2003. Effects of flooding on the growth of seedlings of some deciduous tree species. Page 6 *in* Integration of silviculture and genetics in creating and sustaining oak forests. Joint meeting of IUFRO working groups. Genetics of *Quercus* and improvement and silviculture of oaks. OAK 2003, Tsukuba, Japan.

Sánchez-Gómez, D., F. Valladares, and M. A. Zavala. 2006*a*. Performance of seedlings of Mediterranean woody species under experimental gradients of irradiance and water availability: trade-offs and evidence for niche differentiation. New Phytologist **170**:795–806.

Sánchez-Gómez, D., M. A. Zavala, and F. Valladares. 2006*b*. Survival responses to irradiance are differentially influenced by drought in seedlings of forest tree species of the temperate-Mediterranean transition zone. Acta Oecologica, *in press*.

Schaffrath, J. 2000. Auswirkungen des extremen Sommerhochwassers des Jahres 1997 auf die Gehölzvegetation in der Oderaue bei Frakfurt (O.). Naturschutz und Landespflege in Brandenburg **9**:4–13.

Scharf, F. S., F. Juanes, and M. Sutherland. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. Ecology **79**:448–460.

Schmidt, M., and A. W. Schneider-Poetsch. 2002. The evolution of gymnosperms redrawn by phytochrome genes: the Gnetatae appear at the base of gymnosperms. Journal of Molecular Evolution **54**:715–724.

Shidei, T. 1974. Forest vegetation zones. Pages 87–124 *in* M. Numata, editor. The flora and vegetation of Japan. Kodansha, Tokyo, Japan.

Siebel, H. N., and C. W. P. M. Blom. 1998. Effects of irregular flooding on the establishment of tree species. Acta Botanica Neerlandica **47**:231–240.

Siebel, H. N., M. v. Wijk, and C. W. P. M. Blom. 1998. Can tree seedlings survive increased flood levels of rivers? Acta Botanica Neerlandica **46**:219–230.

Silvertown, J., M. Dodd, and D. Gowing. 2001. Phylogeny and the niche structure of meadow plant communities. Journal of Ecology **79**:448–460.

Smith, J. K., editor. 2004. Fire effects information system (FEIS). FEIS plants species reviews. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Missoula, Montana, USA. ⟨http://www.fs.fed.us/database/feis⟩

Smith, T., and M. Huston. 1989. A theory of the spatial and temporal dynamics of plant communities. Vegetatio **83**:49–69.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry. The principles and practice of statistics in biological research. Third edition. W. H. Freeman, New York, New York, USA.

Soltis, D. E., et al. 2000. Angiosperm phylogeny inferred from 18S rDNA, *rbc*L, and *atp*B sequences. Botanical Journal of the Linnean Society **133**:381–461.

Sperry, J. S., K. L. Nichols, J. E. M. Sullivan, and S. E. Eastlack. 1994. Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. Ecology **75**:1736–1752.

Spurr, S. H., and B. V. Barnes. 1980. Forest ecology. Third edition. John Wiley and Sons, Toronto, Canada.

Stange, C., D. Ogle, and L. St. John. 2002. Tree planting, care and management. USDA Natural Resources Conservation Service Technical Notes, 42. USDA NRCS, Boise, Idaho, USA

Streng, D. R., J. S. Glitzenstein, and P. A. Harcombe. 1989. Woody seedling dynamics in an East Texas floodplain forest. Ecological Monographs **59**:177–204.

Sumida, A. 1995. Three-dimensional structure of a mixed broad-leaved forest in Japan. Vegetatio **119**:67–80.

Suzuki, E. 1997. The dynamics of old *Cryptomeria japonica* forest on Yakushima Island. Tropics **6**:421–428.

Takahashi, K., Y. Fujimura, and T. Koike. 1988. Tolerance of deciduous broad-leaved trees in Hokkaido to flooding. II. Seasonal change of the tolerance. Transactions of the meeting in Hokkaido branch of the Japanese Forestry Society **36**:99–101.

Talbot, R. J., and J. R. Etherington. 1987. Comparative studies of plant growth and distribution in relation to waterlogging. XIII. The effect of Fe^{2+} on photosynthesis and respiration of *Salix caprea* and *S. cinerea* ssp. *oleifolia*. New Phytologist **105**:575–583.

Tanaka, H. 1996. Survival and growth of two coexisting evergreen oak species after germination under different light conditions. International Journal of Plant Sciences **157**:516–522.

Tanouchi, H., and S. Yamamoto. 1995. Structure and regeneration of canopy species in an old-growth evergreen broad-leaved forest of Aya district, southwestern Japan. Vegetatio **117**:51–60.

Tapper, P.-G. 1993. The replacement of *Alnus glutinosa* by *Fraxinus excelsior* during succession related to regenerative differences. Ecography **16**:212–218.

Tapper, P.-G. 1996. Tree dynamics in a successional *Alnus–Fraxinus* woodland. Ecography **19**:237–244.

Terazawa, K., and K. Kikuzawa. 1994. Effects of flooding on leaf dynamics and other seedling responses in flood-tolerant *Alnus japonica* and flood-intolerant *Betula platyphylla* var. *japonica*. Tree Physiology **14**:251–261.

ter Steege, H. 1994. Flooding and drought tolerance in seeds and seedlings of two *Mora* species segregated along a soil hydrological gradient in the tropical rain forest of Guyana. Oecologia **100**:356–367.

Tesche, M. 1992. Klimaresistenz. Pages 279–306 *in* H. Lyr, H. J. Fiedler, and W. Tranquillini, editors. Physiologie und Ökologie der Gehölze. Gustav Fischer Verlag, Jena, Germany.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Monographs in population biology, 26. Princeton University Press, Princeton, New Jersey, USA.

Tilman, D. 1993. Community diversity and succession: the roles of competition, dispersal, and habitat modification. Pages 327–344 *in* E.-D. Schulze and H. A. Mooney, editors. Biodiversity and ecosystem function. Ecological studies, 99. Springer Verlag, Berlin, Germany.

Timmermann, G. 1992. Rosa L. 1753. Pages 64–101 *in* O. Sebald, S. Seybold, and G. Philippi, editors. Die Farn- und Blütenpflanzen Baden-Württembergs. Verlag Eugen Ulmer, Stuttgart, Germany.

Tschaplinski, T. J., G. M. Gebre, and T. L. Shirshac. 1998. Osmotic potential of several hardwood species as affected by manipulation of throughfall precipitation in an upland oak forest during a dry year. Tree Physiology **18**:291–298.

Tsukahara, H. 1985. Studies of the flood tolerance of some tree species. Bulletin of the Yamagata University, Agricultural Science **9**:425–448.

Tyree, M. T., and J. D. Alexander. 1993. Hydraulic conductivity of branch junctions in three temperate tree species. Trees: Structure and Function **7**:156–159.

USDA NRCS. 1996. Chapter 16. Streambank and shoreline protection. *In* National engineering field handbook, Part 650. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, D.C., USA.

USDA NRCS. 2005. The PLANTS Database, Version 3.5. Data compiled from various sources by Mark W. Skinner. National Plant Data Center, Information Technology Center, Baton Rouge, Louisiana, USA. ⟨http://plants.usda.gov⟩

Vaga, A., et al., editors. 1960. Eesti NSV floora. Eesti Riiklik Kirjastus/Valgus, Tallinn, Estonia.

Valladares, F. 2003. Light heterogeneity and plants: from ecophysiology to species coexistence and biodiversity. Pages 439–471 in K. Esser, U. Lüttge, W. Beyschlag, and F. Hellwig, editors. Progress in botany. Springer Verlag, Berlin, Germany.

Valladares, F., S. Arrieta, I. Aranda, D. Lorenzo, D. Tena, D. Sánchez-Gómez, F. Suarez, and J. A. Pardos. 2005a. Shade tolerance, photoinhibition sensitivity and phenotypic plasticity of Ilex aquifolium in continental-Mediterranean sites. Tree Physiology 25:1041–1052.

Valladares, F., I. Dobarro, D. Sánchez-Gómez, and R. W. Pearcy. 2005b. Photoinhibition and drought in Mediterranean woody saplings: scaling effects and interactions in sun and shade phenotypes. Journal of Experimental Botany 56: 483–494.

Valladares, F., and R. W. Pearcy. 1997. Interactions between water stress, sun–shade acclimation, heat tolerance and photoinhibition in the sclerophyll Heteromeles arbutifolia. Plant, Cell and Environment 20:25–36.

Valladares, F., and R. W. Pearcy. 2002. Drought can be more critical in the shade than in the sun: a field study of carbon gain and photo-inhibition in a Californian shrub during a dry El Niño year. Plant, Cell and Environment 25:749–759.

van Splunder, I. 1998. Floodplain forest recovery. Softwood development in relation to hydrology, riverbank morphology and management. Dissertation. Katholieke Universiteit, Nijmgen, Japan.

van Splunder, I., H. Coops, L. A. C. J. Voesenek, and C. W. P. M. Blom. 1995. Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination characteristics and water-level fluctuations. Acta Botanica Neerlandica 44:269–278.

van Splunder, I., L. A. C. J. Voesenek, H. Coops, X. J. A. de Vries, and C. W. P. M. Blom. 1996. Morphological responses of seedlings of four species of Salicaceae to drought. Canadian Journal of Botany 74:1988–1995.

Walter, H. 1968. Die Vegetation der Erde in öko-physiologischer Betrachtung. G. Fischer, Stuttgart, Germany.

Walters, M. B., and P. B. Reich. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology 81:1887–1901.

Warming, E. 1909. Oecology of plants. An introduction to the study of plant communities. Oxford University Press, Oxford, UK.

Warton, D. I., and N. C. Weber. 2002. Common slope tests for bivariate errors-in variables models. Biometrical Journal 44: 161–174.

Webb, S. L., and C. K. Kaunzinger. 1993. Biological invasion of the Drew University (New Jersey) Forest Preserve by Norway maple (Acer platanoides L.). Bulletin of the Torrey Botanical Club 120:334–343.

Westoby, M. 1999. Generalization in functional plant ecology: the species sampling problem, plant ecology strategy schemes, and phylogeny. Pages 847–872 in F. I. Pugnaire and F. Valladares, editors. Handbook of functional plant ecology. Marcel Dekker, New York, New York, USA.

White, P. S. 1983. Corner's rules in eastern deciduous trees: allometry and its implications for the adaptive architecture of trees. Bulletin of the Torrey Botanical Club 110:203–212.

White, R. M. 1973. Plant tolerance for standing water: an assessment. Cornell Plantations 28:50–52.

Whitley, R. E., S. Black-Samuelsson, and D. Clapham. 2003. Development of microsatellite markers for the European white elm (Ulmus laevis Pall.) and cross-species amplification within the genus Ulmus. Molecular Ecology Notes 3:598–600.

Whitlow, T. H., and R. W. Harris. 1979. Flood tolerance in plants: a state-of-the-art review. National Technical Information Service, U.S. Deptartment of Commerce, Washington, D.C., USA.

Wiesner, J. 1907. Der Lichtgenuss der Pflanzen. Photometrische und physiologische Untersuchungen mit besonderer Rücksichtnahme auf Lebensweise, geographische Verbreitung und Kultur der Pflanzen. Verlag von Wilhelm Engelmann, Leipzig, Germany.

Woodward, F. I. 1990. From ecosystems to genes: the importance of shade tolerance. Trends in Ecology and Evolution 5:111–114.

Wright, I. J., and K. Cannon. 2001. Relationships between leaf lifespan and structural defences in a low-nutrient, sclerophyll flora. Functional Ecology 15:351–359.

Yamamoto, F., T. Sakata, and K. Terazawa. 1995. Physiological, morphological and anatomical responses of Fraxinus mandshurica seedlings to flooding. Tree Physiology 15:713–719.

Yevstigneyev, O. I. 1990. Fitotsenotipy i otnosheniye listvennyh derevyev k svetu. (Phytocoenotypes and the behaviour of deciduous trees with respect to light.) Dissertation. Moskovskii Gosudarstvennyi Pedagogicheskii Institut imeni V. I. Lenina, Moscow, Russia.

Yin, Y., J. C. Nelson, G. V. Swenson, H. A. Langrehr, and T. A. Blackburn. 1994. Tree mortality in the upper Mississippi river and floodplain following an extreme flood in 1993. Pages 41–60 in Long term resource monitoring program, 1993 flood observations. National Biological Service, Environmental Management Technical Center, Onalaska, Wisconsin, USA.

Zon, R., and H. S. Graves. 1911. Light in relation to tree growth. U.S. Department of Agriculture, Forest Service, Bulletin 92. Government Printing Office, Washington, D.C., USA.

APPENDIX A

A table showing shade, drought, and waterlogging tolerance for 806 species of woody plants from the temperate Northern Hemisphere (*Ecological Archives* M076-020-A1).

APPENDIX B

Additional details on the protocol followed and the original sources used to build the tolerance data set and to standardize the rankings of tolerance obtained from different sources and for species from different continents (*Ecological Archives* M076-020-A2).