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Polytolerance to abiotic stresses: how universal is the shade-drought tolerance trade-off in woody species?

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Abstract

Aims—According to traditional ecophysiological theories stress tolerance of plants is predominately determined by universal physiochemical constraints. Plant acclimation to environmental stress therefore compromises plant performance under a different stress, hindering successful toleration of several abiotic stress factors simultaneously. Yet, recent studies have shown that these trade-offs are less exclusive than postulated so far, leaving more wiggle room for gaining polytolerance through adaptations. We tested whether the polytolerance to shade and drought depends on cold and waterlogging tolerances – hypothesizing that polytolerance patterns in different species groups (angiosperms vs. gymnosperms; deciduous vs. evergreen; species originating from North America, Europe and East Asia) depend on the length of the vegetation period and species's dormancy through limiting the duration of favourable growing season.

Location—Northern hemisphere

Methods—Our study analyzed four main abiotic stress factors – shade, drought, cold and waterlogging stress – for 806 Northern hemisphere woody species using cross-calibrated tolerance rankings. The importance of trade-offs among species ecological potentials was evaluated using the species-specific estimates of polytolerance to chosen factors.

Results—We found that both cold and waterlogging tolerance are negatively related to species' capabilities of simultaneously tolerating low light and water conditions. While this pattern was different in angiosperms and gymnosperms, species region of origin and leaf type had no effect on this relationship.

Main conclusions—Our results demonstrate that adaptation to different abiotic stress factors in woody plants is highly complex. Vegetation period length and dormancy are the key factors explaining why woody plants are less capable of tolerating both shade and drought in habitats where vegetation period is relatively short and water table high. While dormancy enables angiosperms to more successfully face additional stress factors besides shade and drought,

gymnosperms have lower polytolerance, but are better tolerators of shade and drought when other environmental factors are favorable.

Keywords

abiotic stress; woody plants; shade tolerance; drought tolerance; cold tolerance; waterlogging tolerance; plant functional type; trade-offs; polytolerance; macrophysiology

Introduction

Tolerance to different abiotic stresses is a key shaper of species distribution patterns (Hawkins *et al.*, 2014), in particular for sessile organisms like plants (Bartlett *et al.*, 2012). According to traditional ecological knowledge, basic physical and chemical laws, like thermodynamics and process stoichiometry, largely determine the presence and strength of biological trade-offs (Smith & Huston 1989; Sack 2004). Temperature extremes, water and light availability are considered to be the main abiotic stress factors limiting worldwide plant distribution as well as affecting plant competitive relations within any specific community (Valladares & Niinemets 2008; Martinez-Tilleria *et al.*, 2012). Trade-offs between these factors have been mainly deemed to be rather universal, predominately depending on physiochemical constraints, whereas the relative effects of biological factors like adaptations are regarded as less important. Thus, the degree of polytolerance – capability of tolerating multiple stress factors simultaneously – is thought to be rather low among plants (Niinemets & Valladares 2006).

Indeed, a comprehensive meta-analysis on tolerance to key abiotic stresses demonstrated that there are significant trade-offs between all combinations of shade, drought and waterlogging tolerance, irrespective of species leaf longevity (evergreen vs. deciduous), phylogeny (angiosperm vs. gymnosperm) and origin (North America, Europe or Asia) (Niinemets & Valladares 2006). Yet, for these 806 woody species from temperate Northern Hemisphere, the explained variance in the negative relationships between stress tolerances was only 2-53%. In fact, analogously low and variable explanatory power has been observed in several other studies looking at trade-offs between species ecological potentials from temperate to tropical biomes (Sack 2004; Markesteijn & Poorter 2009; Markesteijn *et al.*, 2011a).

Trade-off patterns with low explanatory power have pushed research towards implementing new theories and mechanisms to explain plants' polytolerance to abiotic stresses or the lack of it. Adaptations via phenology (Martinez-Paltee & Aronne 1999), higher biomass allocation to roots (Sack *et al.*, 2003) and concurrent physiological and morphological adaptations (Pivovarov *et al.*, 2014) and leaf-level functional traits (Hallik *et al.*, 2009) have been proposed as alternative determinants of the shape and strength of trade-offs enabling polytolerance in some species. Various trait-based approaches have become the main alternative way to explain the variability of these patterns (e.g. Hallik *et al.*, 2009; Markesteijn & Poorter 2009; Niinemets *et al.*, 2009; Ouedraogo *et al.*, 2013).

Due to the scarcity of data, polytolerance analyses including a representative species pool do not usually consider trade-offs between more than two stress factors (i.e. polytolerance), and

do not explore how other simultaneously acting factors affect these trade-offs (Valladares & Niinemets 2008). In addition to multiple, and often species-specific ways of how polytolerance has been achieved during evolution, mapping general patterns of trade-off dynamics of abiotic stresses demands larger sampling sizes and analysis on a wider spatial range (Hallik *et al.*, 2009; Stahl *et al.*, 2013). The present study attempts to examine broad-scale polytolerance patterns considering the main abiotic stress factors – temperature, light and limited and excess water conditions – in a large number of species. We focused primarily on the polytolerance or polyintolerance of shade and drought stress (henceforth SADTO – Shade And Drought Tolerance) as the restricted co-tolerance of these two key stress factors is considered the main constraint limiting the combinations of species in forests across gradients of soil water availability and through stand development from early successional open communities to dense late-successional stands (Niinemets & Valladares 2006).

Because the adaptations that allow plants to grow in shade can compromise their ability to grow in dry conditions, SADTO has often been considered to be physically inevitable (see Premise 3 in Smith & Huston 1989). However, experimental studies have indicated that there might be a certain capacity to tolerate both stresses in warmer climate species (Markesteijn & Poorter 2009; Markesteijn *et al.*, 2011a). Likewise, it has been proposed that the strength of SADTO might vary in dependence on other climatic factors that ultimately determine the effective length of the growing season. Valladares and Niinemets (2008) suggested that the length of the growing season and co-occurrence of other stress factors can dramatically affect SADTO through altering a plant's capability of tolerating low light.

In addition, the SADTO dynamics can differ depending on species background – for example, a recent study by Stahl and others (2013) confirmed the findings of Niinemets and Valladares (2006) that gymnosperms and angiosperms have different strategies for coping with abiotic stress factors. Also leaf physiognomy could affect stress polytolerance patterns, as the onset of dormancy at the end and breaking dormancy in the beginning of the growing season and the strategy of dealing with limiting factors depends largely on whether the plants are evergreen or deciduous (Press 1999; Kozłowski & Pallardy 2002). The occurrence of dormancy can have similar impact on species' polytolerance as the length of the vegetation period – limiting the available favourable time for growing. Thus the effect of dormancy on polytolerance steepens concurrently with the vegetation period length.

As a follow up of the meta-study of Niinemets and Valladares (2006) we added cold tolerance data to shade, drought and waterlogging tolerance data, and analyzed the shade-drought trade-off in relation to cold and waterlogging tolerance to gain insight into the determinants of polytolerance to principal abiotic stresses in Northern hemisphere woody species. Our main hypothesis was to test how the polytolerance of shade and drought depends on species' cold and waterlogging tolerances – whether the polytolerance patterns in different species groups (angiosperms vs. gymnosperms; deciduous vs. evergreen; species originating from North America, Europe and East Asia) depend on the length of vegetation period and species's dormancy due to limiting the duration of favourable growing season.

Methods

The species shade, drought and waterlogging tolerance data with species region of origin and plant functional type were taken from Niinemets and Valladares (2006). The aim of that study was to analyze tolerance to three crucially important stresses for almost half of the species pool of self supporting tree and shrub species in the temperate zone of the Northern Hemisphere (Niinemets & Valladares 2006). In order to have comparable data for each stress factor, available data from the literature was synchronized by cross-calibrating different scales using multiple measurements of the same species available across the scales. Ultimately, uniform stress tolerance scales ranging from 1 (very intolerant) to 5 (very tolerant) were derived for each stress factor.

The final dataset of Niinemets and Valladares (2006) contained 806 species of which 566 were winter-deciduous and 240 evergreen. There were 118 gymnosperms, including 11 winter-deciduous species. Nearly half of the species (364) were native to North America, 262 to Europe/West Asia, and 211 to East Asia. Overall, the data set covered about 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 & Ricklefs 1999, 2000, Ricklefs *et al.*, 2004).

Shade tolerance in Niinemets and Valladares (2006) was defined as the capacity for growth in low light availability. The five-level scale used for shade tolerance roughly correspond to given proportions of light availability compared with full sunlight: 1, >50%; 2, 25–50%; 3, 10–25%; 4, 5–10%; 5, 2–5% (Niinemets & Valladares 2006). However, as Niinemets and Valladares (2006) note, the shade tolerance characterizes species potential to tolerate shaded conditions relative to other competing species. The minimum relative light availability any given species can tolerate will depend on species ontogeny and other environmental drivers, but the key assumption is that these factors alter minimum light requirement similarly in all species such that the relative species ranking is maintained. **Drought tolerance** estimations were based on site characteristics of species dispersal and physiological potentials. The relevant site features considered were total annual precipitation, ratio of precipitation to potential evapotranspiration (P:PET ratio), and duration of dry period. As the drought tolerance rankings used by Niinemets and Valladares (2006) were based on a wide array of structural and physiological traits, drought tolerance rankings were determined as rather abstract estimations: 1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; 5, very tolerant. **Waterlogging tolerance** ranking relied on qualitative scale of Whitlow and Harris (1979) that was based on duration and severity of waterlogging during growing season: 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) (Niinemets & Valladares 2006). A separate study (Stahl *et al.*, 2013) analyzing shade and drought tolerance of 305 species of North-American woody plants and independently working out continuous tolerance scales observed significant

correlations of these independent estimates with the data from Niinemets and Valladares (2006).

To these three tolerance rankings, we added **cold tolerance**, which is based on United States Department of Agriculture (USDA) Plant Hardiness index (<http://planthardiness.ars.usda.gov/PHZMWeb/Default.aspx>). USDA plant hardiness mapping is based on average minimum yearly temperatures in species habitats (Daly *et al.*, 2012). The hardiness map is divided into 13 zones ranging from long-term annual minimum temperature of below -53.9 °C (zone 0) to above 12.8 °C (zone 12), and thus covering arctic to tropical ecosystems. Although USDA Plant Hardiness index has been specifically developed for US, including continental US as well as Pacific islands and Puerto Rico (Daly *et al.*, 2012), it covers an extremely broad gradient from arctic to tropics and it has been successfully fitted to other parts of the world, especially in global scale meta-studies (e. g. Tonitto *et al.*, 2006) and various floristic databases (e. g. www.chileflora.com).

Various botanical and gardening web pages (mainly: davesgarden.com; hgtvgardens.com; plantlust.com) that provide USDA Plant Hardiness data were used for extracting species-specific data of the coldest zone where given species is capable of growing (i.e. cold tolerance). To be fully comparable to other studied tolerance estimates, cold tolerance data were inverted and transformed to a 5-level scale, with 5 indicating the highest cold tolerance (capability of tolerating the coldest temperatures) and 1 the lowest.

The polytolerance between any two stress factor was evaluated by pairwise summing the scale tolerance indices for every species. For example, while the shade and drought tolerance scores of *Acer platanoides* are 4.2 and 2.73, respectively, shade and drought tolerance scores of *Acer pensylvanicum* are 3.56 and 2. The shade-drought tolerance of *Acer platanoides* is therefore 6.93 (out of maximum 10), while *Acer pensylvanicum* has a SADTO of 5.56. Lower sums indicate polyintolerance – the species is not capable of tolerating both stresses concurrently –, while higher sums indicate polytolerance. Simple adding up of different tolerance factors was used for calculating the trade-off values based on following reasoning: a) tolerance scale ranging from 1 to 5 does not allow for elaboration of more complicated quantitative i.e., there is currently no objective means to “weight” tolerances to different abiotic stresses; and b) as the tolerance to a certain factor can vary between 1 and 5 independently of other tolerance factors, the sum of tolerances (that can range between 2 and 10) comprises species overall capability of tolerating multiple factors at the same time. The differences in polytolerance emerge similarly to Liebig’s law of the minimum. If a given species has a low tolerance to either factor, its overall polytolerance index cannot be much above the average, even when the tolerance to the other factor is high.

Statistical analyses were carried out with Statistica 8.0 (Stat Soft Inc. 2007).

Results

Mean values for any tolerance score exhibited only limited variation between species regional or leaf physiognomic groupings (Table 1). Nearly half of the species (46%) in our sample tolerated long term average temperature minimums between -40 °C to -29 °C (Fig. A

in Appendix S1 in Supporting Information). One third of species exhibited shade-drought polytolerance scores between 5 and 6, while 79% of species had SADTO scores between 4 and 7 out of possible range of 2 to 10 (Fig. B in Appendix S1). Thus, within any given species grouping, there was a large interspecific variability, but the proportions of species with given tolerance rankings were similar among the groups. This indicates that the results demonstrated here are not driven by different species ecological potentials in different continents or by plant functional type specific performance differences.

Our analyses demonstrate that the shade-drought polytolerance is significantly related to other primary abiotic stress factors, indicating that the length of the vegetation period plays a crucial role in the quantitative importance of polytolerance across different climates. SADTO was negatively related to species cold tolerance (Fig. 1). In particular, species that were more cold tolerant tended to have a stronger trade-off between shade and drought tolerances. A similar trend was also found between SADTO and waterlogging tolerance (Fig. 2). Species that were more cold tolerant were slightly inclined to have higher waterlogging tolerance as well (Fig. 2) – indeed, cold tolerance and waterlogging tolerance were positively correlated ($y = 6.73 + 0.2766x$; $r = 0.16$; $p = 0.00$). Therefore, the regression between cold and waterlogging tolerance trade-off and shade and drought trade-off was even more pronounced (Fig. 3).

Our hypothesis that the dynamics of shade-drought tolerance depends on both species cold and waterlogging tolerance was proven as well – species that are capable of tolerating colder climates and more flooding were less capable of simultaneously tolerating shady and dry conditions (Fig. 3; Fig. C in Appendix S1). Analysis involving additional variables (phylogenetic distance, genus diversification, cold niche breadth, evolutionary age) showed that interactions among different abiotic stress factors are indeed the main influence on SADTO (see additional methods and tables in Appendix S2).

The most pronounced dissimilarity in the shade-drought polytolerance was between angiosperms and gymnosperms. SADTO of angiosperms was negatively related to cold and waterlogging tolerance in both evergreen and deciduous species, but gymnosperms exhibited no relationship whatsoever (Fig. 4, Fig. 5). The leaf longevity did not play a significant role in shaping the tolerances that were basically the same in evergreen and deciduous species (Fig. 4). Species' geographic origin did not affect the tolerances qualitatively – all regional species pools (East Asia, Europe, North America) showed equally significant negative regression between shade-drought and cold-waterlogging tolerance (Fig. 5).

Discussion

The decisive role of physiochemical limitations in determining how well plants can tolerate different abiotic stress factors has been questioned in recent literature (Sack 2004; Bartlett *et al.*, 2012; Pivovarov *et al.*, 2014). According to classical ecological models, fundamental physiological and physical constraints regulate plants' capability of using resources and essentially preclude the possibility of polytolerance (Smith & Huston 1989). While these constraints indeed limit plant growth and survival, high variability in abiotic polytolerance in existent species indicates that the comprehensiveness of these fundamental physiochemical

constraints is debatable (Sack 2004; Pivovarov *et al.*, 2014). Our results suggest that the role of adaptations in tolerating abiotic factors in woody species is much higher than expected on the basis of classical models (Figs. 1-3). While some woody species exhibit high polytolerance, other species have strong trade-offs between different abiotic stress factors. The gradient of polytolerance follows species cold tolerance – species distributed in colder climates are more prone to lower SADTO due to shorter vegetation period and species-specific adaptations preventing growth during unsuitable seasons (i.e. dormancy). Additionally, polytolerance seems to depend on broad species evolutionary classification (unlike gymnosperms, angiosperms exhibit strong interrelated patterns between abiotic stress factors), but not on species region of origin (Figs. 4-5).

Shade-drought and cold-waterlogging polytolerance: general patterns

The key premise in studying such trade-offs is that any stress factor temporarily reduces the plant carbon gain, and the strength of the overall effect depends on the cumulative duration of stressed period relative to the total growing season length (Valladares & Niinemets 2008).

Duration of cold period is particularly relevant as it determines the overall growing season length. Thus, a drought period of moderate duration under shade has a much less severe effect on whole canopy carbon gain in warmer climates than an equally long period in cooler climates where it constitutes a greater proportion of overall growing season length. Furthermore, the higher the species cold tolerance, the deeper the dormancy they develop to cope with the frost period, the earlier they start to develop dormancy in the autumn and the later they break it in the following spring (Cox & Stushnoff 2001; Hänninen 2006; Beaubien & Hamann 2011). This would effectively reduce the growing season length at a given cumulative heat sum in species with higher cold tolerance, further reducing the effective growing season length.

In fact, dormancy is not only relevant in the context of winter survival, but it can be the principal way how plants avoid unfavorable periods other than frost (Poorter & Markesteijn 2008). Dormancy could be the key adaptation shaping SADTO in places where unfavorable seasons are long and regular, as it enables to effectively reduce the adverse growing season length. Both low temperatures and occasional waterlogging can elongate dormancy period (Butt *et al.*, 2008); flooding can also alternate with extremely dry periods, creating different dynamics in open and understory habitats, therefore affecting the strength of SADTO even if the communities in both consists of the same species (Garcia-Sanchez *et al.*, 2007; Bailey-Serres & Voesenek 2008).

Hence, in places with longer growing period, the shade-drought tolerance trade-off could be weak or even non-existent (Markesteijn & Poorter 2009), while at higher latitudes, short growing season can reinforce species adaptations to the dominant stress source (Sack 2004). From species point of view, plants that exhibit higher tolerance to cold temperatures and waterlogging are expected to have lower tolerance to shade and drought (Pearson *et al.*, 2003; Valladares & Niinemets 2008). The frequency of dormancy presence in a species pool more or less correlates with climate extremes (Kollas *et al.*, 2013), therefore species' cold tolerance should be a rather good proxy for indicating the dynamics of SADTO.

The situation is similar with waterlogging tolerance. High waterlogging tolerance requires continuous carbon input to meristematic tissues in roots and stems that are needed to develop adventitious roots (Rich *et al.*, 2012; Cardoso *et al.*, 2013). Such higher respiratory activity, that can decrease leaf photosynthesis rate (Romina *et al.*, 2014), could strongly curb plant capacity to resist severe co-occurring stresses (D'Odorico *et al.*, 2013). In addition, several waterlogging tolerant species have unique structural adjustments such as aerial roots that inherently require greater carbon inputs and compromise the plant capacity for large leaf area formation (Kozłowski 1997). Therefore adaptations to both cold and waterlogging tolerance are expected, through the prolongation of dormancy period, to reduce plants' capability of avoiding damage from simultaneous shade and drought conditions.

Significant relationships between SADTO and all combinations of cold and waterlogging tolerance suggest that enduring abiotic stress factors is even on the macroecological or macrophysiological scale substantially related to specific adaptations that create niche differences (like suggested by Sack 2004). Physiochemical constraints that do not allow plants exhibiting high growth rate in low resource and otherwise stressful conditions (see Smith & Huston 1989) are not as strict as traditional theories state and there is much more evolutionary wiggle room than previously suggested. When taking into account all the species analyzed, our results show that polytolerance in woody plants tends to depend more on interspecific variability than rather strict and ubiquitous physiochemical constraints, the effective strength of which can be actually quite a bit ameliorated by dormancy.

Differences between angiosperms and gymnosperms: phylogeny vs. leaf longevity

Differences between angiosperms and gymnosperms (Fig. 4, Fig. 5) suggest that in some species groups basic physiochemical constraints have a bigger impact on how species tolerate abiotic stress, while other species groups indicate more adaptive diversity. Thus we can assume that phylogeny plays an important role in blazing the trail for new adaptations, and indeed, several recent macroecological studies (Stahl *et al.*, 2013; Zanne *et al.*, 2013; Hawkins *et al.*, 2014) have reached very similar conclusions. Therefore we also carried out species-level phylogenetic analysis, but although phylogeny turned out to be a significant factor in univariate analysis of SADTO (Table A in Appendix S2; see that appendix also for methods and additional results regarding phylogenetic analysis), the importance of species-level phylogeny was marginal compared with cold and waterlogging tolerance.

Crucial phylogenetic signal seems to run at taxonomically very high level – between gymnosperms and angiosperms. Similar niche conservatism patterns on a higher taxonomic level has been found to be affecting how well woody species tolerate low temperatures (Hawkins *et al.*, 2014), and how adapting to colder climates is predominately induced by developing small hydraulic conduits (Zanne *et al.*, 2013). Unlike dormancy, which evolves under straightforward environmental pressure(s), adjusting the size of hydraulic conduits is claimed to have happened already before angiosperm woody species moved from tropical conditions to colder climates (Zanne *et al.*, 2013). In contrast to angiosperms, neither evergreen nor deciduous gymnosperms showed SADTO differences at different levels of cold and waterlogging tolerance (Fig. 4). Gymnosperms are predominately evergreen (91.7% of gymnosperm species in our sample were evergreen; compared to 20.1% evergreen

species among angiosperms). In the case of evergreens, development of winter-dormancy is often delayed or may be even absent in warmer climates (Olsen 2010). Therefore, the length of vegetation period in most gymnosperms in their specific habitat is often longer compared with most co-occurring angiosperms.

According to the whole-plant trait spectra analysis made in 305 North-American woody plant species (Stahl *et al.*, 2013), angiosperms have much higher functional diversity regarding tolerances to various abiotic stress factors than gymnosperms. Stahl *et al.* (2013) also found that the shade and drought tolerance of gymnosperm species were inversely correlated on a PCA axis, while angiosperms had inverse correlation between drought and waterlogging tolerance (Stahl *et al.*, 2013). When studying 339 woody species from Northern hemisphere, Hallik *et al.* (2009) also found that leaf functional traits showed significant trade-off patterns between shade and drought tolerance in all functional groups except deciduous broad-leaved species.

While gymnosperms in our sample tolerated, on average, both shade and drought better than angiosperms, and they also had a weaker trade-off between shade and drought. In contrast, angiosperms exhibited much higher waterlogging tolerance and also cold-waterlogging polytolerance (Table 1). Because of these differences, we suggest that gymnosperms are actually better shade-drought tolerators than angiosperms even if the shade and drought tolerating functional traits are more polarized than in angiosperms (Stahl *et al.* 2013). However, this higher polytolerance capacity only realizes if the climate and water conditions do not add on too much extra abiotic stress. On the other hand, prolonged dormancy favors deciduous angiosperms in places where in addition to shade and drought stress there are also spring or floods or other events causing waterlogging.

Species ecological site occupancy, tolerances and growing season length

It's important to separate among the species ecological potentials *per se* and species occurrence across different habitats. Clearly, having a greater tolerance to a given environmental factor provides an important basis to colonize habitats where this particular factor is limiting. On the other hand, due to the unique physiological, morphological and allocational modifications that lead to enhanced tolerance to the given factor, the species might become less competitive in other environments (Niinemets 2010).

In the case of polytolerance, species stack traits that enhance their persistence in multiple habitats. However, typically enhanced stress tolerance is associated with reduced carbon gain capacity in non-stressed environments (Grime *et al.*, 1997; Wright *et al.*, 2004; Hallik *et al.*, 2009). Thus, polytolerance should not mean an enhanced niche breath. Species with a greater tolerance to abiotic factors are actually more likely to experience shorter vegetation period, whether through global patterns (prolonged cold season) or local patterns (prolonged flooding season). Combinations of multiple stresses appear also in a different manner – they can occur either simultaneously or successively (Niinemets 2010). Shorter vegetation period enhances the chance of several stress factors acting upon plants simultaneously, which in turn generates evolutionary pressure, especially on sessile organisms like plants, for adapting to habitats that exhibit wide variety of climatic conditions. Polytolerance can therefore be interpreted as an adaptation that is not so much in the service of population's dispersal, but

it's more likely a way to survive in places with short vegetation period and high climatic variability (i.e. more frequent and severe abiotic stress).

Also, if a species has adapted to periodically low temperatures and excessive water conditions, its capability to concurrently cope with low light and dry conditions is significantly reduced, as cold and waterlogging adaptations employ contingent trait solutions with shade and drought tolerance: shaded habitats tend to be moist and waterlogged habitats usually do not experience root zone drought (Niinemets & Valladares 2006). While cold tolerance affects vegetation patterns on a larger scale, tolerating excessive soil water or waterlogging tolerance acts more locally – in low-lying areas, places with poor drainage and/or extreme fluctuations in precipitation (Poot & Lambers 2003). So far, relatively little is known about the broad set of mechanisms and underlying traits that make tolerating excessive water possible in woody species (Cardoso *et al.*, 2013), and therefore further research is needed to look for the causes behind these tolerance differences.

Conclusions

A trait-based approach has been the principal alternative way to explain the variability in species ecological potentials and trade-offs (Niinemets *et al.*, 2009; Ouedraogo *et al.*, 2013). According to the critics of traditional physiochemical constraint model, the high rate of interspecific variability in tolerating different stress types points to key roles of adaptive evolution and ecological filtering in making polytolerance possible (Sack 2004; Niinemets & Valladares 2006; Valladares & Niinemets 2008). Although the trait-based approach has been demonstrated correlative patterns among species ecological potentials and plant physiological traits (e.g. Hallik *et al.*, 2009; Markesteijn & Poorter 2009; Markesteijn *et al.*, 2011b; Brenes-Arguedas *et al.*, 2013), explanation of polytolerance patterns among stresses has been rather unsuccessful. In fact, these analyses have mainly shown that plants survive unfavorable conditions by exploiting stress-specific traits that often vary the same way in response to different stresses, e.g., increase in leaf longevity both in drought- and shade-tolerant species (Hallik *et al.*, 2009; Brenes-Arguedas *et al.*, 2013).

The results of our study demonstrate that different abiotic stress factors in woody plants are significantly integrated with each other, and traditional physiochemical constraints do not explain these patterns. Tolerance to low temperatures and waterlogging had a clear trade-off with tolerance to shade and drought. The length of the vegetation period and dormancy are the key factors explaining why woody plants are less capable of tolerating both shade and drought in habitats where the vegetation period is relatively short and/or the water level is high. While dormancy enables angiosperms to face additional stress factors besides shade and drought, gymnosperms have lower polytolerance, but are better tolerators of shade and drought in case other stress factors have weak effects. These results imply that we need to revise our understanding of global abiotic stress patterns in woodlands. More emphasis is clearly needed on the specific stress response trait data, geographic variability of environmental conditions and evolutionary history of species.

There are several promising directions for further studies. First, there is a need to have better understanding of the exact mechanisms and traits that allow for polytolerance. As our results demonstrate, woody species polytolerance patterns depend significantly on species

functional qualities and therefore, the associated mechanisms could vary in different types of species. Second, we should also strive for having a better idea of how much does intraspecific variability, with its ecotypic and plastic components (Niinemets 2014), affect trade-off patterns between different stress factors.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Biosketches

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Figure 1.

Relationship between species shade-drought tolerance and species cold tolerance. The species shade-drought tolerance is defined as the sum of species potential to tolerate shade and drought on a 10-level scale (1 is low and 10 high polytolerance), and the cold tolerance is the species potential to tolerate low temperatures in a 5-level scale (1 is low and 5 is high). Both the regression line and its 95% confidence intervals are demonstrated. Every dot corresponds to one species.

Figure 2.
Relationship between species shade-drought tolerance and species waterlogging tolerance.
Data fitting and categorization as in Fig. 1.

Figure 3.

Species shade-drought tolerance in relation to species cold-waterlogging tolerance. The cold-waterlogging tolerance is defined as the sum of species capability of tolerating both cold and waterlogging in a 10-level scale (1 is low and 10 high polytolerance). Data fitting and categorization as in Fig. 1.

Figure 4.

Results of linear regression analyses between shade-drought tolerance and cold-waterlogging tolerance (both expressed on a 10-level scale, 1 being polyintolerant and 10 polytolerant) separately fitted for evergreen vs. deciduous (upper vs. lower graphs) and angiosperms vs. gymnosperms (left vs. right graphs). Every dot stands for one species.

Figure 5.

Results of linear regression between shade-drought tolerance and cold-waterlogging tolerance separately demonstrated according to species origin (which exhibited no difference among the continents) and for angiosperms and gymnosperms. Data fitting and categorization as in Fig. 4.

Table 1

Average stress tolerance values ($\pm$ SE) for 806 Northern hemisphere temperate species classified according to phylogeny, plant functional type and geographic origin. *Nr* indicates the number of species in each group; all single stress tolerances (unitless) range from 1 (low) to 5 (high); all paired stress tolerances are sums of two single stress tolerances; and cumulative stress tolerance is the sum of all four single stress tolerances.

Species group	Nr	Cold tolerance	Shade tolerance	Drought tolerance	Waterlogging tolerance	Shade-Drought tolerance	Cold-Waterlogging tolerance
Gymnosperms	118	3.17 $\pm$ 0.06	2.69 $\pm$ 0.12	3.08 $\pm$ 0.11	1.46 $\pm$ 0.07	5.77 $\pm$ 0.09	4.62 $\pm$ 0.09
Angiosperms	688	3.24 $\pm$ 0.02	2.40 $\pm$ 0.04	2.78 $\pm$ 0.03	1.83 $\pm$ 0.03	5.18 $\pm$ 0.04	5.07 $\pm$ 0.03
Evergreen	240	3.45 $\pm$ 0.05	2.61 $\pm$ 0.07	3.10 $\pm$ 0.07	1.68 $\pm$ 0.06	5.70 $\pm$ 0.08	5.13 $\pm$ 0.07
Deciduous	566	3.22 $\pm$ 0.02	2.38 $\pm$ 0.04	2.75 $\pm$ 0.04	1.83 $\pm$ 0.03	5.13 $\pm$ 0.05	5.05 $\pm$ 0.04
East Asia	211	3.43 $\pm$ 0.05	2.58 $\pm$ 0.07	2.67 $\pm$ 0.05	1.77 $\pm$ 0.05	5.25 $\pm$ 0.08	5.20 $\pm$ 0.06
Europe	262	3.09 $\pm$ 0.04	2.19 $\pm$ 0.06	3.04 $\pm$ 0.07	1.95 $\pm$ 0.07	5.23 $\pm$ 0.09	5.04 $\pm$ 0.07
North America	333	3.30 $\pm$ 0.03	2.69 $\pm$ 0.06	2.86 $\pm$ 0.06	1.93 $\pm$ 0.06	5.56 $\pm$ 0.06	5.23 $\pm$ 0.07
Total	806	3.28 $\pm$ 0.09	2.49 $\pm$ 0.09	2.88 $\pm$ 0.09	1.89 $\pm$ 0.09	5.37 $\pm$ 0.09	5.17 $\pm$ 0.09