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A heuristic classification of woody plants based on contrasting shade and drought strategies

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Woody plants vary in their adaptations to drought and shade. For a better prediction of vegetation responses to drought and shade within dynamic global vegetation models, it is critical to group species into functional types with similar adaptations. One of the key challenges is that the adaptations are generally determined by a large number of plant traits that may not be available for a large number of species. In this study, we present two heuristic woody plant groups that were separated using cluster analysis in a three-dimensional trait–environment space based on three key metrics for each species: mean xylem embolism resistance, shade tolerance and habitat aridity. The two heuristic groups separate these species into tolerators and avoiders. The tolerators either rely on their high embolism resistance to tolerate drought in arid habitats (e.g., Juniperus and Prunus) or rely on high shade tolerance to withstand shaded conditions in wet habitats (e.g., Picea, Abies and Acer). In contrast, all avoiders have low embolism resistance and low shade tolerance. In arid habitats, avoiders tend to minimize catastrophic embolism (e.g., most Pinus species) while in wet habitats, they may survive despite low shade tolerance (e.g., Betula, Populus, Alnus and Salix). Because our approach links traits to the environmental conditions, we expect it could be a promising framework for predicting changes in species composition, and therefore ecosystem function, under changing environmental conditions.

**Keywords:** drought responses, embolism resistance, plant functional traits, shade tolerance, wood density.

**Introduction**

In the last decade, many studies have shown drought-induced tree mortality across the world (Phillips et al. 2009, van Mantgem et al. 2009, Canzler et al. 2011, Peng et al. 2011, Field et al. 2014, Allen et al. 2015). Our capability to predict drought-induced mortality is growing (McDowell et al. 2013, Xu et al. 2013, Anderegg et al. 2015, Greenwood et al. 2017) and may eventually rely in part on parameterization of traits and processes key to prediction (Fisher et al. 2018). Prediction of drought-induced tree mortality is challenging because it is difficult to represent the myriad drought strategies that exist among plant species with potential interactions with other strategies for survival, such as shade tolerance.

The first approach for differentiating drought strategies is to evaluate whether plants tolerate or avoid water stress (Levitt 1972, Lo Gullo and Salleo 1988, Larsen et al. 1989, Jones 1992). Plants with a drought-tolerating strategy may markedly drop their xylem water potential during drought as compared with a non-drought period, while partly maintaining photosynthesis (Lo Gullo and Salleo 1988). In contrast, drought-avoiding plants tend to limit transpiration, and hence photosynthesis, to avoid catastrophically low water potential and survive drought (Lo Gullo and Salleo 1988). Additional adaptations include extensive axial...
parenchyma for water storage (Borchert and Pockman 2005), leaf shedding to minimize transpiration and respiration (Hoffmann et al. 2011), deep roots and efficient acquisition of soil water (Lo Gullo and Salleo 1988, Donovan et al. 2000, Johnson et al. 2018), re-sprouting capacity (Bond and Midgley 2003) and forming segmented stems that contain independent, redundant compartments (Schenk et al. 2008). Both drought-tolerating and drought-avoiding plants may utilize these avoiding strategies, but they are crucial for drought-avoiding plants in arid habitats as they may lack high embolism resistance (e.g., Johnson et al. 2018).

Whether a particular species avoids or tolerates drought can be assessed by a set of physiological measurements that include seasonal monitoring of plant water potential, relative water content and stomatal conductance (Lo Gullo and Salleo 1988, Goulden 1996), but these measurements require considerable effort. A second approach is to classify species into groups of drought strategies within the trait–trait space. Ackerly (2004) pointed out that a two-dimensional (2D) strategy space defined by two ‘anchor’ traits (i.e., key plant traits differentiating functional strategies) can be used to distinguish contrasting ecological strategies and thus define functional groups. Specifically, chaparral shrubs were divided into three groups with varied drought strategies based on species’ locations within the 2D space defined by leaf life span and minimum water potentials, including (i) morphological and microsite avoidance of water deficit, (ii) phenological avoidance of water deficit and (iii) tolerance of water deficit (Ackerly 2004). This theoretical framework efficiently classifies a large number of species into tolerators and avoiders. Similar to Ackerly (2004), a third approach is to group species into tolerator and avoider within the trait–environmental space considering that key functional traits are linked to survival niche in a multidimensional environmental space (Westoby et al. 2002, McDowell et al. 2008, Hallik et al. 2009, Adler et al. 2014, Mencuccini et al. 2015, Diaz et al. 2016). Such a trait–environmental space framework may not only improve our understanding of plant physiology but also identify, from a myriad of traits, those combinations most useful in predicting survival or death in the next-generation of Earth System Models (ESMs) (Fisher et al. 2015).

How might this trait–environmental space framework work? Previous studies have shown that a suite of traits can determine fitness of a species within a specific environmental condition (Westoby et al. 2002, Marksteijn et al. 2011a, Greenwood et al. 2017). For wet environmental conditions where it is more critical for the species to compete for light than for water, traits related to shade tolerance could be important for their success (Niinemets and Valladares 2006, Grubb 2016). For dry environmental conditions, because it is critical for the species to survive under water stress, traits related to water uptake and conservation (Johnson et al. 2018), resistance to embolism (Blackman et al. 2012, 2014) and high wood density (Greenwood et al. 2017) could be important for their success. At different levels of aridity, species may be distributed along different ecological strategy axes (e.g., survival under shade vs drought) in order to maximize their fitness (Niinemets and Valladares 2006, Hallik et al. 2009). Therefore, we expect that a key trait related to a certain ecological strategy will adapt to a specific environmental gradient (i.e., aridity) if the trait is critical for the survival and growth of plants along the gradient. If different ecological strategies can lead to distinct adaptations of a certain trait to an environmental gradient (e.g., Westoby et al. 2002, Hallik et al. 2009), we will be able to identify different groups of species related to different ecological strategies within the 2D space between the trait and corresponding environmental gradient.

One of the key traits related to survival and growth during droughts is the water potential recorded at 50% loss of conductivity (P50), which determines resistance to embolism. The more negative this value, the higher the resistance, and the more likely a species will survive drought in an arid environment (Blackman et al. 2012, 2014). However, many arid environments contain species that avoid drought and thereby maintain relatively low resistance to embolism. If all species are plotted within a P50–habitat aridity space, we expect to see two groups of species: (i) the water stress tolerators, which have a relatively negative P50 under high aridity (i.e., Figure 1a) and (ii) the water stress avoiders, which maintain a relatively stable and mild P50 across an aridity gradient (Feature 2 in Figure 1a). The challenge is that the two features with different drought strategies blend together to form a continuous triangular distribution in a 2D P50–habitat aridity space (Figure 1a), and thus it is difficult to statistically separate these two groups.

To improve our understanding and prediction of species performance under drought, we need to find an approach that enables separation of species into functional groups with different drought strategies continuously distributed in the 2D P50–habitat aridity space. One way to proceed is to expand the number of traits considered. If suites of traits are chosen carefully, covaried traits may reflect adaptive tradeoffs and coordination between axis of strategies; in contrast, suites of traits that are orthogonal to each other may indicate independent axes of strategies (Ackerly 2004). Following this idea, we hypothesize that orthogonal traits representing different survival strategies can be added to the 2D P50–habitat aridity space to separate species groups with different drought strategies.

One obvious trait to consider in addition to P50 is the shade tolerance, which represents how species survive in their response to light availability. There is a continuum between pioneer species, which are adapted to full light, and those adapted to shade under denser canopies (Whitmore 1989). With increasing light, there is a concomitant shift in growth rates among species (Kitajima 1994, Kobe et al. 1995, Walters and Reich 1999, Sánchez-Gómez et al. 2006). The requirement for light changes when a species is stressed (Valladares and Niinemets 2008) and the exposure of plants to high irradiance intensifies the effect of drought (Sánchez-Gómez et al. 2006). When we
examine the distribution of woody plants within the 2D space of shade tolerance and aridity, the pattern is also a triangular shape with three features (Figure 1b). One group of species has a lower shade tolerance under more arid environments (Feature 1). Another group of species lives in wet habitats but has relatively low shade tolerance (Feature 2, Figure 1b). A third group of species can tolerate both shade and drought (polytolerance) (Feature 3, Figure 1b). Dense canopy rarely occurs in very arid habitats, which makes adaptation of plants to shade unnecessary (Grubb 2016). In some habitats where dense forests encounter seasonal drought, polytolerance of shade and drought may be adaptively meaningful; the existence of such polytolerance may depend on whether the length of the growing season allows recovery after drought (i.e., polytolerance; Valladares and Niinemets 2008, Laanisto and Niinemets 2015).

We also include waterlogging tolerance and wood density as possible candidates to examine the P50–aridity relationship within a higher dimensional space to reveal different groups of...
species. Waterlogging causes low-oxygen stress for plants as gases diffuse much more slowly in water than in air. Long-lasting waterlogging conditions will lead to hypoxic or anoxic conditions around plant roots that inhibit oxygen-demanding metabolic activities (Dennis et al. 2000). A plants’ waterlogging tolerance is negatively correlated to habitat aridity and shade tolerance (Niinemets and Valladares 2006), and may hence serve as a good candidate to form a covaried axis with habitat aridity and shade tolerance. Moreover, wood density is related to drought survival (Greenwood et al. 2017). Species in more arid environments tend to have high wood density; higher wood density may also be related to more negative P50 and hence the ability to resist xylem embolism (Hacke et al. 2001, Pittermann et al. 2006, 2012, Markesteijn et al. 2011b).

The objective of this study was to develop a framework to quantitatively separate woody plants into functional groups with different survival strategies, which were revealed by orthogonal axes of traits and environmental gradients. This scheme may provide a practical and heuristic solution to separate species that are continuously distributed in 2D trait–trait and trait–environment spaces (e.g., Figure 1). Because the functional groups are derived based on the relationship between traits and environment gradients, we expect that the separation of functional groups will help us to better predict how vegetation composition and function will respond to future environmental conditions.

### Materials and methods

#### Data

We grouped woody plants (trees and shrubs; lianas excluded) based on their traits and habitats for temperate species from the Northern Hemisphere. The major traits we used were P50 and wood density. P50 and wood density data were obtained from the Xylem Functional Traits database (Choat et al. 2012), which is available via the TRY database (Kattge et al. 2011). Wood density data were supplemented by data from a global wood density database (Zanne et al. 2014), Glopnet (Wright 2004) and the BAAD (Biomass And Allometry Database for woody plants) database (Falster et al. 2015).

We used three factors to describe the potential of plants to survive in a multidimensional environment (Table 1). These factors are assumed to be related to a suite of traits that determine plant survival in different environmental conditions. The first factor was the ability to survive under light limitation (i.e., shade tolerance) as determined by the lowest light level plants can grow at (Niinemets and Valladares 2006) (Table 1). The second factor was the ability to survive under water limitations (i.e.,

Table 1. Unified scales from 1 to 5 for shade tolerance, drought tolerance (i.e., habitat aridity) and waterlogging tolerance (Niinemets and Valladares 2006). We used the habitat aridity instead of drought tolerance in this study to avoid confusion with another drought tolerance factor, P50. $\phi_{\text{min}} =$ minimum light at which a given species is able to grow (% of full sunlight), P = precipitation (mm), $\Psi_{\text{s,min}} =$ minimum soil water potential (MPa). The habitat aridity score was the lowest among five criteria: P, P/PET, variations of precipitation during growing season, the length of drought and $\Psi_{\text{s,min}}$ (Niinemets and Valladares 2006).

<table>
<thead>
<tr>
<th>Scale</th>
<th>Shade tolerance</th>
<th>Drought tolerance (habitat aridity)</th>
<th>Waterlogging tolerance</th>
</tr>
</thead>
</table>
| 1. Very intolerant $\phi_{\text{min}} > 50\%$ | Annual P=600 mm
Little variation of P during growing season
P/PET>3.0
Few days of drought
$\Psi_{\text{s,min}} >$−0.3 MPa | Does not tolerate water saturated soils for more than a few days during the growing season |
| 2. Intolerant $\phi_{\text{min}}$ 25–50% | Annual P=500–600 m
Coefficient of P variation in growing season <10%
P/PET from 1.5 to 3
Few weeks of drought
−0.3 > $\Psi_{\text{s,min}}$ > −0.8 | Tolerates 1–2 weeks of waterlogging during the growing season |
| 3. Moderately tolerant $\phi_{\text{min}}$ 10–25% | Annual P=400–500 m
Coefficient of P variation in growing season: 10–15%
P/PET from 0.8 to 1.5
Up to 1 month of drought
−0.8 > $\Psi_{\text{s,min}}$ > −1.5 | Survives waterlogging or saturated soils for 30 consecutive days during growing season |
| 4. Tolerant $\phi_{\text{min}}$ 5–10% | Annual P=300–400 m
Coefficient of P variation in growing season: 20–25%
P/PET of from 0.5 to 0.8
2–3 months of drought
−1.5 > $\Psi_{\text{s,min}}$ > −3 | Survives deep waterlogging for one growing season |
| 5. Very tolerant $\phi_{\text{min}}$ 2–5% | Annual P<300 m
Coefficient of P variation in growing season >25%
P/PET <0.5
>3 months of drought
$\Psi_{\text{s,min}}$ <−3 | Survives deep, prolonged waterlogging for >1 year |

Table 1. Uniform scales from 1 to 5 for shade tolerance, drought tolerance (i.e., habitat aridity) and waterlogging tolerance (Niinemets and Valladares 2006). We used the habitat aridity instead of drought tolerance in this study to avoid confusion with another drought tolerance factor, P50. $\phi_{\text{min}} =$ minimum light at which a given species is able to grow (% of full sunlight), P = precipitation (mm), $\Psi_{\text{s,min}} =$ minimum soil water potential (MPa). The habitat aridity score was the lowest among five criteria: P, P/PET, variations of precipitation during growing season, the length of drought and $\Psi_{\text{s,min}}$ (Niinemets and Valladares 2006).
habitability) as determined by the most limiting factor among annual precipitation, precipitation to potential evapotranspiration ratio and duration of dry periods (Table 1) (Niinemets and Valladares 2006). This factor was named drought tolerance in Niinemets and Valladares (2006), which may be inferred as a trait. However, it specifically describes the habitat aridity where species survive. We hence refer to this factor as habitat aridity or aridity and consider it as an environmental factor instead of a trait to avoid confusion with another physiological drought tolerance trait, P50. Note that the habitat aridity is a semi-quantitative factor (Laanisto and Niinemets 2015): 1, very intolerant; 2, intolerant; 3, moderately tolerant; 4, tolerant; and 5, very tolerant. In the future, thorough bioclimatic analyses are needed to improve this rating, but this dataset was the best one available for our analysis. The third factor was the waterlogging tolerance in terms of the survival duration in waterlogged conditions (Table 1) (Niinemets and Valladares 2006). Multiple species rankings were obtained from different sources for shade tolerance, habitat aridity and waterlogging tolerance (Niinemets and Valladares 2006). For each factor, rankings of the same species from different sources were then cross-calibrated using linear correlations to ensure comparability across sources; after calibration, the final rankings were the averages of calibrated values across different sources (Niinemets and Valladares 2006). The results were unified scales from 1 to 5 of shade tolerance, habitat aridity and waterlogging tolerance for temperate forests across North America, Europe and Asia (Table 1), which enables comparison of different species across continents (Niinemets and Valladares 2006).

The final dataset included 182 species from 73 genera (see Supplementary dataset and Supplementary material Figure S2 available as Supplementary Data at Tree Physiology Online) of temperate species in the Northern Hemisphere across an annual precipitation gradient from 157 to 2392 mm (see Figures S1 and S8 available as Supplementary Data at Tree Physiology Online). Their phylogenetic relationships and data values are shown in Figure S2 available as Supplementary Data at Tree Physiology Online.

**Cluster analysis**

We hypothesized that Features 1 and 2 in Figure 1 may present two orthogonal axes in a higher dimension while their projections in the 2D spaces were distributed in continuous triangular shapes. Features 1 and 2 hence served as a priori expectations in our search for statistical approaches of separations. There are two orthogonal axes in the 3D space of P50–shade tolerance–habitat aridity based on visual judgment, which may help separate Features 1 and 2 (Figure 2 and Supplementary videos available as Supplementary Data at Tree Physiology Online). We hence applied cluster analysis to confirm the visual observation and statistically separated two groups representing two orthogonal axes in this 3D space.

We performed cluster analysis (Fraley and Raftery 2002) with P50, shade tolerance and habitat aridity using the ‘mclust’ package (Scrucca et al. 2016) in R (R Core Team, 2013) to automatically search for groups. The procedure fits a series of combinations of Gaussian components using the expectation-maximization method, where different parameter combinations contain different cluster shapes (Fraley and Raftery 2002). The combination with the highest Bayesian Information Criterion value was selected as optimal combination from the Gaussian distribution. Each cluster can be represented by an ellipsoid-shaped multivariate Gaussian distribution. We did not include wood density and waterlogging tolerance as these two parameters were tightly correlated to ensure comparability across sources; after calibration, the final dataset included 182 species from 73 genera (see Supplementary dataset and Supplementary material Figure S2 available as Supplementary Data at Tree Physiology Online). Their phylogenetic relationships and data values are shown in Figure S2 available as Supplementary Data at Tree Physiology Online.

We ran cluster analysis in the P50–shade tolerance–habitat aridity space for 129 angiosperm species (Figure 2a); the only restriction we set was looking for best clustering of one to four groups. The best answer was two groups, which coincidently matched the notion of our a priori expectation (Features 1 and 2) in general (see Results). For the 53 gymnosperm species, the two groups matching Features 1 and 2 were visibly present (Figure 2b and Supplementary videos available as Supplementary Data at Tree Physiology Online) but could not be separated with cluster analysis in the 3D space with P50, shade tolerance and aridity due to the small sample size and sparse data distributions around the center of shade tolerance–aridity–P50 space. There were only six species in the domain with shade tolerance or aridity between 2 and 4 and P50 < −5 MPa, which created a sparse area in the axis representing Feature 1 in Figure 1. Consequently, we ran cluster analysis in the 2D space based on only P50 and shade tolerance data (Figure 3b), where the data were more tightly clustered than in the shade tolerance–aridity–P50 space. The approach separated gymnosperms matching our priori expectation (Figure 2b). After the segmentation, we tested if the two groups were meaningful in the dimensions with wood density or waterlogging tolerance as these two parameters were tightly related to plants’ habitat aridity.

Caution should be used when evaluating the cluster analysis for the two-group separation. First, we used mean parameter values for species in the cluster analysis; if their sample ranges were geographically biased or sample sizes were insufficient, the grouping of a species may not be accurate. We cannot address this issue in this study but further field measurements.
for traits should be made for species that were insufficiently measured (e.g., species with one P50 measurement, see Supplementary dataset available as Supplementary Data at Tree Physiology Online) to improve the reliability of grouping. Second, the quality of P50 measurements could have effects on our cluster analysis given concerns about measuring xylem embolism resistance especially methodological artefacts that underestimate embolism resistance (Jansen et al. 2015). Such artefacts include a cutting artefact and open vessel artefact (Jansen et al. 2015, Torres-Ruiz et al. 2015, Choat et al. 2016). We hence applied the cluster analysis to a smaller dataset \((n = 144)\) removing data using less reliable measuring approaches to confirm the validity of the two groups. The following criteria were used to exclude data from this second dataset: (i) R-shaped vulnerability curves; (ii) the combination of centrifuge methods (cavitron and standard centrifuge) with ring-porosity and/or long and wide vessels (open-vessel artefact); (iii) air-injection together with ring-porosity and/or long/wide vessels (open-vessel artefact); and (iv) relatively less negative P50 values in combination with wide and long vessels (cutting artefact).

**Results**

**Two-group clustering**

Two distinct groups emerge via the cluster analysis along two orthogonal axes in the P50–shade tolerance–habitat aridity space (Figure 2 and Supplementary videos available as Supplementary Data at Tree Physiology Online). One group is distributed along an axis that occupied the 3D space diagonally from the less negative P50–high shade tolerance–low aridity space (Figures 2 and 3); this group represents a continuum similar to Feature 1 in Figure 1. In this continuum, P50, shade tolerance and aridity are correlated with each other (Figure 3). We call these species the tolerators because they possess traits that allow them to tolerate either drought at one end of the continuum or shade at the other end. The second group clustered around an axis perpendicular to the P50–shade tolerance plane with less negative P50 and low shade tolerance (Figure 2). This group includes species neither embolism resistant nor shade tolerant: species living in high aridity environments despite less...
negative P50 (Figure 3c and d), and species with low shade tolerance despite living in low aridity (Figure 3e and f). We call these the ‘avoiders’ for lack of a better term, because they do not show traits that allow them to tolerate the habitats in which they are found.

**Characteristics of tolerators and avoiders related to shade and drought**

The two new groups represented distinctive strategies for survival under a wide range of habitat aridity. This was revealed by the projections of the two orthogonal axes on 2D planes (Figure 3; shown in evergreen/deciduous and angiosperm/gymnosperm subgroups). The next three paragraphs describe the properties of the two groups in terms of their drought and shade tolerance/avoidance. We summarize the properties of tolerators and avoiders in Table 2. In brief, tolerator species in the arid habitat have the ability to tolerate drought via high embolism resistance, and those in the wet habitats tolerate shade. In contrast, avoider species in the arid habitat avoid catastrophic negative xylem pressure, and those in wet habitats are shade-intolerant. Therefore, our definition of tolerators and avoiders includes both shade and drought tolerance and drought avoidance.

For tolerator species, embolism resistance (i.e., P50) is in coordination with local aridity. Namely, species with more negative P50 can maintain conductivity under more severe water stress and hence tolerate a drier environment (Figure 3c and d). They are therefore desiccation tolerators in arid environments; these include drought-tolerant _Juniperus_, _Prunus_ and _Amelanchier_ species. This group also includes drought intolerant but shade tolerant (see shade tolerance in the next section) _Picea_, _Abies_, _Acer_, _Sequoia_ and _Sequoiadendron_ (see Supplementary dataset, Figure 2 and Figure S6 available as Supplementary Data at *Tree Physiology* Online) with less negative P50. Moreover, tolerators show a negative correlation between shade tolerance and embolism resistance, and between shade tolerance and habitat aridity (Figure 3). Tolerators dwelling in arid environments are embolism resistant (i.e., more negative P50) but shade intolerant, whereas species dwelling in wet environments are embolism vulnerable but shade tolerant. There are also species between extreme shade tolerators and extreme drought tolerators along the axis; their ability to tolerate shade decreases with their ability to tolerant drought and vice versa (Figure 3e and f).

In contrast, avoider species did not follow the limitation of embolism resistance in the sense that many of them exist in some of the most arid environments despite their less negative P50 and hence low embolism resistance (Figure 3c and d). These species may have to apply desiccation-avoiding strategies to limit transpiration and photosynthesis and hence avoid catastrophically low water potential. Avoiders include most _Pinus_ species, most deciduous conifers (_Larix_, _Ginkgo_ and _Taxodium_) except _Metasequoia glyptostroboides_, and nearly all _Betula_, _Populus_, _Alnus_ and _Salix_ species in this study (see Supplementary dataset, Figure 2 and Figure S6 available as Supplementary Data at *Tree Physiology* Online). Besides low embolism resistance, avoiders are also characterized by low shade tolerance, yet they inhabit a full range of habitat aridity. Deciduous angiosperm avoiders had higher shade tolerance in more arid areas (Figure 3e) and higher shade tolerance with more negative P50 (Figure 3a), which was opposite to tolerators.

The difference in shade tolerance is apparent between tolerators and avoiders in wet habitats. All tolerators with habitat aridity ≤2 are relatively shade tolerant with shade tolerance ≥3.3 (eight angiosperm and eight gymnosperm species, Figure 3e and f). However, many shade-intolerant avoiders also exist in wet habitats. There are 16 species with aridity ≤2.0 and shade tolerance ≤2.5 (Figures 3e and 4a), all of which are deciduous avoiders.

**Two groups in other dimensions**

The differences between the two groups also existed beyond the P50–shade tolerance–aridity dimension that defined the two groups. For example, the two groups are visually discernible in the 3D space of aridity–shade tolerance–waterlogging tolerance for angiosperms (Figure 4). The data clouds of the two groups are clearly separated in this 3D space of angiosperms at one end of the cloud of each group: the low aridity–high shade

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**Table 2. Properties of two heuristic groups separated by cluster analysis with xylem P50 (i.e., embolism resistance), shade tolerance and habitat aridity.**

<table>
<thead>
<tr>
<th>Trait-environment coordination</th>
<th>Tolerators</th>
<th>Avoiders</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species in wet habitat</td>
<td>Distributed across the whole spectrum of embolism resistance, shade tolerance and habitat aridity. Shade tolerators.</td>
<td>All are shade intolerant. All have low embolism resistance. Distributed across the spectrum of habitat aridity. Low shade tolerance. Strategies: (i) being pioneers (e.g., <em>Betula</em>, <em>Salix</em>, <em>Populus</em>); (ii) live in a waterlogged habitat where no shade tolerators survive.</td>
</tr>
<tr>
<td>Species in arid habitat</td>
<td>Desiccation tolerators. High embolism resistance.</td>
<td>Desiccation avoiders with low embolism resistance. Avoid catastrophic low xylem tension by various strategies. Distributed across the whole spectrum of waterlogging tolerance.</td>
</tr>
<tr>
<td>Waterlogging tolerant</td>
<td>Not waterlogging tolerant. Cavitation resistance coordinate with habitat aridity.</td>
<td>No coordination between embolism resistance and habitat aridity.</td>
</tr>
<tr>
<td>Wood density coordinate with habitat aridity.</td>
<td>No coordination between wood density and habitat aridity.</td>
<td></td>
</tr>
</tbody>
</table>
tolerance space for tolerators and the high waterlogging tolerance–low shade tolerance space for avoiders. However, the data clouds of the two groups heavily overlap at the low shade tolerance–low waterlogging tolerance space (Figure 5a), which precludes isolation of two groups in the aridity–shade tolerance–waterlogging tolerance space. In comparison, there is little data...
cloud overlap of the two groups in the P50–shade tolerance–aridity space (Figure 2), which made statistical isolation of the two groups straightforward.

Another example of distinctions between the two groups is how wood density is related to P50 and habitat aridity (Figure 4). The correlation between wood density and P50 was significant only for tolerators, but was absent for avoiders (Figure 4c and d). Despite this difference, both groups have higher wood density in more arid environments (Figure 4a and b).

Linear regressions between some metrics were also contrasted in the two groups. Such examples included wood density vs waterlogging tolerance (significant with P ≤ 0.05 only in avoiders, negative correlation), wood density vs shade tolerance (tolerators, negative) and P50 vs waterlogging tolerance (tolerators, positive) (see Table S1 available as Supplementary Data at Tree Physiology Online).

Uncertainty

We use an index of the uncertainty in the cluster analysis to inform the uncertainty of a species’ grouping (see Supplementary dataset for uncertainty values for all species). The possible uncertainty values ranged from 0 to 0.5; the larger uncertainty, the further away a species is from the center of its cluster (Fraley and Raftery 2002). The mean value of uncertainty index is 0.06 for 182 species (range from 0.00 to 0.44, see Supplementary dataset available as Supplementary Data at Tree Physiology Online).

We also applied all analyses of this study to a smaller dataset removing data using less reliable measuring approaches for P50. The two groups could still be clearly discerned with the cluster analysis based on the smaller dataset (144 species; see Supplementary dataset and Figure S5 available as Supplementary Data at Tree Physiology Online). The key conclusions from the large dataset (e.g., Figures 3 and 4) were still valid.

Discussion

This study presents a quantitative approach toward separating two woody plant groups based on only three metrics—an environmental factor (habitat aridity) and two plant traits (shade tolerance and embolism resistance)—for 182 species. This clear separation was achieved by using only simple cluster analysis, but the results indicated connections between plant traits and plant functioning. These two groups formed two distinct axes in the 3D P50–shade tolerance–habitat aridity space. These groups reflect two contrasting survival strategies under drought—either relying on embolism resistance or not—and two more in wet habitats by either being shade tolerant or not (Table 2).

Avoider strategies

As demonstrated above, tolerators are defined by their high shade tolerance in wet habitats and high embolism resistance in arid habitats (Table 2). In contrast, avoiders are defined by an assemblage of strategies in different habitat aridity (Table 2). Shade-intolerant avoiders may survive in wet habitats, which raises a question: how could these shade-intolerant avoiders in wet habitats compete with species with high shade tolerance? The potential solution is to avoid being shaded using two strategies: being pioneers and/or being waterlogging tolerant. First, they could be pioneer species. The 16 species with low aridity ≤2 and low shade tolerance ≤2.5 include six Salix species, five Populus species, two Betula species, two Alnus species and Quercus phellos. Among them, Alnus, Betula, Populus and Salix are pioneer species (Burns and Honkala 1990, Tellenius 1999); they may regenerate after disturbances without being shaded, although they may eventually be shaded out when more shade-tolerating tolerator species emerge from the same habitat. Second, it is also possible that avoiders avoid being shaded out by being waterlogging tolerant. Based on our study, 14 of these 16 species are located in the high waterlogging tolerant domain (>2.5) where few tolerators exist (Figure 5); 12 of these 16 species are among the top 20 of the most tolerant species of all 182 studied species. The ability to survive in the waterlogged environments can provide these avoiders an additional ability to survive in wet areas without being pioneers.

It is complex to define avoiders with regards to how they avoid catastrophically low xylem potential in arid habitats. One might conclude that avoiders are not well adapted to their environments, but the drought response literature has shown that avoiding drought is often a good strategy even in the absence of high tolerance (Levitt 1972). There are many desiccation avoiding strategies that plants can use during drought (Pivovarov et al. 2016, O’Brien et al. 2017), but we cannot tell what strategies separate the avoiders at this stage because these strategies may be shared by both avoiders and tolerators. For example, leaf shedding or wilting in drought can reduce transpiration cost and hence help plants to avoid catastrophic hydraulic failure (Hoffmann et al. 2011). However, both tolerators (e.g., Cornus, Crataegus, Fagus, Ligustrum, Oxystegum, Prunus and Viburnum) and avoiders (e.g., Populus, Salix and Sambucus) can utilize these avoiding strategies (Hoffmann et al. 2011, Grubb 2016). Moreover, active stomatal regulation can be an important drought-avoiding strategy (Lo Gullo and Salleo 1988), but we did not see a distinction between tolerators and avoiders on how strictly they regulate stomata for water loss under drought. Plants may regulate their stomata to declining soil water potential either loosely (anisohydric regulation) to allow a decrease in mid-day leaf water potential (Ψmd), strictly (isohydric regulation) to maintain a relatively constant Ψmd, or moderately between the anisohydric and isohydric regulation (Klein 2014, Martinez-Vilalta et al. 2014, Hochberg et al. 2018). Our data (48 species, Note S2 and Figure S10 available as Supplementary Data at Tree Physiology Online) show that species from both groups lay across the iso- and aniso-hydric continuum, thus strict stomatal regulation to maintain a relatively constant xylem water potential may not be a signature strategy for avoiders.
Two-group classifications

Despite some connections between the two groups and their survival strategies, our separation of tolerators and avoiders should be considered as a useful classification scheme instead of two real natural groups. There could be many reasonable approaches to classify species; different classification schemes may conflict with each other and lead to debate about whether the defined groups are distinct and real (Ackerly 2004). Therefore, future work should define where our two-group classification can be applied and explore how plant traits and their drought and shade strategies are connected within each group. For example, the evolution of drought-resistant xylem of the Cupressaceae family (15 out of 16 in this study are tolerators, Figure S12 available as Supplementary Data at Tree Physiology Online) is coordinated with xylem safety, which increased with increasing habitat aridity from the Oligocene onward (Pittermann et al. 2012); species from this family rely on leaf desiccation to drive stomatal closure during drought (Brodribb et al. 2014). If such physiological and phylogenetic patterns can be related to gymnosperm tolerators, we may use these patterns to determine a natural gymnosperm tolerator group without using the cluster analysis as the main classification scheme. The evolution of drought-resistant xylem of the Cupressaceae family (Pittermann et al. 2012) may also provide an example of the evolutionary connection between shade tolerators and drought tolerators in the tolerator group. Increasingly drought-resistant xylem (more negative P50) of the Cupressaceae family was accompanied by increasing habitat aridity ($R^2 = 0.52, P < 0.001$) and decreasing shade tolerance ($R^2 = 0.21, P = 0.04$) in extant species in this study. If P50 was also correlated with habitat aridity and shade tolerance in Cupressaceae species along the evolutionary path, adaptation to drier environment by natural selection may have created species between the shade-tolerant and the drought-tolerant ends of the tolerator axis.

It may seem counterintuitive to include shade-tolerant and drought-tolerant species in a single group. After all, one would expect fundamentally different traits in species with tolerance to drought vs shade. However, what these tolerators share is the ability to deviate from the requirement for rapid growth. This is represented by very negative P50 in arid habitat (thus low efficiency of transporting water; Gleason et al. 2016) and high shade tolerance in wet habitat. These two traits would both limit photosynthetic rates, at least at high light (Kobe et al. 1995, Sánchez-Gómez et al. 2006, Gleason et al. 2016). Grouping shade-tolerant and drought-tolerant species in a single group may also be supported by the similar phylogenies of some species. For example, as described in the previous paragraph, the species of the Cupressaceae evolved from wet habitats into arid habitats (Pittermann et al. 2012), and now occupy the whole aridity, P50 and shade tolerance spectrum of the tolerator group (see Figure S12 available as Supplementary Data at Tree Physiology Online).

One might expect that all species within the same genus might fall into a similar group. This is the case for all but six genera: Betula, Fraxinus, Pinus, Populus, Quercus and Rhododendron; $N = 4, 5, 16, 9, 17$ and 5, respectively (see Supplementary dataset and Figure 2 and Figure S2 available as Supplementary Data at Tree Physiology Online). The genera Betula, Populus and Rhododendron each had only one species that diverged from their major group (Figure 4). There are two genera with similar numbers of species in each group, Fraxinus (two tolerators vs three avoiders; mean uncertainty = 0.17) and Quercus (7 vs 10; 0.25) (Figure 2 and Figure S2 available as Supplementary Data at Tree Physiology Online). These two genera had the highest uncertainty values among 25 genera with at least two species, which indicated that these species are located at the border of two groups in the P50–shade tolerance–aridity space. The separation of Quercus could be expected because Quercus species were formerly reported as both drought tolerators and avoiders (e.g., Abrams 1990, Lo Gullo and Salleo 1990, Knops and Koenig 1994, Damesin and Rambal 1995, Picon et al. 1996, Nardini et al. 1999, Martinez-Ferri et al. 2000). Quercus species survive drought by traits including deep roots, effective water transport, xeromorphic leaves, and osmotic and elastic adjustment to gas exchange (Abrams 1990). For example, some Quercus species tolerate drought and maintain photosynthesis at negative water potential (Damesin and Rambal 1995, Picon et al. 1996), while some are among the most iconic desiccation avoiders with very deep roots reaching the water table, which enable them to survive severe drought (Abrams 1990, Knops and Koenig 1994, Johnson et al. 2018).

The two heuristic groups may also improve our understanding about triangular trait distributions (Figure 1), which requires only two ‘building blocks’ (avoiders and tolerators) to construct them. Projections of the two groups are all in triangular form in the 2D dimension of any two of five parameters including P50, shade tolerance, habitat aridity, wood density and waterlogging tolerance (Figure S3 available as Supplementary Data at Tree Physiology Online, and Figures 3, and 4c and d), with the only exception being wood density–aridity space (Figure S3 available as Supplementary Data at Tree Physiology Online, and Figure 4a and b); most of these projections have tolerators within the Feature 1 space and only avoiders are within the Feature 2 space (except those 2D dimensions with waterlogging tolerance involved) (see Figure S3 available as Supplementary Data at Tree Physiology Online). It is worth noting that some avoiders are also located in the Feature 1 space and hence overlapped with tolerators in some 2D spaces (see Figure S3 available as Supplementary Data at Tree Physiology Online). They overlap less in the 3D space with P50, shade tolerance and habitat aridity (Figure 1 and Supplementary videos available as Supplementary Data at Tree Physiology Online), and this is why we could separate the two ‘building blocks’ in 3D.
Figure 6. The distributions of species of Brzeziecki and Kienast (1994) in the 3D P50–aridity–shade tolerance (a) and the 2D aridity–shade tolerance (b) space. There were 36 major European tree species classified into groups with three major survival strategies based on the Grime’s model (Grime 1977, 1988): competitive (C), stress-tolerant (S) and ruderal (R). Strategies between these three extremes were also identified (C–S, S–R and C–S–R). All species with C and S strategies in Brzeziecki and Kienast (1994) were avoiders in this study, and all R species were avoiders.

While most of the triangular distributions will have weak correlations among traits or trait and environment gradients, using these heuristic groups can help us better understand the trait–trait or trait–environment coordination and tradeoffs by considering different survival strategies.

We also tested the two-group segmentation against Grime’s model (Grime 1977, 1988). The Grime model describes three main evolutionary strategies of vascular plants based on the intensity of disturbance and stress. The survival of plants with a competitive (C) strategy adapted to low stress and low disturbance habitat is determined by their ability to compete for resources. Stress-tolerant (S) plants adapted to environments with high stress but low disturbance; their survival relies on endurance in low-resource conditions. Ruderal (R) species are adapted to low stress and high disturbance environments; they are characterized by a short life span and high seed production and are typified by annual herbs (Grime 1977). However, tree species can also be considered ruderal when their establishment relies on large forest gaps and openings after disturbance (i.e., pioneers) (Brzeziecki and Kienast 1994). If we apply Grime’s model to this study, the tolerators would span the S and C strategies as they are classified based on how woody plants compete for water and light, and how tolerant they are to water and shade stress. Therefore, the tolerator group can be considered a continuum of species between the S and C strategies in Grime’s framework. Avoiders may be considered R strategists as their existence is not determined by tolerance of drought or shade, and many of them are pioneers (see Avoider strategies above).

We tested the idea by comparing the C–S–R classification with major European tree species (Brzeziecki and Kienast 1994). Within 36 species in Brzeziecki and Kienast (1994), 30 were also grouped in this study (Figure 6). It turned out that all C (n = 6) and S (n = 3) species in Brzeziecki and Kienast (1994) were tolerators in this study, and R (n = 8) species were all avoiders (Figure 6). There were also strategies between the C–S–R extremes, including C–S (n = 5), S–R (n = 6) and C–S–R (n = 2). The two C–S–R species (Pinus sylvestris and Larix decidua), which were considered as pioneers (Brzeziecki and Kienast 1994), were avoiders in this study. All other species with strategies between extremes (C–S and S–R) were tolerators in this study. These results show a promising convergence of our two-group classification into the C–S–R framework where species with C and S strategies are likely tolerators, and those with R strategy are avoiders. However, we only considered light limitation and drought in this study, whereas the classification of Brzeziecki and Kienast (1994) was based on 21 variables including not only shade tolerance and drought resistance, but also reproduction and growth biology (size, life span, seed properties, wood density, etc.) and environmental gradients (temperature, frost, and soil pH, moisture, aeration and nitrate). Therefore, our two-group classification is more parsimonious and perhaps easier to apply in vegetation modeling.

Implications on correlations between shade tolerance, aridity and waterlogging tolerance

Although our dichotomy was originally developed to improve vegetation model parameterization, it illuminates several key ideas in vegetation ecology, such as correlations between shade tolerance, drought tolerance (i.e., aridity) and waterlogging tolerance. Tradeoffs were previously found between drought tolerance and shade tolerance, between drought tolerance and waterlogging tolerance, and between shade tolerance and waterlogging tolerance among woody plants in a seminal study (Niinemets and Valladares 2006). Here we reexamine such relationships under our two-group framework. This reexamination...
has several heuristic advantages. First, negative correlations between shade tolerance and aridity were found only among the tolerators, but not avoiders (Figure 3). Grubb (2016) indicated that the relationship between aridity and shade tolerance should not be considered as a tradeoff; there is no evolutionary pressure for species in arid habitats to be shade tolerant and the leaf area in such environments is low. We cannot determine if the negative correlation between aridity and shade tolerance is a tradeoff based on only the trait and environment data in this study; however, our study indicates that if such a tradeoff exists, the underlying mechanisms are likely to be found only in the tolerator group.

A second insight from the two-group framework is that negative correlations between waterlogging tolerance and aridity emerged only in angiosperm subgroups but not in gymnosperm subgroups (see Figure S9 and Table S1 available as Supplementary Data at Tree Physiology Online). Grubb (2016) indicated that the tradeoff between drought and waterlogging tolerance should be represented by a boundary line instead of a trend line inside a cloud of points. The cloud of points is triangularly distributed in the 2D space of waterlogging tolerance and aridity of angiosperms (see Figure S9a and c available as Supplementary Data at Tree Physiology Online), which is similar to data in Figure 1; the boundary line, which is similar to the Feature 1 space in Figure 1, defines the limit of plant tolerance of waterlogging and drought, beyond which is not attainable by plants. If we examine only angiosperm subgroups, the boundary line is largely represented by the deciduous avoiders group, while most tolerators are inside the ‘cloud’ (see Figure S9 available as Supplementary Data at Tree Physiology Online). Therefore, the tradeoff between waterlogging tolerance and aridity can be represented by both a boundary line and a trend line inside a cloud of points by different subgroups.

Thirdly, in contrast to Niinemets and Valladares (2006), we found no meaningful connection between waterlogging tolerance and shade tolerance under the two-group framework. One likely reason is that there is no significant correlation in any subgroup between waterlogging tolerance and shade tolerance (see Figure S9 and Table S1 available as Supplementary Data at Tree Physiology Online). More importantly, because tolerators accumulated in the low-waterlogging tolerance domain and avoiders in the low-shade tolerance domain, the boundary line in the shade tolerance–waterlogging tolerance space is represented by extreme shade-tolerant tolerators, extreme waterlogging-tolerant avoiders and a few ‘outlier’ species located away from main axes of two groups (Figure 5 and Figure S9 available as Supplementary Data at Tree Physiology Online). Survival strategies change abruptly along the boundary line from tolerator species (tolerate shade but not waterlogging) to avoiders (cannot tolerate shade but tolerate waterlogging); the combination of more than one strategy confounds the relationship between the two metrics.

Fourth, based on the analysis above, the relationships between shade tolerance, aridity and waterlogging tolerance may no longer be treated as a tradeoff surface, where the increased performance at one dimension may worsen the performance in other dimensions. Instead, there are two clearly separated clusters in the shade tolerance–aridity–waterlogging tolerance space (Figure 5a) representing the tolerator and avoider groups with many contrasting surviving strategies.

**Predictions of species composition**

The heuristic two-group framework indicated multiple possibilities in the shift of compositions of avoiders and tolerators, and hence the changes of P50 and shade tolerance to a drier climate (Figure 7). Under future climate conditions with a greater drought frequency and severity (Allen et al. 2015), shifts in environmental conditions may leave behind only species whose functional traits allow them to persist in systems where aridity increases (Keddy 1992, Brenes-Arguedas et al. 2013, Zhang et al. 2018). To test what would occur in an adaptive landscape when aridity increases, we assumed that the aridity increase would act as an environmental filter, shifting species composition of a community to a new state based on plants’ functional traits (Figure 7). While mean wood density should increase with increasing habitat aridity (Figure 7c), the P50 and shade tolerance of ecosystems may change in four possible ways (Figure 7a and b). First, when species composition shifts were mainly within the tolerator group, we would expect a more negative mean P50 (Figure 7a) and a reduced shade tolerance (Figure 7b) for the community. Second, if species composition shifts were mainly within the avoider group, we would expect little change in P50 and shade tolerance for the community (Figure 7a and b). Third, if the majority of shifts in species composition were from avoiders to tolerators, we would expect a more negative P50 (Figure 7a) and increased shade tolerance (Figure 7b). Fourth, if the majority of shifts in species composition were from tolerators to avoiders, we would see less negative P50 values (Figure 7a) and reduced shade tolerances (Figure 7b) for the community. The fourth scenario could be counterintuitive as more negative P50 is normally expected in a drier environment (Blackman et al. 2012, 2014). However, the situation of less negative P50 in a drier climate could happen. For example, during the worst drought event in recorded history in Texas, USA, it was the species with the most negative P50 (i.e., tolerators) that suffered the most mortality, including *Juniperus ashei* (branch P50 < −10 MPa, mortality rate 27%) and *Diospyros texana* (−7 MPa, 18%) (Johnson et al. 2018). In contrast, two drought-avoiding species, benefited by their deep roots, had less negative P50 but low mortality; these were *Quercus fusiformis* (−2 MPa, 4%) and *Prosopis glandulosa* (−4 MPa, 0%) (Johnson et al. 2018). Such a drought-induced dieback of tolerators may change species composition towards more avoiders and drive the mean community P50 to less negative; exactly as the fourth scenario indicates. Similar analyses of
other historic droughts might improve predictions of responses to future droughts.

Conclusion
We established a classification scheme and separated temperate woody plants in the Northern Hemisphere into two groups. The two groups—tolerators and avoiders—represented two distinct axes in the 3D P50–shade tolerance–habitat aridity space with contrasting shade and drought strategies. Tolerator species varied along an axis from high desiccation resistance and low shade tolerance in arid habitats to low desiccation resistance and high shade tolerance in moist habitats; tolerators with higher desiccation resistance survived in more arid habitats and those with higher shade tolerance survived in more humid habitats. In contrast, the avoider group consisted of species of similar low desiccation resistance and similar low shade tolerance along an axis from low to high habitat aridity; thus avoider species vary little among habitats in terms of desiccation resistance and shade tolerance. The two orthogonal axes revealed clear connections between plant traits and plant functions in multidimensional trait–trait and trait–environment dimensions. Moreover, the two orthogonal axes also existed in other dimensions with wood density (Figure 4) or waterlogging tolerance (Figure 5) beyond the P50–shade tolerance–habitat aridity space. The two groups provide a promising framework for studying plant traits and we revisited some key theories in vegetation ecology in light of these insights. Such reevaluations revealed that some ecological theories were better supported in one group than the other, which could be related to different survival strategies of two groups. The two orthogonal axes can also be used in global vegetation models to predict possible changes in species composition and mean traits of a community when habitat aridity changes (Figure 7).

Supplementary Data
Supplementary data for this article are available at Tree Physiology Online.

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Conflict of interest
None declared.

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