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REPORT

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Turgor loss point predicts survival responses to experimental and natural drought in tropical tree seedlings

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Abstract

Identifying key traits that can serve as proxies for species drought resistance is crucial for predicting and mitigating the effects of climate change in diverse plant communities. Turgor loss point (π_{tlp}) is a recently emerged trait that has been linked to species distributions across gradients of water availability. However, a direct relationship between π_{tlp} and species ability to survive drought has yet to be established for woody species. Using a manipulative field experiment to quantify species drought resistance (i.e., their survival response to drought), combined with measurements of π_{tlp} for 16 tree species, we show a negative relationship between π_{tlp} and seedling drought resistance. Using long-term forest plot data, we also show that π_{tlp} predicts seedling survival responses to a severe El Niño-related drought, although additional factors are clearly also important. Our study demonstrates that species with lower π_{tlp} exhibit higher survival under both experimental and natural drought. These results provide a missing cornerstone in the assessment of the traits underlying drought resistance in woody species and strengthen π_{tlp} as a proxy for evaluating which species will lose or win under projections of exacerbating drought regimes.

KEYWORDS

Barro Colorado Island, climate change, dehydration tolerance, drought strategy, El Niño, functional traits, leaf turgor loss point, Panama, plant–water relations, tree mortality

INTRODUCTION

Rainfall is becoming increasingly variable and unpredictable in many locations around the world, with pervasive consequences for biodiversity, ecosystem services, and climate–vegetation feedbacks (IPCC, 2014; Schwalm et al., 2017). Over the last few decades, widespread plant mortality due to an increase in drought intensity and frequency has been observed globally in forests and grasslands (Allen et al., 2010; Moran et al., 2014). Mortality

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induced by drought varies widely among species within and among communities (Meir et al., 2009; Tilman & Elhaddi, 1992). To predict which species will be winners or losers under changing drought regimes, and to project ecosystem consequences, it is crucial to understand the mechanisms contributing to differential drought resistance of plant species (reviewed in O'Brien et al., 2017). Despite decades of studies on plant–water relations, mechanisms related to species differential drought resistance remain elusive (O'Brien et al., 2017; Powers et al., 2020). This is especially acute for tropical forests, which harbor enormous tree diversity and are globally important carbon sinks (Ferreira et al., 2018). Under global change, increased mortality induced by extreme drought events such as El Niño, is expected to accelerate biomass loss and cause changes to forest structure and composition in tropical forests (Rowland et al., 2015; van der Sande et al., 2016).

Turgor loss point (π_{tlp}, MPa), the leaf water potential at which leaf wilting occurs (Bartlett, Scoffoni, Ardy, et al., 2012), has emerged as a promising physiological trait that can be used as a proxy for plant drought resistance (Bartlett, Scoffoni, & Sack, 2012; Sun et al., 2020). Turgor loss point is related to a suite of physiological mechanisms relevant for maintaining critical functions under drought, including the water potential at stomatal closure and the vulnerability to xylem embolism (Bartlett et al., 2016). The importance of π_{tlp} in plant–water relations has long been recognized (e.g., Tyree & Hammel, 1972). However, only recently has a relatively fast method to measure π_{tlp} been developed (Bartlett, Scoffoni, Ardy, et al., 2012), resulting in a surge of studies that have assessed π_{tlp} across multiple species (e.g., Bartlett, Scoffoni, & Sack, 2012; Kunert et al., 2021; Maréchaux et al., 2015; McFadden et al., 2019; McGregor et al., 2021; Sun et al., 2020; Zhu et al., 2018). Most of these studies have related π_{tlp} to species distributions across natural moisture gradients, including at local, regional and biome scales. In woody plants, species with lower π_{tlp} have been generally associated with drier sites (Baltzer et al., 2008; Bartlett, Scoffoni, & Sack, 2012; Kunert et al., 2021; Maréchaux et al., 2015; McFadden et al., 2019; Mitchell et al., 2008; Rosas & Mencuccini, 2019; Zhu et al., 2018). π_{tlp} has therefore frequently been explicitly or implicitly assumed to determine species distributions by being negatively related to species drought resistance, that is, their ability to withstand periods of low water availability (*ensu* Larcher, 2003). However, the direct relation of π_{tlp} to differential survival of woody species under drought conditions has, to our knowledge, only been addressed in one study, which found no relation (Powers et al., 2020). Moreover, studies on π_{tlp} have focused on adult trees (but please refer to Baltzer et al., 2008), whereas seedlings, which are a bottleneck in the life cycle of trees (Harper, 1977) and determine future forest composition, may respond differently to stressors.

Survival of plants under drought conditions in the field, as well as species distribution across moisture gradients, are not only shaped by water availability, but also by other abiotic and biotic factors, namely light, nutrients, herbivore and pathogen pressure, competition, as well as dispersal limitation (Engelbrecht et al., 2005). Because these factors may modulate or even override direct effects of drought in driving species' survival and distributions, experiments are required to isolate the direct effects of reduced water availability on species performance from other factors that determine drought survival (Engelbrecht & Kursar, 2003). To be able to rigorously test the relevance of π_{tlp} for plant survival responses to drought, we need to directly link π_{tlp} to experimental multispecies assessments of comparative whole-plant drought resistance, based on survival responses. However, such studies are still lacking (reviewed in Delzon, 2015). To our knowledge, the only study explicitly linking π_{tlp} to comparative drought performance responses across multiple species was conducted on herbaceous perennials (Sun et al., 2020). They found the opposite of what has been assumed for woody species: herbaceous species with higher π_{tlp} exhibited higher (rather than lower) drought survival. This highlights the need to directly test the relationship between π_{tlp} and drought performance in different life forms and/or ecosystems. At the same time, we need to evaluate if π_{tlp} is a useful proxy for species survival responses to natural drought conditions, such as those associated with El Niño Southern Oscillation (Powers et al., 2020).

Here, we explicitly tested if π_{tlp} of tropical woody species is negatively related to seedling drought resistance by directly linking π_{tlp} to seedling survival under dry, relative to irrigated, conditions in a common garden soil moisture manipulation experiment in the forest understory in central Panama. Using long-term seedling survival censuses across multiple forests, we also tested whether π_{tlp} is related to decreased seedling survival in response to an extreme El Niño event that caused severe drought conditions in the region (Burton et al., 2018; Spinoni et al., 2019). We hypothesized that tree species with lower (i.e., more negative) π_{tlp} exhibit higher experimentally assessed drought resistance (as determined by seedling survival in dry vs. irrigated treatments) and smaller reductions in seedling survival in response to El Niño-related drought.

METHODS

Study species and site

We selected 16 tree species from lowland tropical forests for which seedling comparative drought resistance in terms of survival has been experimentally assessed (please refer to the following paragraphs) and that spanned a wide range of drought resistance, distribution, and families (Appendix S2: Table S1). Seeds were collected in the Panama Canal watershed, including the Barro Colorado Nature Monument (BCNM, 9°9″ N, 79°51″ W).

Leaf turgor loss point (π_{tlp}, MPa) was measured on seedlings (5–28 per species, depending on seed/seedling availability; Appendix S2: Table S1) grown in a shaded screenhouse in central Panama at 5%–10% light under fully watered conditions. Seedlings were ~1 year old and 20–40 cm tall at the time of measurements, comparable with the size at the beginning of their first dry season and the drought experiment (please refer to the following paragraphs). We assessed π_{tlp} following the method of Bartlett, Scoffoni, Ardy, et al. (2012) from measurements of leaf osmotic potential at leaf full turgor (π_o, MPa). In brief, seedlings were rehydrated overnight, and osmotic potential was measured with an osmometer (Vapro 5600; Wescor, Logan, UT, USA) on one mature leaf per individual after freezing in liquid nitrogen. A tight relation between π_{tlp} and π_o holds across life forms, from woody species, including tropical trees, to perennial forbs and grasses (reviewed in Sun et al., 2020).

We analyzed the relation of species' π_{tlp} with their experimentally assessed drought resistance, and their survival response to a strong El Niño drought event. To evaluate if relations between π_{tlp} and species distributions with respect to moisture that have previously been established (e.g., Kunert et al., 2021) also hold for our species set and for the seedling stage, we additionally related π_{tlp} with species abundance at the seedling and adult stages in dry relative to wet habitats in a Forest Dynamics Plot in the BCNM (please refer to Appendix S1).

Seedling drought resistance was based on experimental assessments of seedling survival in dry conditions (covered with rainout shelters) relative to irrigated, wet conditions in the understory of a second growth forest in central Panama during the dry season (for experimental details please refer to Engelbrecht et al., 2007 and Appendix S1). Drought resistance (DR) was assessed as the response ratio of survival of seedlings in dry, relative to wet, plots ($\mathrm{DR} = \log[\mathrm{survival}_{\mathrm{dry}}/\mathrm{survival}_{\mathrm{wet}}]$; please refer to Hedges et al., 1999).

Survival responses of naturally established seedlings to a strong El Niño event in 2015–2016, which resulted in significant precipitation decrease and a more severe dry season in central Panama (Browne et al., 2021; Burton et al., 2018; Spinoni et al., 2019), were analyzed based on annual seedling censuses from 2014 to 2020 in eight 1-ha forest plots across the Isthmus of Panama (Figure 1). Data were available for 425 individuals from 15 of the study species. For more detailed methods please refer to Appendix S1.

Statistical analyses

We tested for differences of π_{tlp} among species using the Kruskal-Wallis with post-hoc least significant difference (LSD) tests. We used linear models to test for a relationship of species mean π_{tlp} with their DR as well as with their abundance in dry and wet habitats (please refer to Appendix S1). Models were weighted based on the variance of π_{tlp} within species, to account for differences in replication number in π_{tlp} among species and to improve heteroscedasticity (weighted least squares model). All models were run for all species as well as for evergreen species only and yielded equivalent results (Appendix S2: Table S2).

To model the relationship between π_{tlp} and seedling survival response to drought during the 2015–2016 El Niño compared with non-El Niño years, we used a hierarchical Bayesian logistic regression controlling for species, plot, and size effects. For model details please refer to Appendix S1.

All analyses were conducted in R (version R 4.0.2, R Core team, 2020).

RESULTS

Leaf water potential at turgor loss point (π_{tlp}) differed significantly among the study species (ANOVA, $F = 63.38$, $p < 0.001$; Figure 2a), with species' mean π_{tlp} showing a wide range from −2.17 to −1.46 MPa. As expected, species' experimentally assessed seedling DR was significantly negatively related to π_{tlp} (Figure 2b). Specifically, species with lower (i.e., more negative) π_{tlp} were more drought resistant.

Consistent with the experimental results, survival responses of naturally established seedlings to the 2015–2016 El Niño drought were related to species' π_{tlp} (Figure 2c). Although species with the lowest π_{tlp} exhibited an estimated 4.2% increase in survival during the El Niño drought compared with baseline non-El Niño years (95% credible interval: −1.7% to 10.6%), the species with the highest (most positive) π_{tlp} exhibited an estimated −3.1% decrease in probability of survival (CI: −12.6% to 3.2%). However, wide credible intervals indicate relatively high levels of uncertainty in the relationship between El Niño response and π_{tlp}, in addition to high variability in the relationship between π_{tlp} and survival rates across census years (Appendix S2: Figure S1).

Seedling local distribution across moisture gradients was significantly related to π_{tlp}, with species relatively

FIGURE 1 Wilting of tropical tree seedlings in the dry season. Barro Colorado Nature Monument, Panama. Photograph credit: Christian Ziegler

more abundant in drier habitats showing lower π_{tlp} (Appendix S2: Figure S2A). A similar trend was seen for adult trees, but the relationship was only statistically significant for evergreen species (i.e., when deciduous species were excluded; Appendix S2: Figure S2B, Table S2).

DISCUSSION

We showed for the first time in woody species that π_{tlp} is directly related to species survival response to drought, that is, whole-plant DR. By experimentally assessing DR through comparisons of survival under dry versus wet treatments in the field, we were able to isolate the effect of low water availability from other factors that may influence plant survival under dry conditions (e.g., differences in soil nutrients, light availability; Engelbrecht et al., 2005) and clearly link species drought responses to π_{tlp}. The experimental approach further assured that all species were exposed to the same drought levels, such that survival responses can be compared among species, and that drought levels are realistic in the field. Our approach also avoided the pitfalls of drought experiments in pots, for example, that water depletion rates depend on plant size (Comita & Engelbrecht, 2014). Multispecies data sets, such as the one described here, remain surprisingly scarce across ecosystems worldwide (reviewed in O'Brien et al., 2017 for woody species), but are crucial to rigorously establish the role of traits for plant performance and their responses to environmental conditions (Shipley et al., 2016). Our study therefore adds a missing link in the effort to identify traits that are suitable proxies for tree species response to drought. Our results substantially solidify the basis for using π_{tlp} in studies of the consequences of global change for the composition, diversity, ecosystem services and plant–atmosphere interactions in tropical forests and beyond.

The relation between π_{tlp} and experimentally assessed DR in the study species was consistent with the survival response of naturally established seedlings to the extreme natural drought imposed by a recent strong El Niño event; drought-sensitive species with higher π_{tlp} tended to experience higher relative decreases in survival compared with drought-resistant species with lower π_{tlp}. The relatively high levels of uncertainty in the relationship between El Niño response and π_{tlp}, however, suggest that other traits and/or other factors besides drought also contribute to seedling mortality. For instance, increased solar irradiance during the El Niño event may have led to the increased survival observed in the more drought-resistant species (please refer to Wright & Calderon, 2006). Using π_{tlp} as a proxy for DR can help us to understand and project species differential responses to drought under current and future climate conditions.

Consistent with these results, we documented for the first time at the seedling stage, that π_{tlp} is related to

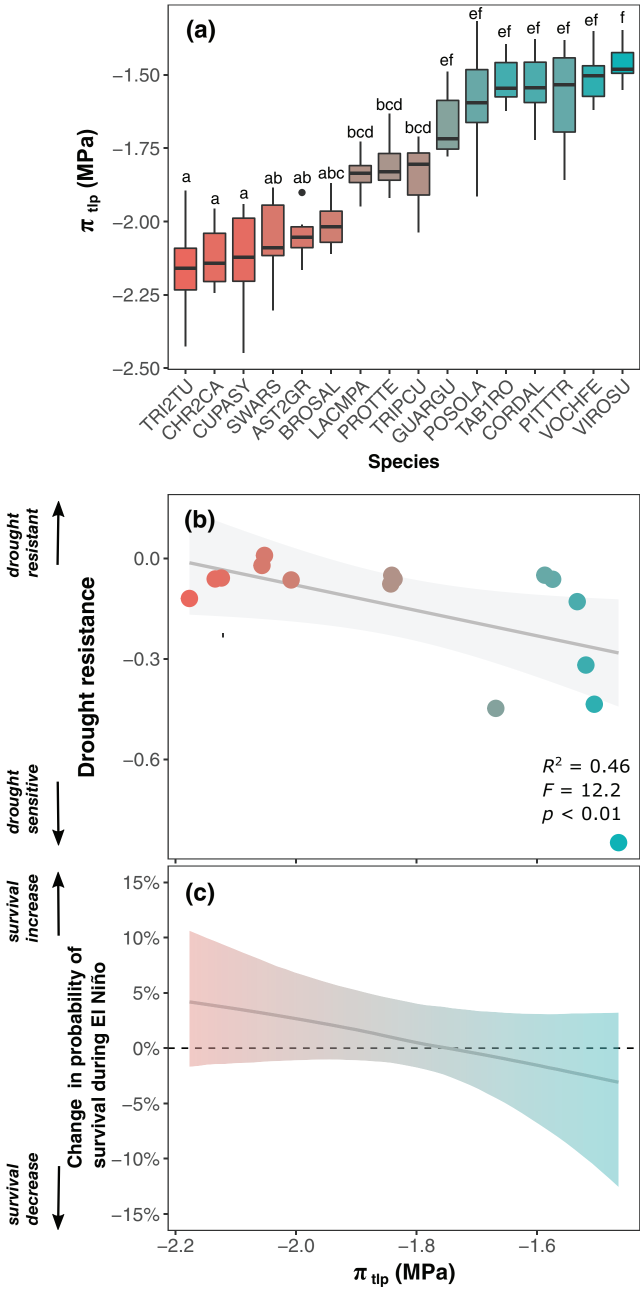

FIGURE 2 (a) Turgor loss point (π_{tlp}) of the 16 study species, (b) relation between species' turgor loss point and their experimentally assessed drought resistance (DR), that is, their response ratio survival dry/irrigated, and (c) relation between species' turgor loss point and their survival response to the 2015–2016 El Niño drought. In (a) different letters at the top of bars indicate significant ($p < 0.05$) differences based on Kruskal-Wallis and post-hoc least significant difference (LSD) test; $N = 5$–28 individuals per species. For species codes please refer to Appendix S2: Table S1. Color coding of bars represents the gradient from low (red) to high (blue) π_{tlp} mean values per species. In (b) linear model R^2, F, and p-values are shown. $N = 16$ (the relation was still significant after removal of the outlier, $R^2 = 0.512$, $p < 0.01$). In (c) the % predicted change in the probability of survival during the 2015–2016 El Niño relative to non-El Niño years is given. The shaded region indicates the 95% credible interval, and the dashed line indicates no change in survival

distribution across local moisture gradients, with seedlings of species with lower π_{tlp} being relatively more abundant in drier habitats. Previous studies at our study site and elsewhere (Kunert et al., 2021; McFadden et al., 2019) have reported significant relationships between π_{tlp} and species adult distributions across local moisture gradients. For our focal species, the relationship between species distributions and π_{tlp} at the adult stage was similar to, but weaker than, at the seedling stage, perhaps because several of our focal species are deciduous (please refer to Kunert et al., 2021). Together, these results support the notion that differential DR of seedlings has pervasive consequences for species abundance and distribution across moisture gradients at the juvenile as well as adult stage (Engelbrecht et al., 2007).

A low (more negative) π_{tlp} can lead to high plant DR as a mechanism of a dehydration tolerance strategy by allowing the leaf to remain turgid despite decreasing leaf water potentials, and to thereby maintain photosynthesis, water transport, transpiration, and growth. Conversely, a high (less negative) π_{tlp} can also improve DR as a mechanism of a dehydration avoidance strategy by leading to early stomatal closure, and therefore enabling plants to maintain high water potentials and hydration, even under declining soil water status. Our finding that π_{tlp} decreases with increasing DR underscores the role of π_{tlp} as a mechanism of dehydration tolerance in woody species. This is consistent with the relation of π_{tlp} to other relevant functional traits, for example, water potential at stomatal closure and vulnerability to xylem embolism (Bartlett et al., 2016; Delzon, 2015), its relation to growth responses to drought (McGregor et al., 2021), as well as with the now widely reported decrease of π_{tlp} with species association to drier sites in woody plants (Baltzer et al., 2008; Bartlett, Scoffoni, & Sack, 2012; Kunert et al., 2021; Maréchaux et al., 2015; McFadden et al., 2019; Mitchell et al., 2008; Zhu et al., 2018). However, the opposite relation between π_{tlp} and DR of survival has emerged in herbaceous temperate plants (including both grasses and forbs), indicating that in these life forms π_{tlp} acts as a mechanism of dehydration avoidance rather than tolerance (Sun et al., 2020). Interestingly, clear links of π_{tlp} to species local and regional distribution have been found for evergreen, but not for deciduous, tree species in a recent study in the same study area in central Panama (Kunert et al., 2021). Similarly, the only available study linking π_{tlp} to tree mortality during a natural drought (also the 2015/2016 El Niño), also found no relation for deciduous species (Powers et al., 2020). The discrepancies among life forms and between trees with different leaf phenology clearly indicate that the mechanistic role of π_{tlp} in the interplay of traits that determine how plants respond to drought can differ between different ecosystems with different functional, ecological, or phylogenetic constraints. Similarly, the relative importance of the direct role of water availability versus other factors determining species mortality, distribution, diversity, and ecosystem functioning across spatial or temporal moisture gradients varies between systems (Baltzer et al., 2008; Comita & Engelbrecht, 2014). Our study established for the first time a direct relation between π_{tlp} and survival under experimental drought in woody species, providing a missing cornerstone in the assessment of the traits underlying DR. Similar studies will be needed that rigorously test links between plant performance responses to environmental factors, and traits in different life forms and ecosystems. These links are crucial in the quest for traits that can serve as reliable and practical proxies for projecting which species will lose or win under exacerbating drought regimes with global change.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Álvarez-Cansino et al., 2022) are available in Dryad athttps://doi.org/10.5061/dryad.crjdfn35v. Code (Browne, 2021) is available in Figshare athttps://doi.org/10.6084/m9.figshare.17695034.v1.

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