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Letter

Can leaf drought tolerance predict species abundance and its changes in tropical-subtropical forests?

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Climate change has resulted in an increase in drought severity in the species-rich tropical and subtropical forests of southern China. Exploring the spatiotemporal relationship between drought-tolerance trait and tree abundance provides a means to elucidate the impact of droughts on community assembly and dynamics. In this study, we measured the leaf turgor loss point (π_{tlp}) for 399 tree species from three tropical forest plots and three subtropical forest plots. The plot area was 1 ha and tree abundance was calculated as total basal area per hectare according to the nearest community census data. The first aim of this study was to explore π_{tlp} abundance relationships in the six plots across a range of precipitation seasonality. Additionally, three of the six plots (two tropical forests and one subtropical forest) had consecutive community censuses data (12–22 years) and the mortality ratios and abundance year slope of tree species were analyzed. The second aim was to examine whether π_{tlp} is a predictor of tree mortality and abundance changes. Our results showed that tree species with lower (more negative) π_{tlp} were more abundant in the tropical forests with relative high seasonality. However, π_{tlp} was not related to tree abundance in the subtropical forests with low seasonality. Moreover, π_{tlp} was not a good predictor of tree mortality and abundance changes in both humid and dry forests. This study reveals the restricted role of π_{tlp} in predicting the response of forests to increasing droughts under climate change.

***Keywords*:** basal area, climate change, drought, mortality, precipitation seasonality, turgor loss point.

Introduction

Functional traits reflect the ecological strategies of plant species and are thus associated with their commonness or rarity at a given site (McGill et al. 2006, Umaña et al. 2015). Exploring the trait abundance relationships within plant communities has long been a core aspect of trait-based ecology (Cornwell and Ackerly 2010, R.H. Li et al. 2021). Shifts in trait–abundance relationships across plant communities along an environmental gradient could reveal environmental filtering processes influencing species abundance (Lebrija-Trejos et al. 2010, Aiba et al. 2020). Based on the long-term community census of permanent forest plots, such trait-based approaches provide a promising strategy to explain the effects of climate change on species abundance changes (Bittencourt et al. 2020), thereby contributing to modeling the fates of forests under future climates (Katabuchi et al. 2017, Aguirre-Gutiérrez et al. 2019).

Several easily measured economic traits (e.g., specific leaf area and wood density) can predict the growth and defense performance of plant species, and have been widely used to examine trait–abundance relationships in various plant communities (Aiba et al. 2020, Sporbert et al. 2021). However, these economic traits are weak predictors of species abundance in many studies, partly due to the fact that a trait with little context shows weak predictive power (e.g., to predict species abundance in a drought-prone environment using a trait unrelated to drought tolerance; Yang et al. 2018).

In many forests, drought exerts a profound effect on community assembly and tree dynamics (Anderegg et al. 2013, Choat et al. 2018, Berdugo et al. 2020). In addition, previous studies have shown that hydraulic failure (loss of xylem hydraulic function due to cavitation) is the primary mechanism underlying drought-induced tree mortality (Rowland et al. 2015, Brodribb et al. 2020). Therefore, hydraulic safety-related traits (e.g., cavitation resistance and hydraulic safety margin) are good proxies for mortality rate and are thus crucial for predicting tree abundance dynamics with increasing extreme droughts (Anderegg et al. 2016, Powers et al. 2020). Nevertheless, measurements of these hydraulic traits are time-consuming and require large amounts of plant materials, which restricts their application in species-rich forests (Kunert et al. 2021).

The leaf turgor loss point (π_{tlp}) defines the water potential at leaf wilting, and lower (more negative) π_{tlp} indicates that plant species could maintain cell turgor pressure and thus sustain hydraulic and photosynthetic functions under lower water availability (Bartlett et al. 2012*a*). Several studies have found that π_{tlp} is closely associated with cavitation resistance (Bartlett et al. 2016), stomatal controlling capacity (Meinzer et al. 2016) and stem sap-flux response to drought (Maréchaux et al. 2018). Particularly, π_{tlp} can be rapidly and easily determined (Bartlett et al. 2012*b*), and is therefore an important parameter in the assessment of plants' drought tolerance in species-rich communities. Several studies have found that π_{tlp} is associated with regional tree abundance in Amazonian forests (Maréchaux et al. 2015), and is a good predictor of the drought-induced mortality rates of tropical tree seedlings (Álvarez-Cansino et al. 2022) and temperate herbaceous species (Stears et al. 2022).

Tropical-subtropical forests in southern China are biodiversity hotspots that play a major role in the global carbon cycle (Yu et al. 2014). Particularly, karst landform (limestone substance) distributes extensively in this region; forests growing on karst experience frequent droughts and thus represent a distinct community structure and preserve many endemic species (Geekiyanage et al. 2019). Under global change, the climate of this region has become hotter and drier in recent decades, resulting in an increase of frequency of extreme droughts in many areas (Qiu 2010, Dai 2013), which is the main environmental driver of alterations in forest composition and ecosystem functioning (Zhou et al. 2014). Previous studies on tree hydraulics have found that regional tropical and subtropical forests differed in hydraulic risks, with tropical tree species operating a narrower hydraulic safety margin compared with subtropical forests (Zhu et al. 2018, 2019, Tan et al. 2020; see Figure S1 available as Supplementary data at *Tree Physiology* Online). Therefore, it would be novel to clarify the relationship between π_{tlp} and abundance and its dynamics across tropical-subtropical forests with contrasting water environments, for a better understanding of forests' responses to drought.

Here, we measured the π_{tlp} of 399 tree species from six 1-ha permanent plots in tropical-subtropical forests, with three of them having long-term community-censuses data. We first analyzed the spatial π_{tlp}–abundance relationships across the six plots with a range of water environments. Subsequently, we explored the temporal patterns of π_{tlp}–abundance relationships during the census periods in the three plots and analyzed the relationships between π_{tlp} and tree abundance changes and mortality ratio (MR). The main objective of this study was to examine whether π_{tlp} can be used as a proxy for predicting tree abundance and its dynamics in tropical-subtropical forests subject to increasing droughts.

Plots and methods

The present study was conducted in six 1-ha (100 m × 100 m) permanent plots in the tropical and subtropical forests of southern China (Figure 1, more details are shown in Table S1 available as Supplementary data at *Tree Physiology* Online). All plots were established in nature reserves without human disturbances. These sites are strongly influenced by a monsoon climate, which results in distinct wet and dry seasons. The three tropical forests exhibited stronger precipitation seasonality than the three subtropical forests (Figure 1). In recent decades, extreme drought episodes have been frequently reported in the tropical forests of southern Yunnan (Figure S2 available as Supplementary data at *Tree Physiology* Online). Consequently, extensive canopy diebacks have been observed (Tan et al. 2020). Despite the clear tendency of climate drying in subtropical regions, subtropical forests are currently hydrologically stable (Song et al. 2017, Zhu et al. 2019).

In each plot, 26–102 tree species were selected, accounting for >90% of total individuals (except for 70% in BN1 (Tropical seasonal rain forest in the ravine area of Xishuangbanna National Nature Reserve; Table S1 available as Supplementary data at *Tree Physiology* Online). Species abundance was estimated as the total basal area in each 1-ha plot, which was calculated as the sum of the cross-sectional areas at breast height of all individuals for that species (Li et al. 2015). The basal area considers both the number and the size of the individuals of tree species and thus reflect the overall abundance status in the plant community (Potvin and Gotelli 2008). For the three plots with long-term community censuses data (i.e., BN1; BN2 (Tropical dry forest in the karst area of Xishuangbanna National Nature Reserve) and DH (subtropical monsoon evergreen broadleaved forest in the Dinghushan National Nature Reserve)), we examined species abundance dynamics using a previously described calculation method (Li et al. 2015; methods available as Supplementary data at *Tree Physiology* Online). For each studied species, we used simple linear regression to

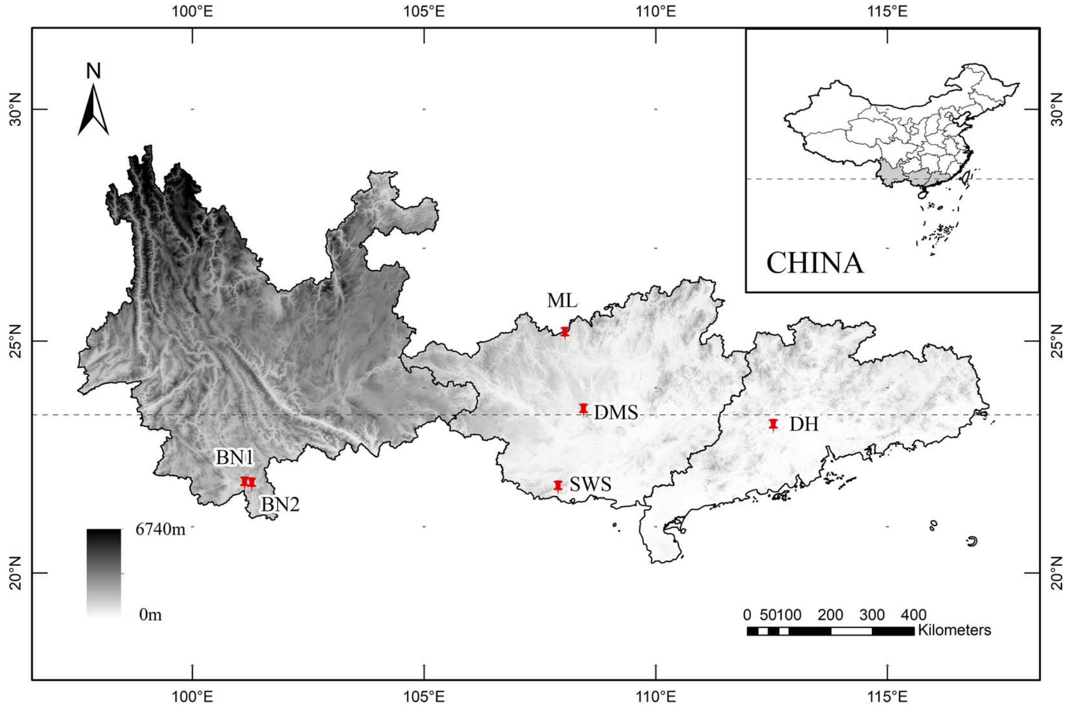

Figure 1. Locations of the six permanent forest plots. BN1, tropical seasonal rain forest in the ravine area of Xishuangbanna National Nature Reserve; BN2, tropical dry forest in the karst area of Xishuangbanna National Nature Reserve; SWS, tropical seasonal rain forest in the Shiwandashan National Nature Reserve; DH, subtropical monsoon evergreen broadleaved forest in the Dinghushan National Nature Reserve; DMS, subtropical montane evergreen broadleaved forest in the Daminshan National Nature Reserve; ML, subtropical mixed evergreen and deciduous broadleaved forest in the Mulun National Nature Reserve. The forest types are recognized according to community structure and composition. Eight-time community censuses have been conducted in BN1 and BN2 during 2004–15, and six times in DH during 1994–2015. Plots in SWS, DMS and ML were established in 2017 without long-term community census data. The dotted line indicates the tropic of cancer.

analyze the response of abundance to the year. The coefficient of regression slope was referred to as 'abundance–year slope', which indicates temporal changes of abundance (Figure S3 available as Supplementary data at *Tree Physiology* Online). Additionally, we calculated the MR (%) during the monitoring period using the following equation:

$$\mathrm{MR} = 100 \times (N_{\mathrm{i}} - N_{\mathrm{s}})\,/N_{\mathrm{i}},$$

where N_{i} is the initial number of individuals in the first survey, and N_{s} is the number of survivors in the last survey.

To determine π_{tlp}, we sampled sun-exposed leaves from three to five healthy and mature individuals per species, and their size was at the average diameter at breast height of that species in the plot. In this study, we used species-level mean value because several studies have reported that intraspecific variations of π_{tlp} was small (Zhu et al. 2019, Kunert et al. 2021, Liu et al. 2022). For tree species from BN1, BN2, DH and ML (Subtropical mixed evergreen and deciduous broadleaved forest in the Mulun National Nature Reserve), π_{tlp} was measured using the traditional pressure–volume curve approach (Zhu et al. 2019). For the tree species from SWS (Tropical seasonal rain forest in the Shiwandashan National Nature Reserve) and DMS (Subtropical montane evergreen broadleaved forest in the Daminshan National Nature Reserve), we used the osmometer measurements technique to determine π_{tlp} (Bartlett et al. 2012*b*, Methods available as Supplementary data at *Tree Physiology* Online). A previous study has proven that π_{tlp} did not differ significantly between the two methods in these tropical-subtropical tree species (Zhu et al. 2018).

Prior to all data analyses, all variables were $\log_{10}$-transformed to improve normal distribution and homogeneity of variance. For the six plots, Pearson correlation analysis was used to examine the relationships between π_{tlp} and abundance of the nearest survey. For the three plots (i.e., BN1, BN2 and DH) with community census data, we analyzed π_{tlp}–abundance relationships using Pearson correlation analysis in each census year, and then used simple linear regression to examine the changes of π_{tlp}–abundance relationship coefficients (represent the strength of the relationships) over year. We conducted a weighted least-squares linear regression analysis to explore the relationship between π_{tlp} and tree abundance changes and MR. All analyses were performed in R 4.1.1 statistical software (R Core Team 2021).

Significant π_{tlp}–abundance relationship in tropical forests with high seasonality

The mean π_{tlp} ranged from −1.58 MPa in DH to −2.24 MPa in BN2 (Figure S1 available as Supplementary data at *Tree Physiology* Online). Our results showed that significant π_{tlp}–abundance

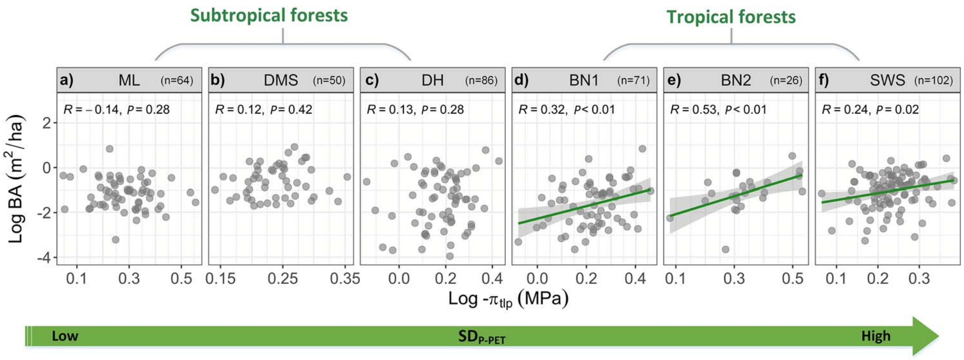

Figure 2. Relationships between leaf turgor loss point ($\pi_{\rm tlp}$) and tree abundance in the six 1-ha plots. Tree abundance is calculated as the total basal area in the plot according to the nearest community census data. Each point represents one species. Plot codes are shown in Figure 1. The standard deviation of monthly P - PET (the difference between precipitation and potential evapotranspiration) during a year was calculated to qualify the degree of seasonality (Table S1 available as Supplementary data at *Tree Physiology* Online).

relationships were only found in tropical forests that suffered from high seasonality and hydraulic risk (Figure 2). Because tree species with lower $\pi_{\rm tlp}$ were more drought-resistant, they thus contributed to a higher abundance (competitive advantages) in the tropical forests. Additionally, $\pi_{\rm tlp}$ has also been found to be a predictor of habitat preference in tropical forest plots, with lower-$\pi_{\rm tlp}$ tree species occurring in relatively drier habitats (Kunert et al. 2021). Taken together, $\pi_{\rm tlp}$ represents an important parameter for investigating drought-driven community assembly in tropical forests.

In a previous study, Maréchaux et al. (2015) found that lower-$\pi_{\rm tlp}$ tree species are currently rare in Amazonian tropical forests but are likely to gain abundance in a more drought-prone future, indicating a profound change of forest composition. Contrary to this finding, our results showed that lower-$\pi_{\rm tlp}$ species are more abundant in the three tropical forests and would become more dominant with climate drying (e.g., BN1). This may be because the high hydraulic risks in the north tropical forests (e.g., BN1 and BN2) exert an environmental selection pressure for highly drought-toleran tree species. From this perspective, this study supports Hubbell (2013) who claimed that conservation efforts should focus more on rare tree species (with low drought tolerance) in tropical forests.

Unlike tropical forests, we found no significant $\pi_{\rm tlp}$–abundance relationships in the three subtropical forests with low seasonality and hydraulic risks (Figure 2 and Figure S1 available as Supplementary data at *Tree Physiology* Online). Moreover, we analyzed the $\pi_{\rm tlp}$–abundance relationship by separating evergreen and deciduous species in ML, and the results showed that there was no significant relationship in both functional groups (Figure S4 available as Supplementary data at *Tree Physiology* Online). Nevertheless, several previous studies have reported that high abundance is associated with lower specific leaf area and high woody density in subtropical evergreen broadleaved forests in southern China (Yan et al. 2013, Wang et al. 2021). In another study carried at DH, R.H. Li et al. (2021) also found tree species with ‘slow-return’ economics traits (e.g., low nutrient concentrations) are more abundant, because such ‘conservative’ strategy is beneficial in the mature subtropical forests where nutrient and light availability (rather than water availability) are limited.

$\pi_{\rm tlp}$ is not related to tree MR and abundance change at the community level

In the tropical seasonal rain forests in BN1, the strength of $\pi_{\rm tlp}$–abundance relationships increased from 2004 to 2015 (Figure 3b). That is, $\pi_{\rm tlp}$–abundance relationship was insignificant before droughts but became significant after extreme droughts (Figure S5 available as Supplementary data at *Tree Physiology* Online). In addition, we found that tree mortality substantially increased following drought episodes, which led to a direct impact on tree abundance changes in the tropical forest (Figure S6 available as Supplementary data at *Tree Physiology* Online). According to these results, we inferred that the tropical forest might exhibit a predictable response to increasing extreme droughts and that tree abundance dynamics (and mortality) could be predicted by $\pi_{\rm tlp}$ (e.g., Álvarez-Cansino et al. 2022). However, inconsistent with our expectations, $\pi_{\rm tlp}$ was not associated with tree mortality and abundance changes across all the tree species in BN1 (Figure 3e and h) or in different functional groups (e.g., canopy and understory; Figure S7 available as Supplementary data at *Tree Physiology* Online). One reason is that extreme drought-induced mortality in BN1 was predicted by vulnerability segmentation, an important hydraulic strategy that is not related to $\pi_{\rm tlp}$ (Wang et al. 2023). Moreover, osmotic potential changes (osmotic adjustment) under different abiotic conditions (Bartlett et al. 2014), and such plasticity might be a better predictor of demographic characteristics than species mean $\pi_{\rm tlp}$ (Zhang et al. 2020).

Although there were significant $\pi_{\rm tlp}$–abundance relationships in each census year in the tropical dry karst forest in BN2, we find insignificant temporal variation of the strength of the

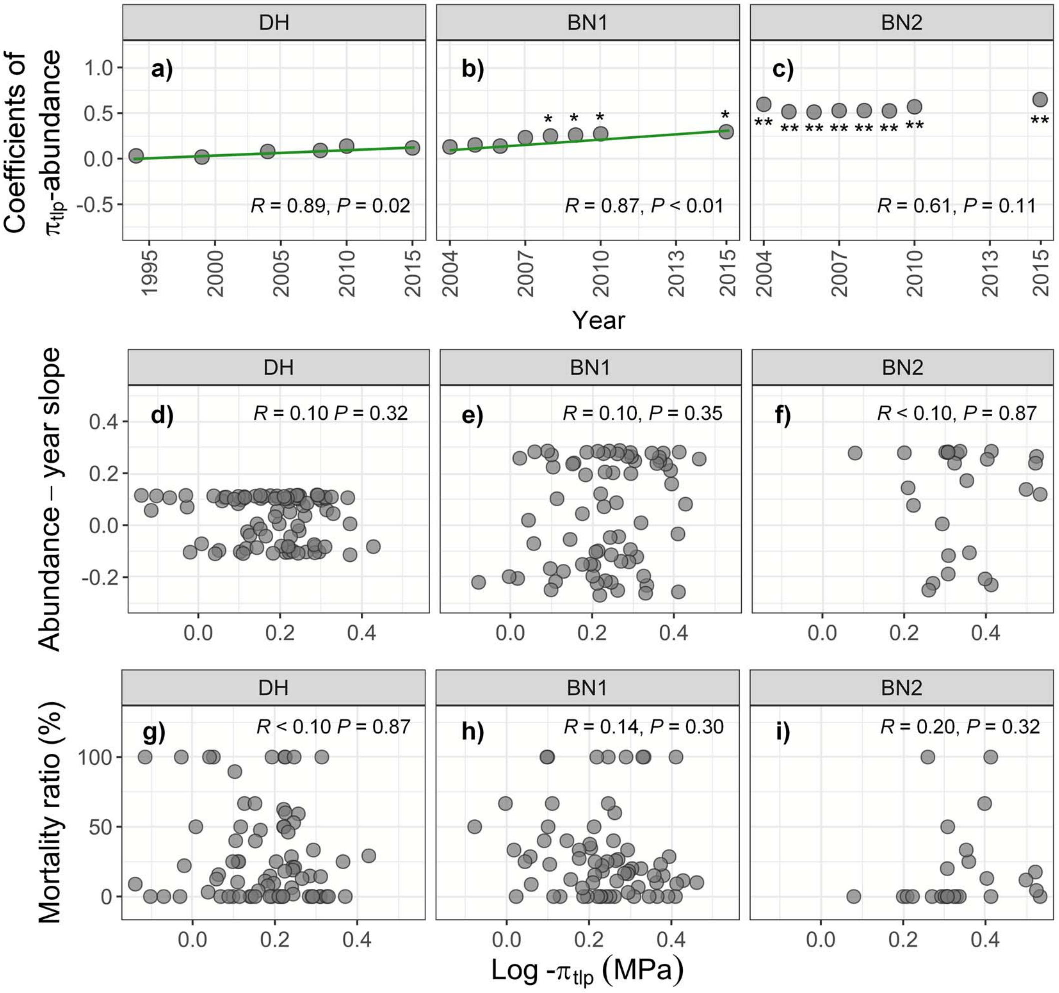

Figure 3. (a–c) Temporal changes of π_{tlp}–abundance correlation coefficient (the strength of the relationship) in the three plots with long-term community censuses. Each point denotes the correlation coefficient in each census year. * and ** indicate significant π_{tlp}–abundance relationships in the census year at $P < 0.05$ and $P < 0.01$, respectively. Solid green lines indicate significant temporal changes, i.e., the strength of π_{tlp}–abundance relationships increase significantly. (d–f) Relationships between π_{tlp} and abundance–year slope (reflect temporal changes of tree abundance; Figure S3 available as Supplementary data at *Tree Physiology* Online). (g–i) Relationships between π_{tlp} and MR. Plots codes are shown in Figure 1. Each point in (d–j) represents one species.

relationship, and a non-significant relationship between π_{tlp} and tree mortality (Figure 3c, f and i). Similarly, π_{tlp} could not predict tree demographic rates in the subtropical evergreen broadleaved forests in DH (Figure 3d and g), because tree mortality in this humid forest has been previously reported to be mainly caused by insect pest attacks (Chen et al. 2017) and typhoons (Y.L. Li et al. 2021).

Conclusion

This study is the first to examine the π_{tlp}–abundance relationship in species-rich tropical and subtropical forests with different water environments. Tree species with lower π_{tlp} were more abundant in tropical forests with high seasonality, but such a π_{tlp}–abundance relationship was not found in subtropical forests with low seasonality. As a key drought-tolerant trait however, π_{tlp} is not a predictor of tree mortality and abundance changes at the community level. This might be because species-mean π_{tlp} could not account for the mechanism underlying drought-induced tree mortality. Therefore, more investigations are necessary before π_{tlp} can be applied in modeling forest responses to global climatic change.

Supplementary data

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

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Conflict of interest

None declared.

Data availability

Data used in this letter are available in Supplementary data at Tree Physiology Online.

Authors' contributions

H.Q.S, Y.Q.W, C.L.Y and W.H.Z performed the experiments; Y.J.C, J.L.Z, H.L. and Q.M.Z provided community censuses data; S.D.Z worked on the experimental design; H.Q.S, Y.Q.W and S.D.Z conducted data analysis and wrote the manuscript. All authors read and approved this paper.

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