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ORIGINAL PAPER

Leaf habit and plant height are associated with mortality risk of trees and shrubs during extreme drought in a Chinese savanna ecosystem

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Abstract Climate change has significantly increased the frequency and severity of droughts and risk of tree death worldwide. Differences in leaf habit, plant size, and species diversity are associated with differences in the risk of drought-induced mortality, but the relative contributions of these factors to the risk of mortality are unclear. In a study of the mortality of tree and shrub species during the extreme drought of 2019 in a savanna ecosystem in Southwest China, we assessed the relative contributions of evergreen and deciduous leaf habit, plant size, and species richness and diversity to the mortality of shrubs and trees after the 2019 extreme drought. The deciduous species had significantly lower hydraulic safety margins than the coexisting evergreen species, resulting in a higher mortality risk. Additionally, species and individuals with taller canopies tended to have deeper root systems, an advantage during extreme drought that reduced mortality risk. Notably, mortality risk was largely independent of stand species richness and diversity. Overall, leaf habit and plant height were better predictors of mortality risk than species richness and diversity. These novel insights provide a better understanding of the mechanisms driving drought-induced mortality in the ecosystems with a low canopy and weak interspecific and intraspecific competition for shared resources. Leaf habit and tree size should be incorporated into hypotheses on the mechanisms underlying drought-induced tree mortality.

Keywords Drought-induced mortality · Hydraulic safety margin · Root depth · Savanna · Species diversity

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Introduction

Climate models predict that droughts are likely to increase in frequency and severity in many regions worldwide (Dai 2012; Petrova et al. 2024). Over the past few decades, droughts have reduced tree growth and killed trees in tropical, temperate, and boreal forests (Allen et al. 2010; Hammond et al. 2022; Sterck et al. 2024), leading to changes in community structure (Saura-Mas et al. 2015), species distribution (Anderegg 2015), biogeochemical cycles (Bonan 2008), and ecosystem functioning (Hartmann et al. 2022). The carbon sequestration capacity of tropical and temperate forests has also been severely reduced by during drought events (Anderegg et al. 2015; Doughty et al. 2015), which may further exacerbate the frequency and intensity of droughts (Trenberth et al. 2014; Bauman et al. 2022). Therefore, it is critical to understand the adaptive strategies of plants to drought and the mechanisms that lead to drought-induced tree mortality.

Plant mortality during droughts is the result of hydraulic failure, carbon depletion, and biotic agents (McDowell et al. 2008, 2011; Choat et al. 2018). Hydraulic failure is considered a primary pathway for drought-induced tree mortality (Arend et al. 2021; Chen et al. 2021; Nolan et al. 2021). Trees require efficient long-distance transport to support canopy transpiration (Tyree and Zimmermann 2002), but in drought conditions, conduits become air-filled (embolization), and damage to hydraulic supply networks decreases xylem hydraulic conductance, potentially leading to dehydration, canopy dieback and mortality (McDowell et al. 2008). In the absence of catastrophic hydraulic failure, prolonged stomatal closure during a drought reduces carbon fixation and increases the likelihood of mortality as carbon reserve pools are depleted (Doughty et al. 2015; Signori-Müller et al. 2021). Plants are also less able to defend themselves against pathogens and insects during droughts, which may exacerbate drought-induced mortality (McDowell et al. 2008; Brandenburger et al. 2020). Thus, tree death results from the complex interplay of physiological, ecological, and environmental factors when water is limited.

In tropical seasonal forests and savanna ecosystems, seasonal drought imposes strong selective pressure for the differentiation of leaf habit (Quigley and Platt 2003; Ishida et al. 2010; Zhang et al. 2022). Evergreen and drought-deciduous species exhibit distinct water-use strategies (Delzon 2015; Vargas et al. 2021). Specifically, deciduous species maintain high hydraulic efficiency and maximize water-use when water availability is optimal, whereas evergreen species tolerate seasonal drought at the cost of growth rate (Choat et al. 2005; Ishida et al. 2010; de Souza et al. 2020; Vargas et al. 2021). During extreme droughts, deciduous species have a higher ratio of drought-induced canopy dieback and tree mortality compared to evergreens, which have greater embolism resistance and wider hydraulic safety margins (HSM) (Chen et al. 2021). Plant size is also critical in determining drought sensitivity. Large and small trees respond differently to drought (Nepstad et al. 2007; McDowell and Allen 2015), with extreme droughts potentially intensifying size-dependent tree mortality (Bennett et al. 2015; Stovall et al. 2019). Taller trees have a higher risk of mortality due to the longer hydraulic pathway required to support the taller canopy and relatively high metabolic demands during extreme droughts (Ryan 2015; Adams et al. 2017). Moreover, root depth is another crucial trait of plant species (Nippert and Holdo 2015), and large trees develop deeper root systems and absorb sufficient water to avoid hydraulic dysfunction in arid habitats (Subedi et al. 2021; Trugman et al. 2021). Although there is a decoupling relationship between tree height and root depth of angiosperms and gymnosperms in different climatic conditions, large trees with a greater ratio of plant height and root depth are more susceptible to drought-induced mortality (Feng et al. 2023). Within plant communities, competition for limiting resources such as light, nutrients, and water also plays a significant role in regulating tree mortality (Luo and Chen 2015; Das et al. 2016). Factors such as standing crowding, tree diversity, and species interactions also influence tree mortality (Luo and Chen 2011; Searle et al. 2022), largely due to asymmetric competition because larger trees require more resources than smaller individuals (DeMalach et al. 2016). Higher plant density and more intense competition in crowded stands can also contribute to increased mortality (Searle et al. 2022). Despite extensive research on tree mortality across forest types worldwide (Allen et al. 2010; Phillips et al. 2010; Greenwood et al. 2017), we have a limited understanding of the relative importance of leaf habit, plant size, and species diversity in drought-induced mortality. This knowledge gap underscores the need for further study into how these factors interact under changing climatic conditions to develop effective forest management and conservation strategies.

Savannas are important ecosystems in tropical and subtropical regions, covering approximately 20% of the Earth's land surface (Grace et al. 2006). In Southwest China, the dry-hot climate in the river valleys nestled among the high mountains supports a unique valley-type savanna (Jin and Ou 2000). Seasonal drought is a limiting factor for leaf habit differentiation in this savanna, where coexisting evergreen and deciduous species have contrasting hydraulic safety strategies to cope with drought stress (Zhang et al. 2017, 2022). Previous studies have shown that drought-induced plant dieback is related to hydraulic vulnerability segmentation (Zhang et al. 2019) and depends on leaf habit and growth form (Chen et al. 2021; He et al. 2022). From 1950 to 2022, frequent severe drought events in the tropical and subtropical regions of China (Liu et al. 2023a), including an extreme drought in 2019 in the river valleys in Southwest

China (Yang et al. 2023), have led to significant reductions in terrestrial net primary productivity (Li et al. 2020).

To gain more understanding of how leaf habit, plant size, and community diversity influence mortality risk during drought events, here we analyzed the mortality patterns of tree and shrub species in a 1-ha (100 × 100 m) plot during an extreme drought in a savanna ecosystem of Southwest China. We calculated species richness and diversity indices using 10 × 10 m quadrats within the plot and measured leaf and wood traits, seasonal minimum water potential, hydraulic safety margins and plotted xylem vulnerability curves. Our primary objective was to explore how leaf habit, tree size, and community diversity influence the mortality of tree and shrub species under extreme drought. Specifically, we tested the following hypotheses:

(1) Deciduous species typically have resource-acquisitive traits such as higher specific leaf area, photosynthesis rate, and lower wood density, and evergreen species have traits that confer high drought resistance (Ishida et al. 2010; Chen et al. 2021; Zhang et al. 2022). Because tree mortality is promoted by lower wood density and higher specific leaf area (Greenwood et al. 2017), we hypothesized that deciduous species will have a higher mortality risk compared to evergreen species in extreme drought conditions (Fig. 1a).

(2) Larger trees generally have more complex water transport systems with longer root-to-canopy pathways and higher metabolic demands (Ryan 2015). Additionally, fast-growing trees can grow taller at a cost of higher vulnerability to hydraulic embolism (Liu et al. 2023b). Consequently, large trees are often more severely affected by droughts and are at a higher risk of mortality (Bennett et al. 2015; Liu et al. 2023b). We hypothesize that mortality risk during extreme drought will increase with plant height (Fig. 1b).

(3) Mortality risk is higher in forest stands with greater plant density and species diversity. The competition for shared limiting resources is considered as a major driver of tree mortality (Luo and Chen 2011). High species richness and diversity also promote higher plant density within forest stands (Searle et al. 2022), which intensifies interspecific and intraspecific competition for limited resources (Luo and Chen 2011). Given that water becomes a critical limiting factor during extreme drought, we hypothesized that stands with higher species richness and diversity will have a greater risk of mortality due to more intense competition for water resources (Fig. 1c).

Materials and methods

Study site

The study site at the Yuanjiang Savanna Ecosystem Research Station, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences is located in Yuanjiang County, Yunnan Province, Southwest China (23°28′25″ N, 102°10′34″ E; 481 m a.s.l.). Due to a rain-shadow effect, the Yuanjiang Valley has a dry-hot climate with two distinct seasons: a rainy season from May to October and a long, dry season from November to April. According to the station's meteorological data (2011–2021), the average annual temperature is 25.0 °C, ranging from 17.6 °C in January to 30.2 °C in June. The average annual precipitation is 681.4 mm, with approximately 80% of this occurring during the rainy season. The

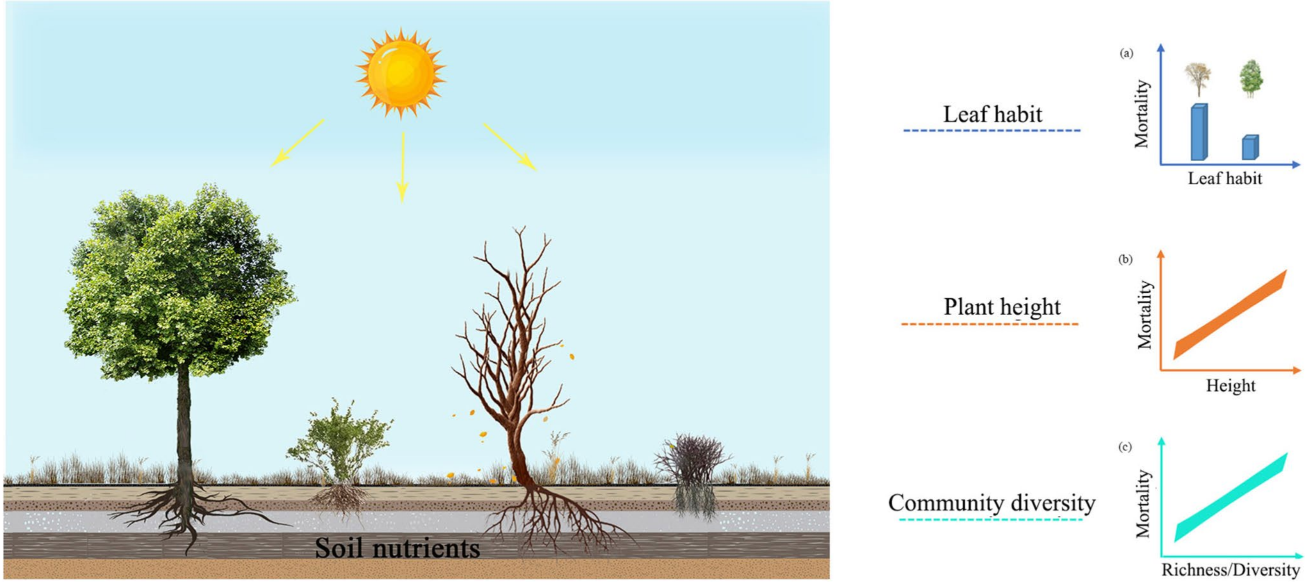


Fig. 1 Overview of the expected relationships between mortality risk of trees and shrubs and different factors. **a** Leaf habit; **b** plant height; **c** plant richness or diversity

soil type is ferralic cambisol, containing 3.57 ± 0.49 g kg^{-1} total nitrogen, 1.34 ± 0.18 g kg^{-1} total phosphorus, and 19.67 ± 1.02 g kg^{-1} total potassium, 5.49 ± 2.48 mg kg^{-1} ammonia nitrogen and 7.86 ± 2.17 mg kg^{-1} nitrate nitrogen. The maximum photosynthetically active radiation (PAR) is 2129 µmol $\mathrm{m}^{-2}\ \mathrm{s}^{-1}$, and did not differ significantly between the upper and lower canopy layers (Liu et al. 2021).

The Yuanjiang Valley is the most representative region of the dry-hot valleys in Southwest China (Jin and Ou 2000). The vegetation is classified as a valley-type savanna, characterized by a dominance of tropical floristic elements (Jin and Ou 2000; Zhu et al. 2020) and featuring a discontinuous layer of trees and shrubs with a canopy height from 3 to 8 m and generally continuous grass layer (Fig. S1). The dominant tree species include *Lannea coromandelica*, *Huberantha cerasoides*, and *Pistacia weinmanniifolia*, and the dominant shrub species are *Campylotropis delavayi*, *Tarenna depauperata*, and *Woodfordia fruticosa*. This vegetation has distinct leaf phenological characteristics, comprising deciduous and evergreen species (Table S1).

Extreme drought in 2019

The mean monthly temperature for 2017, 2018, and 2019 was 24.3 °C, 24.4 °C, and 26.4 °C, respectively (Fig. 2a), and the annual precipitation for these years was 861.7 mm, 780.1 mm, and 390.0 mm, respectively (Fig. 2b). The monthly standardized precipitation evapotranspiration index (SPEI) was used to describe patterns of drought events from 2017 to 2019 (Fig. 2c); more negative SPEI values indicate more severe drought events (Vicente-Serrano et al. 2010). A significant increase in mean air temperature and a sharp decline in annual precipitation coincided with negative SPEI values in 2019. Notably, the most severe drought event in the study area occurred during the extreme drought in 2019.

Monitoring plot and mortality survey

In a typical flat area of this savanna ecosystem, we established a 1-ha (100 × 100 m) long-term monitoring plot in December 2011, using the protocols set by the Center for Tropical Forest Science (CTFS). This plot was subdivided into 100 quadrats of 10 × 10 m. Within each quadrat, every tree and shrub individual with a DBH ≥ 1 cm was identified, tagged, and mapped. The height of each individual was also measured as part of the monitoring protocol.

We conducted the first census of all living individuals of trees and shrubs with DBH of ≥ 1 cm within each quadrat in August 2018 during the pre-drought period. In a second assessment in December 2019, after the extreme drought event, each individual was classified as dead or alive: If there were no living branches, we made a shallow cut into the trunk; if the inner bark and cambium were dry, this individual was scored as dead (Smith et al. 2005; Hoffmann et al. 2011). We then assessed the individuals in the pre- and post-drought censuses to ascertain mortality from the extreme drought event in 2019.

Species richness and diversity

Within each quadrat, we counted all trees and shrubs (N) and the different species (S) and calculated the Margalef (1951) richness index (I_M) (Eq. 1) and assessed species diversity using the Shannon–Wiener index (I_{SW}) (Eq. 2; Shannon et al. 1949) and Simpson index (I_S) (Eq. 3; Simpson 1949):

$$I_M = \frac{S-1}{\log(N)} \tag{1}$$

$$I_{SW} = \sum_{i=1}^{S} P_i \log P_i \tag{2}$$

$$I_S = 1 - \sum_{i=1}^{S} P_i^2, \tag{3}$$

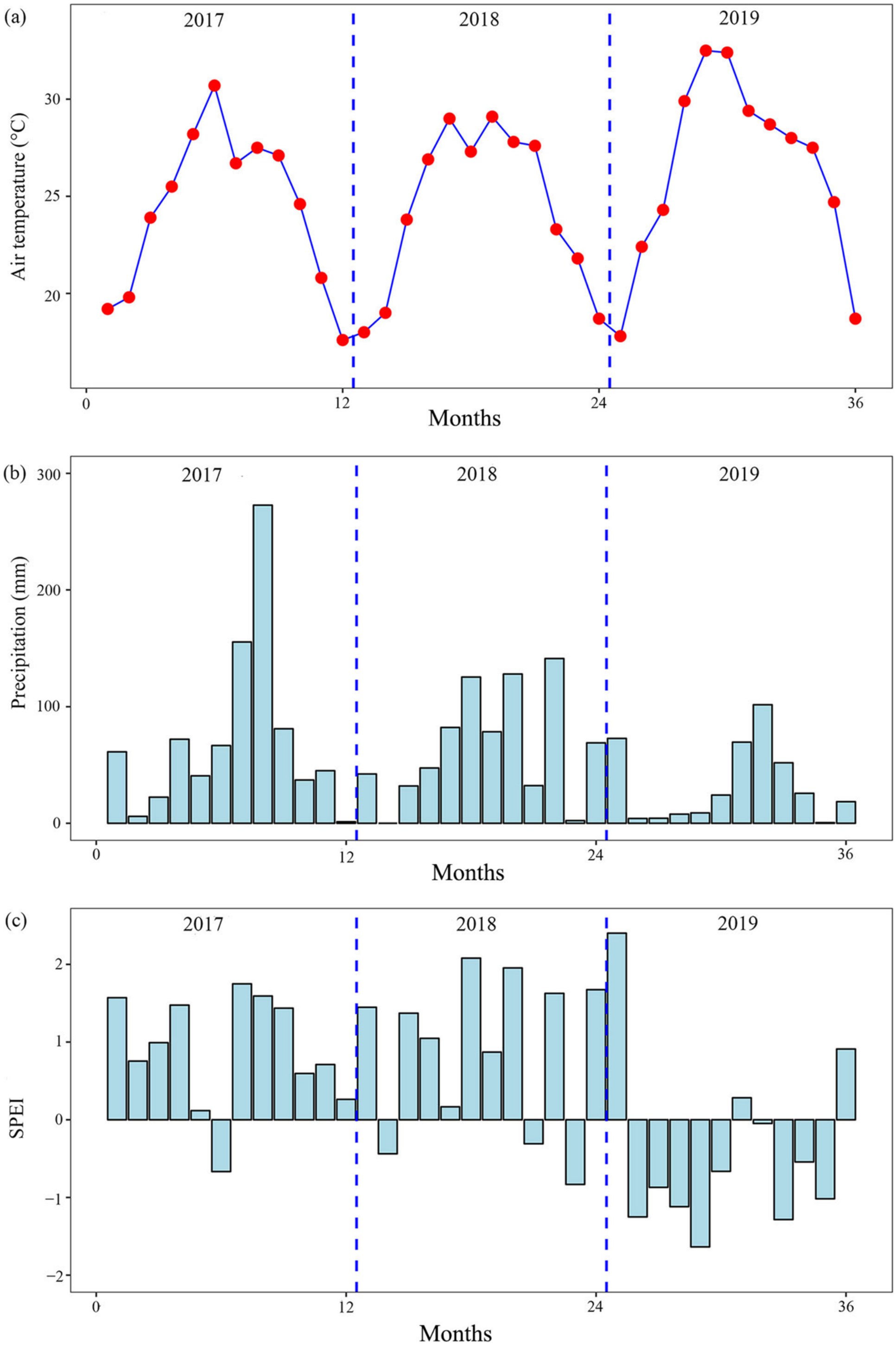
where P_i is the frequency of the ith species.

Hydraulic safety margin

Data for water potential causing 50% loss of stem hydraulic conductivity (P_{50}) was derived from Chen et al. (2021). They collected plant materials from the same species in this long-term monitoring plot and constructed xylem vulnerability curves using the benchtop dehydration method (Chen et al. 2021).

The minimum water potential (Ψ_{min}) was measured in the field for 19 tree and shrub species in this plot on sunny days in April 2019 during the peak of the extreme drought. For each species, three healthy adult individuals were randomly selected within and near the plot; two leaf-bearing branches were collected from each individual for evergreen species, and two leafless terminal twigs were collected from each individual for deciduous species and wrapped in plastic bags and aluminum foil in the evening before the measurement day. Midday water potential of non-transpiring leaves of evergreen species and terminal twigs of deciduous species was measured using a pressure chamber (PMS1505D-EXP, PMS Instrument Co., Albany, OR, USA) between 12:00 and 14:00 h on sunny days. A previous study showed that stem water potentials did not differ significantly when measured using leaves and leafless terminal twigs that had achieved full equilibrium (Chen et al. 2021). The hydraulic safety margin (HSM) was calculated as HSM = Ψ_{min}—P_{50} (Choat et al. 2012).

Fig. 2 Average monthly air temperature **a**, monthly precipitation **b**, and standardized precipitation evapotranspiration index (SPEI, c) between 2017 and 2019 in the study site



Leaf traits and wood density

In August 2018, two branches with leaves were removed from each healthy adult tree or shrub individual during the peak of the rainy season (in total 6 branches per species). Three expanded leaves attached to each terminal branch (in total 18 leaves per species) were scanned at 300 dpi using the HP LaserJet Pro MFP scanner (Hewlett Packard, USA). The images were used to measure leaf area (LA, cm^2) using ImageJ software (https://imagej.nih.gov/ij/). Subsequently, the leaves were oven-dried at 70 °C for at least 48 h to achieve a constant leaf dry mass and weighed using an electronic balance (ME204, Mettler Toledo, Creifensee, Switzerland; accuracy 0.0001 g). Specific leaf area (SLA, cm^2 g^{-1}) was then calculated by dividing the fresh leaf area by leaf dry mass.

A 5 cm segment was cut from each stem to measure hydraulic traits. The bark and pith were carefully removed to assess wood density (WD, g cm^{-3}). The fresh wood volume was measured using the water displacement method. After oven-drying at 70 °C for 72 h, the wood was weighed, then WD was calculated as the ratio of wood dry mass to fresh volume.

Quantification of root depth

A fireproof access road was constructed in 2015 near our long-term monitoring plot and a research platform to study plant adaptation and resilience was built 100 m from the long-term monitoring plot in 2023, providing the opportunity to study the variations in root depth among trees and shrubs. In total, we selected 40 individuals from 14 tree and shrub species, ranging in height from 1.8 to 8.0 m (Table S2) to analyze the relationships among root depth, plant height, and DBH. Of the 40, 28 were deciduous and 12 evergreen, which corresponded to the species composition in the plot. The selected trees and shrubs were felled, and we measured the DBH and plant height of each individual. An excavator was then used to carefully remove the root systems to maintain its integrity. Most species had a prominent taproot; however, *W. fruticosa* had a fibrous root system. We measured the largest vertical root to determine the root depth of 40 sampled individuals.

Data analyses

The mortality risk estimated per individual from the censuses was used as the response variable in a generalized linear model (GLM), with a binary probability for tree and shrub mortality (i.e., 1: dead, 0: alive). Potential explanatory variables included plant height, DBH, leaf habit (evergreen or deciduous), growth form (tree or shrub), plant density, Margalef richness index, Shannon–Wiener index, and Simpson index. Before the data analysis, all the numerical variables were standardized (mean = 0, SD = 1) to ensure that the regression slopes were directly comparable. Given the high correlation between plant height and DBH ($R = 0.79$, $P < 0.001$), we included only plant height as our primary size-related variable because it is commonly used to indicate plant size in relation to tree mortality (Stovall et al. 2019). To assess collinearity among the explanatory variables, we used the variance inflation factor (VIF) function in the R package car (Fox and Weisberg 2011), retaining only variables with VIF values ≤ 5 for the full model construction. Additionally, we conducted a variance partitioning analysis to quantify the relative effects of leaf habit, growth forms, plant size, plant density, richness, and species diversity on mortality risk using the glmm.hp package in R (Lai et al. 2023).

Leaf habit and plant height significantly influenced mortality risk. However, our study included fewer evergreen species than deciduous (Table S1), so the sample sizes for the two leaf-habit groups were unbalanced for making comparisons. We thus compared the mortality risk (predicted probability of mortality) between evergreen and deciduous groups using a nonparametric bootstrap approach with 1000 replicates (Booth et al. 1993). Specifically, we defined a function that calculated the difference in means of predicted probability of mortality between deciduous and evergreen, then we performed bootstrapping with 1000 resamples. If the 95% confidence interval (CI) of the difference in means of predicted probability of mortality did not overlap zero, there was significant difference between two groups. We also compared leaf area (LA), specific leaf area (SLA), wood density (WD), seasonal minimum water potential ($\Psi_{\min}$), and hydraulic safety margin (HSM) between the deciduous ($N = 13$) and the evergreen species ($N = 6$) using the same method (Table S3). Additionally, a standardized major axis (SMA) regression was used to assess the relationships among plant height, diameter at breast height (DBH), and root depth using the 'smatr' package in R (Warton et al. 2012). All statistical analyses were performed using R version 4.3.2 (R Core Team 2023).

Results

Mortality drivers

In this long-term monitoring plot, we studied 926 individuals (including both tree and shrub species), comprising 198 evergreen and 728 deciduous individuals (Table S1). Of these, 840 individuals were still alive after the 2019 extreme drought, and 86 individuals had died. Parameter estimation for the full model revealed that among the six variables examined, leaf habit and plant height significantly influenced mortality risk (Fig. 3; Table S4; $P < 0.001$); growth forms, plant density, Margalef index, and Simpson index had no significant effect on mortality risk. Variance partitioning for the full model indicated that leaf habit and plant height, respectively, accounted for 67.56% and 25.25% of the total variation in mortality risk (Table 1) and that together, they accounted for 92.81% of the observed variation. The other four variables (growth forms, plant density, Margalef index, and Simpson index) together explained only 7.09% of the variation in mortality risk.

We subsequently fitted a reduced model that included leaf habit and plant height (Table S5) and found a significant difference in the mortality risk between the deciduous and evergreen groups (Fig. 4a; Table S6). Furthermore, mortality risk was negatively correlated with plant height in both deciduous and evergreen species (Fig. 4b), and evergreen

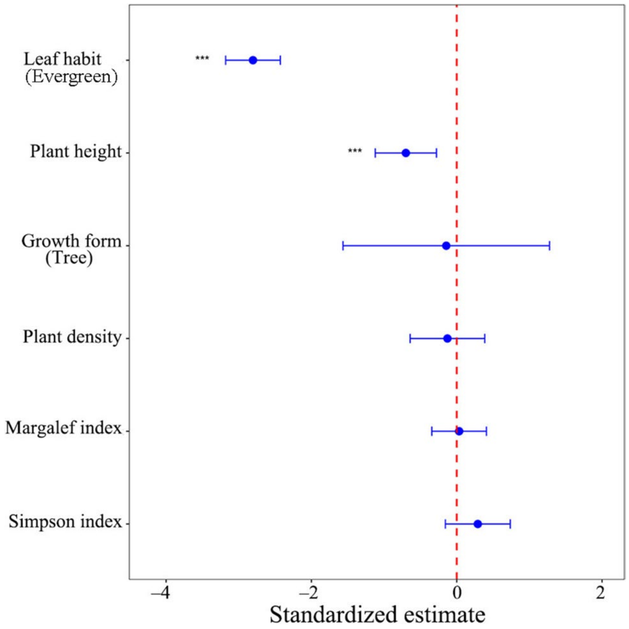


Fig. 3 Standardized estimate of a generalized linear model predicting the mortality risks using leaf habit, growth form, plant height, plant density, Margalef index, and Simpson index. Error bars represent the 95% confidence interval. See detailed results in Supplementary Table S2

Table 1 Relative effects of leaf habit, growth forms, plant size, plant density, richness, species diversity on the mortality risk of trees and shrubs under an extreme drought in a Chinese savanna ecosystem

Variable	Average share	Individual	Percentage (%)
Leaf habit	0.021	0.083	67.56
Plant height	0.095	0.031	25.25
Growth-form	0.004	0.004	3.10
Plant density	0.001	0.002	1.55
Margalef index	0.001	0.001	0.81
Simpson index	0.001	0.002	1.63

species consistently had a lower probability of mortality than the deciduous species at any given plant height.

Differences in traits between evergreen and deciduous groups

Savanna woody species had distinct leaf and wood traits depending on their leaf habit (Fig. 5; Table S7); deciduous species had significantly larger leaf area (LA) and specific leaf area (SLA) but lower wood density (WD) compared to the evergreen. Deciduous and evergreen species had comparable $\Psi_{\min}$ values. On average, deciduous species had a narrower or negative HSM, in contrast to the positive HSM of the evergreen species. In addition, trees and shrubs differed significantly only in WD ($P < 0.05$; Fig. S2), but did not differ significantly in LA, SLA, $\Psi_{\min}$, or HSM.

Relationships among plant size and root depth

A significant positive correlation was found between plant height and diameter at breast height (DBH) across 40 sampled tree and shrub individuals, including 28 deciduous and 12 evergreen individuals ($P < 0.001$; Fig. 6; Table S2). Both plant height and DBH were positively correlated with root depth ($P < 0.001$).

Discussion

Leaf traits and plant size drive drought mortality

Complex physiological mechanisms influence the response of plants to natural drought events and thus their risk of mortality (Choat et al. 2018). Because drought-induced mortality risk is also influenced by plant size (Bennett et al. 2015; Stovall et al. 2019) and species diversity (Shovon et al. 2024), here we analyzed leaf habit, plant size, and species diversity to evaluate their relative contributions to the mortality of trees and shrubs during extreme drought conditions in a savanna ecosystem. Overall, our findings suggest that leaf habit and plant height are stronger predictors of mortality risk than species richness and diversity within quadrats.

Deciduous species have a higher mortality risk than the evergreen

We found a greater risk of mortality for deciduous species than for the evergreen after the extreme drought of 2019, which supports our initial hypothesis, and leaf habit was the strongest predictor of drought-induced mortality for trees and shrubs. Deciduous species, characterized by higher leaf area (LA) and specific leaf area (SLA), may be more susceptible to drought-induced mortality than evergreen species, which have high wood density (WD) and more negative P_{50} values. Therefore, the observed difference in mortality between evergreen and deciduous groups can be attributed to their functional traits and hydraulic strategies. Tree mortality may be exacerbated by higher SLA and lower WD (Greenwood et al. 2017). First, SLA functions as a hub trait closely related to the leaf economic spectrum (Wright et al. 2004), influencing potential water loss and drought resistance of leaves (Bussotti et al. 2015). Evergreen species have relatively lower SLA, thicker leaf blades, and small, thick-walled cells (Wright et al. 2004), which enable them to optimize leaf mass allocation and enhance drought resistance compared to deciduous species (Wright et al.

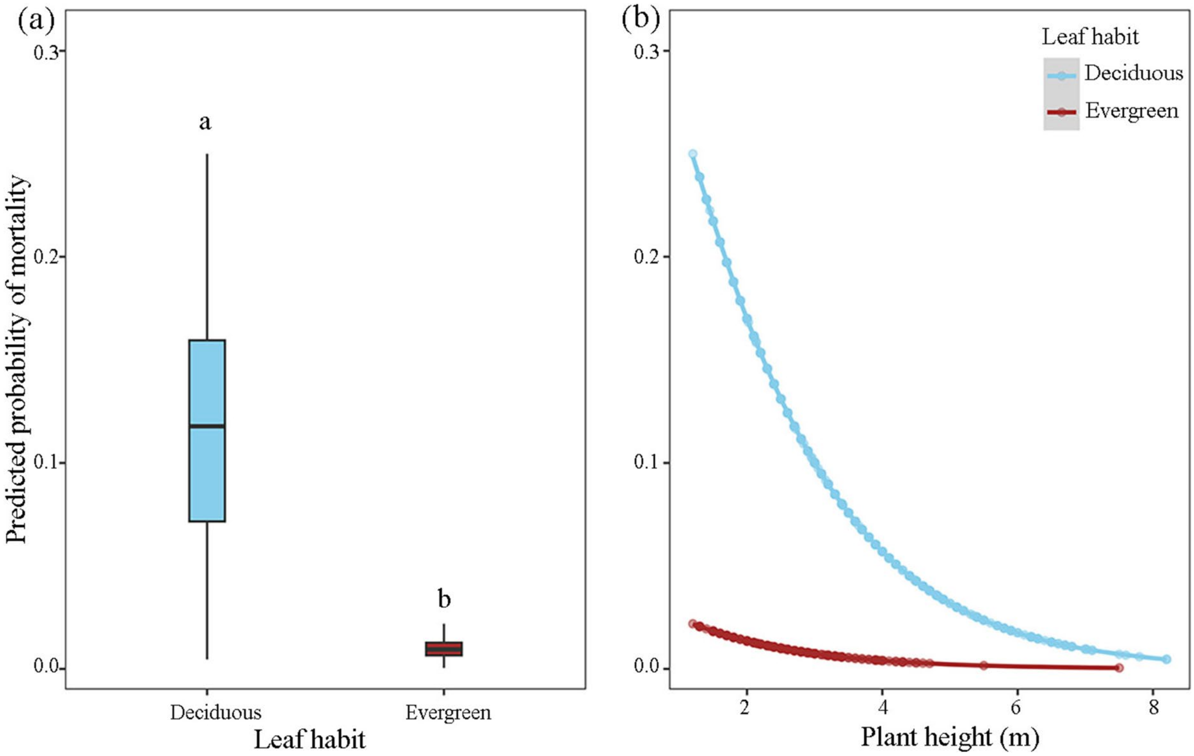


Fig. 4 Predicted mortality risk for evergreen and deciduous species by **a** leaf habit and **b** plant height. The predicted probability of mortality was derived from a reduced model (see Supplementary Table S5), which excluded variables with no significant effects. Different letters above means indicate significant differences in mortality risk between deciduous and evergreen groups (95% CI of the difference in means did not overlap zero). (Statistical results are in Supplementary Table S6.)

2004; Poorter et al. 2009). Furthermore, WD influences water storage, transport, and drought sensitivity (Chave et al. 2009; Bennett et al. 2015; Gleason et al. 2016). In this study, evergreen species had higher WD and were able to sustain more negative P_{50} values (Fig. S3). Thus, evergreen species are more likely to survive extreme drought conditions than co-occurring deciduous species (Wang et al. 2023). Previous studies have also suggested that evergreen and deciduous species differ in crown conductance sensitivity and trunk sapwood capacitance (Siddiq et al. 2017, 2019). Under the same DBH, the crown conductance sensitivity is also significantly higher in evergreen species than in deciduous (Siddiq et al. 2017). Moreover, evergreen species have higher trunk sapwood capacitance than deciduous ones, enhancing drought tolerance and canopy water status (Siddiq et al. 2019). These findings underscore the competitive advantage of evergreen species over deciduous species during prolonged or extreme drought events.

The hydraulic safety margin (HSM) is also critical in determining plant response to drought conditions (Adams et al. 2017). A narrow or negative HSM indicates an elevated risk of hydraulic failure and, consequently, a high rate of drought-induced mortality (Anderegg et al. 2016; Choat et al. 2018). During the extreme drought of 2019, evergreen species were able to maintain relatively wide HSMs, thereby avoiding hydraulic failure. In contrast, deciduous species often rely on their internal water storage or employ avoidance strategies such as deep root systems and drought-deciduousness (Choat et al. 2018). For example, the deciduous species *L. coromandelica* and *Haldina cordifolia* have deep root and shed leaves at the onset of the drought season. These adaptations help maintain hydraulic safety and reduce mortality risk during extreme drought. However, prolonged or extreme drought can lead to water loss through cuticle and bark, causing a gradual decrease in xylem water potential (Kerstiens 1996; Oren and Pataki 2001), potentially below the threshold of hydraulic safety (Chen et al. 2021), thereby resulting in a higher mortality risk for deciduous species.

Higher mortality risks for shorter plants

Contrary to our second hypothesis, our findings revealed that the mortality risk associated with extreme drought decreased with plant height. This result is inconsistent with other site- and region-specific studies (Nepstad et al. 2007; Lindenmayer et al. 2012) and global patterns demonstrating that large trees exhibited greater sensitivity to drought and higher mortality rates than smaller trees (Bennett et al. 2015).

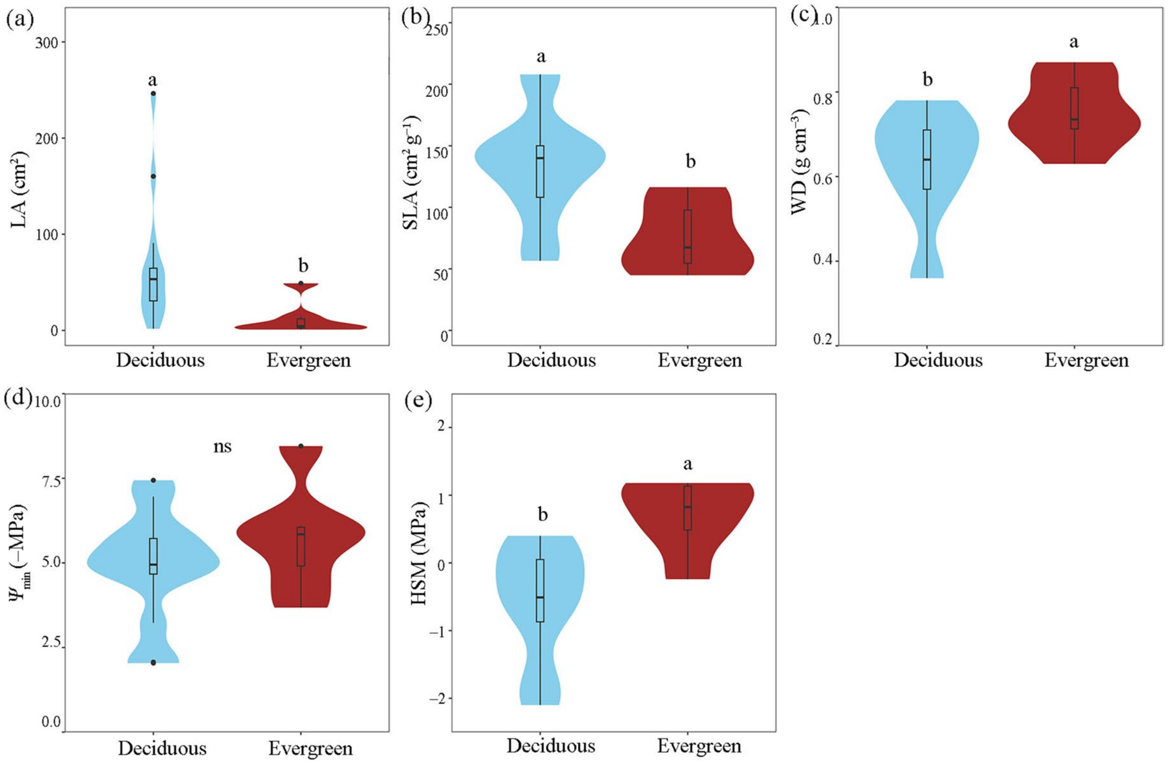


Fig. 5 Leaf area (LA), specific leaf area (SLA), wood density (WD), seasonal minimum water potential (Ψ_{min}), and hydraulic safety margin (HSM) between evergreen and deciduous groups using a non-parametric bootstrap approach with 1000 replications. Different letters in a panel indicate significant differences between deciduous and evergreen groups (95% CI of the difference in means did not overlap zero). (Statistical results are in Supplementary Table S7.)

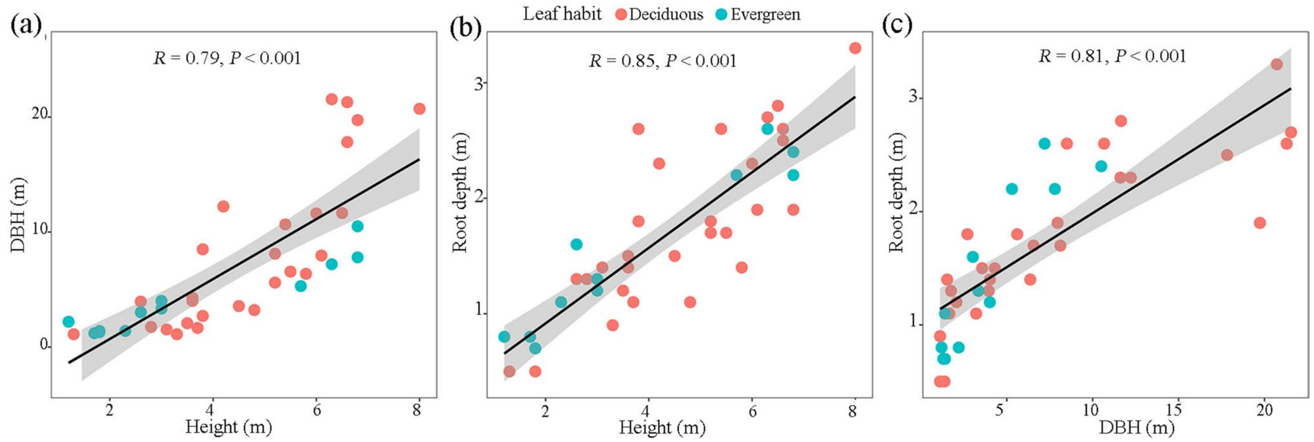


Fig. 6 Relationships between plant height, diameter at breast height, and root depth across 28 deciduous and 12 evergreen individual trees and shrubs

The increased sensitivity of larger trees to drought is often attributed to their greater vulnerability to inherent hydraulic stresses (McDowell and Allen 2015). Within the context of climate change, substantial evidence indicates that drought consistently exerts a more deleterious effect on the growth and survival of large trees (Bennett et al. 2015). Our findings may represent a unique ecological perspective that warrants further investigation regarding plant size-dependent mortality.

Previous studies have shown that taller plant species are more vulnerable to drought-induced mortality, but these findings were primarily derived from ecosystems with significantly taller canopy heights (e.g., more than 30 m for large trees) than in a savanna (Stovall et al. 2019). The savanna ecosystem studied here had much shorter canopies ranging from 3 to 8 m. Therefore, the water supply to the tree and shrub canopies in our study site was less constrained by the resistance of gravity and hydraulic path length, which may explain the decreasing mortality risk with increasing plant height found in our study.

In this study, plant height proved to be a significant predictor of mortality risk for trees and shrubs in extreme drought. Additionally, we found a positive correlation between plant height and root depth across evergreen and deciduous individuals. This finding supports the notion that larger trees develop roots extending into deeper soil profiles, allowing them to absorb more water and nutrients, thereby mitigating hydraulic failure during drought (Bardgett et al. 2014; Subedi et al. 2021). In savanna ecosystems, maximum root depth has been identified as a crucial trait for characterizing the susceptibility of plant species to drought (Nippert and Holdo 2015). Plants with deep root systems are able to exploit a greater volume of soil water, so water availability is more stable (Nippert and Holdo 2015), which is essential for their survival during prolonged dry periods. The maximum root depth determines the extent of soil resource exploration and plays a key role in underground ecological performance. Large trees develop deep roots to absorb sufficient water and nutrients, thereby avoiding hydraulic failure during a water shortage (Trugman et al. 2021) by ensuring a reliable water supply and thus reducing the risk of mortality.

Mortality risk was not related to species richness and diversity

Our analysis revealed that plant density, species richness, and diversity had no significant impact on mortality risk within the studied quadrats. This finding suggests that mortality risk is largely independent of stand species richness and diversity, contrasting with a previous report of a positive effect of species diversity on tree mortality in temperate and boreal forests (Searle et al. 2022). The main reason for this discrepancy might be attributed to increased competition for resources such as light, water, and nutrients in diverse forest stands during drought (Luo and Chen 2011; DeMalach et al. 2016; Mori et al. 2017).

Tree mortality has a critical role in shaping forest ecosystems by influencing tree abundance and species diversity (Jump et al. 2017). However, the valley-type savanna at our study site presents unique ecological characteristics. This ecosystem is characterized by sparse vegetation, an open canopy structure, and abundant light availability (Jin and Ou 2000). Consequently, light availability is not a limiting factor for plant growth and survival. Furthermore, root stratification is a prevalent adaptation in grassland and savanna ecosystems, enabling species to exploit water resources differently in space and magnitude (Nippert and Holdo 2015). This mechanism allows diverse species to access water and nutrients from different soil profiles, thereby reducing direct competition for shared resources. Ecological niche differentiation or resource partitioning further alleviates direct competition among neighboring species and individuals for shared resources (Decarsin et al. 2024). Consequently, the relatively low competition intensity for shared resources among species may explain the lack of significant effects of species richness and diversity on drought-induced mortality risk in this savanna ecosystem. In such open environments where root niche differentiation is pronounced, the influence of plant richness and diversity on mortality dynamics may be less pronounced compared to other forest types.

Conclusion

Overall, our results indicate that mortality risk in the savanna ecosystem during extreme drought is more strongly associated with leaf habit and plant height rather than with species richness or diversity, and leaf habit was the most important in explaining the mortality risk of savanna trees and shrubs. This work provides an integrated framework for understanding drought-induced mortality in ecosystems characterized by a low canopy and low interspecific and intraspecific competition for shared resources of light, water, and soil nutrients. Future research should integrate leaf habit and plant size to better elucidate the mechanisms underlying drought-induced tree mortality across biomes and plant functional groups. For practical applications, we recommend selecting the evergreen native tree species and deep-rooted tree species as high-survival candidates in the future vegetation restoration, particularly in degraded ecosystems in semiarid and arid regions. Restoration efforts can then be more effectively tailored to enhance ecosystem resilience in the face of increasing climatic challenges.

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Data availability The data is available on request from the corresponding author.

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