









## LETTER

# Hydraulic prediction of drought-induced plant dieback and top-kill depends on leaf habit and growth form

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**Funding information**

National Natural Science Foundation of China, Grant/Award Number: 41861144016, 31570406, 32071735 and 31861133008; 'Light of West China' and Youth Innovation Promotion Association Program of the Chinese Academy of Sciences; Yunnan Provincial Science and Technology Department, Grant/Award Number: 2018HB068

Editor: Sally Archibald

**Abstract**

Hydraulic failure caused by severe drought contributes to aboveground dieback and whole-plant death. The extent to which dieback or whole-plant death can be predicted by plant hydraulic traits has rarely been tested among species with different leaf habits and/or growth forms. We investigated 19 hydraulic traits in 40 woody species in a tropical savanna and their potential correlations with drought response during an extreme drought event during the El Niño–Southern Oscillation in 2015. Plant hydraulic trait variation was partitioned substantially by leaf habit but not growth form along a trade-off axis between traits that support drought tolerance versus avoidance. Semi-deciduous species and shrubs had the highest branch dieback and top-kill (complete aboveground death) among the leaf habits or growth forms. Dieback and top-kill were well explained by combining hydraulic traits with leaf habit and growth form, suggesting integrating life history traits with hydraulic traits will yield better predictions.

**KEYWORDS**

dieback and mortality, drought tolerance, embolism, hydraulic failure, hydraulic safety margin, leaf turgor loss point, liana, top-kill, tropical savanna

## INTRODUCTION

Drought is one of the most prevalent environmental stress conditions globally (Burke et al., 2006; IPCC, 2007), limiting the productivity and growth of most terrestrial ecosystems (Reichstein et al., 2013). An increasing number of studies have documented sudden and widespread tree mortality in response to drought across all major biomes (Allen et al., 2010). Rising global temperatures and shifts in precipitation are expected to exacerbate drought stress (Dai, 2013), leading to a greater probability of massive tree mortality events (Anderegg et al., 2019; Brodribb et al., 2020). Therefore, a mechanistic understanding of drought-induced mortality is of paramount importance.

Predicting the impact of drought events on plant survival and distribution patterns requires a detailed understanding of the mechanisms underlying drought-induced tree death, which are thought to include biotic agents, carbon starvation and hydraulic failure (Choat et al., 2018; McDowell, 2011; McDowell et al., 2008). A sound knowledge of plant hydraulic strategies is crucial for understanding and predicting drought-induced mortality (Oliveira et al., 2021), which also determines the species distribution within the community and their biogeographic limits along environmental gradients, for example, water availability (Blackman et al., 2012; Brodribb & Hill, 1999; Larter et al., 2017; Oliveira et al., 2019; Skelton et al., 2021). Previous studies have shown that drought-induced mortality of a given species can be predicted reasonably by hydraulic traits such as the xylem resistance to embolism ( $P_{50}$ ), a hydraulic trait widely used to estimate hydraulic safety (Choat et al., 2012; Hammond et al., 2019), and the hydraulic safety margin (HSM), a widely used indicator of the hydraulic impairment risk (Anderegg et al., 2019; Anderegg et al., 2016; Choat et al., 2012; Skelton et al., 2015). Nevertheless, it is clear that drought-induced plant death is complex, involving many physiological processes. Although hydraulic failure could be one of the major factors associated with drought-induced mortality, particularly in short, high-intensity drought events (Anderegg et al., 2018; McDowell et al., 2018; Rowland et al., 2015), additional processes may include reduced resistance to pathogens (Dietze & Matthes, 2014; Oliva et al., 2014) or bark beetles (Huang et al., 2020), changes in the soil microbiome community (Kaisermann et al., 2017) and soil fertility (Harrison et al., 2015). Consequently, differential impacts of multiple processes during droughts confound the accuracy of predictions of drought-induced mortality (Trugman et al., 2021). Here we consider two additional factors, leaf habit and growth form.

Coexisting species may be affected in different ways by drought (Fensham & Fairfax, 2007; Johnson et al., 2018; Kukowski et al., 2013), and differences in sensitivity to drought and mortality incidence are often associated with plant hydraulic strategies (Anderegg et al., 2016;

Anderegg et al., 2018; Brodribb et al., 2020; Oliveira et al., 2021; Pivovarovoff et al., 2016; Powers et al., 2020). Drought tolerance (e.g., high resistance to xylem embolism and tissue tolerance to desiccation) and avoidance (e.g., deciduousness, deep roots, and timely stomatal closure) are two divergent strategies that allow plants to survive extreme drought (Brodribb et al., 2014; Oliveira et al., 2021) and are found to trade-off across tropical forests (Christoffersen et al., 2016). Generally, drought-avoiding species (i.e., those that rely on drought avoidance strategies) close their stomata early in response to decreasing water availability relative to species that exhibit higher embolism resistance (Brodribb et al., 2014; Gonzalez-Rebeles et al., 2021; Meinzer et al., 2009), whereas species with highly embolism-resistant xylem can maintain water transport under conditions of a more negative water potential and are able to maintain leaves over dry periods (Fu et al., 2012; Johnson et al., 2018). In line with this, evergreen species are expected to be physiologically more resistant to water stress, which allows them to function under moderate drought intensity but places them at risk of catastrophic hydraulic failure when an extreme drought occurs (Anderegg et al., 2019; Kukowski et al., 2013) and may come at the cost of growth rate. In contrast, deciduous species avoid drought by leaf shedding, which helps them to avoid catastrophic failure under extreme drought, and allows them to support fast water flow and rapid growth during the wet season, but forces them to regrow a new leaf canopy each year (Gonzalez-Rebeles et al., 2021; Singh & Kushwaha, 2016).

Data on hydraulic strategies have mainly been collected on trees, but there is evidence to suggest that different growth form plants may differ in their drought tolerance. For example, lianas are reported to show a 'dry season growth advantage' (Schnitzer & van der Heijden, 2019) over trees via deep rooting (Chen et al., 2015) and strong stomatal control (Chen et al., 2017). Drought can be particularly severe for plants in arid and semi-arid habitats, where long and intense periods of water stress occur during the dry season. Plant species growing in semi-arid environments, particularly shrubs and trees, tend to have modular hydraulic systems and typically have multiple aboveground clonal stems with high redundancy (Anest et al., 2021; Schenk et al., 2008); the aboveground tissues may partially or completely die during severe disturbances such as fire and drought (hereafter define as branch 'dieback' or 'top-kill', definitions are provided below), but the species retain living belowground organs that support resprouting, allowing the species to recover post-drought (Bond & Midgley, 2001; Bond & Midgley, 2003). This strategy may reduce the risk to whole-plant death under extreme drought (Schenk et al., 2008).

Savanna is a dryland ecosystem that partly occurs in semi-arid regions and is prone to droughts. Savannas are mainly distributed in tropical and subtropical regions and cover approximately 20% of the land surface

on earth (Grace et al., 2006; Murphy & Bowman, 2012; Ratnam et al., 2016). Savannas in southwest China often contain coexisting species with a wide spectrum of leaf habits (evergreen, semi-deciduous and deciduous) and growth forms (trees, shrubs and lianas), making them excellent study systems for understanding how leaf habit and growth form affect plant responses to drought stress. Compared to forests, the response of savannas to extreme drought has been less studied (cf. with Zhang et al., 2016), and consequently, relatively little information is available regarding the vulnerability of savanna species to extreme drought. Moreover, species are often pooled together in analysis, whilst species with contrasting leaf habits and growth forms are rarely considered independently.

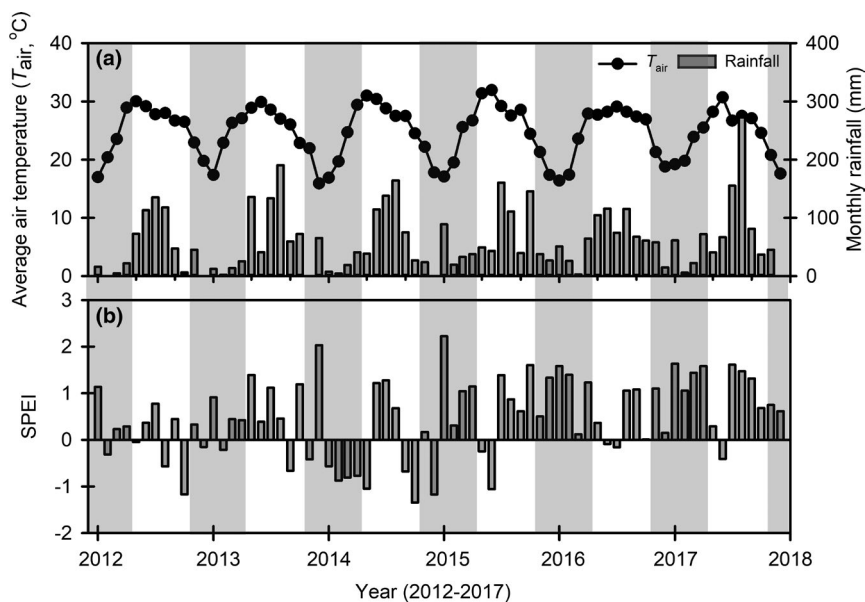
In this study, we investigated 40 common woody species from a semi-arid savanna in southwest China. The species included 17 trees, 16 shrubs and 7 lianas, among which there were 9 evergreen, 16 semi-deciduous and 15 deciduous species. We measured stem and leaf hydraulic traits and related these to a survey of branch dieback and top-kill. During the research period, an extreme drought event occurred in 2015 (Figure 1) caused by strong El Niño (Kogan & Guo, 2017), which enabled us to test the possible linkages between branch dieback and top-kill and plant hydraulic traits. The two main objectives of our study were (1) to examine the xylem embolism resistance in relation to leaf habit and growth form, and (2) to document to what extent hydraulic traits account for branch dieback and/or top-kill across leaf habits and growth forms. Top-kill was defined as the complete death of aboveground biomass, but it does not necessarily mean whole-plant death. Branch dieback was recorded as partial terminal branch death, which is a less severe

form of negative growth in individual shoot axes. Branch dieback may also occur during droughts and may occur across a larger proportion of species under drought. We hypothesised that savanna woody species would be spread along a spectrum from conservative water-use and embolism-resistant strategies to nonconservative but drought-avoiding strategies. Thus, we expected evergreen species would possess high embolism-resistant traits whereas deciduous species would possess drought-avoiding traits, and that semi-deciduous species would possess intermediate traits between these extremes. Consequently, we expected that semi-deciduous species would show the highest risk of dieback and top-kill because of their lesser conservative traits relative to evergreens and greater exposure to drought effects relative to deciduous species. With respect to growth forms, we anticipated that shrubs exhibit greater branch dieback and top-kill than trees and lianas because of their small stature (and presumably associated shallow roots), and their strategy of resprouting allows them to discard relative cheap aboveground biomass during the dry season and thus reshoot in subsequent wet seasons more freely.

## MATERIALS AND METHODS

### Site information and plant materials

This study was conducted at the Yuanjiang Savanna Ecosystem Research Station (Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences; 23°28'56"N, 102°10'40"E, 481 m a.s.l.). This region has a typical semi-arid valley savanna vegetation. The vegetation is dominated by *Lannea coromandelica*, *Bauhinia*



**FIGURE 1** The monthly averaged air temperature ( $T_{air}$ ) and rainfall (a) and the Standardised Precipitation Evapotranspiration Index (SPEI, b) in the study area between 2012 and 2017. Grey areas indicate the dry season of each year. More negative SPEI value indicate a stronger drought intensity

*brachycarpa* and *Vitex negundo* (Zhang et al., 2016). The canopy height is approximately 6 to 8 m for trees and approximately 2 to 3 m for shrubs (Figure S1). According to the meteorological data available for the study period (2012 to 2017), the mean annual temperature was 24.7°C. April to June were the hottest months with a maximum air temperature of 43°C. The mean annual rainfall was ~732.8 mm, with ~80% occurring between May and October. Based on the Köppen-Geiger classification, this area has a dryness threshold of 9.46, classifying the climate as semi-arid (Kottek et al., 2006). In this study, we used a monthly timescale Standardised Precipitation Evapotranspiration Index (SPEI) to describe the characteristics of drought events during the study period (Figure 1). The SPEI value was calculated using the monthly differences between precipitation and potential evapotranspiration. We used a timescale of 1-month data (SPEI-1) of this region, downloaded from the Global SPEI database (<http://spei.csic.es/map/maps.html#months=1#month=7#year=2019>). During the experimental period, the dry seasons in 2013–2015 showed SPEI values below average. Especially in the middle of the year 2015, a prolonged dry season associated with extremely hot and dry climate (SPEI < -3) due to a strong 2015–2016 El Niño (Kogan & Guo, 2017) caused vast plant mortality in the field (Figure S2).

We selected a total of 40 woody species, belonging to 22 families, which included most of the common species in the vegetation (Table S1). Species were classified into three growth forms (trees,  $n = 17$ ; shrubs,  $n = 16$ ; and lianas,  $n = 7$ ) and three leaf habit groups. We defined evergreen (E,  $n = 9$ ) for species with no obvious leaf shedding period throughout the year and without a leafless phase; semi-deciduous (SD,  $n = 16$ ) for species that only partially dropped their leaves but did not show a leafless stage in the dry season; and deciduous (D,  $n = 15$ ) for species that drop all their leaves and went through an obvious leafless stage in the dry season (Powers et al., 2020).

## Leaf and stem hydraulic traits

The leaf and stem hydraulic properties were measured in the wet season (see methodological details in Supplementary Methods for all measurements and trait definition/functional meaning in Table S2). Briefly, we determined the maximum vessel length (MVL, cm) using an air injection method (Ewers & Fisher, 1989) prior to all hydraulic measurements. We measured the maximum sapwood hydraulic conductivity ( $K_s$ ,  $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ ) following Sperry et al. (1988). After performing hydraulic conductivity measurements, we measured the sapwood area to leaf area ratio ( $H_v$ ,  $\text{mm}^2 \text{cm}^{-2}$ ). Subsequently, a 10-cm segment was cut for measurement of wood density ( $\rho$ ,  $\text{g cm}^{-3}$ ) and saturated water content ( $\text{SWC}_{\text{wood}}$ ,  $\text{g g}^{-1}$ ).

Stem vulnerability curves (VCs) were determined using a bench-top dehydration method (see Supplementary Methods 1; Chen et al., 2021). A three-parameter exponential sigmoid function was used to fit the embolism vulnerability curves. Stem water pressures causing 50% ( $P_{50}$ , MPa) and 88% ( $P_{88}$ , MPa) loss of hydraulic conductivity were calculated according to VCs (Figure S3).

Leaf pressure-volume curves ( $P$ - $V$  curves) were determined using a bench dehydration technique (Lenz et al., 2006). Pressure-volume parameters were calculated following Sack et al., (2011) (see methodological details in Supplementary Methods 1 for all measurements and trait definitions/functional meaning in Table S2).

## Seasonal water potential and HSMs

We monitored leaf ( $\Psi_{\text{leaf}}$ ) and stem ( $\Psi_{\text{stem}}$ ) water potentials for 25 species at 2- to 3-month intervals from 2015 to 2017. The minimum  $\Psi_{\text{stem}}$  was used to calculate HSMs (MPa) for each species. We calculated HSM in three ways: (1)  $\text{HSM}_{50} = \text{stem } P_{50} - \text{stem } \Psi_{\text{min}}$  ( $n = 25$  species); (2)  $\text{HSM}_{88} = \text{stem } P_{88} - \text{stem } \Psi_{\text{min}}$  ( $n = 25$  species); and (3)  $\text{HSM}_{\text{tlp}} = \pi_{\text{tlp}} - \text{stem } P_{50}$  ( $n = 37$  species, see methodological details in Supplementary Methods 2).

## Survey of branch dieback and top-kill

We used the term ‘top-kill’ rather than ‘mortality’ to describe individuals that have complete death of above-ground biomass (Hoffmann et al., 2009). We did not assess true mortality because we lack sufficient data to establish whether the individuals regrew or not post-drought. We used the term ‘branch dieback’ to describe individuals that had partial terminal branch death but with living stems. We conducted a top-kill survey (22 species) and a branch dieback survey (29 species) separately. The top-kill ratio was estimated based on two censuses in 2012 and 2017, in a 1-ha permanent plot. We defined top-kill ratio as the percentage of individuals with top-kill to overall living individuals tagged in the first census. We monitored branch dieback in individuals of each species before and after the 2015 drought events. The dieback ratio (%) was calculated as the ratio of the number of individuals with branch dieback over resurveyed individuals for each species (see details in Supplementary Methods).

## Data analysis

All traits were tested for normality and log10-transformed as necessary prior to analysis. Models of trait data assumed normal errors, and models of top-kill and branch dieback ratio data assumed binomial errors as these are both proportions. We used a Bayesian approach to



properly account for differences in sample size (Gelman & Hill, 2007).

We performed a variance partitioning analysis using Bayesian linear mixed models to quantify the ability of leaf habit (evergreen, semi-deciduous and deciduous) and growth form (tree, shrub and liana) to explain the variation in each functional trait and in top-kill and branch dieback data.

We used Bayesian linear mixed model to test for differences in traits, branch dieback ratio and top-kill among leaf habits and growth form. We fitted the models with varying intercepts for leaf habits or growth forms for each variable. To perform multiple comparisons, we applied the Bonferroni corrections for the credible intervals (CI) at the  $\alpha = 0.05$  level (98.3% CI) for each pairwise difference.

To establish which traits affected the drought responses and how they interacted with leaf habit and growth form groups, we modelled the branch dieback and top-kill ratio as a function of a single trait and leaf habit or growth form. An alternative model for demographic rates as a function of all the traits, leaf habit and growth form was considered but not implemented because of the limited sample size. The models above were fitted using the Hamiltonian Monte Carlo (HMC) algorithm implemented in rstanarm (Brilleman et al., 2018; Goodrich et al., 2020).

Additionally, we conducted a principal component analysis (PCA) in R using the 'FactoMineR' package to describe the associations among leaf and stem traits, safety margins and whole-plant variables. We drew the PCA with species points coloured by leaf habit or by growth form to see whether the different groups in each of these classifications were spatially segregated in the biplot. Then, we extracted the first axis of the PCA and tested whether the branch dieback ratio and top-kill data might be significantly related to the first axis and whether the relationship differed by leaf habit or by growth form (separately) using logistic regression. Because the data were over-dispersed, we used the quasibinomial errors. Fitted lines were dropped for groups with prediction confidence intervals that touched zero for all interpolated values.

## RESULTS

### Leaf and stem hydraulic traits

The stem and leaf traits differed substantially among the 40 species studied (Table 1). The  $P_{50}$ ,  $P_{88}$ ,  $H_v$ ,  $MVL$ ,  $\rho_{wood}$ ,  $\rho_{leaf}$ ,  $SWC_{leaf}$ ,  $\pi_o$ ,  $\pi_{tlp}$ ,  $RWC_{tlp}$  and leaf mass per unit area (LMA) varied several-fold across species, whereas  $K_s$ ,  $SWC_{wood}$ ,  $C_{leaf}$  and  $\epsilon$  varied by more than one order of magnitude (Figures S3–S5).

The partitioning of variance in all 21 variables revealed that leaf habit contributed more strongly than

growth form to the variances in most stem and leaf traits that related to drought-resistance, for example,  $P_{50}$ ,  $P_{88}$ ,  $\Psi_{min}$ ,  $\rho_{wood}$ ,  $SWC_{wood}$ , LMA,  $\pi_o$ ,  $\pi_{tlp}$ ,  $SWC_{leaf}$ ,  $C_{leaf}$ ,  $\epsilon$ ,  $RWC_{tlp}$ ,  $\rho_{leaf}$ ,  $HSM_{88}$  and branch dieback ratio (Figure S6). Growth form explained more variance in two traits related to hydraulic efficiency, for example,  $MVL$  and  $K_s$  (Figure S6). Lianas had significantly higher  $K_s$  and  $MVL$  than shrubs and trees (Figure S4).

Species with different leaf habit types had similar  $H_v$  values but were variable in 20 other traits. Specifically, semi-deciduous and evergreen species had similar stem traits that related to drought resistance ( $P_{50}$ ,  $P_{88}$ ,  $\Psi_{min}$ ,  $SWC_{wood}$ ,  $\rho_{wood}$ ,  $HSM_{50}$ ,  $HSM_{88}$  and  $HSM_{tlp}$ ) but not hydraulic efficiency ( $K_s$  and  $MVL$ ). In contrast, deciduous species showed higher  $K_s$ ,  $SWC_{wood}$ , less negative  $P_{50}$ ,  $P_{88}$ ,  $\Psi_{min}$ ,  $\pi_o$ ,  $\pi_{tlp}$ ,  $SWC_{leaf}$  and  $C_{leaf}$  together with lower  $\rho_{wood}$ , LMA and  $\rho_{leaf}$  than evergreen and semi-deciduous species (Table 1). When comparing among the growth forms, tree and lianas showed comparable values for all stem and leaf traits that were related to drought resistance, whereas shrubs differed from trees and lianas in most studied traits (Table 1).

Generally, leaf and stem hydraulic properties related to drought resistance were strongly coordinated (Figure S7); however, these trait correlations differed between leaf habit-type subsets but not for growth form subsets (Figure S7). The 19 leaf and stem variables were analysed using PCA. The first two axes of PCA explained 62.70% of the total variation for the 19 leaf and stem traits (Figure 2), of which the first axis explained 45.31% of the total variation and was positively correlated with xylem embolism resistance traits (stem  $P_{50}$ ,  $P_{88}$  and  $\Psi_{min}$ ), and leaf osmotic regulation ( $\pi_o$ ,  $\pi_{tlp}$ ), but negatively correlated with carbon storage traits, such as  $\rho_{wood}$ ,  $\rho_{leaf}$  and LMA. This reflected a trade-off between drought tolerance strategies on one hand and drought avoidance strategies on the other. The second axis explained 17.39% of the total variation and was related to leaf water storage ( $C_{leaf}$  and  $RWC_{tlp}$ ). Species differing in leaf habit took different positions along the first axis in the PCA diagram (Figure 2a) with deciduous species associated with drought avoidance traits, evergreen species associated with drought tolerance traits and semi-deciduous species in between. Species with different growth forms were more interspersed (Figure 2d).

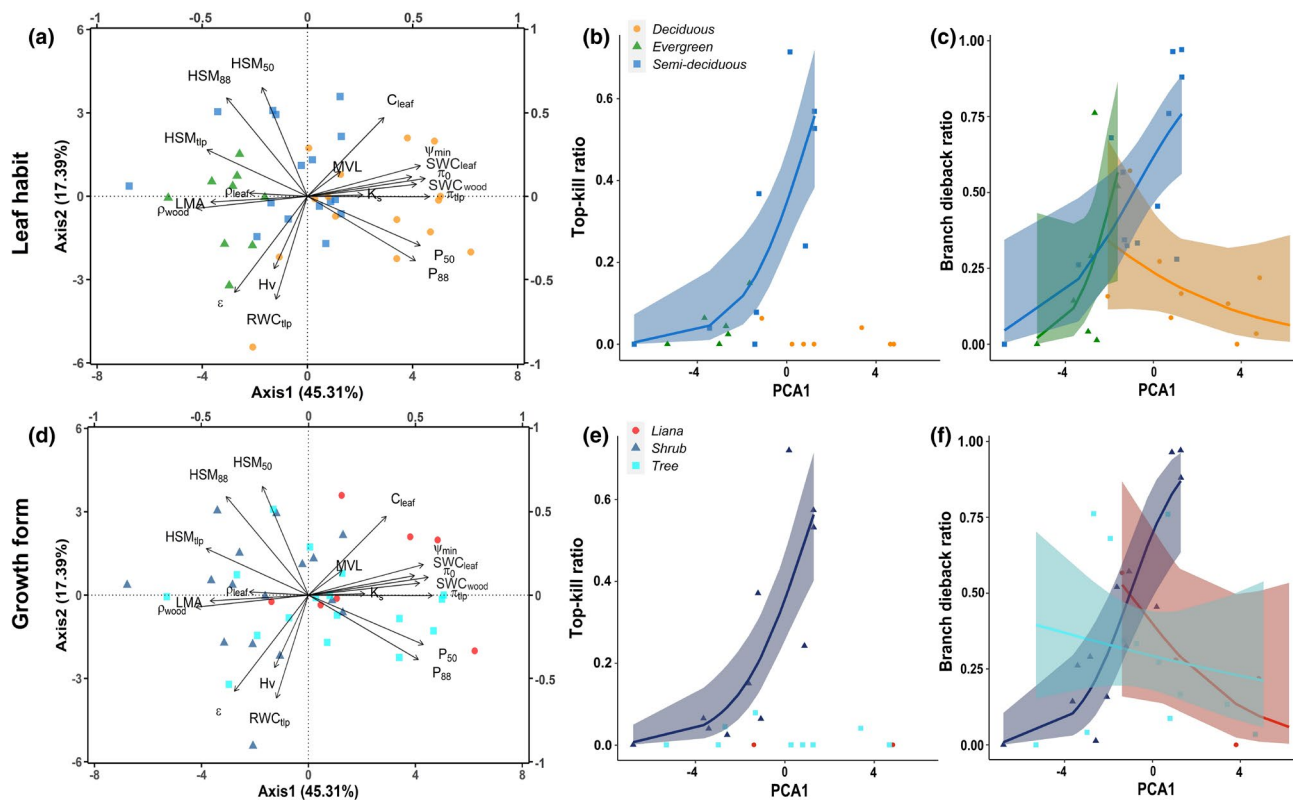
### Seasonal variations in water potential and drought response

During the drought event, the majority of species experienced more negative water potentials than those reported in a previous study in this region (Zhang et al., 2016). The  $\Psi_{min}$  of *Pistacia weinmanniifolia* and *Terminthia paniculata*, two common species, declined from  $-0.88$  to  $-3.81$  MPa and from  $-2.32$  to  $-3.49$  MPa, respectively. During dry periods, the midday water potential of both

**TABLE 1** Comparison on leaf and stem traits, hydraulic safety margins, branch dieback and top-kill ratios among three leaf habit types and three growth forms for 40 species from a hot-dry savanna of southwest China. Values and values in brackets are the posterior mean and the 95% credible interval, respectively. Effects sharing the same letters are not significantly different at the  $\alpha = 0.05$  level (98.3% CI).

Traits	Leaf habit				Growth form		
	Evergreen <i>n</i> = 9	Semi-deciduous <i>n</i> = 16	Deciduous <i>n</i> = 15	Tree <i>n</i> = 17	Shrub <i>n</i> = 16	Liana <i>n</i> = 7	
<b>Stem traits</b>							
$K_s$ ( $\text{kg m}^{-1} \text{s}^{-1} \text{MPa}^{-1}$ )	1.20 [0.66, 2.09] <sup>a</sup>	2.0 [1.38, 2.95] <sup>ab</sup>	2.24 [1.51, 3.39] <sup>b</sup>	1.95 [1.35, 2.75] <sup>a</sup>	1.41 [0.95, 2.09] <sup>ab</sup>	3.31 [1.78, 6.03] <sup>a</sup>	
$P_{50}$ (MPa)	-5.98 [-7.12, -4.80] <sup>a</sup>	-5.15 [-6.01, -4.28] <sup>ab</sup>	-3.66 [-4.74, -2.63] <sup>b</sup>	-4.42 [-5.36, -3.39] <sup>a</sup>	-5.37 [-6.4, -4.42] <sup>a</sup>	-4.45 [-5.71, -2.98] <sup>a</sup>	
$P_{88}$ (MPa)	-10.68 [-12.74, -8.63] <sup>a</sup>	-9.76 [-11.36, -8.16] <sup>a</sup>	-6.65 [-8.62, -4.68] <sup>b</sup>	-8.0 [-9.74, -6.16] <sup>a</sup>	-9.88 [-11.62, -8.21] <sup>a</sup>	-8.95 [-11.2, -6.61] <sup>a</sup>	
MVL (cm)	70.25 [52.38, 86.33] <sup>a</sup>	76.86 [62.69, 92.86] <sup>a</sup>	70.08 [54.45, 84.26] <sup>a</sup>	62.84 [47.76, 77.83] <sup>a</sup>	70.66 [55.94, 85.36] <sup>a</sup>	101.88 [76.07, 125.54] <sup>b</sup>	
Hv ( $\text{mm}^2 \text{cm}^{-2}$ )	1.98 [1.36, 2.67] <sup>a</sup>	1.88 [1.36, 2.36] <sup>a</sup>	1.98 [1.47, 2.52] <sup>a</sup>	1.87 [1.34, 2.39] <sup>a</sup>	2.04 [1.55, 2.59] <sup>a</sup>	1.82 [1.07, 2.45] <sup>a</sup>	
$\Psi_{\min}$ (MPa)	-4.53 [-5.59, -3.47] <sup>a</sup>	-3.83 [-4.6, -3.09] <sup>ab</sup>	-2.76 [-4.0, -1.56] <sup>b</sup>	-3.51 [-4.38, -2.56] <sup>a</sup>	-4.05 [-4.92, -3.22] <sup>a</sup>	-3.48 [-4.65, -2.01] <sup>a</sup>	
$\rho_{\text{wood}}$ ( $\text{g cm}^{-3}$ )	0.73 [0.65, 0.81] <sup>a</sup>	0.66 [0.6, 0.72] <sup>a</sup>	0.49 [0.42, 0.55] <sup>b</sup>	0.58 [0.51, 0.64] <sup>a</sup>	0.70 [0.63, 0.77] <sup>b</sup>	0.48 [0.38, 0.59] <sup>a</sup>	
SWC <sub>wood</sub> ( $\text{g g}^{-1}$ )	0.62 [0.47, 0.79] <sup>a</sup>	0.71 [0.59, 0.87] <sup>a</sup>	1.20 [0.98, 1.48] <sup>b</sup>	0.91 [0.74, 1.12] <sup>a</sup>	0.66 [0.52, 0.83] <sup>ab</sup>	1.20 [0.85, 1.7] <sup>a</sup>	
<b>Leaf traits</b>							
$\pi_0$ (MPa)	-2.27 [-2.49, -2.04] <sup>a</sup>	-1.83 [-2.0, -1.65] <sup>b</sup>	-1.49 [-1.68, -1.32] <sup>c</sup>	-1.8 [-2.0, -1.6] <sup>a</sup>	-1.89 [-2.13, -1.68] <sup>a</sup>	-1.71 [-1.96, -1.39] <sup>a</sup>	
$\pi_{\text{tip}}$ (MPa)	-2.88 [-3.09, -2.66] <sup>a</sup>	-2.34 [-2.51, -2.18] <sup>b</sup>	-1.88 [-2.06, -1.71] <sup>c</sup>	-2.28 [-2.51, -2.05] <sup>a</sup>	-2.4 [-2.67, -2.15] <sup>a</sup>	-2.19 [-2.48, -1.84] <sup>a</sup>	
SWC <sub>leaf</sub> ( $\text{g g}^{-1}$ )	1.29 [1.0, 1.66] <sup>a</sup>	1.62 [1.35, 1.95] <sup>a</sup>	2.4 [1.95, 3.02] <sup>b</sup>	1.74 [1.41, 2.14] <sup>a</sup>	1.66 [1.32, 2.04] <sup>a</sup>	2.04 [1.55, 2.88] <sup>a</sup>	
$C_{\text{leaf}}$ ( $\text{mol m}^{-2} \text{MPa}^{-1}$ )	0.44 [0.30, 0.6] <sup>a</sup>	0.52 [0.41, 0.69] <sup>a</sup>	0.54 [0.41, 0.72] <sup>a</sup>	0.47 [0.35, 0.6] <sup>a</sup>	0.52 [0.40, 0.69] <sup>b</sup>	0.58 [0.42, 0.87] <sup>a</sup>	
$\epsilon$ (MPa)	22.39 [15.49, 31.62] <sup>a</sup>	12.88 [10, 16.6] <sup>b</sup>	14.13 [10.96, 18.2] <sup>b</sup>	16.22 [12.88, 20.42] <sup>a</sup>	15.49 [12.30, 19.95] <sup>a</sup>	13.49 [9.33, 18.20] <sup>a</sup>	
RWC <sub>tip</sub> (%)	87.19 [84.28, 90.67] <sup>a</sup>	84.51 [81.65, 87.05] <sup>a</sup>	86.31 [83.83, 88.98] <sup>a</sup>	86.32 [84.08, 88.88] <sup>a</sup>	85.62 [83, 87.99] <sup>a</sup>	85.31 [82.17, 88.01] <sup>a</sup>	
LMA ( $\text{g cm}^{-2}$ )	144.54 [120.23, 177.83] <sup>a</sup>	91.2 [79.43, 104.71] <sup>b</sup>	67.61 [57.54, 79.43] <sup>c</sup>	87.1 [70.79, 104.71] <sup>a</sup>	104.71 [85.11, 134.9] <sup>b</sup>	79.43 [58.88, 102.33] <sup>a</sup>	
$\rho_{\text{leaf}}$ ( $\text{g cm}^{-3}$ )	0.62 [0.5, 0.76] <sup>a</sup>	0.6 [0.51, 0.71] <sup>a</sup>	0.48 [0.39, 0.58] <sup>a</sup>	0.55 [0.48, 0.65] <sup>a</sup>	0.56 [0.48, 0.66] <sup>a</sup>	0.55 [0.46, 0.66] <sup>a</sup>	
<b>Safety margins</b>							
HSM <sub>50</sub> (MPa)	1.51 [0.54, 2.51] <sup>a</sup>	1.6 [0.82, 2.41] <sup>a</sup>	1.29 [0.18, 2.22] <sup>a</sup>	1.48 [0.64, 2.3] <sup>a</sup>	1.52 [0.74, 2.35] <sup>a</sup>	1.49 [0.38, 2.52] <sup>a</sup>	
HSM <sub>88</sub> (MPa)	6.23 [4.28, 8.52] <sup>a</sup>	6.25 [4.76, 7.95] <sup>a</sup>	4.74 [2.12, 6.9] <sup>a</sup>	5.37 [3.43, 7.03] <sup>a</sup>	6.26 [4.61, 8.07] <sup>b</sup>	6.2 [4.04, 8.84] <sup>b</sup>	
HSM <sub>tip</sub> (MPa)	3.30 [2.03, 4.69] <sup>a</sup>	3.02 [2.05, 4.06] <sup>a</sup>	1.9 [0.64, 3.09] <sup>a</sup>	2.17 [1.03, 3.28] <sup>a</sup>	3.51 [2.40, 4.63] <sup>b</sup>	1.87 [0.28, 3.29] <sup>a</sup>	
<b>Whole-plant performance</b>							
Branch dieback ratio (%)	23.87 [18.24, 30.36] <sup>a</sup>	52 [46.75, 57.2] <sup>b</sup>	19 [14.31, 24.23] <sup>a</sup>	30.36 [25.54, 35.66] <sup>a</sup>	41.34 [36.35, 46.26] <sup>b</sup>	29.94 [21.93, 38.23] <sup>a</sup>	
Top-kill ratio (%)	5.37 [3.29, 8.32] <sup>a</sup>	28.5 [25.73, 31.22] <sup>b</sup>	2.66 [1.37, 4.74] <sup>a</sup>	4.65 [3.36, 6.36] <sup>a</sup>	32.52 [29.53, 35.89] <sup>b</sup>	0.38 [0.0, 4.74] <sup>a</sup>	

Note: (1) Trait abbreviations and functional meanings are provided in Table S2. (2) Those seven traits were modeled in the log-scale but are shown in non-log scale:  $K_s$ , SWC<sub>wood</sub>, SWC<sub>leaf</sub>,  $C_{\text{leaf}}$ , LMA and  $\rho_{\text{leaf}}$ .



**FIGURE 2** Principal-component analysis of leaf traits, stem traits, hydraulic and safety margins, and first axis relationships with top-kill and branch dieback ratios. Species are grouped based on their leaf habits (a–c) and their growth forms (d–f). Fitted lines with 95% confidence intervals follow logistic regressions of species' top-kill and branch dieback values against PCA1 scores, structured by leaf habit or by growth form

leaves and stems fell below  $P_{50}$  in two out of seven evergreen species, four of 12 semi-deciduous species and two of five deciduous species. The deciduous species had less negative stem water potentials than evergreen and semi-deciduous species (Figure S8).

Ten out of the 25 species selected for water potential measurements had narrow ( $< 1$  MPa) or even negative hydraulic safety margins ( $HSM_{50}$ , Figure 3c). In contrast, 10 species, including two evergreen, seven semi-deciduous, and one deciduous species had an  $HSM_{50} > 2$  MPa. Compared to evergreen and semi-deciduous species, deciduous species had relatively high  $HSM_{50}$  values (Table 1). When a more conservative safety margin was applied ( $HSM_{88}$ ), all 25 species had positive values, with  $HSM_{88} > 1.5$  MPa. In contrast, seven out of 37 species for which we had  $HSM_{tip}$  data showed values  $< 1$  MPa.

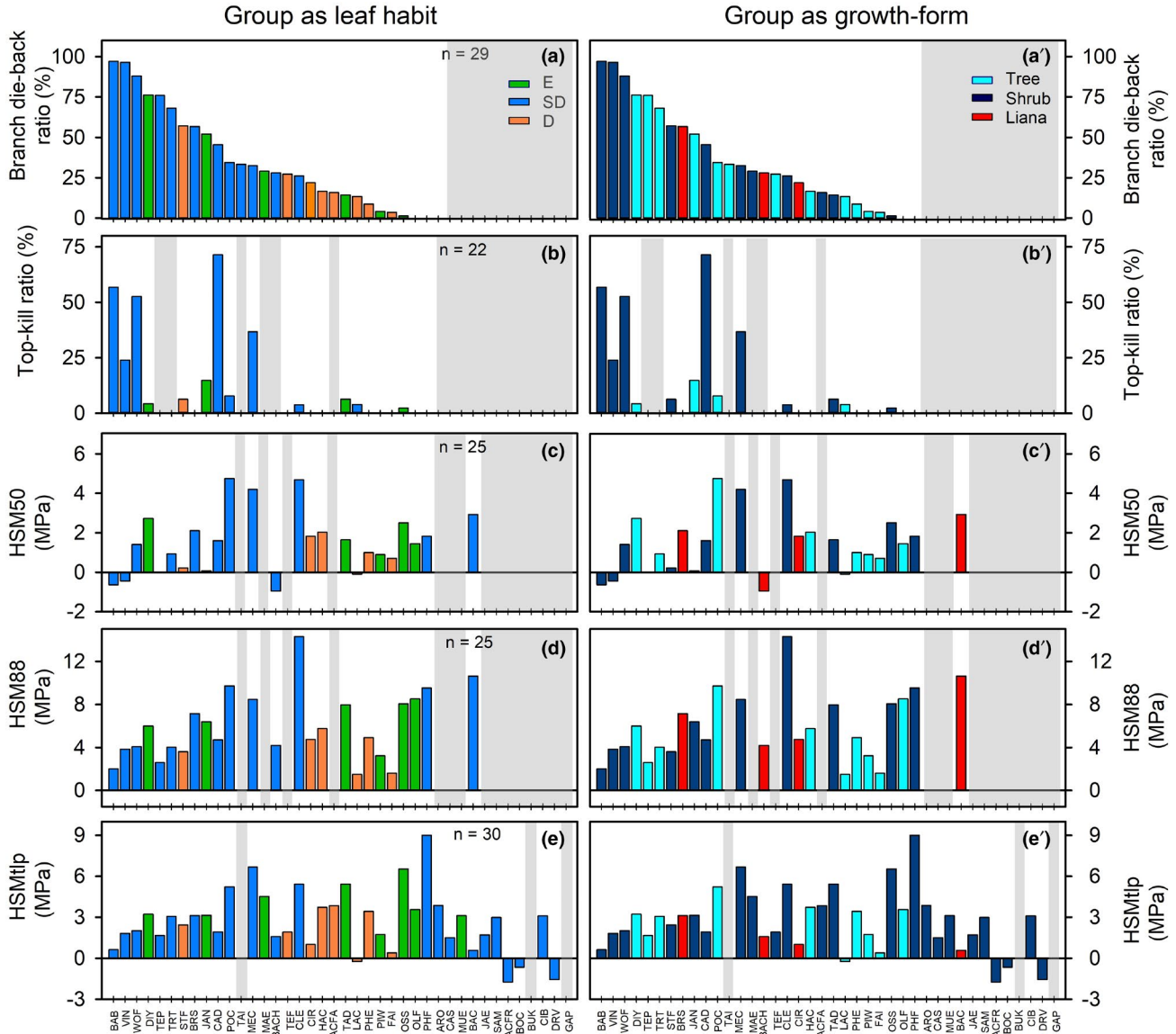
The branch dieback ratio differed substantially among species, ranging from 0% for three species (*Olea ferruginea*, *Phyllanthus urinaria*, and *Argyrea osyrensis*) to approximately 97% in two semi-deciduous species (*Bauhinia brachycarpa*, *Vitex negundo* var. *cannabifolia*; Figure 3). Semi-deciduous species showed a higher branch dieback and top-kill than the evergreen and deciduous species (Figure 3 and Table 1). The 22 targeted species in the 1-ha monitoring plot showed distinctive top-kill ratios among species, ranging from zero to 70%

for a semi-deciduous species (*Campylotropis delavayi*, Figure 3). However, when comparing growth forms, shrubs had much higher branch dieback and top-kill ratios than trees or lianas (Figure 3 and Table 1).

### Relationships between leaf traits, stem traits, and drought response

We found species differing in leaf habit spread along the first PCA axis with evergreen species showing high stem drought resistance traits and high tissue density traits. In contrast, deciduous species were associated with low drought resistance but high capacitance traits (Figure 2a). Species of different growth forms were more interspersed, although shrubs were more common on the negative side of the first axis and lianas were more common on the positive side (Figure 2b). With respect to whole-plant responses, top-kill was only significantly related to semi-deciduous species among leaf habit groups, with increased ratio towards the middle of PCA1 and low ratio at both the tolerance-strategy and the avoidance-strategy ends.

Similarly, branch dieback ratio differed within leaf habit and growth form groups. Both the highest top-kill and highest branch dieback were observed in the middle of the PCA1, with lower top-kill towards either



**FIGURE 3** Branch dieback, top-kill, and hydraulic safety margins (HSM) in relation to different leaf habits (a–e) and growth forms (a’–e’), respectively. We defined HSM following three methods:  $HSM_{50} = \Psi_{min} - P_{50}$ ;  $HSM_{88} = \Psi_{min} - P_{88}$ ;  $HSM_{tip} = \pi_{tip} - P_{50}$ . Species are ordered from high to low branch dieback ratio, and grey areas indicate missing data. Species and trait abbreviations are shown in Table 1, Tables S1 and S2

end. Branch dieback ratio was largely associated with hydraulic traits in semi-deciduous and evergreen species, and to some extent in deciduous species (Figure 4), whereas top-kill was explained by hydraulic traits only in semi-deciduous species (Figure 5). Tighter relationships between hydraulic traits and branch dieback or top-kill were found when combining evergreen and semi-deciduous species but excluding deciduous species when analyzing each group separately (Figures S9 and S10).

When comparing growth forms, branch dieback and top-kill ratios were mainly explained by hydraulic traits for shrubs, unlike trees or lianas (Figures S11 and S12). We found that  $P_{50}$ ,  $P_{88}$ ,  $HSM_{50}$ ,  $HSM_{88}$  and  $HSM_{tip}$  were good predictors of branch dieback and top-kill ratio for semi-deciduous species and shrub species, and only for

branch dieback in the case of evergreen species (Figures 4, 5 and Figures S11, S12).

## DISCUSSION

Our results highlight the importance of considering growth form and leaf habit in research on drought-induced mortality and dieback. Species differing in leaf habit in a tropical semi-arid savanna region diverge in stem hydraulic traits related to either drought resistance or drought avoidance. The data showed that drought-induced branch dieback and top-kill were substantially different among leaf habits and among growth forms. Semi-deciduous and shrub species showed the highest branch dieback and top-kill caused by extreme drought





**FIGURE 4** The relationships between branch dieback ratio, leaf habits and leaf and stem traits. Each dot represents the mean value of a species. The solid lines indicate the posterior mean of the dieback ratio, and the shaded regions represent 95% credible intervals (CI) of the posterior distributions. The posterior means of Bayesian  $r^2$  are shown in each panel. Note that the model with leaf habit alone explained 28% of the variances in branch dieback ratio ( $r^2 = 0.28$ ). Acronyms are shown in Table S2. Note: outliers are excluded from the regression analysis but are shown as grey symbols

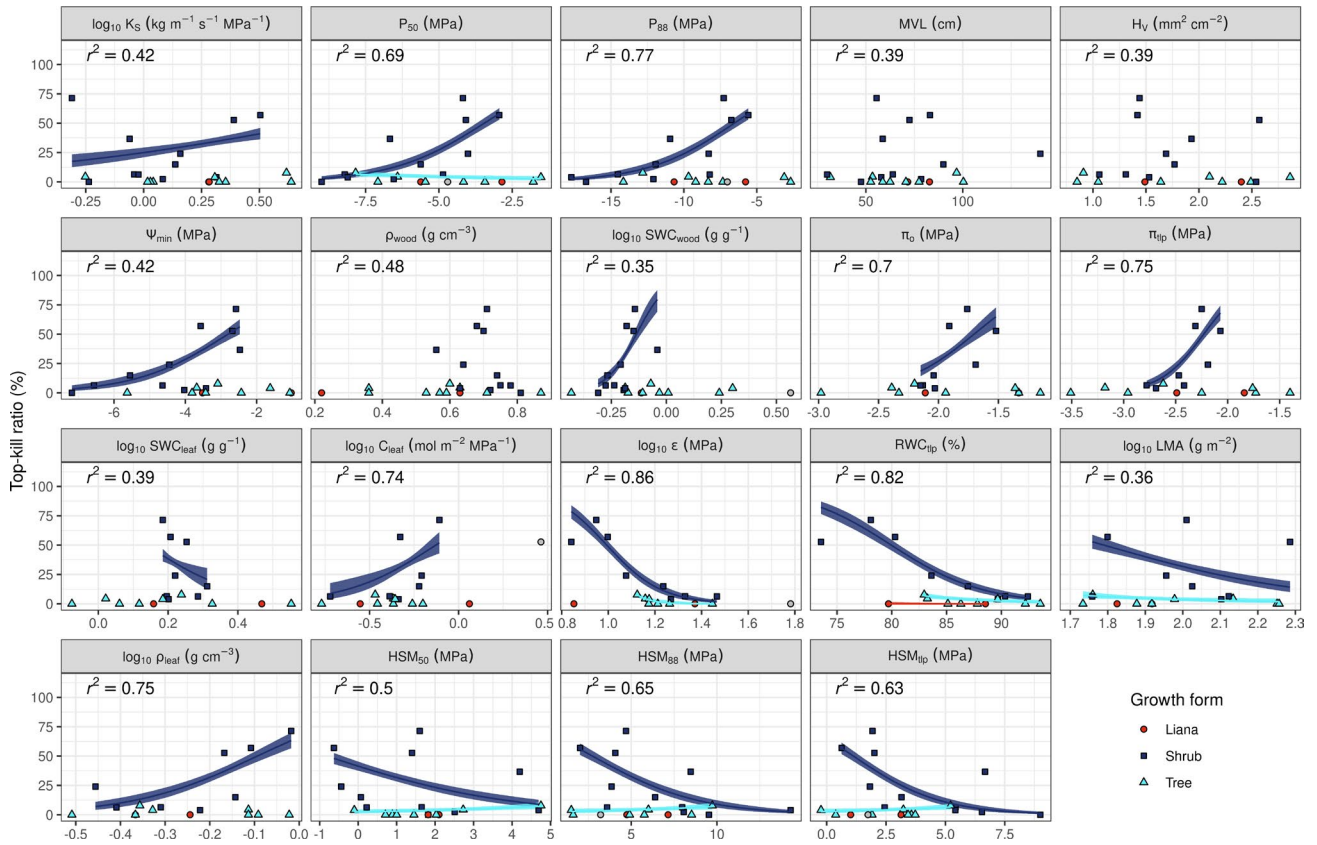
during the 2015 strong El Niño. Overall, widely used hydraulic safety traits, such as  $P_{50}$ ,  $P_{88}$ , safety margins and  $\pi_{tip}$ , explained the drought-induced branch dieback and top-kill to a great extent, but these were also dependent on leaf habit and growth form.

### Variation in plant hydraulic traits in relation to leaf habit and growth form

A recent study showed that canopy leaf persistence, an ordinal variable, was a better predictor of whole-plant scale physiology than the commonly used categorical term ‘leaf habit’ in 10 Sonoran desert tree species (Gonzales-Rebelez et al., 2021). However, our results confirmed the usefulness of categorical terms. Evergreen species showed denser leaves, denser wood and more embolism-resistant xylem as well as more negative water potentials and lower saturated water content when compared with deciduous species (Choat et al., 2005). Generally, a lower  $\pi_{tip}$  indicates greater drought tolerance (Bartlett et al., 2012; Zhu et al., 2018). The more negative  $\pi_{tip}$  and  $\pi_o$  values in evergreen species may enable carbon assimilation at lower leaf water potentials

than in deciduous or semi-deciduous species (Table 1). Evergreen species may continue to extract soil water at lower water potentials and maintain water transport and stomatal conductance for a longer time during drought than deciduous species. In contrast, deciduous species showed a lower tolerance to leaf desiccation and less resistance to stem embolism, whilst deciduousness allowed species to avoid very negative xylem water potentials under persistent drought (Table 1). However, the longer growth period of semi-deciduous species increases the risk of hydraulic failure, potentially making them more susceptible to catastrophic hydraulic failure under severe drought (Kukowski et al., 2013), which may explain the high branch dieback ( $52.5 \pm 8.5\%$ ) and top-kill ( $28.2 \pm 9.1\%$ ) ratio recorded here for semi-deciduous species (Figure 3).

Among growth forms, trees and lianas had relatively more negative  $P_{50}$  and  $P_{88}$  values compared to shrubs. The lianas are usually reported to be susceptible to embolism, whereas the lianas in our study had a relatively lower  $P_{50}$  and  $P_{88}$  than previous studies in tropical wet forests (De Guzman et al., 2017; van der Sande et al., 2019; Zhang et al., 2019; Zhu & Cao, 2009). Greater embolism resistance of lianas in savannas may help them to



**FIGURE 5** The relationships between top-kill ratio, leaf habits and leaf and stem traits. Each dot represents the mean value of a species. The solid lines indicate the posterior mean of the top-kill ratio, and the shaded regions represent 95% credible intervals (CI) of the posterior distributions. The posterior means of Bayesian  $r^2$  are shown in each panel. Note that the model with leaf habit alone explained 34% of the variance in top-kill ratio ( $r^2 = 0.34$ ). Acronyms are shown in Table S2. Note: outliers are excluded from the regression analysis but are shown as grey symbols

cope with drought (De Deurwaerder et al., 2018; Smith-Martin et al., 2020).

### To what extent do hydraulic traits account for branch dieback and/or top-kill?

Generally, branch dieback (0% to 97.1%, with a mean of 35.3%) and top-kill (0% to 71.4%, with a mean of 13.3%) were relatively high in our savanna site (Figure 3 and Table 1). In contrast, Powers et al., (2020) reported 0% to a high of 34% annual mortality rate (aboveground and belowground death) for tropical trees caused by the same El Niño in 2015. However, high top-kill mainly occurred in semi-deciduous species and not in evergreen or deciduous species, and in shrub species but not in liana and tree species (Figure 3 and Table 1). Therefore, we emphasise the importance of the life history in mediating drought responses in savanna systems.

Semi-deciduous species have a relatively higher embolism resistance than deciduous species, whereas the findings suggest their tolerance strategy may only be favoured under moderate drought but may not be

useful in case of extreme drought, as occurred during the strong El Niño phenomenon in 2015. This finding supports a recent study that showed species with strong drought-resistant stems (more negative  $P_{50}$ ) ultimately experience higher mortality when exposed to extreme drought because these species continue to function during drought and hence are likely to reach more negative internal water potentials (Anderegg et al., 2019). Nevertheless, the persistence of semi-deciduous species in this savanna site indicates that in most years, dry season conditions are mild enough to support their leaf habit.

Unlike liana and tree species, shrubs showed a strong resistance to embolism yet still had the highest branch dieback and top-kill ratios among growth forms (Figure 3). It is likely that the smaller stature of shrubs may have compromised their water connectivity more than that of taller trees and lianas, whereas trees and lianas may have deeper roots to enable them to use ground water. It has been reported that lianas appear to have deep roots (Chen et al., 2015) and strong stomatal control (Chen et al., 2017) to cope with drought, which may partially explain their low top-kill ratio.

It is reported that woody plants in dry environments show a more segmented hydraulic system than those in wet habitats (Schenk et al., 2008), and growth of multiple, segmented basal stems (i.e., modular systems) represent a common syndrome of plants in arid systems (Anest et al., 2021). Moreover, the degrees of modularity also differ among growth forms. Compared with liana and tree species, shrubs have greater functional redundancy, with the possibility to isolate systems with hydraulic dysfunction from remaining, functional ones, helping to increase their genet survival through droughts. Therefore, high top-kill may not be directly related to lower performance for these species, because aboveground death may be compensated for by their vigorous, resprouting capacity (Bond & Midgley, 2001).

Understanding the mechanisms underlying drought-induced plant mortality during and after drought events and the prediction of such occurrence is a long standing and challenging scientific question (Trugman et al., 2021). Although great efforts have been made in the past decades to incorporate plant hydraulics into models, the accuracy of prediction of drought-induced mortality continues to be debated (Trugman et al., 2021). Our results provided clear evidence that widely used hydraulic traits, for example,  $P_{50}$ ,  $P_{88}$  and HSMs, can explain the plant drought responses, as found in other recent studies (Hammond et al., 2019; Powers et al., 2020). However, we propose that these associations may differ for species with a given leaf habit or growth form. Notably, most of the studied species had positive HSMs (Figure 3). As we used the minimum water potentials during extreme drought to calculate HSMs, positive HSMs suggest that plants may not approached the point of catastrophic hydraulic failure, such as  $P_{50}$ . Therefore, although hydraulic traits could be predictors of drought-induced mortality, other indirect mechanisms, such as decreased carbon assimilation and tissue desiccation due to loss of hydraulic conductivity, may be equally important determinants of tree death (Oliveira et al., 2021; Trugman et al., 2021). An alternative explanation is that the minimum water potentials measured during our experiment represent a seasonal average, whilst extreme water potentials occurring in plants under extreme conditions (e.g., extremely hot days) were not captured. Moreover, embolism resistance parameters ( $P_{50}$  and  $P_{88}$ ) provide a threshold for hydraulic failure (Choat et al., 2018). It is equally important to understand the time taken to reach the threshold water potential required for hydraulic failure, which requires knowledge of a range of other traits such as canopy area, stomatal closure, rooting depth, cuticular conductance and internal water storage (Blackman et al., 2019; Blackman et al., 2016; Martin-StPaul et al., 2017). Thus, instead of a single-mechanism-based model, an integrated model is essential for accurately predicting drought-induced plant responses to future drought (Trugman et al., 2021).

## CONCLUSION

Our findings provide evidence that semi-deciduous and shrub species had higher branch dieback and top-kill than other savanna plant groups under an extreme drought event in 2015. We found that drought-induced branch dieback and top-kill were largely explained by plant hydraulic traits (e.g.,  $P_{50}$ ,  $P_{88}$ , safety margins and  $\pi_{tip}$ ), but the prediction power largely depended on leaf habit and growth form. These findings shed light on the importance of combining plant hydraulic traits with life history in trait-based predictions of plant responses to drought.

## ACKNOWLEDGEMENTS

The authors wish to thank Lian-bin Tao, Song Lv, Ai-Guo Chen and Wan-You Dao for their assistance with field measurements, and Yun-Hong Tan for species identification. We are grateful to the three anonymous reviewers who provided very constructive suggestions on this manuscript. The Yuanjiang Savanna Ecosystem Research Station of XTBG provided climate and survey data and supported the field work. This work was funded by the National Natural Science Foundation of China (Nos: 41861144016, 31570406, 32071735, 31861133008), Youth Innovation Promotion Association (No. 2016351) and 'Light of West China' Program and Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences (151C53KYSB20200019), the CAS 135 program (Nos. 2017XTBG-T01, 2017XTBG-F01), and Yunnan Provincial Science and Technology Department (2018HB068). PM acknowledges financial support from CAS-TWAS President's Fellowship for International Doctoral Students. SJ and CKF acknowledge financial support from a joint DFG-NSFC project (No. 410768178). MK acknowledges CAS President's International Fellowship Initiative (2020FYB0003). RSO acknowledges the CNPq productivity scholarship.

## AUTHOR CONTRIBUTIONS


YJC designed the study. YJC, MP, SBZ and JXS carried out the measurement. YJC, MP, MK, KT, SBZ and KFC analysed the results. YJC, FS and SJ led the manuscript writing, with additional contributions from BC, KT, YJZ, RSO and KFC. All other authors contributed to discussions and revised the final version of the manuscript.

## DATA AVAILABILITY STATEMENT

Authors confirm that, if the manuscript is accepted, all the data supporting the results will be archived in an appropriate public repository such as Dryad.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Chen, Y.-J., Choat, B., Sterck, F., Maenpue, P., Katabuchi, M., Zhang, S.-B., et al (2021) Hydraulic prediction of drought-induced plant dieback and top-kill depends on leaf habit and growth form. *Ecology Letters*, 00, 1–14. <https://doi.org/10.1111/ele.13856>