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Physiological response and photosynthetic recovery to an extreme drought: Evidence from plants in a dry-hot valley savanna of Southwest China

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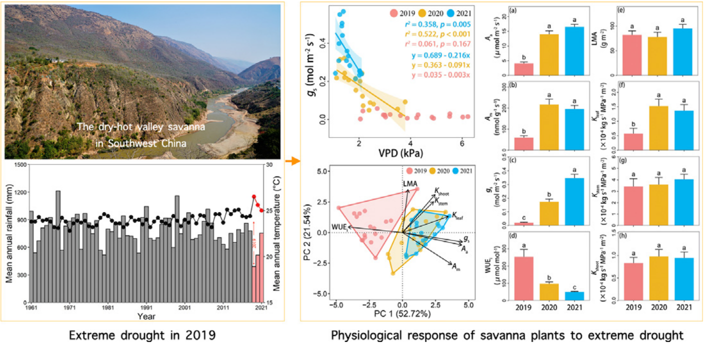
HIGHLIGHTS

- Extreme drought affected leaf hydraulic and stomatal conductance but not stem hydraulic conductance.
- Under extreme drought savanna plants showed strong stomatal control.
- After extreme drought leaf stomatal conductance and photosynthesis recovered.
- Physiological response to extreme drought was similar among leaf habits and growth forms.

GRAPHICAL ABSTRACT



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ABSTRACT

The frequency of extreme drought events has been rising worldwide, but due to its unpredictability, how plants will respond remains poorly understood. Here, we aimed to characterize how the hydraulics and photosynthesis of savanna plants respond to extreme drought, and tested whether they can subsequently recover photosynthesis after drought. There was an extreme drought in 2019 in Southwest (SW) China. We investigated photosynthetic gas exchange, leaf-, stem-, and whole-shoot hydraulic conductance of 18 plant species with diverse leaf habits (deciduous, semi-deciduous and evergreen) and growth forms (tree and shrub) from a dry-hot valley savanna in SW China for three rainy seasons from 2019 to 2021. We also compared photosynthetic gas exchange to those of a regular year (2014). We found that leaf stomatal and hydraulic conductance and maximum photosynthetic rate were significantly lower during the drought in 2019 than in the wetter years. In 2019, all studied plants maintained stomatal conductance at their minimum level observed, which could be related to high vapor pressure deficits (VPD, >2 kPa). However, no significant difference in stem and shoot hydraulic conductance was detected across years. The reductions in leaf hydraulic conductance and stomatal regulation under extreme drought might help keep the stem hydraulic function. Stomatal conductance and photosynthesis after drought (2020 and 2021) showed comparable or even higher values compared to that of 2014, suggesting high recovery of photosynthetic gas exchange. In addition, the response of hydraulic and photosynthetic traits to extreme drought was convergent across leaf habits and growth forms. Our results will help better understand the physiological mechanism underlying the response of savanna ecosystems to climate change.

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1. Introduction

The severity and frequency of drought has been rising over recent decades and will continue to intensify due to climate change (Coumou and Rahmstorf, 2012; Trenberth et al., 2014; IPCC, 2016; Naumann et al., 2018; Yu and Zhai, 2020). Extreme drought events can affect plant physiological function and growth (Anderegg et al., 2015), and impact productivity and mortality (McDowell et al., 2011; Choat et al., 2018; Xu et al., 2019; McDowell et al., 2022). Therefore, revealing the physiological mechanisms of how plants respond to extreme drought is of paramount importance for predicting plant performance under future climate change.

The physiological response of plants to extreme drought events has received significant attention globally (McDowell et al., 2008, 2011; Martin-StPaul et al., 2017; Choat et al., 2018; Creek et al., 2018). However, for many studies on physiological responses to extreme drought, drought treatments were applied to fully developed plant tissues under controlled experimental conditions. The response of plants to natural extreme drought may be different compared to that under a controlled environment. Natural drought events can happen during the leaf expansion period and/or leaf maturity stage, whereas controlled drought experiments are generally carried out when plant leaves become mature. In addition, the timing of drought matters; drought in different seasons has distinct impacts on plant physiology and growth (van Kampen et al., 2022). The difficulty of timing field measurements of physiological traits to coincide with extreme drought events limits our capacity to predict the physiological response of plants to natural droughts (Skelton et al., 2017; Arend et al., 2021).

There are many physiological mechanisms for plants coping with drought stress (Pivovaroff et al., 2016; Oliveira et al., 2021; Hajek et al., 2022), including timely stomatal closure (Hochberg et al., 2017), leaf xylem embolism and shedding (Brodribb and Holbrook, 2003), and utilization of shoot water storage (Zhang et al., 2013; Bryant et al., 2021). Timely closure of stomata can minimize plant water loss via transpiration and thus protect the water-transport system against a drought-induced hydraulic failure (Brodribb and Holbrook, 2003; Blackman et al., 2009; Martínez-Vilalta and Garcia-Forner, 2017), and even avoid soil water potential decline around roots (Carminati et al., 2020). Such stomatal closure will depress leaf gas exchange and photosynthetic rates (Schulze et al., 1974; Iio et al., 2004) and may decrease carbon supply (Anderegg et al., 2012; McDowell et al., 2022). Plants can also minimize drought-induced hydraulic dysfunction and catastrophic hydraulic failure through leaf-stem hydraulic segmentation (Zimmermann, 1983). High resistance in leaves can act as a bottleneck or 'safety valve' and can be sacrificed under unfavorable water conditions to protect more carbon-costly basal parts (stems) (Bucci et al., 2013; Pivovaroff et al., 2014; Scholz et al., 2014; Levionnois et al., 2020). The degree of segmentation varies among species (Pivovaroff et al., 2014; Levionnois et al., 2020). Theoretically, a combination of a timely stomata regulation and then sacrificing leaves could protect the costly stem hydraulic integrity under natural extreme droughts, although there is very limited direct field evidence to test this hypothesis under natural extreme drought.

The responses to drought events may differ among plant functional groups (i.e., leaf habit and growth form) (Chen et al., 2021; Oliveira et al., 2021). For example, plant drought-induced xylem embolism or dieback is related to differences in leaf habits (deciduous, semi-deciduous and evergreen) in savannas (Chen et al., 2021). Under extreme drought, deciduous species generally shed their leaves and avoid catastrophic hydraulic failure (Singh and Kushwaha, 2016; Gonzalez-Rebeles et al., 2021), while evergreen species must tolerate drought stress (Kukowski et al., 2013; Oliveira et al., 2021). In addition, shrubs growing in semi-arid environments tend to have more modular water transport systems and multiple aboveground stems with high redundancy (Schenk et al., 2008; Anest et al., 2021). The semi-deciduous shrubs have higher drought-induced branch dieback than other co-existing growth forms, i.e., tree or liana (Chen et al., 2021). These findings suggest that plants with different leaf habits and growth forms may have distinct responses to extreme drought.

Savannas are one of the most important vegetation types in the world, covering 20 % of land surface and accounting for 30 % of net primary production (Scholes and Archer, 1997; Field et al., 1998). Savannas are widely distributed in tropical and subtropical regions of Africa, South America, Australia, and Asia (Solbrig et al., 1996; Scholes and Archer, 1997; Lehmann et al., 2014; Ratnam et al., 2016). In southwestern China, moist monsoon from the Indian Ocean is blocked by the eastern extensions of the Himalayan Mountains, which reduces precipitation. Thus, valley savannas under a dry-hot climate with distinct dry seasons are formed in the river valleys between these mountains (Wu, 1995; Yao et al., 2012). The dry-hot valley savanna vegetation with diverse woody plant species includes different leaf habits (deciduous, semi-deciduous, and evergreen) and growth forms (tree, shrub, and liana) (Chen et al., 2021). In 2019, a valley savanna in Yuanjiang, China experienced an extreme drought with the lowest annual rainfall, and the highest temperatures in the past 61 years (Fig. 1), with the drought starting at the beginning of the regularly rainy season (Fig. S1). This extreme drought event in 2019 gave us a unique chance to test how woody plants across diverse functional groups physiologically respond to a natural extreme drought.

In this study, we measured hydraulic conductance of leaf, stem and whole-shoots, leaf gas exchange, and leaf mass per area of 18 common woody species during three rainy-seasons from 2019 to 2021 in a dry-hot valley savanna. Leaf gas exchange during and after the drought was also compared to that of a regular pre-drought year (2014). We investigated how hydraulic traits and gas exchange parameters of savanna plants with different leaf habits (deciduous, semi-deciduous and evergreen) or growth forms (tree and shrub) respond to the extreme drought in 2019. We hypothesized that leaf stomatal conductance (g_s) and leaf hydraulic conductance were significantly lower during the drought year compared to subsequent wetter years, while g_s and maximum photosynthetic rates could recover largely in subsequent wet years compared to 2014. Given that g_s is sensitive to changes in vapor pressure deficit (VPD) and high VPD can cause stomatal closure (Martin-StPaul et al., 2017), we hypothesized a significantly negative relationship between g_s and VPD across years, while the low g_s in the extreme drought year was associated with high VPD. Furthermore, since deciduous plants generally use a drought-avoidance strategy and evergreen species are more drought-resistant (Anderegg et al., 2019; Chen et al., 2021), we also hypothesized that leaf stomatal conductance and maximum photosynthetic rates would decrease more in deciduous plants than in evergreen counterparts in the extreme drought year.

2. Materials and methods

2.1. Study site

The study was conducted in a valley savanna near the Yuanjiang Savanna Ecosystem Research Station (YSERS; 102°10′34″E, 23°28′25″N, elevation of 481 m) of the Xishuangbanna Tropical Botanical Garden, CAS, located in Yuanjiang County, Yunnan Province, Southwestern China. This is a typically dry-hot valley with rainy (May to October) and dry (November to April) seasons. The mean annual rainfall and mean annual temperature is 782 mm, and 24 °C for 1961–2021. According to the monitoring records of the meteorological station in YSERS of 2012–2021 (the station was established in 2011), 76.5 % of the precipitation falls in the rainy season, while the mean annual potential evaporation is 1750 mm. The mean annual air temperature and extreme maximum and minimum temperatures are 25.0 °C, 45.0 °C and 3.6 °C, respectively. The mean annual ground temperature and extreme maximum and minimum ground temperature are 28.8 °C, 77.9 °C and 2.1 °C, respectively. The mean annual air humidity is 67.3 %, and the mean annual sunshine hours are 2350 h. The soil type of this site is ferralic cambisol with pH value of 6.63–7.75, soil nitrogen of 0.196–0.427 %, soil phosphorus of 0.055–0.12 % and soil potassium of 1.601–1.737 % within 0–20 cm depth (Zhang et al., 2012).

This region has a typical dry-hot valley savanna vegetation with diverse plant species, including the tree layer dominated by *Lannea coromandelica*, *Terminthia paniculata*, *Polyalthia cerasoides* and *Haldina cordifolia* with the

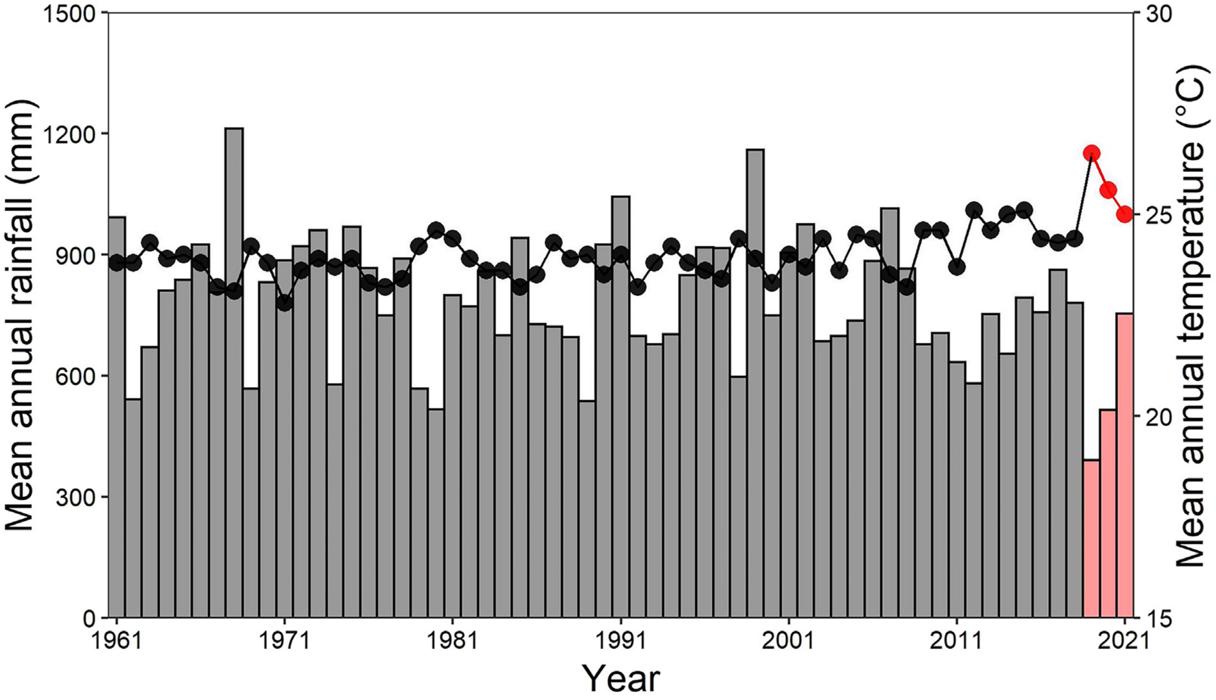

Fig. 1. The mean annual rainfall (bar) and mean annual temperature (dot) in the study area between 1961 and 2021 in Yuanjiang. In 2019, this area experienced an extreme drought event during the past 61 years, with the lowest mean annual rainfall and the highest mean annual temperature. Red colour indicates the experimental period (2019–2021).

height of 3–8 m and coverage of 20 %–30 %, the shrub layer dominated by *Woodfordia fruticosa* and *Tarenna depauperata* with the height of 0.5–3 m and the coverage of 35 %–45 %, and the grass layer by *Heteropogon contortus* and *Paraboea rufescens* with the height of 0.1–0.6 m and the coverage of 60 %–80 %. The majority of trees and shrubs are deciduous species. The vegetation around the YSERS is a part of the Yuanjiang State-level Nature Reserves established in 1980s, although it is occasionally disturbed by grazing.

2.2. Natural extreme drought in 2019

The mean annual rainfall at YSERS in 2014, 2019, 2020, and 2021 was 653.5 mm, 390 mm, 514.9 mm, and 754.1 mm, respectively (Fig. 1). In 2019, Yuanjiang experienced the most extreme drought of the past 61 years, with the highest mean annual temperature and the lowest mean annual rainfall (Fig. 1). According to the standardized precipitation evapotranspiration index, the drought lasted from May of 2019 (usually the start of rainy season) to January of 2020 (Fig. S1). The maximum temperature in 2014, 2019, 2020, and 2021 was 43.7 °C, 45 °C, 44 °C and 44.1 °C, respectively (Fig. S1). The days over 40 °C in 2014, 2019, 2020, and 2021 were 40, 61, 34, and 22, respectively. The Yuanjiang valley savanna in 2019 only has half of the mean annual precipitation (782 mm) of 1961–2021. In 2019, it also showed the highest values of the maximum temperature and the most number of days with temperatures over 40 °C. In addition, we downloaded monthly Standardized Precipitation Evapotranspiration Index (SPEI) data from the Global SPEI database (http://spei.csic.es/map/maps.html#months=1#month=7#year=2022), and more negative SPEI values indicate stronger drought intensity (Vicente-Serrano et al., 2010). The monthly averaged SPEI showed the lowest values (the strongest drought intensity) in 2019 (Fig. S1b). Thus, the 2019 drought was a record-breaking drought and was classified as extreme drought (Shen et al., 2022). Branch dieback can be observed during and after extreme drought event (Fig. 2). However, the mechanism underlying branch dieback induced by extreme drought was out of the scope of this study. The annual precipitation in 2020 was similar to that of some periodical drought years (e.g., 1962, 1980, 1989). Thus, 2020 is characterized by a periodically moderate drought year. The annual precipitation in 2021 becomes normal. Similarly, the annual precipitation in 2014 is close to normal.

2.3. Plant materials

The observations were made during the rainy season (July–October) in 2019, 2020 and 2021. We selected 18 common woody species with three leaf habits (five deciduous, nine semi-deciduous and four evergreen species), and two growth forms (eight shrub and 10 tree species) (Table 1). For the definition of deciduous, semi-deciduous and evergreen species, we followed Chen et al. (2021). Specifically, evergreen plants (E, $n = 4$) are species with no obvious leaf shedding and without a leafless phase; semi-deciduous plants (SD, $n = 9$) are species that only partially drop their leaves but do not show a leafless stage in the dry season; and deciduous plants (D, $n = 5$) are species that drop all their leaves and go through an obvious leafless stage in the dry season (Powers et al., 2020; Chen et al., 2021). Shrubs 1–3 m and trees 3–8 m in height were selected for this study. Three-to-five individuals of every species ($n = 3$ or 5) were sampled randomly in similar habitats near the YSERS to reduce the effect of environmental heterogeneity on the results. Leaf, stem, and whole-branch hydraulic conductance, as well as leaf gas exchange were measured (Table 2).

2.4. Measurements of leaf, stem, and whole-branch hydraulic conductance

For each of the 18 species, whole-branch hydraulic conductance was measured using a high-pressure flow meter (HPFM-Gen3, Dynamax Inc., Houston TX, USA) on six branches sampled three-to-five individuals for each species ($n = 3$ or 5) during each rainy season (late July-early October) of 2019–2021. This technique has been previously described in detail (Yang et al., 2019). Briefly, the branches 1.5–2 m in length for trees or 0.5–1 m in length for the shrubs were cut off, at dawn and the cut end of the branch was then immediately re-cut (~5 cm off) under water. We used an opaque plastic bag to cover the whole sampled branches and kept the cut ends in water during transportation to the laboratory. The perfusion

Fig. 2. An aerial view of the dry-hot valley savanna ecosystem. The upper-left inset shows the branch dieback in some savanna plants caused by the extreme drought in 2019 in the study site. Photos were taken in the rainy season of 2021.

solution used for hydraulic measurements was deionized and boiled water filtered through a purifier (Parker Hannifin Corp., Havehill, MA USA), to remove possible micro-bubbles. To minimize xylem cavitation formation, the cut ends of the branches were always immersed in water throughout the measurement process. Firstly, whole-branch hydraulic conductance with all leaves (K_{shoot}) was measured using a quasi-steady-state mode of the HPFM with a pressure of 0.4 MPa. After the shoot was connected, all leaves of the branch were covered by a dark plastic bag. When a stable flow rate was reached (mostly within 30 min), data was recorded and collected automatically by the HPFM. Then, all distal leaves of the branch were removed, and the hydraulic conductance of the branch including stem and attached twigs (K_{stem}) were measured. These measurements allowed us to calculate leaf hydraulic conductance (K_{leaf}). K_{leaf} was calculated as $1/(1/K_{shoot}\text{-}1/K_{stem})$. After all hydraulic measurements were done for a branch, the hydraulic conductance was normalized by its total leaf area. Specifically, after the measurement of hydraulic conductance, 6–20 simple leaves or 3–6 compound leaves per branch were selected. These fresh leaves were scanned (CanoScan 9000F Mark II, CANON, Tokyo, Japan) at 300 d.p.i. resolution and their total area (LA_{scan}, cm^2) was determined by the ImageJ software (US National Institutes of Health, Bethesda, MD, USA). Then, the scanned leaves and all other leaves were removed from the branch and oven-dried at 80 °C for at least 48 h and the mass (LM_{scan} and LM_{rest}, g) weighed, respectively. Leaf mass per area (LMA, $g\ m^{-2}$) was calculated as $(LM_{scan}/LA_{scan}) \times 10{,}000$. The total leaf area

Table 1
List of 18 tree species selected in this study. Nomenclature follows Flora of China (http://www.iplant.cn/foc/).

Species	Family	Growth form	Leaf habit
Strophioblachia fimbricalyx	Euphorbiaceae	Shrub	Deciduous
Tarenna depauperata	Rubiaceae	Shrub	Evergreen
Bauhinia brachycarpa	Fabaceae	Shrub	Semi-deciduous
Campylotropis delavayi	Fabaceae	Shrub	Semi-deciduous
Clausena excavata	Rutaceae	Shrub	Semi-deciduous
Trigonostemon tuberculatum	Euphorbiaceae	Shrub	Semi-deciduous
Vitex negundo	Lamiaceae	Shrub	Semi-deciduous
Woodfordia fruticosa	Lythraceae	Shrub	Semi-deciduous
Cipadessa baccifera	Meliaceae	Tree	Deciduous
Haldina cordifolia	Rubiaceae	Tree	Deciduous
Lannea coromandelica	Anacardiaceae	Tree	Deciduous
Terminalia franchetii	Combretaceae	Tree	Deciduous
Diospyros yunnanensis	Ebenaceae	Tree	Evergreen
Olea ferruginea	Oleaceae	Tree	Evergreen
Pistacia weinmannifolia	Anacardiaceae	Tree	Evergreen
Polyalthia cerasoides	Annonaceae	Tree	Semi-deciduous
Tamarindus indica	Fabaceae	Tree	Semi-deciduous
Terminthia paniculata	Anacardiaceae	Tree	Semi-deciduous

Table 2
Information of physiological traits measured in this study.

Traits	Abbreviation	Unit
Stomatal conductance	g_s	$mol\ m^{-2}\ s^{-1}$
Maximum photosynthesis rate per area	A_a	$\mu mol\ m^{-2}\ s^{-1}$
Maximum photosynthesis rate per mass	A_m	$nmol\ g^{-1}\ s^{-1}$
Photosynthetic water use efficiency	WUE_i	$\mu mol\ mol^{-1}$
Leaf mass per area	LMA	$g\ m^{-2}$
Leaf hydraulic conductance	K_{leaf}	$kg\ s^{-1}\ MPa^{-1}\ m^{-2}$
Stem hydraulic conductance	K_{stem}	$kg\ s^{-1}\ MPa^{-1}\ m^{-2}$
Whole–branch hydraulic conductance	K_{shoot}	$kg\ s^{-1}\ MPa^{-1}\ m^{-2}$

(m^2) of the branch was calculated as (LM_{scan} + LM_{rest})/LMA. The K_{shoot}, K_{stem}, K_{leaf}, and LMA were averaged to represent the species-level values.

2.5. Measurements of leaf gas exchange

In each rainy season (late July-early October) of 2019–2021, we used a portable photosynthesis system (model Li-6400 XT, Li-Cor Biosciences, Lincoln, NE, USA) to measure stomatal conductance (g_s) and light-saturated photosynthetic rate per leaf area (A_a) on three-to-five sun-exposed mature leaves from three-to-five plant individuals ($n = 3$ or 5) in situ for each species between 9:00 and 12:00 solar time. We recorded the values after ~30 min of exposure to an irradiance of 1000 μmol m^{-2} s^{-1} with a reference CO_2 of 400 μmol mol^{-1}. Intrinsic photosynthetic water use efficiency (WUE_i) was calculated as the ratio of A_a to g_s for each sampling leaf. The g_s, A_a and WUE_i measured for each species were averaged to represent the species-level values. The species-level light-saturated photosynthetic rate per mass (A_m, nmol g^{-1} s^{-1}) was calculated as (A_a /LMA) × 1000. In addition, we also collected pre-drought data on g_s and A_a of 16 same species in the same site as this study in 2014 (a regular year), which were measured by a YSERS colleague (Shu-Bin Zhang, unpublished).

2.6. Statistics

The species-level trait values were tested for normality and $\log_{10}$-transformed when necessary, prior to subsequent analyses. All analyses were performed in R v.4.0.3 (R Core Team, 2021). One-way multivariate analysis of variance (ANOVA) was used to test differences of all traits among the three years with the *aov* function in the 'stats' package and multiple comparison based on least significant difference was tested with the *LSD.test* function in the 'agricolae' package when normality and homogeneity were satisfied, while the Kruskal Wallis test and the criterium Fisher's least significant difference was used with the *kruskal* function in the 'agricolae' package when normality or homogeneity were not satisfied. In multiple comparisons, the Bonferroni correction was used to adjust *p* values. Pearson's correlation was used to analyze the relationships between pair of traits via *corr.test* function in the 'psych' package. Principal component analysis (PCA) was performed to characterize the trait space and species space by using *PCA* function in the 'FactoMineR' package. Permutational multivariate analysis (PERMANOVA) and three-way multivariate analysis of variance (MANOVA) were used to test whether these savanna plants for different leaf habits and growth forms have contrasting responses to the 2019 extreme drought with the *adonis* function in the 'vegan' package and the *aov* function in the 'stats' package. All figures were plotted with the *ggplot* function in the 'ggplot2' package in R.

3. Results

Overall, the values for leaf hydraulic and photosynthetic traits were lowest in 2019 during the extreme drought, but leaf mass per area (LMA), stem and whole-branch hydraulic conductance (K_{stem} and K_{shoot}, respectively) showed no difference across years (Fig. 3). Both stomatal conductance (g_s) and leaf hydraulic conductance (K_{leaf}) were significantly lower in 2019 than in 2020 and 2021 (Fig. 3). Consistently, in 2019 the plants showed significantly lower area-based (A_a) and mass-based maximum photosynthetic rates (A_m), but higher intrinsic photosynthetic water-use efficiency (Fig. 3). In addition, g_s and A_a after drought (2020 and 2021) showed comparable or even higher values compared to that in 2014, a regular year (Fig. 4). Compared to 2014, significant and similar declines in g_s and A_a were found under the extreme drought in 2019 across all species, leaf habits (deciduous, semi-deciduous and evergreen) and growth forms (tree and shrub; Fig. 4).

Stomatal conductance (g_s) was negatively correlated with vapor pressure deficit (VPD) in wetter years, whereas in the drought year the g_s-VPD relationship became nonsignificant because all VPDs in 2019 were higher than 2 kPa, under which stomatal conductance reached their minimum values observed (Fig. 5a). Maximum photosynthetic rate per area (A_a) showed a positive relationship with g_s across years (Fig. 5b; Table S1).

Based on the PCA results, the plants showed a clear separation between 2019 and 2020, or between 2019 and 2021, and high overlap between 2020 and 2021 (Fig. 6). The permutational multivariate analysis (PERMANOVA) and three-way multivariate analysis of variance (MANOVA) showed that the factor year (drought) with a maximum explanation of trait variation (50.3 %) had a significant impact on the physiological traits (Table S2). Although leaf habit also showed a significant impact on the physiological traits, it had a relatively low explanation of trait variation (8.7 %). In addition, savanna plants showed similar responses of hydraulic and photosynthetic traits to the 2019 extreme drought among different leaf habits (deciduous, semi-deciduous, and evergreen species) and between growth forms (tree and shrub) (Figs. S2, S3). Specifically, deciduous, semi-deciduous and evergreen species showed a similar trend for all traits studied, except for K_{leaf} (Fig. S2), and trees and shrubs also showed a consistent trend in response to the natural extreme drought in all traits (Fig. S3).

4. Discussion

Our study reveals high physiological resilience of savanna plants to extreme drought in terms of recovery in leaf photosynthesis. Their carbon assimilation in the years after drought (2020 and 2021) was nearly back to their level in pre-drought 2014 (Fig. 4). The photosynthetic recovery could be related to the maintenance of hydraulic integrity in stem xylem. Studied savanna plants showed significant declines in leaf hydraulic and stomatal conductance during an extreme drought (Fig. 3), which could reduce plant water loss and the risk to stem hydraulic integrity for valley-savanna plants during the drought.

Consistent with our expectation, we found that the g_s of the studied plants was highly sensitive to increasing vapor pressure deficit (VPD). When VPD in 2019 was higher than 2 kPa, all studied plants maintained stomatal conductance at their minimum levels observed, suggesting a strong stomatal regulation under extreme drought (Fig. 5). The stomata, as the final pathway of water transport in plants, are a major controller of plant water loss when water stress occurs (Jones and Sutherland, 1991; Martínez-Vilalta and Garcia-Forner, 2017; Brodribb et al., 2016; Creek et al., 2020) and has important impacts on survival of savanna plants under drought conditions (Martínez-Vilalta and Garcia-Forner, 2017; Martin-StPaul et al., 2017; Creek et al., 2018). Closing stomata minimizes water loss and delays catastrophic xylem dysfunction under drought given that stomatal closure protects against large gradients in water potential between the soil and foliage (Creek et al., 2020; Carminati et al., 2020). In addition, low g_s during the drought could be related to lower leaf hydraulic conductance (Deans et al., 2020; Lu et al., 2020; Xu et al., 2021). The low g_s in the drought may partly be the result of less water supply via leaf xylem to stomata induced by lower K_{leaf}.

Low g_s and K_{leaf} suppress carbon assimilation (Sperry et al., 2017; Lawson and Vialet-Chabrand, 2018). Indeed, A_a and A_m were significantly lower during the 2019 extreme drought (Figs. 3, 5). This suppression of photosynthesis may reduce carbon supply for plant growth, and even cause carbon starvation, a possible mechanism of tree mortality during extreme drought (McDowell et al., 2008; Anderegg et al., 2012; Hajek et al., 2022; McDowell et al., 2022). However, some studies have shown that carbon starvation may not be the mechanism explaining drought-induced mortality based on high tissue non-structural carbohydrate (NSC) concentrations during the drought (Adams et al., 2017; Kannenberg and Phillips, 2020; Shen et al., 2022). In contrast, the high percentage loss of xylem hydraulic conductivity (> 60 %) is consistent with proposed theoretical and modeled survival thresholds across species, suggesting that xylem hydraulic failure is an important physiological mechanism explaining drought-induced mortality (Adams et al., 2017). In addition, the higher photosynthetic water use efficiency under extreme drought can partly compensate for the drought-induced decline in xylem water potential by

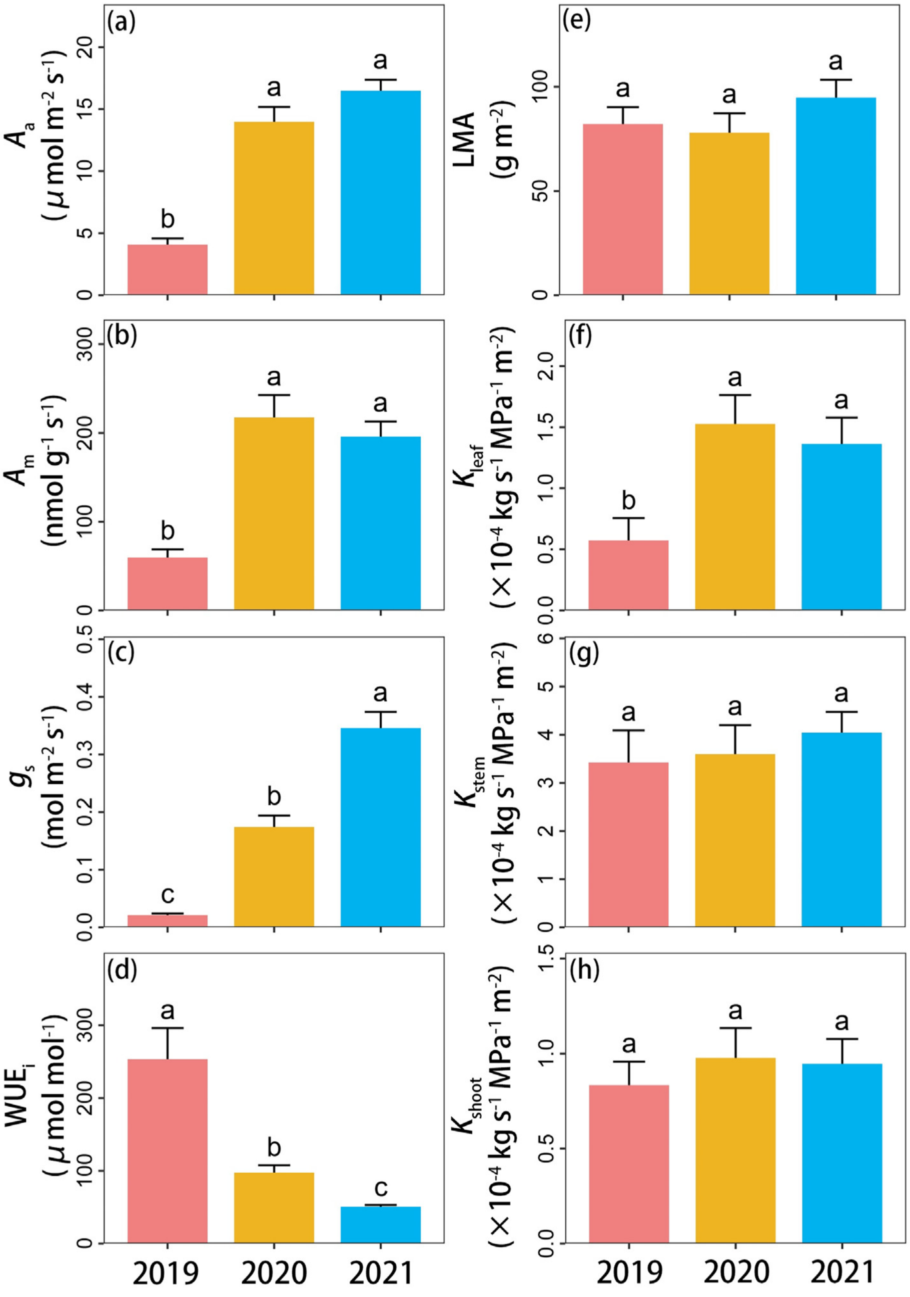

Fig. 3. Differences in mean trait values for all 18 species among three years (2019, 2020 and 2021). (a) maximum photosynthetic rate per area (A_a), (b) maximum photosynthetic rate per mass (A_m), (c) stomatal conductance (g_s), (d) photosynthetic water use efficiency (WUE$_i$), (e) leaf mass per area (LMA), (f) leaf hydraulic conductance (K_{leaf}), (g) stem hydraulic conductance (K_{stem}), and (h) the whole branch hydraulic conductance (K_{shoot}). Error bars represent +1 SE. Different letters on top of the error bars indicate significant differences in traits among years ($p < 0.05$). One-way multivariate analysis of variance (ANOVA) was used to test the difference in traits, and the Bonferroni correction was used to adjust p values in multiple comparisons.

decreasing stomatal conductance and less water loss (Ponton et al., 2002; Hentschel et al., 2016; Driscoll et al., 2020).

Despite lower K_{leaf} in 2019 compared to 2020 and 2021, stem water transport capacity (K_{stem}) during the 2019 extreme drought was comparable to that of 2020 and 2021 (Fig. 3). This suggests maintenance of hydraulic integrity of stems, which may benefit from less water loss due to the down-regulation of both g_s and K_{leaf}. This could be because the 2019 drought started at the beginning of the rainy season, which inhibited leaf xylem growth resulting in low K_{leaf}. However, stem cambium growth was less impacted. Lower K_{leaf} (high hydraulic resistance in leaf) can produce a greater water potential gradient within leaves in a given transpiration rate and leaf water potential, and thus help keep a higher water potential in upstream stems (Zimmermann, 1983; Tyree and Ewers, 1991), which helps avoid catastrophic hydraulic failure due to embolism (Hao et al., 2008; Bucci et al., 2013; Scholz et al., 2014; Charrier et al., 2016). In addition, although leaf-stem hydraulic segmentation in terms of vulnerability to embolism has not been studied here, leaf xylem embolism could function as a 'safety valve' under the drought (Zimmermann, 1983; Pivovaroff et al., 2014; Hochberg et al., 2017; Levionnois et al., 2020).

Unexpectedly, savanna woody plants with different leaf habits (deciduous, semi-deciduous and evergreen groups) and growth forms (growth form: tree and shrub groups) showed similar responses to the 2019 extreme drought (Figs. S2, S3). This convergent behavior suggests that, for this region and climate, maintenance of hydraulic integrity is critical for plant survival (Chen et al., 2021; Oliveira et al., 2021). Savanna habitats can show strong water deficits even during a regular dry season (Sankaran,

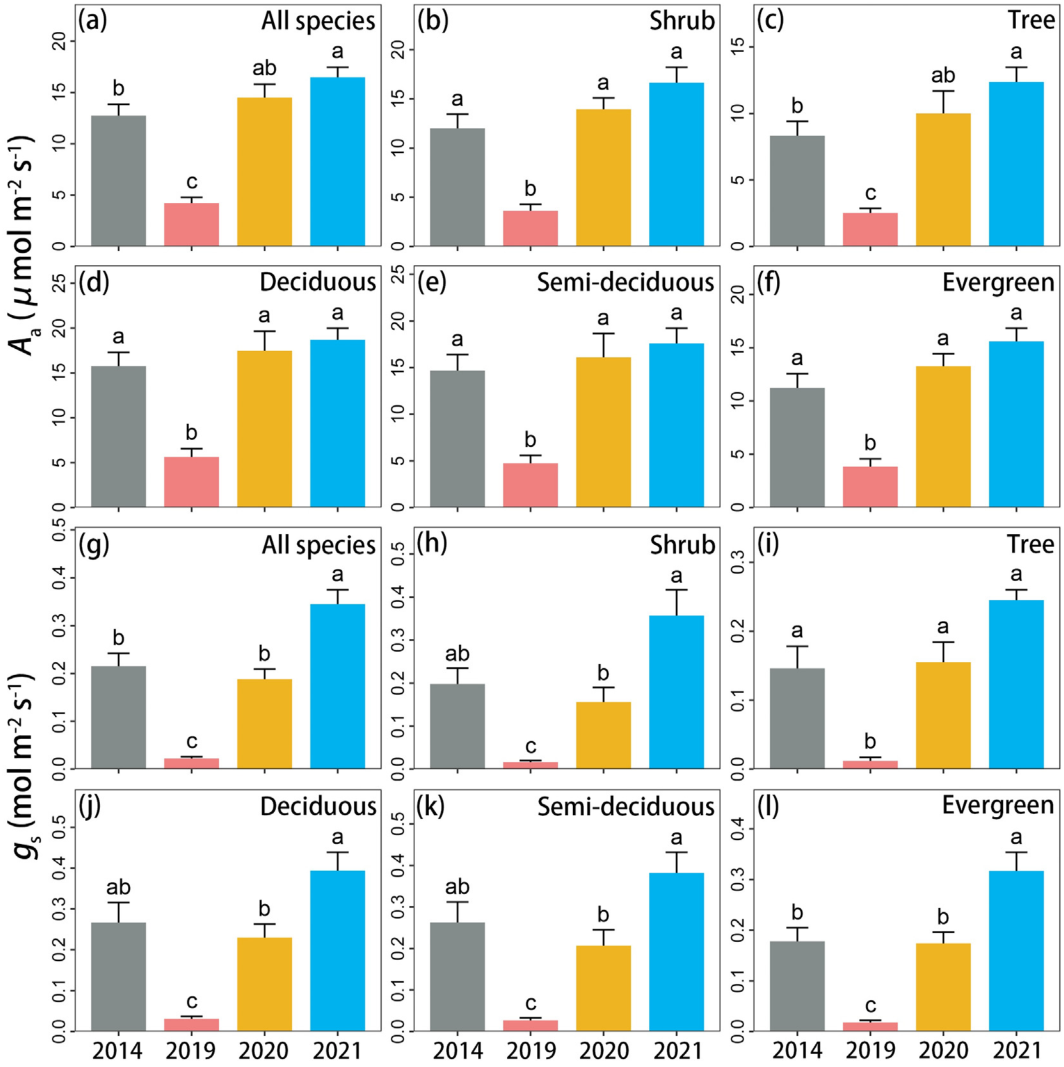

Fig. 4. Differences in mean trait values of (a)-(f) maximum photosynthetic rate per area (A_a,) and (g)-(l) stomatal conductance (g_s) among four years (2014, 2019, 2020 and 2021) for all 16 species, different growth forms (shrub and tree) and leaf habits (deciduous, semi-deciduous and evergreen). Data on A_a and g_s of the 16 same species as in this study at the same site in 2014 (a regular year) were measured by Shu-Bin Zhang during the rainy season of 2014 (unpublished data). Error bars represent +1 SE. Different letters on top of the error bars indicate significant difference in traits among years ($p < 0.05$). One-way multivariate analysis of variance (ANOVA) was used to test the difference in traits, and the Bonferroni correction was used to adjust p values in multiple comparisons.

2019; Zhang et al., 2022), due to negligible rainfall and high evaporative demand caused by high irradiance and temperature (Sankaran, 2019). The diversity of savanna trees is limited by the narrow niche due to the water-limited environment condition (Schwinning and Kelly, 2013). Thus, this convergent physiological response of these plants among leaf habits and growth forms to extreme drought may be related to long-term adaptation to the powerful selecting stress in the dry-hot valley savanna ecosystem.

5. Conclusions

In conclusion, our study shows the maintenance of stem hydraulic integrity during the drought and the recovery of leaf-level photosynthesis after the drought, suggesting high physiological resilience of savanna plants under extreme drought. Declines in leaf hydraulic conductance and strong stomatal regulation can decrease water loss and help plants survive under extreme drought and recover after drought (Shen et al., 2022). In the face of extreme drought, savanna plants across different leaf habits and growth forms show a similar physiological response, despite that different leaf habits or growth forms may have different hydraulic traits and drought-induced branch dieback (Chen et al., 2021; Zhang et al., 2022). This study provides important physiological results for understanding how savanna plants across diverse leaf habits and growth forms respond to natural extreme drought, which can help predict the response of savanna ecosystems to future climate change.

CRediT authorship contribution statement

Da Yang: Conceptualization, Methodology, Supervision, Writing – Original draft. Yang-Si-Ding Wang: Conceptualization, Data collection, Analysis, Methodology, Writing – Original draft. Qin Wang: Data collection and Analysis. Yan Ke: Data collection and Analysis. Yun-Bing Data collection and Analysis. Shi-Bao Zhang: Writing – Review and Editing. Yong-Jiang Zhang: Conceptualization, Supervision, Writing – Review and Editing. Nate G. McDowell: Writing – Review and Editing. Jiao-Lin Zhang: Conceptualization, Supervision, Writing – Review and Editing.

Data availability

Data will be made available on request.

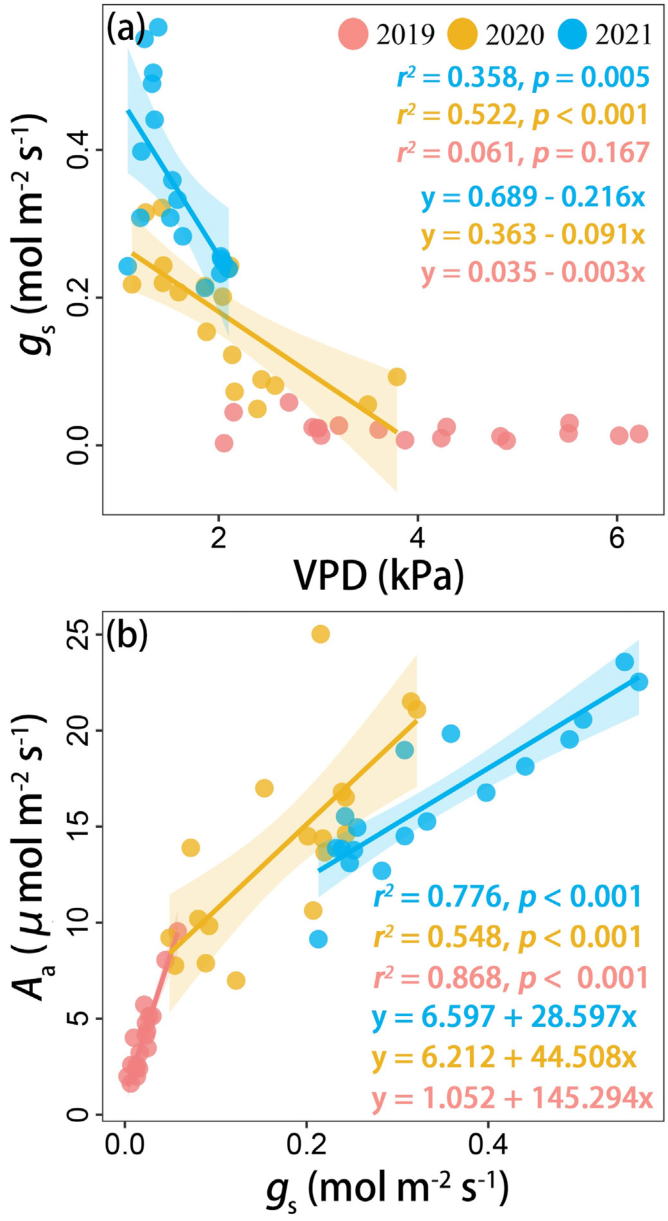

Fig. 5. Relationships between (a) stomatal conductance (g_s) and vapor pressure deficit (VPD), and (b) maximum photosynthetic rate per area (A_a) and g_s across 18 species in 2019 (light red), 2020 (light yellow) and 2021 (light blue), respectively.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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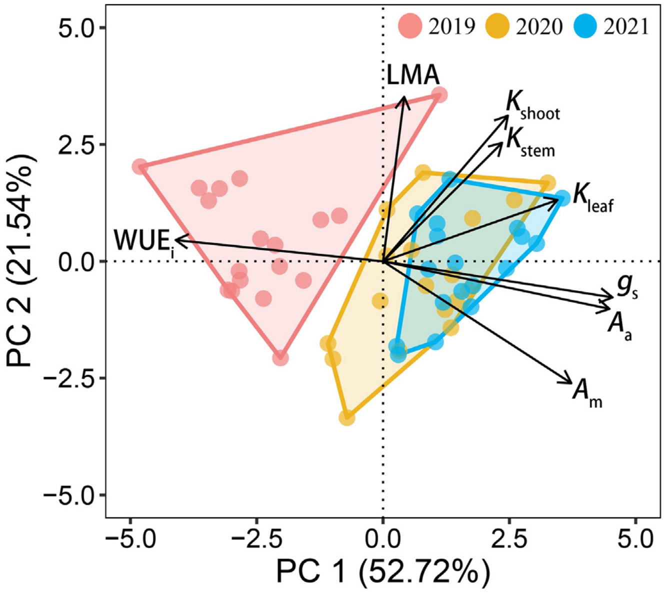

Fig. 6. Principal component analysis (PCA) using $\log_{10}$-transformed mean values for eight traits of 18 species in 2019 (light red), 2020 (light yellow) and 2021 (light blue). See trait abbreviations in Table 2.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.161711.

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