Environmental and Experimental Botany 203 (2022) 105046

Contents lists available at ScienceDirect

Environmental and Experimental Botany

journal homepage: www.elsevier.com/locate/envexpbot

Physiological traits and response strategies of four subtropical tree species exposed to drought

Ting Wu[a,b,c,e,f,1,2], Nadan Tan[a,e,f,1], David T. Tissue[b,c,3], Juan Huang[a,e,f], Honglang Duan[d], Wei Su[a,e,f], Yuting Song[a,e,f], Xujun Liu[a,e,f], Yue Liu[a,e,f], Xu Li[a,e,f], Zhiyang Lie[a,e,f], Shimin Yang[a,e,f], Shuyidan Zhou[a,e,f], Junhua Yan[a,e,f], Xuli Tang[a,e,f], Shizhong Liu[a,e,f], Guowei Chu[a,e,f], Xinghua He[a], Juxiu Liu[a,e,f,*,4]

[a] *Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, South China Botanical Garden, Chinese Academy of Sciences, Xingke Road 723, Tianhe District, Guangzhou 510650, China*
[b] *Hawkesbury Institute for the Environment, Western Sydney University, Hawkesbury Campus, Richmond, NSW 2753, Australia*
[c] *Global Centre for Land-based Innovation, Western Sydney University, Hawkesbury Campus, Richmond, NSW 2753, Australia*
[d] *Institute for Forest Resources and Environment of Guizhou, Key Laboratory of Forest Cultivation in Plateau Mountain of Guizhou Province, College of Forestry, Guizhou University, Guiyang, China*
[e] *Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, 723 Xingke Road, Tianhe District, Guangzhou 510650, China*
[f] *University of Chinese Academy of Sciences, Beijing 100039, China*

ARTICLE INFO

Keywords:
Drought adaptation strategy
Photosynthesis
Stomatal regulation
Subtropical plantations
Water relation

ABSTRACT

World-wide, forests are experiencing drought-induced mortality. However, physiological adaptation to drought is highly variable, which may lead to differential mortality patterns and alter community structure. In this study, saplings of four common tree species (*Ormosia pinnata*, *Dalbergia odorifera*, *Castanopsis fissa* and *Michelia macclurei*) grown in subtropical plantations in southern China were subjected to average rainfall and three drought treatments, consisting of low (25% rainfall reduction), moderate (50% rainfall reduction) and high (75% rainfall reduction) drought. To investigate their drought response strategies and select tree species with higher drought tolerance, we examined plant traits, including tree growth, stomatal regulation, water relations, carbon dynamics and morphology, that might contribute to drought tolerance. We found that *O. pinnata* adapted to drought by decreasing turgor loss point (TLP) and increasing leaf dry matter content and leaf mass per area (LMA). *D. odorifera* exhibited low leaf minimum conductance and high LMA as the key drought traits to reduce water loss. *C. fissa* was slowest to initiate stomatal closure but completed stomatal closure more rapidly than the other species. Drought reduced light-saturated photosynthetic rates (A_{sat}) for *O. pinnata*, *D. odorifera* and *C. fissa* primarily due to declining stomatal conductance (g_s), with lesser limitations due to the biochemical capacity of Rubisco carboxylation (V_{cmax}) and electron transport (J_{max}). *M. macclurei* was the first species to close stomata. Drought did not affect A_{sat} for *M. macclurei* due to stable photosynthetic biochemical processes; however, V_{cmax} regulation of A_{sat} increased with drought intensity. There was trait variation in the capacity of study trees to tolerate drought, with *M. macclurei* exhibiting the highest capacity to tolerate drought due to key stomatal (earlier stomatal closure) and hydraulic (lower TLP) traits reducing plant water loss with progressive drought stress.

---

[*] Correspondence to: No.723, Xingke Road, Tianhe District, Guangzhou, China.
E-mail address: ljxiu@scbg.ac.cn (J. Liu).
[1] Ting Wu and Nadan Tan contributed equally to this work.
[2] ORCID: 0000–0001-6045–036X
[3] ORCID: 0000–0002-8497–2047
[4] ORCID: 0000–0001-7850–1006

https://doi.org/10.1016/j.envexpbot.2022.105046
Received 5 June 2022; Received in revised form 11 August 2022; Accepted 17 August 2022

Table 1
Summary of species background information and measured predawn leaf water potential (ψ_{pd}, MPa, n = 12), midday leaf water potential (ψ_{md}, MPa, n = 12), the light-saturated photosynthetic rate (A_{sat}, μmol m^{-2} s^{-1}, n = 12), stomatal conductance (g_s, mol m^{-2} s^{-1}, n = 12) and leaf mass per area (LMA, g cm^{-2}, n = 4) for the four tree species with similar size at pre-drought. Values are means ± standard errors. P50, the xylem water potential at which stem hydraulic conductivity was reduced by 50%; TLP, turgor loss point. P50 and TLP were derived from Li et al. (2015) and Liu et al. (2019). P50 and TLP for *D. odorifera* were not studied in previous study.

Species	Family	ψ_{pd}	ψ_{md}	A_{sat}	g_s	LMA	P50	TLP
Ormosia pinnata	Leguminosae	-0.21 ± 0.03	-1.06 ± 0.05	7.22 ± 0.37	0.12 ± 0.01	168.65 ± 11.11	-1.74	-1.39
Dalbergia odorifera	Leguminosae	-0.45 ± 0.06	-1.16 ± 0.07	11.07 ± 1.61	0.29 ± 0.04	254.55 ± 12.44	no	no
Castanopsis fissa	Fagaceae	-0.19 ± 0.01	-1.01 ± 0.09	8.82 ± 1.10	0.26 ± 0.02	154.74 ± 24.66	-1.27	-2.35
Michelia macclurei	Magnoliaceae	-0.20 ± 0.01	-0.70 ± 0.12	7.12 ± 1.15	0.19 ± 0.03	161.22 ± 4.22	-3.54	-1.52

1. Introduction

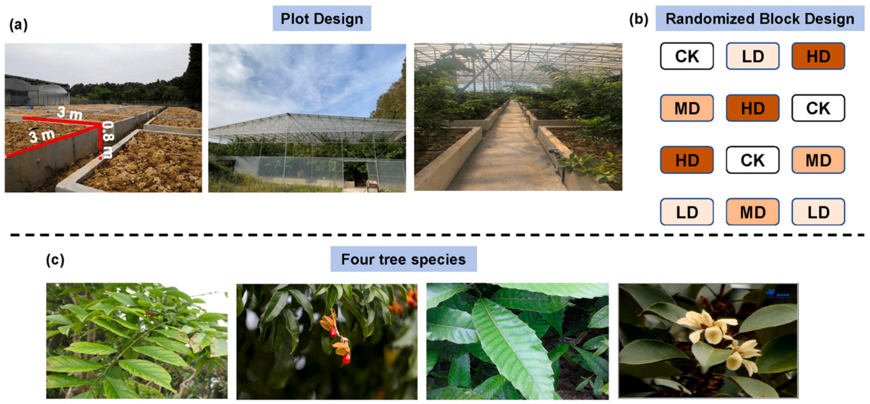
The distribution pattern of rainfall has been altered by climate change, which increases drought frequency and intensity at global and regional scales (Lobell et al., 2011; IPCC, 2021). Drought is the principal environmental factor limiting plant physiological processes and growth in forest ecosystems (Li et al., 2018b; Duan et al., 2019), while drought-induced tree mortality events have been widely observed in a large variety of forest biomes (van Mantgem et al., 2009; Allen et al., 2010, 2015). Tropical forests have high biodiversity and represent large carbon sinks, as well as play important global roles in carbon and biogeochemical cycles, and biodiversity conservation (Yu et al., 2014; Lie et al., 2021). Trees exhibit highly variable physiological and morphological plasticity to drought, such that the adaptive potential of trees to drought remains unclear (Isaac-Renton et al., 2018). Tree death caused by drought has altered forest community structure (Zhou et al., 2013, 2014a) and reduced carbon sinks in tropical forests (Corlett, 2016).

Plant drought response strategies are complex and differ among co-occurring species, thereby affecting plant survival (Blackman et al., 2019). Stomatal regulation is one of the protective strategies used to minimize the negative effects of water stress (Brodribb et al., 2003). Species with tight stomatal regulation close stomata and reduce plant water loss to maintain stable midday leaf water potential (Ψ_L) and avoid dehydration (Kumagai and Porporato, 2012), but this also limits CO_2 availability for photosynthesis and inhibits plant growth (Quentin et al., 2012). In contrast, species with weak stomatal regulation maintain stomatal opening to sustain photosynthesis, but at a cost of significant water loss, resulting in declines in Ψ_L (Tardieu and Simonneau, 1998). Generally, species with tight stomatal regulation exhibit earlier stomatal closure than those with weak stomatal regulation in response to declining water availability (Gonzalez-Rebeles et al., 2021), which might be a vital strategy to avoid xylem cavitation (Li et al., 2019). However, it is unclear which stomatal strategy is more favorable during periods of drought (Fu and Meinzer, 2019). The Ψ_L at 50% and 90% stomatal closure (P_{gs50} and P_{gs90}, respectively) is associated with embolism thresholds (Klein, 2014), which represents the sensitivity of stomata during progressive dehydration (Henry et al., 2019). For instance, species with lower (more negative) P_{gs50} and P_{gs90} indicate that plants maintain open stomata under more severe water stress (Bartlett and Sinclair, 2021). Plant stomatal response to decreasing Ψ_L influences the dynamics of gas exchange, drought tolerance and productivity (Bartlett et al., 2016).

In the context of extreme drought, water is still lost from the cuticle after complete stomatal closure. The rate of water loss from the cuticle is expressed as leaf minimum conductance (g_{min}) (Sack et al., 2003; Barnard and Bauerle, 2013), which is considered a key drought tolerance trait used to predict plant mortality (Martin-StPaul et al., 2017; Duursma et al., 2019). Leaf turgor loss point (TLP) is the negative water potential at which leaf cells lose turgor and close stomata, leading to reductions in gas exchange and plant growth (Brodribb et al., 2003). Plants cannot take up water to recover from wilting when soil water potential is lower than TLP. Plants that exhibit more negative TLP under drought, which allows them to maintain hydraulic conductance, gas exchange and growth under lower water availability, have higher capacity to tolerate water stress (Bartlett et al., 2012b, 2014). TLP is a commonly used trait to quantify plant drought resistance and hence adaptive capacity to water stress (Bartlett et al., 2012b).

Photosynthesis plays a critical role in determining plant fitness, but may be substantially limited by drought (Talbi et al., 2020; Li et al., 2021). Leaf light-saturated photosynthetic rate (A_{sat}) is decreased by drought, as a function of reductions in light-saturated stomatal conductance (g_{ssat}), mesophyll conductance and biochemical processes (Carmo-Silva et al., 2012). Stomatal limitation is represented by reductions in stomatal conductance that generate lower A_{sat}, which is the first process limiting A_{sat} (Limousin et al., 2010). Additionally, lower mesophyll conductance during drought could reduce CO_2 diffusion into chloroplast stroma (Flexas et al., 2008). Under long-lasting drought, biochemical limitations to photosynthesis are generated by reductions in biochemical processes, including the maximum capacity for Rubisco carboxylation (V_{cmax}) and electron transport (J_{max}), which reduce A_{sat} (Damour et al., 2009; Zhou et al., 2014b). Plant water uptake and transport induced by transpiration promote nutrient acquisition from soil (Cernusak et al., 2011). Thus, reduced transpiration due to stomatal limitation might impair plant nutrient acquisition, which would further inhibit photosynthetic biochemical processes (Yates et al., 2010; Pignon and Long, 2020). Previous studies demonstrate that stomatal limitation may transition to biochemical limitation when drought stress is intensified (Misson et al., 2010; Drake et al., 2017). However, few studies have explored the contribution of stomatal and biochemical limitations (J_{max} and V_{cmax}) to A_{sat} under drought for species with different stomatal regulation (Drake et al., 2017; Salazar-Tortosa et al., 2018).

Four common tree species (*Ormosia pinnata*, *Dalbergia odorifera*, *Castanopsis fissa* and *Michelia macclurei*) grown in subtropical plantations in southern China were chosen for this study, which exhibited contrasting drought sensitivities defined by the xylem water potential of the traits of stem hydraulic conductivity (P50) and TLP (Table 1). Zhou et al. (2011) demonstrated that the annual number of no-rain days significantly increased but soil moisture and water yield coefficient significantly decreased in this region over the past few decades, indicating that the frequency and intensity of drought have increased and further affected tree survival and community structure (Zhou et al., 2013). Li et al. (2015) reported that species with high drought tolerance often increase their abundance in subtropical China. It has been shown that *M. macclurei* exhibits a drought-avoidance strategy by accessing shallow soil water (Ouyang et al., 2020), while it was still unknown whether the other three tree species utilized drought-avoidance or drought-tolerance strategies to adapt to drought. Here, we analyzed the responses of process traits (stomatal regulation, water relations, gas exchange, photosynthetic capacity, leaf minimum conductance and turgor loss point) and pattern traits (leaf dry matter content and mass per area), and their impacts on plant growth in response to a well-watered control (100% water) and three drought treatments: low intensity (25% reduction), moderate intensity (50% reduction) and high intensity (75% reduction). Our objectives were to determine (a) the process and pattern traits that confer drought avoidance or tolerance for the four tree species; (b) the main factors that lower A_{sat} for the four tree species; and (c) selection of the most drought tolerant tree species in the subtropical region.



Dalbergia odorifera *Ormosia pinnata* *Castanopsis fissa* *Michelia macclurei*

Fig. 1. Representation of plot (a) and randomized block design for plots (b). Photos of four tree species (c).

2. Materials and methods

2.1. Plant material and experimental design

In 2018, twelve plots were constructed in the South China Botanical Garden, CAS, Guangzhou, Guangdong province, China (N23°10'30.97'', E113°21'9.81''). The mean annual temperature is approximately 21 °C, and the relative humidity averages 80% throughout the year. The mean annual precipitation is approximately 1900 mm; nearly 80% of the rainfall occurs during the wet season (April–September) and 20% during the dry season (October–March) (Wu et al., 2020). A plastic film extended above the tops of the trees, to exclude natural rainfall from the plots. Each plot had an edge length of 3 m, with a height of 0.8 m (Fig. 1a). The wall of the plot was made of brick-cement and concrete, and the bottom of the plot was filled with local forest soil (Table S1). *Ormosia pinnata*, *Dalbergia odorifera*, *Castanopsis fissa* and *Michelia macclurei* exhibit different drought sensitivities according to their P50 and TLP values (Fig. 1b and Table 1) and are widely distributed in subtropical plantations; hence, they were chosen for this experiment. In May 2019, one year-old, similar-sized seedlings (height was ca. 30 cm and stem basal diameter was ca. 4 mm), grown outdoors in natural environmental conditions, were purchased from a nursery near South China Botanical Garden. Five individuals of each of the four species (20 trees) were randomly transplanted into each of the 12 plots (total of 240 trees) using a randomized block design; spacing between individual trees was approximately 50 cm in each plot.

2.2. Watering treatments

In 2010–2019, the average annual rainfall at our site in Guangzhou was 1900 mm (Chen and Zhang, 2021). We used this value as the baseline for our four water treatments: 1) *control (CK)*: the average natural rainfall; total watering volume per day was 47 L; 2) *low drought (LD)*: 25% reduction of control; total watering volume per day was 35 L; 3) *moderate drought (MD)*: 50% reduction of control; total watering volume per day was 23 L; and 4) *high drought (HD)*: 75% reduction of control; total watering volume per day was 12 L. The amount and frequency of watering was controlled by an automatic irrigation system, which was located on the soil surface. Watering occurred every night over four intervals per night to reduce potential run-off. All trees were maintained in control conditions for 15 months after planting, and then the drought treatments were initiated in August 2020, and lasted 4 months until final tree growth measurements were completed in December 2020. Each plot was distributed randomly with three replicates per water treatment.

2.3. Growth measurements

The stem diameter (D, mm) and height (H, cm) of all seedlings per species in each plot were measured in December 2019 (19 month-old trees; well-watered), July 2020 (26 month-old trees; well-watered), September 2020 (28 month-old trees; 1 month drought treatment) and December 2020 (31 month-old trees; 4 months drought treatment). The stem volume (V, cm^3) of all seedlings per species in each plot was also calculated as 3.14 * (D / 2) ^ 2 * H (Wu et al., 2022). Additionally, we calculated the growth rate of V (V_{rate}, %).

2.4. Water potentials

Pre-dawn water potential (Ψ_{pd}, MPa) and mid-day leaf water potential (Ψ_{md}, MPa) were measured every two weeks, following gas exchange measurements using a Scholander-type pressure chamber (PMS 1505D, PMS instruments, Corvalis, Oregon USA). Three seedlings per treatment per species were randomly selected. Approximately one hour before sunrise, Ψ_{pd} of two leaves from each seedling was measured. Following gas exchange measurements during the day, another two leaves from each seedling were sampled for the determination of Ψ_{md}.

2.5. Leaf gas exchange measurements

The net assimilation vs. rate-intercellular CO_2 concentration (A-Ci) curves were measured on fully expanded leaves from three or four seedlings per plot per species (n = 3–4) between 0900 and 1400 h on clear days at the beginning of the drought treatments (August 2020) and 2.5 months later (October 2020), using a portable open path gas exchange system (Licor-6800, Li-Cor, Lincoln, NE, USA) equipped with a leaf chamber fluorometer (6800–40). The measurements of leaf water potential and gas exchange were completed on the same day. A-Ci curves were measured at saturating PAR of 1500 μmol m^{-2} s^{-1}, leaf temperature (25 ℃) and ambient relative humidity inside the leaf chamber (~ 60%). A-Ci curves were generated using leaf chamber CO_2 values of (in order): 400, 300, 200, 100, 50, 400, 600, 800, 1000 and 1200 μmol mol^{-1}. Leaf light-saturated photosynthesis (A_{sat}, μmol m^{-2} s^{-1}) and stomatal conductance (g_s, mol m^{-2} s^{-1}) were selected, at CO_2 of 400 μmol mol^{-1}. The maximum rate of photosynthetic ribulose 1,·5-bisphosphate carboxylase/oxygenase (Rubisco) carboxylation (V_{cmax}, μmol m^{-2} s^{-1}) and apparent maximum rate of photosynthetic electron transport (J_{max}, μmol m^{-2} s^{-1}) were estimated from A-Ci curves. A-Ci curves were terminated when g_s was lower than 0.03 mol m^{-2} s^{-1} (Bartholomew et al., 2020).

Table 2

Effects of drought treatments (D), drought duration (T), species (S) and their interactions on the stem volume (V, cm^3, $n = 15$); the growth rate of stem volume (V_{rate}, %, $n = 15$); leaf water potential (ψ_{pd} and ψ_{md}, MPa, $n = 6$); gas exchange (A_{sat}, $\mu mol\ m^{-2}\ s^{-1}$, $n = 9$; g_s, $mol\ m^{-2}\ s^{-1}$, $n = 9$); photosynthetic capacity (J_{max} and V_{cmax}, $\mu mol\ m^{-2}\ s^{-1}$, $n = 3$); leaf minimum conductance (g_{min}, $mmol\ m^{-2}\ s^{-1}$, $n = 9$); turgor loss point (TLP, MPa, $n = 6$); dry matter content (LDMC, %, $n = 6$) and leaf mass per area (LMA, $g\ cm^{-2}$, $n = 6$).

Factors	V	V_{rate}	ψ_{pd}	ψ_{md}	A_{sat}	g_s	J_{max}	V_{cmax}	g_{min}	TLP	LDMC	LMA
D	0.270	0.326	**0.018**	0.053	**0.004**	**0.006**	**0.028**	**0.029**	**< 0.001**	0.428	**0.001**	**0.038**
T	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.003**	–	–	–	–
S	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
D * T	**0.041**	0.454	**< 0.001**	**0.001**	**< 0.001**	**0.001**	0.220	0.247	–	–	–	–
D * S	0.054	0.185	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.002**	**0.002**	**0.001**	0.087	**< 0.001**	**< 0.001**
T * S	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**	**0.001**	**0.001**	0.077	**0.016**	–	–	–	–
D * T * S	0.928	**0.011**	0.398	0.106	**0.014**	**0.001**	0.822	0.987	–	–	–	–

2.6. Minimum leaf water conductance

Leaf minimum water conductance (g_{min}, mmol m^{-2} s^{-1}) represents water loss through the leaf when stomata are maximally closed (Slot et al., 2021). g_{min} was determined from the consecutive weight loss of desiccating leaves in an incubator in the dark with low air humidity (Slot et al., 2021). After 40 days of drought treatment, the mature leaves were selected at the end of the day (~15:00) and immediately double-bagged for transport to the lab. Samples were immediately hydrated overnight (~12 hr), and cut ends were sealed with wax after hydration. Then, samples were dried on the lab bench with a fan for 30 min at photosynthetically active radiation of < 10 μmol m^{-2} s^{-1} to induce stomatal closure and weighed every 30 min over eight intervals. g_{min} was calculated by plotting water loss versus time; the slope was highly linear and therefore taken to represent transpiration after stomata had closed (Pivovaroff et al., 2018).

2.7. Pressure volume analysis

Seven leaves per treatment (7 leaves x 4 treatments x 4 species = 112 leaves) were collected for leaf pressure volume (PV) determination after 40 days of drought treatment; for species with reduced leaf petioles, a terminal shoot was used instead. Leaves were excised under water on the previous night and transported to the lab with the petiole kept under water. Leaf water potential (Ψ_{leaf}, MPa) was measured using the Scholander pressure chamber (PMS, Corvallis, Oregon, USA), and fresh weight (FW, g) was measured with a digital balance (weighted to 0.001 mg). Then, leaves were bench dried and Ψ_{leaf}, and FW were measured periodically. Finally, leaves were oven dried at 70 °C for at least 48 hr to obtain dry weight. Data were used to plot the inverse of leaf water potential (1 / Ψ_{leaf}) against leaf relative water content (RWC_{leaf}, %). Leaf turgor loss point (TLP, MPa) was taken as the point where the line became non-linear (Brodribb et al., 2003). TLP of previous studies (Table 1) was also measured by this method.

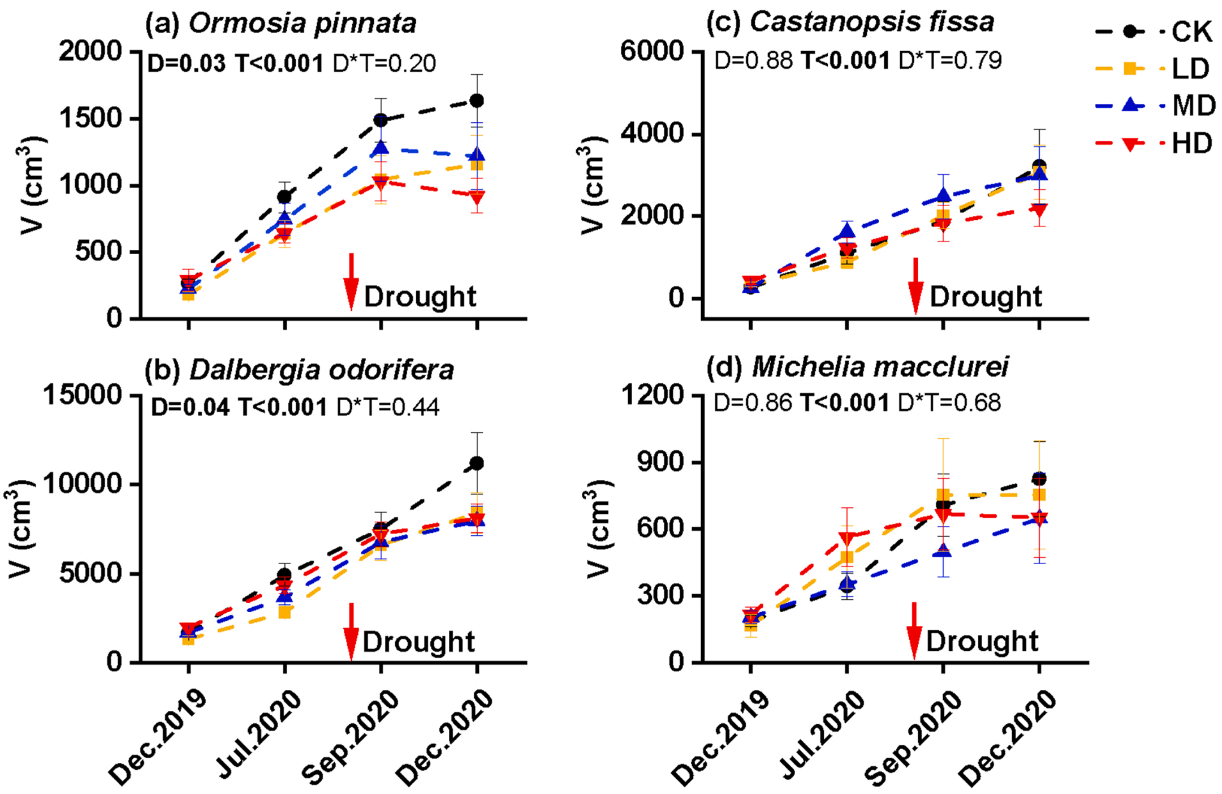


Fig. 2. The stem volume (V, cm^3, $n = 15$) for *Ormosia pinnata* (a), *Dalbergia odorifera* (b), *Castanopsis fissa* (c) and *Michelia macclurei* (d) subjected to control (CK), low drought (LD), moderate drought (MD) and high drought (HD) treatments. Values are means ± standard errors. D, drought treatment; T, time. Arrows indicated the start of drought treatments.

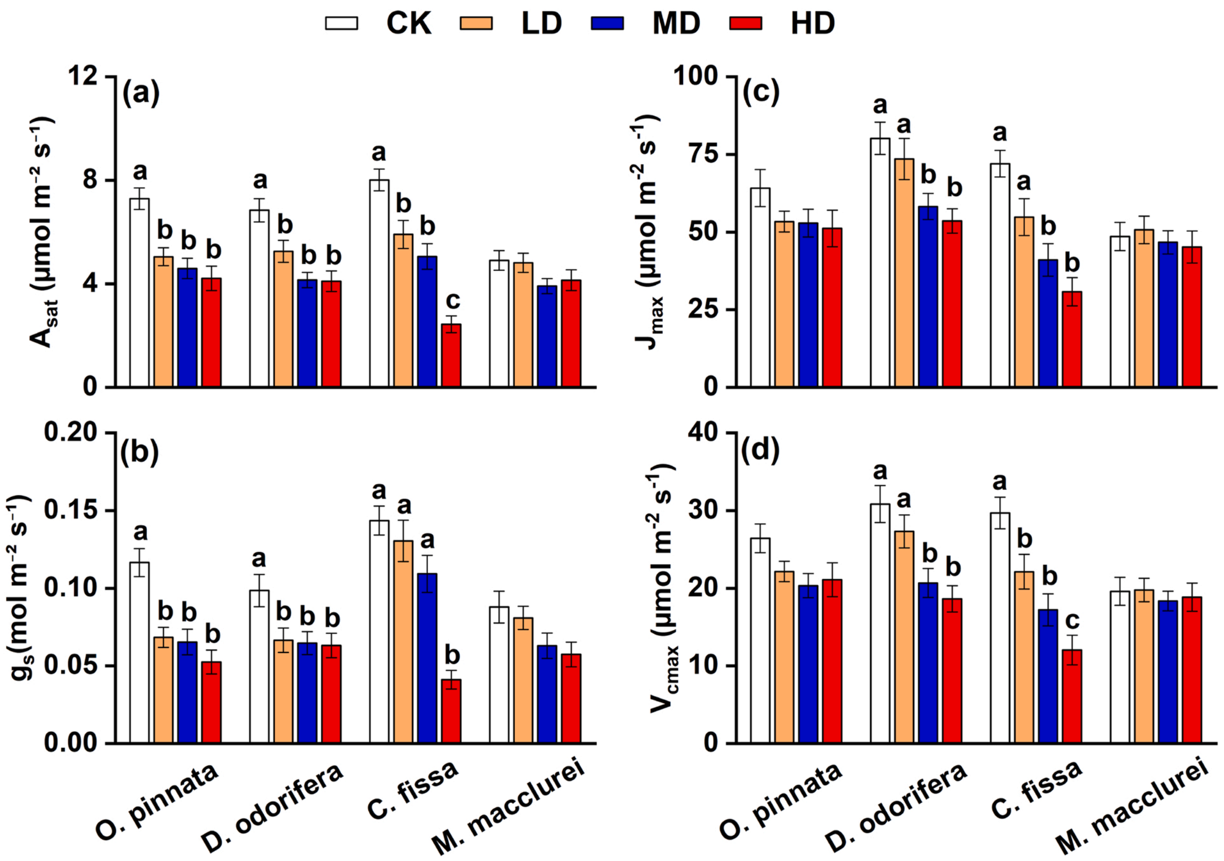


Fig. 3. (a) The light-saturated photosynthetic rate (A_{sat}, μmol m^{-2} s^{-1}, n = 9); (b) stomatal conductance (g_s, mol m^{-2} s^{-1}, n = 9); (c) the area-based maximum rate of photosynthetic electron transport (J_{max}, μmol m^{-2} s^{-1}, n = 3); (d) the area-based maximum rate of photosynthetic Rubisco carboxylation (V_{cmax}, μmol m^{-2} s^{-1}, n = 3) for *Ormosia pinnata*, *Dalbergia odorifera*, *Castanopsis fissa* and *Michelia macclurei* subjected to control (CK), low drought (LD), moderate drought (MD) and high drought (HD) treatments over the course of the experiment. Different lowercase letters above the error bars (standard errors) indicate significant differences in A_{sat}, g_s, J_{max} and V_{max} among drought treatments.

2.8. *Leaf dry matter content and mass per area*

Ten mature leaves per species per treatment (10 leaves x 4 treatments x 4 species = 160 leaves) were selected to measure leaf fresh weight (LFW, g) and leaf area (LA, cm^2) with a leaf area meter (LI-3100, Li-Cor Biosciences, Lincoln, NE, USA). Leaves were then dried in a drying oven for 48 hr at 65 ℃, before measuring leaf dry mass (LDW, g). Leaf dry matter content (LDMC, %) was calculated as 100% * LDW / LFW. Leaf mass per area (LMA, g cm^{-2}) was calculated as LDW / LA (Bartlett et al., 2012a).

2.9. *Statistical analysis*

Data were assessed using Kolmogorov-Smirnov test for normality and Levene's test for homogeneity of variance prior to statistical analysis. When the data did not conform to the assumption of normality and homogeneity of variances, they were logarithmically transformed. Time-series measurements including V, V_{rate}, Ψ_{pd}, Ψ_{md}, A_{sat}, g_s, J_{max} and V_{cmax} were analyzed using repeated-measures mixed effects, in which the fixed factors were drought treatment, drought duration and species, but the random factor was plot. In addition, V, V_{rate}, Ψ_{pd}, Ψ_{md}, A_{sat}, g_s, J_{max} and V_{cmax} for each species were analyzed using repeated-measures mixed effects, in which the fixed factors were drought treatment and duration, but the random factor was plot. The mixed effects models were used to evaluate the fixed effects of drought treatment and species on g_{min}, TLP, LDMC and LMA, in which the random factor was plot. Liner mixed models were performed by the "*lmer*" function in the "lme4" package. One-way analysis (ANOVA) was conducted to compare the differences of g_{min}, TLP, LDMC and LMA among control and drought treatments, following by Tukey post-hoc test. Differences were considered statistically significant at $P < 0.05$.

g_s was plotted against Ψ_{md} to extract P_{gs50} and P_{gs90}, using R with the "fitplc" package (Duursma and Choat, 2017). Correlations between A_{sat} and g_s, J_{max} and V_{cmax} were also tested using liner regression, using Original 2018. The relative importance of stomatal limitation (g_s) and biochemical limitation (J_{max} and V_{cmax}) in explaining variation in photosynthetic rate (A_{sat}), was determined using variation partitioning analysis (VPA) and redundancy analysis (RDA) using the "*varpart*" function in the "Vegan" package. All statistical analyses were conducted with the open-source statistical software platform R (version 4.2.0; R Foundation for Statistical Computing).

3. Results

3.1. *Tree growth*

Overall, V and V_{rate} were obviously influenced by drought duration and species (Table 2, $P < 0.05$). V for *O. pinnata* was significantly reduced by drought treatment across drought duration (30.7%, 20. 5% and 33.3% for LD, MD and HD, respectively; Fig. 2a, $P < 0.01$). V for *D. odorifera* was significantly decreased by drought treatment across drought duration, with declines of 27.8%, 20.5% and 14.4% under LD, MD and HD, respectively (Fig. 2b, $P < 0.05$). V for *C. fissa* and *M. macclurei* declined with drought duration (Fig. 2c and d, $P < 0.001$). Drought duration significantly decreased V_{rate} for the four tree species (Fig. S1).

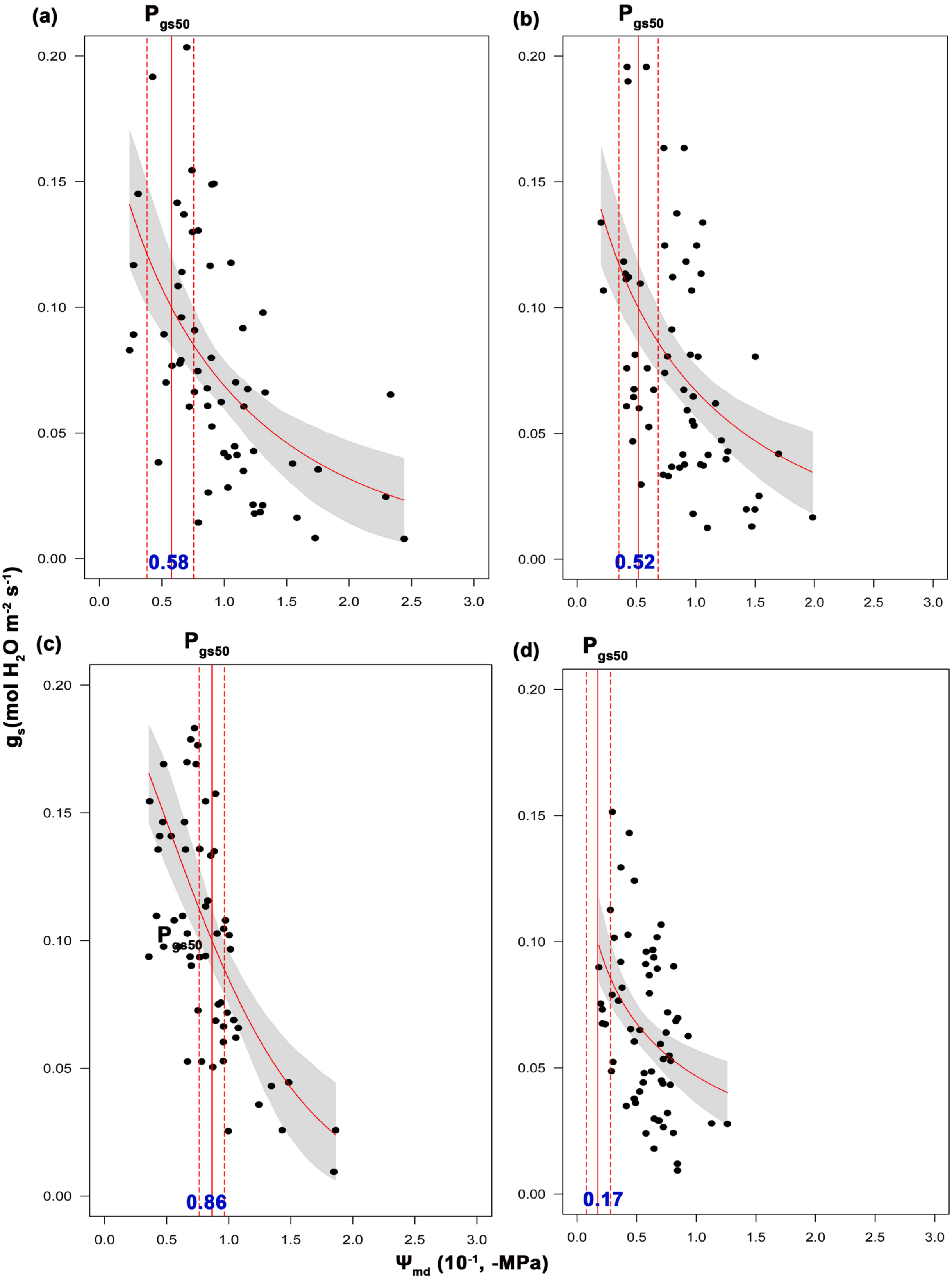


Fig. 4. Leaf stomatal conductance response to water potential for *Ormosia pinnata* (a), *Dalbergia odorifera* (b), *Castanopsis fissa* (c) and *Michelia macclurei* (d). Red vertical lines indicate leaf water potential at 50% stomatal closure (P_{gs50}).

Table 3

Leaf minimum conductance (g_{min}, mmol m^{-2} s^{-1}, n = 9), turgor loss point (TLP, MPa, n = 6), dry matter content (LDMC, %, n = 6), leaf mass per area (LMA, g cm^{-2}, n = 6), leaf water potential at 50% of maximum stomatal conductance (P_{gs50}, MPa) and leaf water potential at 90% of maximum stomatal conductance (P_{gs90}, MPa) for *Ormosia pinnata* (*O. pinnata*), *Dalbergia odorifera* (*D. odorifera*), *Castanopsis fissa* (*C. fissa*) and *Michelia macclurei* (*M. macclurei*) subjected to control (CK), low drought (LD, 75% of CK), moderate drought (MD, 50% of CK) and high drought (HD, 25% of CK) treatments. Values of g_{min}, TLP, LDMC and LMA are shown in means ± standard errors. Values of P_{gs50} and P_{gs90} are shown means with lower and upper bounds of 95% confidence intervals (CI, bracketed). Different lowercase letters above the bold values indicate significant differences in g_{min}, TLP, LDMC and LMA.

	Treatments	*O. pinnata*	*D. odorifera*	*C. fissa*	*M. macclurei*
g_{min} mmol m^{-2} s^{-1})	CK	1.97 ± 0.22	**9.79 ± 0.48^a**	2.30 ± 0.11	1.13 ± 0.07
	LD	1.97 ± 0.17	**9.55 ± 0.58^a**	2.70 ± 0.10	1.61 ± 0.09
	MD	1.80 ± 0.11	**7.72 ± 0.46^b**	2.38 ± 0.12	1.03 ± 0.08
	HD	2.06 ± 0.17	**8.21 ± 0.54^b**	2.71 ± 0.09	1.22 ± 0.06
TLP (MPa)	CK	**-1.21 ± 0.05^a**	-1.66 ± 0.14	-1.64 ± 0.12	-1.61 ± 0.1
	LD	**-1.12 ± 0.03^{ab}**	-1.70 ± 0.07	-1.79 ± 0.08	-1.36 ± 0.10
	MD	**-1.37 ± 0.04^b**	-1.58 ± 0.10	-1.63 ± 0.08	-1.42 ± 0.10
	HD	**-1.42 ± 0.06^b**	-1.67 ± 0.12	-1.54 ± 0.06	-1.69 ± 0.04
LDMC (%)	CK	**34.35 ± 1.37^b**	34.87 ± 1.06	**40.11 ± 0.91^a**	31.07 ± 0.85
	LD	**37.66 ± 0.97^{ab}**	36.79 ± 1.08	**42.05 ± 0.89^a**	30.88 ± 1.28
	MD	**41.44 ± 0.94^a**	34.80 ± 1.23	**40.87 ± 0.90^a**	34.04 ± 0.74
	HD	**39.82 ± 1.69^a**	33.19 ± 0.83	**35.46 ± 1.23^b**	33.13 ± 0.84
LMA (10^{-2}, g cm^{-2})	CK	**0.56 ± 0.03^b**	**0.63 ± 0.03^{ab}**	0.81 ± 0.04	**0.70 ± 0.03^b**
	LD	**0.59 ± 0.02^b**	**0.66 ± 0.03^{ab}**	0.76 ± 0.03	**0.85 ± 0.05^a**
	MD	**0.73 ± 0.03^a**	**0.54 ± 0.04^b**	0.83 ± 0.02	**0.85 ± 0.03^a**
	HD	**0.70 ± 0.03^a**	**0.70 ± 0.03^a**	0.69 ± 0.03	**0.64 ± 0.03^b**
P_{gs50} (-MPa)		0.58 [0.38, 0.78]	0.52 [0.35, 0.69]	0.86 [0.76, 0.96]	0.17 [0.07, 0.27]
P_{gs90} (-MPa)		2.66 [1.80,]	2.94 [1.93,]	1.97 [1.54,]	2.94 [1.92,]

3.2. Leaf water potential

At pre-drought, Ψ_{pd} and Ψ_{md} were the lowest (i.e., more negative) for *D. odorifera* ($\Psi_{pd} = -0.45 \pm 0.06$ MPa, $\Psi_{md} = -1.16 \pm 0.07$ MPa), but *M. macclurei* exhibited the highest (i.e., less negative) Ψ_{md} (-0.70 ± 0.12 MPa) (Table 1). In general, drought treatment, drought duration and species significantly affected Ψ_{pd}, and Ψ_{md} was significantly influenced by drought duration and species (Table 2, $P < 0.05$). Ψ_{pd} for *O. pinnata* and *D. odorifera* both decreased after Day 52 of drought treatment (Fig. S2a and b). Ψ_{pd} for *C. fissa* and *M. macclurei* sharply decreased after Day 24 and Day 64 of drought treatment, respectively (Fig. S2c and d). Compared to the control, four tree species under drought treatment had significantly lower Ψ_{pd} and Ψ_{md} across drought duration. *O. pinnata* and *C. fissa* in HD treatment had lower Ψ_{pd} and Ψ_{md} than *D. odorifera* and *M. macclurei* (Fig. S2a-h, $P < 0.001$).

3.3. Photosynthesis

At pre-drought, A_{sat} and g_s were the highest for *D. odorifera*, followed by *C. fissa*, *O. pinnata* and *M. macclurei pinnata* (Table 1). Overall, A_{sat} and g_s were significantly affected by drought treatment, drought duration and species (Table 2, $P < 0.01$). Drought treatment led to significant decreases in A_{sat} for *O. pinnata* across drought duration (30.8%, 37.0% and 42.2% for LD, MD and HD, respectively; Figs. S3a and 3a, $P < 0.001$). A_{sat} for *D. odorifera* was significantly reduced by drought treatment throughout drought duration (23.2%, 39.3% and 40.0% for LD, MD and HD, respectively; Figs. S3b and 3a, $P < 0.001$). LD and MD significantly reduced A_{sat} for *C. fissa*, with declines of 26.2% and 36.9%, respectively. *C. fissa* under HD had lower A_{sat} than CK, LD and MD, with declines of 69.6%, 16.4% and 8.5%, respectively (Figs. S3c and 3a, $P < 0.001$). A_{sat} for *M. macclurei* was significantly reduced by drought duration (Figs. S3d and 3a, $P < 0.001$), but not drought treatment. Drought treatments significantly reduced g_s for *O. pinnata* and *D. odorifera* (Figs. S3e, f and 3b, $P < 0.01$). g_s for *C. fissa* was significantly lower in HD than CK, LD and MD (Figs. S3g and 3b, $P < 0.001$). g_s for *M. macclurei* declined with drought duration (Figs. S3h and 3b, $P < 0.001$).

J_{max} and V_{cmax} were significantly affected by drought treatment, drought duration and species (Table 2, $P < 0.05$). MD and HD significantly reduced J_{max} for *D. odorifera* by 27.4% and 33.2%, respectively (Figs. S3j and 3c, $P < 0.01$). J_{max} for *C. fissa* was significantly decreased by MD and HD across drought duration, with declines of 43.0% and 57.3%, respectively (Figs. S3k and 3c, $P < 0.05$). Drought treatment did not affect J_{max} for *O. pinnata* and *M. macclurei* (Figs. S3i, S3l and 3c). MD and HD significantly reduced V_{cmax} for *D. odorifera* across drought duration by 33.0% and 39.6%, respectively (Figs. S3n and 3d, $P < 0.05$). Drought treatment significantly decreased V_{cmax} for *C. fissa* (25.5%, 42.0% and 59.4% for LD, MD and HD, respectively; Figs. S3o and 3d, $P < 0.001$). Drought treatment did not affect V_{max} for *O. pinnata* and *M. macclurei* (Figs. S3m, S3p and 3d).

3.4. g_s responds to declining Ψ_{pd}

Across large ranges of Ψ_{md} for *O. pinnata* ([−0.24, −2.44] MPa), *D. odorifera* ([−0.20, −1.99] MPa) and *C. fissa* ([−0.36, −1.86] MPa), g_s slowly decreased. However, over a small range of Ψ_{md} for *M. macclurei* ([−0.18, −1.26] MPa), g_s declined very quickly (Fig. 4). P_{gs50} for *M. macclurei* was the highest (i.e., less negative) (−0.17 [−0.27, −0.07] MPa), followed by *D. odorifera* (−0.52 [−0.69, −0.35] MPa), *O. pinnata* (−0.58 [−0.78, −0.38] MPa) and *C. fissa* (−0.86 [−0.96, −0.76] MPa). While P_{gs90} for *C. fissa* was the highest (i.e., less negative) (−1.97 [, −1.54] MPa), followed by *O. pinnata* (−2.66 [, −1.80] MPa), *D. odorifera* (−2.94 [, −1.93] MPa) and *M. macclurei* (−2.94 [, −1.92] MPa) (Fig. 4 and Table 3).

3.5. Plant water relations and leaf morphological traits

At pre-drought, LMA for *C. fissa*, *M. macclurei*, *O. pinnata* and *D. odorifera* were 154.7, 161.2, 168.7 and 254.6 g cm^{-2}, respectively (Table 1). In generally, drought treatment and species both affected g_{min}, LDMC and LMA (Table 2, $P < 0.05$); TLP was not influenced by drought treatment, but varied among species (Table 2, $P < 0.001$). g_{min} for *D. odorifera* was significantly reduced by MD and HD compared to CK and LD (Table 3, $P < 0.001$). MD and HD lowered TLP for *O. pinnata* (Table 3, $P < 0.05$). MD and HD significantly increased LDMC for *O. pinnata*, while reduced LDMC was observed in *C. fissa* under HD (Table 3, $P < 0.05$). LMA for *O. pinnata* was higher under MD and HD than CK and LD. HD induced higher LMA for *D. odorifera*. *M. macclurei* had higher LMA under LD and MD compared with CK and HD (Table 3, $P < 0.05$).

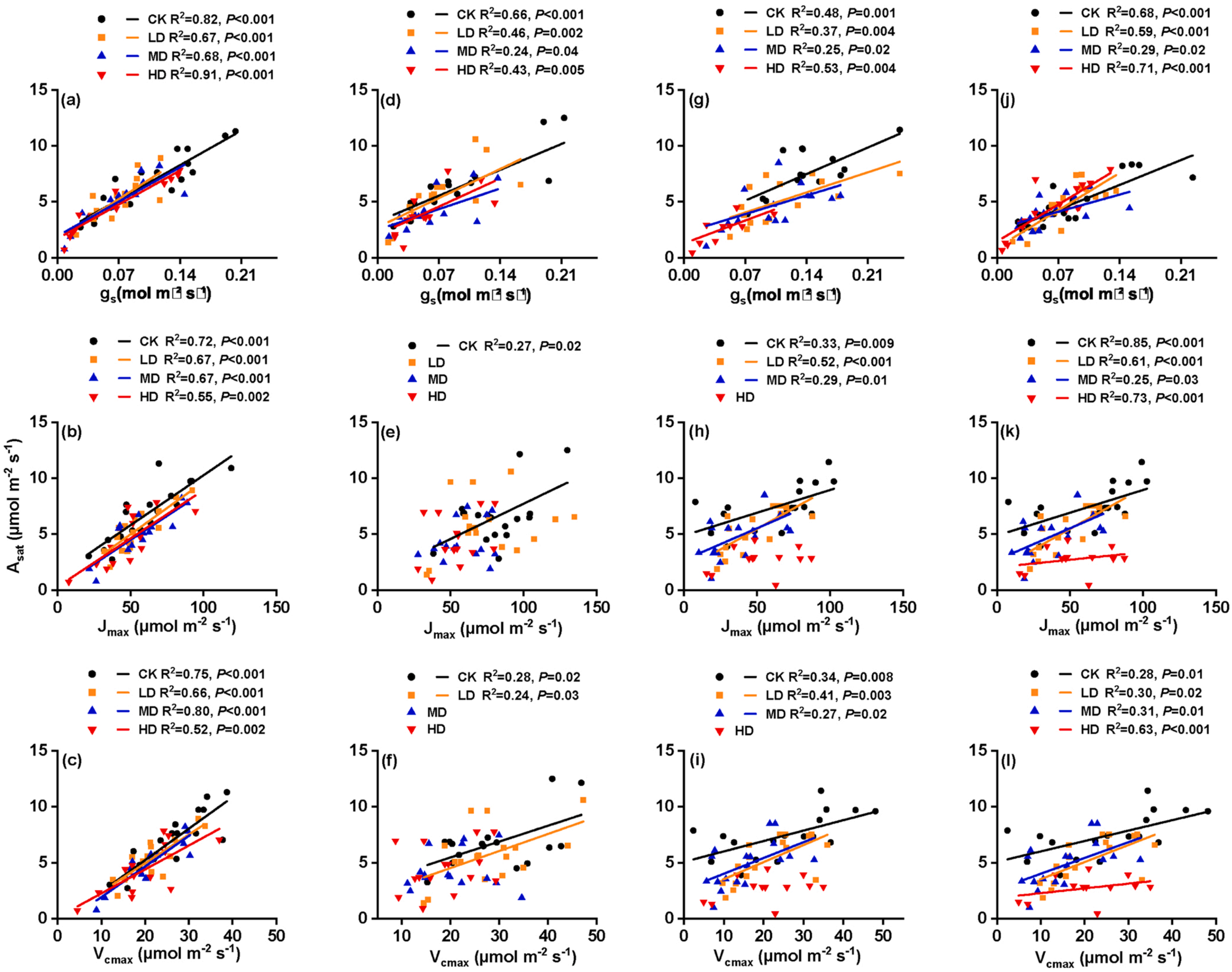


Fig. 5. Relationship between the light-saturated photosynthetic rate (A_{sat}) and stomatal conductance (g_s, a, d, g and j), area-based maximum rate of photosynthetic electron transport (J_{max}, b, e, h and k) and area-based maximum rate of photosynthetic Rubisco carboxylation (V_{cmax}, c, f, i and l) for *Ormosia pinnata*, *Dalbergia odorifera*, *Castanopsis fissa* and *Michelia macclurei*.

3.6. Correlations between A_{sat} and g_s, J_{max} and V_{cmax}

A_{sat} for *O. pinnata* and *M. macclurei* were positively correlated with g_s, J_{max} and V_{cmax} (Table S2). The slopes between A_{sat} and V_{cmax} for *O. pinnata* decreased with increasing drought intensity (Table S2 and Fig. 5c, $P < 0.01$), while that for *M. macclurei* increased with increasing drought intensity (Table S2 and Fig. 5l, $P < 0.05$). A_{sat} for *D. odorifera* and *C. fissa* were positively correlated with g_s, while there were no significant correlations between A_{sat} and J_{max}, or between A_{sat} and V_{cmax} in MD or HD (Table S2 and Fig. 5).

The effects of stomatal and biochemical limitations on A_{sat} for the four tree species.

Stomatal and biochemical limitations explained lower A_{sat} for *O. pinnata* by 14% and 9%, respectively (Fig. 6a). Reduced A_{sat} for *D. odorifera* was explained by stomatal and biochemical limitations, accounting for 42% and 13%, respectively (Fig. 6b). Stomatal and biochemical limitations explained decreased A_{sat} for *C. fissa* by 40% and 12%, respectively (Fig. 6c). Biochemical and stomatal limitations explained lower A_{sat} for *M. macclurei* by 22% and 16%, respectively (Fig. 6d).

4. Discussion

In this drought treatment experiment, we tested our objectives and found that (a) *O. pinnata* adapted to drought by decreasing TLP and increasing LDMC and LMA, while *D. odorifera* decreased g_{min} and increased LMA. *C. fissa* was the most susceptible to water loss due to slow stomatal closure, while *M. macclurei* closed stomata quickly to reduce water loss; (b) drought reduced A_{sat} for *O. pinnata*, *D. odorifera* and *C. fissa*, which was primarily driven by declining g_s and further decreased growth for *O. pinnata* and *D. odorifera*. A_{sat} for *M. macclurei* was not affected by drought due to stable J_{max} and V_{cmax}; (c) Overall, the seedling of *M. macclurei* might be most suitable in plantations during soil water drought stress due to earlier stomatal closure and lower TLP.

4.1. Adaptive strategies to drought for the four tree species

g_s for *C. fissa* was less sensitive to drought, while *M. macclurei* was most sensitive to drought. Reduced Ψ_{pd}, Ψ_{md} and g_s had been observed in the four tree species, which was due to declining soil water moisture (Garcia-Forner et al., 2016). *O. pinnata*, *D. odorifera* and *C. fissa* had more negative P_{gs50}, suggesting that they could maintain gas exchange until more negative water potentials (Klein, 2014; Bartlett et al., 2016; Henry et al., 2019). *C. fissa* exposed to drought initiated stomatal closure

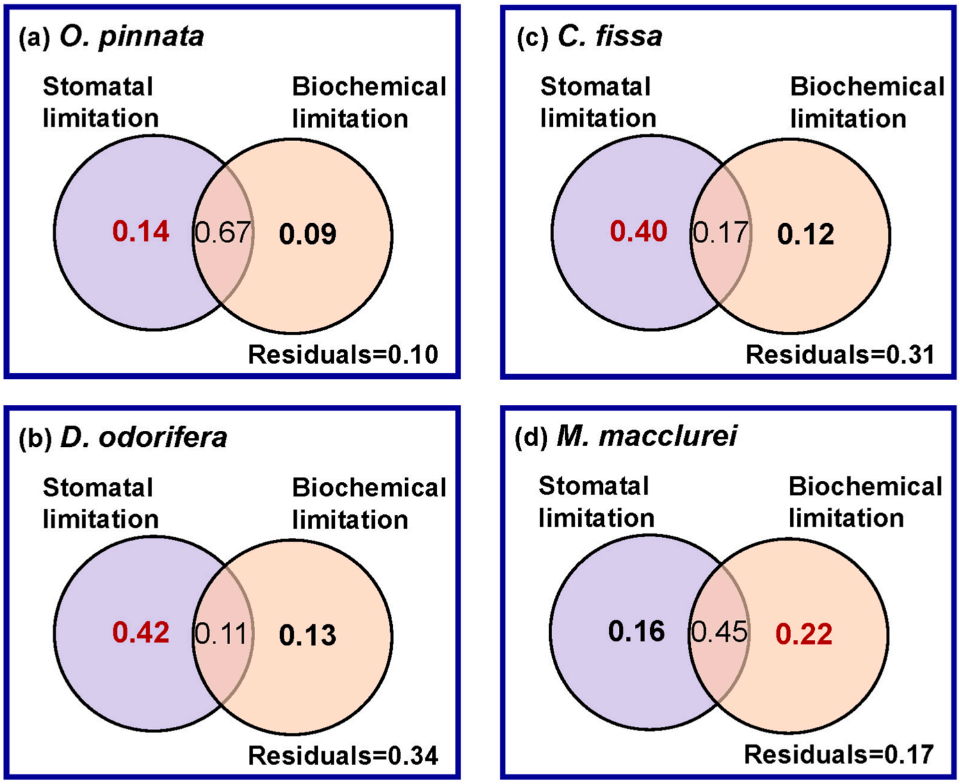


Fig. 6. Variation partitioning analysis (VPA) showing the effects of stomatal limitation (g_s) and biochemical limitation on photosynthetic rate (A_{sat}) for *Ormosia pinnata*, *Dalbergia odorifera*, *Castanopsis fissa* and *Michelia macclurei*. Biochemical limitation contains area-based maximum rate of photosynthetic Rubisco carboxylation (V_{cmax}) and area-based maximum rate of photosynthetic electron transport (J_{max}).

latest (P_{gs50}) but completely closed stomata earliest (P_{gs90}), indicating small differences in water potential between initial and complete stomatal closure (Brodribb et al., 2016; Li et al., 2019). *C. fissa* slowly initiated stomatal closure, which would contribute to its faster water loss (Farrell et al., 2017). *M. macclurei* sustained stable Ψ_{md} before Day 62 regardless of declining soil moisture, which might be due to tighter stomatal regulation (Nolan et al., 2017; Fu and Meinzer, 2019). *M. macclurei* had less negative P_{gs50} among the four tree species, suggesting that it was most sensitive to water stress and closed stomata earliest to avoid cavitation (Henry et al., 2019). Similar to Li et al. (2018a), early stomatal closure for *M. macclurei* was a critical strategy to adapt to drought, resulting in less water loss. *M. macclurei* sustained open stomata until leaf water potential was low, reflected by a more negative P_{gs90}, which might be related to early stomatal closure.

Drought decreased g_{min} for *D. odorifera*, which could reduce water loss for *D. odorifera* and increase the time to hydraulic failure and plant desiccation (Brodribb et al., 2014; Duursma et al., 2019; Challis et al., 2021; Levionnois et al., 2021). The alteration in chemical composition of the cuticle may lead to decreased g_{min}, as supported by other studies (Bueno et al., 2019; Duursma et al., 2019). Although *O. pinnata*, *C. fissa* and *M. macclurei* exhibited low plasticity in reducing g_{min}, they had lower water loss than *D. odorifera* after stomatal closure due to lower g_{min}. Future studies should further investigate the contribution of g_{min} to plant desiccation time (Martin-StPaul et al., 2017; Levionnois et al., 2021).

Lower TLP was observed in *O. pinnata* under drought, which could delay stomatal closure to maintain hydraulic transport, photosynthesis and growth until soil water potential was low (Brodribb et al., 2003; Blackman et al., 2010; Zhang et al., 2021). Reduced TLP for *O. pinnata* might be due to solutes accumulation, including ions, sugars, amino acids, and organic acids (Chen and Jiang, 2010; Bartlett et al., 2014; Zhang et al., 2021), which would enhance water retention capacity and maintain turgor pressure by increasing water uptake from soil (Inoue et al., 2017). *D. odorifera* and *M. macclurei* had more negative TLP than *O. pinnata* and *C. fissa* in the high drought treatment, suggesting that *D. odorifera* and *M. macclurei* might have higher drought tolerance and lower hydraulic vulnerability (Bucci et al., 2019).

Drought enhanced LDMC for *O. pinnata* but decreased it for *C. fissa*, and increased LMA for *O. pinnata* and *D. odorifera* but reduced it for *M. macclurei*. Increased LDMC for *O. pinnata* might be driven by higher leaf toughness, reducing its water loss (Blumenthal et al., 2020). Lower LDMC caused by drought had been observed in *C. fissa*, which would promote water loss and not be beneficial for its growth and survival (Jung et al., 2014). Drought-induced enhancements in LMA for *O. pinnata* and *D. odorifera* might be due to enhanced leaf thickness, which would help them conserve water and enable them to better adapt to drought (Chen and Wang, 2009; Limousin et al., 2010; Michaletz et al., 2015). In addition, Binks et al. (2016) demonstrated that drought increased the thickness of spongy mesophyll to store more water, which may contribute to higher LMA for *O. pinnata* and *D. odorifera*. However, thinner leaves for *M. macclurei* might lead to its declining LMA, as demonstrated by Mitchell et al. (2008).

4.2. Stomatal and biochemical limitations to A_{sat}

We found that drought significantly decreased A_{sat} for *O. pinnata*, *D. odorifera* and *C. fissa*, thereby inhibiting growth for *O. pinnata* and *D. odorifera*; however, A_{sat} in *M. macclurei* was not affected by drought. Drought reduced J_{max} and V_{cmax} for *D. odorifera* and *C. fissa*. Limited rubisco-1, 5-bisphosphate regeneration induced by drought might contribute to lower J_{max} for *D. odorifera* and *C. fissa* (Carmo-Silva et al., 2010). Drought reduced V_{cmax} for *D. odorifera* and *C. fissa*, which might be related to lower Rubisco activity and changes in leaf structural traits (Limousin et al., 2010; Misson et al., 2010). Drought-induced lower A_{sat} for *O. pinnata*, *D. odorifera* and *C. fissa* were positively associated with declining g_s, but biochemical limitations decreased with drought intensity. Contrary to our results, previous studies demonstrated that lower A_{sat} induced by high drought was mainly due to non-stomatal (biochemical and mesophyll) limitations, which exceeded stomatal limitation (Misson et al., 2010; Sperlich et al., 2016). Lower A_{sat} for *O. pinnata* and *D. odorifera* contributed to their declining growth (Aaltonen et al., 2017). Many studies demonstrated that tight stomatal regulation led to nutrient deficiency due to reduced nutrient transport as a function of declining transpiration, which would further inhibit photosynthetic biochemical processes (Vaz et al., 2010; Salazar-Tortosa et al., 2018). However, drought did not affect J_{max} and V_{cmax} for *M. macclurei*, which might be related to long-term nutrient uptake, as a result of its prolonged stomatal closure (Li et al., 2016; Shrestha et al., 2021). Additionally, the correlation between A_{sat} and V_{cmax} for *M. macclurei* increased with drought intensity. Thus, no change in A_{sat} for *M. macclurei* under drought was driven by stable J_{max} and V_{cmax}. Overall, stomatal limitation exerted greater impact than biochemical limitation on declining A_{sat} for *O. pinnata*, *D. odorifera* and *C. fissa*, while biochemical limitations were greater than stomatal limitations for *M. macclurei*.

4.3. Species best adapted to drought

Warmer and drier environments increased tree mortality in subtropical plantations (Duan et al., 2022), while physiological plasticity in response to drought may improve tree growth and reduce mortality (Liu et al., 2018). In response to future climate change, selecting tree species with physiological and morphological traits that confer high drought tolerance and resistance will be critical for maintaining growth during drought periods and potentially generating higher wood carbon storage and lumber production in plantations (Rahman et al., 2019). Among the four tree species, *M. macclurei* exhibited the lowest negative effects of soil water deficit due to high drought avoidance (earlier stomatal closure) and resistance (lower TLP) (Choat et al., 2018; McDowell et al., 2022). Earlier stomatal closure might reduce the potential for impairment of leaf hydraulic conductivity in *M. macclurei*, and hence following re-rewatering there might be more rapid recovery of physiological processes in the whole plant (Li et al., 2021; Manzi et al., 2022). Thus, *M. macclurei* may exhibit higher drought resilience than other three tree species due to fast physiological recovery (Li et al., 2021). In addition, *M. macclurei* maintained photosynthesis, while drought reduced photosynthesis for the other three tree species. Stable photosynthesis in *M. macclurei* may facilitate non-structural carbohydrate (NSC) accumulation, which may provide carbon to improve osmotic regulation, thereby increasing water acquisition during drought (Li et al., 2021). Overall, *M. macclurei* might be the best adapted plantation tree for growth in future drier climates.

CRediT authorship contribution statement

Ting Wu and Nadan Tan wrote the draft. Juxiu Liu, David T. Tissue and Honglang Duan revised the draft. Wei Su, Yuting Song, Xujun Liu, Yue Liu, Xu Li, Zhiyang Lie, Shuyidan Zhou and Shimin Yang helped complete experiment. Juan Huang, Junhua Yan, Xuli Tang, Shizhong Liu, Guowei Chu and Xinghua He helped design the drought experiment.

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.

Data availability

Data will be made available on request.

Acknowledgments

This study was jointly funded by the Key Research and Development Program of Guangdong Province (Grant No. 2020B1111530004), the National Natural Science Foundation of China (Grant Nos. 41977287, 41991285, 32101342 and 31971459) and the China Postdoctoral Science Foundation (Grant Nos. 2021M703259, 2021M703260, 2021M693220).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2022.105046.

References

Aaltonen, H., Linden, A., Heinonsalo, J., Biasi, C., Pumpanen, J., 2017. Effects of prolonged drought stress on *Scots pine* seedling carbon allocation. Tree Physiol. 37, 418–427. https://doi.org/10.1093/treephys/tpw119.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. . Ecol. Manag. 259, 660–684. https://doi.org/10.1016/j.foreco.2009.09.001.

Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6, 129. https://doi.org/10.1890/ES15-00203.1.

Barnard, D.M., Bauerle, W.L., 2013. The implications of minimum stomatal conductance on modeling water flux in forest canopies. J. Geophys. Res-Biogeo. 118, 1322–1333. https://doi.org/10.1002/jgrg.20112.

Bartholomew, D.C., Bittencourt, P.R.L., da Costa, A.C.L., Banin, L.F., Costa, P.D., Coughlin, S.I., Domingues, T.F., Ferreira, L.V., Giles, A., Mencuccini, M., Mercado, L., Miatto, R.C., Oliveira, A., Oliveira, R., Meir, P., Rowland, L., 2020. Small tropical forest trees have a greater capacity to adjust carbon metabolism to long-term drought than large canopy trees. Plant Cell Environ. 43, 2380–2393. https://doi.org/10.1111/pce.13838.

Bartlett, M.K., Sinclair, G., 2021. Temperature and evaporative demand drive variation in stomatal and hydraulic traits across grape cultivars. J. Exp. Bot. 72, 1995–2009. https://doi.org/10.1093/jxb/eraa577.

Bartlett, M.K., Scoffoni, C., Ardy, R., Zhang, Y., Sun, S., Cao, K., Sack, L., 2012a. Rapid determination of comparative drought tolerance traits: using an osmometer to predict turgor loss point. Methods Ecol. Evol. 8, 880–888. https://doi.org/10.1111/j.2041-210X.2012.00230.x.

Bartlett, M.K., Scoffoni, C., Sack, L., 2012b. The determinants of leaf turgor loss point and prediction of drought tolerance of species and biomes: a global meta-analysis. Ecol. Lett. 15, 393–405. https://doi.org/10.1111/j.1461-0248.2012.01751.x.

Bartlett, M.K., Zhang, Y., Kreidler, N., Sun, S.W., Ardy, R., Cao, K.F., Sack, L., 2014. Global analysis of plasticity in turgor loss point, a key drought tolerance trait. Ecol. Lett. 17, 1580–1590. https://doi.org/10.1111/ele.12374.

Bartlett, M.K., Klein, T., Jansen, S., Choat, B., Sack, L., 2016. The correlations and sequence of plant stomatal, hydraulic, and wilting responses to drought. Proc. Natl. Acad. Sci. U. S. A. 113, 13098–13103. https://doi.org/10.1073/pnas.1604088113.

Binks, O., Meir, P., Rowland, L., da Costa, A.C.L., Vasconcelos, S.S., de Oliveira, A.A.R., Ferreira, L., Mencuccini, M., 2016. Limited acclimation in leaf anatomy to experimental drought in tropical rainforest trees. Tree Physiol. 36, 1550–1561. https://doi.org/10.1093/treephys/tpw078.

Blackman, C.J., Brodribb, T.J., Jordan, G.J., 2010. Leaf hydraulic vulnerability is related to conduit dimensions and drought resistance across a diverse range of woody angiosperms. N. Phytol. 188, 1113–1123. https://doi.org/10.1111/j.1469-8137.2010.03439.x.

Blackman, C.J., Creek, D., Maier, C., Aspinwall, M.J., Drake, J.E., Pfautsch, S., O'Grady, A., Deizon, S., Medlyn, B.E., Tissue, D.T., Choat, B., 2019. Drought response strategies and hydraulic traits contribute to mechanistic understanding of plant dry-down to hydraulic failure. Tree Physiol. 39, 910–924. https://doi.org/10.1093/treephys/tpz016.

Blumenthal, D.M., Mueller, K.E., Kray, J.A., Ocheltree, T.W., Augustine, D.J., Wilcox, K. R., Cornelissen, H., 2020. Traits link drought resistance with herbivore defence and plant economics in semi-arid grasslands: The central roles of phenology and leaf dry matter content. J. Ecol. 108, 2336–2351. https://doi.org/10.1111/1365-2745.13454.

Brodribb, T.J., Holbrook, N.M., Edwards, E.J., GutiERrez, M.V., 2003. Relations between stomatal closure, leaf turgor and xylem vulnerability in eight tropical dry forest trees. Plant Cell Environ. 26, 443–450. https://doi.org/10.1046/j.1365-3040.2003.00975.x.

Brodribb, T.J., McAdam, S.A., Jordan, G.J., Martins, S.C., 2014. Conifer species adapt to low-rainfall climates by following one of two divergent pathways. Proc. Natl. Acad. Sci. U. S. A. 111, 14489–14493. https://doi.org/10.1073/pnas.1407930111.

Brodribb, T.J., Skelton, R.P., McAdam, S.A., Bienaime, D., Lucani, C.J., Marmottant, P., 2016. Visual quantification of embolism reveals leaf vulnerability to hydraulic failure. N. Phytol. 209, 1403–1409. https://doi.org/10.1111/nph.13846.

Bucci, S.J., Silletta, L.M.C., Garre, A., Cavallaro, A., Efron, S.T., Arias, N.S., Goldstein, G., Scholz, F.G., 2019. Functional relationships between hydraulic traits and the timing of diurnal depression of photosynthesis. Plant Cell Environ. 42, 1603–1614. https://doi.org/10.1111/pce.13512.

Bueno, A., Alfarhan, A., Arand, K., Burghardt, M., Deininger, A.C., Hedrich, R., Leide, J., Seufert, P., Staiger, S., Riederer, M., 2019. Effects of temperature on the cuticular transpiration barrier of two desert plants with water-spender and water-saver strategies. J. Exp. Bot. 70, 1613–1625. https://doi.org/10.1093/jxb/erz018.

Carmo-Silva, A.E., Keys, A.J., Andralojc, P.J., Powers, S.J., Arrabaca, M.C., Parry, M.A., 2010. Rubisco activities, properties, and regulation in three different C4 grasses under drought. J. Exp. Bot. 61, 2355–2366. https://doi.org/10.1093/jxb/erq071.

Carmo-Silva, A.E., Gore, M.A., Andrade-Sanchez, P., French, A.N., Hunsaker, D.J., Salvucci, M.E., 2012. Decreased CO_2 availability and inactivation of Rubisco limit photosynthesis in cotton plants under heat and drought stress in the field. Environ. Exp. Bot. 83, 1–11. https://doi.org/10.1016/j.envexpbot.2012.04.001.

Cernusak, L.A., Winter, K., Turner, B.L., 2011. Transpiration modulates phosphorus acquisition in tropical tree seedlings. Tree Physiol. 31, 878–885. https://doi.org/10.1093/treephys/tpr077.

Challis, A., Blackman, C., Ahrens, C., Medlyn, B., Rymer, P., Tissue, D.T., 2021. Adaptive plasticity in plant traits increases time to hydraulic failure under drought in a foundation tree. Tree Physiol. 42, 708–721. https://doi.org/10.1093/treephys/tpab096.

Chen, H., Jiang, J.G., 2010. Osmotic adjustment and plant adaptation to environmental changes related to drought and salinity. Environ. Rev. 18, 309–319. https://doi.org/10.1139/A10-014.

Chen, L., Wang, R.Z., 2009. Anatomical and physiological divergences and compensatory effects in two *Leymus chinensis* (Poaceae) ecotypes in Northeast China. Agric. Ecosyst. Environ. 134, 46–52. https://doi.org/10.1016/j.agee.2009.05.015.

Chen, S.G., Zhang, Y., 2021. Water saving potential and economic viability assessment of rainwater harvesting system for four different climatic regions in China. Water Supply 21, 386–400. https://doi.org/10.2166/ws.2020.30.

Choat, B., Brodribb, T.J., Brodersen, C.R., Duursma, R.A., Lopez, R., Medlyn, B.E., 2018. Triggers of tree mortality under drought. Nature 558, 531–539. https://doi.org/10.1038/s41586-018-0240-x.

Corlett, R.T., 2016. The impacts of droughts in tropical forests. Trends Plant Sci. 21, 584–593. https://doi.org/10.1016/j.tplants.2016.02.003.

Damour, G., Vandame, M., Urban, L., 2009. Long-term drought results in a reversible decline in photosynthetic capacity in mango leaves, not just a decrease in stomatal conductance. Tree Physiol. 29, 675–684. https://doi.org/10.1093/treephys/tpp011.

Drake, J.E., Power, S.A., Duursma, R.A., Medlyn, B.E., Aspinwall, M.J., Choat, B., Creek, D., Eamus, D., Maier, C., Pfautsch, S., Smith, R.A., Tjoelker, M.G., Tissue, D. T., 2017. Stomatal and non-stomatal limitations of photosynthesis for four tree species under drought: A comparison of model formulations. Agric. . Meteorol. 247, 454–466. https://doi.org/10.1016/j.agrformet.2017.08.026.

Duan, H.L., Li, Y.Y., Xu, Y., Zhou, S.X., Liu, J., Tissue, D.T., Liu, J.X., 2019. Contrasting drought sensitivity and post-drought resilience among three co-occurring tree species in subtropical China. Agric. For. Meteorol. 272, 55–68. https://doi.org/10.1016/j.agrformet.2019.03.024.

Duan, H.L., de Dios, V.R., Wang, D.F., Zhao, N., Huang, G.M., Liu, W.F., Wu, J.P., Zhou, S.X., Choat, B., Tissue, D.T., 2022. Testing the limits of plant drought stress and subsequent recovery in four provenances of a widely distributed subtropical tree species. Plant Cell Environ. 45, 1187–1203. https://doi.org/10.1111/pce.14254.

Duursma, R., Choat, B., 2017. fitplc—An R package to fit hydraulic vulnerability curves. J. Plant Hydraul. 4, 002.

Duursma, R.A., Blackman, C.J., Lopez, R., Martin-StPaul, N.K., Cochard, H., Medlyn, B. E., 2019. On the minimum leaf conductance: its role in models of plant water use, and ecological and environmental controls. N. Phytol. 221, 693–705. https://doi.org/10.1111/nph.15395.

Farrell, C., Szota, C., Arndt, S.K., 2017. Does the turgor loss point characterize drought response in dryland plants. Plant Cell Environ. 40, 1500–1511. https://doi.org/10.1111/pce.12948.

Flexas, J., Ribas-Carbo, M., Diaz-Espejo, A., Galmes, J., Medrano, H., 2008. Mesophyll conductance to CO_2: current knowledge and future prospects. Plant Cell Environ. 31, 602–621. https://doi.org/10.1111/j.1365-3040.2007.01757.x.

Fu, X.L., Meinzer, F.C., 2019. Metrics and proxies for stringency of regulation of plant water status (iso/anisohydry): a global data set reveals coordination and trade-offs among water transport traits. Tree Physiol. 39, 122–134. https://doi.org/10.1093/treephys/tpy087.

Garcia-Forner, N., Adams, H.D., Sevanto, S., Collins, A.D., Dickman, L.T., Hudson, P.J., Zeppel, M.J.B., Jenkins, M., Powers, H., Martinez-Vilalta, J., McDowell, N.G., 2016. Responses of two semiarid conifer tree species to reduced precipitation and warming reveal new perspectives for stomatal regulation. Plant Cell Environ. 39, 38–49. https://doi.org/10.1111/pce.12588.

Gonzalez-Rebeles, G., Terrazas, T., Mendez-Alonzo, R., Paz, H., Brodribb, T.J., Tinoco-Ojanguren, C., 2021. Leaf water relations reflect canopy phenology rather than leaf life span in Sonoran Desert trees. Tree Physiol. 41, 1627–1640. https://doi.org/10.1093/treephys/tpab032.

Henry, C., John, G.P., Pan, R.H., Bartlett, M.K., Fletcher, L.R., Scoffoni, C., Sack, L., 2019. A stomatal safety-efficiency trade-off constrains responses to leaf dehydration. Nat. Commun. 10, 3398. https://doi.org/10.1038/s41467-019-11006-1.

Inoue, Y., Ichie, T., Kenzo, T., Yoneyama, A., Kumagai, T., Nakashizuka, T., 2017. Effects of rainfall exclusion on leaf gas exchange traits and osmotic adjustment in mature canopy trees of *Dryobalanops aromatica* (Dipterocarpaceae) in a Malaysian tropical rain forest. Tree Physiol. 37, 1301–1311. https://doi.org/10.1093/treephys/tpx053.

IPCC, 2021. Summary for Policymakers. In: Climate Change. In: Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock, T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (Eds.), The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. 3–32. https://doi.org/10.1017/9781009157896.001.

Isaac-Renton, M., Montwe, D., Hamann, A., Spiecker, H., Cherubini, P., Treydte, K., 2018. Northern forest tree populations are physiologically maladapted to drought. Nat. Commun. 9, 5254. https://doi.org/10.1038/s41467-020-15177-0.

Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G., Spiegelberger, T., Cornwell, W., 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. J. Ecol. 102, 45–53. https://doi.org/10.1111/1365-2745.12177.

Klein, T., 2014. The variability of stomatal sensitivity to leaf water potential across tree species indicates a continuum between isohydric and anisohydric behaviours. Funct. Ecol. 28, 1313–1320. https://doi.org/10.1111/1365-2435.12289.

Kumagai, T., Porporato, A., 2012. Strategies of a Bornean tropical rainforest water use as a function of rainfall regime: isohydric or anisohydric? Plant Cell Environ. 35, 61–71. https://doi.org/10.1111/j.1365-3040.2011.02428.x.

Levionnois, S., Ziegler, C., Heuret, P., Jansen, S., Stahl, C., Calvet, E., Goret, J.Y., Bonal, D., Coste, S., 2021. Is vulnerability segmentation at the leaf-stem transition a drought resistance mechanism? A theoretical test with a trait-based model for Neotropical canopy tree species. Ann. Sci. 78, 87. https://doi.org/10.1007/s13595-021-01094-9.

Li, R.H., Zhu, S.D., Chen, H.Y.H., John, R., Zhou, G.Y., Zhang, D.Q., Zhang, Q.M., Ye, Q., 2015. Are functional traits a good predictor of global change impacts on tree species abundance dynamics in a subtropical forest. Ecol. Lett. 18, 1181–1189. https://doi.org/10.1111/ele.12497.

Li, X.M., Blackman, C.J., Choat, B., Duursma, R.A., Rymer, P.D., Medlyn, B.E., Tissue, D. T., 2018a. Tree hydraulic traits are coordinated and strongly linked to climate-of-origin across a rainfall gradient. Plant Cell Environ. 41, 646–660. https://doi.org/10.1111/pce.13129.

Li, X.M., Blackman, C.J., Rymer, P.D., Quintans, D., Duursma, R.A., Choat, B., Medlyn, B. E., Tissue, D.T., 2018b. Xylem embolism measured retrospectively is linked to canopy dieback in natural populations of *Eucalyptus piperita* following drought. Tree Physiol. 38, 1193–1199. https://doi.org/10.1093/treephys/tpy052.

Li, X.M., Blackman, C.J., Peters, J.M.R., Choat, B., Rymer, P.D., Medlyn, B.E., Tissue, D. T., 2019. More than iso/anisohydry: Hydroscapes integrate plant water use and drought tolerance traits in 10 eucalypt species from contrasting climates. Funct. Ecol. 33, 1035–1049. https://doi.org/10.1111/1365-2435.13412.

Li, X.M., Bao, J.T., Wang, J., Blackman, C., Tissue, D.T., 2021. Antecedent drought condition affects responses of plant physiology and growth to drought and post-drought recovery. Front. For. Glob. Change 4. https://doi.org/10.3389/ffgc.2021.704470.

Li, X.N., Jiang, D., Liu, F.L., 2016. Soil warming enhances the hidden shift of elemental stoichiometry by elevated CO_2 in wheat. Sci. Rep. 6, 23313. https://doi.org/10.1038/srep23313.

Lie, Z.Y., Huang, W.J., Liu, X.J., Zhou, G.Y., Yan, J.H., Li, Y.L., Huang, C.M., Wu, T., Fang, X., Zhao, M.D., Liu, S.Z., Chu, G.W., Kadowaki, K., Pan, X.P., Liu, J.X., 2021. Warming leads to more closed nitrogen cycling in nitrogen-rich tropical forests. Glob. Change Biol. 27, 664–674. https://doi.org/10.1111/gcb.15432.

Limousin, J.M., Misson, L., Lavoir, A.V., Martin, N.K., Rambal, S., 2010. Do photosynthetic limitations of evergreen *Quercus ilex* leaves change with long-term increased drought severity? Plant Cell Environ. 33, 863–875. https://doi.org/10.1111/j.1365-3040.2009.02112.x.

Liu, H., Gleason, S.M., Hao, G.Y., Hua, L., He, P.C., Goldstein, G., Ye, Q., 2019. Hydraulic traits are coordinated with maximum plant height at the global scale. Sci. Adv. 5, eaav1332. https://doi.org/10.1126/sciadv.aav1332.

Liu, Y.Y., Wang, A.Y., An, Y.N., Lian, P.Y., Wu, D.D., Zhu, J.J., Meinzer, F.C., Hao, G.Y., 2018. Hydraulics play an important role in causing low growth rate and dieback of aging *Pinus sylvestris* var. *mongolica* trees in plantations of Northeast China. Plant Cell Environ. 41, 1500–1511. https://doi.org/10.1111/pce.13160.

Lobell, D.B., Schlenker, W., Costa-Roberts, J., 2011. Climate trends and global crop production since 1980. Science 333, 616–620. https://doi.org/10.1126/science.1204531.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the Western United States. Science 323, 521–524. https://doi.org/10.1126/science.1165000.

Manzi, O.J.L., Bellifa, M., Ziegler, C., Mihle, L., Levionnois, S., Burban, B., Leroy, C., Coste, S., Stahl, C., 2022. Drought stress recovery of hydraulic and photochemical processes in Neotropical tree saplings. Tree Physiol. 42, 114–129. https://doi.org/10.1093/treephys/tpab092.

Martin-StPaul, N., Delzon, S., Cochard, H., 2017. Plant resistance to drought depends on timely stomatal closure. Ecol. Lett. 20, 1437–1447. https://doi.org/10.1111/ele.12851.

McDowell, N.G., Sapes, G., Pivovaroff, A., Adams, H.D., Allen, C.D., Anderegg, W.R.L., Arend, M., Breshears, D.D., Brodribb, T., Choat, B., Cochard, H., De Caceres, M., De Kauwe, M.G., Grossiord, C., Hammond, W.M., Hartmann, H., Hoch, G., Kahmen, A., Klein, T., Mackay, D.S., Mantova, M., Martinez-Vilalta, J., Medlyn, B.E., Mencuccini, M., Nardini, A., Oliveira, R.S., Sala, A., Tissue, D.T., Torres-Ruiz, J.M., Trowbridge, A.M., Trugman, A.T., Wiley, E., Xu, C.G., 2022. Mechanisms of woody-plant mortality under rising drought, CO_2 and vapour pressure deficit. Nat. Rev. Earth Environ. 3, 294–308. https://doi.org/10.1038/s43017-022-00272-1.

Michaletz, S.T., Weiser, M.D., Zhou, J.Z., Kaspari, M., Helliker, B.R., Enquist, B.J., 2015. Plant thermoregulation: energetics, trait-environment interactions, and carbon economics. Trends Ecol. Evol. 30, 714–724. https://doi.org/10.1016/j.tree.2015.09.006.

Misson, L., Limousin, J.M., Rodriguez, R., Letts, M.G., 2010. Leaf physiological responses to extreme droughts in Mediterranean *Quercus ilex* forest. Plant Cell Environ. 33, 1898–1910. https://doi.org/10.1016/j.tree.2015.09.006.

Mitchell, P.J., Veneklaas, E.J., Lambers, H., Burgess, S.S., 2008. Leaf water relations during summer water deficit: differential responses in turgor maintenance and variation in leaf structure among different plant communities in south-western Australia. Plant Cell Environ. 31, 1791–1802. https://doi.org/10.1111/j.1365-3040.2008.01882.x.

Nolan, R.H., Tarin, T., Santini, N.S., McAdam, S.A.M., Ruman, R., Eamus, D., 2017. Differences in osmotic adjustment, foliar abscisic acid dynamics, and stomatal regulation between an isohydric and anisohydric woody angiosperm during drought. Plant Cell Environ. 40, 3122–3134. https://doi.org/10.1111/pce.13077.

Ouyang, L., Gao, J.G., Zhao, P., Rao, X.Q., 2020. Species-specific transpiration and water use patterns of two pioneer dominant tree species under manipulated rainfall in a low-subtropical secondary evergreen forest. Ecohydrology 13, e2234. https://doi.org/10.1002/eco.2234.

Pignon, C.P., Long, S.P., 2020. Retrospective analysis of biochemical limitations to photosynthesis in 49 species: C4 crops appear still adapted to pre-industrial atmospheric [CO_2]. Plant Cell Environ. 43, 2606–2622. https://doi.org/10.1111/pce.13863.

Pivovaroff, A.L., Cook, V.M.W., Santiago, L.S., 2018. Stomatal behaviour and stem xylem traits are coordinated for woody plant species under exceptional drought conditions. Plant Cell Environ. 41, 2617–2626. https://doi.org/10.1111/pce.13367.

Quentin, A.G., O'Grady, A.P., Beadle, C.L., Mohammed, C., Pinkard, E.A., 2012. Interactive effects of water supply and defoliation on photosynthesis, plant water status and growth of *Eucalyptus globulus* Labill. Tree Physiol. 32, 958–967. https://doi.org/10.1093/treephys/tps066.

Rahman, M., Islam, M., Brauning, A., 2019. Species-specific growth resilience to drought in a mixed semi-deciduous tropical moist forest in South Asia. . Ecol. Manag. 433, 487–496. https://doi.org/10.1016/j.foreco.2018.11.034.

Sack, L., Cowan, P.D., Jaikumar, N., Holbrook, N.M., 2003. The 'hydrology' of leaves: co-ordination of structure and function in temperate woody species. Plant Cell Environ. 26, 1343–1356. https://doi.org/10.1046/j.0016-8025.2003.01058.x.

Salazar-Tortosa, D., Castro, J., Villar-Salvador, P., Vinegla, B., Matias, L., Michelsen, A., de Casas, R.R., Querejeta, J.I., 2018. The "isohydric trap": A proposed feedback between water shortage, stomatal regulation, and nutrient acquisition drives differential growth and survival of *European pines* under climatic dryness. Glob. Chang. Biol. 24, 4069–4083. https://doi.org/10.1111/gcb.14311.

Shrestha, R.K., Lei, P., Shi, D., Hashimi, M.H., Wang, S., Xie, D.T., Ni, J.P., Ni, C.S., 2021. Response of maize (*Zea mays* L.) towards vapor pressure deficit. Environ. Exp. Bot. 181, 104293 https://doi.org/10.1016/j.envexpbot.2020.104293.

Slot, M., Nardwattanawong, T., Hernandez, G.G., Bueno, A., Riederer, M., Winter, K., 2021. Large differences in leaf cuticle conductance and its temperature response among 24 tropical tree species from across a rainfall gradient. N. Phytol. 232, 1618–1631. https://doi.org/10.1111/nph.17626.

Sperlich, D., Barbeta, A., Ogaya, R., Sabate, S., Penuelas, J., 2016. Balance between carbon gain and loss under long-term drought: impacts on foliar respiration and photosynthesis in *Quercus ilex* L. J. Exp. Bot. 67, 821–833. https://doi.org/10.1093/jxb/erv492.

Talbi, S., Rojas, J.A., Sahrawy, M., Rodriguez-Serrano, M., Cardenas, K.E., Debouba, M., Sandalio, L.M., 2020. Effect of drought on growth, photosynthesis and total antioxidant capacity of the saharan plant *Oudeneya africana*. Environ. Exp. Bot. 176, 104099 https://doi.org/10.1016/j.envexpbot.2020.104099.

Tardieu, F., Simonneau, T., 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. J. Exp. Bot. 49, 419–432. https://doi.org/10.1093/jexbot/49.suppl_1.419.

Vaz, M., Pereira, J.S., Gazarini, L.C., David, T.S., David, J.S., Rodrigues, A., Maroco, J., Chaves, M.M., 2010. Drought-induced photosynthetic inhibition and autumn recovery in two Mediterranean oak species (*Quercus ilex* and *Quercus suber*). Tree Physiol. 30, 946–956. https://doi.org/10.1093/treephys/tpq044.

Wu, T., Liu, S.Z., Lie, Z.Y., Zheng, M.H., Duan, H.L., Chu, G.W., Meng, Z., Zhou, G.Y., Liu, J.X., 2020. Divergent effects of a 6-year warming experiment on the nutrient productivities of subtropical tree species. For. Ecol. Manag. 461. https://doi.org/10.1016/j.foreco.2020.117952.

Wu, T., Tissue, D.T., Zhou, G.Y., Yan, J.H., Zheng, M.H., Li, X., Song, Y.T., Li, Y.L., Tang, X.L., Liu, S.Z., Chu, G.W., Meng, Z., Ye, Q., Liu, J.X., 2022. Direct and indirect effects of long-term field warming methods on the physical environment and biological responses in a subtropical forest. Front. For. Glob. Change 5. https://doi.org/10.3389/ffgc.2022.877025.

Yates, M.J., Verboom, G.A., Rebelo, A.G., Cramer, M.D., 2010. Ecophysiological significance of leaf size variation in Proteaceae from the Cape Floristic Region. Funct. Ecol. 24, 485–492. https://doi.org/10.1111/j.1365-2435.2009.01678.x.

Yu, G.R., Chen, Z., Piao, S.L., Peng, C.H., Ciais, P., Wang, Q.F., Li, X.R., Zhu, X.J., 2014. High carbon dioxide uptake by subtropical forest ecosystems in the East Asian monsoon region. Proc. Natl. Acad. Sci. U. S. A. 111, 4910–4915. https://doi.org/10.1073/pnas.1317065111.

Zhang, H.X., Li, X.R., Wang, W.Z., Pivovaroff, A.L., Li, W.B., Zhang, P.P., Ward, N.D., Myers-Pigg, A., Adams, H.D., Leff, R., Wang, A.Z., Yuan, F.H., Wu, J.B., Yabusaki, S., Waichler, S., Bailey, V.L., Guan, D.X., McDowell, N.G., 2021. Seawater exposure causes hydraulic damage in dying *Sitka-spruce* trees. Plant Physiol. 187, 873–885. https://doi.org/10.1093/plphys/kiab295.

Zhou, G.Y., Wei, X.H., Wu, Y.P., Liu, S.G., Huang, Y.H., Yan, J.H., Zhang, D.Q., Zhang, Q.M., Liu, J.X., Meng, Z., Wang, C.L., Chu, G.W., Liu, S.Z., Tang, X.L., Liu, X.D., 2011. Quantifying the hydrological responses to climate change in an intact forested small watershed in Southern China. Glob. Change Biol. 17, 3736–3746. https://doi.org/10.1111/j.1365-2486.2011.02499.x.

Zhou, G.Y., Peng, C.H., Li, Y.L., Liu, S.Z., Zhang, Q.M., Tang, X.L., Liu, J.X., Yan, J.H., Zhang, D.Q., Chu, G.W., 2013. A climate change-induced threat to the ecological resilience of a subtropical monsoon evergreen broad-leaved forest in Southern China. Glob. Chang. Biol. 19, 1197–1210. https://doi.org/10.1111/gcb.12128.

Zhou, G.Y., Houlton, B.Z., Wang, W.T., Huang, W.J., Xiao, Y., Zhang, Q.M., Liu, S.Z., Cao, M., Wang, X.H., Wang, S.L., Zhang, Y.P., Yan, J.H., Liu, J.X., Tang, X.L., Zhang, D.Q., 2014a. Substantial reorganization of China's tropical and subtropical forests: based on the permanent plots. Glob. Chang. Biol. 20, 240–250. https://doi.org/10.1111/gcb.12385.

Zhou, S.X., Medlyn, B., Sabate, S., Sperlich, D., Prentice, I.C., 2014b. Short-term water stress impacts on stomatal, mesophyll and biochemical limitations to photosynthesis differ consistently among tree species from contrasting climates. Tree Physiol. 34, 1035–1046. https://doi.org/10.1093/treephys/tpu072.