

ORIGINAL RESEARCH

Physiological responses of rosewoods *Dalbergia cochinchinensis* and *D. oliveri* under drought and heat stresses

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Abstract

Dalbergia cochinchinensis and *D. oliveri* are classified as vulnerable and endangered, respectively, in the IUCN Red List and under continued threat from deforestation and illegal harvesting for rosewood. Despite emerging efforts to conserve and restore these species, little is known of their responses to drought and heat stress, which are expected to increase in the Greater Mekong Subregion where the species co-occur and are endemic. In this study of isolated and combined drought and heat effects, we found that *D. oliveri* had an earlier stomatal closure and more constant midday water potential in response to increasing drought level, suggesting that *D. oliveri* is relatively isohydric while *D. cochinchinensis* is relatively anisohydric. Heat shock and drought had synergistic effects on stomatal closure. Our results indicate contrasting relationships in water relations, photosynthetic pigment levels, and total soluble sugars. An increase in chlorophyll a was observed in *D. cochinchinensis* during drought, and a concomitant increase in carotenoid content likely afforded protection against photo-oxidation. These physiological changes correlated with higher total soluble sugars in *D. cochinchinensis*. By contrast, *D. oliveri* avoided drought by reducing chlorophyll content and compromising productivity. Anisohydry and drought tolerance in *D. cochinchinensis* are adaptations which fit well with its ecological niche as a pioneering species with faster growth in young trees. We believe this understanding of the stress responses of both species will be crucial to their effective regeneration and conservation in degraded habitats and in the face of climate change.

KEYWORDS

drought tolerance, ecophysiology, heat shock, rosewoods, stress response

Tin Hang Hung and Rosemary Gooda are co-first authors.

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1 | INTRODUCTION

The pantropical genus *Dalbergia* Linn. f. (Fabaceae: Faboideae) contains around 250 species (Vatanparast, 2013), many of which produce valuable heartwood timber known as rosewood (Winfield, Scott, & Graysn, 2016), which is used to manufacture luxury furniture, boats, and musical instruments (Bhagwat, Dholakia, Kadoo, Balasundaran, & Gupta, 2015). Growing demand and diminishing supply have drastically increased the economic value of rosewood, resulting in much illegal harvesting and poorly regulated exploitation of natural populations. Among these are *Dalbergia cochinchinensis* Pierre and *D. oliveri* Gamble ex Prain (Figure 1), both of which are endemic to Cambodia, Laos, Thailand, and Vietnam within the Greater Mekong Subregion (GMS). *D. cochinchinensis* was once the most sought-after rosewood species globally, but it is now virtually commercially extinct, as is *D. oliveri* (EIA, 2017). They were classified as vulnerable and endangered, respectively, in the IUCN Red List in 1998, with international trade strictly regulated since 2017 under CITES Appendix II.

Responses to their declining populations have seen new initiatives in the Greater Mekong Subregion to conserve and restore both species, such as through improving capacity for seed collection, germplasm supply, and propagation (APFORGEN, 2018; CDRI, 2014; Luoma-aho, Hong, Ramanatha Rao, & Sim, 2003). In addition, some *Dalbergia* species are deemed suitable candidates for use in forest landscape restoration in the region (Aerts, 2009), where intense land conversion has degraded sites (Tanaka, 2008). Successful incorporation of valuable and endangered species like *Dalbergia* in forest restoration programs can achieve both conservation and restoration goals (Kaewkrom, Gajaseeni, Jordan, & Gajaseeni, 2005; Sakai, 2009). A sustainable supply of diverse germplasm is essential for the success of such projects (Maningo & Thea). Recently, the importance of investigating the response to climatic stresses of germplasm used in forest restoration and other tree planting has been recognized (2017), since many forest restoration projects around the world have

neglected the adaptability of seeds in the planting sites (Jalonen, Valette, Boshier, Duminil, & Thomas, 2018). For reforestation to succeed, it is crucial to know about the ranges of abiotic conditions that a species can tolerate, allowing their planting in appropriate regions. There is particular concern for the effect of climate change within the Greater Mekong Subregion with evidence pointing to increased temperature, variability in runoff, and prolonged agricultural droughts (MRC, 2010). Simultaneously, water availability may decrease in the region due to increasing urbanization and changes in river infrastructure such as upstream dams in China (Hughes, 2017). However, we have little understanding of the physiological adaptations of *D. cochinchinensis* and *D. oliveri*, which hinders informed decision-making in both conservation and forest restoration initiatives.

Imminent effects of climate change will, in many areas, result in rapid increases in temperatures, drought, and extreme weather (Li, 2015). The sessile habit and longevity of tree species mean they must have sufficient phenotypic plasticity to tolerate the wide range of environmental conditions that occur during their lifespans (Estravis-Barcala, 2019). Similarly, trees are potentially more vulnerable than other plants under changing climate scenarios as they have long generation times, with the persistence of a particular tree species dependent on adaptive capacity to stress, plasticity, and migration potential (Aitken, Yeaman, Holliday, Wang, & Curtis-McLane, 2008). Extreme abiotic conditions caused by climate change will potentially be detrimental to primary productivity, ecological functions, and associated biodiversity of these forests (Sitch, 2008). Vulnerability of forests to tree die-off due to climate change has become a focus of forest sustainability (Allen, Breshears, & McDowell, 2015), with extensive tree climate-induced mortality well-documented worldwide (Allen, 2010; McDowell, 2008; Pollastrini, Puletti, Selvi, Iacopetti, & Bussotti, 2019). In particular, seedling recruitment and survival are considered critical bottlenecks in tree life history and have an important role in shifts in species' range under changing climate (Canham & Murphy, 2016). Migration to adapted ecological niches and acclimation in an existing range are important mechanisms for

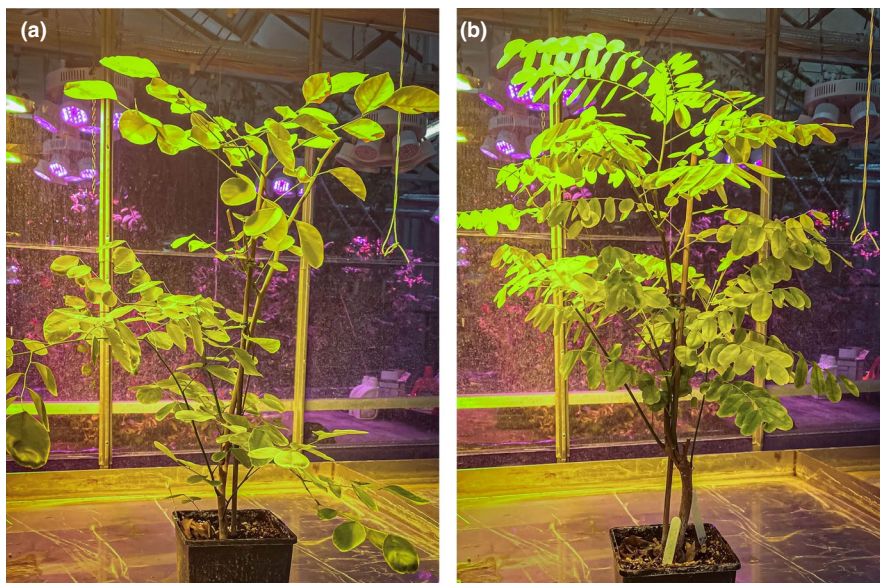
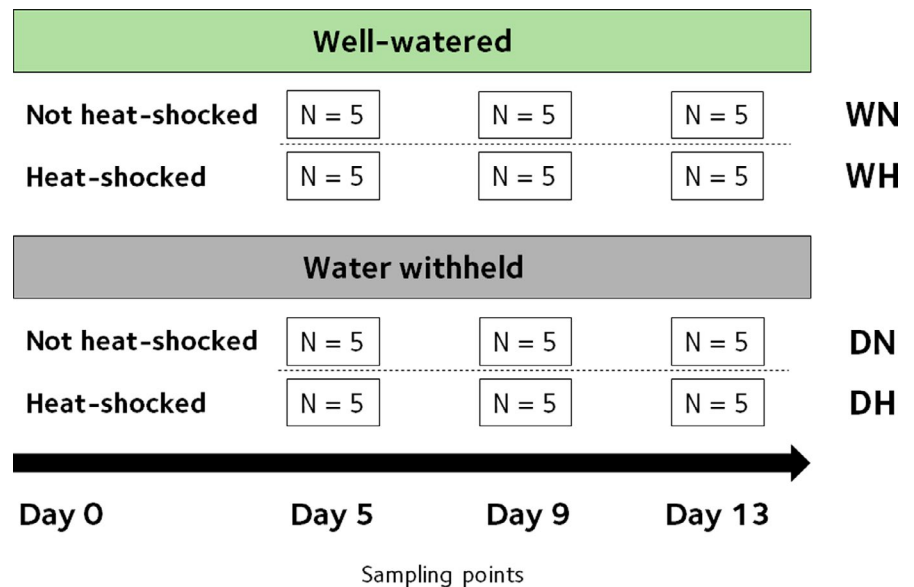


FIGURE 1 Photograph of (a) *Dalbergia cochinchinensis* and (b) *D. oliveri* in a greenhouse (not taken during this study)

FIGURE 2 Conceptual diagram of the experimental design in this study



tree survival in a changing climate (Brodrribb, Powers, Cochard, & Choat, 2020).

Although knowledge of the ability of tree species to tolerate environmental stresses is essential for our understanding of how trees will respond to the effects of climate change (Estravis-Barcala, 2019), we lack data on the stress tolerance of specific taxa (Chaves, 2002). Water availability varies spatially and temporally and has also been found to be an important determinant of functional traits in trees (Terra, 2018). Trees have evolved strategies to balance hydraulic conductance and resource allocation in response to water deficit. One of these strategies is establishing barriers for evaporation to achieve homeostasis of tissue water status (Estravis-Barcala, 2019). Other strategies exist to maintain their metabolism at a lower water potential (Polle, Chen, Eckert, & Harfouche, 2019) through osmotic adjustment and protection from photo-oxidation (Pintó-Marijuan & Munné-Bosch, 2014). However, prolonged drought stress that exceeds the drought resistance threshold can lead to mortality associated with hydraulic failure, carbon starvation, and the demography of biotic agents (McDowell, 2008).

Temperature also plays a major role in determining the distribution of tree species, as it significantly regulates tree growth and development. Trees can usually utilize transpiration to allow water evaporation for temperature regulation (Urban, Ingwers, McGuire, & Teskey, 2017), but excessive heat stress is an important driver of tree die-off in natural ecosystems (McDowell, 2018). Studies have shown that heat stress impairs photosystems, stimulates photorespiration, and encourages production of volatile compounds (Li, 2014; Rizhsky, Liang, & Mittler, 2002). Extreme heat reduces tree vigor, fecundity, and growth, significantly affecting survival (Teskey, 2015).

Different stresses often occur simultaneously in the field but there are few reports on interactions between such stresses in trees (Chaves, 2002). It has been proposed that drought and heat stresses are intrinsically linked and produce positive feedbacks to intensify their effects (Stéfanon, Drobinski, D'Andrea, Lebeauin-Brossier, & Bastin, 2014), but new evidence indicates that combinations

of stresses can invoke responses that are distinct from those of the individual stresses (Zandalinas, Mittler, Balfagón, Arbona, & Gómez-Cadenas, 2018). For example, the combination of heat and drought stress could reduce the negative effect of drought stress by preserving predawn water potential and malondialdehyde (Correia, 2018). These interactions and responses are species-specific and are expected to be complex and difficult to predict, as response mechanisms vary between stresses (Sheel, Göran, Löfvenius, & Marie-Charlotte, 2013).

The objective of the present study is to develop an understanding of the physiological responses of 3-month-old *D. cochinchinensis* and *D. oliveri* seedlings under controlled conditions of heat and drought stress. First, we compare and characterize the hydraulic responses in the two species when exposed to drought. Second, we determine the effects of isolated and combined stresses of heat and drought on hydraulic, leaf, and photosynthetic traits. We discuss the findings in relation to life-history traits and ecological niches of these species and formulate implications for their conservation and use in restoration.

2 | METHODS

2.1 | Plant materials

Dried seeds of *D. cochinchinensis* and *D. oliveri* were provided by the Forest Research Center, Lao PDR, and the Institute of Forest & Wildlife Research & Development, Cambodia, respectively, in 2018. We scarified the seeds by placing them in 70°C distilled water, which was then left to cool to room temperature overnight and germinated them on 1% agar in a plant growth cabinet MLR-350 (Sanyo, Watford, United Kingdom) at 25°C and photoperiod 12L/12D. Germinants were transferred to 1-L pots in a soil-perlite 3:1 (v:v) mixture in a greenhouse set to 30°C, 80% RH, and 12L/12D. 128 plants were kept in trays of 8 pots and randomized with equal

numbers of individuals of *D. cochinchinensis* and *D. oliveri*. Plants were watered to maintain at substrate capacity and fertilized once a week using N-P-K 20:20:20 fertilizer (Chempak, Suffolk, United Kingdom).

2.2 | Experimental design

After 3 months of growth in the greenhouse, the experiment began on the 12 June 2019 (Day 0), on which all plants were watered. The design included a total of 4 treatments: drought treatment (D), well-watered control (W), heat shock treatment (H), or non-heat shock control (N) (Figure 2). Each of the trays of 8 plants was randomly assigned as either D or W, while each plant of the trays was then randomly assigned to H or N. This resulted in each individual being assigned to one of four treatment combinations: drought and heat shock (DH), well-watered and heat shock (WH), drought and non-heat shock (DN), and well-watered and non-heat shock (WN). The well-watered plants were watered every other day to maintain them at substrate capacity and all water was withheld from the drought plants. Each individual plant was randomly assigned to one of the three sampling points: 5, 9, and 13 days from the beginning of treatments according to Figure 2, each five biological replicates were present for each sampling group.

For the heat shock treatment, we placed half of the individuals to be sampled at a given time point in a plant growth cabinet MLR-350 (Sanyo, Watford, United Kingdom) at 38°C for 4 hr from 08:00 to 12:00 before sampling. Five biological replicates were finally present for each sampling group. The samples were made up of homogeneous leaves that were snap-frozen in liquid nitrogen and kept at -80°C for subsequent analyses. Fully expanded branches were also cut at the nodes and kept in cooler bags for water potential, mass, and area measurements.

2.3 | Water relation measurements

Soil water content (SWC) was measured daily using a ML3 ThetaProbe Soil Moisture Sensor (Delta-T Devices Ltd. Cambridge, England) by placing the sensor probe in the soil at the center of the pot. Stomatal conductance (g_s) was determined daily using an SC-1 leaf porometer (METER Group, Inc.) to measure vapor flux through the stomata on fully expanded leaves for 30 s. Midday water potential (Ψ_{MD}) was measured by using a scholander-type pressure chamber SKPM140 (Skye Instruments Ltd.) on a fully expanded branch. Pressure was increased inside the chamber with compressed nitrogen, until moisture appeared on the cut end and the reading recorded.

2.4 | Leaf dry matter content and specific leaf area

An office scanner was used to obtain electronic images of leaves on a fully expanded branch from each plant. The program ImageJ 1.52s

(Schneider, Rasband, & Eliceiri, 2012) was then used to measure the total leaf area of a fully expanded branch for each individual. These leaves were then dried in an oven at 65°C until the weight reading remained constant for two consecutive days.

Leaf dry matter content (LDMC) and specific leaf area (SLA) were deduced using the following equations (Pérez-Harguindeguy, 2013):

$$\text{Leaf dry matter content} = \frac{\text{Oven-dried mass of leaf (mg)}}{\text{Fresh mass of leaf (mg)}} \quad (1)$$

$$\text{Specific leaf area (cm}^2\text{/mg)} = \frac{\text{Area of leaf (cm}^2\text{)}}{\text{Oven-dried mass of leaf (mg)}} \quad (2)$$

2.5 | Pigment quantification

Photosynthetic pigments were extracted using cold acetone-50 mM Tris buffer pH 7.8 (80:20 v:v) following Sims & Gamon's protocols (Sims & Gamon, 2002). Absorbances of the extract were read at 470, 537, 647, and 663 nm using Helios Gamma UV-Vis Spectrophotometer (Thermo Fisher Scientific). Concentrations of anthocyanin (Ac), chlorophyll a (Chl_a), b (Chl_b), and carotenoids were determined using Sims and Gamon's formulae:

$$Ac (\mu\text{mol/ml}) = 0.08173A_{537} - 0.00697A_{647} - 0.002228A_{663} \quad (3)$$

$$Chl_a (\mu\text{mol/ml}) = 0.01373A_{663} - 0.000897A_{537} - 0.003046A_{647} \quad (4)$$

$$Chl_b (\mu\text{mol/ml}) = 0.02405A_{647} - 0.004305A_{537} - 0.005507A_{663} \quad (5)$$

$$\text{Carotenoids } (\mu\text{mol/ml}) = (A_{470} - (17.1 \times (Chl_a + Chl_b) - 9.479Ac)) \times 119.26 \quad (6)$$

2.6 | Total soluble sugars quantification

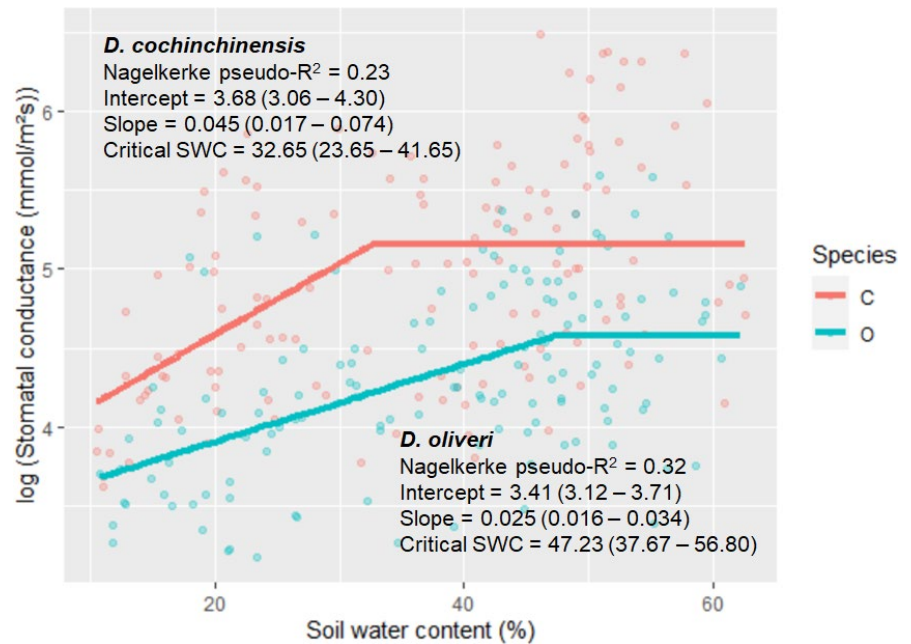
Total soluble sugars (TSS) were extracted from 50 mg of frozen leaves in 80% (v/v) ethanol for 1 hr at 80°C. TSS concentration was determined by Osaki's anthrone method (Osaki, Shinano, & Tadano, 1991), in which the extract was mixed with anthrone and sulfuric acid. After heating the mixture at 100°C for exactly 10 min, absorbance was read at 625 nm using Helios Gamma UV-Vis Spectrophotometer (Thermo Fisher Scientific). The concentration was determined according to a D-glucose standard curve.

2.7 | Statistical analysis

The experiment used a split-plot design: The drought treatment was randomized at the tray level (main-plot), while heat shock was randomized at the individual plant level (split-plot). We log-transformed the g_s , SLA, Ac, Chl_b , and carotenoids content to correct for normality.

To compare and characterize the hydraulic responses in the two species over time, we applied linear-plateau regression of g_s against

FIGURE 3 Linear-plateau regression of stomatal conductance (g_s) against soil water content (SWC) of *Dalbergia cochinchinensis* (red) and *D. oliveri* (blue). Goodness of fit was tested using Nagelkerke method. Values in the brackets represent 95% confidence interval



SWC in the drought treatment groups for both species. Best-fit estimates of the intercept (c), the slope (m), and the critical value of SWC (x') were predicted using nonlinear least-squares method (Bates & Watts, 1988) with the following equation:

$$g_s = \begin{cases} mx + c, & \text{if } x < x' \\ mx' + c, & \text{if } x \geq x' \end{cases} \quad (7)$$

To test the effects of isolated and combined stresses on the hydraulic, leaf, and photosynthetic traits, we performed main-plot analyses on data subsets which averaged the response variables, including g_s , Ψ_{MD} , LDMC, SLA, Ac , Chl_a , Chl_b , carotenoids, and TSS, over the combinations of block, species, and two treatments, and performed split-plot analyses on the full dataset while controlling for block. The fixed effects of the two stresses and their interaction were tested with the following equation:

$$Y = \mu + \text{drought}_a + \text{block}_i + \eta_{ai} + \text{species}_b + \text{day}_c + \text{heatshock}_d + (\text{drought} * \text{heatshock} * \text{day} * \text{species})_{abcd} + \epsilon_{abcdi} \quad (8)$$

Y: response variable; μ : mean; drought_a: fixed effect of drought treatment; block_i: fixed effect of block; η_{ai} : whole-plot error; species_b: fixed effect of species; day_c: fixed effect of number of days since water withholding; heatshock_d: fixed effect of heat shock treatment; (drought*heatshock*day*species)_{abcd}: interaction between explanatory variables; ϵ_{abcdi} : split-plot error.

We used R 3.6.2 to perform the randomization for experimental design, statistical analysis, and data visualization. An analysis of variance (ANOVA) table was computed for the statistical model of each response variable.

3 | RESULTS

The plants were divided into drought (D) and well-watered control (W) treatment groups following a split-plot experimental design. Physiological traits were measured after 5, 9, and 13 days of treatment. On the sampling days only, we also applied a heat shock (H) treatment to half of the individuals in each sampling group with the other not exposed to heat (N). Hence, there were four treatment groups: DH, DN, WH, WN (Figure 2).

3.1 | Stomatal conductance

We found a statistically significant difference in slopes of stomatal conductance (g_s) ($p = .0134$; Table S1) between the drought and well-watered (control) treatments but not in intercepts ($p = .2308$; Table S2). This observation indicated that water relations were similar among the two groups at the start of the experiment and that g_s decreased with the drought treatment in both species.

We employed a linear-plateau nonlinear least-squares fit to model the relationship between g_s and soil water content (SWC) and searched for a critical value of SWC that affects the stomatal aperture (Figure 3). We found that the critical SWC of *D. cochinchinensis* (32.65%, $p = 4.65e-11$) was lower than *D. oliveri* (47.23%, $p < 2e-16$), suggesting that *D. cochinchinensis* closed its stomata later than *D. oliveri* in response to decreasing SWC.

When analyzing all four treatment groups on sampling days, we obtained the same significant decrease in g_s in drought treatment ($p = 2.401e-5$; Table S3 and Figure 4a). We found that *D. oliveri* had a lower g_s than *D. cochinchinensis* ($p = 3.366e-06$). In addition, we found a significant decrease in heat shock treatment ($p = 2.936e-15$)

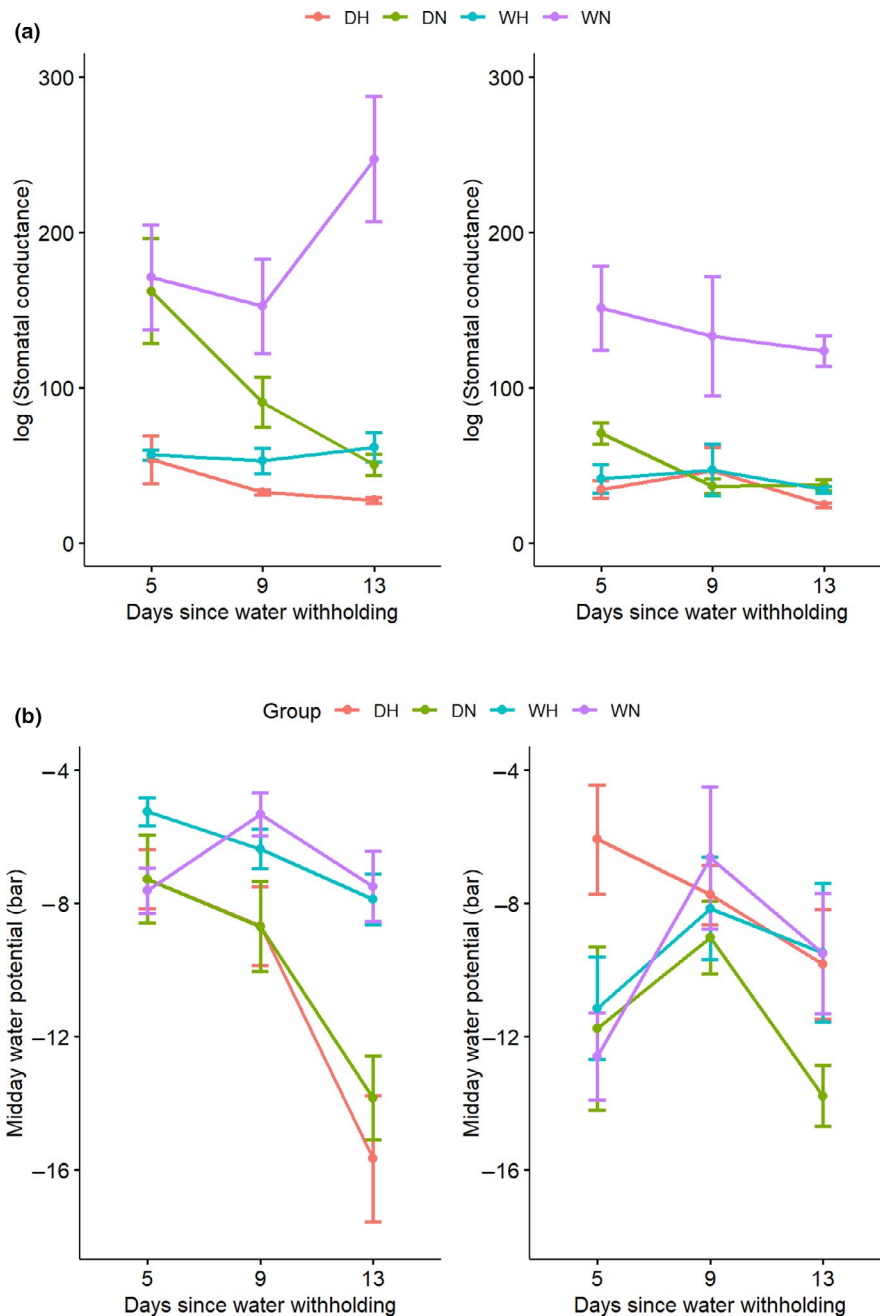


FIGURE 4 (a) Stomatal conductance (g_s) and (b) midday branch water potential (Ψ_{MD}) of *Dalbergia cochinchinensis* (left) and *D. oliveri* (right) at 5, 9, and 13 days from the beginning of drought treatment. Treatment groups were as follows: DH (drought and heat shock), DN (drought and non-heat shock), WH (well-watered and heat shock), and WN (well-watered and non-heat shock)

and a significant drought \times heat interaction in g_s ($p = .000666$). The interaction effect was the strongest on day 13: The g_s of combined stress was lower (27.54 mmol/m²s) than either drought (50.48) or heat (61.8) alone in *D. cochinchinensis*. In *D. oliveri*, the g_s of combined stress was also lower (24.56 mmol/m²s) than either drought (37.46) or heat (34.66) alone.

3.2 | Midday water potential

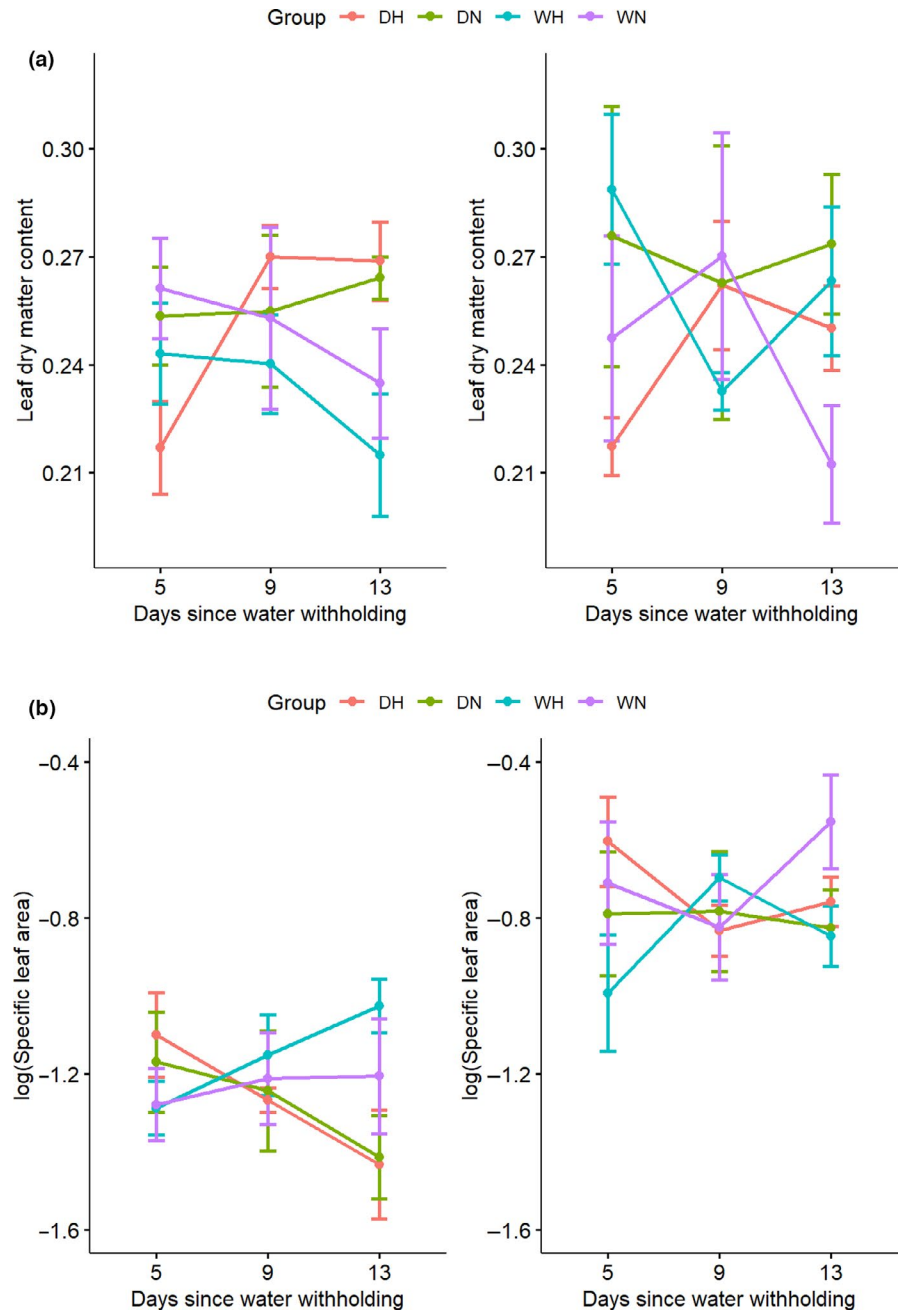
We observed a significant decrease in midday water potential (Ψ_{MD}) in the drought treatment ($p = .03955$; Table S4 and Figure 4b). A significant interaction was found between the drought treatment and

species, ($p = .004137$), indicating differential responses and vulnerabilities, with *D. cochinchinensis* displaying a faster decrease in Ψ_{MD} over time than *D. oliveri*. The Ψ_{MD} of the *D. cochinchinensis* drought treatment group dropped drastically from -7.27 to -13.84 bar between day 5 and 13, while that for *D. oliveri* remained relatively stable from -11.75 to -13.78 bar.

3.3 | Leaf dry matter content and specific leaf area

We found no significant effect of the drought and heat treatments on leaf dry matter content (LDMC) and specific leaf area (SLA) (Table S5 and Figure 5a). However, SLA was significantly different between

FIGURE 5 (a) Leaf dry matter content (LDMC) and (b) specific leaf area (SLA) of *Dalbergia cochinchinensis* (left) and *D. oliveri* (right) at 5, 9, and 13 days from the beginning of drought treatment. Treatment groups were as follows: DH (drought and heat shock), DN (drought and non-heat shock), WH (well-watered and heat shock), and WN (well-watered and non-heat shock)



species ($p = 1.061e-12$; Table S6 and Figure 5b), with *D. cochinchinensis* having a lower SLA ($0.30 \text{ cm}^2/\text{mg}$) than *D. oliveri* ($0.48 \text{ cm}^2/\text{mg}$).

3.4 | Pigments

We observed no significant effect of either drought or heat shock stresses on anthocyanin content (Table S7 and Figure 6a). Chlorophyll a content (Chl_a) was significantly affected by drought treatment ($p = .02927$; Table S8 and Figure 6b), species ($p = .039284$), and the interaction between both stresses and species ($p = .034303$). We found opposite trends of change in Chl_a content between species, such that combined stresses increased Chl_a

from 1.15 to $1.43 \mu\text{mol/g FW}$ in *D. cochinchinensis* and decreased Chl_a from 0.876 to $0.568 \mu\text{mol/g FW}$ in *D. oliveri*. The drought treatment seemed to amplify the difference between species, resulting in the highest Chl_a in *D. cochinchinensis* and lowest in *D. oliveri*. We observed no significant effect of drought and heat shock stresses on chlorophyll b content (Chl_b) (Table S9 and Figure 6c).

Carotenoid content was significantly affected by the drought treatment ($p = .03966$; Table S10 and Figure 6d) and the combination of drought, species, and days ($p = .003470$). An opposite trend between species was observed in carotenoids similar to Chl_a , where carotenoid content increased over time following drought from 11.27 to 11.54 mmol/g FW in *D. cochinchinensis* but decreased from 14.27 to 8.63 mmol/g in *D. oliveri*.

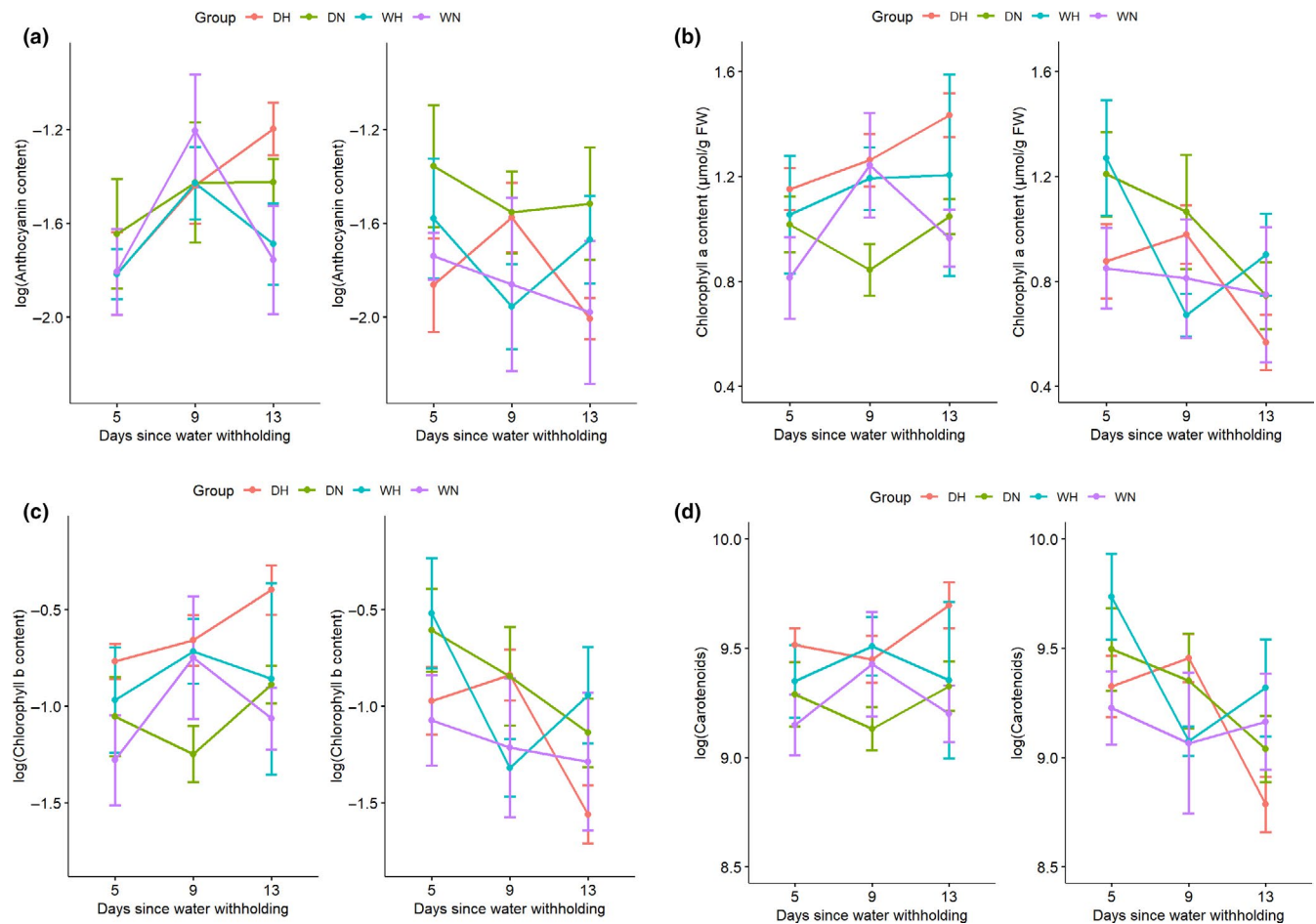


FIGURE 6 (a) Anthocyanin content, (b) chlorophyll a content (Chl_a), (c) chlorophyll b content (Chl_b), and (d) carotenoid content of *Dalbergia cochinchinensis* (left) and *D. oliveri* (right) at 5, 9, and 13 days from the beginning of drought treatment. Treatment groups were as follows: DH (drought and heat shock), DN (drought and non-heat shock), WH (well-watered and heat shock), and WN (well-watered and non-heat shock)

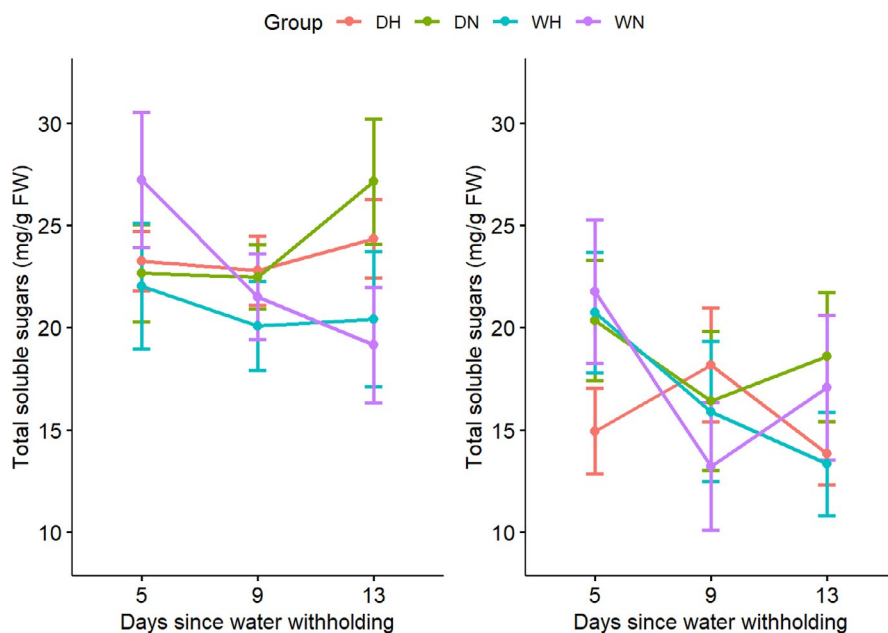


FIGURE 7 Total soluble sugars content (TSS) of *Dalbergia cochinchinensis* (left) and *D. oliveri* (right) at 5, 9, and 13 days from the beginning of drought treatment. Treatment groups were as follows: DH (drought and heat shock), DN (drought and non-heat shock), WH (well-watered and heat shock), and WN (well-watered and non-heat shock)

3.5 | Total soluble sugars

We found that the total soluble sugars content (TSS) changed significantly with the drought treatment ($p = .03993$; Table S11 and Figure 7) and increased slightly from 22.66 to 27.14 mg/g FW in *D. cochinchinensis*, but decreased slightly from 20.34 to 18.58 mg/g FW in *D. oliveri*. *D. cochinchinensis* maintained a higher TSS than *D. oliveri* ($p = 2.586e-6$).

4 | DISCUSSION

We report short-term physiological changes in seedlings of *D. cochinchinensis* and *D. oliveri* in response to isolated and combined stress treatments of drought and heat. Most of the responses are found to be induced by drought only but the two stresses have an additive effect on reducing stomatal conductance. These stress responses included several physiological factors and may highlight metabolic vulnerabilities, which follow from adaptations to environmental conditions. Our observations indicate changes in water relations, photosynthetic pigments, and soluble sugars. Our results suggest possible trade-offs between hydraulic integrity and gas exchange associated with photosynthesis during drought, or between hydraulic integrity and temperature regulation during combined heat and drought stress. We discuss our findings as potential indicators of adaptation to different ecological niches for *D. cochinchinensis* and *D. oliveri* and the implications for their conservation and restoration.

4.1 | Water relations

The observed differences in stomatal conductance (g_s) and water potential (Ψ_{MD}) over time reflected contrasting hydraulic responses in the two species: (1) stomatal closure occurred at a higher soil water content (or lower water deficit) in *D. oliveri* leaves than in *D. cochinchinensis*, and (2) Ψ_{MD} was relatively stable in *D. oliveri* until the last day of the drought treatment but decreased rapidly in *D. cochinchinensis*. The ability to maintain Ψ_{MD} and regression of g_s in response to increasing water deficit is common differentiators of iso-anisohydric behaviors (Hochberg, Rockwell, Holbrook, & Cochard, 2018): *D. oliveri* fit more closely with an isohydric response, characterized by earlier stomatal closure and thus maintaining a more constant Ψ_{MD} (Lavoie-Lamoureux, Sacco, Risse, & Lovisolo, 2017). By contrast, *D. cochinchinensis* was more anisohydric, maintaining stomatal aperture until experiencing severe drought, when Ψ_{MD} decreases drastically (Bergel-Landefeldt, 1936). However, recent research suggests that species naturally present a continuum of iso-anisohydry, and very few species could be categorized in a strict dichotomy of iso-anisohydry (Klein, 2014; Martínez-Vilalta, Poyatos, Aguadé, Retana, & Mencuccini, 2014). Iso-anisohydry is closely related to a plant's life-history traits and survival strategy. Isohydricity implies a more conservative water-balance management strategy to prevent loss of water via transpiration (Sade, Gebremedhin, & Moshelion, 2012),

which can protect plants from hydraulic failures and xylem embolism. Anisohydricity maintains higher carbon assimilation at mild drought conditions and thus achieves an overall higher productivity (Uri, 2013). A previous study among species of Bornean rain-forest found that anisohydricity is more prevalent and reduces the risk of drought-induced hydraulic failure (Kumagai & Porporato, 2012). However, satellite data suggested the contrary, that is, that isohydricity is more dominant in wet areas (Li, 2017). These conflicting results reflect an important role that environment plays in shaping water relations and call for investigation of more aspects of plant hydraulic functions (Hochberg et al., 2018). More studies on specific systems and species are also needed to improve our understanding of species' responses to drought in tropical forests under progressive climate change.

The heat shock applied in this study resulted in rapid closure of stomata in both well-watered and drought-stressed plants of both species, suggesting that drought and heat shock stress were additive in reducing g_s . Transpiration via the stomatal aperture is a mechanism of heat regulation (Zhou, Chen, Li, & Chen, 2010). Previous studies have shown that many plants achieve heat loss via transpiration, with stomatal conductance either maintained at normal levels (Correia, 2018) or increased (Urban et al., 2017) to prevent leaf temperatures from reaching harmful levels. By contrast, our findings are similar to those reported in olive trees (Haworth, 2018), in which g_s decreased with heat shock, and this could be a mechanism for plants adapted to low water availability to reduce the risk of xylem embolism. The level of heat stress tested here produced a conservative response in both *D. oliveri* and *D. cochinchinensis*. Stomatal responses may vary at different levels and durations of heat.

4.2 | Leaf traits

We found no significant effect of drought or heat shock on leaf dry matter content (LDMC) or specific leaf area (SLA). LDMC and SLA are two leaf traits related to resource use and trade-offs. High SLA or low LDMC implies rapid assimilation for growth and production, whereas low SLA or high LDMC implies efficient conservation of nutrients within structural and well-protected tissues (Vitra, 2019). The temporal limitation in this study may not reflect effects in SLA as leaf development potentially operates over a longer timeframe. Previous studies mainly suggested that drought stress caused decreased SLA to reduce the surface area for transpiration and thus prevent water loss (Liu & Stützel, 2004; Pandey, Ramegowda, & Senthil-Kumar, 2015).

We found a higher SLA in *D. oliveri* than *D. cochinchinensis*; however, *D. oliveri* was more isohydric in terms of hydraulic traits. This observation seems to contradict the above claim that SLA decreases plastically in response to drought. However, there is little understanding of variation of SLA across species. Poorter, Niinemets, Poorter, Wright, and Villar (2009) in their meta-analysis suggested that SLA varies strongly with many factors including light, temperature, nutrient, and functional groups. An increase in SLA could be

a compensating mechanism for reduced carbon allocation to the leaves during stress (Aspelmeier & Leuschner, 2006). In response to heat stress, increase in SLA could provide a mechanism for temperature regulation by increasing surface area (Pandey, Ramegowda, & Senthil-Kumar, 2015). These features suggest that isohydric *D. oliveri* may suffer an impaired carbon assimilation under drought stress and compensate through associated leaf traits.

4.3 | Photosynthetic pigments and carbon assimilation

We found that levels of chlorophyll a and carotenoids increased in *D. cochinchinensis* in response to drought and decreased in *D. oliveri*. Chlorophyll content is one of the most commonly used parameters to measure the severity of drought stress (Ying, 2015) as drought stress is thought to damage photosynthetic apparatus and diminish chlorophyll content (Fu & Huang, 2001). By maintaining lower chlorophyll content under severe drought conditions, plants are protected from photo-oxidative damage by inhibiting photosynthesis and avoiding excess light excitation energy (Aranjuelo, Molero, Erice, Avicé, & Nogué, 2011; Pintó-Marijuan & Munné-Bosch, 2014). As such, the decreasing trend of chlorophyll a in *D. oliveri* implies correspondence to drought avoidance as may be expected with an isohydric behavior. On the contrary, some studies have suggested that chlorophyll content is positively associated with drought tolerance and recovery (Chen, 2016) and that the potential photo-oxidative damage can be remediated by increasing levels of carotenoids, which play a central role in the assembly of the light-harvesting complex in the photosystem, regulate photomorphogenesis, and provide photoprotection (Munné-Bosch & Alegre, 2000). Carotenoids are also precursors for two plant hormones, strigolactones, and abscisic acid (ABA) from carotenoid cleavage (Nisar, Li, Lu, Khin, & Pogson, 2015), while ABA has a dominant role in regulation of stomatal conductance in response to drought stress (Pirasteh-Anosheh et al., 2016). Therefore, the contrasting trends of photosynthetic pigments further support the conclusion that *D. oliveri* avoids drought by reducing carbon assimilation and maintaining water potential, while *D. cochinchinensis* tolerates drought and maintains its productivity.

The higher levels of photosynthetic pigments associated with these increases in *D. cochinchinensis* may explain its higher total soluble sugars (TSS). Higher TSS may also provide an energy buffer to sustain metabolic activity during drought stress (Duan, 2015). The lower TSS in *D. oliveri* potentially implies a carbon limitation, which is commonly associated with isohydric species and could lead to carbon starvation in the long term (McDowell, 2008). Our finding that TSS increased in response to drought stress may suggest a mechanism of osmoregulation (Granda & Camarero, 2017), in which osmotically active soluble sugars can help maintain water potential and hydraulic integrity (O'Brien, Leuzinger, Philipson, Tay, & Hector, 2014).

In our study, we found little response specifically to heat shock in either species, thus potentially suggesting that these trees could have a higher heat threshold than 38°C for 4 hr. We did not observe any

synergistic or antagonistic effect of both drought and heat stresses as in previous studies (Correia, 2018; Sheel et al., 2013; Zandalinas et al., 2018), except g_s . There is an emerging interest in studying plant responses to a suite of stress factors, as different stresses may lead different signaling pathways to interact and conflict to produce novel physiological responses (Zandalinas et al., 2018).

4.4 | Relating life-history traits with potential ecological niches

D. cochinchinensis and *D. oliveri* are endemic to and geographically co-occur in Cambodia, Laos, Thailand, and Vietnam. *D. cochinchinensis* is described as an intermediate pioneering species, characteristic of faster growth rate in young age (2000). Its anisohydric behavior, described here as maximizing carbon assimilation at the risk of hydraulic failure during drought, may be associated with its higher productivity for more efficient colonization in early ecological succession. This fits well with an earlier formulation by Smith and Huston (1989) that light-demanding pioneers would optimize growth and outcompete shade-tolerant species in drier habitats. Other studies also support the theory that pioneers run the risk of drought-induced cavitation in order to maintain higher hydraulic efficiency and meet the water demand for photosynthesis and fast growth during drought (Markesteijn, Poorter, Bongers, Paz, & Sack, 2011; Markesteijn, Poorter, Paz, Sack, & Bongers, 2011). Such a trade-off between short-term growth and long-term survival aligns with the spectrum from pioneers to shade-tolerant species (Poorter & Bongers, 2006).

On the other hand, *D. oliveri* demonstrates a wider ecological amplitude within the deciduous forest, from relatively rich, deep soils to poor, shallow soils (Aerts et al., 2009). Aerts et al. (2009) suggested that *D. oliveri* can grow on shallow, eroded regosols where drought stress is persistent during the dry season. We report a more isohydric behavior in *D. oliveri* and hypothesize that it is more conservative in order to allow survival under low water availability of the region's deciduous forests.

The controlled nature of the experiment in this study allowed isolating the effects of multiple stressors and assessing their interactions (Seebacher & Franklin, 2012). Although the controlled experiment does not replicate the environmental and growth conditions in the field, its focus on seedlings shows close relevance to a crucial regeneration stage when mortality and selection pressures are high (Muscarella, 2013; Qie, 2019). We believe our results need further validation with field experiments and observations. At the same time, our results inform design of such field studies, for example by indicating the need to study multiple stressors and the divergent response strategies of individual species.

The contrasting hydraulic strategies of *D. cochinchinensis* and *D. oliveri* may reflect adaptation to their current ecological niche, but such dynamics may change drastically with changing climate and affect their survival and regeneration. The extent to which these water-carbon trade-offs affect growth and survival depends on

species-specific vulnerability to and capacity for recovery from hydraulic failure and carbon starvation. We recommend that research is needed to study responses and recovery to the extreme stresses at different life stages and under probable climate scenarios within their ranges.

5 | CONCLUSION

To date, our understanding of physiology and ecological function in *D. cochinchinensis* and *D. oliveri* is poorly developed compared to that of their mating and genetic structure (Hartvig, 2018, 2020). This knowledge gap hinders informed decision-making for the conservation and restoration of these valuable species. We present the first study on hydraulic traits and carbon assimilation of *D. cochinchinensis* and *D. oliveri* in their seedling stages and characterize their isohydric behavior in response to drought and heat stresses. We suggest potential thresholds and interactions of drought and heat stresses, which will open the opportunity for further studies to gain a better understanding of their physiology and stress response. Such an approach would also be beneficial to studying stress responses in other *Dalbergia* species to similarly inform their conservation and use.

Dalbergia species regenerate naturally when circumstances permit, but are also suited to use for planting in restoring degraded forests and restoring deforested sites (Koonkhunthod, Sakurai, & Tanaka, 2007). Seedling establishment is a crucial life stage of trees and an understanding of their stress responses will contribute to appropriate site selection and effective long-term regeneration (Abiyu, Teketay, Glatzel, & Gratzer, 2016; Fontaine, 2007), especially with regard to restoration efforts and climate change.

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CONFLICT OF INTERESTS

The authors declare no competing interests.

AUTHOR CONTRIBUTION

Tin Hang Hung: Conceptualization (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing-original draft (equal); Writing-review & editing (equal). **Rosemary Gooda:** Data curation (equal); Formal analysis (equal); Investigation (equal); Visualization (equal); Writing-original draft (equal); Writing-review & editing (equal). **Gabriele Rizzuto:** Methodology (equal); Validation (equal); Writing-review & editing (equal). **Thea So:** Funding acquisition (equal); Project administration (equal); Resources (equal); Validation (equal); Writing-review & editing (equal). **Bansa Thammavong:** Funding acquisition (equal);

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DATA AVAILABILITY STATEMENT

The research materials supporting this publication can be publicly accessed in Dryad (<https://doi.org/10.5061/dryad.v6wwpzgt1>).

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SUPPORTING INFORMATION

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

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