Research paper

Nocturnal warming accelerates drought-induced seedling mortality of two evergreen tree species

Ruiling Lu[1], Ying Du[1], Huanfa Sun[1], Xiaoni Xu[1], Liming Yan[1] and Jianyang Xia [ID][2]

[1]Tiantong Forest Ecosystem National Observation and Research Station, Research Center for Global Change and Complex Ecosystems, School of Ecological and Environmental Sciences, East China Normal University, 500 Dongchuan Road, Minhang District, Shanghai 200241, China; [2]Corresponding author (jyxia@des.ecnu.edu.cn)

Extreme drought is one of the key climatic drivers of tree mortality on a global scale. However, it remains unclear whether the drought-induced tree mortality will increase under nocturnal climate warming. Here we exposed seedlings of two wide-ranging subtropical tree species, *Castanopsis sclerophylla* and *Schima superba*, with contrasting stomatal regulation strategies to prolonged drought under ambient and elevated night-time temperature by 2 °C. We quantified the seedling survival time since drought treatment by measuring multiple leaf traits such as leaf gas exchange, predawn leaf water potential and water-use efficiency. The results showed that all seedlings in the ambient temperature died within 180 days and 167 days of drought for *C. sclerophylla* and *S. superba*, respectively. Night warming significantly shortened the survival time of *C. sclerophylla*, by 31 days, and *S. superba* by 28 days, under the drought treatment. A survival analysis further showed that seedlings under night warming suffered a 1.6 times greater mortality risk than those under ambient temperature. Further analyses revealed that night warming suppressed net leaf carbon gain in both species by increasing the nocturnal respiratory rate of *S. superba* across the first 120 days of drought and decreasing the photosynthetic rate of both species generally after 46 days of drought. These effects on net carbon gain were more pronounced in *S. superba* than *C. sclerophylla*. After 60 days of drought, night warming decreased the predawn leaf water potential and leaf water-use efficiency of *C. sclerophylla* but not *S. superba*. These contrasting responses are partially due to variations in stomatal control between the two species. These findings suggest that stomatal traits can regulate the response of leaf gas exchange and plant water-use to nocturnal warming during drought. This study indicates that nocturnal warming can accelerate tree mortality during drought.

- Night warming accelerates the mortality of two subtropical seedlings under drought.
- Night warming differently affects the drought response of leaf gas exchange and plant water-use between the two species due to species-specific stomatal morphological traits.
- Carbon metabolism changes and hydraulic damage play differential roles in driving night-warming impacts on the drought-induced mortality between the two species.

Introduction

Droughts have triggered widespread tree mortality in all forested biomes with profound impacts on the carbon balance and ecosystem functions (Allen et al. 2010, Hartmann, et al. 2018b). The negative effects of drought on tree survival can be further exacerbated by warmer temperatures, as reported by extensive forest dieback across the globe (Phillips et al. 2009, Peng et al. 2011, Allen et al. 2015, Breshears et al. 2021). In most forest areas, the night warms more quickly than the day (Easterling et al. 1997, Xia et al. 2014, Thorne et al. 2016). Hence, a mechanistic understanding of the sensitivity of drought mortality to nocturnal warming is essential for predicting forest dynamics in the future.

Drought mortality has been linked to temperature-dependent physiological processes in plants. First, rising temperature directly elevates carbon loss by stimulating respiratory rates and reducing photosynthetic capacity (Crafts-Brandner and Salvucci 2000, Dusenge et al. 2020), intensifying the risk of carbon starvation during drought (Galbraith et al. 2010, McDowell et al. 2018). For example, diurnal warming induces earlier stomatal closure and causes negative carbon balance over the whole plant under drought treatment (Zhao et al. 2013). If the carbon deficit persists, plants grown at higher temperature will suffer a more severe reduction in stored carbohydrates than ambient plants (Du et al. 2020), leading to a higher risk of carbon starvation (Hartmann 2015, Hartmann, et al. 2018a). Furthermore, elevated cumulative respiration induced by increased daily temperature triggers more rapid seedling mortality from drought (Adams et al. 2009, 2017). Second, elevated temperature also modulates plant water-use through its positive effects on vapor pressure deficit (VPD), yielding more significant risks of hydraulic failure via higher evaporative demand (McDowell and Allen 2015, Grossiord et al. 2020). For example, along a grassland–forest ecotone, the warming-induced increase in daily temperature and VPD hastens desiccation-induced mortality by enhancing plant transpiration rates and xylem water potentials (Will et al. 2013). Diurnal warming has been found to accelerate drought-induced tree mortality by inducing more extensive water-use, lower net carbon gain and earlier vascular dysfunction (Duan et al. 2014, 2015). The warming effect on these physiological characteristics interactively affects the water-for-carbon trade-offs on tree functioning during drought (Meir et al. 2015, Novick et al. 2016). Although the critical role of increasing mean diurnal temperature in driving tree eco-physiological processes is known, how nocturnal warming can influence drought-driven tree mortality remains unclear.

Nocturnal warming can affect plant survival during drought by enhancing the respiratory loss of carbon at night. For example, regional analyses of tropical forest plot data have shown that increased night-time temperature stimulates leaf respiration and causes higher tree mortality rates (Clark et al. 2010). By contrast, some experimental studies also suggest that night-warming-induced carbon losses from respiration can increase foliar carbohydrate depletion overnight and trigger a compensatory increase in tree daytime photosynthesis (Turnbull et al. 2002, 2004). The photosynthetic compensation under nocturnal warming can strengthen carbon sequestration (Wan et al. 2009, Xia et al. 2014) and community resistance to drought in arid and semi-arid grasslands (Yang et al. 2016). However, soil drought can convert the night-warming impact on tree growth from positive to negative in forests (Zhu et al. 2020). On the global scale, the elevated respiratory loss at higher night temperature is one of the mechanisms to explain the reduced tropical tree growth (Clark et al. 2003, Feeley et al. 2007) and interannual variability of terrestrial carbon sink (Anderegg et al. 2015).

Warming at night can also influence drought-induced tree mortality by altering plant hydraulic functions, such as stimulating plant nocturnal water loss by increasing evaporative loads (Zeppel et al. 2012, Zhao et al. 2013). Consequently, the increased leaf water loss can reduce the recovery of xylem embolism and hydraulic redistribution during the night (Howard et al. 2009, Fuentes et al. 2013), causing higher vulnerability to drought stress and mortality (Zeppel et al. 2012, Choat et al. 2018). A field experiment has shown that night warming with drought can increase the mortality rate of *Pinus halepensis* seedlings by inducing a higher loss of xylem hydraulic conductivity (Balducci et al. 2014). However, the evidence is still lacking to show the potential impacts of night-time warming on drought-induced tree mortality via daytime water-use in plants (Sadok and Jagadish 2020).

Despite the proximate cause of hydraulic dysfunction to drought-induced mortality, the degree of carbohydrate depletion varies between species among studies (Anderegg and Anderegg 2013, Anderegg et al. 2016). Differences in the physiological mechanisms of drought-induced mortality among experiments have been linked to uncertainty in traits and the associated ecological strategies among species, including plant growth form, species or genetic differences or plant water-use strategy. For instance, two Eucalyptus species exhibit rapid declines in water status and complete losses of xylem hydraulic conductance under severe water deficit. In comparison, the conservative growth and water-use strategy of *Pinus radiata* resulted in a longer duration to drought mortality, but significant carbohydrate depletion (Mitchell et al. 2013). However, alternative evidence indicates stomatal regulation strategies did not generally change the relative contributions of hydraulic failure and carbohydrate depletion during tree mortality from drought (Anderegg and Anderegg 2013, Duan et al. 2015). Studies using two species of contrasting stomatal regulation strategies further observed that diurnal warming accelerates drought-induced mortality for relatively isohydric *P. radiata*, but not for relatively anisohydric species (e.g., *Callitris rhomboidea*) (Duan et al. 2015). In addition, the different sensitivities to water stress

among tree species partly depend on xylem anatomy, which is functionally related to a suite of traits that govern plant drought response (Taneda and Sperry 2008, Klein 2014, Elliott et al. 2015). The large earlywood vessels of ring-porous species with anisohydric behaviors have been suggested to be more susceptible to hydraulic damage, potentially causing embolism at low water potentials (Kannenberg et al. 2019). However, little is known about the consequences of trait combinations on species performance during drought, especially under warmer conditions.

Subtropical evergreen broadleaf forests in East Asia store a large amount of carbon and are critical in regulating terrestrial feedbacks to climate change (Yu et al. 2014, Cui et al. 2019). This region has undergone pronounced night warming (Xia et al. 2014) and increasingly severe seasonal drought due to hydrothermal changes (Dai 2013, Zhao and Dai 2017). Thus, understanding the vulnerability of subtropical tree species to drought mortality under nocturnal climate warming is crucial for predicting future forest productivity and dynamics. To identify whether night warming can exacerbate water stress during drought, we imposed a drought treatment on two subtropical species of contrasting stomatal regulation with fundamentally different xylem anatomic architecture (i.e., relatively anisohydric ring-porous *Castanopsis sclerophylla* and relatively isohydric diffuse-porous *Schima superba*) in a greenhouse under ambient and elevated night-time temperature. We assessed the effects of night-time warming on the tree survival time and its controlling processes and traits, such as leaf photosynthesis, night-time respiration, transpiration, leaf water potential and water-use efficiency. We hypothesized that (1) night warming would shorten the survival time of seedlings during drought for both species, (2) night warming would accelerate seedling mortality by inducing a faster decline in predawn leaf water potential due to increased water loss during the night and enhanced carbohydrate consumption due to higher respiration during drought, resulting in higher susceptibility to both hydraulic failure and carbon starvation, (3) the rather anisohydric *C. sclerophylla* would experience a faster decline in water status under night warming than rather isohydric *S. superba*. In contrast, night warming would trigger earlier stomatal closure in *S. superba* than *C. sclerophylla* during drought and result in considerable carbohydrate depletion compared with that in *C. sclerophylla*.

Materials and methods

Plant material

This study selected two common evergreen species (i.e., *C. sclerophylla* and *S. superba*) that are widely distributed throughout subtropical ecosystems across East China. The two species were chosen as representative of two different types of xylem anatomic architecture (ring- vs diffuse-porous) and contrasting stomatal regulation strategies (anisohydric vs isohydric) (Figures S2-1 and S2-2, Table S2-1 available as Supplementary

data at *Tree Physiology* Online). *Castanopsis sclerophylla* is a ring-porous species and exhibits a rather anisohydric behavior. In comparison, diffuse-porous *S. superba* adopts a more anisohydric strategy and has greater cavitation-resistant xylem than *C. sclerophylla* (xylem water potential inducing 50% loss of hydraulic conductivity: $P50 = -5.65$ MPa vs -4.39 MPa, respectively, Table S2-1 available as Supplementary data at *Tree Physiology* Online). We obtained 3-year-old seedlings of two species from a seedling nursery in Ningbo city, Zhejiang, China (29°32′N, 120°21′E). In May 2019, 18 seedlings per species were planted into 19 l circular pots and kept well-watered within a naturally lit greenhouse at East China Normal University, Shanghai, China (31°14′N, 121°24′E). At the start of the experiment, the mean plant height and basal stem diameter were 71.1 ± 2.3 (mean ± SE) cm and 5.7 ± 0.3 cm for *C. sclerophylla*, and 76 ± 2.1 cm and 6.6 ± 0.3 cm for *S. superba*, respectively.

Experimental design

Following roughly 2 months of growth, one-half of the seedlings from each species (9 of 18 individuals from each species) with similar height and stem size were randomly assigned into two treatments, including control and 2 °C warming during the night (06:00 p.m.–06:00 a.m.). The warming treatment was conducted with infrared radiators (Langpu Co. Ltd, Guangzhou, China), positioned 0.5 m above the target leaves. Identical heaters without lamps were positioned in ambient treatments to consider the shading effects of the infrared radiator. On average, the temperature treatment resulted in average night warming by 3.1 °C ($P < 0.001$), rising mean night-time temperature from 31.6 °C to 34.7 °C (Figure S1 available as Supplementary data at *Tree Physiology* Online). Initially, the mean soil volumetric water content (VWC) was similar between the temperature treatments in both species with a mean of 0.35 ± 0.32 m³/m³, and plants were then left to dry with no water addition until all nine seedlings for each species in each temperature treatment were dead (Figure S2 available as Supplementary data at *Tree Physiology* Online). VWC from 0 to 10 cm depth was measured in each plant with FieldScout TDR 350 Soil Moisture Meter (Spectrum Technologies, IL).

Plant growth metrics

We measured the height of the main stem and basal diameter of nine seedlings in each temperature treatment at the initial and end stages of the experiment. Leaf area was measured with a Li-3100 leaf area meter (Li-Cor, Lincoln, NE, USA) and leaf mass per unit area was calculated as leaf mass after drying for 48 h at 70 °C, divided by leaf area. All seedlings were measured for height, diameter and leaf area.

Gas exchange and tree water status measurements

Leaf gas exchange was measured on one leaf of each seedling with a Li-Cor 6800 portable photosynthesis system (Li-Cor)

equipped with the red/blue LED light source. Night-time respiration (μmol m^{-2} s^{-1}) was determined between 21:00 and 24:00h, and net photosynthesis (μmol m^{-2} s^{-1}) was measured between 9:00–11:00h during the following day in weekly intervals. These repeated measurements were done on fully developed leaves randomly selected from the upper canopy at each point. The reference CO_2 concentration and relative humidity in chambers were set to 400 p.p.m. and 50–60%, respectively. The light environment in the chamber was regulated at 0 μmol m^{-2} s^{-1} for respiration at night and 1000 μmol m^{-2} s^{-1} for photosynthesis during the day. After 30 days of drought, leaf water potential was measured before dawn between 05:00 and 06:00h during the same day for gas exchange measurement using a Scholander pressure chamber (model 670, PMS Instrument Co., Corvallis, OR, USA).

Stomatal size and density

On 6 August 2019, sun-exposed leaves were collected early in the morning for measuring stomatal anatomical traits. The stomata were taken from the abaxial side of the leaves. The abaxial epidermis of the leaves was cleaned by a degreased cotton ball and then applied clear nail varnish at the maximum leaf width for about half an hour. Stomatal size and counts were determined from the clear nail varnish impression at $\times 400$ magnification by light microscopy (Olympus BX51, Tokyo, Japan), and digital images were captured with a digital microscope eyepiece (HiROCAM MA88-300A, Shanghai, China). Stomatal size S was calculated as the guard cell length $\times$ guard cell pair width. Stomatal density D was expressed as the number of stomata per 400 $\times$ 400 μm field of view. The pore area of the stomata was used to represent the stomatal aperture. The leaves used for stomatal morphology were fully mature under the well-watered control environment, so a potential drought and night-warming effect could not be tested.

Non-structural carbohydrates sampling and analysis

To detect the dynamic of leaf non-structural carbohydrates (NSCs) over the night, we sampled leaves before sunrise at the 41 days of drought (three to five seedlings per species per treatment). Before NSC quantification, foliar samples were dried at 105 °C for an hour and at 70 °C for 48 h and ground to a powder fine enough to pass a 100-mesh screen. The NSC mainly includes soluble sugars and starch, which were analyzed using 0.1 g of dried tissue following the anthrone method and UV spectrophotometry methods.

Seedling mortality

Plants were monitored daily for leaf defoliation, and we defined mortality as 100% of their canopy foliage turning brown or respiration approaching zero (Lu et al. 2019).

Statistical analyses

In this study, WUE was calculated for each treatment using the following equation:

$$\text{WUE} = \frac{A_{\text{net}}}{E}$$

where WUE is water-use efficiency (μmol CO_2 mmol^{-1} H$_2$O), A_{net} is leaf net photosynthesis (μmol m^{-2} s^{-1}) and E is transpiration (mmol m^{-2} s^{-1}).

We analyzed how night-time warming shaped tree mortality using survival analysis with Kaplan–Meier survivorship curves for each treatment with the 'survival' package (Therneau 2020). This analysis compared the probability of survival through time and produced a log-rank test P-value. We also performed a t-test to examine the effects of night warming on the average survival time under drought. In addition, we used the Cox proportional hazards model to combine species and treatment effects into a single survival model (Therneau 2020) and estimate the proportional hazard ratios related to the species and temperature treatment.

All data are reported as means $\pm$ SE. Two-way ANOVAs were used to analyze the main and interactive effects of temperature treatment and species on plant growth metrics. For the time-series data during drought, we used a linear mixed-effects model to evaluate the main and interactive effects of temperature treatment, species and time, with time treated as a continuous variable and the number of sample sizes considered as a random factor. The response variables accessed in this model include the time-varying VWC, night-time leaf temperature (night-time T_{air}), night-time respiration (R_{night}), night-time stomatal conductance (g_{night}), night-time transpiration (E_{night}), predawn leaf water potential (Ψ_{pd}), net photosynthesis (A_{net}), daytime stomatal conductance (g_s), daytime transpiration (E) and WUE (Table S1 available as Supplementary data at Tree Physiology Online). We repeated the same analysis for two species separately (Table S2 available as Supplementary data at Tree Physiology Online). All analyses were performed in R version 4.0.3 (http://www.R-project.org/), and results were considered significant if $P < 0.05$.

Results

Effects of night warming on soil moisture and plant growth

The mean soil VWC of plants gradually decreased with time under treatments of both species and temperatures. Soil VWC declined faster under warming treatment with C. sclerophylla ($P < 0.05$, Figure S2 available as Supplementary data at Tree Physiology Online) but not S. superba. At the beginning of the drought experiment, there was no difference in plant height and stem basal diameter between temperature treatment ($P > 0.05$) and species ($P > 0.05$). The warming treatment did not change the plant height or stem basal diameter at the time of death in
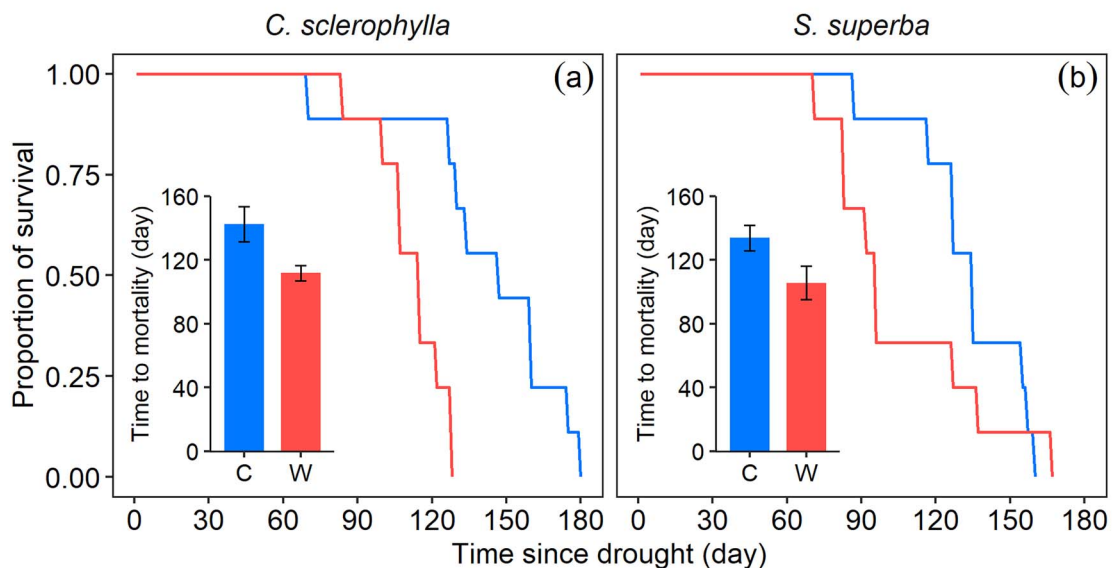
Figure 1. Effect of night warming on drought-induced mortality for seedlings of (a) *C. sclerophylla* and (b) *S. superba*. The main plot represents the percentage of seedlings surviving during drought. Inset denotes the mean days to drought mortality under control (C) and night warming (W) for each species. Error bars depict ± SE ($n = 9$).

both species ($P > 0.05$, Figure S3 available as Supplementary data at *Tree Physiology* Online).

Effects of night warming on drought mortality

When exposed to drought treatment, all seedlings of *C. sclerophylla* and *S. superba* died within 180 days and 167 days, respectively. Under the ambient temperature treatment, the mean time-to-mortality of *C. sclerophylla* and *S. superba* was 143 and 134 days, respectively. On average, seedlings under night warming died 31 ± 5 and 28 ± 10 days earlier than under the ambient temperature for *C. sclerophylla* and *S. superba*, respectively (Figure 1). Night warming significantly shortened the seedling death time caused by drought ($P < 0.05$) and the reduction in *C. sclerophylla* (21.6%) was similar to that in *S. superba* (21.1%). Based on the Cox proportional hazard model, seedlings under night warming had a 1.6 (95% CI: 1.03–2.17, $P < 0.05$) times greater mortality risk than those under ambient temperature. No significant difference in mortality risk was found between the two species.

Effects of night warming on nocturnal respiration, leaf water potential and leaf NSC

After the start of the drought treatments, nocturnal respiration rates and predawn leaf water potential of both species declined over time ($P < 0.001$). Nocturnal respiration of *C. sclerophylla* did not differ between the ambient and elevated night-time temperature treatments (Figure 2a). In contrast, *S. superba* under night warming had higher nocturnal respiration than those under ambient temperature. The warming-induced stimulation of nocturnal respiration was consistent across the first 120 days of drought ($P < 0.001$, Figure 2b), but exhibited

large variability after that. Predawn leaf water potential of *C. sclerophylla* was markedly reduced by night warming, and the treatment effects were increased over time ($P < 0.001$, Figure 2c). In comparison, a negative effect of night warming on the leaf water potential of *S. superba* was only observed at 51, 58 and 65 days of drought. The overall effect of warming was not statistically significant for the leaf water potential of *S. superba* ($P = 0.227$, Figure 2d). Moreover, total NSC and starch concentrations in leaves of both species were unchanged by night warming (Figure 3). Only the soluble sugar concentration in the leaves of *C. sclerophylla* exhibited a significant increase under night warming ($P < 0.05$).

Effects of night warming on WUE

During drought, *C. sclerophylla* consistently maintained higher A_{net} and transpiration rates, and smaller WUE than *S. superba* at both temperatures (Figure 4). In both species, A_{net} and transpiration rates of the ambient-temperature seedlings declined over time and reached zero around 177 and 140 days of drought for *C. sclerophylla* and *S. superba*, respectively (Figure S4a and b available as Supplementary data at *Tree Physiology* Online). Night warming significantly affected the responses of A_{net} and transpiration rates to drought stress. A_{net} of both species showed a more marked decline under night warming generally after 46 days of drought and was near zero around 120 days of drought (Figure S4a and b available as Supplementary data at *Tree Physiology* Online). Transpiration rates of *C. sclerophylla* were not significantly different between temperature treatments over time and therefore led to decreased WUE under night warming (Table S2 available as Supplementary data at *Tree Physiology* Online, Figure 4). A significant decline in WUE of
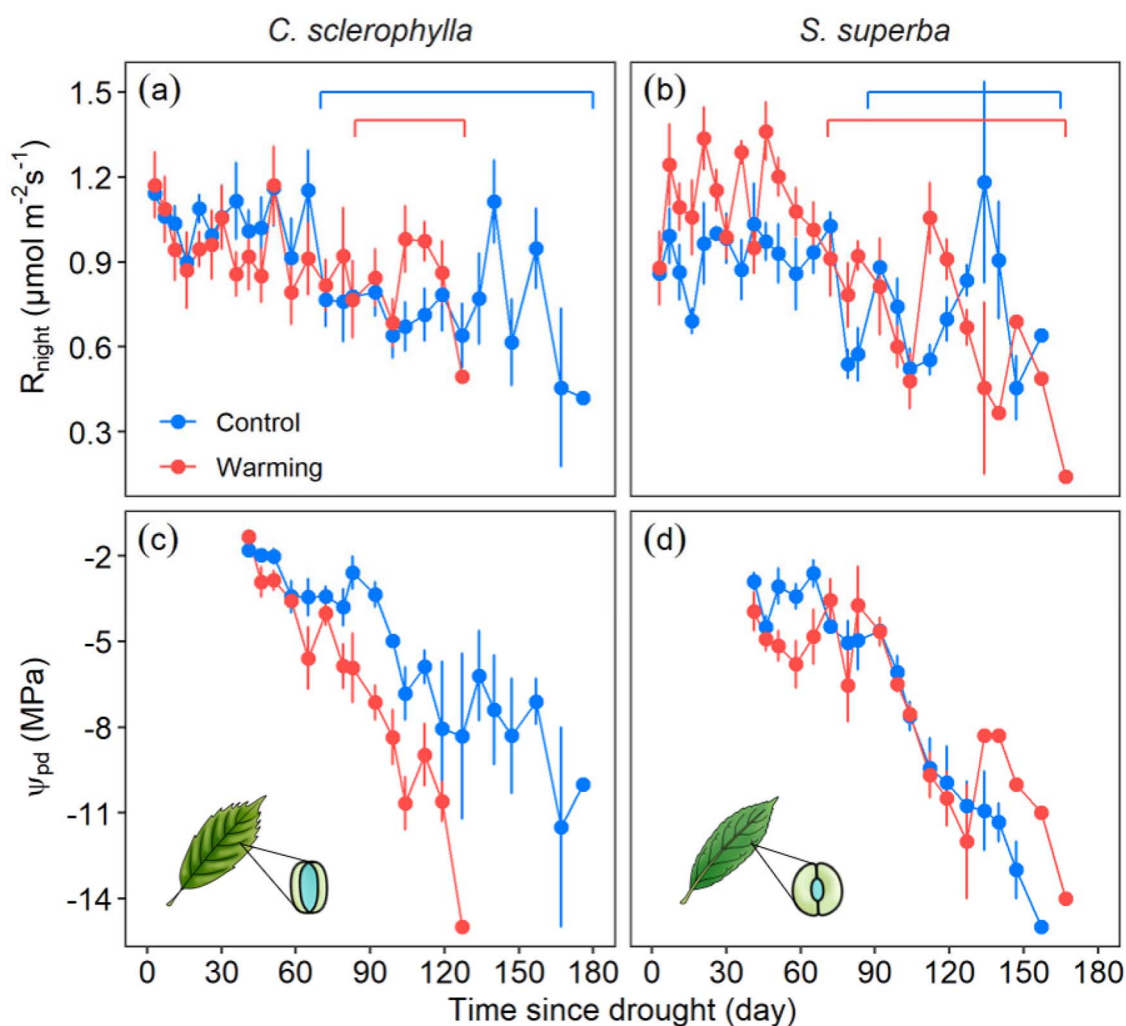
Figure 2. (a, b) Nocturnal respiration rate (R_{night}) and (c, d) predawn leaf water potential (ψ_{pd}) of (a, c) *C. sclerophylla* and (b, d) *S. superba* during drought. Blue symbols, grown under ambient temperature, red symbols, grown under night warming. Error bars depict ± SE (*n* = 9). The colored bracket lines indicate days when the number of seedlings was <9. Graphical summary of stomatal traits is modified from micrographs of stomata for two species.

C. sclerophylla was detected at day 36 and 58 of drought (Figure S4e available as Supplementary data at *Tree Physiology* Online). By contrast, the trend in transpiration rates of *S. superba* was similar to the trend observed in A_{net}, thus contributing to an unchanged WUE for *S. superba* (*P* = 0.96, Figure 4). No interaction between night warming and measurement time on A_{net} (*P* = 0.242) or transpiration rates (*P* = 0.58) was observed for *S. superba*.

In both species, WUE showed a peak response with predawn leaf water potential under drought stress (Figure 5). Maximum WUE of *C. sclerophylla* (calculated at the water potential when the value peaked) was lower in seedlings under night warming (3.11 μmol CO_2 mmol^{-1} H_2O) compared with those under ambient temperature (4.61 μmol CO_2 mmol^{-1} H_2O). In contrast, the shape of WUE against predawn leaf water potential for *S. superba* did not differ between temperature treatments

with the maximum WUE as 4.72 and 4.57 μmol CO_2 mmol^{-1} H_2O under control and elevated night-time temperatures.

Differences in stomatal morphology between two tree species

The two species, i.e., *C. sclerophylla* and *S. superba*, differed in stomatal shape and pattern. Stomata of *C. sclerophylla* had dumb-bell-shaped guard cells (Figure 6a), whereas *S. superba* had kidney-shaped guard cells (Figure 6b). *Castanopsis sclerophylla* had a significantly smaller guard cell area than *S. superba* on the abaxial epidermis, ranging from 340 to 941 μm^2 in *C. sclerophylla* and between 540 and 1355 μm^2 in *S. superba* (*P* < 0.05, Figure 6c). Conversely, the stomatal aperture was 1.31 higher in *C. sclerophylla* than *S. superba* (*P* < 0.05, Figure 6d). Stomatal density in *C. sclerophylla* was significantly higher on the adaxial epidermis than *S. superba* (*P* < 0.05, Figure 6e).
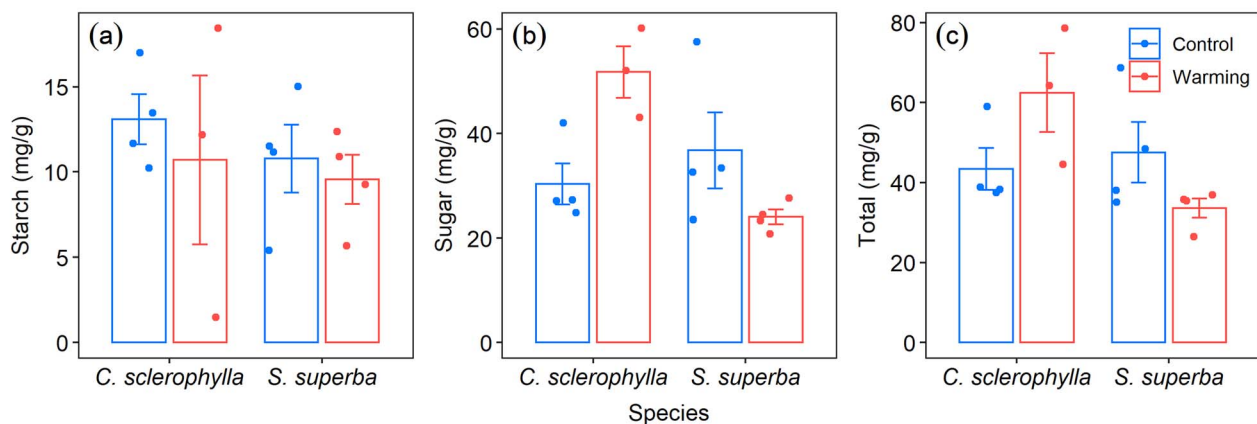
Figure 3. Foliar NSCs of *C. sclerophylla* and *S. superba* at Day 41 of drought. Blue bars, grown under ambient temperature; red bars, grown under night warming. Error bars depict ± SE (*n* = 3–4).

Discussion

Nocturnal warming shortens seedling survival time under drought

Our results support the hypothesis that night warming shortened the seedling survival time of the two subtropical species during drought (Figure 1). The increased mortality at higher night-time temperatures reported by other experimental (Balducci et al. 2014) and observational (Clark et al. 2010) studies also support our hypothesis. A drought mortality experiment simulated an array of increasing temperatures from 3.6 to 7.7 °C on two conifer species (Adams et al. 2017). They found that time-to-mortality during drought linearly decreased with increasing temperature, suggesting that the response of time-to-mortality during drought was a constant proportion of the temperature change. To better understand the response magnitudes of drought-induced mortality under diurnal and night-time warming, we further calculated a mean reduction in time-to-mortality during drought per 1 °C temperature increase, from our experimental results as well as results reported for *Pinus edulis* (Adams et al. 2009, 2017), *Eucalyptus radiata* (Duan et al. 2014), *P. radiata* (Duan et al. 2015), *Pinus ponderosa* (Adams et al. 2017) and 10 tree species from the south-central USA (Will et al. 2013). In this study, night warming can reduce the time to drought-induced mortality of *C. sclerophylla* and *S. superba* by 7.0% and 6.8%, respectively, by per 1 °C increase of night temperature. In comparison, those diurnal-warming experiments with 3–4 °C increase found similar decreases in survival time from 0 to 4.7% under per 1 °C increase of daily temperature (Adams et al. 2017). The reduction in drought survival time under night warming is more significant than the reported negative effect of diurnal warming on seedling mortality of other tree species. The strong response of drought mortality to nocturnal warming suggests that subtropical trees may exhibit higher vulnerability to extreme drought under the rapid increase in night-time temperature.

Different roles of leaf respiration and water potential in regulating drought mortality

During drought, the night-warming treatments had contrasting effects on nocturnal respiration between *C. sclerophylla* and *S. superba* (Figure 2a and b). Nocturnal respiration of *C. sclerophylla* was not affected by night warming, whereas it was increased in *S. superba*. It has been shown that warming effects on leaf nocturnal respiration diverged under differential water regimes. For instance, the warming-induced increase in nocturnal respiration disappeared during drought in *Eucalyptus* (Duan, et al. 2013). In our experiment, night warming increased nocturnal respiration under well-watered conditions (Unpublished data), but this positive response of *C. sclerophylla* was erased under drought stress (Figure 2a). Under drought stress, no effect of warming on the carbohydrates was observed in the leaves of both species (Figure 3). Therefore, the insignificant effect of night warming on nocturnal respiration of *C. sclerophylla* was not linked to substrate supply differences. Instead, decreased demand for respiratory products under drought conditions was most likely responsible for the unchanged nocturnal respiration during drought (Atkin and Macherel 2009, Kumarathunge et al. 2020). In contrast, *S. superba* exhibited higher nocturnal respiration under night warming combined with drought (Figure 2b). The increased nocturnal respiration of *S. superba* could reflect drought-mediated increases in the need for maintenance respiration to support hydraulic repair in dry soils (Atkin and Macherel 2009, Brodersen and McElrone 2013, Rowland et al. 2015). No response of NSC consumption to night warming despite changes in nocturnal respiration and photosynthesis indicates adjustments to internal tree NSC dynamics. Potential explanatory processes include feedback inhibition of photosynthesis, translocation of NSC between other tree tissues and leaves and sink limitation (Myers et al. 1999, Körner 2003, Adams et al. 2013). The
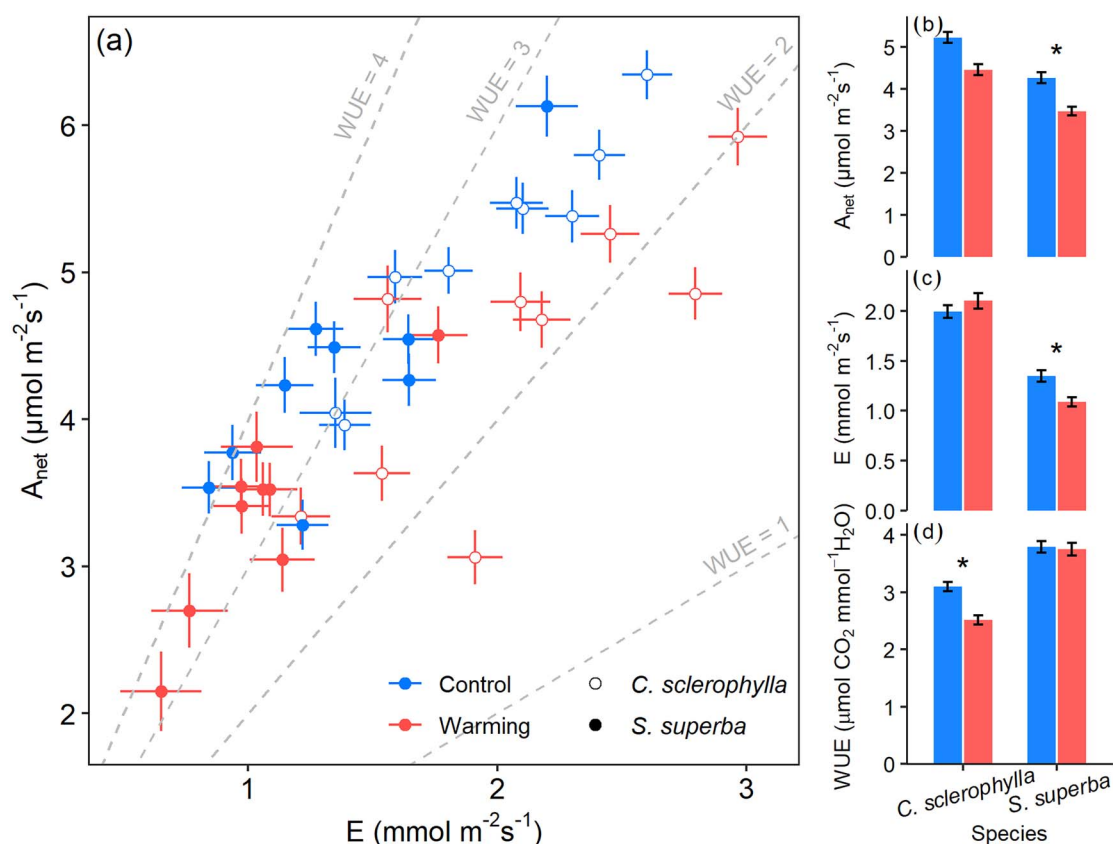
Figure 4. (a) The relationship between net photosynthesis rate (A_{net}) and evaporation rate (E) of *C. sclerophylla* (open symbols) and *S. superba* (closed symbols). Blue symbols, grown under ambient temperature; red symbols, grown under night warming. Data are the means of each plant. (b) A_{net}, (c) E and (d) WUE of two tree species grown under ambient and warmer night temperature. Error bars depict ± SE ($n = 14$–40). Asterisks in b–d denote significant difference of treatment effects at $P < 0.05$.

warming-induced reduction in survival time during drought is consistent with a pioneer mortality experiment in which warming increased cumulative respiration (Adams et al. 2009) but did not affect foliar NSC (Adams et al. 2013). Our result in *S. superba* additionally provides evidence that the warming-induced increases in respiration were not reflected in changes to foliar NSC. However, substantial reductions in net carbon gain induced by night warming suggest clear signs of disturbing carbon metabolism, which may lead to greater susceptibility to drought mortality.

Night warming accelerated the decline in predawn leaf water potential of *C. sclerophylla* with increasing drought stress (Figure 2c). In contrast, the warming effects were only pronounced during early drought in *S. superba* (Figure 2d). The negative effect of night warming on predawn leaf water potential could be explained by increased evapotranspiration associated with an elevated VPD (Zeppel et al. 2011, Sadok and Jagadish 2020). Nocturnal transpiration of *C. sclerophylla* was enhanced under night warming (Figure S5, Table S2 available as Supplementary data at *Tree Physiology* Online). This positive response could partially account for the more rapid soil dry-down (Figure S2 available as Supplementary data at *Tree Physiology*

Online) and may inhibit overnight water potential recovery during the night (Howard et al. 2009). Moreover, in both species, drought substantially decreased leaf water potential to values close to −15 MPa in both temperature treatments. Given the low water availability in branch tissue of droughted trees, we suggest that stems and branches of these trees experienced extensive cavitation under heat and drought stress. Thus, regardless of temperature treatments, drought-induced mortality in this study is linked to the immediate hydraulic dysfunction.

Contrasting responses of WUE to night warming between the two species

Our results showed that night warming could amplify lethal drought stress by negatively affecting plant WUE (Figure 4, Table S1 available as Supplementary data at *Tree Physiology* Online). Many studies have reported improved WUE under drought stress (Brodribb 1996, Peters et al. 2018) and night warming (Xia et al. 2009). However, such water-saving effect quickly disappeared during the combined heat-drought stress (Birami et al. 2020). Our findings suggest that night warming may shrink or even reverse the potential benefits of WUE upregulation during droughts (Coupel-Ledru et al. 2016,
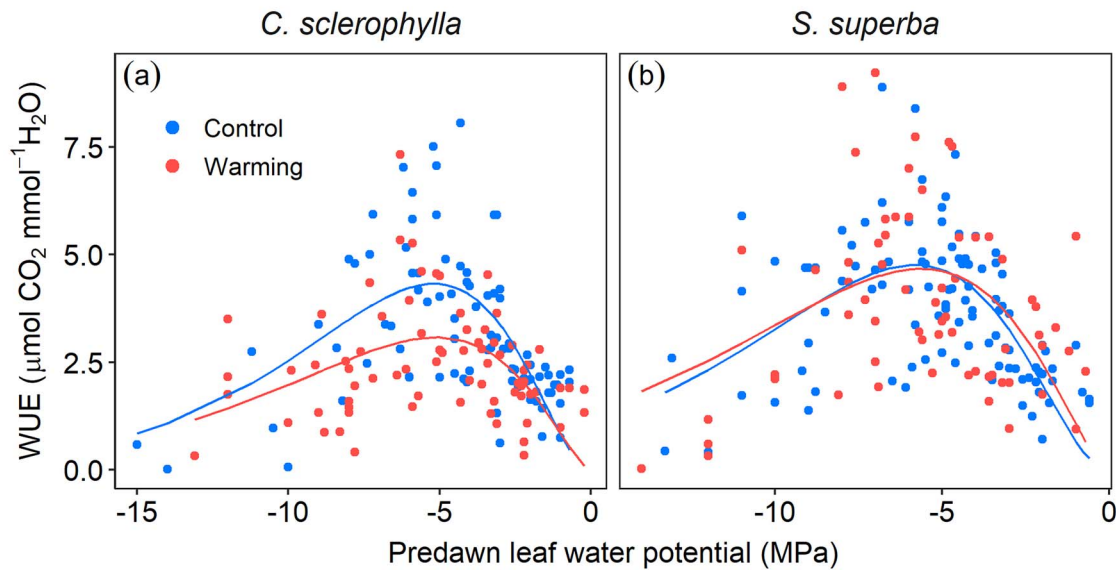
Figure 5. The relationships between water-use efficiency (WUE) and decreasing leaf water potential of (a) *C. sclerophylla* and (b) *S. superba* under ambient and warmer night temperature. The regression model used to fit the data as: control = $0.94 \times \frac{x^{2.34}}{e^{0.44x}}$ ($R^2 = 0.44$, $P < 0.001$), night warming = $1.04 \times \frac{x^{1.58}}{e^{0.29x}}$ ($R^2 = 0.16$, $P < 0.05$) in *C. sclerophylla*, and control = $0.84 \times \frac{x^{2.24}}{e^{0.38x}}$ ($R^2 = 0.44$, $P < 0.001$), night warming = $2.17 \times \frac{x^{1.24}}{e^{0.25x}}$ ($R^2 = 0.18$, $P < 0.05$) in *S. superba*.

Sadok and Jagadish 2020). In this study, the reduction in WUE induced by night warming could exacerbate the negative impact of night warming on plant assimilation, meaning plants face a higher risk of carbon starvation and drought mortality (Gessler et al. 2018).

At the species level, WUE was significantly reduced by night warming in *C. sclerophylla*, whereas was unaltered in *S. superba* (Figure 4, Table S2 available as Supplementary data at *Tree Physiology* Online). Reduced WUE of *C. sclerophylla* was related to a warm-induced decrease in photosynthesis, considering the unchanged transpiration (Figure 4b–d). The photosynthetic reduction induced by night warming is also observed in other species (Mohammed et al. 2013, Liao et al. 2020) and could be explained by the increased night-time water loss under night warming (Sadok and Jagadish 2020). However, *S. superba*, in which photosynthesis and transpiration declined at a similar rate, exhibited constant WUE under night warming (Figure 4). The steady WUE of *S. superba* may efficiently save water and maintain hydraulic functions under drought conditions but may cause severe carbon deficiency over long-time periods (Gessler et al. 2018). During extreme water stress, the responses of WUE observed in *S. superba* could be explained by deficient carbon and water fluxes rather than physiological recovery (Hartmann et al. 2013, Wang et al. 2021).

Consistent with some previous studies (Yang et al. 2021, Yao et al. 2021), our results observed a peak response of WUE to decreasing predawn leaf water potential (Figure 5). Upregulated WUE is a vital adaptive capacity for plants to cope with water deficit under both ambient and warming

environments (Duan et al. 2018). However, plants may have reached a physiological threshold in their ability to improve WUE owing to drought-induced stomatal closure under severe heat and drought stress and ultimately cause the breakdown of WUE (Linares et al. 2009). It has been suggested that a threshold may exist in the adaptive capacity of the trees to face drought (Penuelas et al. 2008, Carnicer et al. 2011). In addition, as the drought progressed, photosynthesis decreased at a greater rate than transpiration in response to night warming, inducing a lower maximum WUE of *C. sclerophylla*. The warming-induced downregulation of WUE could indicate biochemical limitations on carbon assimilation, which are known to become considerable under severe drought (Flexas and Medrano 2002, Zhao et al. 2013).

Role of stomatal morphology in affecting drought mortality under night warming

Our study found no significant differences in warming effects on time-to-mortality during drought between *C. sclerophylla* and *S. superba*. However, night warming had contrasting impacts on carbon and water dynamics between the two species under water deficit. The differential responses of two species to night warming can be linked to species-specific stomatal traits and water-use strategies (Figure 6). Even though *C. sclerophylla* had small guard cells, wider stomatal apertures with higher stomatal density correspondingly induce larger stomatal conductance for *C. sclerophylla* than *S. superba*. These morphological traits feature *C. sclerophylla* with relatively high gas exchange capacities and evaporation but low WUE (Figure S2-3
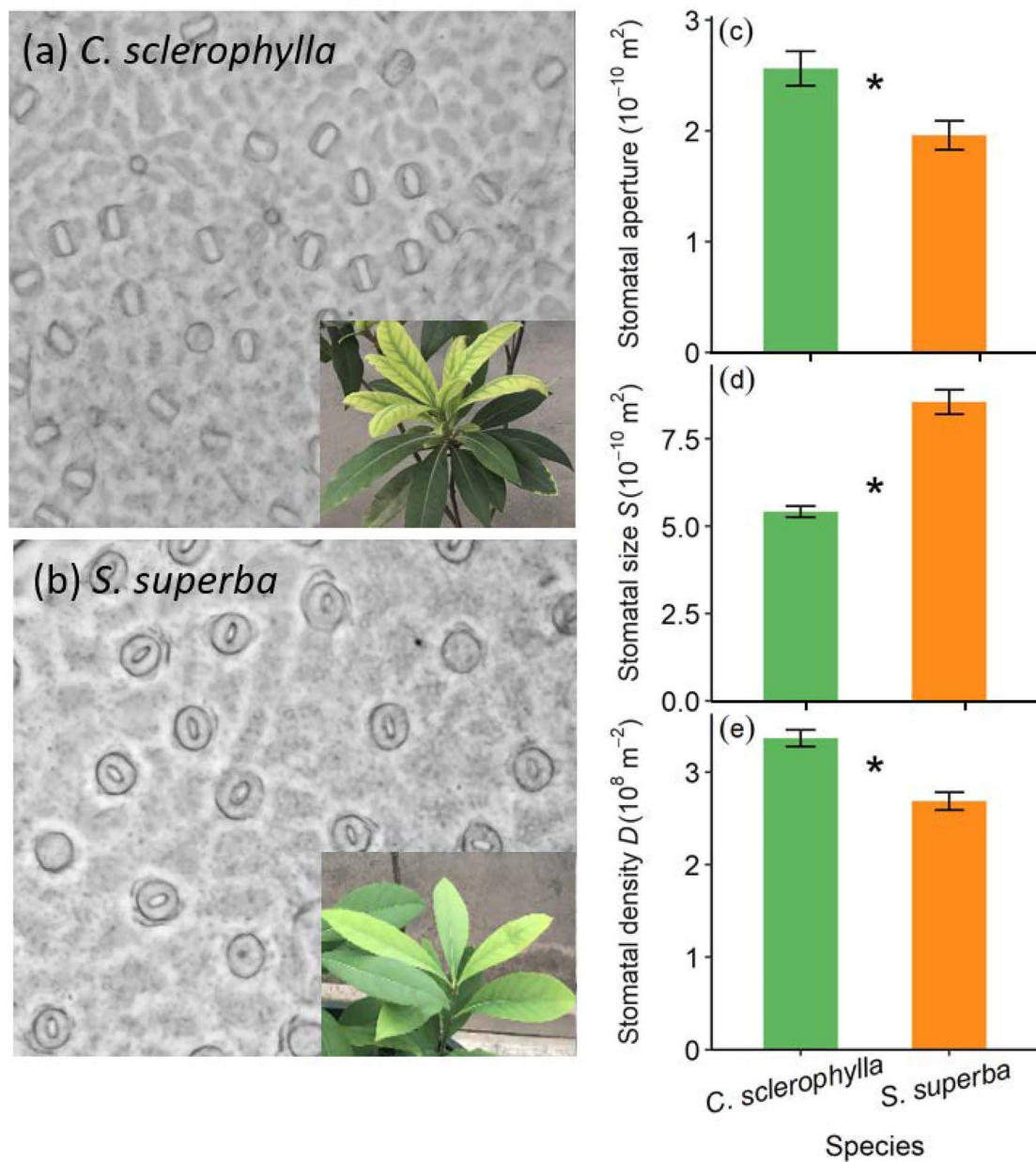
Figure 6. Light micrographs showed contrasting stomatal traits between (a) *C. sclerophylla* and (b) *S. superba*. The bar plot is the mean value of (c) stomatal aperture, (d) stomatal size S and (e) stomatal density D. Error bars are ± SE ($n = 9$). Asterisks in c–e denote significant difference of treatment effects at $P < 0.05$.

available as Supplementary data at *Tree Physiology* Online) (Franks and Casson 2014). However, ineffective stomatal control of water loss makes *C. sclerophylla* prone to cavitation as drought stress progressed. By contrast, *S. superba* has a tighter stomatal regulation, higher and stable WUE, and more isohydric behavior than *C. sclerophylla* (Figures S2-1, S2-2 and S2-3 available as Supplementary data at *Tree Physiology* Online). Such conservative strategies allow this species to sustain hydrated and thus mitigate hydraulic failure during drought (Martin-StPaul et al. 2017, Yi et al. 2019). Consequently, anisohydric *C. sclerophylla* dropped leaf water potential in response to night warming during drought, whereas isohydric

S. superba holds similar water potential between ambient and elevated night-time temperature treatments.

Many studies have indicated that species with a strong control on stomata may be advantageous under water deficit due to their conservative water-use strategies (Brodribb et al. 2009, McAdam and Brodribb 2012). Our results suggest that the impacts of night warming on drought survival are affected by differences in physiological and anatomical adjustments among tree species to cope with drought. Therefore, when dealing with species-specific responses to drought, it is crucial to quantity multiple leaf traits among species to detect physiological mechanisms involved in drought mortality and predict plant

vulnerability to future climate change (Linares and Camarero 2012, Medlyn et al. 2016, Gessler et al. 2018). As competition is the primary driver of small-tree mortality in forests (Lu et al. 2021), we also suggest future work to access the competition effects among species of different drought tolerance in understanding the carbon and water responses to drought under night warming (Medlyn et al. 2007, Lu et al. 2020, Jiang et al. 2021).

Conclusions

Night warming accelerated seedling mortality of two subtropical species during drought. Predawn leaf water potential and leaf WUE of *C. sclerophylla* were significantly lower under night warming, which could explain the earlier drought mortality of *C. sclerophylla* under night warming. Although night warming showed no effect on nocturnal total NSC in leaves of both species, increasing nocturnal respiratory losses of *S. superba* and reducing photosynthetic rates of both species resulted in reduced leaf net carbon gain in both species under night warming. These negative effects were more pronounced in *S. superba* than *C. sclerophylla*. Drought mortality in *S. superba* appears to be related to carbon metabolism changes under night warming. The distinct responses of *C. sclerophylla* and *S. superba* to nocturnal warming during drought result from their contrasting drought response strategies and related stomatal morphological traits. This study underlined the importance of considering the integration of both morphological and physiological traits contributing to drought mortality, along with their responses to night warming. Our findings underscore the importance of nocturnal warming in mediating the tree survival process during drought.

Authors' contributions

Y.D., R.L. and H.S. conducted the experiment. R.L. and J.X. performed the data analysis and wrote the manuscript. X.X. and L.Y. contributed to the manuscript development.

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Conflict of interest

The authors declare no conflict of interest.

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