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Plant photosynthetic overcompensation under nocturnal warming: lack of evidence in subtropical evergreen trees

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- **Background and Aims** Increased plant photosynthesis under nocturnal warming is a negative feedback mechanism to overcompensate for night-time carbon loss to mitigate climate warming. This photosynthetic overcompensation effect has been observed in dry deciduous ecosystems but whether it exists in subtropical wet forest trees is unclear.
- **Methods** Two subtropical evergreen tree species (*Schima superba* and *Castanopsis sclerophylla*) were grown in a greenhouse and exposed to ambient and elevated night-time temperature. The occurrence of the photosynthetic overcompensation effect was determined by measuring daytime and night-time leaf gas exchange and non-structural carbohydrate (NSC) concentration.
- **Key Results** A reduction in leaf photosynthesis for both species and an absence of persistent photosynthetic overcompensation were observed. The photosynthetic overcompensation effect was transient in *S. superba* due to respiratory acclimation and stomatal limitation. For *S. superba*, nocturnal warming resulted in insufficient changes in night-time respiration and NSC concentration to stimulate overcompensation and inhibited leaf stomatal conductance by increasing the leaf-to-air vapour pressure deficit.
- **Conclusions** The results indicate that leaf stomatal conductance is important for the photosynthetic overcompensation effect in different tree species. The photosynthetic overcompensation effect under nocturnal warming may be a transient occurrence rather than a persistent mechanism in subtropical forest ecosystems.

Key words: Climate warming, photosynthetic overcompensation, respiration, subtropical forest, tree ecophysiology.

INTRODUCTION

The global mean surface temperature was ~0.99 °C higher in 2001–2020 compared with 1850–1900 (IPCC, 2021). Significant attention has been given to the effects of nocturnal warming on the terrestrial ecosystem and its feedback on climate change (Alward, 1999; Wan *et al.*, 2009; Peng *et al.*, 2013; Anderegg *et al.*, 2015) because temperatures rise faster at night than during the day (Xia *et al.*, 2014; Thorne *et al.*, 2016). Previous studies have demonstrated that nocturnal warming increases the respiratory rate of leaves at night (Atkin and Tjoelker, 2003; Atkin *et al.*, 2005; Jing *et al.*, 2016). According to the sink–source hypothesis of photosynthesis (Paul and Foyer, 2001; Paul *et al.*, 2001; McCormick *et al.*, 2006), the overdepletion of substrates during the previous night results in a compensatory enhancement of photosynthesis the following day (Turnbull *et al.*, 2002, 2004; Wan *et al.*, 2009). Therefore, nocturnal warming may enhance daytime leaf photosynthesis to overcompensate for night-time carbon loss, resulting in increased net carbon uptake on the diurnal scale (Griffin *et al.*, 2002; Turnbull *et al.*, 2002, 2004; Wan *et al.*, 2009). This phenomenon, the photosynthetic overcompensation effect (POE), occurs under nocturnal warming in temperate ecosystems (Wan *et al.*, 2009; Xia *et al.*, 2014). However, whether POE occurs in other regions, especially in the wet tropical and subtropical ecosystems, is unclear. Thus, a mechanistic understanding of POE under nocturnal warming conditions is essential for establishing and predicting vegetation productivity in subtropical forests during future climate change events.

The enhanced leaf respiratory rate regulates the occurrence of POE on warm nights (Xia *et al.*, 2014). However, night-time carbon loss does not always increase under nocturnal warming because of the thermal acclimation of plant respiration (Atkin and Tjoelker, 2003; Smith and Dukes, 2017). The thermal acclimation may occur quickly, even within a few days when plants are exposed to a higher temperature (Slot *et al.*, 2014; Slot and Kitajima, 2015). Also, the acclimation of leaf respiration is reversible during changes in ambient temperature (Bostad *et al.*, 2003). As a product of daytime photosynthesis and the primary substrate of night-time respiration (Göttlicher *et al.*, 2006; Gibon *et al.*, 2009), the content of non-structural carbohydrates (NSC) is an important trait that regulates photosynthesis and links the day–night physiological process (Turnbull *et al.*, 2002, 2004; Wan *et al.*, 2009; Mohammed *et al.*, 2013; Jing *et al.*, 2016). The two main NSC components, soluble sugar and starch, account for NSC fluctuations over time (Hartmann and Trumbore, 2016; Du *et al.*, 2020). Soluble sugar is synthesized during daytime photosynthesis (Chapin *et al.*, 1990), which supports immediate plant metabolism, and it is translocated to various organs at night (Geiger and Servaites, 1994; Geiger *et al.*, 2000). Moreover, starch is produced from sugar that accumulates when the photosynthetic carbon gain exceeds the carbon demand for metabolic activities during the daytime (Chapin *et al.*, 1990; Hartmann *et al.*, 2016). It is then converted to soluble sugar and consumed as the primary carbon source during the night (Gibon *et al.*, 2009; Sulpice *et al.*, 2009). Climate warming stimulates more starch consumption compared with soluble sugar in plants, as revealed in a recent meta-analysis (Du *et al.*, 2020). Thus, starch content is a better substrate depletion indicator under nocturnal warming conditions compared with soluble sugar. Besides participating in metabolism, translocation at night contributes to carbohydrate consumption. Nocturnal warming inhibits the export of carbohydrates from the leaves to other tissues in the plants (Tombesi *et al.*, 2018), resulting in the accumulation of carbohydrates in the leaves. Thus, the occurrence of POE under nocturnal warming depends on the extent of carbohydrate depletion throughout the night.

In addition to carbon metabolism, the use of water is essential for linking daytime and night-time processes. Stomatal conductance is critical to regulating leaf carbon dioxide (CO_2) and water (H_2O) exchange and is sensitive to microclimate changes (Urban *et al.*, 2017; Merilo *et al.*, 2018). The stomata are traditionally assumed to be closed at night because of the absence of photosynthetic carbon gain. However, many studies have shown that stomata are not fully closed during the night, although this increases water loss (Caird *et al.*, 2007; Resco do Dios *et al.*, 2019). Night-time leaf conductance is sensitive to air humidity and is negatively associated with night-time vapour pressure deficit (VPD; Caird *et al.*, 2007; Mott and Peak, 2010; Ogle *et al.*, 2012). The inhibited stomatal conductance may limit respiratory rates under elevated VPD because of the linear relationship between stomatal conductance and night-time respiration (Yu *et al.*, 2019). A tight correlation also exists between daytime and night-time transpiration or stomatal conductance (Christman *et al.*, 2008; Schoppach *et al.*, 2014; Coupel-Ledru *et al.*, 2016). This suggests that leaf photosynthesis may be affected by the day–night linkage of stomatal conductance under nocturnal warming conditions. A previous study indicates that daytime stomatal conductance is increased and reduced under nocturnal warming in the short (hours to days) and long (months to years) terms, respectively (Jing *et al.*, 2016). Therefore, plant stomata closure may downregulate the probability of POE occurrence under nocturnal warming conditions.

A nocturnal warming experiment was conducted in this study to determine whether POE occurs in the seedlings of two subtropical tree species, i.e. *Schima superba* (Theaceae) and *Castanopsis sclerophylla* (Fagaceae). The two tree species are common in subtropical evergreen broad-leaved forests (Ni and Song, 1997; Wang *et al.*, 2019; Lu *et al.*, 2021; Cui *et al.*, 2022). Three hypotheses (Fig. 1) were generated based on the literature: (1) POE will not occur without stimulated night-time respiration (R_{night}); (2) although R_{night} is stimulated, POE will not occur when leaf photosynthesis is not enhanced because of insufficient substrate depletion or stomatal limitation; and (3) POE occurs when R_{night} and leaf photosynthesis are simultaneously enhanced. Thus, whether POE under nocturnal warming occurs persistently in the seedlings of two widely distributed evergreen trees from subtropical forests was determined.

MATERIALS AND METHODS

Plant materials

Three-year-old *S. superba* and *C. sclerophylla* seedlings were obtained from a forestry centre in Zhejiang, China (29°52′N, 121°34′E), in March 2018. The seedlings were transplanted into 19-L cylindrical pots containing homogenized soil and grown in a naturally lit greenhouse at the East China Normal University, Shanghai, China (31°14′N, 121°24′E). Only one seedling was placed in each pot. The plants were watered for 5 d to prevent water deficiency. After 2 months, 36 healthy seedlings of similar size for each species were selected for the experiment. At the beginning of the experiment, the plant height and basal stem diameter (mean ± s.e.) were 70.0 ± 1.4 and 8.2 ± 0.2 cm (*S. superba*) and 70.3 ± 1.6 and 6.9 ± 0.2 cm (*C. sclerophylla*), respectively.

Experimental design

A complete random block design was used to divide the greenhouse (18 m × 4 m) into 12 blocks of equal spacing, which were assigned to control or nocturnal warming treatments (1800–0600 h the next day, local time). Each treatment for each species was done in triplicate, and each replicate contained six seedlings. Infrared heaters (Langpu Co. Ltd, Guangzhou, China) were suspended 2.2 m above the ground.

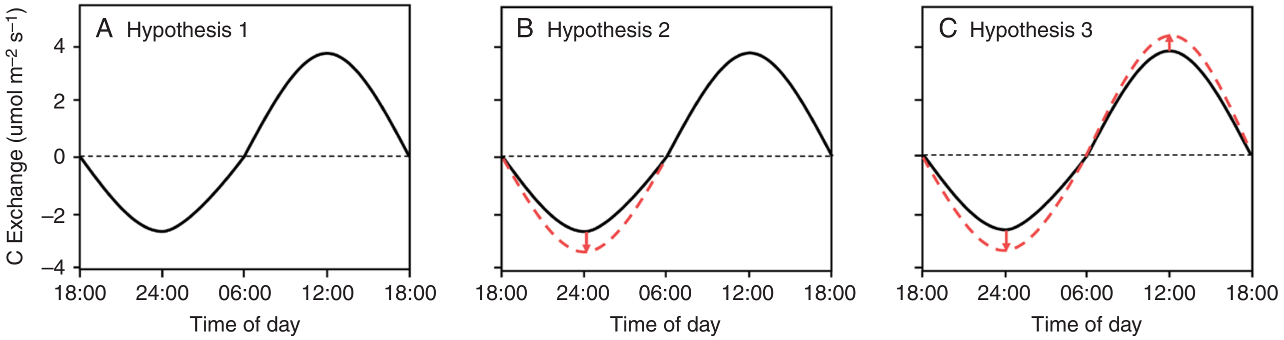

Fig. 1. Conceptual diagram of warming effects on night-time respiration (R_{night}, 1800–0600 h) and photosynthesis (A_{sat}, 0600–1800 h).

Heaters without lamps were used in control blocks to avoid shading effects. Soil temperature at a depth of 5 cm was measured and automatically recorded every hour with a data logger (DS1923, Bobang Co. Ltd, Shanghai, China). The average of 24 measurements per day was calculated as the daily mean. Nocturnal warming elevated the average soil temperature by 1.0 °C ($P < 0.05$, Supplementary Data Fig. S1). The air temperature in the glasshouse was monitored with a greenhouse controller (TD400C, Siemens, Germany). The average air temperature during the experiment was 32.58 and 27.72 °C during the day and night, respectively (Supplementary Data Fig. S2). The experiment was conducted from May 2018 to January 2019.

Plant growth metrics

Plant height and basal stem diameter were measured on 17 May 2018 (before the beginning of the experiment), 23 September 2018 (day 117 of the experiment) and 13 January 2019 (day 221 of the experiment) to determine the growth of the two species at the initial, medium-term and final phases of the experiment, respectively. Moreover, four or five fully expanded upper leaves in each well-grown seedling were sampled after sunset on 5 July 2018 (day 38), 25 August 2018 (day 87) and 12 January 2019 (day 220) and before sunrise on 6 July 2018 (day 39), 26 August 2018 (day 88) and 13 January 2019 (day 221). The leaf area was immediately measured with a leaf area meter (LI-3100, Lincoln, NE, USA). The leaves were then dried at 105 and 70 °C for 1 and 48 h, respectively, to a constant mass. After measuring the dry mass, the oven-dried leaves were ground and passed through a 100-mesh screen for NSC (i.e. soluble sugar and starch) analysis.

Gas exchange and chlorophyll fluorescence measurements

One fully expanded leaf at the upper part of each seedling was selected for gas exchange measurements. According to the diurnal pattern of leaf gas exchange (Supplementary Data Figs S3 and S4), night-time measurements (e.g. night-time respiration, R_{night}; night-time leaf conductance, g_{night}) were taken weekly between 2100 and 2400 h, whereas daytime measurements (e.g. net photosynthesis under saturating light, A_{sat}; daytime stomatal conductance, g_{day}) were taken weekly between 0900 and 1200 h on the following day. The temperature of each leaf (T_{leaf}) was measured with a portable photosynthesis system (LI-6800, Lincoln, NE, USA), which was compared with T_{leaf} measured using an infrared gun (H10, Hikmicro Co. Ltd, Hangzhou, China). The difference was insignificant (Supplementary Data Fig. S5). The leaf-to-air vapour pressure deficit (VPD_{leaf}) was recorded during each gas exchange measurement. A calibrated T_{leaf} was used to recalculate VPD_{leaf}. The calibrated VPD_{leaf} did not alter the original findings (Supplementary Data Fig. S6). The environmental conditions for the gas exchange measurements in the LI-6800 were air relative humidity (kept at 60 %), reference CO_2 (maintained at 400 p.p.m.), and flow rate (500 μmol s^{-1}) through the leaf chamber. These environmental parameters were similar for daytime and night-time measurements. Light intensity was maintained at 1000 μmol m^{-2} s^{-1} when measuring daytime gas exchange. The dynamics of the environmental conditions and CO_2 and H_2O exchange rates were simultaneously monitored during the measurements. Data were recorded after environmental conditions had been stabilized. To reduce the bias in the measurements, the standard for judging the stability of the gas exchange data was the slope of respiration or photosynthesis versus time (<0.02 μmol m^{-2} s^{-1} min^{-1}) and the slope of stomatal conductance versus time (<0.0025 mol m^{-2} s^{-1} min^{-1}).

Five or six seedlings were selected from each species to measure the short-term temperature response of R_{night} with LI-6800. Temperature response curves were measured from 22 to 38 °C with an increment of 2 °C by adjusting leaf temperature. The leaf was allowed to equilibrate for 20 min following a temperature change for each measurement. Data were recorded with similar judging standards as regular gas exchange measurements. Q_{10} represents the temperature sensitivity of respiration, indicating the proportional change in respiration per 10 °C rise in temperature. The observations of temperature and R_{night} were used to fit the following equation (Slot *et al.*, 2014):

$$\log_{10}\left(R_{\text{night}}\right) = a + bT_{\text{leaf}}$$

where R_{night} is the night-time respiratory rate, T_{leaf} is the leaf temperature to measure R_{night}, and a and b are coefficients describing the temperature response of R_{night}. The Q_{10} value was calculated as:

$$Q_{10} = 10^{10b}$$

Chlorophyll fluorescence can reflect the functionality of the photosynthetic system (Chen *et al.*, 2010). For example, the maximum quantum efficiency of photosystem II (F_v/F_m) indicates whether the plants are healthy. The F_v/F_m was measured with an LI-6800 before night-time gas exchange measurements on dark-adapted leaves (2000–2100 h).

NSC analysis

NSC was estimated from 100 mg of ground sample. Soluble sugar was extracted with water, and the water-insoluble residual was used to extract starch using perchloric acid. The soluble sugar and starch concentrations were quantified by the anthrone method using a UV-5500 spectrophotometer (Metash, Shanghai, China) at a wavelength of 620 nm. After sunset, the carbohydrate concentration reflects the accumulation of daytime carbohydrates and the available substrate for night-time respiration. Before sunrise, the carbohydrate concentration exhibits a potential sink regulation on photosynthesis on the following day. Thus, the concentration of NSC and its components were analysed before sunrise. The daily consumptions of NSC and its components were calculated as:

$$\text{Carbohydrate consumption} = \text{NSC}_{\text{sunset}} - \text{NSC}_{\text{sunrise}}$$

where $\text{NSC}_{\text{sunset}}$and $\text{NSC}_{\text{sunrise}}$ are the concentration of NSC and its components sampled after sunset and before sunrise, respectively.

In addition to participating in night-time respiration, NSC is translocated from the source (mainly leaves) to sink organs at night (Geiger and Servaites, 1994; Geiger *et al.*, 2000). Consumption of NSC used in carbon metabolism was calculated based on night-time respiration (Tombesi *et al.*, 2018).

Moreover, 1 mol of glucose was assumed to produce 6 mol of CO_2. The respiratory NSC consumption was calculated as follows: The night-time respiratory rate of each seedling (umol $m^{-2}\ s^{-1}$) was multiplied by time (12 h), by the average specific leaf area (SLA) of each seedling [$m^2\ g^{-1}$ dry matter (DM)] and the molar weight of glucose (180.16 g mol $^{-1}$), then dividing 6. . After unit conversion, the respiratory NSC consumption was expressed as mg g^{-1} DM. In addition, NSC consumption used in translocation was estimated as the difference between the overall and respiratory NSC consumption.

Phenological analysis

The A_{sat} time-series was used to fit the logistic function and extract the phenological metrics using the *phenopix* package in *R* 3.6 (Filippa *et al.*, 2016). A widely used logistic model was selected to capture the seasonal dynamics (Zhang *et al.*, 2003). Based on local extremes in the first derivative, the ending date of the growing season was extracted. The start of the growing season was not calculated because the experiment was conducted in May when plants had already begun to grow.

Statistical analysis

In this study, intrinsic water use efficiency (WUE_i) for each measurement was calculated as:

$$\mathrm{WUE}_i = \frac{A_{\mathrm{sat}}}{g_{\mathrm{day}}}$$

where A_{sat} is net photosynthesis at a saturated light intensity and g_{day} is daytime stomatal conductance.

Time-series measurements (i.e. R_{night}, A_{sat}, g_{night}, g_{day}, WUE_i, F_v/F_m, T_{leaf}, VPD_{leaf}, consumption of NSC and its components, the concentration of NSC and its components, plant height, basal stem diameter, leaf area and SLA) were analysed using a repeated-measures mixed-effect model using the *nlme* package in *R* 3.6 (R Development Core Team, 2016). Time and warming were considered fixed factors for the analysis. The subject (seedling here) was a random factor. A one-way analysis of variance was conducted to test the warming effects on A_{sat}, R_{night}, T_{leaf}, VPD_{leaf}, the consumption of NSC and its components, the concentration of NSC and its components, plant height, basal stem diameter, leaf area and SLA for each measurement in *R* 3.6.

To generate a mechanistic understanding of how g_{night} is affected by nocturnal warming, a modified Lohammar's function was used to describe stomatal responses to VPD (Oren *et al.*, 1999):

$$g_s = -m \times \ln D + b$$

where g_s is stomal conductance, *D* is VPD, *m* is stomatal sensitivity and *b* is the reference conductance.

The relative contributions of several factors (R_{night}, ΔNSC, g_{night}, and g_{day}) to A_{sat} changes were quantified. The relative contributions in multiple linear regression models were estimated with a relative importance analysis method using the *relaimpo* package in *R* 3.6 (R Development Core Team, 2016) and based on variance decomposition (Grömping, 2007). The metric known as the Lindeman–Merenda–Gold method in the *relaimpo* package was used to assess the relative importance of these factors in multiple linear regression models (Grömping, 2007).

RESULTS

Effects of nocturnal warming on temperature and VPD

Warming significantly increased night-time T_{leaf} on most of the measurement dates ($P < 0.05$) for the two species. Overall, nocturnal warming significantly increased T_{leaf} by 2.50 °C ($P < 0.001$) in *S. superba* ($P < 0.001$) and by 2.24 °C ($P < 0.001$) in *C. sclerophylla* ($P < 0.001$). Daytime T_{leaf} was unchanged in the two species during the experimental period (Supplementary Data Fig. S7). Nocturnal warming significantly elevated VPD_{leaf} at night on most measurement dates ($P < 0.05$). Overall, night-time VPD_{leaf} increased by 0.28 kPa in both species (both $P < 0.001$), whereas daytime VPD_{leaf} was unaffected by nocturnal warming (Supplementary Data Fig. S8).

Effects of nocturnal warming on plant growth

No difference in plant height or basal stem diameter was noted between temperature treatments ($P > 0.05$) at the beginning of the experiment. The warming treatment did not alter the plant height or basal stem diameter of either species at the medium (day 117) or final (day 221) experimental phase ($P > 0.05$, Supplementary Data Fig. S9). The leaf area was the highest at the second measurement (25 August). Nocturnal warming did not affect the leaf area or SLA in either species during the experiment ($P > 0.05$, Supplementary Data Fig. S10). The end of the growing season was estimated as day 150 of the experiment for both species. However, nocturnal warming did not affect the ending date of the growing season (Supplementary Data Fig. S11).

Leaf gas exchange and controlling factors

For *S. superba*, nocturnal warming stimulated R_{night} on days 1, 20, 109 and 125 and A_{sat} on day 1, whereas it inhibited A_{sat} on days 144, 165, 193, 207 and 235 (Fig. 2). Overall, R_{night} and A_{sat} significantly increased and decreased by 20.3 and 12.6 %, respectively (Fig. 2; Table 1). For *C. sclerophylla*, nocturnal warming stimulated R_{night} on day 193 but inhibited A_{sat} on days 109, 138, 151, 165, 179 and 235. Overall, R_{night} was unchanged and A_{sat} was reduced by 10.1 % (Fig. 2; Table 1). A significant difference in the warming effect on R_{night} was observed between the two species ($P < 0.05$; Fig. 2).

A regression analysis revealed a non-linear relationship between the warming effects on R_{night} and warming duration in *S. superba* (Fig. 3). The minimum warming effect occurred when the duration was between 100 and 150 d. The warming effect on A_{sat} decreased linearly with experimental duration (Fig. 3A). Taking these results together, R_{night} and A_{sat} were stimulated within the first 50 d of the experiment. Subsequently, the warming effect on R_{night} began to decrease, and the effect on A_{sat}

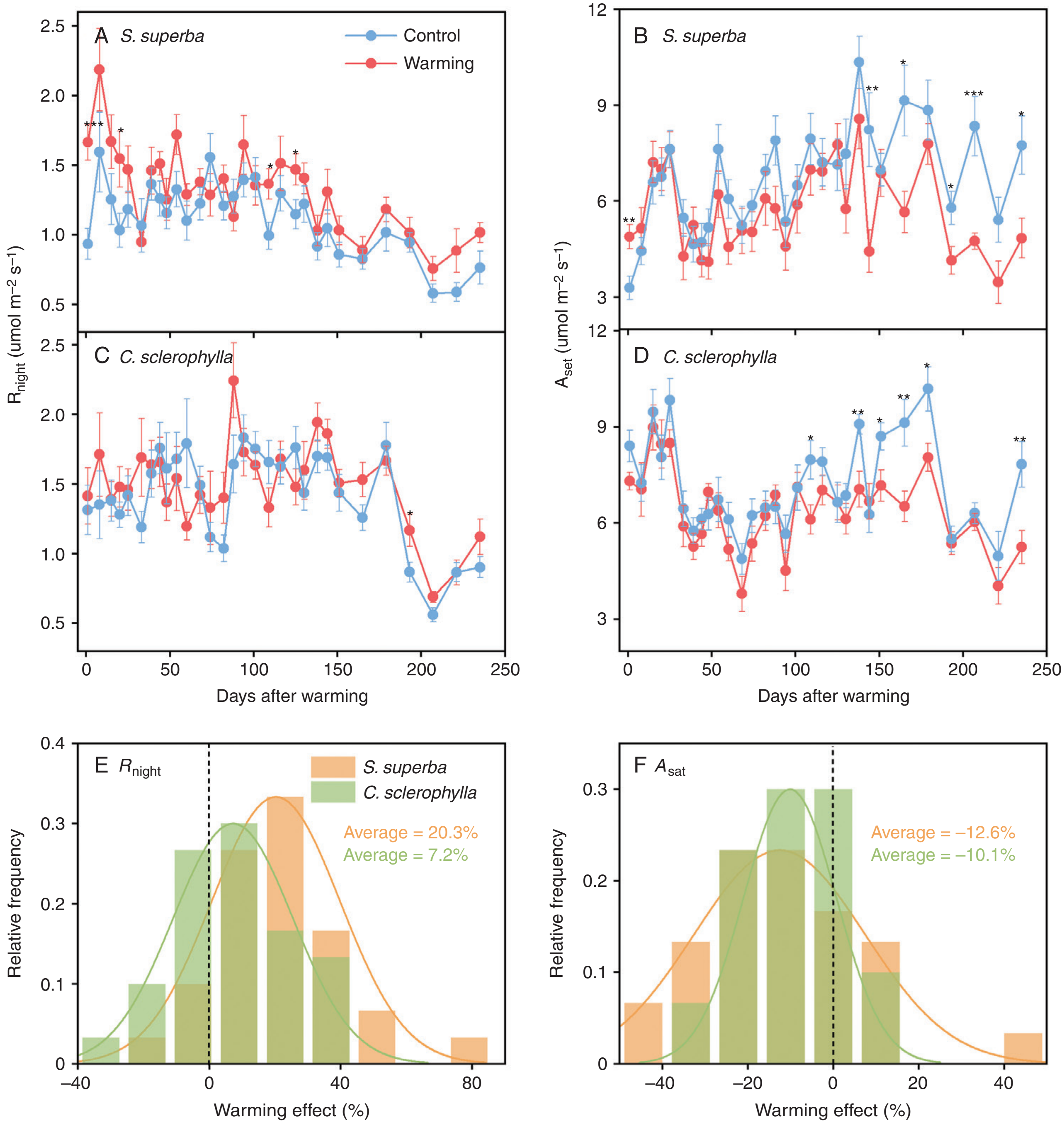

FIG. 2. Dynamics of night-time respiration (R_{night}) and photosynthesis (A_{sat}) in two species. Time series of R_{night} and A_{sat} in *S. superba* (A, B) and *C. sclerophylla* (C, D). Values are mean ± s.e. (n = 12–18). The solid curves are Gaussian distributions fitted to the warming effect on R_{night} (E) and A_{sat} (F) in the two species ($P < 0.01$). The warming effect was calculated as [(warming − control)/control]. The asterisks in A–D denote significant difference of treatment effects: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

turned out to be negative. Around day 125 of the experiment, R_{night} was stimulated again, but A_{sat} was reduced persistently by nocturnal warming. For *C. sclerophylla*, the warming effects on R_{night} and A_{sat} were not affected by the experimental duration (Fig. 3B).

Nocturnal warming significantly reduced the g_{night} and g_{day} of *S. superba* by 31.6 and 25.3 %, respectively (Table 1; Fig. 4A). For *C. sclerophylla*, nocturnal warming significantly reduced g_{night} and g_{day} by 13.7 and 16.0 %, respectively (Table 1; Fig. 4B). Moreover, g_{night} exhibited a significant negative relationship with VPD$_{leaf}$ under nocturnal warming conditions in both species (Fig. 5). A positive linear relationship between warming effects on g_{night} (Δg_{night}) and g_{day} (Δg_{day}) was observed in both species (Supplementary Data Fig. S12). However, no clear relationship was noted between the changes in g_{night} (Δg_{night}) and night-time respiration (ΔR_{night}; Supplementary Data Fig. S13).

TABLE 1. *Results* (P*-values) of repeated measures linear mixed-effects models for the effects of nocturnal warming (NW), time (T) and their interactions on time-series measurements [i.e. photosynthesis (*A_{sat}*), night-time respiration (*R_{night}*), night-time leaf conductance (*g_{night}*), daytime stomatal conductance (*g_{day}*), night-time* VPD_{leaf}*, and night-time leaf temperature (*T_{leaf}*)]*

Treatment	A_{sat}	R_{night}	g_{night}	g_{day}	VPD_{leaf}	T_{leaf}
S. superba						
NW	<0.050	<0.001	<0.001	<0.050	<0.001	<0.001
T	<0.001	<0.001	<0.001	<0.010	<0.001	<0.001
NW × T	<0.001	0.181	0.122	<0.050	0.165	<0.001
C. sclerophylla						
NW	<0.001	0.162	<0.010	<0.050	<0.001	<0.001
T	<0.010	<0.001	<0.001	<0.050	<0.001	<0.001
NW × T	0.082	0.777	<0.001	0.955	0.070	<0.001

A_{sat} and g_{day} both decreased, whereas WUE_i was unaffected by nocturnal warming (Supplementary Data Fig. S14). The WUE_i in *S. superba* was significantly higher compared with that in *C. sclerophylla* ($P < 0.001$). The relative importance analysis suggested that g_{day} contributed >50 % of A_{sat} for the two species under ambient temperature. In addition, g_{night} was the most important of all factors in explaining A_{sat} under nocturnal warming (Fig. 6).

Consumption of leaf NSC

The concentration and consumption of NSC and its components were analysed (Supplementary Data Figs S15 and 16; Supplementary Data Table S1). Starch and NSC concentrations for *S. superba* were significantly decreased by nocturnal warming on day 39 ($P < 0.05$). However, lower NSC concentration at elevated temperature for *C. sclerophylla* was observed compared with ambient temperature on day 221 ($P < 0.05$). Consumption of NSC was significantly affected by nocturnal warming on day 221. For example, soluble sugar and NSC consumption were significantly increased by nocturnal warming in *S. superba* ($P < 0.05$), and starch consumption was significantly increased by warming in *C. sclerophylla* ($P < 0.01$).

Consumption of NSC at night was separated into consumption from respiration and translocation. NSC was primarily used in night-time respiration when leaf temperature was >28 °C in the experiment of the current study. NSC was translocated when leaf temperature was downregulated. The increased NSC translocation was observed when leaf temperature was increased to 25 °C by nocturnal warming (Fig. 7).

DISCUSSION

Species-specific occurrence of photosynthetic overcompensation under nocturnal warming

A species-specific occurrence of POE under nocturnal warming was demonstrated in this study. For the two species, a transient POE was observed in *S. superba*, but not in *C. sclerophylla*.

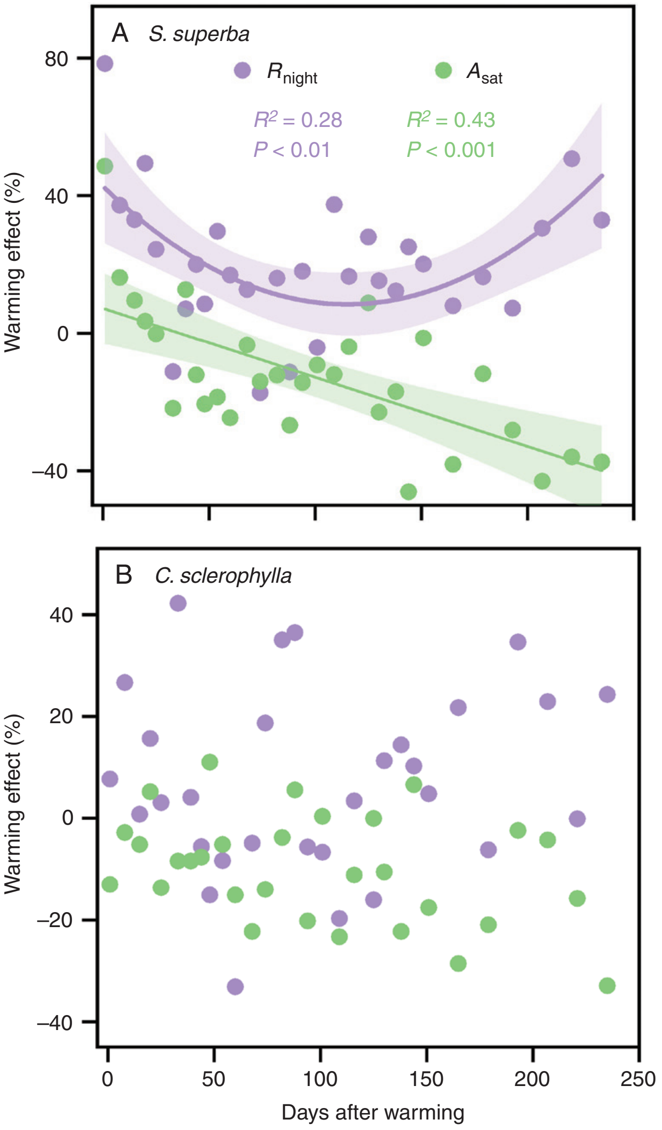

FIG. 3. Relationship between warming effect on carbon exchange rates and experimental duration in *S. superba* (A) and *C. sclerophylla* (B). The purple and green symbols indicate night-time respiration and net photosynthesis, respectively. The warming effect was calculated as [(warming − control)/control].

Such a species-specific occurrence of POE resulted from the different response of R_{night} to nocturnal warming in the two species (Fig. 1). For example, the temperature sensitivity of R_{night} was higher in *S. superba* ($Q_{10} = 2.17$) compared with *C. sclerophylla* ($Q_{10} = 1.72$; Supplementary Data Fig. S17). This finding suggests that the POE under nocturnal warming is more likely to occur in thermosensitive plants. For example, *Deschampsia antarctica* rather than *Colobanthus quitensis* upregulates photosynthesis under nocturnal warming because the former plant is more thermosensitive (Sanhueza *et al.*, 2019). On a global scale, the temperature sensitivity of plant respiration increases from tropical to arctic regions (Heskel *et al.*, 2016). Thus, one implication of this finding is the probability that the occurrence of POE may be lower in subtropical compared with temperate and boreal regions (Turnbull *et al.*, 2004; Wan *et al.*, 2009; Sanhueza *et al.*, 2019).

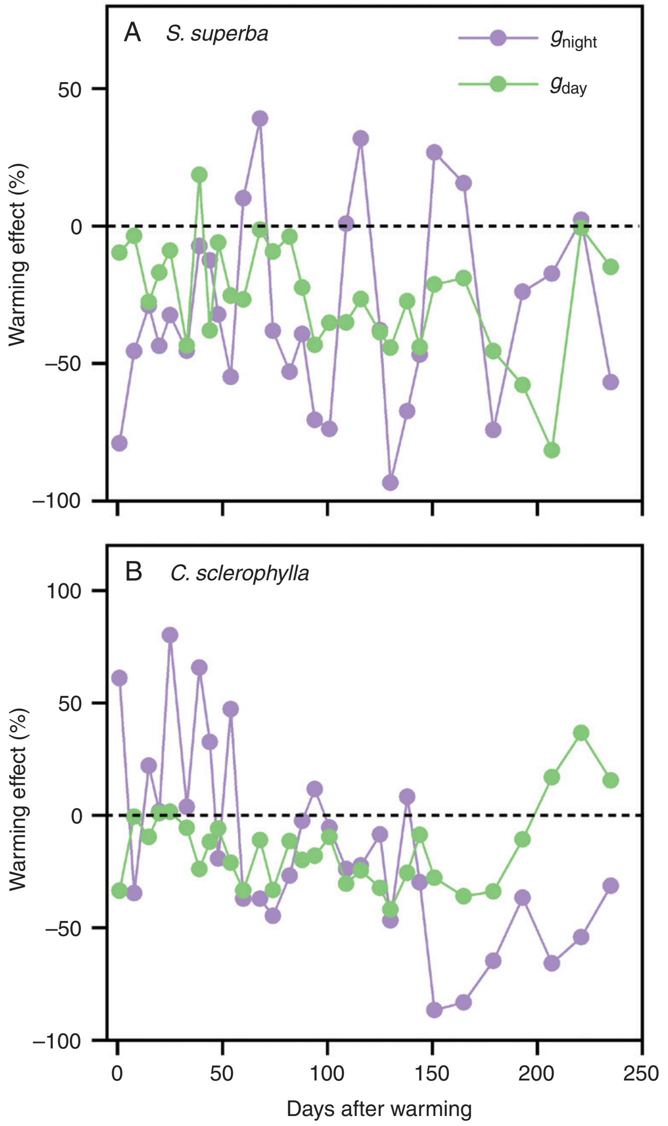

FIG. 4. Temporal dynamics of the warming effect on night-time leaf conductance (g_{night}) and daytime stomatal conductance (g_{day}) in *S. superba* (A) and *C. sclerophylla* (B). The warming effect was calculated as [(warming − control)/control].

Role of NSC in POE occurrence under nocturnal warming

The occurrence of POE under nocturnal warming conditions may be reflected by the warming response of the NSC status before sunrise and NSC consumption at night (Turnbull *et al.*, 2004). The concentration of NSC and its response to nocturnal warming was measured on days 39, 88 and 221 following treatment (Supplementary Data Figs S15 and S16). On day 39, nocturnal warming reduced leaf NSC concentration in *S. superba* before sunrise (Supplementary Data Fig. S15) but did not affect A_{sat} (Fig. 2B). For *C. sclerophylla*, nocturnal warming reduced NSC concentration before sunrise, but not A_{sat} on the following morning on day 221. These results suggest that the reduction of NSC is not the primary cause of POE under nocturnal warming conditions in this study. However, this result is inconsistent with a previous experiment in a temperate steppe, which reported unchanged NSC concentrations before sunrise with enhanced A_{sat} under nocturnal warming (Wan *et al.*, 2009).

Nocturnal warming was found to increase the night-time consumption of NSC and its components on a cold night (Supplementary Data Fig. S16). The consumption of NSC results from the enhanced R_{night} and translocation in the leaves to other plant tissues (Bunce, 2007). Further analysis revealed that NSC consumption resulting from translocation may be significant at low ambient temperatures (Fig. 7). The temperature dependence of translocation, affecting night-time NSC consumption, has also been reported in other plant species, e.g. *Vitis vinifera* (Tombesi *et al.*, 2018). On a global scale, climate warming can stimulate greater plant NSC consumption in boreal and temperate compared with subtropical biomes (Martínez-Vilalta *et al.*, 2016; Du *et al.*, 2020; Fermaniuk *et al.*, 2021). Thus, NSC consumption may play a more important role in driving POE under nocturnal warming in boreal and temperate ecosystems (Turnbull *et al.*, 2004; Wan *et al.*, 2009; Sanhueza *et al.*, 2019) compared with subtropical forests.

Stomatal limitation on POE occurrence under nocturnal warming

A reduction in plant photosynthesis was observed in both species under nocturnal warming (Fig. 2). The primary cause was the lower g_{night} and g_{day} on warmer nights (Fig. 4). The important role of stomatal limitation is supported by the positive linear relationship between warming effects on g_{night} (Δg_{night}) and g_{day} (Δg_{day}) in the two species (Supplementary Data Fig. S12). Water loss at night is typically 5–30 % of daytime loss (Caird *et al.*, 2007; Howard *et al.*, 2009). Plants close night-time stomata and reduce g_{night} in response to a higher VPD_{leaf} (Caird *et al.*, 2007). Plants use water with a similar strategy at night as in the daytime (Christman *et al.*, 2008; Schoppach *et al.*, 2014), so the increased water loss at night downregulates predawn leaf water potential (Sadok and Jagadish, 2020; Lu *et al.*, 2022). In the experiment of the current study, *C. sclerophylla* is a rather anisohydric species characterized by profligate water use, whereas *S. superba*, with a more isohydric behaviour, regulates stomata more tightly in response to water stress (Lu *et al.*, 2022). Thus, WUE_i in *S. superba* was higher compared with that in *C. sclerophylla* ($P < 0.001$; Supplementary Data Fig. S14).

Nocturnal warming increased R_{night} but decreased g_{night} in *S. superba* in the present study (Figs 2–4), suggesting that the change in R_{night} is unrelated to g_{night} (Supplementary Data Fig. S13). The g_{night} of plants under the warming treatment was 0.02–0.04 mol m^{-2} s^{-1}, which may not be low enough to trigger the inhibitive effect on respiration (Resco de Dios *et al.*, 2019). However, the stomatal responses to increasing evaporative demands in the air and leaves are an essential contributor to plant productivity and growth (Ocheltree *et al.*, 2014; Sanginés de Cárcer *et al.*, 2018). The regulation of photosynthesis by *gnight* occurs through multiple processes, e.g. nutrient supply, hydraulic redistribution, water use and carbon gain (Caird *et al.*, 2007). Although g_{night} was inhibited because of high VPD_{leaf} in the current study (Fig. 5), g_{night} may be unchanged or increased with higher VPD (Barbour *et al.*, 2005; Dawson *et al.*, 2007; Rogiers and Clarke, 2013). The different stomatal responses may be related to plant functional type (Hoshika *et al.*, 2018), circadian rhythm (Chowdhury *et al.*, 2022), genetic regulation (Resco de Dios *et al.*, 2016) or phylogenetic and biogeographic controls (Yu *et al.*, 2019). The

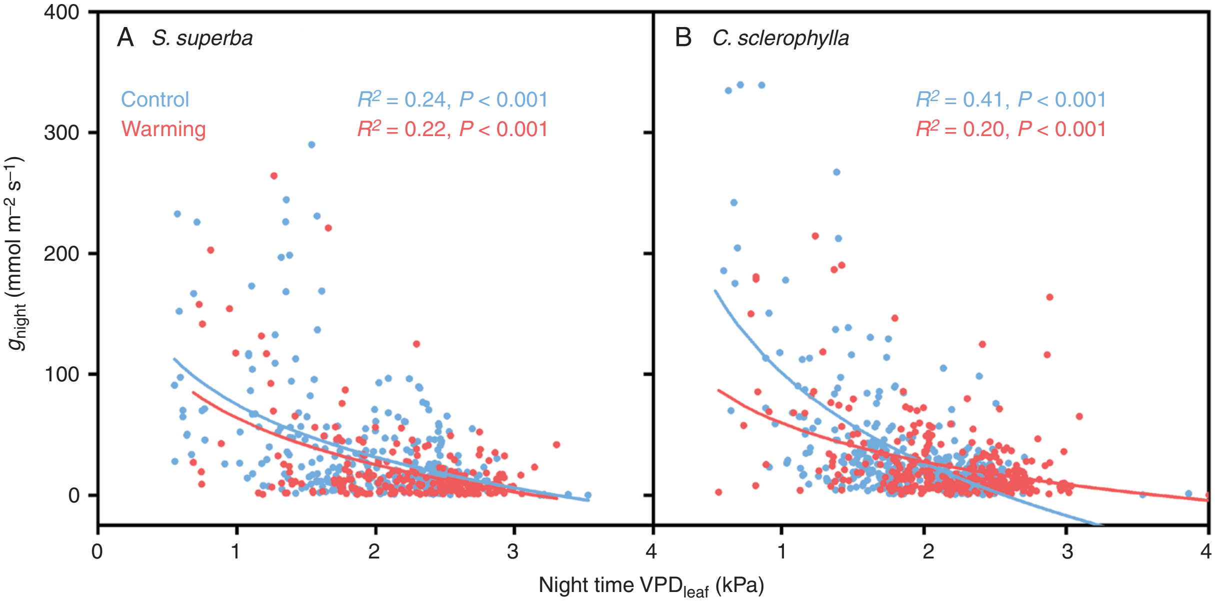

FIG. 5. Relationships between night-time leaf conductance (g_{night}) and night-time VPD$_{leaf}$ in *S. superba* (A) and *C. sclerophylla* (B).

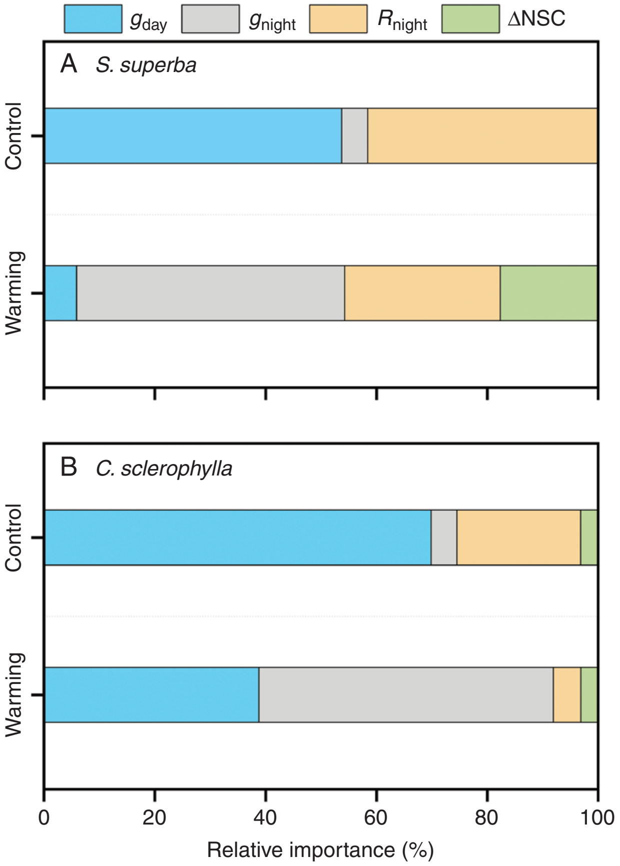

FIG. 6. Relative importance of different factors to light-saturated photosynthesis (A_{sat}) based on multiple regression in *S. superba* (A) and *C. sclerophylla* (B). Factors include night-time respiration (R_{night}), NSC consumption (ΔNSC), night-time leaf conductance (g_{night}) and daytime stomatal conductance (g_{day}).

findings of the current study warrant further studies to explore the mechanisms of stomatal regulation of POE occurrence in tree species.

Other traits influencing photosynthesis under nocturnal warming conditions

Several plant traits have been reported to affect leaf photosynthesis under nocturnal warming aside from the day–night linkage between carbon and water processes. Leaf fluorescence parameters, e.g. maximal photochemical efficiency of PSII (i.e. F_v/F_m), mediate the photosynthetic response to temperature changes (Prasad *et al.*, 2008; Djanaguiraman *et al.*, 2013). The damage to PSII typically occurs in herbs or from extreme heat stress (Satoh *et al.*, 1998; Djanaguiraman *et al.*, 2013; Jing *et al.*, 2016). However, F_v/F_m was unchanged in the two species in the present study (Supplementary Data Fig. S18). High night-time T_{leaf} exerts a positive influence on SLA, leaf area ratio and the number of leaves (Cheesman and Winter, 2013; Jing *et al.*, 2016). Capturing light and increasing photosynthesis is beneficial for plants (Jing *et al.*, 2016; Tang *et al.*, 2016). However, SLA was unchanged in the current study and had no impact on photosynthesis (Supplementary Data Fig. S10).

Conclusions

The current study determined whether POE under nocturnal warming occurs in the seedlings of subtropical evergreen trees. POE in *S. superba*, which was transient because of respiratory acclimation and stomatal limitation, was detected. The stomatal limitation under nocturnal warming induces a persistent reduction in photosynthesis. This finding highlights the important role of water processes in regulating day–night carbon cycling under non-uniform diurnal climate warming. However, the attention given to night-time ecology is limited (Xia *et al.*, 2014; Gaston, 2019). The lack of a persistent POE occurrence in the experiment of the current study supports a large-scale determination of accelerated respiratory carbon loss in tropical regions under nocturnal warming (Anderegg *et al.*, 2015). Thus, more studies to explore the differential response and connections of

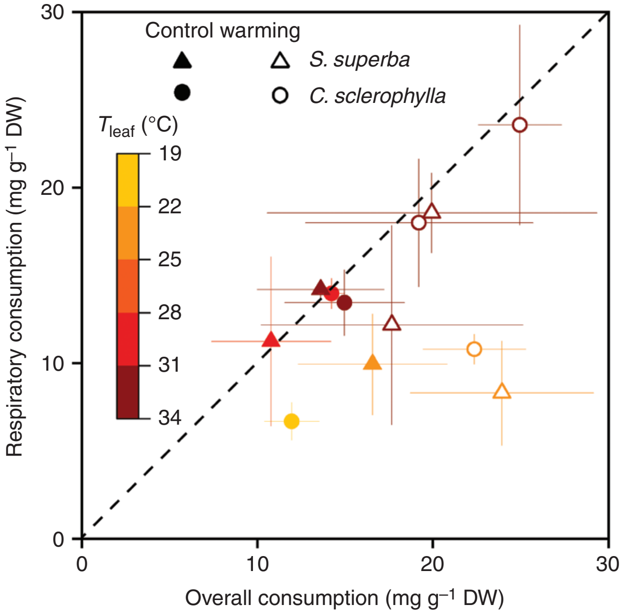

FIG. 7. Overall NSC consumption and respiratory NSC consumption in the two species. The colour of symbols indicates leaf temperature (indicated in T_{leaf} scale bar). Plants were grown under ambient temperature or nocturnal warming (symbols indicated in the key). Each symbol represents the mean ± s.e. of $n = 3–4$.

plant ecophysiological processes on the diurnal scale during climate warming are recommended.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Figure S1: daily soil temperature at 5 cm depth in control and warming groups. Figure S2: temporal dynamics of air temperature during daytime and night in the glasshouse. Figure S3: diurnal patterns of leaf gas exchange rates measured at 3-h intervals in *S. superba* and *C. sclerophylla.* Figure S4: temporal dynamics of stomatal conductance in *S. superba* and *C. sclerophylla*. Figure S5: comparison of leaf temperature measured with an LI-6800 and an infrared gun. Figure S6: relationships between night-time stomatal conductance and night-time VPD_{leaf} measured with an LI-6800 or recalculated with calibrated T_{leaf}. Figure S7: night-time and daytime T_{leaf} for *S. superba* and *C. sclerophylla*. Figure S8: night-time and daytime VPD_{leaf} for *S. superba* and *C. sclerophylla*. Figure S9: plant height and stem diameter of two species in the initial, medium-term and final experimental phases. Figure S10: leaf area and specific leaf area on days 39, 88 and 221. Figure S11: average timing of the end of the growing season in the two species. Figure S12: relationships between change in night-time stomatal conductance and change in daytime stomatal conductance in *S. superba* and *C. sclerophylla*. Figure S13: relationships between change in night-time stomatal conductance and change in night-time respiration in *S. superba* and *C. sclerophylla*. Figure S14: intrinsic water use efficiency in *S. superba* and *C. sclerophylla*. Figure S15: mean concentration of NSC and its components before sunrise in *S. superba* and *C. sclerophylla* on three measurement dates. Figure S16: mean consumption of NSC and its components in *S. superba* and *C. sclerophylla* on three measurement dates. Figure S17: temperature response of night-time respiration in *S. superba* and *C. sclerophylla*. Figure S18: relationships between change in night-time stomatal conductance and change in night-time respiration in *S. superba* and *C. sclerophylla*. Table S1: results of repeated-measures linear mixed-effects models for the effects of nocturnal warming, time, and their interactions on consumptions of NSC and its components.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

AUTHOR CONTRIBUTIONS

J.X. designed the study. Y.D., R.L. and H.S. contributed to experimental measurements. Y.D. conducted the analysis and wrote the manuscript. Y.D., E.C., L.Y. and J.X. contributed to the revisions.

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