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Tropical rainforest species have larger increases in temperature optima with warming than warm-temperate rainforest trees

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Summary

- While trees can acclimate to warming, there is concern that tropical rainforest species may be less able to acclimate because they have adapted to a relatively stable thermal environment. Here we tested whether the physiological adjustments to warming differed among Australian tropical, subtropical and warm-temperate rainforest trees.
- Photosynthesis and respiration temperature responses were quantified in six Australian rainforest seedlings of tropical, subtropical and warm-temperate climates grown across four growth temperatures in a glasshouse. Temperature-response models were fitted to identify mechanisms underpinning the response to warming.
- Tropical and subtropical species had higher temperature optima for photosynthesis (T_{optA}) than temperate species. There was acclimation of T_{optA} to warmer growth temperatures. The rate of acclimation (0.35–0.78°C °C^{-1}) was higher in tropical and subtropical than in warm-temperate trees and attributed to differences in underlying biochemical parameters, particularly increased temperature optima of V_{cmax25} and J_{max25}. The temperature sensitivity of respiration (Q_{10}) was 24% lower in tropical and subtropical compared with warm-temperate species.
- Overall, tropical and subtropical species had a similar capacity to acclimate to changes in growth temperature as warm-temperate species, despite being grown at higher temperatures. Quantifying the physiological acclimation in rainforests can improve accuracy of future climate predictions and assess their potential vulnerability to warming.

Introduction

The effect of climate warming on rainforest trees is uncertain and under debate (e.g. Huntingford *et al.*, 2013; Mercado *et al.*, 2018; Smith *et al.*, 2020). Some modelling studies have suggested that tropical Amazonian forests are seriously threatened by climate warming (Malhi *et al.*, 2008; Cook *et al.*, 2012; Fu *et al.*, 2013; Bastin *et al.*, 2019) and project a large reduction in vegetation biomass by 2100 (Cox *et al.*, 2004). Moreover, drought stress and associated tree mortality are also predicted to increase in tropical rainforests (Rowland *et al.*, 2015) leading to reduced carbon stocks (Brando *et al.*, 2019). Such an extensive loss of tropical rainforest would have major feedbacks to the global climate (Lewis *et al.*, 2009; Fu *et al.*, 2013) and pronounced effects on the global carbon budget (Malhi, 2012). However, these predictions depend in part on the representation of physiological responses to warming, which is one of the major uncertainties in current global vegetation models (Lombardozzi *et al.*, 2015; Huntingford *et al.*, 2017). Many models do not account for the possibility that tree species can acclimate to rising temperatures. Several studies have highlighted the need to incorporate thermal acclimation of photosynthetic and respiratory processes to improve the accuracy of future climate projections (Atkin *et al.*, 2008; Smith & Dukes, 2013; Mercado *et al.*, 2018). The potential adjustment of the photosynthetic capacity in tropical species could reduce their predicted vulnerability to warming (e.g. Mercado *et al.*, 2018), so it is important to quantify how much rainforest species can adjust to warming.

Generally, plants can maintain or increase carbon gain via increased photosynthetic capacity (Kattge & Knorr, 2007; Sage & Kubien, 2007) and/or an increase in the temperature optimum of photosynthesis (T_{optA}) (Cowling & Sage, 1998; Gunderson *et al.*, 2010; Yamori *et al.*, 2014; Scafaro *et al.*, 2017; Crous *et al.*, 2018) in response to warmer growth temperatures. Given that tropical species are adapted to stable climatic conditions with high growth temperatures within a narrow temperature range (Janzen, 1967; Wright *et al.*, 2009; Perez *et al.*, 2016), we might expect that their physiological capacity to adjust to warming would be more limited compared with temperate species. Previous studies have found that tropical species were more susceptible to growth declines at increased temperatures, whereas temperate species had enhanced growth with warming (Way & Oren, 2010; Drake *et al.*, 2015), suggesting that tropical species may have constrained capacity to adjust to climate warming (Perez *et al.*, 2016; Crous *et al.*, 2018).

The limited studies investigating thermal acclimation of photosynthesis in rainforest species have generally reported reduced, not increased, photosynthetic rates with warming (Cunningham & Read, 2003; Slot & Winter, 2016; Scafaro *et al.*, 2017; Dusenge *et al.*, 2021). Slot & Winter (2017) found that tropical seedlings can acclimate to moderate warming via an increase in T_{optA}, but photosynthesis declined under a high level of warming.

T_{optA} may be related to species' climate of origin (Slatyer, 1978; Robakowski *et al.*, 2012), but other studies reported a lack of T_{optA} response to a species' climate of origin (Gunderson *et al.*, 2000; Kumarathunge *et al.*, 2019; Dusenge *et al.*, 2021). A change in growth temperatures was found to be the most common driver of T_{optA} (Kumarathunge *et al.*, 2019). Our study compared the response of T_{optA} using a range of growth temperatures rather than just two levels to understand how T_{optA} adjusted across temperatures, whether there were limits to this adjustment (range of warming up to 10°C) and how rainforest species from different climates adjusted their T_{optA} across this temperature range. We also aimed to identify the mechanisms underpinning the physiological responses of temperate and tropical species to warming.

Several underlying physiological processes contribute to the temperature response of net photosynthesis (A_{net}), including stomatal conductance (Lin *et al.*, 2012), biochemical processes, particularly changes in the carboxylation of ribulose-1,5-bisphosphate (RuBP) activity (V_{cmax}) and regeneration of RuBP (i.e. the maximum rate of electron transport, J_{max}) (Farquhar *et al.*, 1980), each of which have their own temperature dependency. The direct dependence of g_s on temperature has not been consistent across studies (Sage & Sharkey, 1987; von Caemmerer & Evans, 1991), but low g_s in response to increased vapour pressure deficit (VPD) can reduce the temperature optimum of photosynthesis (Lin *et al.*, 2012; Slot & Winter, 2016). In addition, changes in the biochemical component processes of the photosynthesis temperature response may be involved in T_{optA} adjustments. Some studies have found increased T_{optA} to be associated with an increase in the activation energy of V_{cmax}, E_{aV}, together with a decrease in the $J_{max} : V_{cmax}$ ratio with increasing growth temperatures (Hikosaka *et al.*, 2006). Other studies have found that the adjustment of T_{optA} was associated with a decline in V_{cmax25} or J_{max25} (Medlyn *et al.*, 2002b; Yamori *et al.*, 2005; Sage & Kubien, 2007; Scafaro *et al.*, 2017). Identifying which of these parameters changed across several growth temperatures will give us better insights into the principal processes responsible for photosynthetic temperature acclimation and whether any relationships underlie these processes.

Similar to photosynthesis, leaf respiration responds to short- and long-term changes in growth temperatures. Leaf respiration typically shows an exponential increase with short-term changes in temperature (Atkin & Tjoelker, 2003; Heskel *et al.*, 2016), but can adjust rapidly to warmer temperatures via thermal acclimation in a manner that promotes homeostasis in metabolic function (Lee *et al.*, 2005; Crous *et al.*, 2011; Atkin *et al.*, 2015; Aspinwall *et al.*, 2016) via reduced rates of respiration at a standard temperature or via reduced temperature sensitivity of respiration (Atkin & Tjoelker, 2003). However, at higher growth temperatures, temperature acclimation of respiration may be constrained and not achieve homeostasis (Drake *et al.*, 2017). A meta-analysis including 103 species from different biomes found a general pattern of acclimation of respiration to warming, via reduced respiration rates at a set temperature (Slot & Kitajima, 2015). In addition, respiration rates at a set temperature can vary geographically, with higher rates of dark respiration at a standard temperature (25°C) in temperate species compared with tropical species (Atkin *et al.*, 2015). Based on these reports, we would expect that respiration would be reduced with long-term warming in all species to minimise carbon loss.

The magnitude of physiological adjustments in rainforest tree species and whether these physiological adjustments differed in tropical vs temperate tree species are currently not well known. This study aimed to determine the key components responsible for the photosynthesis and respiration temperature responses in Australian woody rainforest species from different climates. We also tested whether there was a difference between tropical and temperate species in their capacity to acclimate photosynthesis and leaf respiration to a range of warmer growth temperatures. As growth temperature is an important driver of thermal acclimation (Kumarathunge *et al.*, 2019), using a range of growth temperatures in our experimental design enabled us to develop relationships across growth temperatures, while comparing how rainforest species from different climate zones differed across this temperature gradient. We addressed the following hypotheses: (1) the temperature optima of photosynthesis (T_{optA}), V_{cmax} (T_{optV}) and J_{max} (T_{optJ}) will increase with increasing growth temperatures; (2) physiological processes at a common temperature including net photosynthesis at 25°C (A_{net25}), V_{cmax25} and J_{max25} will be downregulated with increasing T_{growth}; (3) respiration rate at 25°C (R_{25}) will be reduced with warming; and (4) adjustments in T_{optA}, A_{opt} and R_{25} will be larger in temperate than tropical species. Using growth temperatures experienced within the native range, we aimed to imitate some of the growth conditions in the field. However, disentangling these detailed mechanisms would be hard to realise in the field. Our study in a controlled environment across similar soils focuses on the mechanistic differences in acclimation responses of rainforest species to warming across a large geographical scale.

Materials and Methods

Plant materials and experimental design

We grew seedlings of six Australian rainforest tree species at a range of growth temperatures. All species' distributions were located along the east-coast margin of Australia between 12 and 40°S (Table 1). We selected common rainforest species with minimally overlapping distribution ranges. The species included two tropical species (*Atractocarpus fitzalanii* (F. Muell.) Puttock and *Xanthostemon chrysanthus* (F. Muell.) Benth.), two subtropical species (*Backhousia citriodora* F. Muell. and *Flindersia australis*

Table 1 Six rainforest species from three climates including their distributional range and the corresponding average summer temperatures at the southernmost and northernmost latitude occurrence based on WorldClim climatology data (WorldClim1.4; Hijmans *et al*., 2005).

Rainforest group	Species	Family	Latitude range of native distribution	Average summer temperature (°C)	Coordinates of seed collection
Warm-temperate	*Cryptocarya laevigata*	Lauraceae	24.6–31°S	22.9–25.0°C	28°08′56″S, 153°25′05″E (Tallabugera, QLD)
	Tristaniopsis laurina	Myrtaceae	24.6–40°S	17.4–25.4°C	28°31′16″S, 153°32′28″E (Big Scrub, NSW)
Subtropical	*Backhousia citriodora*	Myrtaceae	17.1–33.9°S	22.0–23.4°C	27°28′13″S, 153°01′28″E (Brisbane, QLD)
	Flindersia australis	Rutaceae	17.2–35.2°S	19.7–23.4°C	28°23′16″S, 153°33′29″E (Pottsville, NSW)
Tropical	*Atractocarpus fitzalanii*	Rubiaceae	14.4–27.6°S	24.8–28.3°C	17°15′58″S, 145°29′09″E (Atherthon, QLD)
	Xanthostemon chrysanthus	Myrtaceae	12.4–19.2°S	27.1–27.2°C	17°07′40″S, 145°25′40″E (Walkamin, QLD)

Collection coordinates (latitude, longitude) are included in the last column.

R. Brown), and two warm-temperate species (*Cryptocarya laevigata* Blume and *Tristaniopsis laurina* Sm.). All plant species are evergreen angiosperms with similar leaf traits (i.e. size, thickness) and none is classified as a pioneer species. Seedlings of the six species were obtained from two commercial nurseries (Burringbar Rainforest nursery, NSW and Yuruga nursery, QLD) with seeds of each species locally obtained from one seed source (Table 1). While rainforest species have a similar natural history, selecting species with similar traits from different climates enabled us to test whether acclimation capacity would differ depending on climate origin while also reflecting a temperature range that they currently experience. Species distributions were obtained from Atlas of Living Australia, and WorldClim climatology data (WorldClim 1.4; Hijmans *et al*., 2005) were used to calculate the average summer temperature (December–February) of the southernmost and northernmost latitude of each species' native occurrence (Table 1).

To assess the effects of warming, seedlings of each species were grown under four growth temperatures. Six mean diel temperature treatments ranging from 17 to 34.5°C in 3.5°C increments were implemented in six adjacent, natural sunlit glasshouse bays. All growth temperature regimes were implemented with a diurnal range of 10°C. Therefore, temperatures during the day were warmer than the average diel temperatures reported above, with the target daily maximum temperatures ranging from 23 to 40°C in the coolest to hottest bays, respectively. The temperature treatments for each rainforest group included three temperature regimes that spanned the average summer temperatures in their native range and one temperature regime that was *c*. 3.5°C warmer than average summer temperatures currently experienced. We included a growth temperature of 24°C for tropical species (cooler than their average summer temperature) to obtain four growth temperatures for all species. Warm-temperate species were grown under mean diel temperatures of 17, 20.5, 24 or 27.5°C, while subtropical and tropical species were grown at 24, 27.5, 31 or 34.5°C. Relative humidity in the respective glasshouse bays (17–34.5°C) were on average 81%, 84%, 88%, 72%, 76% and 72%, respectively, over 24 h (Carel Humidisk 65 humidifier, Sydney, Australia).

The experiment ran at Western Sydney University (Richmond, NSW, Australia) during the Austral summer of 2017–2018 (November–February). Seedlings were transplanted individually into 7 l pots of loamy sand soil. Ten seedlings of each of the six species were randomly assigned to each of the four temperature treatments on 6 November 2017. While some species grew faster than others, all seedlings within a given species started with similar heights. Seedling height at the beginning of the experiment ranged from 10 to 32 cm across species. After transplanting and before measurements, plants were allowed to establish for at least 4 wk to develop new leaves under the experimental conditions. After the establishment period, most species developed two to four new leaves every 2 wk with the exception of *Backhousia citriodora* and *Tristaniopsis laurina* which developed more than five leaves per fortnight. Seedlings were generally growing well following an exponential growth curve. Throughout the experiment, plants were kept well watered with an automated irrigation system and were fertilised weekly with a commercial fertiliser (50 ml at 2 g l^{-1}; 25% N, 5% P, 8.8% K, 0.004% Zn, 0.005% Cu, 0.001% Mo, 0.01% Mn, 0.18% Fe, 0.005% B; Thrive soluble, Yates, Padstow, NSW, Australia).

Leaf photosynthesis and A_{net}–C_i curves

Three plant replicates per species were randomly selected within each temperature treatment (6 species × 4 growth temperatures × 3 replicates = 72 plants) for leaf physiological measurements. Gas-exchange measurements were conducted using several portable open gas-exchange systems using the 2 × 3 cm leaf chamber with red and blue lamps (LI-6400XT; Li-Cor, Lincoln, NE, USA). One newly developed, fully expanded leaf was marked and measured on each plant replicate across 1–3 d to accommodate all leaf temperatures but avoid measurement 'fatigue'. Leaves were measured at one point in time for light-saturated photosynthesis (A_{net}) between 08:30 h and 16:00 h, local time. Initial A_{net} measurements were conducted at saturating light (1800 μmol m^{-2} s^{-1}) and ambient CO_2 concentration (*c.* 415 μmol mol^{-1}) using a flow rate of 300 μmol s^{-1}, followed by an A_{net}–C_i response curve using a sequence of CO_2 concentration levels (40, 150, 235, 330, 415, 700, 1200, 1500, 1800 μmol mol^{-1}).

To establish the temperature responses of the apparent maximum carboxylation rate, V_{cmax} and the apparent maximum electron transport rate, J_{max}, these A_{net}–C_i response curves were measured at five leaf temperatures (17, 25, 30, 35 and 40°C) on the same leaf (6 species × 4 growth temperatures × 3 replicates × 5 leaf temperatures = 360 A_{net}–C_i curves). The temperature-response curves were started at the respective growth temperature of each replicate, after which the rest of the temperatures were measured from low to high. Leaf temperature was controlled to within ±1°C of the target leaf temperature by manually adjusting the temperature of the chamber block. To achieve good temperature control, plants were temporarily moved to different bays for each of the five target measurement temperatures and measured after at least a 1-h adjustment period. The relative humidity in the leaf cuvette was controlled between 50% and 70%. The leaf-to-air VPD during these measurements increased consistently with leaf temperature among the target measurement temperatures (from *c.* 1 to 4 kPa; Supporting Information Fig. S1).

Net photosynthesis temperature responses

Based on the initial A_{net} measurements at each of five leaf temperature temperatures, temperature responses of photosynthesis were fitted using the following parabolic equation (Gunderson *et al.*, 2010):

$$A_{net} = A_{opt} - b(T - T_{opt})^2 \qquad \text{Eqn 1}$$

where A_{net} is the light-saturated net photosynthetic rate ({mol m^{-2} s^{-1}) at a given leaf temperature (T in °C); T_{opt}, the temperature optimum for photosynthesis (°C). A_{opt} is the light-saturated net photosynthetic rate at T_{opt}, and the parameter b describes the broadness of the curvature of the parabola.

Net photosynthesis at a common C_i (A_{300})

We also examined A_{300}, the net photosynthesis rate at the mean C_i (300 μmol mol^{-1}), which was obtained from each A_{net}–C_i curve by interpolating the curve using the Farquhar model (Farquhar *et al.*, 1980) with parameters fitted to that curve. When the photosynthetic rate is scaled to a common C_i, it eliminates the effect of variation in stomatal conductance on C_i, therefore isolating the temperature effects on photosynthetic biochemistry (Kumarathunge *et al.*, 2019). The temperature optimum for photosynthesis at the mean C_i ($T_{optA300}$) was estimated for each species by fitting Eqn 1. By comparing $T_{optA300}$ and T_{optA}, we estimated the effect of variation in stomatal conductance on the temperature optimum for photosynthesis.

Stomatal limitation

The stomatal limitation (S_l) of net photosynthesis was calculated by comparing photosynthesis from the fitted A_{net}–C_i curve at the measured ambient C_i ($A_{measuredCi}$) and photosynthesis from the fitted curves at the mean C_i (A_{300}) using the following equation:

$$S_l = A_{measuredCi} - A_{300} \qquad \text{Eqn 2}$$

Stomatal limitation (S_l) was compared among species at each T_{growth} in relation to leaf temperature.

Temperature dependence of photosynthetic biochemistry parameters

Each A_{net}–C_i curve was fitted to the Farquhar *et al.* (1980) photosynthesis model using the 'fitacis' function in the PLANTECOPHYS package in R (Duursma, 2015). We used the standardised kinetics parameters using the parameterisation given by Bernacchi *et al.* (2001). The reported rates of photosynthetic capacity are apparent J_{max} and apparent V_{cmax} values were based on data from intracellular CO_2 (C_i) concentrations rather than CO_2 concentrations at the site of carboxylation. The temperature dependencies of apparent V_{cmax} and J_{max} were fitted using the modified version of the Arrhenius equation to reflect a peaked function (Medlyn *et al.*, 2002a):

$$f(T_k) = k_{25} \exp\left[\frac{E_a(T_k - 298)}{298\,T_k}\right] \frac{1 + \exp\left(\frac{298\Delta S - H_d}{298R}\right)}{1 + \exp\left(\frac{T_k \Delta S - H_d}{T_k R}\right)} \qquad \text{Eqn 3}$$

where: k_{25}, value of V_{cmax} or J_{max} at 25°C; R, universal gas constant (8.314 J mol^{-1} K^{-1}; T_k, leaf temperature in K; E_a (J mol^{-1}), activation energy. E_a describes the exponential rise of enzyme activity with increasing temperature. H_d (J mol^{-1}), deactivation energy and ΔS is the entropy term (J K^{-1}). H_d and ΔS together describe the rate of decrease in the function above the optimum. To avoid overparameterisation, H_d was held at a constant of 200 kJ mol^{-1} for all species (Medlyn *et al.*, 2002a; Kattge & Knorr, 2007).

The optimum temperatures (T_{opt}) of V_{cmax} and J_{max} were calculated from the following equation (Medlyn *et al.*, 2002a):

$$T_{opt} = \frac{H_d}{\Delta S - R \log_e\left[\frac{E_a}{(H_d - E_a)}\right]} \qquad \text{Eqn 4}$$

where the variable abbreviations are explained above and $\log_e$ represents the natural log.

Temperature dependence of dark respiration

The short-term temperature dependence of leaf dark respiration (R_T) was measured on three plants of each species in two of the four growth temperatures. Different pairs of growth temperatures were measured for temperate (17 and 20.5°C), subtropical (24 and 27.5°C) and tropical (27.5 and 31°C) species to assess the effect of +3.5°C warming on leaf respiration in each group. Leaves were kept in darkness for at least 30 min before measurements by covering them with aluminium foil. Measurements on excised leaves were conducted during the day using a flow rate of 300 µmol s^{-1} and a reference CO_2 concentration of 400 µmol mol^{-1}. Dark respiration was measured over a temperature range from 14 to 60°C, using a large gas-exchange chamber (3010-GWK1; HeinzWalz GmbH, Effeltrich, Germany) connected to an infrared gas analyser (IRGA, LI-6400XT; Li-Cor). The leaf temperature was raised at a rate of 1°C min^{-1} to obtain high-resolution temperature-response curves of dark respiration (O'Sullivan *et al.*, 2017). The following equation was fitted to the data between 15 and 45°C:

$$R_T = R_{25} \cdot Q_{10}^{(T-25)/10} \qquad \text{Eqn 5}$$

where: R_T, respiration rate measured at a given temperature; T, leaf temperature, and the parameters R_{25} and Q_{10} characterise the respiration rate at 25°C and the proportional increase in respiration with a 10°C increase in temperature, respectively.

Data analysis

All graphs and statistical analysis were conducted in R v.3.3.2 (R Development Core Team, 2018). Data were checked for homogeneity and normality. Temperature-response curves (Eqns 1, 4) were fitted to the data using the 'nls' function within the NLSTOOLS package (Baty *et al.*, 2015). We used ANCOVA to distinguish effects of growth temperatures vs rainforest groups, including an interaction term. Regressions against T_{growth} were compared across rainforest groups using ANCOVA; the slopes and intercepts of the groups were obtained using LSTRENDS within LSMEANS package. As R_{25} and Q_{10} were only measured at two growth temperatures, an ANOVA was used with growth temperature and rainforest group as categorical variables.

Results

Temperature responses of net photosynthesis

The optimum temperature for leaf net photosynthesis ($T_{optA300}$ and T_{optA}) was higher in tropical and subtropical species than in warm-temperate species (Figs 1, 2). The optimum temperature of net photosynthesis at mean C_i, $T_{optA300}$ in tropical and subtropical species ranged from 30.1 to 38.9°C, whereas in warm-temperate species $T_{optA300}$ ranged from 25.9 to 28.3°C (Table 2). Similar differences among rainforest groups were observed for both T_{optA} and $T_{optA300}$, indicating a minor role of stomatal conductance in causing the difference in optimum temperature.

We observed acclimation of both T_{optA} and $T_{optA300}$ to growth temperature (Table 3). T_{optA} increased with growth temperature and the rate of increase was similar across groups (Fig. 2a). When normalised for differences in stomatal conductance, $T_{optA300}$ displayed relationships with T_{growth} that differed among rainforest groups $P = 0.02$; Table 3; Fig. 2b). The sensitivity (i.e. slope) of $T_{optA300}$ to T_{growth} was higher in the subtropical (0.78 ± 0.20°C °C^{-1} increase in T_{growth}) and tropical species (0.35 ± 0.17°C °C^{-1} increase in T_{growth}) than in warm-temperate species that showed little increase in $T_{optA300}$ ($P = 0.020$; ANCOVA; Table 3; Fig. 2).

Consistent with the higher T_{optA}, the photosynthetic rate at the temperature optimum (A_{opt}) was significantly higher in tropical and subtropical species than in temperate species ($P = 0.03$; Table 3; Fig. S2). However, there was no evidence that either A_{opt} or A_{opt300} acclimated to growth temperature ($P > 0.64$; Table 3). Net photosynthesis at 25°C (A_{net25}) also showed no difference with growth temperatures but tended to be decreased more in tropical and subtropical species compared with temperate species ($P = 0.08$; Table 3), especially at higher growth temperatures (Table 2; Fig. S2).

Stomatal component of the photosynthetic response to temperature

Temperature responses of photosynthesis can potentially be affected by stomatal closure at high VPD associated with high leaf temperatures (Fig. S3), which was the case for warm-temperate *T. laurina* and subtropical *B. citriodora* (Fig. S3) while only *B. citriodora* significantly decreased its conductance at higher leaf temperatures (Fig. 3). However, the g_s responses to T_{leaf} did not differ at different T_{growth} in any species (Fig. S4), indicating that changes in T_{optA} with T_{growth} were not caused by changes in stomatal response (Fig. 3). Moreover, stomatal limitation was not significantly related to leaf temperature ($P > 0.05$) for most species at any growth temperature, except in three out of 24 instances for *C. laevigata* grown at 17°C, *B. citriodora* grown at 31°C and *F. australis* grown at 27.5°C (Fig. S5).

Biochemical component of the photosynthetic response to temperature

The observed acclimation of T_{optA} was mainly driven by adjustments of photosynthetic biochemistry, which showed significant differences in response to growth temperatures in most parameters (Table 3). Temperature responses of V_{cmax} and J_{max} are shown for each species and growth temperature in Figs S6 and S7, while the parameters extracted by fitting Eqn 3 to these curves are shown in Fig. 4 and Table 4.

In general, J_{max25} declined with increasing growth temperature ($P = 0.009$; Table 3) with an interaction between growth temperature and rainforest group ($P = 0.015$). The interaction indicated significantly higher reduction of J_{max25} in pooled subtropical and tropical species (−6.13 ± 1.33 for each °C increase in T_{growth}) than warm-temperate species (−0.12 ± 1.33 for each °C increase in T_{growth}) (Fig. 4b). Several species exhibited large J_{max25} reductions (Table 4): tropical *A. fitzalanii* displayed more than 75% reduction of J_{max25} at the highest T_{growth} compared with 27.5°C, while subtropical *B. citriodora* reduced J_{max25} by *c.* 39% at 34.5°C compared with 24°C. By contrast, V_{cmax} measured at 25°C (V_{cmax25}) showed no difference in response to growth temperatures ($P = 0.77$; Fig. 4a; Table 3)

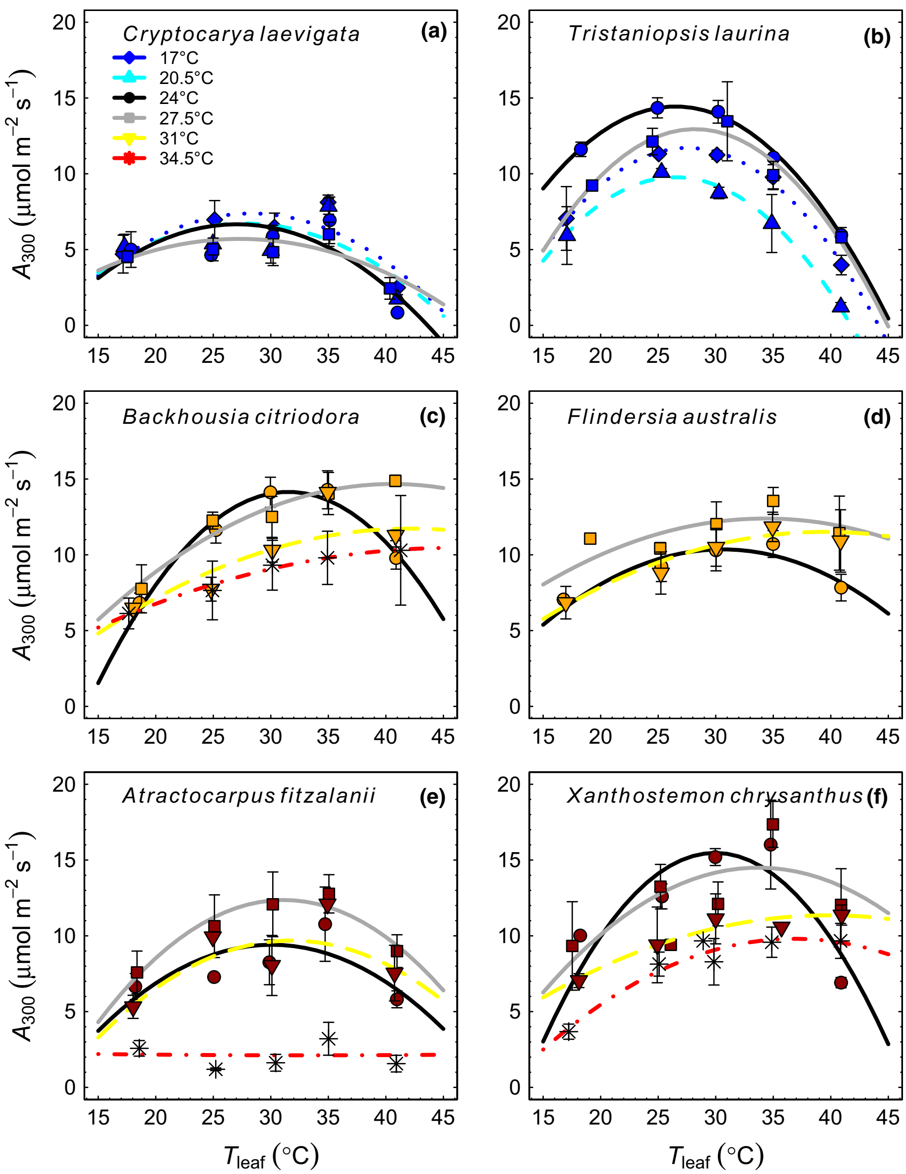

Fig. 1 Temperature response of photosynthesis of six rainforest tree species at an intercellular CO_2 concentration of 300 μmol mol^{-1} (A_{300}) at four different growth temperatures (means ± 1 SE): (a, b) warm-temperate species, (c, d) subtropical species (*Flindersia australis* could not be fit at 34.5°C, data not shown) and (e, f) tropical species. Symbols representing growth temperatures are maintained in relevant subsequent graphs. The temperature response fits at each growth temperature is represented by different line types and colours: dashed blue lines, 17°C; dashed cyan lines 20.5°C; : solid black lines, 24°C; solid grey lines, 27.5°C; : long-dashed yellow lines, 31°C; dashed red lines, 34.5°C.

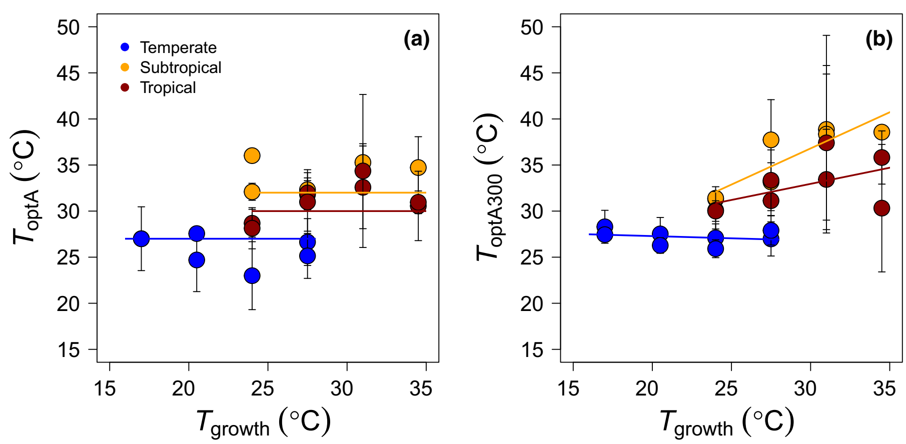

Fig. 2 Means and ± SE of the temperature optimum for (a) leaf net photosynthesis (T_{optA}) and (b) net photosynthesis at an intercellular CO_2 concentration of 300 μmol mol^{-1} ($T_{optA300}$) at different growth temperatures (T_{growth}) for each rainforest group: warm-temperate species in blue, subtropical species in orange and tropical species in red.

Table 2 Mean coefficients (± 1 SE) from the photosynthesis temperature response fits at mean C_i (300 μmol mol^{-1}) and net photosynthesis at 25°C (A_{net25}) for six rainforest tree species at four different growth temperatures.

Rainforest group	Species	Growth temperature	A_{opt300} (μmol m^{-2} s^{-1})	$T_{optA300}$ (°C)	*b* (broadness)	A_{net25} (μmol m^{-2} s^{-1})
Warm temperate	*Cryptocarya laevigata*	17.0°C	6.62 ± 0.65	28.3 ± 1.8	0.020 ± 0.008	5.71 ± 0.81
		20.5°C	6.12 ± 0.66	27.5 ± 1.8	0.018 ± 0.007	5.48 ± 0.50
		24.0°C	6.24 ± 0.69	27.1 ± 1.5	0.023 ± 0.008	4.19 ± 1.21
		27.5°C	5.37 ± 0.60	27.0 ± 2.4	0.013 ± 0.006	3.59 ± 0.75
	Tristaniopsis laurina	17.0°C	11.01 ± 0.44	27.4 ± 0.5	0.040 ± 0.005	11.23 ± 0.33
		20.5°C	9.17 ± 0.66	26.3 ± 0.8	0.04 ± 0.007	10.00 ± 0.35
		24.0°C	13.10 ± 0.55	25.9 ± 0.9	0.038 ± 0.007	11.34 ± 0.63
		27.5°C	12.24 ± 0.94	27.9 ± 1.6	0.043 ± 0.015	10.58 ± 1.46
Subtropical	*Backhousia citriodora*	24.0°C	13.33 ± 0.59	31.3 ± 0.6	0.044 ± 0.007	12.01 ± 0.77
		27.5°C	13.71 ± 0.61	37.7 ± 4.3	0.016 ± 0.008	14.50 ± 0.76
		31.0°C	10.84 ± 0.61	38.9 ± 6.0	0.011 ± 0.006	9.93 ± 0.17
		34.5°C	10.32 ± 1.12	38.6 ± 10.6	0.011 ± 0.011	8.34 ± 1.21
	Flindersia australis	24.0°C	9.58 ± 0.67	31.4 ± 1.2	0.027 ± 0.008	6.68 ± 1.24
		27.5°C	12.19 ± 0.80	33.2 ± 2.1	0.026 ± 0.009	10.89 ± 0.58
		31.0°C	10.58 ± 0.85	38.3 ± 10.7	0.009 ± 0.009	5.66 ± 0.43
		34.5°C	–	–	–	2.78 ± 0.30
Tropical	*Atractocarpus fitzalanii*	24.0°C	8.54 ± 1.01	30.1 ± 2.0	0.022 ± 0.012	7.00 ± 0.39
		27.5°C	11.38 ± 0.93	31.1 ± 1.6	0.028 ± 0.011	8.94 ± 0.63
		31.0°C	8.25 ± 1.24	33.4 ± 5.4	0.014 ± 0.014	8.24 ± 2.092
		34.5°C	2.36 ± 0.48	30.3 ± 6.9	0.003 ± 0.005	1.76 ± 0.70
	Xanthostemon chrysanthus	24.0°C	14.54 ± 1.22	30.0 ± 1.1	0.055 ± 0.016	10.73 ± 0.99
		27.5°C	13.62 ± 1.00	33.3 ± 3.3	0.022 ± 0.014	9.37 ± 2.06
		31.0°C	10.58 ± 0.77	37.4 ± 8.4	0.009 ± 0.008	9.72 ± 1.73
		34.5°C	9.25 ± 0.47	35.8 ± 2.9	0.016 ± 0.006	7.98 ± 0.88

A parabolic function was used to fit according to Eqn 1 in the Materials and Methods section. *Flindersia australis* fits at 34.5°C had $T_{optA300}$ outside the measurement range.

Table 3 Analysis of covariance *F*-statistic and *P*-values of the regressions of photosynthetic parameters against T_{growth} across rainforest groups (Group).

	T_{growth} *df* = 1		Group *df* = 2		T_{growth} × Group *df* = 2		
Parameter	*F*-statistic	*P*-value	*F*-statistic	*P*-value	*F*-statistic	*P*-value	Resid *df*
T_{optA}	25.10	**0.00016**	19.52	**< 0.0001**	1.54	0.25	15
$T_{optA300}$	55.58	**< 0.0001**	15.44	**0.00015**	5.00	**0.020**	17
A_{opt}	0.23	0.64	4.27	**0.034**	0.82	0.46	15
A_{opt300}	0.07	0.79	3.00	*0.077*	1.60	0.23	17
A_{net25}	1.67	0.21	2.69	*0.081*	0.74	0.54	16
V_{cmax25}	0.09	0.77	1.37	0.28	0.52	0.60	17
J_{max25}	8.77	**0.0088**	1.48	0.25	5.47	**0.015**	17
J_{max25} : V_{cmax25}	2.33	0.14	0.74	0.49	1.48	0.25	18
T_{optV}	15.48	**0.0012**	1.69	0.22	1.34	0.29	16
T_{optJ}	22.18	**0.0002**	5.95	**0.012**	0.78	0.47	16
E_{aV}	0.46	0.50	1.79	0.20	1.73	0.21	17
E_{aJ}	0.15	0.70	1.40	0.27	1.98	0.17	17
ΔS_V	8.28	**0.011**	0.38	0.69	0.19	0.82	16
ΔS_J	15.05	**0.0013**	3.94	**0.040**	0.32	0.73	16

Parameters are: the temperature optima of net photosynthesis (T_{optA}) and of photosynthesis at [CO_2] = 300 μmol mol^{-1} ($T_{optA300}$), and the maximum photosynthesis rates at the temperature optima (A_{opt} and A_{opt300}), the maximum carboxylation rate at 25°C (V_{cmax25}) and its activation energy (E_{aV}), the maximum electron transport rate at 25°C (J_{max25}) and its associated activation energy (E_{aJ}), while its deactivation energy (H_d) was kept constant at 200 kJ mol^{-1}. T_{optV} and T_{optJ} represent the temperature optima of V_{cmax} and J_{max} fits, respectively. ΔS represents the entropy factor in the model (ΔS_V and ΔS_J for V_{cmax} and J_{max} fits, respectively). *df* stands for degrees of freedom, including the residual *df* in the last column. Bold values are the significant relationships at $P < 0.05$; italic values are significant at $P < 0.1$.

and there were also no differences among rainforest groups (P = 0.28). While the ratio of J_{max25} to V_{cmax25} (J_{max25} : V_{cmax25}) did not decline with higher growth temperatures (P = 0.14) and was similar among rainforest groups (P = 0.49; Fig. S8a), J_{max} : V_{cmax} did reduce significantly across all growth temperatures (P = 0.003).

Similar to T_{optA}, the optimum temperatures of both V_{cmax} (T_{optV}) and J_{max} (T_{optJ}) increased significantly with increasing

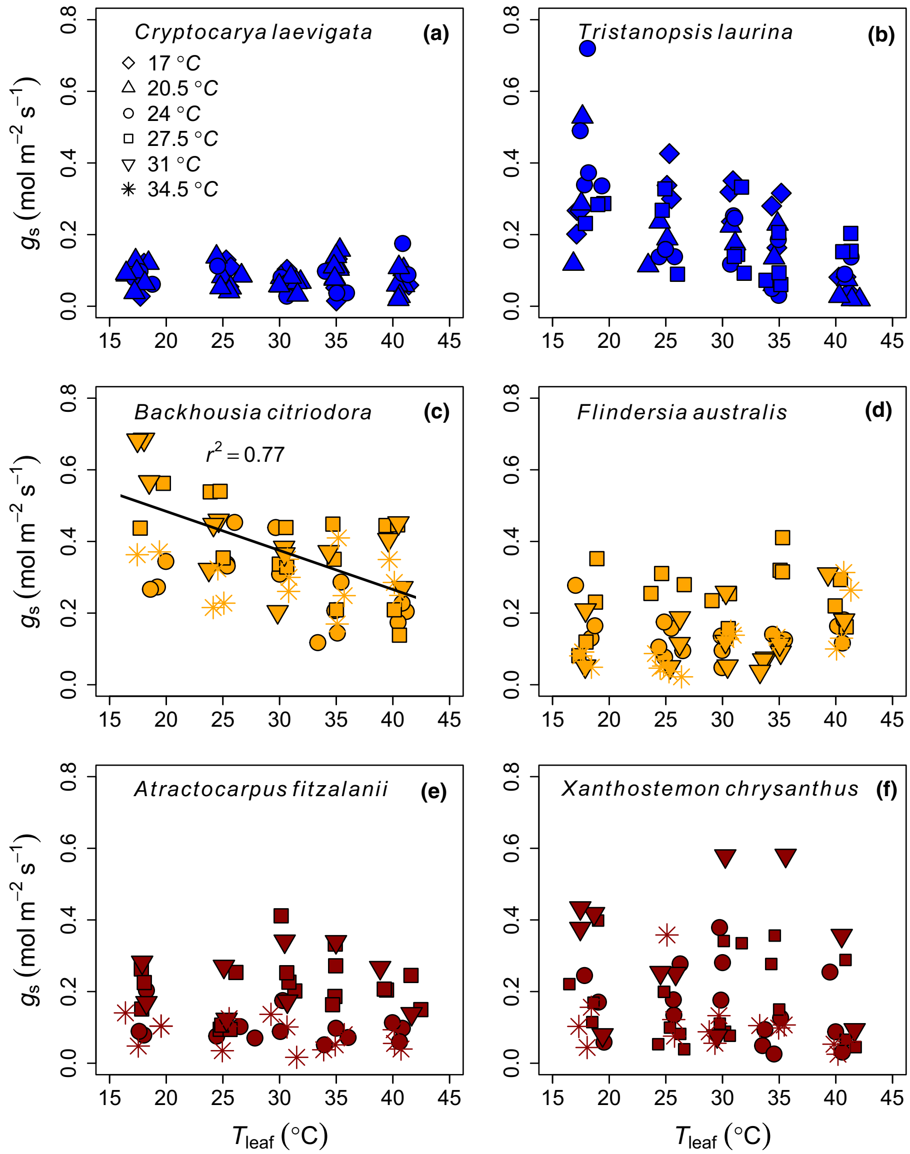

Fig. 3 Relationships between leaf temperature (T_{leaf}) and stomatal conductance (g_s) at different growth temperatures (different symbols) in six rainforest tree species: (a, b) warm-temperate species in blue, (c, d) subtropical in orange, and (e, f) tropical species in red. The relationship was only significant for *B. citriodora* ($g_s = -0.0109$, $T_{leaf} + 0.70$, $R^2 = 0.77$, $P = 0.01$).

growth temperatures across species ($P < 0.0012$; Fig. 4c,d; Table 3). The slopes of linear regressions of T_{optV} and T_{optJ}, with growth temperature were 0.49 ± 0.13°C °C^{-1} and 0.56 ± 0.14°C °C^{-1}, respectively (Fig. 4c,d) and slopes were not different among groups, indicating a similar degree of acclimation for all rainforest groups ($P > 0.05$; Table 4). The change in T_{optA} was not associated with a change in activation energy (E_a) of either V_{cmax} or J_{max}; both E_{aJ} and E_{aV} were independent of growth temperature ($P > 0.5$; Fig. 4e,f; Table 3). Across growth temperatures, the increases in T_{optV} and T_{optJ} were associated with a significant decline in ΔS_V and ΔS_J ($P < 0.011$; Fig. 4g,h; Table 3). Therefore, several biochemical parameters (J_{max25}, T_{optV}, T_{optJ}, ΔS_V, ΔS_J) responded to higher growth temperatures across species, suggesting a strong influence of growth temperatures on the underlying biochemical components of the temperature response of photosynthesis. Similarly to J_{max25}, the associated parameters T_{optJ} and ΔS_J varied among rainforest groups ($P < 0.041$; Table 3) resulting in higher T_{optJ} and lower ΔS_J in subtropical and tropical species compared with warm-temperate species (different intercepts in Fig. 4d,h).

There were strong relationships between several biochemical parameters and the temperature optimum of photosynthesis, $T_{optA300}$ (Fig. 5). We found a positive relationship between $T_{optA300}$ and the optimum temperatures of V_{cmax} (T_{optV}) and of J_{max} (T_{optJ}) (Fig. 5a,b), indicating that higher T_{opt} in V_{cmax} and J_{max} were correlated with a higher temperature optimum of photosynthesis. A low $J_{max25} : V_{cmax25}$ ratio was also related to high temperature optima of photosynthesis (Fig. 5c). While there was no significant relationship between $T_{optA300}$ and the activation energy (either E_{aV} or E_{aJ}, data not shown), a strong negative relationship was found between ΔS_J and $T_{optA300}$ ($R^2 = 0.43$; Fig. 5d) and between ΔS_V and $T_{optA300}$ ($R^2 = 0.17$, data not shown), in line with the reduction of ΔS_V and ΔS_J with increasing growth temperature across species (Fig. 4g,h; Table 3).

Temperature response of respiration

The response of dark respiration to leaf temperature acclimated differently to warming in warm-temperate vs

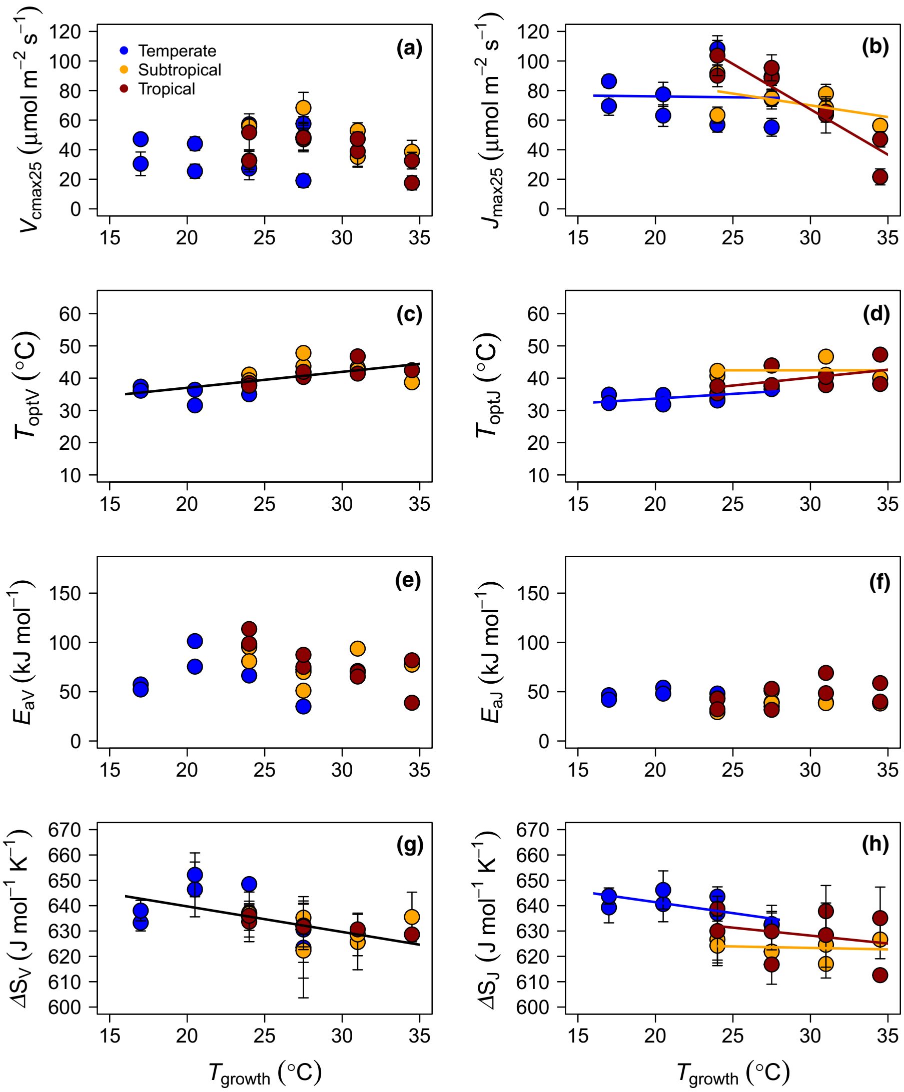

Fig. 4 Means and ± SE of parameter values of individually fitted functions to characterise the temperature dependence of maximum carboxylation rate (V_{cmax}) (a, c, e, g) and maximum electron transport rate (J_{max}) (b, d, f, h) at 25°C across growth temperatures. (a, b) Standard value of V_{cmax} and J_{max} at 25°C, (c, d) optimum temperature (T_{opt}) of V_{cmax} and J_{max}, (e, f) activation energy (E_a) for V_{cmax} and J_{max}, (g, h) entropy term (ΔS) for V_{cmax} and J_{max} fits. Warm-temperate species are indicated in blue, subtropical species are orange and tropical species are red. ANCOVA of linear regressions across growth temperatures and rainforest groups are reported in Table 3. Significant linear regressions (and no significant differences between neither slopes nor intercepts) were found: (c) T_{optV} and T_{growth} (T_{optV} = 0.49, T_{growth} + 27.12; R^2 = 0.38, P = 0.001); (g) ΔS_V and T_{growth} (ΔS_V = −1.00, T_{growth} + 659.86; R^2 = 0.29, P = 0.005).

subtropical and tropical species (Figs 6, S9), reflected by adjustments in both respiration rates at a common temperature, R_{25} and the temperature sensitivity of respiration, Q_{10}. While R_{25} rates tended to increase with warming in temperate species, and decrease in tropical species (Fig. 6a), there were no differences in response to 3.5°C warming (P = 0.88). There were differences among rainforest groups in R_{25} (P = 0.045) with subtropical species having the highest R_{25} (Fig. 6a) while tropical and warm-temperate species exhibited similar rates.

Similarly, the decrease in the temperature sensitivity of respiration (Q_{10} between 15 to 45°C) was significantly different among rainforest groups (P = 0.027) but not different with categorical growth temperatures (P = 0.90). On average, Q_{10} was reduced by 24% in subtropical and tropical species, compared with the average Q_{10} of warm-temperate species (P < 0.025). These adjustments resulted in homeostasis in the respiration rate at T_{growth} ($R_{Tgrowth}$) among subtropical and tropical species, while warm-temperate species had lower $R_{Tgrowth}$ (Fig. 6c; P = 0.003).

Discussion

We found that Australian rainforest species adjusted both photosynthesis and respiration to warming. Tropical and subtropical species showed as much, if not more, capacity to acclimate as did warm-temperate species, despite being grown at a higher range of temperatures. The optimum temperature for photosynthesis increased with growth temperature and the rate of increase was higher in tropical and subtropical species than in warm-temperate species. We showed that adjustments of biochemical processes, particularly changes in J_{max25}, ΔS and the optimal temperatures for RuBP regeneration and Rubisco carboxylation, were the principal mechanisms underlying the shift in temperature optimum of photosynthesis in response to increased growth temperatures. Tropical species showed greater acclimation of respiration rates via both a reduction in R_{25} and Q_{10} whereas warm-temperate species did not reduce R_{25} at higher growth temperatures. These adjustments resulted in similar respiration rates at higher growth temperatures in tropical species, rather than enhanced $R_{Tgrowth}$ by warming in temperate species.

Table 4 Table of coefficients ± 1 SE from temperature response fits for two warm-temperate, two subtropical and two tropical rainforest species across four growth temperatures reflecting warming within and beyond their native range.

			Rubisco carboxylation					Electron transport				
Rainforest group	Species	T_{growth}	V_{cmax25} (μmol m^{-2} s^{-1})	E_{aV} (kJ mol^{-1})	ΔS_V (J mol^{-1} K^{-1})	T_{optV} (°C)	R^2	J_{max25} (μmol m^{-2} s^{-1})	E_{aJ} (kJ mol^{-1})	ΔS_J (J mol^{-1} K^{-1})	T_{optJ} (°C)	R^2
Warm temperate	*Cryptocarya laevigata*	17°C	30.4 ± 8.0	57.3 ± 23.2	640 ± 20	37.36	0.37	69.6 ± 6.3	46.4 ± 15.8	640 ± 10	34.90	0.72
		20.5°C	25.4 ± 5.0	101.3 ± 48.8	650 ± 10	36.40	0.70	63.1 ± 7.3	54.1 ± 21.0	641 ± 10	34.80	0.52
		24°C	27.3 ± 8.0	96.9 ± 75.6	650 ± 20	35.00	0.55	56.9 ± 5.0	43.4 ± 14.8	637 ± 4	33.58	0.59
		27.5°C	19.0 ± 4.0	72.4 ± 29.0	630 ± 10	41.66	0.65	55.2 ± 6.0	39.3 ± 14.1	632 ± 8	37.45	0.54
	Tristaniopsis laurina	17°C	47.8 ± 3.3	61.3 ± 11.8	638 ± 4	36.11	0.77	86.3 ± 4.2	41.9 ± 10.2	640 ± 4	32.26	0.77
		20.5°C	44.0 ± 4.6	75.4 ± 36.6	652 ± 8	31.57	0.75	77.4 ± 8.2	48.0 ± 24.9	646 ± 8	31.84	0.60
		24°C	57.2 ± 3.0	66.4 ± 8.6	637 ± 3	37.89	0.92	108.3 ± 5.7	48.1 ± 10.9	644 ± 4	33.07	0.72
		27.5°C	57.5 ± 4.8	35.0 ± 11.1	623 ± 10	40.58	0.68	89.6 ± 6.2	34.9 ± 10.4	633 ± 5	36.60	0.68
Subtropical	*Backhousia citriodora*	24°C	55.7 ± 5.4	80.9 ± 13.5	640 ± 3	39.34	0.93	91.8 ± 5.4	29.3 ± 8.0	620 ± 10	42.27	0.80
		27.5°C	68.3 ± 10.4	51.0 ± 18.8	610 ± 40	47.81	0.78	74.9 ± 5.5	38.6 ± 4.7	*		0.88
		31°C	53.0 ± 5.3	71.0 ± 14.7	630 ± 10	42.50	0.93	68.4 ± 6.0	38.4 ± 12.9	620 ± 10	41.06	0.73
		34.5°C	38.7 ± 7.6	77.4 ± 28.3	640 ± 10	38.71	0.73	56.2 ± 3.6	38.1 ± 8.7	630 ± 10	40.00	0.81
	Flindersia australis	24°C	32.8 ± 6.1	95.1 ± 26.6	640 ± 10	41.12	0.86	63.4 ± 5.4	43.2 ± 12.4	630 ± 10	40.65	0.73
		27.5°C	48.6 ± 10.0	70.0 ± 25.3	630 ± 20	43.70	0.78	74.3 ± 6.7	50.8 ± 11.7	620 ± 10	43.90	0.89
		31°C	35.1 ± 7.0	93.7 ± 23.2	630 ± 10	43.19	0.89	77.8 ± 6.4	39.1 ± 9.2	610 ± 30	46.68	0.82
		34.5°C	25.5 ± 7.0	85.2 ± 23.2	620 ± 40	40.58	0.68	47.8 ± 6.2	44.3 ± 17.3	620 ± 30	44.40	0.74
Tropical	*Atractocarpus fitzalanii*	24°C	32.5 ± 7.5	113.6 ± 45.5	640 ± 10	38.50	0.83	90.0 ± 7.4	42.9 ± 16.1	640 ± 5	35.30	0.71
		27.5°C	47.0 ± 7.5	75.2 ± 21.8	630 ± 10	40.36	0.78	88.3 ± 8.8	52.9 ± 14.8	630 ± 10	37.86	0.67
		31°C	38.9 ± 10.2	70.0 ± 38.0	630 ± 20	41.42	0.76	63.6 ± 12.3	69.1 ± 34.2	640 ± 10	37.82	0.75
		34.5°C	17.6 ± 4.8	8.7 ± 35.1	620 ± 40	42.46	0.21	21.6 ± 5.4	58.7 ± 37.5	640 ± 10	38.20	0.47
	Xanthostemon chrysanthus	24°C	51.7 ± 12.6	98.7 ± 46.8	640 ± 10	37.65	0.68	103.6 ± 13.5	32.2 ± 19.7	630 ± 10	37.54	0.33
		27.5°C	48.2 ± 8.4	87.4 ± 23.3	630 ± 10	42.00	0.79	95.4 ± 8.8	31.6 ± 13.4	620 ± 3	43.95	0.52
		31°C	47.3 ± 4.7	65.4 ± 12.7	620 ± 20	46.76	0.96	65.7 ± 7.1	48.5 ± 18.4	630 ± 10	40.40	0.82
		34.5°C	33.1 ± 4.4	80.2 ± 7.3	*		0.95	47.0 ± 5.2	39.9 ± 14.2	610 ± 50	47.30	0.74

Each fit was performed across three replicates per treatment using a peaked Arrhenius function, except two fits for which a standard Arrhenius was used (indicated with *) because they did not show a peak (V_{cmax} of *X. chrysanthus* at 34.5°C and J_{max} of *B. citriodora* at 27.5°C). Coefficients are the maximum carboxylation rate at 25°C (V_{cmax25}), the maximum electron transport at 25°C (J_{max25}), the activation energy (E_{aV} and E_{aJ} for V_{cmax} and J_{max}, respectively), and the entropy (ΔS_V and ΔS_J, respectively). The temperature optimum (T_{opt}) of each fit was calculated. R^2 represents the overall model fit.

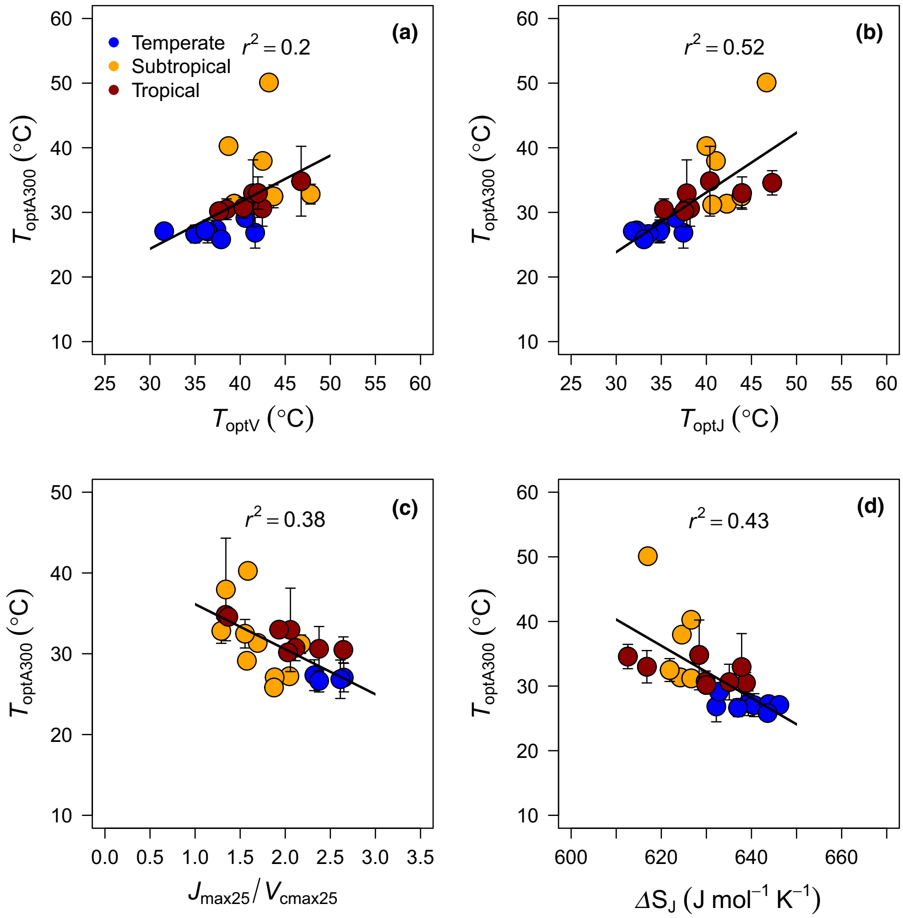

Fig. 5 Relationships of means and ± 1 SE between several biochemical parameters and the temperature optimum of photosynthesis at a common C_i of 300 μmol mol^{-1} ($T_{optA300}$) among six rainforest tree species. Warm-temperate species are indicated in blue, subtropical species are orange and tropical species are red: (a) $T_{optA300}$ and T_{optV} ($T_{optA300} = 0.72,\ T_{optV} + 2.72$; $R^2 = 0.20$, $P = 0.02$), (b) $T_{optA300}$ and T_{optJ} ($T_{optA300} = 0.92\ T_{optJ} - 3.85$; $R^2 = 0.52$, $P < 0.01$), (c) $T_{optA300}$ and J_{max25}/V_{cmax25} ($T_{optA300} = -5.57,\ J_{max25}/V_{cmax25} + 41.71$; $R^2 = 0.38$, $P = 0.001$), (d) $T_{optA300}$ and ΔS_J ($T_{optA300} = -0.41,\ \Delta S_J + 287.43$; $R^2 = 0.43$, $P < 0.01$).

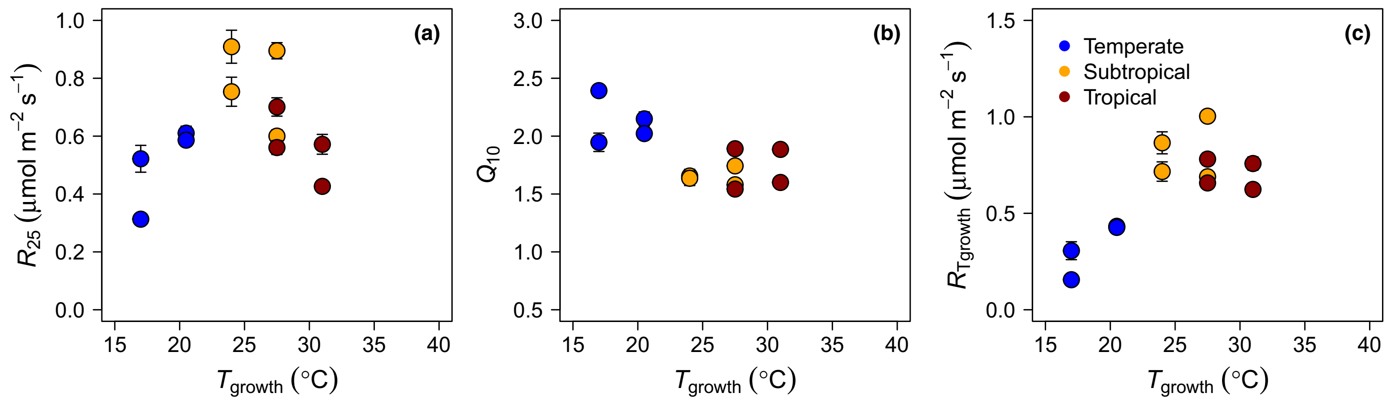

Fig. 6 Means and ± SE of (a) dark respiration rate at 25°C (R_{25}) across six rainforest tree species, (b) Q_{10} of respiration (calculated across 15–45°C), and (c) dark respiration each at two T_{growth} ($R_{Tgrowth}$). Warm-temperate species are indicated in blue, subtropical species are orange and tropical species are red.

The photosynthetic response to growth temperature

The rate of increase in $T_{optA300}$ was 0.35–0.78°C °C^{-1} increase in T_{growth}, a shift similar in magnitude to that observed in earlier studies (e.g. Berry & Björkman, 1980; Kumarathunge *et al.*, 2019). Tropical and subtropical species showed a higher increase of $T_{optA300}$ (*c.* 8°C increase) with warming than warm-temperate species (*c.* 3°C increase), similar to Cunningham & Read (2002). The larger shift in $T_{optA300}$ in our study in tropical species compared with temperate species could, in part, be related to the fact the tropical species were exposed to higher growth temperatures compared with temperate species.

The increase in $T_{optA300}$ with higher growth temperatures was underpinned by an increase in T_{opt} of V_{cmax25} and T_{opt} of J_{max25} (Fig. 4) supporting our hypothesis that the temperature optima of photosynthesis (T_{optA}), V_{cmax} (T_{optV}), and J_{max} (T_{optJ}) would increase with increasing growth temperatures. The magnitude of acclimation of T_{optV} (0.49°C °C^{-1}) was similar to Dreyer *et al.*

(2001), in a study of seven European tree species, and Kattge & Knorr (2007) (0.44°C °C^{-1}), in a meta-analysis of 36 species. There was a strong relationship between $T_{optA300}$ and T_{optV} and between $T_{optA300}$ and T_{optJ} (Fig. 5a,b) suggesting that biochemical components strongly influenced the temperature optimum of photosynthesis.

A strong negative correlation between ΔS_J and $T_{optA300}$ (Fig. 5d) indicated that the reduction in ΔS also contributed to an increased temperature optimum of photosynthesis in response to warming. Using a peaked Arrhenius function, the change in T_{optV} and T_{optJ} is generally explained by the sensitivity of ΔS to temperature (Kattge & Knorr, 2007; Kumarathunge *et al.*, 2019). We observed a decline of ΔS_V and ΔS_J in response to growth temperature, and the magnitude of this decline (-1.00 ± 0.32 and -1.10 ± 0.31 J mol^{-1} K^{-1} °C^{-1}, for ΔS_V and ΔS_J, respectively) was very similar to Kattge & Knorr (2007) and to Kumarathunge *et al.* (2019). There was no positive relationship observed between either activation energy (E_{aV} or E_{aJ}) and T_{growth}. While some studies have found a positive relationship between activation energy and growth temperature (Hikosaka *et al.*, 1999, 2006; Onoda *et al.*, 2005), these studies typically did not use a peaked temperature-response function in which the ΔS parameter is quantified. Kattge & Knorr (2007) also found lack of E_{aV} and E_{aJ} responses to T_{growth} in 36 rainforest species. Overall, the selected rainforest species clearly adjusted the underlying biochemical components of photosynthesis to warmer growth temperatures, mainly via reduced J_{max25}, reduced ΔS and increased temperature optima (T_{optV} and T_{optJ}).

The reduction in J_{max25} with increased growth temperatures supported our hypothesis of downregulation of photosynthetic capacity at warmer T_{growth} via the decline of J_{max25}, but not V_{cmax25} (Fig. 4). By contrast, Scafaro *et al.* (2017) associated the decline in net photosynthetic rate with a decline in V_{cmax25} as T_{growth} increased across six temperate and four tropical rainforest species. However, other studies have reported increased V_{cmax25} with warming (Hikosaka *et al.*, 1999; Onoda *et al.*, 2005; Ghannoum *et al.*, 2010; Smith & Dukes, 2017; Lamba *et al.*, 2018). While photosynthetic capacity can be adjusted by either a change in V_{cmax25} of J_{max25} or both, many studies have reported a reduced $J_{max25} : V_{cmax25}$ ratio with increasing growth temperatures across many species (Atkin *et al.*, 2006; Hikosaka *et al.*, 2006; Kattge & Knorr, 2007; Sage & Kubien, 2007; Lin *et al.*, 2012; Crous *et al.*, 2013; Dusenge *et al.*, 2020). The reduction of J_{max}/V_{cmax} is likely to be related to the greater dependence of J_{max} upon membrane stability than V_{cmax} at higher temperatures (Hikosaka *et al.*, 2006; Sage & Kubien, 2007). Moreover, a lower $J_{max25} : V_{cmax25}$ ratio was related to a higher $T_{optA300}$ (Fig. 5; Kumarathunge *et al.*, 2019; Dusenge *et al.*, 2020). As J_{max} and V_{cmax} have different temperature optima, the optimum temperature of photosynthesis is determined by the most limiting component process of photosynthesis. At lower $J_{max25} : V_{cmax25}$, there is less Rubisco limitation compared with a higher $J_{max25} : V_{cmax25}$, an adjustment that leads to a higher T_{optA} at higher growth temperatures (Hikosaka *et al.*, 2006).

Our study was designed to distinguish the acclimation capacity among rainforest species from different climates in a controlled environment. Most biochemical parameters describing the temperature response of photosynthesis responded to a change in growth temperatures without a difference among rainforest groups (Table 3), suggesting similar acclimation capacity among rainforest groups. Similar acclimation to experimental warming has also been reported in Slot & Kitajima (2015), Slot & Winter (2017) and Crous *et al.* (2022). One novel result here was that J_{max25} not only reduced with increased growth temperatures but the reduction was stronger in tropical and subtropical species compared with warm-temperate rainforest species. The reduction in J_{max25} was underpinned by lower ΔS_J in tropical and subtropical species. While a reduction in J_{max25} could lead to impaired photosynthesis rates with warming, this reduction was counteracted by increased temperature optima with warming, resulting in similar photosynthesis rates (A_{net25} and A_{opt300}) across rainforest groups ($P = 0.08$; Table 3). Similar photosynthesis rates across a range of growth temperatures were also reported for a tropical montane species, *Syzygium guineense* (Dusenge *et al.*, 2021), although rates did decrease above 30°C. Other studies have found reduced rates of photosynthesis in tropical species with warming especially at growth temperatures above 30°C (Cunningham & Read, 2003; Slot & Winter, 2016; Scafaro *et al.*, 2017; Crous *et al.*, 2018; Dusenge *et al.*, 2021). While not statistically significant, photosynthesis tended to decline at the highest growth temperatures in our study (Table 2) suggesting that some species may decline photosynthesis at high growth temperatures despite thermal acclimation. There is clearly a need to understand how acclimation capacity differs among species from different latitudes or biogeographic regions, which our study addressed in Australian rainforest species. Recently, Crous *et al.* (2022) reviewed the acclimation responses in evergreen species from boreal to tropical latitudes and found more negative responses of photosynthesis to warming in species experiencing higher growth temperatures.

Another factor potentially contributing to reduced photosynthesis at higher growth temperatures could be reduced stomatal conductance. In contrast to most biochemical components, the stomatal conductance response to growth temperatures remained mostly unchanged and stomatal limitation was generally not related to leaf temperature in our study. This implies that g_s was not a major component driving a shift in the temperature response of photosynthesis in these rainforest species, which is likely due to the well watered conditions in this experiment. Gunderson *et al.* (2010), Crous *et al.* (2018) and Kumarathunge *et al.* (2019) also demonstrated that stomatal conductance was not a major component driving the adjustments of the photosynthesis temperature response. However, water limitations can reduce the temperature optima for photosynthesis in trees (Lin *et al.*, 2012; Kumarathunge *et al.*, 2020). A recent study found that the stomatal response to high VPD could be a major driver of the decline of photosynthesis at higher temperatures in tropical forests (Smith *et al.*, 2020), especially when VPD is not manipulated, which is in contrast with most controlled environments in which VPD is minimised via high humidity. The decrease of g_s with increasing temperatures is not uncommon and has been observed in several studies (e.g. Slot *et al.*, 2016; Carter *et al.*, 2021) suggesting that photosynthesis rates could additionally be constrained by stomatal conductance at higher growth temperatures.

Response of leaf dark respiration to growth temperature

Since photosynthesis and respiration are coupled (Reich *et al.*, 1998; Whitehead *et al.*, 2004; Dusenge *et al.*, 2019), plants with strong photosynthetic acclimation might also show strong thermal respiratory acclimation. $R_{Tgrowth}$ tended to increase with warming in temperate rainforest species (Fig. 6c) while tropical and subtropical species displayed similar respiration rates regardless of growth temperature. This homeostatic response of $R_{Tgrowth}$ can be explained via the adjustments of both a reduced temperature sensitivity (Q_{10}) and reduced rates of R_{25} in tropical compared with temperate rainforest species (Fig. 6).

Subtropical and tropical species showed 24% lower temperature sensitivity (Q_{10}) compared with warm-temperate species. Changes in Q_{10} enabled respiration to adjust dynamically to changes in growth temperature (Atkin & Tjoelker, 2003), probably via changes in substrate and/or adenylate control (Armstrong *et al.*, 2008). This reduction in Q_{10} in subtropical and tropical species was likely related to the higher growth temperatures they experienced compared with temperate species, and enabled tropical and subtropical species to reduce carbon loss via reduced respiration. Therefore tropical species had similar R_{25} as found for temperate species, regardless of warming combined with a lower Q_{10}. While we could not attribute this response to warming, reduced respiration rates in response to long-term warming are commonly observed in many species (Atkin *et al.*, 2005; Crous *et al.*, 2011; Aspinwall *et al.*, 2016; Drake *et al.*, 2015, 2017), including in tropical species (Slot & Kitajima, 2015). Adjustments in R_{25} and Q_{10} resulted in homeostasis in the respiration rate at T_{growth} ($R_{Tgrowth}$) among subtropical and tropical species, regardless of warming, while warm-temperate species had lower $R_{Tgrowth}$ (Fig. 6c).

Because tropical species reduced both R_{25} and Q_{10}, respiration rates in tropical species adjusted more than respiration rates in temperate species, refuting our fourth hypothesis. Therefore tropical and subtropical species have a large capacity to acclimate respiration in response to moderate warming (Slot & Kitajima, 2015). The adjustment of leaf dark respiration in tropical and subtropical species partly offsets the decrease of photosynthetic capacity (J_{max25}), although acclimation of stem or root respiration to warming may be more limited (Drake *et al.*, 2017; Noh *et al.*, 2020). In terms of leaf-level responses, tropical species may adjust to warming via a combined effect of an increased T_{optA} and reduced respiration, but it is unclear whether these responses are enough to prevent reduced photosynthesis with future warming.

Mercado *et al.* (2018) showed that thermal acclimation of photosynthetic capacity reduced the vulnerability of temperate and tropical species to warming in an Earth system model, although acclimation of respiration was not accounted for. Moreover, recent field studies on tropical tree species have observed limited thermal acclimation (Carter *et al.*, 2021; Dusenge *et al.*, 2021). Our findings extends this work by investigating the mechanisms controlling the photosynthesis temperature response across a range of growth temperatures to determine differences in acclimation capacity in rainforest trees from different climates. While acclimation capacity of photosynthesis may be more limited with higher growth temperatures, including in the tropics (Carter *et al.*, 2021; Crous *et al.*, 2022), there is a need to investigate the limits of thermal acclimation across latitudes, including at extreme temperatures (Zhu *et al.*, 2018). Understanding how thermal acclimation varies geographically and what factors are controlling this response would contribute to reduce uncertainties regarding physiological responses to warming and improve projections of future carbon uptake in models.

Contrasting responses between tropical and warm-temperate rainforest trees

According to our hypothesis, the shift in the optimum temperature of photosynthesis (T_{optA}) would be larger in warm-temperate than subtropical and tropical species due to the larger seasonal temperature variation temperate species experience. In contrast with this hypothesis, we found larger adjustments of $T_{optA300}$ in tropical and subtropical species compared with warm-temperate species related to an increase in T_{optJ} and T_{optV}. While other studies have generally found a higher T_{opt} of photosynthesis in tropical species compared with temperate species (Cunningham & Read, 2003; Scafaro *et al.*, 2017; Mau *et al.*, 2018; Crous *et al.*, 2022), our study also found that the adjustment in T_{optA} was larger in tropical species (8°C range) compared with warm-temperate species (4.5°C range).

Tropical species also exhibited stronger reductions in J_{max25} compared with temperate species in response to warmer growth temperatures. Other studies also reported reduced rates of J_{max25} in response to warming in several broadleaf evergreen species (Aspinwall *et al.*, 2016; Scafaro *et al.*, 2017; Smith & Dukes, 2017; Crous *et al.*, 2018; Carter *et al.*, 2020) especially in species exposed to higher growth temperatures. Reduced J_{max} rates are likely to be related to reduced photosystem II (PSII) electron flow at moderately high temperatures (Havaux, 1996; Pastenes & Horton, 1996; Sharkey, 2005). The shift away from a linear electron flow by PSII towards increased cyclic electron flow can help to maintain a pH gradient (and proton motive force) across the thylakoid membrane in response to high temperatures and counteracts increased membrane leakiness of the thylakoid membrane (Bukhov *et al.*, 1999; Schrader *et al.*, 2004; Sharkey & Zhang, 2010). This mechanism, together with other structural changes in the thylakoid membrane, can help to avoid thermal damage and support thermostability in response to higher growth temperatures. Other adjustments to cope with high temperatures can be increased content of saturated fatty acids (Zhu *et al.*, 2018), induction of heat-shock proteins (Vierling, 1991) and changes in osmotic potential (Hüve *et al.*, 2006).

While warming may have negative effects on carbon storage, tropical species have some thermal resilience with moderate warming. Tropical and subtropical species have a large capacity to adjust to warmer temperatures via increases in the temperature optimum of photosynthesis and reduced respiration rates. Sullivan *et al.* (2020) reported that high daytime temperatures (> 32°C) contributed most to reduced growth rates in the tropics. Therefore, it remains important to further investigate the responses to warming in tropical forests (Cavaleri *et al.*, 2015) both in the short term and over longer time periods (Sullivan *et al.*, 2020) and evaluate how resilient tropical species are to future warming. This is especially true for mature trees rather than seedlings. Mature individuals may not exhibit the same responses as seedlings and much fewer studies have involved large trees (Doughty & Goulden, 2008; Crous *et al.*, 2013; Slot *et al.*, 2014; Aspinwall *et al.*, 2016). Based on these and other studies conducted on large trees in the field, our evidence of thermal acclimation of photosynthesis and respiration is similar in magnitude and direction. Moreover, other evidence points to convergent acclimation of photosynthesis and respiration to both seasonal and experimental warming (Vanderwel *et al.*, 2015; Reich *et al.*, 2016). While this is the case for the processes of carbon uptake and loss, other processes such as growth and water transport regulation are likely to be different between seedlings and mature trees.

Overall, this study provided insights into the mechanisms controlling the photosynthesis temperature response in rainforest tree species and their capacity to adjust to warming. Subtropical and tropical species showed greater adjustments of $T_{optA300}$, and leaf respiration compared with warm-temperate species. Photosynthetic capacity was reduced via a stronger reduction in J_{max25} in tropical compared with warm-temperate species. Therefore, our study found that tropical and subtropical rainforest tree species substantially acclimated to higher temperatures while exhibiting reductions in photosynthetic capacity at higher growth temperatures (> 32°C), indicating that tropical species are likely to reduce carbon uptake at higher growth temperatures. Photosynthetic biochemistry, but not stomatal limitation, was the main driver of the shift in the temperature response of photosynthesis and the increase of the temperature optimum of photosynthesis.

Both the temperature-driven shifts in photosynthesis and respiration should be considered together when forecasting future warming impacts at larger scales (Smith & Dukes, 2013; Mercado *et al.*, 2018). In addition, there is a need to understand how the responses to experimental warming are different from responses to extreme temperatures. Our findings indicated that the magnitude of acclimation can differ depending on climate zone, and that warming responses at 3.5°C warming may not be the same compared with larger temperature changes. These differences in acclimation capacity can be modified in combination with other climate change factors, for example limited water availability, a common co-limitation with warming in the field (Kumarathunge *et al.*, 2020). These are important questions to be addressed in future research to reflect more realistic climate change scenarios when predicting carbon exchange in land surface models.

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Author contributions

KYC designed the study with input of ZC and MGT. ZC led the data collection with help of AW-K, AB and NPB. ZC performed the data analyses with the guidance of KYC, BEM and MGT. Manuscript writing was led by ZC and KYC with input from all co-authors.

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Data availability

The data used in this manuscript are publicly available at https://figshare.com/s/173c66190ae77ccc6dd6.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Relationships between leaf temperature (T_{leaf}) and leaf-to-air vapour pressure deficit (VPD) at different growth temperatures.

Fig. S2 Temperature responses of photosynthesis at the mean C*i* (300 ppm) and different growth temperatures in six rainforest species from three different rainforest groups (means ± 1 SE, $n = 3$) (warm-temperate species, subtropical species and tropical species).

Fig. S3 Relationships between stomatal conductance (g_s) and vapour pressure deficit (VPD) at different growth temperatures in warm-temperate species, subtropical species and tropical species).

Fig. S4 Means and SE between stomatal conductance measured at 25°C (g_{s25}) and different growth temperatures (T_{growth}) across six rainforest species.

Fig. S5 Relationships between $A_{measuredCi}$–A_{300} and leaf temperature (T_{leaf}) at different growth temperatures in warm-temperate species, subtropical species and tropical species at each growth temperature.

Fig. S6 Temperature responses of the apparent maximum carboxylation (V_{cmax}) for each of six rainforest species measured in their respective growth temperatures at five leaf temperatures (T_{leaf}) in three replicates per growth temperature (means ± 1 SE).

Fig. S7 Temperature response of the apparent maximum electron transport rate (J_{max}) for each of six rainforest species measured in their respective growth temperatures at five leaf temperatures (T_{leaf}) in three replicates per growth temperature (means ±1 SE).

Fig. S8 Mean and SE of fitted values (3 replicates) of $J_{max} : V_{cmax}$ at a common leaf temperature (25°C) as a function of six growth temperatures across three rainforest groups: $J_{max25}/V_{cmax25} = -0.04 \times T_{growth} + 3.03$ ($P = 0.01$; $R^2 = 0.20$).

Fig. S9 The short-term temperature response of mitochondrial leaf respiration (R_{dark}) as a function of leaf temperature (T_{leaf}) measured at two different growth temperatures (different symbols) to assess the responses to +3.5°C warming among rainforest groups.

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