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Photosynthetic temperature responses of tree species in Rwanda: evidence of pronounced negative effects of high temperature in montane rainforest climax species

Angelica Varhammar
University of Wollongong, University of Gothenburg

Goran Wallin
University of Gothenburg

Christopher M. McLean
University of Wollongong, chrismc@uow.edu.au

Mirindi Eric Dusenge
University of Gothenburg

Belinda E. Medlyn
Macquarie University

See next page for additional authors

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Abstract

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Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

Publication Details

Authors

Angelica Varhammar, Goran Wallin, Christopher M. McLean, Mirindi Eric Dusenge, Belinda E. Medlyn, Thomas B. Hasper, Donat Nsabimana, and Johan Uddling

Photosynthetic temperature responses of tree species in Rwanda: evidence of pronounced negative effects of high temperature in montane rainforest climax species

Angelica Vårhammar[1], Göran Wallin[1], Christopher M. McLean[2], Mirindi Eric Dusenge[1,3], Belinda E. Medlyn[4], Thomas B. Hasper[1], Donat Nsabimana[3] and Johan Uddling[1]

[1]Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden; [2]Department of Biological Sciences, University of Wollongong, Wollongong, NSW 2522, Australia; [3]Department of Biology, University of Rwanda, Huye, Rwanda; [4]Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109, Australia

Author for correspondence:
Johan Uddling
Tel: +46 317863757
Email: johan.uddling@bioenv.gu.se

Summary

• The sensitivity of photosynthetic metabolism to temperature has been identified as a key uncertainty for projecting the magnitude of the terrestrial feedback on future climate change. While temperature responses of photosynthetic capacities have been comparatively well investigated in temperate species, the responses of tropical tree species remain unexplored.

• We compared the responses of seedlings of native cold-adapted tropical montane rainforest tree species with those of exotic warm-adapted plantation species, all growing in an intermediate temperature common garden in Rwanda. Leaf gas exchange responses to carbon dioxide (CO_2) at different temperatures (20–40°C) were used to assess the temperature responses of biochemical photosynthetic capacities.

• Analyses revealed a lower optimum temperature for photosynthetic electron transport rates than for Rubisco carboxylation rates, along with lower electron transport optima in the native cold-adapted than in the exotic warm-adapted species. The photosynthetic optimum temperatures were generally exceeded by daytime peak leaf temperatures, in particular in the native montane rainforest climax species.

• This study thus provides evidence of pronounced negative effects of high temperature in tropical trees and indicates high susceptibility of montane rainforest climax species to future global warming.

Introduction

Observations have unequivocally demonstrated increasing global surface air temperatures (Hartmann *et al.*, 2013), and global climate change models project a continuation of temperature increase over the coming century, irrespective of the chosen emission scenario (IPCC, 2013; Burrows *et al.*, 2014). As temperature is one of the most important environmental factors controlling physiological processes (Hughes, 2000; Poethig, 2003; Root *et al.*, 2003; Hegland *et al.*, 2009), increased temperature is expected to have significant effects on the fitness of all living organisms.

Improving the understanding of the effect of temperature on terrestrial plant species is particularly important, as most migrate far more slowly than would be necessary to remain in a suitable climate under mid- and high-range rates of global warming (IPCC, 2013, 2014). Furthermore, terrestrial vegetation has important biogeochemical, hydrological and biophysical interactions with the atmosphere and its responses thus affect both local and global climate (Denman *et al.*, 2007; Bonan, 2008). In particular, it is paramount to understand the responses of plant

primary production to climate change in order to project terrestrial feedbacks on the carbon cycle along with the potential of the terrestrial biosphere to be either mitigative or promotive to further global warming (Cox *et al.*, 2000; Cao *et al.*, 2001; Bonan, 2008). The sensitivity of photosynthetic metabolism to temperature has been identified as the most important uncertainty with respect to projections of the magnitude of the terrestrial feedback on future climate change, highlighting the need for a better understanding of plant photosynthetic responses to high temperature (Booth *et al.*, 2012).

In global vegetation models, photosynthesis of terrestrial plants is modelled using the well-established biochemical model of photosynthesis developed by Farquhar *et al.* (1980; Sellers *et al.*, 1997; Pitman, 2003; Prentice *et al.*, 2007). This model requires parameters of two photosynthetic capacities; the maximum carboxylation rate of ribulose-1,5-bisphosphate carboxylase/oxygenase (Rubisco; V_{cmax}) and the maximum rate of electron transport (J_{max}), necessary to regenerate ribulose-1,5-bisphosphate. The maximum rates of photosynthetic carboxylation and electron transport depend on multiple factors, of which the most important include light (Carswell *et al.*, 2000; Kenzo *et al.*, 2006),

nutrient availability (particularly nitrogen and phosphorus; Kattge *et al.*, 2009; Domingues *et al.*, 2010; Mercado *et al.*, 2011) and intercellular carbon dioxide (CO_2) concentration (C_i), which is dependent on stomatal conductance (g_s; Farquhar & Sharkey, 1982), as well as temperature (Kattge & Knorr, 2007). Increasing temperature causes J_{max} and V_{cmax} to rise to a maximum followed by a rapid decrease at supraoptimal temperatures (Berry & Björkman, 1980; Medlyn *et al.*, 2002a). Electron transport is considered to be particularly sensitive to high temperatures, because of its greater dependence on membrane stability (Murakami *et al.*, 2000; Sage & Kubien, 2007). Thus, the temperature at which the maximum rates occur, the optimum temperature (T_{opt}), is often found to be significantly lower for J_{max} than for V_{cmax} (Walcroft *et al.*, 1997; Dreyer *et al.*, 2001; Medlyn *et al.*, 2002a).

In temperate tree species, the T_{opt} values for V_{cmax}, J_{max} and leaf net photosynthesis (A_n) correlate with the prevailing temperature regimes (Battaglia *et al.*, 1996; Dreyer *et al.*, 2001; Medlyn *et al.*, 2002a; Kattge & Knorr, 2007; Gunderson *et al.*, 2010). Furthermore, plant photosynthesis has been shown to acclimate to prevailing growth temperature by shifting its T_{opt}, particularly that of J_{max}, towards the temperature of the ambient air if subjected to warming (Battaglia *et al.*, 1996; Cunningham & Read, 2002; Kirschbaum, 2004; Hikosaka *et al.*, 2006; Gunderson *et al.*, 2010). Photosynthetic thermal acclimation abilities have also been demonstrated in studies taking advantage of temperature differences with season (Battaglia *et al.*, 1996; Gunderson *et al.*, 2000; Medlyn *et al.*, 2002a; Crous *et al.*, 2013), altitude (Cavieres *et al.*, 2000; Zhang *et al.*, 2007) and provenance (Hill *et al.*, 1988; Gunderson *et al.*, 2000; Cunningham & Read, 2002; Medlyn *et al.*, 2002b).

While the photosynthetic temperature responses of temperate tree species are comparatively well studied, the responses of tropical tree species remain unexplored (Medlyn *et al.*, 2002a; Kattge & Knorr, 2007; Gunderson *et al.*, 2010). This is unfortunate, as tropical forests are inhabited by over half of all plant and animal species on Earth, represent one-fourth of the global terrestrial carbon storage and are responsible for at least one-third of the global primary production (Denman *et al.*, 2007; Bonan, 2008; Beer *et al.*, 2010; Zhou *et al.*, 2013). Tropical forests play a crucial role in regulating both regional and global climate (Lewis, 2006), and better understanding of the effect of increased temperature on tropical forests is therefore paramount (Denman *et al.*, 2007). Most studies investigating the photosynthetic temperature responses of tropical trees have focused on responses of A_n and not the underlying biochemical mechanisms (i.e. J_{max} and V_{cmax}). They predominantly focus on species and ecosystems in South America, primarily Amazonia (Rada *et al.*, 1996; Clark *et al.*, 2003; Wittich *et al.*, 2012; Cheesman & Winter, 2013), South East Asia (Mori *et al.*, 1990; Ishida *et al.*, 1999) and Australia (Pearcy, 1987; Read, 1990; Cunningham & Read, 2002), whereas to date, no temperature response assessments have been conducted on tropical African trees. These studies have indicated that tropical trees may have a more narrow optimum temperature range, with A_n quickly declining as temperatures become suboptimal or supraoptimal, compared with temperate and boreal species. This is believed to be a consequence of adaptation to a more stable climate and may imply that tropical species are more sensitive to future temperature increases (Berry & Björkman, 1980; Read, 1990; Battaglia *et al.*, 1996; Cunningham & Read, 2002; Way & Oren, 2010). Observations of considerable declines in growth rates of tropical trees resulting from only subtle increases in air temperature (Clark *et al.*, 2003; Feeley *et al.*, 2007; Doughty & Goulden, 2008; Way & Oren, 2010) further support this hypothesis. Tropical forests are thus suspected of being close to a thermal threshold, above which CO_2 uptake is strongly reduced (Doughty & Goulden, 2008).

This study aimed to improve the limited understanding of temperature responses of tropical primary production by providing the first temperature response assessments of photosynthetic capacities (i.e. J_{max} and V_{cmax}) in tropical tree species. This was achieved by examining leaf gas exchange responses to CO_2 at different temperatures (20–40°C) in three native cold-adapted, tropical montane rainforest species and three common exotic warm-adapted plantation species, in an intermediate temperature common garden in Rwanda. We hypothesized that: (1) J_{max} is more sensitive to high temperature than V_{cmax}, as has been found in temperate and boreal tree species. (2) Cold-adapted native montane rainforest species have lower photosynthetic optimum temperatures (i.e. T_{opt} for J_{max}, V_{cmax} and A_n) than warm-adapted exotic plantation species, as a consequence of adaptation to the species' climate of origin, which is not erased by acclimation to the common garden conditions. (3) The optimum temperatures of photosynthesis are commonly exceeded in the native tropical species growing in the common garden, but not in the exotic plantation species, demonstrating limited acclimation ability and high sensitivity to future global warming.

Along with increased temperatures, climate change also includes continued increases in atmospheric CO_2 concentrations (C_a; IPCC, 2013, 2014). The expected CO_2 rises are predicted to increase the optimum temperature of photosynthesis, such that the negative effects of increased temperature will be mitigated (Long, 1991; Cao *et al.*, 2001; Kirschbaum, 2004; Lloyd & Farquhar, 2008). A fourth hypothesis explores the temperature sensitivity under higher atmospheric CO_2 concentration conditions, according to the photosynthesis model parameterized for the investigated species: (4) in a moderate climate change scenario for year 2100 (IPCC, 2013, 2014), a 50% increase in atmospheric CO_2 concentration cancels the negative effects of 3°C warming such that heat-induced reductions in photosynthesis remain similar compared with today.

Materials and Methods

Study site and plant material

The study was carried out on seedlings cultivated in the Rwasave nursery, located on the edge of the Ruhande Arboretum (Rwanda; 2°36′S, 29°44′E; *c.* 1640 m above sea level (asl)) and surrounded by vegetation in all directions. At a meteorological station *c.* 2 km from the arboretum (1765 m asl; Nsabimana *et al.*, 2009), the average day and night air temperatures at 7.5 m

above ground were 20.8 and 17.1°C, respectively, the average relative humidity was 74% and annual rainfall was 1231 mm during 2006–2013. The climate of the region is tropical humid and the difference in mean temperature between the warmest and coldest months is 1.5°C. The rainfall is bimodal with most rain in March–May and lighter occurrence in September–December, separated by a major drought period in June–August and a moderately dry period in January–February. Maximum temperatures and the average diurnal temperature range at the meteorological station are provided in Table 1.

Daytime air temperature (Model TinyTag Plus 2; Gemini Data Loggers Ltd, Chichester, UK; placed inside self-ventilating radiation shields) at 1.8 m above ground in the nursery was similar to that at 1.8 m above ground at the meteorological station, but predawn temperature was c. 3°C lower at the lower location of the nursery. The vertical variation in air temperature was considerable, with the temperatures at 1.8 and 0.4 m above ground being 2°C and 4°C higher compared with the temperature at 7.5 m in the nursery.

The taxa selected (Table 2) were either native tropical montane rainforest tree species or silviculturally important exotics, planted in the Ruhande Arboretum one to two generations ago. The native species included two climax taxa from the Meliaceae family, *Carapa grandiflora* Sprague and *Entandrophragma excelsum* (Dawe & Sprague) Sprague, along with one pioneer species from the Rosaceae family, *Hagenia abyssinica* (Bruce) J. F. Gmelin. *Carapa grandiflora* is a dominant species in transitional Afromontane rainforest and has an altitudinal distribution ranging between 1600 and 2500 m asl (White, 1983; Fischer & Killmann, 2008; Bloesch *et al.*, 2009). *Entandrophragma excelsum* is a dominant species in Afromontane rainforest and occurs between 1500 and 2100 m asl (White, 1983; Fischer & Killmann, 2008; Bloesch *et al.*, 2009) and *H. abyssinica*, which is the diagnostic species for *H. abyssinica* forest, occurs at altitudes of 1800–3400 m asl (White, 1983; Fischer & Killmann, 2008;

Bloesch *et al.*, 2009). The plant material of the three native species originates from the Nyungwe national park montane rainforest (Rwanda; 2°15′–2°55′S, 29°00′–29°30′E; 1500–2950 m asl). At a meteorological station located at Uwinka (2°28′43″S, 29°12′00″E; 2465 m asl; Nsabimana, 2009), the average day and night air temperatures at 7.5 m above ground were 15.7 and 13.5°C, respectively, the relative humidity was 81%, and annual rainfall was 1879 mm during 2007–2013. At another meteorological station located at 1935 m asl in Nyungwe, the annual mean temperature was 1.5°C higher than at Uwinka. Maximum temperatures and average diurnal temperature range experienced at Uwinka are provided in Table 1.

Three common exotic plantation taxa were selected to represent warm-adapted exotics (Table 2): two Myrtaceae species, *Eucalyptus microcorys* F. Muell and *Eucalyptus maidenii* F. Muell, along with a deciduous pioneer species from the Meliaceae family, *Cedrela serrata* Royal. *Eucalyptus maidenii* occurs in temperate southern coastal New South Wales and Victoria, Australia (Hill, 1991), whereas *E. microcorys* is distributed in warmer subtropical coastal areas of New South Wales and Queensland, Australia (Hill, 1991). *Cedrela serrata* is known to occur from Central to South East Asia (Orwa *et al.*, 2009). Maximum temperatures and average diurnal temperature range experienced by the exotic species in their known native distributions are provided in Table 1.

The seedlings were cultivated in pots containing clay soil from the surrounding area (ISAR, 2011) and were irrigated twice daily with water sourced from the local creek. The pots were placed in monospecific plots, some partially shaded from the sun by basic shade houses. Seedling dimensions are provided in Table 2.

Gas exchange measurements

Gas exchange measurements were completed on two seedlings per day during July and August 2011. One fully developed sun leaf with a healthy appearance (i.e. normal colouration and no

Table 1 Temperature parameters (°C) for Nyungwe montane rainforest, the common garden of Ruhande Arboretum, and the known native distribution of three exotic tree species

Air temperature parameter	Nyungwe montane rainforest[1]	Common garden[2]	*Eucalyptus microcorys*[3]	*Eucalyptus maidenii*[3]	*Cedrela serrata*[4,5]
Mean diurnal range[6]	2.2	3.7	11.5	12.0	10.7
Mean daily maximum of warmest month[7]	19.2	24.8	26.9	24.3	n/a
Mean monthly maximum of warmest month[8]	22.1	27.5	33.1	32.6	29.6
Mean annual maximum[9]	22.6	27.8	40.8	40.4	n/a

Data for the native species refers to footnotes 1 and 2 and for the exotic species to footnotes 3–9. Values for the exotic species are based on climate extracted for coordinates where species observations have been recorded (*Eucalyptus*: 5598 records, 1940–2012; *Cedrela serrata*: nine records, dates not available). n/a, data not available.
[1]Measured at Uwinka meteorological station at 2465 m above sea level (asl) during 2007–2013.
[2]Measured at a nearby (c. 2 km away) meteorological station at 1765 m asl during 2006–2013.
[3]ALA (2014).
[4]GBIF (2014).
[5]Hijmans *et al.* (2005).
[6]Mean diurnal range (average of years 1950–2000; °C).
[7]Daily maximum of warmest month (average of years 1927–1995; °C).
[8]Monthly maximum of warmest month (average of years 1957–2004; °C).
[9]Annual maximum (average of years 1957–2004; °C).

Table 2 Information on species native distribution, average plant height, leaf size (taken as 0.7 × length × width), leaf mass per unit area, leaf nitrogen content per unit area (N_a) and mass (N_m) and leaf phosphorus content per unit area (P_a) and mass (P_m)

Species	Native distribution	Plant height (m)	Leaf size (cm^2)	Leaf mass per unit area (g m^{-2})	N_a (g m^{-2})	P_a (mg m^{-2})	N_m (%)	P_m (%)
Carapa grandiflora[1,2,3]	East African montane forest endemic	0.85 ± 0.04	85.9 ± 6.6A	81.4 ± 3.4A	2.14 ± 0.09A	106 ± 10AB	2.63 ± 0.08A	0.13 ± 0.01A
Entandrophragma excelsum[2,3,4]	Central East African forest	0.23 ± 0.02	35.7 ± 4.3B	55.5 ± 2.0BC	1.33 ± 0.04B	172 ± 14A	2.39 ± 0.10A	0.31 ± 0.03B
Hagenia abyssinica[2,3]	African montane forest endemic	0.39 ± 0.05	24.0 ± 2.9B	44.4 ± 2.8C	1.58 ± 0.11B	86.4 ± 17B	3.56 ± 0.14B	0.20 ± 0.04AB
Cedrela serrata[5]	South-east Asia	0.82 ± 0.03	19.2 ± 1.6B	56.8 ± 2.9BC	2.18 ± 0.20A	96.2 ± 12AB	3.82 ± 0.24B	0.17 ± 0.02A
Eucalyptus maidenii[6]	East Australia; NSW and VIC	0.89 ± 0.06	60.2 ± 9.3C	65.5 ± 1.5B	2.26 ± 0.11A	82.5 ± 7.9B	3.45 ± 0.16B	0.13 ± 0.01A
Eucalyptus microcorys[6]	East Australia; NSW and QLD	0.35 ± 0.04	15.7 ± 1.1B	67.6 ± 8.0AB	1.83 ± 0.18AB	145 ± 42AB	2.80 ± 0.20A	0.20 ± 0.05AB
Among species		***	***	***	***	**	***	***
Native vs exotic		ns	ns	ns	ns	ns	ns	ns

Species investigated include native tropical montane species (*Carapa grandiflora*, *Entandrophragma excelsum* and *Hagenia abyssinica*) and exotic plantation species (*Cedrela serrata*, *Eucalyptus maidenii* and *Eucalyptus microcorys*). Values represent mean ± SE. The significance of results from ANOVA (species comparison) and Student's *t*-test (native vs exotic species) is reported as: ns, $P > 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The same capital letter indicates no significant difference between species according to Tukey's *post hoc* test.
[1]Kenfack (2011). [2]Bloesch *et al.* (2009). [3]Fischer & Killmann (2008). [4]Lemmens (2008). [5]Orwa *et al.* (2009). [6]Brooker & Klenig (2006).

visible damage) was measured on each seedling and five to six seedlings per species were investigated. The species to be measured each day was selected randomly and different monospecific plots within the nursery were used for each replicate when available.

Measurements of the response of A_n to varying C_i (A–C_i curves) were conducted at leaf temperatures (T_{leaf}) of 20, 25, 30, 35 and 40°C using an LI–6400XT Portable Photosynthesis System equipped with an LED light source as well as an expanded temperature control kit (Li-Cor Inc., Lincoln, NE, USA). The measurements were conducted at a photosynthetic photon flux density of 1800 µmol m^{-2} s^{-1} and were commenced as soon as leaf temperature and g_s were stable. The A–C_i curves included measurements at the following CO_2 concentrations of air entering the leaf chamber: 400, 60, 125, 225, 400, 800, 1200, 1600, 2000 and 400 µmol mol^{-1}. As a result of difficulties in measuring at 40°C with acceptable levels of g_s (> 0.015 mol H$_2$O m^{-2} s^{-1}) and reaching 20°C on hotter days, not all desired leaf temperatures could be measured for some replicates. As a result, the temperature range for the native species *C. grandiflora* was 20–35°C (i.e. no measurements were completed at 40°C), four replicates were possible at 20°C for the exotic species *E. maidenii* and three replicates were possible at 40°C for the native species *E. excelsum*.

A sensitivity analysis was performed to assess the possible influence of cuticular transpiration on the estimated values of J_{max} and V_{cmax}. In this analysis, cuticular conductance was assumed to be 2% of maximum g_s (at 20°C), which is typical for nonsucculents (Larcher, 2003). Subtraction of this cuticular conductance from the original value of g_s (and the consequent recalculation of C_i) had relatively small effects on the parameterization of V_{cmax}

and J_{max}. In *C. grandiflora* at 35°C and *E. excelsum* at 40°C (the measurements with lowest g_s), the mean effects on J_{max} and V_{cmax} were +3 and +8%, respectively, while the effects for the other species or temperatures were considerably smaller. Results for J_{max} temperature responses are thus only slightly influenced by possible cuticular transpiration. The larger influence on V_{cmax} is probably a minor concern, as lack of discernible peaks within the measured temperature range for half of the species introduced a comparatively large uncertainty regarding the V_{cmax} high temperature responses (see the 'Photosynthetic temperature responses' subsection).

Parameterization of photosynthesis models

The photosynthesis model by Farquhar *et al.* (1980), with modifications of photosynthetic temperature dependences (Bernacchi *et al.*, 2001; Medlyn *et al.*, 2002a), was used to parameterize the photosynthetic capacities V_{cmax} and J_{max}, as well as the nonphotorespiratory CO_2 release in the light (R_d), from A–C_i curve data using the least-square method. The rates of V_{cmax}-limited photosynthesis (A_c) and J_{max}-limited photosynthesis (A_j) were estimated using Eqns 1 and 2:

$$A_c = \left(1 - \frac{\Gamma^*}{C_i}\right) \frac{V_{cmax^*} C_i}{C_i + K_c(1 + \frac{O}{K_o})} - R_d \qquad \text{Eqn 1}$$

$$A_j = J \frac{C_i - \Gamma^*}{4 C_i + 8 \Gamma^*} - R_d \qquad \text{Eqn 2}$$

(K_c and K_o, Michaelis–Menten constants for CO_2 and O_2, respectively; Γ^*, the CO_2 concentration at which the carboxylation reaction of Rubisco equals the oxygenation reaction.) Values

(at 25°C) and temperature sensitivities of Γ^*, K_c and K_o were taken from Bernacchi *et al.* (2001). Values of R_d are not reported because A–C_i curve based estimates of R_d are subject to rather large uncertainty.

Leaf mesophyll conductance to CO_2 was not estimated and therefore apparent V_{cmax} and J_{max} values were determined, based on C_i rather than the CO_2 concentration at the chloroplast. The uncertainty of the values of curvature of the light response (0.9) and quantum yield of electron transport (0.3 mol electrons mol^{-1} photons) used when calculating J_{max} from actual electron transport (J) has only a slight effect on the estimated value of J_{max} (Medlyn *et al.*, 2002a). The only *a priori* restriction placed on the V_{cmax} and J_{max} determination through A–C_i fitting was that data points with C_i below 100 μmol mol^{-1} were forced to be V_{cmax}-limited. Triose phosphate use limitation of photosynthesis, which mainly occurs at high C_i and low temperature (Sage, 2002), was not observed in the A–C_i curves of the present study (data not shown). As a consequence of low g_s at higher temperatures, the C_i did not reach values high enough for A_n to be limited by the rate of electron transport in some A–C_i curves. Determination of J_{max} required that A_n was clearly limited by J in at least one data point, for which the value predicted by electron transport limitation was > 10% lower than that predicted by carboxylation limitation (according to data at lower C_i). Inclusion of J_{max} data also required that there were at least two J_{max} values for each species and temperature combination. As a result, J_{max} data were unavailable for 20 of the 150 A–C_i curves obtained; mainly values at high temperatures in the exotic species *C. serrata* and the native species *C. grandiflora* and *E. excelsum*.

The temperature responses of photosynthetic capacities were determined by regressing V_{cmax} and J_{max} against measured T_{leaf} using a peaked Arrhenius equation (Eqn 3), where a deactivation term accounts for the negative effects at higher temperatures (Medlyn *et al.*, 2002a):

$$f(T_k) = k_{opt} \frac{H_d \exp\left(\frac{H_a(T_k - T_{opt})}{T_k R T_{opt}}\right)}{H_d - H_a\left(1 - \exp\left(\frac{H_d(T_k - T_{opt})}{T_k R T_{opt}}\right)\right)} \qquad \text{Eqn 3}$$

(H_a, the activation energy (kJ mol^{-1}); T_{opt}, optimum temperature (°K); k_{opt}, the value of J_{max} or V_{cmax} at T_{opt} (μmol m^{-2} s^{-1}); H_d, the deactivation energy (kJ mol^{-1}); T_k, the measured leaf temperature (°K); R, the universal gas constant (8.314 J mol^{-1} K^{-1}).) By fitting the observed data to Eqn 3, H_a, T_{opt}, k_{opt} and H_d could be estimated. However, the peaked Arrhenius equation is overparameterized if all four parameters are allowed to vary (Dreyer *et al.*, 2001; Medlyn *et al.*, 2002a; Kattge & Knorr, 2007) and, in such a case, data may be insufficient to reliably estimate all parameters. Therefore, following the method of previous studies on temperate and boreal species, H_d was held at a constant 200 kJ mol^{-1} for all species (Medlyn *et al.*, 2002a; Kattge & Knorr, 2007). In an analysis where H_d was also allowed to vary, it was only significantly different from 200 kJ mol^{-1} in one case (V_{cmax} in *E. maidenii*).

As all replicates did not have data covering the entire temperature range, Eqn 3 was fitted to data pooled for each species. Fitted parameters were considered to significantly differ between two species if $P \le 0.01$, that is, if the following relationship between mean values (x) and SE was true:

$$(x_1 - x_2) - 2.58\sqrt{SE_1^2 + SE_2^2} > 0 \qquad \text{Eqn 4}$$

While the probability of obtaining at least one significant difference by pure chance is 14% ($1 - 0.99^{15}$) when making 15 pairwise comparisons, the probability of obtaining at least two significant differences (as found here; Table 3) is just 2%.

Net photosynthesis temperature responses

To estimate biochemical limitations of A_n at varying temperatures, the Farquhar *et al.* (1980) photosynthesis model parameters from each A–C_i curve were used to calculate A_n at a common C_i and saturating photosynthetic photon flux density (1800 μmol m^{-2} s^{-1}), for each leaf replicate and measurement temperature. The intercellular to ambient CO_2 concentration ratio (C_i:C_a) was assumed to be 0.7. As the global ambient CO_2 concentration at the time of measurement was 389 μmol mol^{-1} (Thoning *et al.*, 2014), the common C_i was set to a constant value of 272 μmol mol^{-1}. In an additional analysis to assess the effect of 50% elevated CO_2 concentration on photosynthetic temperature optimum, A_n was calculated at a common C_i of 408 μmol mol^{-1}.

In order to also account for stomatal limitations of A_n at increasing temperature, a third analysis was conducted in which the decrease in C_i with increasing temperature and leaf-to-air vapour pressure deficit (VPD) was calculated according to a coupled stomatal-photosynthesis model assuming optimal stomatal behaviour (A_{nT}; Medlyn *et al.*, 2011). The atmospheric vapour pressure was held constant at 1.6 kPa (the mean predawn value from the nearby meteorological station, which varied little over the year and remained fairly constant during the day). The C_i concentrations calculated with this stomatal behaviour model were, for each 5°C increase between 20 and 40°C, 284, 253, 229, 209 and 192 μmol mol^{-1}. For a +50% atmospheric CO_2 concentration scenario, the corresponding values were 427, 380, 344, 314 and 287 μmol mol^{-1}.

The temperature responses of A_n at C_i of 272 μmol mol^{-1} (A_{n272}) and C_i of 408 μmol mol^{-1} (A_{n408}) were parameterized for each leaf replicate using nonlinear regression of a second-order equation (Säll & Pettersson, 1994; Battaglia *et al.*, 1996; Gunderson *et al.*, 2010), where $A_n(T)$ is the A_n (μmol m^{-2} s^{-1}) at a given air temperature T (°C) and A_{opt} is the A_n at the optimum temperature (T_{opt}):

$$A_n(T) = A_{opt} - b(T - T_{opt})^2 \qquad \text{Eqn 5}$$

Eqn 5 was fitted to A_{n272} and A_{n408} data for individual leaves, and the significance of differences in T_{opt} among species and provenances (i.e. cold-adapted vs warm-adapted) was determined

Table 3 Temperature response parameters estimated for maximum electron transport rate, maximum Rubisco carboxylation rate (T_{opt}, H_a, H_d, J_{max}^{25} and V_{cmax}^{25}, see Eqn 3), stomatal conductance (g_s) and optimum temperatures for net photosynthesis at an intercellular CO_2 concentration of 272 and 408 µmol mol^{-1}

Species	J_{max} T_{opt} (°C)	J_{max} H_a (kJ mol^{-1})	J_{max} H_d (kJ mol^{-1})	J_{max}^{25} (µmol m^{-2} s^{-1})	V_{cmax} T_{opt} (°C)	V_{cmax} H_a (kJ mol^{-1})	V_{cmax} H_d (kJ mol^{-1})	V_{cmax}^{25} (µmol m^{-2} s^{-1})	g_s (µmol m^{-1} s^{-1})	A_{n272} T_{opt} (°C)	A_{n408} T_{opt} (°C)
Carapa grandiflora	29.3 ± 1.1A	55.7 ± 62	200	81.6 ± 3.1A	36.0 ± 2.7AB	72.9 ± 43	200	43.6 ± 2.6A	0.09 ± 0.01A	29.3 ± 1.35	31.1 ± 2.22
Entandrophragma excelsum	32.4 ± 1.0AC	48.2 ± 29	200	56.7 ± 3.1B	38.4 ± 1.5AB	73.2 ± 30	200	30.2 ± 2.5A	0.04 ± 0.01A	28.7 ± 0.29	29.9 ± 0.71
Hagenia abyssinica	30.3 ± 0.9A	32.6 ± 34	200	160 ± 6.4CE	35.5 ± 1.2A	75.6 ± 46	200	69.6 ± 5.8BC	0.36 ± 0.05B	24.1 ± 2.35	25.7 ± 1.90
Cedrela serrata	34.5 ± 1.3C	45.7 ± 16	200	124 ± 7.4DE	34.6 ± 1.6A	66.4 ± 65	200	73.1 ± 5.5BCE	0.15 ± 0.02A	22.8 ± 2.90	28.8 ± 0.58
Eucalyptus maidenii	37.8 ± 0.7BC	36.7 ± 6.8	200	158 ± 2.4CE	41.9 ± 1.2B	51.6 ± 8.6	200	96.3 ± 2.9DE	0.41 ± 0.04B	26.5 ± 0.71	29.3 ± 0.56
Eucalyptus microcorys	38.3 ± 4.2ABC	26.1 ± 24	200	144 ± 10CDE	39.0 ± 2.1AB	63.2 ± 32	200	91.5 ± 5.9CDE	0.66 ± 0.09C	26.6 ± 1.93	29.8 ± 1.82
Among species	**	ns		**	**	ns		**	**	ns	ns
Native vs exotic	**	ns		ns	ns	*		*	ns	ns	ns

T_{opt}, optimum temperature; H_a, activation energy; H_d, deactivation energy; J_{max}^{25}, maximum electron transport rate at 25°C; V_{cmax}^{25}, maximum Rubisco carboxylation rate at 25°C; g_s, stomatal conductance at 25°C and [CO2] of 400 µmol mol^{-1}; $T_{opt} A_{n272}$, optimum temperature of net photosynthesis at internal [CO2] of 272 µmol mol^{-1}; $T_{opt} A_{n408}$, optimum temperature of net photosynthesis at internal [CO2] of 408 µmol mol^{-1}.
The native tropical montane species are Carapa grandiflora, Entandrophragma excelsum and Hagenia abyssinica. The exotic plantation species are Cedrela serrata, Eucalyptus maidenii and Eucalyptus microcorys. Values represent mean ± SE. The significance of results from ANOVA (species comparison) and Student's t-test (native vs exotic species) is reported as: ns, P > 0.05; *, P < 0.05; **, P < 0.01. The same capital letter indicates no significant difference between species according to Eqn 4.

by one-way ANOVA and Student's *t*-test, respectively. Five leaves that had restricted A_{n272} or A_{n408} temperature ranges, and presumably as a result of this did not peak within the range of available data, were excluded from the analysis. Eqn 5 was not applied to the A_{nT} data as its highest values were commonly found at or near the lower end of the measured temperature range (i.e. there was often no discernible peak).

Leaf traits and energy balance

Leaf size (length and width) was recorded with a ruler to the nearest millimetre. A hole punch (13 mm diameter) was used to collect discs from each leaf, avoiding major veins, in order to determine leaf mass per unit area (LMA) and leaf nitrogen and phosphorus content expressed per unit area (N_a and P_a, respectively) and mass (N_m and P_m, respectively). The collected leaf material was oven-dried at 70°C for at least 48 h before dry mass was recorded. The discs were milled using a ball mill with stainless steel grinding jars (Model MM 301; Retsch, Haan, Germany). Leaf nitrogen content was determined using an elemental analyser (EA 1108; Fison Instruments, Rodano, Italy). Leaf phosphorus content was determined by extracting and oxidating leaf phosphorus into phosphate (Valderrama, 1981), followed by determining phosphate content through spectrophotometry (Ames, 1966). Eighteen leaf samples were analysed for phosphorus content using a different method, inductively coupled plasma mass spectrometry (ICP-MS; Basic Suite 1VE1; ACME Analytical Laboratories, Vancouver, BC, Canada), in order to calibrate the spectrophotometric method.

Data on g_s (at 25°C) and leaf dimensions, together with micrometeorological data collected at 7.5 m above ground from the local meteorological station, were used to model the annual mean leaf temperature (modelled T_{leaf}) of horizontal leaves at the hottest hour of the day (15:00 h) for each species. As a result of the large variation in vertical air temperature, the micrometeorological input data for the T_{leaf} modelling were corrected for the 3°C higher temperature at canopy height (c. 1.0 m) and the corresponding vertical difference in VPD (assuming no variation in absolute air humidity). The horizontal wind speed at canopy height was estimated by assuming a logarithmic wind profile (Campbell & Norman, 1998). The micrometeorological data used in the energy balance calculations included mean annual air temperature (26.0°C; 23.0°C at 7.5 m), wind speed (0.45 m s^{-1}; 1.52 m s^{-1} at 7.5 m), total incoming irradiance (381 W m^{-2}) and VPD (2.12 kPa; 1.57 kPa at 7.5 m) at 15:00 h. In an additional analysis, T_{leaf} was estimated based on mean daytime (06:30–18:30 h) environmental conditions at canopy height (air temperature 23.9°C; wind speed 0.35 m s^{-1}; incoming radiation 285 W m^{-2}; VPD 1.36 kPa). Leaf energy balance equations were taken from Campbell & Norman (1998), with particular attention being paid to expressing variables on a relevant leaf area basis (i.e. one- or two-sided). The photosynthetically active radiation was assumed to be 50% of the total incoming radiation.

Leaf temperatures were also measured with infrared thermometers (Model IR-66; CEM, Shenzhen, China) on seedlings of all species except the exotic species *E. microcorys*. These

measurements were conducted on similarly sized plants growing in the nursery in March 2014, under sunny conditions in the early afternoon (13:00–15:00 h) of four days. On each day, T_{leaf} was measured on 20–30 leaves per species, selecting leaves with a horizontal leaf angle.

Results

Photosynthetic temperature responses

Values of J_{max} and V_{cmax} at 25°C differed among all six species (Table 3; Fig. 1; J_{max}: $P < 0.01$; V_{cmax}: $P < 0.01$), but all had a similar J_{max} to V_{cmax} ratio ($J : V$; mean 1.75 ± 0.07 SE), except for *H. abyssinica* which had a mean ratio of 2.29 ± 0.14 SE ($P < 0.001$). The native species, *E. excelsum* and *C. grandiflora*, had the lowest values of both J_{max} and V_{cmax} (Table 3; Fig. 1). Additionally, g_s at 25°C differed significantly among species ($P < 0.01$; Table 3), in a similar pattern as for photosynthetic capacities. Comparisons between native tropical montane species and the exotic plantation species demonstrated that native species had significantly lower values of V_{cmax} ($P = 0.04$) and higher $J : V$ ratios than exotic species ($P = 0.01$), while J_{max} and g_s did not differ between these two groups (Table 3).

Both J_{max} and V_{cmax} at 25°C had significant positive relationships with leaf nitrogen content, expressed on both an area (N_a) and a mass basis (N_m; $P \leq 0.04$; Fig. 2); however, stronger relationships were found for N_m (Fig. 2). Leaf nitrogen content also differed significantly among species ($P < 0.01$; Table 2), where higher N_m was found in *C. serrata*, *E. maidenii* and *H. abyssinica*, and higher N_a was found in *C. serrata*, *E. maidenii* and *C. grandiflora*. The species also differed in LMA ($P < 0.01$; Table 2), with the highest values found in *C. grandiflora* and the lowest in *H. abyssinica*. Neither LMA nor leaf nutrient content significantly differed between native and exotic taxa (Table 2).

The leaf phosphorus content also differed among species ($P < 0.01$), but not between native and exotic taxa (Table 2). The response of J_{max} and V_{cmax} at 25°C to leaf phosphorus content varied among species, on both a mass (P_m) and an area basis (P_a; data not shown). The data could therefore not be pooled, as for the response to leaf nitrogen content, and data replication was deemed insufficient to conclude that there were any effects of leaf phosphorus content on photosynthetic capacities at an individual species level.

The activation energy (H_a) of V_{cmax} and J_{max} did not significantly differ among species, but H_a was generally higher for V_{cmax} than for J_{max} (paired t-test: $P = 0.002$). H_a for V_{cmax} was also significantly higher in the native than in the exotic species ($P = 0.04$; Table 3), while H_a for J_{max} did not differ between the two groups.

Values of T_{opt} for V_{cmax} and J_{max} differed among species and ranged between 29.3 and 38.3°C and between 34.6 and 41.9°C, respectively (Table 3; Fig. 1). Values of T_{opt} were lower for J_{max} than for V_{cmax} in native species, but not in exotics (Table 3; Fig. 1). Native species also had significantly lower T_{opt} for J_{max} than exotic species ($P = 0.01$), whereas T_{opt} for V_{cmax} did not differ (Table 3).

For J_{max}, the temperature response curves had clear discernible peaks within the measured temperature range, particularly for the three native species (Fig. 1a). Similarly, clear peaks within the temperature responses for V_{cmax} could be produced for *E. excelsum*, *H. abyssinica* and *C. serrata*. However, the lack of clear peaks causes uncertainty in the T_{opt} estimates of V_{cmax} for the remaining three species, particularly *C. grandiflora*, for which measurements only occurred up to 35°C (Fig. 1b).

Three different parameters of A_n were determined: A_n at a constant $C_i : C_a$ ratio of 0.7 (A_{n272}); A_n at a constant $C_i : C_a$ ratio of 0.7 in an atmosphere with 50% higher CO_2 concentration (A_{n408}) and A_n at a $C_i : C_a$ ratio that decreased with increasing temperature, as predicted by an optimal stomatal behaviour model (A_{nT}; Medlyn *et al.*, 2011; Fig. 3). The optimum temperatures of A_{n272} and A_{n408} did not significantly differ among species or between native and exotic species (Table 3). The average T_{opt} values for A_{n272} and A_{n408} across species were 26.3°C (± 0.85

● *Carapa grandiflora*   ○ *Cedrela serrata*
■ *Entandrophragma excelsum*   □ *Eucalyptus maidenii*
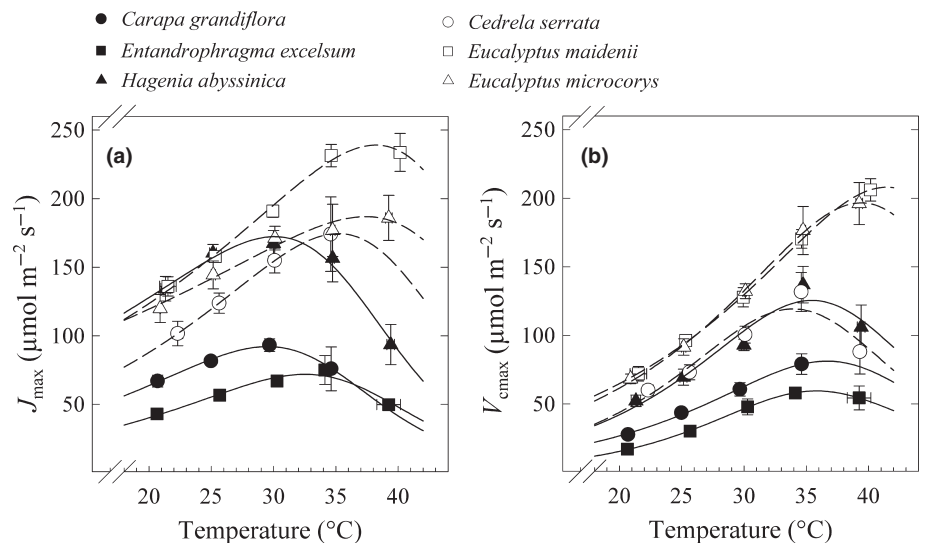▲ *Hagenia abyssinica*   △ *Eucalyptus microcorys*

Fig. 1 Responses of (a) maximum electron transport rate (J_{max}) and (b) maximum rate of Rubisco carboxylation (V_{cmax}) to temperature. Species include native tropical montane species (closed symbols and solid lines) and exotic species (open symbols and dashed lines). Error bars indicate $\pm$ SE. Lines represent the fitted peaked Arrhenius equations.
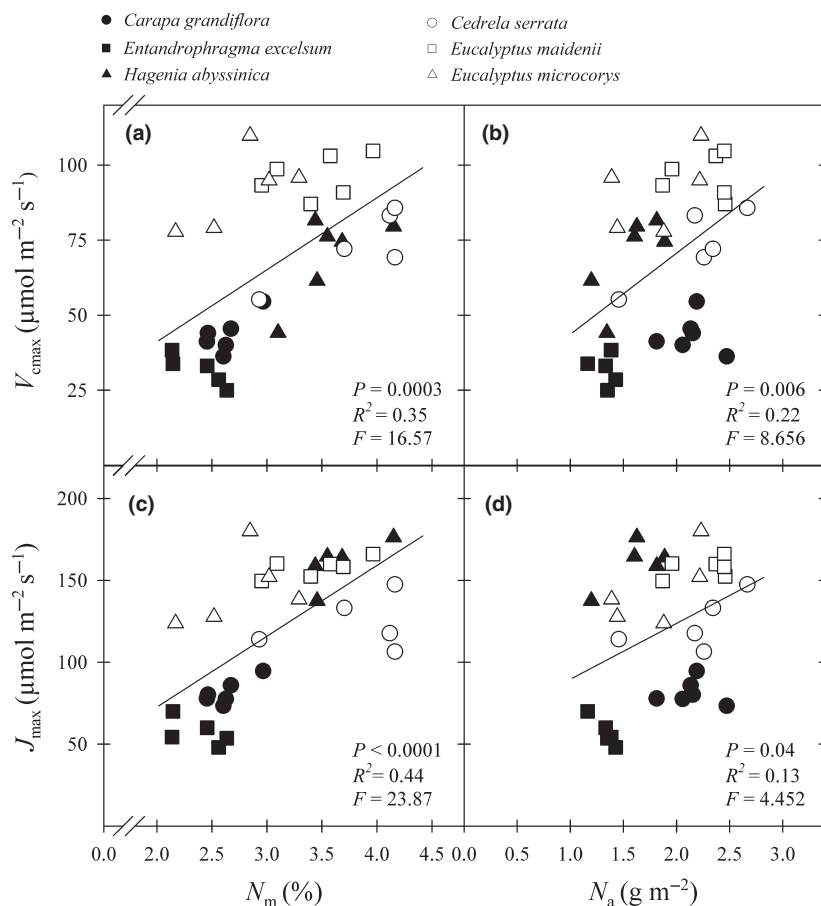
● *Carapa grandiflora* ○ *Cedrela serrata*
■ *Entandrophragma excelsum* □ *Eucalyptus maidenii*
▲ *Hagenia abyssinica* △ *Eucalyptus microcorys*

(a) $P = 0.0003$ $R^2 = 0.35$ $F = 16.57$

(b) $P = 0.006$ $R^2 = 0.22$ $F = 8.656$

(c) $P < 0.0001$ $R^2 = 0.44$ $F = 23.87$

(d) $P = 0.04$ $R^2 = 0.13$ $F = 4.452$

y-axes: V_{cmax} (µmol m^{-2} s^{-1}), J_{max} (µmol m^{-2} s^{-1})

x-axes: N_m (%), N_a (g m^{-2})

Fig. 2 Linear regressions of (a, b) maximum Rubisco carboxylation rate (V_{cmax}) and (c, d) maximum electron transport rate (J_{max}) at 25°C with increasing leaf nitrogen (N) content. N content is expressed on a mass basis (a, c; N_m) and an area basis (b, d; N_a) for native tropical montane species (closed symbols) and exotic plantation species (open symbols).

SE) and 29.0°C (± 0.75 SE), respectively (Figs 3a,b, 4). The A_{nT} at ambient atmospheric CO_2 concentrations was negatively affected by temperatures above 20–25°C in all species and its T_{opt} could thus not be confidently estimated (Fig. 3c). This demonstrates that, when stomatal responses are also considered, photosynthetic optima drastically decrease. For a +50% atmospheric CO_2 concentration scenario, A_{nT} peaked at 24–27°C (Fig. 3d). In a sensitivity analysis, we assessed the influence of a 6% downregulation in V_{cmax} under elevated CO_2; a typical response of trees to growth in elevated CO_2 (Ainsworth & Long, 2005). Such down-regulation had only a minor effect on T_{opt} of A_{n408}, which was increased from 29.0 to 29.5°C (± 1.2 SE) across all species (Supporting Information Fig. S1).

Leaf temperatures in relation to photosynthetic optimum temperatures

Leaf width, length and g_s (Table 2) along with micrometeorological parameters were used to model the annual mean T_{leaf} of the six species at the hottest hour (15:00 h) in the common garden. Modelled T_{leaf} values were considerably higher for species with large leaves and low g_s as compared with species with smaller leaves and/or higher g_s (Fig. 4; Table 2). Consequently, *C. grandiflora* and *E. excelsum* (large leaves, low g_s) were found to have the highest modelled T_{leaf} and *E. microcorys* (small leaves, high g_s) had the lowest, while the

other species had intermediate values of leaf size, g_s and modelled T_{leaf}. Field measurements collected at 15:00 h on four days in March 2014 confirmed the pattern of differences in modelled T_{leaf} among species (Fig. 4). During these observations, air temperature at the meteorological station was 25.3°C; that is, somewhat above the mean annual air temperature at 15:00 h of 23.0°C. Estimates of T_{leaf} based on average daytime (06:30–18:30 h) environmental conditions were 1–2°C lower than the estimates for 15:00 h (Fig. 4).

As the optimum temperature of photosynthesis (J_{max}, V_{cmax}, A_{n272} and A_{n408}) refers to leaf temperature, the results were compared with modelled and observed T_{leaf} values in order to determine acclimation capacity to the temperature of the common garden and potential sensitivity to global warming. Daytime mean and peak T_{leaf} greatly exceeded the T_{opt} for J_{max} in the native species *C. grandiflora* and *E. excelsum* (Fig. 4). In *H. abyssinica* and *C. serrata*, values of T_{leaf} and T_{opt} for J_{max} were similar, while the two *Eucalyptus* species had considerably lower T_{leaf} than T_{opt} for J_{max}. Daytime mean and peak T_{leaf} values were similar to T_{opt} for V_{cmax} in *C. grandiflora*, *E. excelsum* and *C. serrata* but lower than T_{opt} for V_{cmax} in the other three species (Fig. 4). As for J_{max}, the difference between optimal temperatures of photosynthetic capacities and T_{leaf} was largest (c. 10°C) for the two *Eucalyptus* species.

The optimal temperature of A_n at a C_i of 272 µmol mol^{-1} was 26.3°C averaged across all six species (± 0.85 SE), and thus
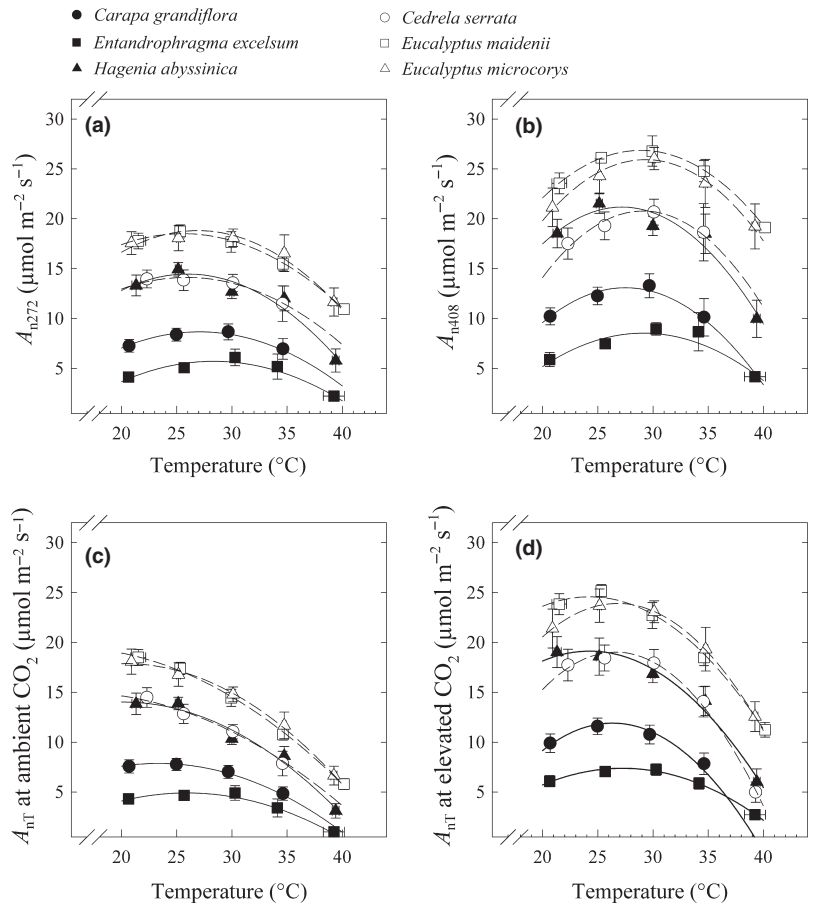
Fig. 3 Temperature responses of net photosynthetic rates are shown at (a) a common ambient atmospheric [CO_2] of 272 µmol mol^{-1} (A_{n272}), (b) a common elevated atmospheric [CO_2] of 408 µmol mol^{-1} (A_{n408}), (c) a temperature-dependent intercellular [CO_2] that decreases from 284 µmol mol^{-1} at 20°C to 192 mol mol^{-1} at 40°C in ambient atmospheric [CO_2] (A_{nT}), and (d) a temperature-dependent intercellular [CO_2] that decreases from 427 to 287 µmol mol^{-1} in elevated atmospheric [CO_2] (see Net photosynthesis temperature responses section in Materials and Methods), for native tropical montane species (closed symbols and solid lines) and exotic plantation species (open symbols and dashed lines). Error bars indicate ± SE. Lines represent the fitted net photosynthesis equation (Eqn 5).

significantly lower than daytime mean and peak T_{leaf} in all species (Fig. 4; Table 3). Increasing the CO_2 concentration by 50% increased the average optimum temperature of A_n by 2.7°C, from 26.3 to 29°C, across all six species (Fig. 4; Table 3). The T_{opt} for A_{n408}, however, remained significantly below T_{leaf} in all species except *E. microcorys*. The exceedance of T_{opt} for both A_{n272} and A_{n408} by T_{leaf} was largest in the two climax montane rainforest tree species *C. grandiflora* and *E. excelsum*.

Accounting also for stomatal responses to increasing VPD as temperature rises, peak daytime T_{leaf} exceeded the T_{opt} for A_{nT} in all species under ambient CO_2 concentrations (Figs 3c, 4). For a +50% atmospheric CO_2 concentration scenario, T_{leaf} exceeded the T_{opt} for A_{nT} in all species except *E. microcorys* (Figs 3d, 4).

Discussion

The overall objective of this study was to improve the limited understanding of temperature responses of photosynthesis in tropical tree species. This study has provided the first temperature response assessments of photosynthesis in tropical African montane trees and, to the best of our knowledge, the first estimates of temperature responses of photosynthetic capacities (i.e. J_{max} and V_{cmax}) in tropical tree species.

Hypothesis (1) predicted that J_{max} would be more sensitive to increased temperature than V_{cmax}, which was confirmed for the tropical montane species, with T_{opt} being 5–7°C lower for J_{max}

than for V_{cmax} (Table 3). This finding conforms to the concept of a greater dependence of electron transport than of Rubisco carboxylation on thylakoid membrane stability and, thus, higher sensitivity to high temperatures (Murakami *et al.*, 2000; Sage & Kubien, 2007). It is also consistent with findings of previous studies on temperate and boreal species (Dreyer *et al.*, 2001; Medlyn *et al.*, 2002a; Kattge & Knorr, 2007). In contrast to the native montane rainforest species, the exotic plantation species had similarly high T_{opt} for both J_{max} and V_{cmax} (Table 3). The T_{opt} values for J_{max} in the exotic species were in the upper range of those reported previously (Kattge & Knorr, 2007), indicating that the photosynthesis of these species is well adapted to high temperatures.

Hypothesis (2) predicted that the native montane species would have lower optimum temperatures for photosynthesis than the exotic plantation species, as a consequence of being adapted to a cooler climate combined with expected lower acclimation ability (Cunningham & Read, 2002; Way & Oren, 2010). This was confirmed for J_{max} but not for V_{cmax} (Table 3; Figs 1, 4), suggesting that thylakoid electron transport capacity does not readily acclimate to the environmental conditions of the common garden in the native montane species. This implies that there are genetically controlled differences in photosynthetic temperature responses between the native and exotic species of this study, relating to their adaptations to a colder or warmer origin.
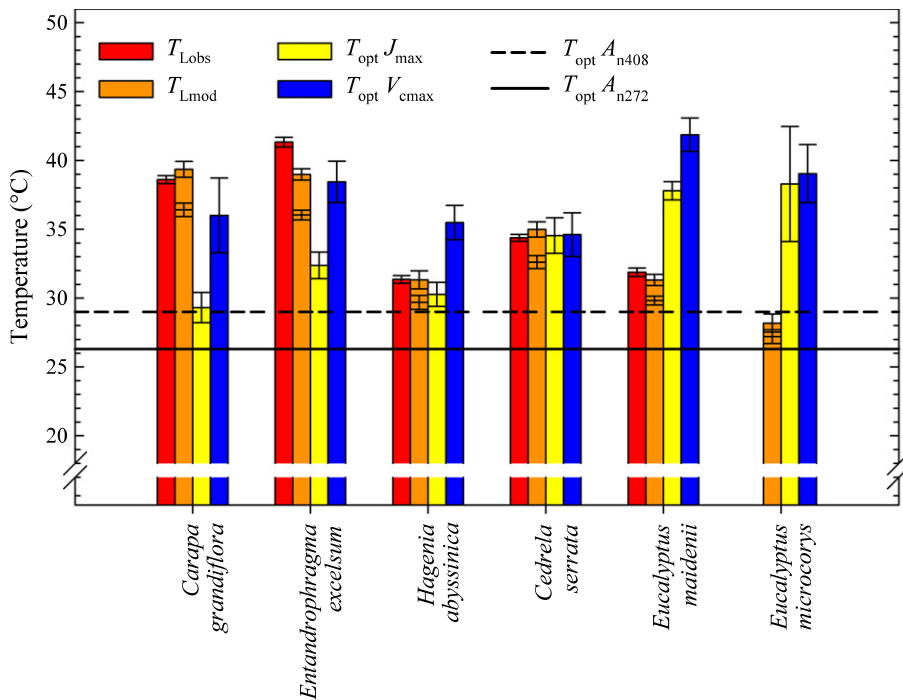
Fig. 4 Leaf temperatures in relation to photosynthetic optimum temperatures. Leaf temperatures are observations from four clear days (T_{Lobs}; red; 28.3°C air temperature at 1 m above ground) or modelled estimates based on mean annual weather data (T_{Lmod}; orange; upper values for 15:00 h weather; lower values for mean 06:30–18:00 h weather) for the native tropical montane species *Carapa grandiflora*, *Entandrophragma excelsum* and *Hagenia abyssinica* and the exotic plantation species *Cedrela serrata*, *Eucalyptus maidenii* and *Eucalyptus microcorys*. Also shown are optimum temperature (T_{opt}) of maximum electron transport rate (J_{max}; yellow) and maximum Rubisco carboxylation rate (V_{cmax}; blue). Error bars indicate ± SE. Horizontal lines indicate the optimum temperature for net photosynthesis at a constant internal [CO_2] of 272 (T_{opt} for A_{n272}; solid line; 26.3°C) and 408 μmol mol^{-1} (T_{opt} for A_{n408}; dashed line; 29°C).

The apparent contradiction of native and exotic species having different T_{opt} for J_{max} but not for A_n at a common C_i (A_{n272} and A_{n408}) is caused by A_n at CO_2 concentrations of 272 and 408 μmol mol^{-1} typically being V_{cmax} limited. The T_{opt} for V_{cmax} was not significantly different between native and exotic species (Table 3).

Hypothesis (3) predicted that limited acclimation ability of the native montane rainforest species would cause their estimated photosynthetic optimum temperatures to be frequently surpassed by their leaf temperatures, whereas the exotic plantation species, adapted to a warmer and more variable climate (Table 1), would not be as susceptible to high temperatures and thus would be better acclimated to the common garden conditions. This hypothesis was confirmed by the finding of very large (c. 10°C) exceedances of T_{opt} for A_{n272} by T_{leaf} at the hottest hour of the day in the two climax montane rainforest species, *C. grandiflora* and *E. excelsum*, compared with considerably smaller but significant exceedances in the other species in the common garden (Table 3; Fig. 4). The larger exceedances in the two climax montane rainforest species compared with the other species were related to differences in leaf energy balance, rather than differences in A_n optimum temperatures (Table 3; Fig. 4). The large interspecific variation in T_{leaf} highlights the importance of considering leaf traits influencing the leaf energy balance (i.e. leaf size and g_s) when evaluating plant sensitivity to air temperature and global warming. Different species grown together may have similar physiological temperature responses but still experience very different degrees of heat stress as a result of differences in their leaf energy budgets.

Our results demonstrate that photosynthesis of native montane rainforest climax tree species (i.e. *C. grandiflora* and *E. excelsum*) grown in a c. 5°C warmer habitat (Table 1) regularly operates at supraoptimal temperatures with respect to biochemical limitations (i.e. A_{n272}; Fig. 4), and that this situation is worsened if also

considering stomatal limitations (A_{nT}; Fig. 3c). Our results thus support earlier suggestions that the commonly observed midday dips in photosynthesis are linked to supraoptimal temperatures and that tropical trees may be especially susceptible to warming (Clark *et al.*, 2003; Clark, 2004; Doughty & Goulden, 2008). The finding of tropical climax species being particularly sensitive to high temperature is also in line with evidence from investigations of warming effects on the growth of tropical South American seedlings. For example, Cheesman & Winter (2013) have demonstrated a stronger negative effect of warming on growth in seedlings of tropical climax species than in those of tropical pioneer species. While not conclusive or directly applicable to mature forest, this suggests that warmer ambient temperatures have the potential to threaten seedling growth and recruitment and potentially migration and survival rates of tropical montane rainforest climax species (Medjibe *et al.*, 2014; Zhu *et al.*, 2014). This may also affect not only canopy species, but co-occurring biota which may not be able to persist in nonclimax vegetation communities (Poulsen *et al.*, 2011).

Hypothesis (4), predicting that a moderate climate change scenario (+50% increased atmospheric CO_2 concentration and +3°C) would have minimal effects on heat-induced reductions in photosynthesis, was corroborated by the finding that 50% increased atmospheric CO_2 concentration increased the optimum temperature of A_n by 2.7°C across all species (Table 3). This finding of balancing effects of projected increases in CO_2 and temperature on the T_{opt} exceedances of photosynthesis in tropical trees is in line with findings by Lloyd & Farquhar (2008). While heat-induced reductions in the photosynthesis of a given species may be unaltered by concurrently rising atmospheric CO_2 and temperature, global warming will probably affect the competitive balance between tropical tree species with different magnitudes of optimum temperature

exceedances. Our results (Fig. 4) as well findings in earlier experiments (Cheesman & Winter, 2013; Zhu *et al.*, 2014) indicate that such effects would be to the disadvantage of montane rainforest climax species, which may be outcompeted by species exhibiting smaller heat-induced reductions in photosynthesis; that is, pioneer species or species adapted to a warmer climate.

In conclusion, results presented here demonstrate that the photosynthesis of seedlings of cool-adapted montane rainforest climax tree species is very sensitive to high temperature. The leaf temperatures of sunlit foliage at the hottest hour of the day in these species (*c.* 40°C) greatly exceeded the photosynthetic optimum temperatures, as a result of low transpiratory cooling (i.e. low g_s) and inefficient heat dissipation (i.e. large leaf size). Furthermore, montane rainforest tree species had lower optimum temperatures for J_{max} compared with warm-adapted exotic plantation species, indicating that they do not readily acclimate to the *c.* 5°C warmer conditions in the common garden. Our results suggest that montane rainforest climax species may be particularly sensitive to future global warming and highlight the urgent need for more research on thermal responses of photosynthesis (considering biochemical and stomatal limitations as well as leaf energy balance) in tropical trees in order to better assess their sensitivity to global warming.

Acknowledgements

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Temperature responses of net photosynthesis at an elevated atmospheric $[CO_2]$ of 408 µmol mol^{-1} (A_{n408}) using 6% lower V_{cmax} values.

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