

Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate–vegetation model

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Abstract

The response of plant respiration (R) to temperature is an important component of the biosphere's response to climate change. At present, most global models assume that R increases exponentially with temperature and does not thermally acclimate. Although we now know that acclimation does occur, quantitative incorporation of acclimation into models has been lacking. Using a dataset for 19 species grown at four temperatures (7, 14, 21, and 28 °C), we have assessed whether sustained differences in growth temperature systematically alter the slope and/or intercepts of the generalized log–log plots of leaf R vs. leaf mass per unit leaf area (LMA) and vs. leaf nitrogen (N) concentration. The extent to which variations in growth temperature account for the scatter observed in log–log R –LMA–N scaling relationships was also assessed. We show that thermal history accounts for up to 20% of the scatter in scaling relationships used to predict R , with the impact of thermal history on R –LMA–N generalized scaling relationships being highly predictable. This finding enabled us to quantitatively incorporate acclimation of R into a coupled global climate–vegetation model. We show that accounting for acclimation of R has negligible impact on predicted annual rates of global R , net primary productivity (NPP) or future atmospheric CO_2 concentrations. However, our analysis suggests that accounting for acclimation is important when considering carbon fluxes among thermally contrasting biomes (e.g. accounting for acclimation decreases predicted rates of R by up to 20% in high-temperature biomes). We conclude that acclimation of R needs to be accounted for when predicting potential responses of terrestrial carbon exchange to climatic change at a regional level.

Keywords: acclimation, leaf mass per unit area, leaf traits, modeling, nitrogen, respiration, scaling, temperature

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Introduction

Climate-dependent changes in plant respiration (R) are accepted as important components of the biosphere's response to global climatic change (Atkin & Tjoelker, 2003). Each year, plant R releases $\approx 60 \text{ GtC}$ into the

atmosphere while producing the energy and carbon intermediates necessary for biosynthesis and cellular maintenance (Houghton *et al.*, 2001; Schimel *et al.*, 2001). This is a large flux compared with the CO_2 release from burning of fossil fuels ($\approx 6 \text{ GtC yr}^{-1}$; Raich & Schlesinger, 1992; Amthor, 1997). Variations in rates of plant R [e.g. due to climate (Ryan, 1991; Atkin & Tjoelker, 2003) and/or genotypic differences in energy demand (Lambers *et al.*, 1998)] thus have the potential to affect

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the functioning of individual ecosystems (Ryan, 2002) and the extent to which atmospheric CO₂ will be sequestered by the terrestrial biosphere (King *et al.*, 2006).

At present, most dynamic vegetation models that have been coupled to global circulation models (GCMs) such as that by the Hadley Centre (Cox *et al.*, 2000) assume a single temperature response function for plant R that is constant even after long-term changes in temperature (i.e. plant R does *not* thermally acclimate). Similarly, although some leaf/canopy models have attempted to account for acclimation (Amthor, 1994), most large-scale models estimating ecosystem net primary productivity (NPP) and ecosystem-level R fail to take into account acclimation of plant R (e.g. Cox, 2001). Acclimation is common in a wide range of plant species representative of different functional groups (Tjoelker *et al.*, 1999a; Loveys *et al.*, 2003; Campbell *et al.*, 2007); it results in R adjusting to compensate for a change in temperature (Atkin & Tjoelker, 2003), often within a few days of a temperature shift (Atkin *et al.*, 2000b; Bolstad *et al.*, 2003; Lee *et al.*, 2005). Recent modeling studies have suggested that acclimation has the potential to alter the strength of the positive climate–carbon feedback and change the amount of carbon stored in plants and soil (Wythers *et al.*, 2005; King *et al.*, 2006). It is also thought to contribute to the relative stability of annual rates of ecosystem R among sites that differ in average temperature (Enquist *et al.*, 2003).

Thermal acclimation of R is often assessed by measurement of R at a reference temperature (R_{mT} , e.g. 25 °C); acclimation to lower temperatures typically results in increased R_{mT} (Atkin & Tjoelker, 2003). Conversely, acclimation to high temperatures results in R_{mT} decreasing. Because cold and warm acclimation have opposing effects on R_{mT} , the effect of acclimation on predicted rates of R_{mT} and long-term carbon loss can vary seasonally and differ among thermally contrasting biomes (Reichstein *et al.*, 2005). The effects of acclimation may also vary through time in response to global warming (Cox *et al.*, 2000; Hansen *et al.*, 2006; IPCC, 2007). Importantly, not all species acclimate to the same extent (e.g. Tjoelker *et al.*, 1999a; Atkin *et al.*, 2006b). A major goal for plant ecology and predictive climate–vegetation modeling is, therefore, to account for the interspecific variations in the thermal acclimation of plant R into coupled climate–carbon simulations. Although recent reports have incorporated simple approximations of acclimation of leaf R into models at the canopy (Amthor, 1994), ecosystem (Wythers *et al.*, 2005) and global scale (King *et al.*, 2006), no attempt has yet been made to quantitatively account for the interspecific differences in proportional and/or absolute changes in R_{mT} , resulting from acclimation of leaf R and/or whole-plant R .

Analyses of leaf phenotypes from a wide range biome have shown that interspecific variations in leaf R_{mT} scale on a log–log basis with a range of other leaf traits such as the leaf mass to area ratio (LMA) and mass-based leaf nitrogen (N) concentration (Reich *et al.*, 1997, 1998; Wright *et al.*, 2004b). Such scaling relationships provide a way to parameterize vegetation–climate models for predicting genotypic variability in rates of leaf R (Wright *et al.*, 2005). Typically, most studies reporting log–log R –LMA–N scaling relationships report considerable scatter in the scaling relationships (e.g. Reich *et al.*, 1998; Wright *et al.*, 2004b), reflecting interspecific differences in the coupling between respiratory metabolism and associated traits, as well as spatial gradients in environmental favorability. Although spatial gradients in nutrients, rainfall and/or temperature are known to impact on leaf R –LMA–N scaling relationships (Wright *et al.*, 2001, 2004a), the importance of individual climate parameters (e.g. growth temperature) in determining variations among co-varying leaf traits has not previously been quantified.

Our study sought to (1) determine the extent to which differences in growth temperature account for the scatter in log–log R –LMA–N scaling relationships; (2) establish whether scaling relationships linking leaf R to N and LMA are systematically altered by growth temperature; and (3) formulate a new approach that would enable interspecific variations in leaf R and/or ability to thermally acclimate to be incorporated into large-scale, predictive vegetation–climate models. Our results show that thermal history accounts for up to 20% of the scatter in scaling relationships used to predict respiration, with its impact on overall R –LMA–N scaling relationships being highly predictable; the latter finding provides a formula that allows generalized acclimation of plant R in a wide range of contrasting plant species to be accounted for in large-scale models. As a first application of this formula, we assess the potential impacts of accounting for generalized acclimation of leaf and plant R using a widely used coupled global climate–vegetation model (Cox *et al.*, 2000; Cox, 2001). Although photosynthesis is also known to thermally acclimate (Berry & Björkman, 1980; Sage & Kubien, 2007), no account was made for photosynthetic acclimation in the modified coupled model. This allowed us to identify the potential importance of respiratory acclimation *per se* in predicted global and regional carbon exchange.

Materials and methods

Dataset and statistics

The data used in these analyses (leaf R , LMA, and N concentration values) were compiled from a recent

study, where 19 contrasting plant species covering a wide range of traits from the 'leaf economics spectrum' were grown under controlled environment conditions (Campbell *et al.*, 2007). Campbell *et al.* (2007) assessed interfunctional group differences in long-term temperature responses of leaf gas exchange and the biochemical changes underpinning photosynthetic and respiratory acclimation, but did not analyze the effect of growth temperature on log-log R_{mT} -LMA-N scaling relationships. In Campbell *et al.* (2007), 19 species were used, representing three functional groups: grasses (*Bromus ramosus*, *Bromus erectus*, *Poa trivialis* L., *Poa costiniana* J. Vickery); forbs [*Achillea millefolium*, *Achillea ptarmica*, *Plantago major*, *Plantago euryphylla*, *Silene dioica*, *Silene uniflora*, and the single species *Arabidopsis thaliana* (ecotype Ost-0)]; and evergreen shrubs and trees (*Acacia melanoxylon* R. Br., *Acacia aneura* R. Muell Ex Benth, *Cistus ladanifer* L., *Cistus laurifolius* L., *Eucalyptus dumosa*, *Eucalyptus delegatensis*, *Quercus suber*, and *Quercus ilex* ssp. *ballota*). Details of the origin and natural distribution of some of these species can be found in Loveys *et al.* (2002); the rest can be found in Campbell *et al.* (2007). The trees and shrubs were chosen for having long-lived leaves (more than one growing season) to contrast these responses with the responses of plants with short-lived leaves (forbs and grasses). Plants were initially grown at constant 21 °C; thereafter, some plants were kept at 21 °C, whereas others were shifted to constant 7, 14, and 28 °C for 10 days. The impact of 10 days at each growth temperature on 21 °C-measured rates of R of preexisting leaves was established for each new growth temperature treatment (Campbell *et al.*, 2007); a 10-day temperature treatment was used as in preexisting leaves, a high degree of respiratory acclimation is achieved within this time period (Atkin *et al.*, 2000b; Lee *et al.*, 2005). Dark leaf R was measured on fully expanded leaves using a Li-Cor 6400 infrared gas analyzer (Li-Cor BioSciences, Lincoln, NE, USA). Measurements were performed on one or more leaves of three plants for each treatment, and the results were averaged. The temperature regimes were maintained for a further 20–50 days, until new leaves had developed under the four growth temperatures. These new leaves were measured in the same way as the preexisting leaves (*note*: in a small number of species, newly developed leaves did not form at 7 or 28 °C). None of the plants had flowers at the time measurements were made (i.e. all plants were in the vegetative stage of growth). By measuring responses in both leaf types (i.e. preexisting and newly developed), we sought to gain an insight into how fully formed leaves might respond to sustained changes in temperature as occur in seasonally variable environments, and how leaves developed under thermally contrasting conditions might differ in predicted scaling relationships.

Statistical analyses of the dataset were carried out using SPSS v.10, SIGMAPLOT v8.02 (SPSS Science, Birmingham, UK), and MICROSOFT EXCEL 2000 (Microsoft Inc.). Log₁₀ transformations were carried out on the data and linear regressions then fitted. Hierarchical multiple regression and analysis of covariance (ANCOVA) was carried out using SPSS v.10. Homogeneity of variance in the ANCOVAs was checked using Levene's test. Previous statistical tests (Campbell *et al.*, 2007) had shown that functional group had no independent effect on R after the LMA of the individual species had been taken into effect. When the data were expressed relative to plant grown at 21 °C, the relative difference in respiration in plants grown at any shifted temperature was unaffected by functional group (Campbell *et al.*, 2007).

Using temperature dependence of scaling relationships to account for acclimation

As outlined in 'Results', our analysis demonstrates that long-term changes in growth temperature have no significant effect on slopes of generalized log-log R_{mT} -LMA (and/or R_{mT} -N) relationships when using multispecies datasets. Because of this, we could use the following to quantify how changes in growth temperature altered log-log R_{mT} -LMA (and/or R_{mT} -N) relationships:

$$\log R_{mT} = [A + C \times (T_A - mT)] + (b \times \log \text{LMA}), \quad (1)$$

where A is the y -axis intercept at reference temperature (mT), C is a constant that takes into account the variation in A that results from variations in the preceding average daily temperature (T_A), and b is the slope of the log-log R_{mT} -LMA or R_{mT} -N plot; A , b , and C values were calculated using all growth temperature data within each leaf type (preexisting or newly developed); we first found A and b in each case using first-order linear regressions fitted to log-log R_{mT} -LMA or R_{mT} -N plot data. The constant C [which is independent of measuring temperature and the short-term temperature dependence (i.e. Q_{10}) of R] takes into account variations in R_{mT} that result from changes in T_A . C was found by fitting equation Eqn (1) to the datasets shown in each plot of log-log R_{mT} -LMA or R_{mT} -N data (using iteration).

Existing models that ignore acclimation do not take into account C when predicting rates of R_{mT} at a given LMA (and/or N concentration). In cases that ignore acclimation,

$$\log R_{mT} = (b \times \log \text{LMA}) + A. \quad (2)$$

As b and A are constants, we find that

$$R_{mT} = \text{LMA}^b \times 10^A, \quad (3)$$

so that at any prevailing temperature (T):

$$R_T = R_{mT} \times Q_{10}^{(T-mT)/10}. \quad (4)$$

Therefore,

$$R_T = LMA^b \times 10^A \times Q_{10}^{(T-mT)/10}. \quad (5)$$

Given Eqn (2), it can be shown that

$$R_{mT} = LMA^b \times 10^{A+C \times (T_A-mT)}, \quad (6)$$

and that

$$R_A = LMA^b \times 10^{A+C \times (T_A-mT)} \times Q_{10}^{(T-mT)/10}. \quad (7)$$

Eqn (7) is the product of the factors operating at two distinct time scales – the acclimated T_A (i.e. the thermal history) and the current T . Given the similarities in Eqns (5) and (7) (and the identical way they treat the Q_{10} of R), we can account for acclimation using:

$$R_A = R_T \times 10^{C \times (T_A-mT)}, \quad (8)$$

where R_A is the rate of leaf R exhibited by plants acclimated to T_A , R_T represents the modeled rates of R when acclimation is not taken into account, mT is the reference measurement temperature (25 °C in the model; Cox *et al.*, 2000), and C is the constant that accounts for variations in R_{mT} that result from changes in T_A [Eqn (1)]. Importantly, Eqn (8) enabled us to account for acclimation of R_T regardless of how the Q_{10} was treated (i.e. fixed or temperature dependent).

Incorporating acclimation of R into a coupled climate–carbon model

To investigate the potential impacts of thermal acclimation on vegetation–climate CO_2 exchange over large spatial and temporal scales, we incorporated Eqn (8) into the JULES (Joint UK Land Environmental Simulator) land surface model. An earlier version of JULES (MOSES-TRIFFID) was used by the Hadley Centre to show the importance of positive carbon feedbacks in determining future atmospheric CO_2 concentrations and global temperatures (Cox *et al.*, 2000); until now, JULES has relied on static respiration parameters (i.e. R_{mT} does not acclimate). JULES was driven globally within the IMOGEN land surface model (Huntingford & Cox, 2000). IMOGEN is an analog representation of the UK Met Office Hadley Centre HADCM3 model. The land surface representation is identical to that used in HADCM3, but the climate is derived from a baseline preindustrial climate, onto which climate anomalies are added. Climate variation within grid cells is assumed to be linear with respect to atmospheric CO_2 , and the coefficients determining this are derived from patterns generated by HADCM3. Atmospheric CO_2 is derived from prescribed emissions and from the carbon balance of the land surface. The land surface model consists of

a surface-exchange scheme, MOSES (Essery *et al.*, 2001), coupled to a dynamic vegetation model, TRIFFID (Cox, 2001). In control runs of JULES, vegetation cover is allowed to change in response to climate, resulting in large changes in fractional coverage of different plant functional types (PFTs) over time.

In MOSES, leaf N is used to predict rates of leaf R at a measuring temperature (R_{mT}) of 25 °C, after which rates of R at the daily average temperature (R_T) are calculated assuming a Q_{10} of 2. Rates of root and stem R are assumed to have the same temperature and N dependence as leaf R and are estimated from patterns of whole-plant N partitioning to stems and roots. Thermal acclimation was incorporated into the model [using Eqn (8) and C values obtained from log–log R_{mT} – N plots] both in the absence and presence of feedbacks from the dynamic vegetation model. The IMOGEN system was used to assess whether inclusion of acclimation of plant R (using leaf R acclimation as a proxy for acclimation in stems and roots) alters predicted rates of annual global CO_2 exchange between the plants and the atmosphere. The existing rates of plant R (i.e. with no acclimation) served as a control. For each acclimation scenario, the model was initially spun-up to equilibrium. The model was then re-run over two 12-month periods (1861 and 2100, respectively, using the distributions of PFTs present within each of these years in the absence of acclimation), with leaf or whole-plant R allowed to acclimate to T_A . Finally, the model was run with acclimation over the full 1861–2100 period to assess whether acclimation alters predicted atmospheric CO_2 concentration in 2100.

For modeling, we used a T_A value taken as the average daily temperature from the preceding 10 days. The decision to use a 10-day average was based on the assumption that a high degree of acclimation of R would have occurred within a 10-day period, as has been reported previously (Atkin *et al.*, 2000b; Bolstad *et al.*, 2003; Lee *et al.*, 2005). Moreover, even if R had acclimated in a period less than 10 days, our previous modeling work (Atkin *et al.*, 2000a) suggests that it is unlikely that the long-term respiratory CO_2 release estimate would have been significantly different from that of our model.

Acclimation of plant R was incorporated into the model using three scenarios: (a) acclimation-dependent changes in fractional coverage of PFTs were allowed to feed back into gross primary productivity (GPP) and plant R within each given year; (b) no acclimation-dependent changes in fractional coverage of PFTs were allowed; and (c) global vegetation from 1861 was exposed to the warmer climate regime predicted for 2100 – here, the aim was to quantify potential impacts of acclimation of plant R alone on global R and NPP

per se (i.e. excluding climate-dependent changes in vegetation distribution).

Results

Leaf trait relationships and thermal history

When considered collectively (i.e. all species, leaf types, and temperature treatments together), pair-wise comparisons showed that all traits were highly correlated (Fig. 1, Table 1), with intertrait correlations similar to those reported previously across the range of traits of our selected species (Reich *et al.*, 1998; Wright *et al.*, 2004b). Using hierarchical multiple regression for log-log leaf trait data in Fig. 1, we found that an additional 1.8–3.5% of variation could be accounted for by including both N and LMA as predictors for R (data not shown). Comparison of log-log $R_{\text{mass}}-N_{\text{mass}}$ and $R_{\text{mass}}-\text{LMA}$ plots revealed that the data collected from controlled-environment-grown plants fall within global relationships (Wright *et al.*, 2004b) reported previously for field-grown plants (Fig. 2), with considerable scatter around the generalized scaling relationships (Table 1); for example, 23% and 29% of the variability in $\log R_{\text{mass}}$ was explained by $\log \text{LMA}$ and $\log N_{\text{mass}}$, respectively.

In preexisting leaves, generalized log-log relationships between LMA and leaf N concentration (either on a mass or area basis) were not affected by growth temperature (Table 2). By contrast, formation of newly developed leaves in the cold was associated with lower average LMA for any given mass-based N concentration (compared with warm-grown newly developed leaves, when considering generalized relationships; Table 2). Analysis of covariance showed that for both preexisting and newly developed leaves, the slopes of the log-log $R_{\text{mT}}-\text{LMA}$ (and $R_{\text{mT}}-N$) relationships (Fig. 3) were similar for all temperature treatments, as shown by the lack of interaction between the covariate and temperature in Tables 2 and 3. However, for each of these relationships, temperature treatment had a significant effect on the *elevation* of the slopes (i.e. the intercept differed; Table 3). As a result, average rates of leaf R_{mT} at any given average N concentration (or average LMA) increased with decreasing growth temperature in both preexisting and newly developed leaves (Fig. 3 shows mass-based data). The slopes of the log-log $R_{\text{mT}}-N_{\text{mass}}$ relationships were similar in preexisting and newly developed leaves (Table 3), indicating that predictions of average rates of leaf R_{mT} based on N_{mass} can be made using data on thermal history alone rather than having to account for the temperature during leaf development. For generalized log-log $R_{\text{mT}}-\text{LMA}$ relationships, the slopes were

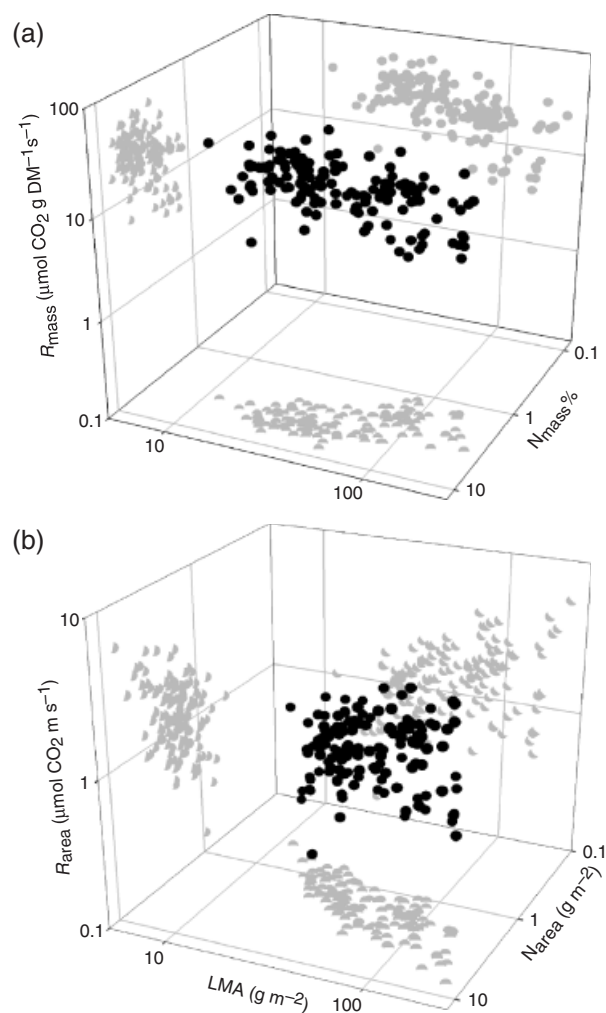


Fig. 1 Three-way relationships among leaf respiration (R) and nitrogen (N) concentration with reference to leaf mass per unit leaf area (LMA). Data shown are for the 19 species exposed to 7–28 °C under controlled environment conditions, both for 10-day temperature-treated preexisting leaves and newly developed leaves formed at each growth temperature. The direction of the data cloud in three-dimensional space can be determined from the shadows projected on the floor and walls of the three-dimensional space: (a) mass-based dark respiration (R_{mass}), LMA, and mass-based leaf nitrogen concentration (N_{mass}); (b) area-based dark respiration (R_{area}), LMA, and N_{area} . Table 1 shows linear regression bivariate relationships between each set of traits.

significantly steeper in preexisting leaves than in newly developed leaves (Tables 2 and 3).

With knowledge of the recent thermal history of mature leaves, we can now account for some of the scatter in the data around the predicted log-log scaling relationships, when considering the multispecies data-set collectively (Fig. 3, Table 4). In preexisting leaves, variations in $\log \text{LMA}$ and $\log N$ accounted for 41.7%

Table 1 Bivariate relationships between leaf traits for data shown in Fig. 1

x-axis	y-axis	r^2	y-axis intercept (\log_{10})	y-axis intercept (normal)	Slope (\log_{10})	P
N_{mass} (%)	LMA (g m^{-2})	0.419	2.203	159.6	-0.900	***
N_{area} (g m^{-2})	LMA (g m^{-2})	0.487	1.481	30.3	0.911	***
LMA (g m^{-2})	R_{mass} ($\text{nmol CO}_2 \text{ g DM}^{-1} \text{ s}^{-1}$)	0.233	2.080	120.2	-0.451	***
N_{mass} (%)	R_{mass} ($\text{nmol CO}_2 \text{ g DM}^{-1} \text{ s}^{-1}$)	0.288	0.924	8.40	0.700	***
LMA (g m^{-2})	R_{area} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.206	-0.648	0.225	0.429	***
N_{area} (g m^{-2})	R_{area} ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.261	-0.075	0.841	0.627	***

All species, growth temperature treatments, and leaf types (preexisting and newly developed) are combined in this linear regression analysis applied to log-log plots of leaf traits. Coefficients of determination (r^2), y-axis intercepts, and standardized major axis slopes are given, with the y-axis intercept values being shown a \log_{10} and untransformed basis. Significance of the slopes of log-log plots compared with zero are shown (*** $P < 0.001$). LMA, leaf mass per unit leaf area; N_{mass} and N_{area} , N concentration per unit dry mass and per unit leaf area, respectively; R_{mass} and R_{area} , leaf respiration per unit dry mass and per unit leaf area, respectively.

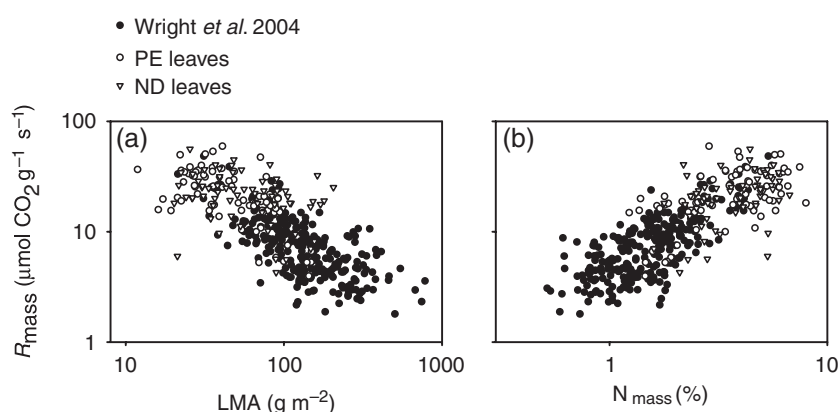


Fig. 2 Comparison of log-log datasets from the current study and from (Wright *et al.*, 2004b). Rates of leaf R in 10-day temperature-treated preexisting leaves (PE, open circles) and newly developed leaves formed at each growth temperature (ND, open triangles) used in the current study are shown. Also shown are data from Wright *et al.* (2004b) (closed circles). Rates of leaf R are plotted against (a) leaf mass per unit leaf area (LMA) and (b) leaf nitrogen concentration per unit mass (N_{mass}), with the x and y-axes shown on a \log_{10} scale. For preexisting and newly developed leaves, rates of leaf R were measured at 21 °C. While the measurement temperature was not stated in Wright *et al.*, we assume that fluxes were measured at a similar moderate temperature. For preexisting and newly developed rates, data shown are for the 19 species exposed to 7–28 °C under controlled environment conditions.

and 35.3% of the variation in $\log R_{\text{mass}}$, respectively, when growth temperatures were combined, with these covariates explaining a lower percentage of the variation in R in newly developed leaves (Table 4). Hierarchical multiple regression showed that in preexisting leaves, temperature accounted for 8.8% and 7.6% of the overall scatter between R vs. LMA and R vs. N concentration (Fig. 3, Table 4), respectively. Temperature accounted for a greater proportion of the scatter between R and its covariates in newly developed leaves (19.6% and 10.6% of the overall scatter between R vs. LMA and R vs. N , respectively; Fig. 3, Table 4).

We further examined the relationship of the scaling exponent with growth temperature (Fig. 3, Tables 2 and 3) to help us assess whether or not species located on different parts of the 'leaf economics spectrum' (Wright

et al., 2004b) show different patterns of acclimation. Although growth temperature alters average rates of leaf R_{mT} at any given LMA or N (when considering the multispecies dataset collectively), no temperature-mediated changes in the scaling exponent were observed, either in preexisting or newly developed leaves (Fig. 3, Table 2). Changes in growth temperature thus have similar proportional impacts on predicted average rates of leaf R_{mT} along the 'leaf economics spectrum', suggesting that, on an average, there is no systematic difference in the degree of acclimation among species located on different parts of the 'leaf economics spectrum'. To further explore the extent to which the degree of acclimation differed systematically among species, we calculated individual species acclimation ratios, using the 'set temperature method' (Acclim_{SetTemp};

Table 2 Analysis of covariance for log–log leaf trait data

x-axis	y-axis	Leaf type					
		Preexisting			Newly developed		
		(a)	(b)	(c)	(a)	(b)	(c)
N_{mass} (%)	LMA (g m^{-2})	0.000	0.800 ^{ns}	0.939 ^{ns}	0.000	0.025	0.991 ^{ns}
N_{area} (g m^{-2})	LMA (g m^{-2})	0.000	0.707 ^{ns}	0.982 ^{ns}	0.000	0.629 ^{ns}	0.989 ^{ns}
LMA (g m^{-2})	R_{mass} ($\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$)	0.000	0.009	0.994 ^{ns}	0.001	0.002	0.918 ^{ns}
N_{mass} (%)	R_{mass} ($\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$)	0.000	0.032	0.925 ^{ns}	0.000	0.032	0.845 ^{ns}
LMA (g m^{-2})	R_{area} ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)	0.030	0.005	0.848 ^{ns}	0.000	0.001	0.566 ^{ns}
N_{area} (g m^{-2})	R_{area} ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)	0.028	0.002	0.928 ^{ns}	0.000	0.021	0.828 ^{ns}

Values represent significance levels for (a) the relationship between the covariate (x) and the dependent variable (y), (b) the effect of temperature treatment, and (c) the interaction between the covariate and temperature for 10-day-treated preexisting leaves and for newly developed leaves formed under each new temperature regime. Superscript 'ns' denotes nonsignificant relationships. LMA, leaf mass per unit leaf area; N_{mass} and N_{area} , N concentration per unit dry mass and per unit leaf area, respectively; R_{mass} and R_{area} , leaf respiration per unit dry mass and per unit leaf area, respectively.

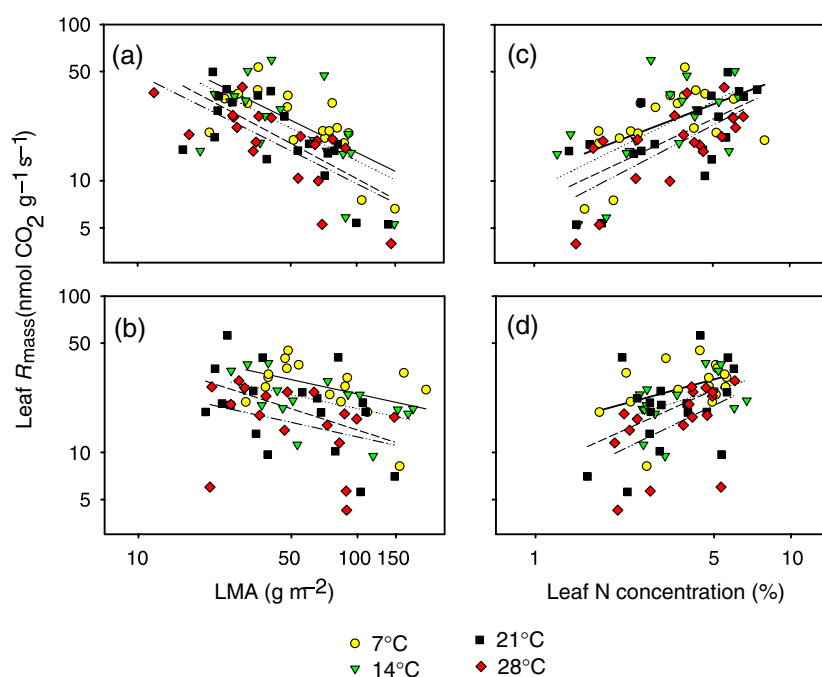


Fig. 3 Rates of mass-based leaf respiration (measured at 21 °C in all cases) in relation to leaf mass per unit leaf area (LMA; a and b) and leaf N concentration (c and d), with the x and y -axes shown on a \log_{10} scale. Data shown are for the 19 species exposed to 7–28 °C under controlled environment conditions, both for 10-day temperature-treated preexisting leaves (a and c) and newly developed leaves formed at each growth temperature (b and d) ($n = 3$ –6). In no case did growth temperature significantly alter the slope of the scaling relationships shown in each figure (regressions for each temperature were 7 °C, solid line; 14 °C, dotted line; 21 °C, dashed line; 28 °C, dash-dotted line; see SI for details on individual regressions for each growth temperature/leaf type combination).

Loveys *et al.*, 2003; Atkin *et al.*, 2005). Using this approach, rates of leaf R_{mT} (i.e. measured at 21 °C) exhibited by plants acclimated to 7, 14, and 28 °C were expressed as a ratio of those exhibited by plants at 21 °C. When comparing 7 °C-acclimated and 14 °C-acclimated plants with those kept at 21 °C, $\text{Acclim}_{\text{SetTemp}}$ ratios

were expected to be greater than 1.0 in species that had cold-acclimated, whereas $\text{Acclim}_{\text{SetTemp}}$ ratios were expected to be lower than 1.0 in species where R_{mT} had acclimated to 28 °C. Figure 4 shows individual species $\text{Acclim}_{\text{SetTemp}}$ ratios for plants acclimated to 7 °C, plotted against the corresponding LMA values exhib-

Table 3 Analysis of covariance and linear regression values for log–log leaf trait data for the comparison of preexisting and newly developed leaves, using data shown in Fig. 3

<i>x</i> -axis	<i>y</i> -axis		r^2	<i>A</i>	<i>b</i>	<i>C</i>	(a)	(b)	(c)
N_{mass} (%)	R_{mass} (nmol CO ₂ g ^{−1} s ^{−1})	PE	0.353	0.925	0.724	−0.00794	0.000	0.408 ^{ns}	0.785 ^{ns}
		ND	0.204	0.926	0.669	−0.00783			
LMA (g m ^{−2})	R_{mass} (nmol CO ₂ g ^{−1} s ^{−1})	PE	0.417	2.418	−0.664	−0.00980	0.000	0.307 ^{ns}	0.004
		ND	0.093	1.767	−0.263	−0.01242			

Values represent the coefficient of determination (r^2); *y*-axis intercept (*A*); scaling relationship slope (*b*); temperature correction factor (*C*); and the significance levels for (a) the relationship between the covariate (*x*) and the dependent variable (*y*), (b) the effect of leaf type (preexisting or newly developed), and (c) the interaction between the covariate and leaf type. Superscript 'ns' denotes nonsignificant relationships. Linear regressions were calculated on all preexisting or newly developed data combined across temperature treatments. LMA, leaf mass per unit leaf area; N_{mass} , N concentration per unit dry mass; R_{mass} , leaf respiration per unit dry mass.

Table 4 Hierarchical multiple regression for log–log leaf trait data

<i>x</i>	<i>y</i>	Leaf type					
		Preexisting			Newly developed		
		(a) Covariate	(b) Temperature	(c) Total	(a) Covariate	(b) Temperature	(c) Total
N_{mass} (%)	LMA (g m ^{−2})	0.346	0.091	0.437	0.563	0.006	0.569
N_{area} (g m ^{−2})	LMA (g m ^{−2})	0.304	0.013	0.317	0.642	0.010	0.652
LMA (g m ^{−2})	R_{mass} (nmol CO ₂ g ^{−1} s ^{−1})	0.417	0.088	0.505	0.093	0.196	0.289
N_{mass} (%)	R_{mass} (nmol CO ₂ g ^{−1} s ^{−1})	0.353	0.076	0.429	0.204	0.106	0.310
LMA (g m ^{−2})	R_{area} (μmol CO ₂ m ^{−2} s ^{−1})	0.085	0.153	0.238	0.320	0.160	0.480
N_{area} (g m ^{−2})	R_{area} (μmol CO ₂ m ^{−2} s ^{−1})	0.066	0.173	0.239	0.440	0.081	0.521

Values of r^2 representing (a) the variability in *y* accounted for by the covariate, *x*; (b) the additional variability in *y* accounted for by temperature; and (c) the total variability in *y* accounted for by both predictors are shown. LMA, leaf mass per unit leaf area; N_{mass} , N concentration per unit dry mass; R_{mass} , leaf respiration per unit dry mass.

ited by plants kept at 21 °C throughout the experiment. $\text{Acclim}_{\text{SetTemp}}$ varied substantially among species. However, this variation was not correlated with LMA values exhibited by plants kept at 21 °C (Fig. 4); the same conclusion was reached when assessing acclimation to 14 and 28 °C, and when comparing plotting acclimation ratios against 21 °C-grown N_{mass} values (data not shown). Thus, while it is clear that not all species acclimate to the same degree, overall there are no systematic differences among contrasting species from different parts of the 'leaf economics spectrum' in their ability to thermally acclimate leaf R_{mT} .

Table 3 shows the values of parameters in Eqn (1) for log–log leaf R_{mT} –N and leaf R_{mT} –LMA plots; *C* was nearly identical in preexisting and newly developed leaves when calculated using log–log leaf R_{mT} –N data, with *C* values being higher when predicting rates of R_{mT} using log–log leaf R_{mT} –LMA plots. The equivalent *C* value for log–log root R_{mT} –N data (calculated using data from Atkinson *et al.*, 2007) is −0.00703, demonstrat-

ing that similar average degrees of acclimation are exhibited by leaves and roots, when considering multi-species datasets collectively.

Our finding that the scaling exponent of generalized relationships linking leaf R_{mT} to other leaf traits remains, on an average, constant in warm- and cold-grown plants has potential importance for plant, ecosystem, and coupled climate–carbon simulations; we suggest that models predicting leaf R_{mT} from related leaf traits might be able to assume, on an average, equal *proportional* changes in leaf *R* following sustained changes in temperature. This greatly simplifies the task of quantitatively incorporating acclimation (averaged across species) into large-scale climate–vegetation models.

Case study: assessing the impacts of Eqn (8) on a coupled climate–vegetation model

We used Eqn (8) to assess the potential impacts of acclimation of *R* alone on predicted output of a coupled

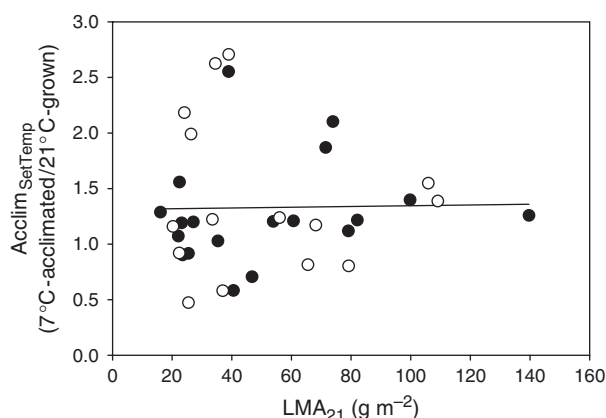


Fig. 4 Variations in respiratory acclimation ratios ($\text{Acclim}_{\text{SetTemp}}$) of preexisting (●) and newly developed (○) leaves for 19 species plant species differing in leaf dry mass per unit leaf area (LMA , g m^{-2}). LMA values are for plants grown throughout the experiment at 21°C . The $\text{Acclim}_{\text{SetTemp}}$ values in (a) represent ratios for 7°C -acclimated plants relative to plants kept at 21°C ($R_{\text{mT}} 7^\circ\text{C}$ -acclimated/ $R_{\text{mT}} 21^\circ\text{C}$ -grown); similarly, in (b) and (c) $\text{Acclim}_{\text{SetTemp}}$ ratios are provided for $R_{\text{mT}} 14^\circ\text{C}$ -acclimated/ $R_{\text{mT}} 21^\circ\text{C}$ -grown and $R_{\text{mT}} 28^\circ\text{C}$ -acclimated/ $R_{\text{mT}} 21^\circ\text{C}$ -grown plants, respectively. Values of LMA of the 21°C -grown plants are from Campbell *et al.* (2007). In all cases, R_{mT} was measured at 21°C . Each symbol represents a different species. Line is a linear regression fitted through both preexisting and newly developed values ($r^2 = 0.0003$).

global climate–vegetation model (Cox *et al.*, 2000). Because C was less than zero in all cases (Table 4), accounting for acclimation [using Eqn (8)] was expected to increase modeled plant R at low daily temperatures and decrease R at high daily temperatures that exceed mT (Fig. 5). Given that N is used to predict R_{mT} in MOSES, we used C values from log–log $R_{\text{mass}}\text{--}N_{\text{mass}}$ plots (from preexisting leaf plots; Table 3). Calculations were made either assuming that acclimation only occurred in leaves or assuming that acclimation occurs in stem and root R , as has been reported previously (Gansert *et al.*, 2002; Atkinson *et al.*, 2007); as the C value of leaves and roots for $R_{\text{mass}}\text{--}N_{\text{mass}}$ was similar, for simplicity, we applied a single leaf-based C value to whole plants.

Initially, JULES was run using scenario (a) to assess the potential effect of acclimation in leaves alone (data not shown) vs. acclimation of whole-plant R (Table 5). To assess the impacts of acclimation by R before and after the onset of recent climatic change, we compared modeled carbon exchange in 1861 and 2100 and for a transient simulation from 1861 to 2100. In 1861, accounting for acclimation of plant R in leaves alone resulted in a slight increase in predicted global plant R (+2.0% compared with the control values shown in Table 5); in 2100, accounting for acclimation of leaf R alone had

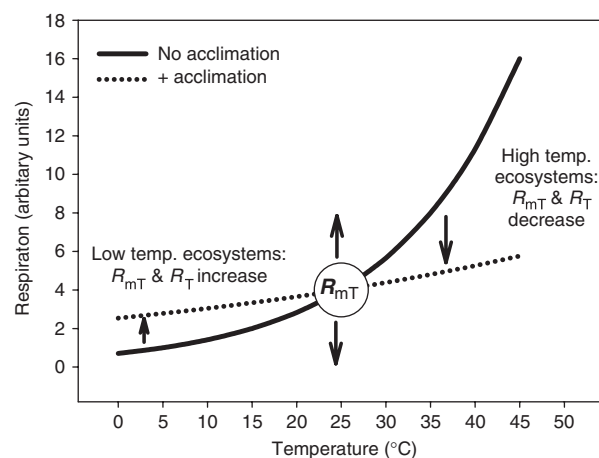


Fig. 5 Schematic to illustrate the impacts of thermal acclimation on modeled rates of respiration. Rates of plant R at a set measuring temperature (R_{mT}) are used to model rates of R at daily average temperatures (R_T) higher and lower than the mT of 25°C . In a no-acclimation scenario, rates of R_T are calculated assuming a constant Q_{10} of 2 (shown here as the thick solid line). The dotted line shows calculated rates of R_T , assuming that acclimation does occur, whereby R_{mT} is allowed to increase/decrease depending on the prevailing average daily temperatures (e.g. in the past 10 days). In this figure, we have shown the net effect of changes in R_{mT} on calculated rates of R_T at daily temperatures below and above the mT of 25°C (again assuming a Q_{10} of 2). Acclimation to low daily temperatures results in increased rates of R_T (mediated by increased rates of R_{mT} , as indicated by the vertical arrow above R_{mT}), whereas acclimation to high daily temperatures is associated with a decrease in calculated rates of R_T (mediated by decreased rates of R_{mT}).

even less effect on predicted global plant R (+0.2%). Similarly, accounting for acclimation of whole-plant R (by applying a common C value to existing rates of leaf, stem, and root R_{mT}) resulted in small increases in global plant R in 1861 (+2.3%) and no change in 2100 (Table 5). As acclimation has been shown to occur in both stems and roots, in subsequent analyses we assumed that acclimation of R occurs in all tissues. Comparison of scenarios (a) and (b) in Table 5 showed that model-based changes in PFT coverage caused by the inclusion of acclimation (and thus GPP) had little impact on the predicted effects of acclimation on global rates of plant R or NPP. Similarly, accounting for acclimation appeared to have little impact on predicted global plant R or NPP when the vegetation distribution from 1861 was exposed to the warmer climate of 2100 [i.e. scenario (c); Table 5]. Thus, irrespective of whether dynamic changes in vegetation are included in the coupled model, failure to account for acclimation of plant R does not appear to result in substantive changes in predicted rates of global plant R or NPP. Moreover, accounting for acclimation of whole-plant R in the model had almost

Table 5 Effect of acclimation of whole-plant respiration (R) on annual global annual CO_2 exchange ($\text{g C m}^{-2} \text{yr}^{-1}$) predicted by the JULES coupled climate-carbon model (Cox *et al.*, 2000; Cox, 2001)

Simulation	Year	Flux	Control (no acclimation)	Acclimated	% change due to acclimation
(a) Vegetation varying within each year	1861	Global GPP	1185	1189	+ 0.3
		Global plant R	569	582	+ 2.28
		Global NPP	616	607	− 1.46
	2100	Global GPP	1894	1920	+ 1.37
		Global plant R	905	908	+ 0.33
		Global NPP	989	1012	+ 2.33
(b) Vegetation static within a given year	1861	Global plant R	569	581	+ 2.11
		Global NPP	616	603	− 2.11
	2100	Global plant R	906	901	− 0.55
		Global NPP	989	994	+ 0.50
	Combined	Global plant R	961	951	− 1.04
		Global NPP	894	904	+ 1.11

Three vegetation distribution simulation runs are shown. In (a) and (b), vegetation cover was allowed to change in response to climate as reported in Cox *et al.* (2000), resulting in changes in control run (i.e. no acclimation) fractional coverage of different plant functional types (PFTs) between 1861 and 2100. In (a), further changes in fractional coverage of PFTs were allowed to occur within each year (i.e. 1861 or 2100) as a result of feedbacks from acclimation-dependent changes in plant R to gross primary productivity (GPP). In (b), vegetation cover within each year was kept constant (i.e. there was no feedback to GPP by acclimation-dependent changes in plant R). In (c), vegetation cover from 1861 was exposed to the climate scenario of 2100 (Cox *et al.*, 2000), with no feedback to GPP by acclimation-dependent changes in plant R being allowed. GPP values are shown for (a), both for the control and acclimation runs. As there was no feedback from acclimation into GPP in (b) and (c), GPP values for these runs are simply the control values in (a). For each scenario, net primary productivity (NPP, equal to GPP minus plant R) values are shown. Acclimation was assumed to have occurred to all tissues to the same degree as observed in leaves. The impacts of acclimation are shown as the percentage increase or decrease, relative to the value in the absence of acclimation. Rates of whole-plant R were calculated assuming a rate of R at a reference measurement temperature (R_{mT} ; see text) and assuming a Q_{10} of 2.0 (Cox *et al.*, 2000; Cox, 2001) when calculating rates of R at average daily temperatures (R_T).

no effect on modeled atmospheric CO_2 concentrations between 1861 and 2100 (data not shown).

Incorporating Eqn (8) into JULES resulted in marked spatial heterogeneity of predicted responses of plant R (Fig. 6) and NPP (data not shown) between cold and warm ecosystems. Control runs of JULES predicted that rates of plant R and NPP would be highest in the equatorial tropics, East Asia, south-west North America, and Western Europe. In 1861 (when average temperatures were lower than present, but vegetation distribution was relatively similar to current distributions), accounting for acclimation of plant R substantially increased predicted plant R in northern ecosystems (Fig. 6); predicted R was decreased in higher temperature ecosystems, with the greatest percentage changes occurring in dry-land/desert ecosystems. This pattern was continued in 2100, with the predicted reductions in plant R (and concomitant increases in NPP) in warm/hot ecosystems being more pronounced, and the stimulatory effect of acclimation on plant R in cold regions being less pronounced than in 1861. Accounting for acclimation had the greatest stimulatory effect on predicted absolute rates of NPP in central Africa, with the greatest percentage increases in NPP

occurring in hot dry-land ecosystems on all continents (data not shown); this pattern was also maintained under a static vegetation distribution scenario from 1861 to 2100 (data not shown).

Discussion

Leaf traits: the importance of thermal history

We sought to determine the extent to which differences in growth temperature account for scatter in generalized scaling relationships linking leaf R to leaf N and LMA, and whether these scaling relationships are systematically altered by growth temperature. Our analysis of the Campbell *et al.* (2007) dataset demonstrates, for the first time, that thermal history explains much of the scatter in the scaling relationships shown in Fig. 1. In particular, the temperature during leaf development accounts for up to 20% of the scatter in log-log R -LMA- N plots (Table 4). This finding raises the possibility that thermal history, in particular seasonal variations in temperature during leaf development, could account for a considerable proportion of the scatter reported in several field-based studies (Reich *et al.*, 1997, 1999;

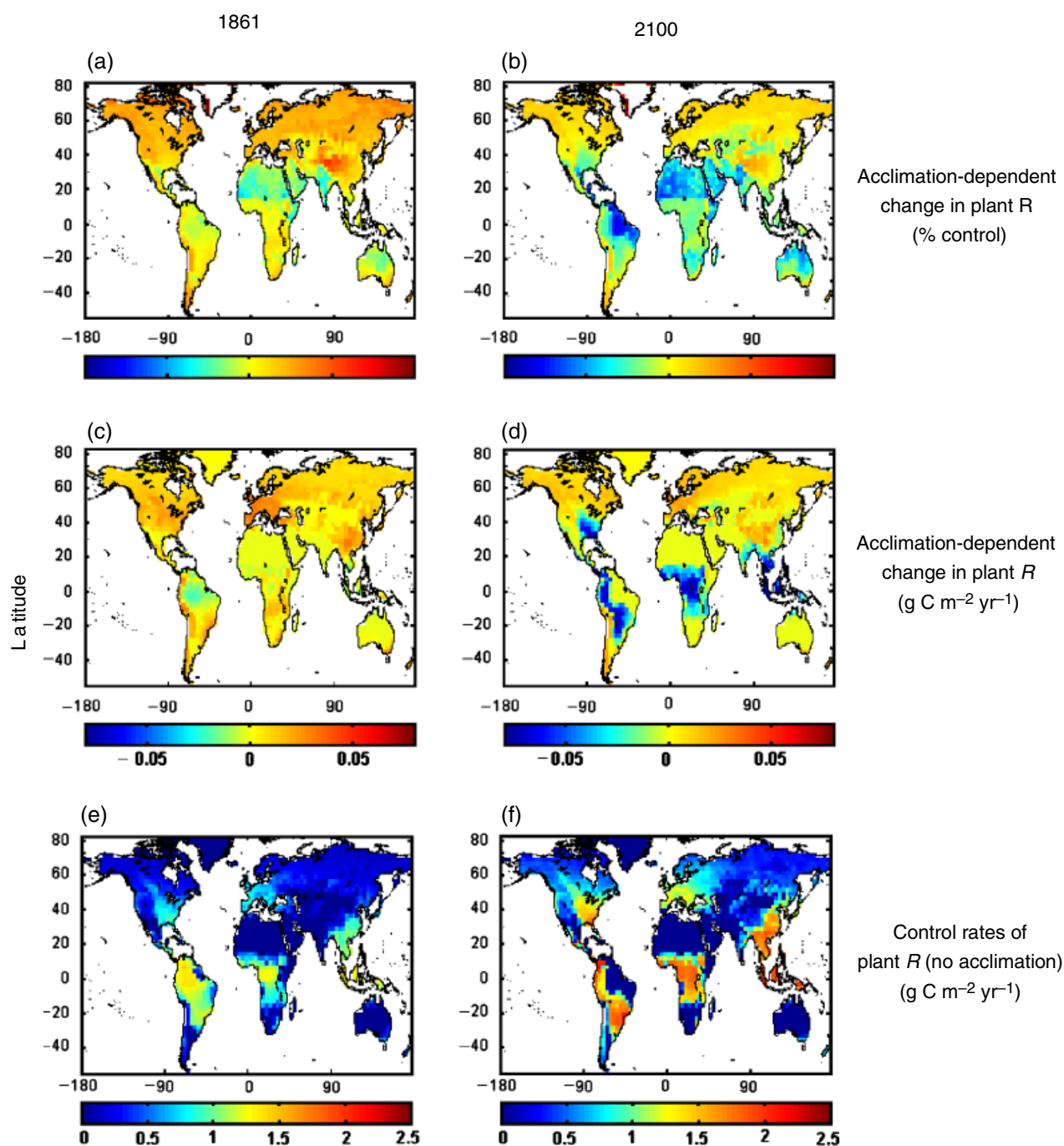


Fig. 6 Impact of acclimation of plant R on spatial heterogeneity of annual rates of plant respiration (R) around the globe in 1861 and 2100. Maps show predicted rates of plant R and the effect of acclimation on plant R in 1861 and 2100. For each year, (a) and (b) show the percentage changes due to inclusion of thermal acclimation of whole-plant R (assuming that stems and roots acclimate to a similar degree as leaves), (c) and (d) show the absolute changes ($\text{g C m}^{-2} \text{yr}^{-1}$) due to acclimation, and (e) and (f) show the control values of plant R ($\text{g C m}^{-2} \text{yr}^{-1}$) when not taking into account acclimation. Impacts of acclimation were calculated using the 'Vegetation static within a given year' scenario (Table 5). See Table 5 for mean annual totals of global R in 1861 and 2100.

Wright & Westoby, 1999; Wright *et al.*, 2001, 2004a,b). Such studies have acknowledged the potential importance of climate in determining scatter in generalized leaf trait relationships linking leaf R to LMA and N

concentration and have shown that at given LMA and N concentration values, rates of leaf R are generally higher in plants growing at sites characterized by hot, dry, and high-irradiance conditions (Wright *et al.*, 2001,

2006); however, due the complexity of multiple abiotic factors varying in the field, these field-based studies have not been able to quantify the role of thermal history *per se* in determining variations in leaf R –LMA–N scaling relationships. As leaves often develop under thermally contrasting conditions (e.g. in deciduous species, where multiple cohorts of leaves are produced through the year, and in evergreen species, where leaves live for many years), accounting for thermal history is likely to be important in studies seeking to understand the role of environmental variability vs. variations in genetic composition in determining scatter in R –LMA–N scaling relationships.

What mechanisms could explain why scatter in generalized leaf R –LMA–N scaling relationships is influenced by thermal history, particularly in leaves that develop at different temperatures? To answer this question, we need to consider the extent to which thermal history impacts on each trait and the underlying factors responsible for changes in the magnitude of each trait. Past studies have shown that cold-developed leaves exhibit higher LMA values and higher nitrogen concentrations (Körner, 1989; Ryan, 1995; Tjoelker *et al.*, 1999b; Loveys *et al.*, 2003; Atkin *et al.*, 2006b). Higher concentrations of N in cold-developed leaves reflect the fact that protein concentrations (in particular those involved in photosynthetic metabolism and sucrose synthesis; Strand *et al.*, 1999; Campbell *et al.*, 2007) are greater in cold-developed leaves. Cold-grown leaves are also thicker and denser (reflecting decreased cell size) than their warm-grown counterparts (Körner *et al.*, 1989; Atkin *et al.*, 2006a) and exhibit higher concentrations of nonstructural carbohydrates; collectively, these changes result in an increase in leaf dry mass per unit leaf area (i.e. higher LMA). Higher rates of leaf R_{mT} in cold-grown leaves (compared with warm-grown leaves) likely reflect an increase in the density and ultrastructure of mitochondria (Miroslavov & Kravkina, 1991; Armstrong *et al.*, 2006a,b) and an increase in the capacity of individual mitochondria (Armstrong *et al.*, 2006b). Temperature-dependent increases in substrate supply and/or ATP turnover may also contribute to higher rates of leaf R in cold-grown leaves, both in preexisting leaves shifted to the cold and cold-developed leaves (Atkin & Tjoelker, 2003). Collectively, such temperature-mediated changes in R , LMA, and N concentration result in thermal history accounting for much of the scatter in log–log R –LMA–N plots that contain data from leaves that experienced contrasting growth temperatures leading up to measurement/leaf harvesting.

The second objective of our study was to establish whether generalized scaling relationships linking leaf R to N and LMA in multispecies datasets are systematically altered by growth temperature. Our analysis

suggests that in addition to the value of each trait varying (on average) with growth temperature, the generalized scaling relationships linking R , LMA, and N concentration are temperature dependent; for example, compared with warm-grown leaves, cold-developed leaves exhibited lower average LMA values for any given mass-based N concentration (Table 2) and higher average rates of R_{mT} at any given N concentration (or LMA). Thermal history systematically affected the y -axis intercept (but not slope) of the generalized log–log scaling relationships linking R_{mass} to LMA and N_{mass} (Tables 2 and 6, Fig. 3), reflecting the fact that the proportional change in average rates of R was greater than changes in LMA or N concentration. Importantly, the impact of growth temperature on generalized scaling between leaf R and LMA and N concentration was consistent, demonstrating that, notwithstanding variability among species in $Acclim_{SetTemp}$ ratios (Fig. 4), there is no *systematic* difference among contrasting species in their ability to thermally acclimate.

Quantitative incorporation of acclimation into large-scale models

Our finding that thermal history has predictable impacts on generalized leaf R –LMA–N scaling relationships enabled a new approach to be formulated, whereby acclimation of R (averaged across a multispecies dataset) can be quantitatively incorporated into large-scale, coupled climate–carbon models. Recent studies that included acclimation in large-scale models (Wythers *et al.*, 2005; King *et al.*, 2006), while highlighting the potential importance of acclimation, did not include scaling parameters based on empirical datasets using large numbers of plant species representative of the ‘leaf economics spectrum’ (Wright *et al.*, 2004b). Indeed, our study provides a set of ‘ C ’ constants that could enable other large-scale models to adjust existing average rates of plant R for acclimation (where data on average N concentrations or LMA values are available), irrespective of existing rates of R present in such models.

Our analysis suggests that accounting for acclimation of plant R could result in two divergent impacts. Firstly, acclimation-dependent changes in R in cold and warm regions of the earth might essentially cancel each other out, resulting in no net change in global plant R or NPP by 2100. On first inspection, this suggestion appears to contrast with that of King *et al.* (2006); however, in their analysis (which used a limited dataset to incorporate acclimation of leaf R into a GCM), the potential effect of acclimation was small, particularly when compared with differences among models. Thus, when considering changes in climate up to 2100, we suggest that accounting for acclimation of plant R does not necessa-

Table 6 Regression values for two-trait log-log relationships

		Growth temperature																
		7 °C				14 °C				21 °C				28 °C				
x-axis	y-axis	Leaf type	r ²	A	b	Sig.	r ²	A	b	Sig.	r ²	A	b	Sig.	r ²	A	b	Sig.
N _{mass} (%)	LMA (g m ⁻²)	PE	0.547	2.190	-0.917	0.000	0.712	2.167	-0.967	0.000	0.586	2.115	-0.860	0.000	0.414	2.084	-0.803	0.003
		ND	0.427	2.454	-1.027	0.006	0.278	2.370	-1.008	0.044	0.464	2.311	-1.149	0.002	0.474	2.295	-1.047	0.002
N _{area} (g m ⁻²)	LMA (g m ⁻²)	PE	0.356	1.521	0.882	0.007	0.241	1.523	0.912	0.039	0.236	1.493	0.742	0.035	0.384	1.484	0.793	0.005
		ND	0.596	1.396	1.020	0.000	0.726	1.433	1.003	0.000	0.652	1.443	1.095	0.000	0.491	1.533	0.922	0.002
LMA (g m ⁻²)	R _{mass} (nmol CO ₂ g DM ⁻¹ s ⁻¹)	PE	0.523	2.552	-0.686	0.000	0.376	2.516	-0.694	0.007	0.539	2.510	-0.748	0.000	0.524	2.380	-0.700	0.000
		ND	0.199	1.983	-0.304	0.083 ^{ns}	0.257	1.867	-0.293	0.045	0.221	2.047	-0.452	0.049	0.101	1.714	-0.307	0.214 ^{ns}
N _{mass} (%)	R _{mass} (nmol CO ₂ g DM ⁻¹ s ⁻¹)	PE	0.283	1.053	0.626	0.019	0.381	0.947	0.802	0.006	0.450	0.860	0.767	0.002	0.497	0.762	0.850	0.001
		ND	0.172	1.158	0.444	0.110 ^{ns}	0.212	1.047	0.501	0.084 ^{ns}	0.204	0.889	0.732	0.060 ^{ns}	0.242	0.749	0.791	0.045
LMA (g m ⁻²)	R _{area} (μmol CO ₂ m ⁻² s ⁻¹)	PE	0.142	-0.342	0.294	0.112 ^{ns}	0.081	-0.289	0.250	0.252 ^{ns}	0.063	-0.357	0.208	0.298 ^{ns}	0.013	-0.171	0.074	0.643 ^{ns}
		ND	0.442	-0.712	0.565	0.005	0.507	-0.789	0.548	0.002	0.282	-1.061	0.629	0.023	0.140	-0.491	0.278	0.127 ^{ns}
N _{area} (g m ⁻²)	R _{area} (μmol CO ₂ m ⁻² s ⁻¹)	PE	0.023	0.125	0.177	0.532 ^{ns}	0.072	0.053	0.437	0.282 ^{ns}	0.094	-0.091	0.387	0.201 ^{ns}	0.104	-0.102	0.267	0.179 ^{ns}
		ND	0.506	-0.021	0.799	0.002	0.482	-0.036	0.604	0.004	0.285	-0.193	0.856	0.023	0.345	-0.170	0.602	0.010

Values are for 10-day-treated preexisting leaves (PE) and newly developed leaves (ND) developed at each growth temperature, showing coefficients of determination (r^2), the values as the \log_{10} value (A), scaling relationship slope (b), and the significance of the slope of the log-log plots compared with 0 (Sig.) for each relationship/temperature combination. LMA, leaf mass per unit leaf area; N_{mass} and N_{area} N concentration per unit dry mass and per unit leaf area, respectively; R_{mass} and R_{area} leaf respiration per unit dry mass and per unit leaf area, respectively.

rily alter the strength of the positive, global climate-carbon feedback (Cox *et al.*, 2000). Why did not incorporating acclimation into JULES [using Eqn (8)] result in a reduction of the predicted positive feedback from respiratory CO₂ as the world warms? The suggestion that acclimation should reduce the predicted positive feedback from respiratory CO₂ is based on the observation that acclimation reduces rates of plant *R* at high growth temperatures (Atkin & Tjoelker, 2003). However, in most coupled models, existing rates of *R* are calculated with reference to a set measuring temperature (*mT*), which is typically 25 °C. In such cases, allowing for acclimation increases average rates of rates of *R* when *T_A* is lower than 25 °C and decreases *R* when *T_A* is greater than 25 °C (Fig. 5). Temperatures greater than 25 °C are common near the equator and are likely to increase in frequency and spatial distribution in a future, warmer world; however, temperatures well below 25 °C are dominant across much of the globe (both now and in the future), particularly in high-latitude and high altitudinal regions. The earth's surface is thus made of up areas where accounting for acclimation of plant *R* will decrease (e.g. hot equatorial regions and deserts) and increase (e.g. boreal forests, arctic/alpine tundra, temperate forests, and grasslands) predicted average rates of respiratory CO₂ release. The net result is that accounting for acclimation of plant *R* appears to be of little consequence when considering average terrestrial carbon exchange on a global basis (Table 5).

The second divergent impact concerns predicted rates of CO₂ exchange in thermally contrasting ecosystems. If we assume that acclimation is widespread and results in reduced average rates of *R_{mT}* in plants experiencing *T_A*'s greater than 25 °C, then existing models might be underestimating the strength of the carbon sink for atmospheric CO₂ in hot ecosystems. For tropical ecosystems, this suggestion is highly relevant, as existing process-based models (that do not account for acclimation) currently predict strong negative effects of global warming in the tropics (Clark *et al.*, 2003). Conversely, our analysis suggests that boreal forests (which represent 40% of the world's forests) might be a weaker than predicted carbon sink.

In JULES, tissue N concentrations are used to predict *R_{mT}* (Cox, 2001). Although our analysis suggests that all species exhibit similar degrees of acclimation when assessed on a *proportional* basis, accounting for acclimation should have its greatest *absolute* effect on *R_{mT}* in species with the highest N concentration. Thus, in hot equatorial regions, it is possible that acclimation-dependent reductions in *R_{mT}* (and thus the greatest increases in NPP) would be greatest in species with the highest N concentrations. Thus, if land clearance in the tropics (DeFries *et al.*, 2002; Laporte *et al.*, 2007) results in

replacement of low N-concentration tropical trees (Reich, 2005; Townsend *et al.*, 2007) by species with high tissue N concentrations (e.g. pasture, cash crops and/or faster growing tree species), we would predict even greater acclimation-dependent changes in *R_{mT}* than shown by our analysis. Consideration, therefore, needs to be given to the importance of changes in tissue chemistry resulting from land clearing when calculating the impact of acclimation of plant *R* on tropical carbon exchange. Similarly, more general changes in tissue chemistry resulting from climate change need to be considered when considering the impacts of acclimation generally. Acclimation also needs to be considered when comparing the contribution of tropical and northern terrestrial ecosystems to global CO₂ uptake. In a recent global study (Stephens *et al.*, 2007), tropical ecosystems were found to represent a stronger carbon sink than suggested by existing coupled GCMs. We suggest that one factor that might contribute to this discrepancy could be the failure of existing coupled GCMs to account for acclimation of plant *R*.

Future challenges

Our analysis was carried out using data obtained from young, controlled-environment-grown plants (Campbell *et al.*, 2007) and is, thus, not necessarily representative of how more mature, field-grown plants would respond to temperature. However, numerous field studies have reported seasonal adjustments in *R_{mT}* that are indicative of acclimation occurring in the field (see Atkin *et al.*, 2005 and references cited therein). Moreover, comparison of plants growing at low- and high-temperature sites have reported differences in *R_{mT}* that are consistent with acclimation (Atkin *et al.*, 2005). Thus, while the coefficient '*C*' that accounts for growth temperature-dependent changes in *R_{mT}* is not necessarily the same for field and laboratory-grown plants, we suggest that our approach provides a first step toward quantitatively accounting for acclimation in large-scale models. In future studies, we suggest that the effects of growth temperature on plant *R* be assessed for a wider range of plant species from all biomes, both in young and mature plants. Moreover, given that we have not addressed the issue of how GPP responds/acclimates to long-term changes in temperature, we also suggest that efforts be made to quantitatively account for acclimation of both plant *R* and photosynthesis in GCMs. Acclimation of plant *R* and photosynthesis is often tightly coupled (Berry & Björkman, 1980; Berry & Raison, 1981; Gifford, 1995; Tjoelker *et al.*, 1998, 1999b; Gunderson *et al.*, 2000; Loveys *et al.*, 2003; Atkin *et al.*, 2006b; Campbell *et al.*, 2007; Sage & Kubien, 2007), and thus successful prediction of future CO₂ exchange over

wide temporal and spatial scales will require acclimation of both parameters to be accounted for. Some attempts have been made to adjust both photosynthesis and leaf R for long-term changes in temperature in process-based models (e.g. Amthor, 1994); however, it remains unclear as to whether contrasting species also differ in their ability to thermally acclimate photosynthesis. If we assume that photosynthetic thermal acclimation is widespread and predictable, and that acclimation to low growth temperatures results in increased rates of photosynthesis at low temperatures (Stitt & Hurry, 2002), then accounting for photosynthetic acclimation should increase predicted rates of GPP in low-temperature biomes; in such cases, accounting for acclimation of both photosynthesis and plant R would result in higher estimates of NPP compared with when acclimation of plant R alone is accounted for. Conversely, accounting for acclimation of both photosynthesis and plant R might result in lower estimates of NPP in the tropics than was the case in our study when acclimation of plant R alone was accounted for. Thus, a long-term goal must be the development of predictive criteria that accounts for thermal acclimation of both plant R and photosynthesis.

How might acclimation of plant R and photosynthesis to be incorporated into GCMs? Our current study describes an approach that enables quantitative incorporation of acclimation of plant R in GCMs using temperature-dependent changes in log-log scaling relationships. Unfortunately, however, we currently lack the predictive criteria necessary to allow thermal acclimation of photosynthesis to be accounted for in GCMs. Nevertheless, it may be possible to establish predictive criteria by quantifying the impact of growth temperature on scaling relationships linking leaf net photosynthesis to related functional traits, such as N concentration and/or the LMA (i.e. following an approach analogous to that used in our current study for plant R). Alternatively, the impacts of long-term changes in growth temperature on the link between the maximum rate of carboxylation of Rubisco (V_{cmax}) and N concentration in a wide range of contrasting species may provide a way forward, as linear V_{cmax} -N relationships are currently used in JULES to predict current and future rates of GPP (Cox, 2001). Armed with an understanding of how photosynthetic parameters of contrasting species acclimate to long-term changes in temperature should enable future studies to better predict future rates of CO_2 exchange in thermally contrasting biomes. Clearly, further work is needed in this area.

Although we found no systematic difference in thermal acclimation of leaf R among contrasting species (as reported previously; Larigauderie & Körner, 1995;

Loveys *et al.*, 2003), our analysis and that of previous studies (Tjoelker *et al.*, 1999a; Loveys *et al.*, 2003; Atkin *et al.*, 2006b) clearly show that not all species acclimate to the same extent. Thus, while our coefficient ' C ' provides a tool to account for average degrees of acclimation in studies predicting rates of CO_2 exchange over large spatial and temporal scales, it may not correctly predict the impacts of acclimation on plant R for individual species. In such cases, a better understanding of the mechanistic basis for interspecific variability in acclimation will be needed if we are to predict the impacts of acclimation on a species-by-species basis. One way of doing this might be via establishing relationships between respiratory acclimation and variations in tissue N and carbohydrate concentrations, as suggested recently by Tjoelker *et al.* (2008).

When incorporating acclimation of plant R into JULES, no change was made to the assumed short-term temperature dependence of R (i.e. a Q_{10} of 2.0 was used). This enabled us to assess the impacts of acclimation alone on predicted rates of R over wide spatial and temporal scales. We are aware, however, that the outputs of our analysis could differ if temperature-dependent variations in the Q_{10} (Tjoelker *et al.*, 2001) were taken into account. For example, in their analysis of how variable Q_{10} 's and acclimation affected net CO_2 exchange in several selected ecosystems, Wythers *et al.* (2005) found that accounting for higher Q_{10} 's in cold ecosystems greatly diminished predicted rates of annual R (whereas accounting for acclimation increased annual R in these ecosystems), with the magnitude of variable Q_{10} effect often being greater than that of the acclimation effect. It is, therefore, important that future GCM modeling exercises account for both acclimation of R [using Eqn (8)] and temperature-dependent changes in the Q_{10} .

Conclusions

Our analysis has shown that growth temperature has predictable effects on the scaling relationships linking leaf R with two commonly measured leaf traits (LMA and N concentration), with thermal history accounting for much of the scatter in such scaling relationships. The fact that thermal history has predictable effects on generalized R -LMA-N scaling relationships (based in multispecies comparisons) provides, for the first time, a means of quantitatively accounting for an average degree of thermal acclimation of plant R in large-scale, predictive climate-vegetation models. Our analysis suggests that failure to account for acclimation of plant R alone in coupled climate-carbon models may have little effect on the predicted positive feedback from respiratory CO_2 as the world warms; however, failure to account for acclimation of plant R alone could have

profound implications for predicted rates of net carbon exchange in future forest management by nation-states using the Clean Development Mechanism as part of their Kyoto protocol commitments.

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