

# General patterns of acclimation of leaf respiration to elevated temperatures across biomes and plant types

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**Abstract** Respiration is instrumental for survival and growth of plants, but increasing costs of maintenance processes with warming have the potential to change the balance between photosynthetic carbon uptake and respiratory carbon release from leaves. Climate warming may cause substantial increases of leaf respiratory carbon fluxes, which would further impact the carbon balance of terrestrial vegetation. However, downregulation of respiratory physiology via thermal acclimation may mitigate this impact. We have conducted a meta-analysis with data collected from 43 independent studies to assess quantitatively the thermal acclimation capacity of leaf dark respiration to warming of terrestrial plant species from across the globe. In total, 282 temperature contrasts were included in the meta-analysis, representing 103 species of forbs, graminoids, shrubs, trees and lianas native to arctic, boreal, temperate and tropical ecosystems. Acclimation to warming was found to decrease respiration at a set temperature in the majority of the observations, regardless of the biome

of origin and growth form, but respiration was not completely homeostatic across temperatures in the majority of cases. Leaves that developed at a new temperature had a greater capacity for acclimation than those transferred to a new temperature. We conclude that leaf respiration of most terrestrial plants can acclimate to gradual warming, potentially reducing the magnitude of the positive feedback between climate and the carbon cycle in a warming world. More empirical data are, however, needed to improve our understanding of interspecific variation in thermal acclimation capacity, and to better predict patterns in respiratory carbon fluxes both within and across biomes in the face of ongoing global warming.

**Keywords** Climate change · Global patterns · Meta-analysis · Plant ecophysiology · Warming

## Introduction

Climate warming is predicted to increase the release of carbon dioxide (CO<sub>2</sub>) from the terrestrial biosphere into the atmosphere, thus triggering a positive climate–terrestrial carbon feedback that accelerates warming (Cox et al. 2000; Luo 2007). However, plant respiration (non-photorespiratory mitochondrial CO<sub>2</sub> release) may be downregulated in response to warming of temperature regimes over days to months, and such acclimation may reduce the potential decline in net primary productivity (NPP) (King et al. 2006; Smith and Dukes 2013; Slot et al. 2014a). High and mid-latitude ecosystems experience more rapid, and greater degrees of warming than the tropics (Stocker et al. 2013), and temperature effects on plant and ecosystem functions have been studied more extensively in temperate and boreal ecosystems than in the tropics. Although tropical regions

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may only experience moderate warming, tropical forests contribute disproportionately to the global carbon cycle (Pan et al. 2013), so even small temperature-induced changes in NPP may have consequences for the global carbon cycle. Despite an increasing interest in the role of acclimation of physiological processes to environmental changes from the modeling community in recent years (e.g. Arneth et al. 2012; Booth et al. 2012; Smith and Dukes 2013), little is known about global variation in thermal acclimation potential of plant respiration.

This paper is an attempt to synthesize results from empirical studies on thermal acclimation of leaf dark respiration from across the globe. First, we briefly review the current understanding of thermal acclimation of respiration. We then discuss the aspects of warm climates that lead to the supposition that warm-climate vegetation may respond differently to climate warming than vegetation in cooler biomes and that biome-specific climate warming responses can be expected. Finally, we analyze published data on thermal acclimation of leaf dark respiration and discuss the results of the meta-analysis in the context of climate warming as anticipated for the current century.

#### Thermal acclimation of leaf dark respiration

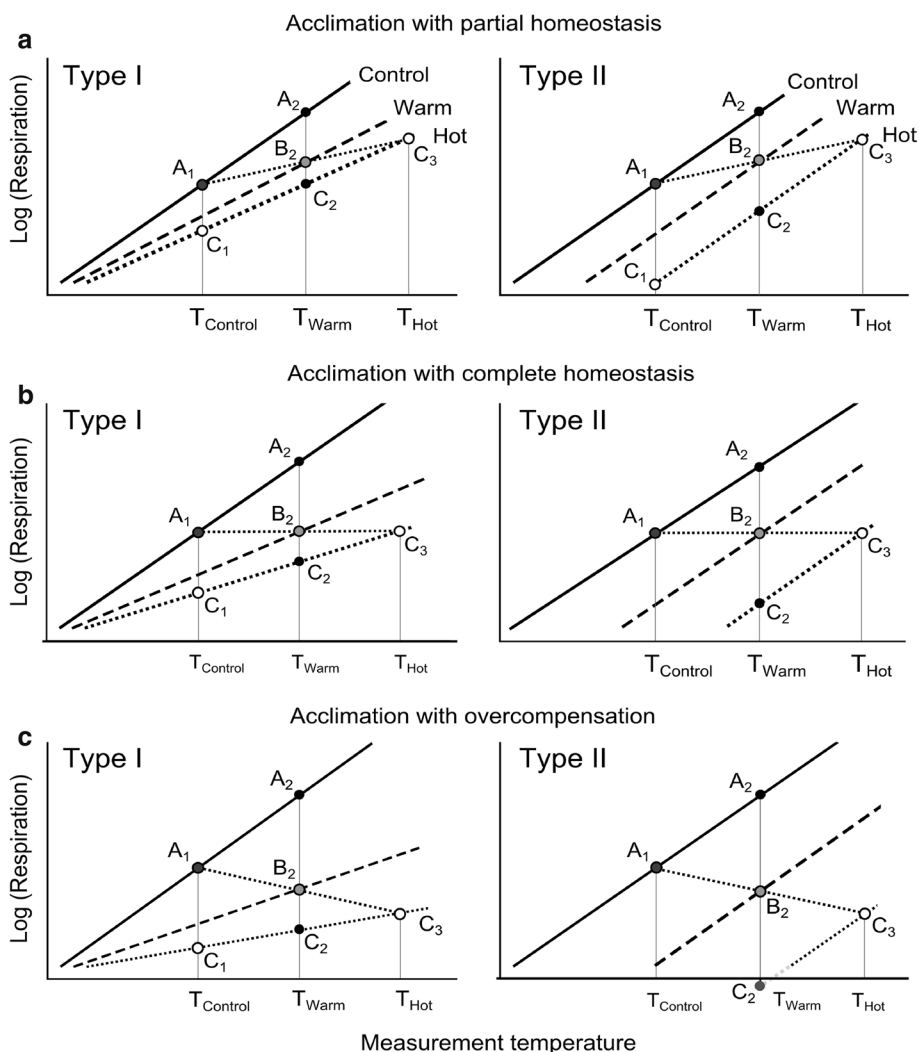
Respiration increases exponentially with short-term temperature increment. This sensitivity of respiration to changes in temperature is primarily driven by an increase in the demand for cellular maintenance, associated with increased protein turnover and membrane leakage at higher temperatures (Amthor 1984; Ryan 1991). Respiration is essential for the growth and survival of plants as it provides energy and carbon skeletons for biosynthesis (Penning de Vries 1975), but respiration associated with growth is believed to increase with warming only when growth itself increases (e.g. Frantz et al. 2004). Thus, thermal acclimation of respiration primarily involves changes in respiration associated with maintenance processes.

Thermal acclimation of respiration is a physiological, structural or biochemical adjustment by an individual plant in response to a change in the temperature regime that is manifested as an alteration in the short-term response to temperature (Smith and Dukes 2013) (Fig. 1). Plants that have been acclimated to a higher temperature regime generally have a decreased respiration rate at the new, elevated temperature relative to that of non-acclimated plants measured at that temperature (Atkin and Tjoelker 2003; Atkin et al. 2005). Thermal acclimation of respiration helps to maintain the optimal supply of ATP and carbon skeletons while minimizing carbon loss from respiration associated with maintenance processes. This may be achieved by changes in mitochondrial membrane composition to minimize ion leakage under warmer conditions (Raison et al.

1980) or by a reduction in the overall protein turnover rate, such as by a change in mitochondrial protein composition (Atkin et al. 2005). When respiration under warmed conditions equals the respiration rate exhibited by leaves under control conditions, perfect homeostasis of respiration is achieved, but even when homeostasis is not achieved, acclimation may have taken place (Fig. 1).

Two types of acclimation of respiration have been recognized (Atkin and Tjoelker 2003) (Fig. 1), and they are hypothesized to reflect differences in physiological mechanisms that underlie the acclimation process. Type I acclimation involves a decrease in the slope of the respiration–temperature response curve (i.e. lower short-term temperature sensitivity in warm-acclimated leaves), such as a reduction in  $Q_{10}$  (temperature sensitivity coefficient: the proportional change in respiration with a 10 °C temperature change), probably under influence of regulatory changes in existing respiratory enzymes (Atkin et al. 2005). Type II acclimation, a decrease in the elevation of the temperature response curve of respiration (i.e. lower respiration across the temperature range, without a change in  $Q_{10}$ ), typically involves a change in overall respiratory capacity. The respiratory capacity may change under the influence of a change in the relative amounts of individual respiratory enzymes or in the concentration of mitochondrial proteins (Atkin et al. 2005). Type II acclimation is expected to be more common for leaves that developed at elevated temperature than for those that developed under the former temperature regime, whereas Type I acclimation, associated with changes in existing enzymes, is thought to be more common in leaves that had matured prior to the change in temperature (Atkin and Tjoelker 2003; Atkin et al. 2005). Ultimately, both types of acclimation result in a reduction in respiration in leaves developed at warm conditions compared to that in non-acclimated leaves. It will nevertheless be valuable to identify patterns in acclimation type to aid in predictions of changes in respiratory fluxes, as the short-term sensitivity ( $Q_{10}$ ) changes in Type I acclimation but not in Type II.

Acclimation may occur within a few days of a temperature change (Rook 1969; Billings et al. 1971; Atkin et al. 2000; Bolstad et al. 2003; Lee et al. 2005; Slot et al. 2014a), but longer exposure to a new temperature may result in a greater degree of homeostasis (Smith and Haldley 1974). Longer exposure enables the plant to make a more complete thermal adjustment—for example, through changes in mitochondrial size and density in leaves (Armstrong et al. 2006). We would therefore expect the duration of warming to have a positive effect on the degree of acclimation. Leaves developed under an experimental temperature are often more completely acclimated than fully formed leaves transferred to that temperature (e.g. Campbell et al. 2007). Acclimation of pre-existing leaves



**Fig. 1** Leaves acclimate to warming by downregulating the respiration rate ( $R$ ). In the case of Type I acclimation,  $R$  is downregulated at high temperature, but remains unchanged at low temperature [i.e. the  $Q_{10}$  (temperature sensitivity coefficient: the proportional change in respiration with a 10 °C temperature change) decreases]. Under Type II acclimation,  $R$  decreases at all temperatures (i.e. no change in  $Q_{10}$ ). The degree of acclimation can be expressed with the set temperature method as  $Acclim_{SetTemp} = \frac{R_{Control}at\ T_{Set}}{R_{Warm}at\ T_{Set}}$ . (e.g.  $A_2/B_2$  or  $A_2/C_2$  in the graphs above). The degree of homeostasis of  $R$  achieved by acclimation can be expressed as  $Acclim_{Homeo} = \frac{R_{Control}at\ T_{Control}}{R_{Warm}at\ T_{Warm}}$  (e.g.  $A_1/B_2$  or

$A_1/C_3$ ). Three scenarios of Type I and Type II acclimation are illustrated. **a** Acclimation with partial homeostasis:  $R$  acclimates to warm or hot conditions ( $Acclim_{SetTemp} > 1$ ), but is not completely homeostatic across temperatures ( $Acclim_{Homeo} < 1.0$ . i.e.  $A_1 < B_2 < C_3$ ). **b** Acclimation with complete homeostasis: acclimation causes  $R$  to be identical for control and warm- and hot-acclimated leaves at their respective growth temperatures ( $Acclim_{Homeo} = 1.0$ . i.e.  $A_1 = B_2 = C_3$ ). **c** Acclimation leading to overcompensation: downregulation of  $R$  in warm- and hot-acclimated leaves is such that warmed leaves respire less under warmed conditions than control leaves under control temperature ( $Acclim_{Homeo} > 1.0$ . i.e.  $A_1 > B_2 > C_3$ )

depends on the physiological plasticity to temperature change alone, whereas acclimation of newly developed leaves employs both physiological and developmental plasticity, which together can be expected to achieve greater thermal adjustment than physiological plasticity alone. In line with previous work we therefore expect newly developed leaves to show systematically greater acclimation than pre-existing leaves. The degree of temperature change may also affect the degree of acclimation achieved, with greater temperature changes imposing a greater challenge on the

physiological system, presumably reducing the degree of homeostasis that can be achieved. Moderate warming can thus be expected to result in more complete acclimation than stronger warming. Tjoelker et al. (1999) found boreal evergreen tree species to acclimate better to experimentally imposed temperature differences than deciduous tree species, thereby providing support for the notion that leaves that experience greater temperature fluctuations in their lifetime have evolved greater thermal plasticity. Campbell et al. (2007), however, found no systematic differences

in acclimation among different growth forms in a growth cabinet study with forbs, grasses, trees and shrubs. Given that most dynamic global vegetation models use plant functional types based on growth form and leaf habit to characterize vegetation, it would be valuable to identify systematic differences in acclimation potential among plant functional types—if such differences were to exist.

#### Potential differences in warming response across biomes

Based primarily on results from mid- and high-latitude acclimation studies, the current consensus is that most plant species can, in principle, acclimate to changes in temperature (Atkin and Tjoelker 2003; Atkin et al. 2005), although the degree of acclimation responses is often species-specific (e.g. Larigauderie and Körner 1995). There are, however, several differences between the comparatively well-studied mid- and high-latitude systems and the warmer ecosystems closer to the equator that may result in systematic differences in thermal acclimation potential across biomes.

First, respiration at ambient temperature increases exponentially with mean annual temperature (Wright et al. 2006). It is therefore already high in tropical forests that experience much warmer temperature regimes year-around compared to vegetation at higher latitudes (Slot et al. 2013, 2014b). The absolute increase in respiration per degree of warming above ambient will be greater in low-latitude habitats than in high-latitude ones as warming will occur along the steeper end of the exponential temperature response curve (Dillon et al. 2010). Compared to the effect of warming on cool-biome plants, a much greater downregulation of respiration is required in warm-biome plants to achieve perfect homeostasis of respiration per degree of increase in temperature. This may constitute a considerably greater challenge than downregulation of the relatively small change in absolute metabolic rates with warming on the cooler end of the temperature spectrum.

Second, a large variation exists across biomes in the extent of seasonal changes in temperature regimes and, consequently, species from different biomes are likely to differ in their capacity to adjust to changing temperatures. For example, tropical forests experience only small seasonal changes of temperature regimes (Wright et al. 2009), and the thermally stable environment of the tropics may not have favored evolution of the capacity to acclimate to temperature changes (Janzen 1967; Cunningham and Read 2003a; Ghalambor et al. 2006). Comparative studies of thermal acclimation of photosynthesis of temperate and tropical rainforest species in Australia indeed found that tropical species do not acclimate as completely as temperate species (Cunningham and Read 2002, 2003b).

Third, whereas a few degrees warming might move mid- and high-latitude vegetation closer towards the physiological optimum of the local vegetation, tropical forests are believed to be close to exceeding their thermal optimum temperature (Doughty and Goulден 2008), and further warming will push the majority of tropical forests into a climate envelope currently not occupied by closed-canopy forest (Wright et al. 2009). The proximity of tropical vegetation to experiencing supra-optimal leaf temperatures makes the issue of high-temperature stress particularly pressing in the tropics. For the past 2.6 million years of the Quaternary Period (current and most recent period of the Cenozoic Era), tropical regions have experienced conditions that were relatively cool compared to current and near-future temperatures, and natural selection would not have favored heat-protective genes and traits (Corlett 2011, 2012). Heat stress can lead to protein denaturing and increased membrane fluidity, factors that increase the respiratory demand for maintenance and which are as such conflicting with an acclimatory decrease in respiration. Based on these three points, we expect the capacity for acclimation to warming to depend on the temperature regime of the biome of origin of the plants, with the acclimation capacity increasing with decreasing mean temperature, as well as with increasing temperature variability of the biome.

In this meta-analysis we sought to determine the effects on thermal acclimation of respiration of (1) the biome, or climatic region of origin of the study species, (2) the duration of exposure to warming, (3) the developmental status of the leaf (pre-existing when temperature change was imposed, or newly developed at the experimental temperature), (4) the growth form under investigation and (5) the degree of warming or the temperature difference across contrasting temperatures.

## Methods

### Data selection

We analyzed the results of studies in which leaf dark respiration had been measured for plants grown at different temperatures; leaf dark respiration had been measured repeatedly under changing ambient temperature conditions; plants were grown in common gardens at different ambient temperature regimes, or plants were exposed to experimental warming above ambient temperature. We searched Google Scholar and the Institute for Scientific Information (ISI) Web of Science for studies that (1) used non-cultivated plant species, (2) exposed plants to at least two growth/acclimation temperatures and (3) measured respiration at the respective ambient temperatures,

or at the same temperature for both groups, or both (e.g. by measuring full temperature response curves of respiration of control and warmed leaves). Most studies used growth cabinets to assess the effect of growth temperature or short-term temperature changes. Research on physiological acclimation to low temperatures commonly uses the same set-up, but these are not included in this study. In total, we identified 43 studies that met the above criteria and included these in the meta-analysis [see Table 1; 42 published and one unpublished dataset (Electronic Supplementary Material (ESM) 1)]. These studies include data on 282 temperature contrasts of 103 species, with a varying number of leaves or plants measured at each temperature contrast, and report on species from alpine, arctic and Antarctic, boreal, temperate and tropical climates, including forbs, graminoids (sedges and grasses) and evergreen and deciduous shrubs, trees and lianas (Table 1). All studies used infrared gas analyzers to quantify respiration rates. Only measurements on fully expanded leaves are included, so the acclimation data reported here reflect changes in respiration associated with maintenance processes only. Only a small number of studies compared respiration at ambient temperature with respiration of leaves warmed to above-ambient temperatures (29 out of a total of 282 species-by-temperature contrasts; 20 of 103 species). Studies that warmed plants or leaves during the night only were also included, as respiration does not necessarily acclimate to mean daily temperature (e.g. Atkin et al. 2000) and has been shown to acclimate to nighttime temperature instead (Bruhn et al. 2007). Data were extracted from tables, (enlarged) figures or from information provided in the Electronic Supplementary Material.

#### Data analysis

To assess acclimation responses quantitatively we extracted information from these studies that enabled us to calculate ‘acclimation ratios’ based on the ‘set temperature method’ and the ‘homeostasis method’ as described by Loveys et al. (2003) (Table 2). In the set temperature method, leaf respiration of warmed and control plants is measured at the same temperature (e.g. at 25 °C, at the temperature of the warmed plants, or at the control temperature). The degree of acclimation is determined from the ratio of these two measurements as  $\text{Acclim}_{\text{SetTemp}} = R_{\text{Control}}/R_{\text{Warm}}$ , where  $R_{\text{Control}}$  is the leaf respiration rate of plants at the control temperature and  $R_{\text{Warm}}$  is the leaf respiration rate of warmed plants, with the higher the value of  $\text{Acclim}_{\text{SetTemp}}$ , the greater the degree of acclimation. In the homeostasis method, the degree of homeostasis achieved by acclimation is assessed, where  $\text{Acclim}_{\text{Homeo}}$  is the ratio of leaf respiration of control and warmed plants at their respective temperatures. When complete homeostasis has been achieved,  $\text{Acclim}_{\text{Homeo}} = 1.0$ ; when acclimation is

incomplete,  $\text{Acclim}_{\text{Homeo}} < 1.0$ . For studies that used growth cabinets to expose plants to two or more different temperatures, the lower of the two was considered to be the control temperature. Similarly, when temperature changes associated with seasons, changes in weather systems or geographical range of common gardens were used, the lower temperature regime was considered to represent the control. Data were available to calculate both acclimation ratios for 62 temperature contrasts (46 species), but more commonly only  $\text{Acclim}_{\text{SetTemp}}$  (167 contrasts, 62 species) or  $\text{Acclim}_{\text{Homeo}}$  (43 contrasts, 37 species) could be calculated, and the set temperature used to calculate  $\text{Acclim}_{\text{SetTemp}}$  differed across studies. Because the long-term acclimation ratio  $\text{Acclim}_{\text{LTR}_{10}}$ , proposed by Atkin et al. (2005) (Table 2) requires information on both the initial  $Q_{10}$  and the long-term acclimation ratio  $\text{LTR}_{10}$  (Larigauderie and Körner 1995), this metric could not be calculated for most studies and was not included in the following analyses. It was not always possible to determine the uncertainty associated with the values used to calculate the acclimation ratios; variances were not always given, and in some cases values were extracted from fitted curves for which no confidence intervals were presented, or tables did not specify whether standard deviations or standard errors of the mean were presented. When sample size and standard errors were available, we tested whether respiration of the control and warmed leaves were significantly different by assuming a normal distribution of the data and calculating 95 % confidence intervals.

#### Acclimation type

To properly assess which type of acclimation has occurred, one would ideally have temperature response curves that go down to the low-temperature ‘basal respiration.’ In the case of Type I acclimation, the control and acclimation curve would hinge at this point, whereas in case of Type II acclimation the curves would never intersect. Generally, however, respiration is not measured at sufficiently low temperatures to identify where the temperature response curves would intersect. It is more common to compare the slopes of log-transformed temperature response curves to test the difference in slopes. When the slope of the warm-acclimated leaf is lower, Type I acclimation is supposed; if the slopes are not significantly different, but have a lower intercept for warm-acclimated leaves, then Type II acclimation is implied. Accordingly, when data were available to compare the slopes of control and acclimated leaves, results were classified as Type I or Type II acclimation. When Type I and Type II acclimation could not clearly be distinguished, no acclimation type was assigned.

To explore whether certain environmental factors may influence either  $\text{Acclim}_{\text{SetTemp}}$  or  $\text{Acclim}_{\text{Homeo}}$ , we tested general linear models for the following explanatory

**Table 1** Mean  $Acclim_{SetTemp}$  and  $Acclim_{Homeo}$  across studies are shown by biome, growth form and leaf habit

| Biome                | Laboratory |          |                  |                    | Field            |           |          |                 | Total              |                  | References <sup>a</sup> |           |                                     |
|----------------------|------------|----------|------------------|--------------------|------------------|-----------|----------|-----------------|--------------------|------------------|-------------------------|-----------|-------------------------------------|
|                      | $n_{con}$  | $n_{sp}$ | $\Delta T$ (°C)  | $Acclim_{SetTemp}$ | $Acclim_{Homeo}$ | $n_{con}$ | $n_{sp}$ | $\Delta T$ (°C) | $Acclim_{SetTemp}$ | $Acclim_{Homeo}$ |                         | $n_{con}$ | $n_{sp}$                            |
| Alpine               |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Forbs                | 15         | 15       | 10.4 (10.0–11.0) | 1.65 ± 0.32        | 0.62 ± 0.26      | 1         | 1        | 1.5             | 1.21               | nd               | 16                      | 16        | 4, 9, 16, 26                        |
| Graminoids           | 4          | 4        | 10.3 (10.0–11.0) | 1.86               | 0.59 ± 0.19      | 5         | 1        | 4.8 (1.5–8.2)   | 1.87 ± 1.31        | nd               | 9                       | 6         | 9, 16, 24, 26                       |
| Arctic and Antarctic |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Forbs                | 3          | 2        | 7.7 (5.0–10.0)   | 1.52 ± 0.40        | 0.94 ± 0.12      |           |          |                 |                    |                  | 3                       | 2         | 1, 4, 40                            |
| Graminoids           | 2          | 1        | 6.5 (5.0–8.0)    | 1.46 ± 0.22        | 1.04 ± 0.01      |           |          |                 |                    |                  | 2                       | 1         | 40                                  |
| Shrubs               |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Evergreen            | 2          | 1        | 15.0             | 1.42 ± 0.02        | 0.54 ± 0.07      |           |          |                 |                    |                  | 2                       | 1         | 30                                  |
| Boreal               |            |          |                  |                    |                  |           |          |                 |                    |                  | 19                      | 9         |                                     |
| Trees                |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Deciduous            | 7          | 4        | 8.6 (6.0–12.0)   | 1.39 ± 0.32        | 0.68 ± 0.15      | 4         | 2        | 4.3 (3.4–5.3)   | 1.27 ± 0.49        | nd               | 11                      | 5         | 13, 27, 34                          |
| Evergreen            | 5          | 3        | 8.8 (6.0–12.0)   | 1.42 ± 0.22        | 0.80 ± 0.15      | 3         | 2        | 4.0 (1.5–8.0)   | 1.06 ± 0.19        | nd               | 8                       | 4         | 33–35, 37, 38, 42                   |
| Temperate            |            |          |                  |                    |                  |           |          |                 |                    |                  | 205                     | 57        |                                     |
| Forbs                | 71         | 18       | 11.3 (5.0–21.0)  | 1.61 ± 0.59        | 0.88 ± 0.42      | 3         | 3        | 1.1             | 0.94 ± 0.06        | nd               | 74                      | 21        | 1, 14, 16                           |
| Graminoids           | 32         | 7        | 13.0 (5.0–21.0)  | 1.76 ± 0.57        | 0.73 ± 0.35      | 2         | 2        | 1.6 (1.1–2.1)   | 1.17 ± 0.34        | nd               | 34                      | 9         | 7, 12, 16, 18, 43                   |
| Shrubs               |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Deciduous            | 17         | 4        | 12.8 (6.0–21.0)  | 1.66 ± 0.60        | 0.71 ± 0.16      | 1         | 1        | 14              | 1.78 ± 0.58        |                  | 3                       | 3         | 31                                  |
| Evergreen            |            |          |                  |                    |                  |           |          |                 | 2.37               |                  | 18                      | 4         | 7, 31, 36                           |
| Trees                |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Deciduous            | 18         | 6        | 11.7 (5.0–21.0)  | 1.87 ± 0.90        | 0.43 ± 0.18      | 12        | 7        | 5.0 (1.0–10)    | 1.31 ± 0.31        | nd               | 30                      | 10        | 5, 7, 8, 13, 17, 19, 20, 25         |
| Evergreen            | 37         | 8        | 12.1 (4.0–21.0)  | 1.54 ± 0.41        | 0.76 ± 0.18      | 9         | 5        | 1.5 (0.3–3.9)   | 1.03 ± 0.14        | 1.12 ± 0.30      | 46                      | 10        | 2, 63, 7, 18, 19–21, 23, 32, 39, 41 |
| Tropical             |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Lianas               |            |          |                  |                    |                  |           |          |                 |                    |                  | 26                      | 11        |                                     |
| Deciduous            |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Evergreen            |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Trees                |            |          |                  |                    |                  |           |          |                 |                    |                  |                         |           |                                     |
| Deciduous            | 11         | 2        | 6.4 (3.0–10.0)   | 1.23 ± 0.52        | 0.72 ± 0.29      | 6         | 4        | 2.5 (2.3–3.5)   | 1.05 ± 0.08        | 0.88 ± 0.04      | 17                      | 5         | 10, 11, 15, 28, 29                  |
| Evergreen            | 2          | 1        | 6.0              | 1.20 ± 0.31        | 0.97             | 2         | 1        | 2.7 (2.3–3.2)   | 1.37 ± 0.32        | 0.87             | 4                       | 3         | 10, 11                              |

Data are presented as the mean ± standard deviation

$Acclim_{SetTemp} = R_{Control}/R_{Warm}$  where  $R_{Control}$  = leaf respiration rate of plants at the control temperature and  $R_{Warm}$  = leaf respiration rate of warmed plants;  $Acclim_{Homeo}$  = ratio of leaf respiration of control and warmed plants at their respective temperatures;  $\Delta T$ , Mean degree (and range) of warming;  $n_{con}$ ,  $n_{sp}$ , the number of temperature and species contrasts, respectively; nd, no data

<sup>a</sup> 1. Arnone and Körner (1997), 2. Atkin et al. (2000), 3. Ayub et al. (2011), 4. Billings et al. (1971), 5. Bolstad et al. (2007), 6. Bruhn et al. (2007), 7. Campbell et al. (2007), 8. Centritto et al. (2011), 9. Chabot and Billings (1972), 10. Cheesman and Winter (2013a), 11. Cheesman and Winter (2013b), 12. Chi et al. (2013), 13. Dillaway and Kruger (2011), 14. Gandin et al. (2014), 15. Krause et al. (2013), 16. Larigauderie and Körner (1995), 17. Lee et al. (2005), 18. Loveys et al. (2003), 19. Ow et al. (2010), 20. Ow et al. (2008a), 21. Ow et al. (2010), 22. Rodríguez-Valcarrada et al. (2010), 23. Rook (1969), 24. Searle et al. (2011), 25. Searle and Turnbull (2011), 26. Shi et al. (2010), 27. Silim et al. (2010), 28. Slot et al., unpublished dataset (see S11 for details), 29. Slot et al. (2014a), 30. Smith and Hadley (1974), 31. Strain (1969), 32. Teskey and Will (1999), 33. Tjoelker et al. (2009), 34. Tjoelker et al. (1999), 35. Tjoelker et al. (2008), 36. Tjoelker et al. (2008), 37. Wang et al. (1995), 38. Way and Sage (2008), 39. Werten et al. (2000), 40. Xiong et al. (2000), 41. Yin et al. (2008), 42. Zha et al. (2002), 43. Zhou et al. (2007)

**Table 2** Quantifying acclimation of respiration. Several methods have been proposed to quantify thermal acclimation of respiration. These are all based on quantifying the degree of downregulation of

respiration in warm-acclimated leaves, but they use different temperatures and timescales over which the change in respiration is assessed

| Method                          | Parameter                 | References                     | Description   |
|---------------------------------|---------------------------|--------------------------------|---|
| Set temperature method          | Acclim <sub>SetTemp</sub> | Loveys et al. (2003)           | Compares $R$ of control and warmed leaves at a set temperature ( $R_{\text{Control}}/R_{\text{Warm}}$ ). Any set temperature ( $T_{\text{Set}}$ ) can be used, but when Type I acclimation (Fig. 1) has occurred, Acclim <sub>SetTemp</sub> increases with the $T_{\text{Set}}$ . When $R$ has acclimated Acclim <sub>SetTemp</sub> >1.0 <sup>a</sup>   |
| Long-term acclimation ratio     | LTR <sub>10</sub>         | Larigauderie and Körner (1995) | Compares $R$ of warm-acclimated leaves at a high temperature with $R$ of control leaves at a temperature 10 °C lower ( $R_{\text{Warm}}$ at $T_{\text{Warm}}/R_{\text{Control}}$ at $T_{\text{Warm}} - 10$ ). In effect, the LTR <sub>10</sub> represents the long-term $Q_{10}$ . When $R_{\text{Warm}}$ at $T_{\text{Warm}}$ is not significantly different from $R_{\text{Control}}$ at $T_{\text{Warm}} - 10$ , $R$ has fully acclimated to warming   |
| Long-term acclimation ratio (2) | Acclim <sub>LTR10</sub>   | Atkin et al. (2005)            | This is a modification of LTR <sub>10</sub> in which LTR <sub>10</sub> is directly compared to the short-term $Q_{10}$ . Acclim <sub>LTR10</sub> is calculated as $1 - [(LTR_{10} - 1)/(Q_{10} - 1)]$ . The more LTR <sub>10</sub> has decreased with acclimation, the larger Acclim <sub>LTR10</sub>   |
| Homeostasis method              | Acclim <sub>Homeo</sub>   | Loveys et al. (2003)           | This determines the degree of homeostasis of $R$ in leaves acclimated to contrasting temperatures by comparing $R$ of control leaves at control temperature to warmed leaves at warm temperature ( $R_{\text{Control}}$ at $T_{\text{Control}}/R_{\text{Warm}}$ at $T_{\text{Warm}}$ ). When $R_{\text{Control}}$ at $T_{\text{Control}}$ and $R_{\text{Warm}}$ at $T_{\text{Warm}}$ are not significantly different, $R$ has fully acclimated. When the temperature difference between two sets of plants/leaves equals 10 °C, Acclim <sub>Homeo</sub> is the inverse of LTR <sub>10</sub> |

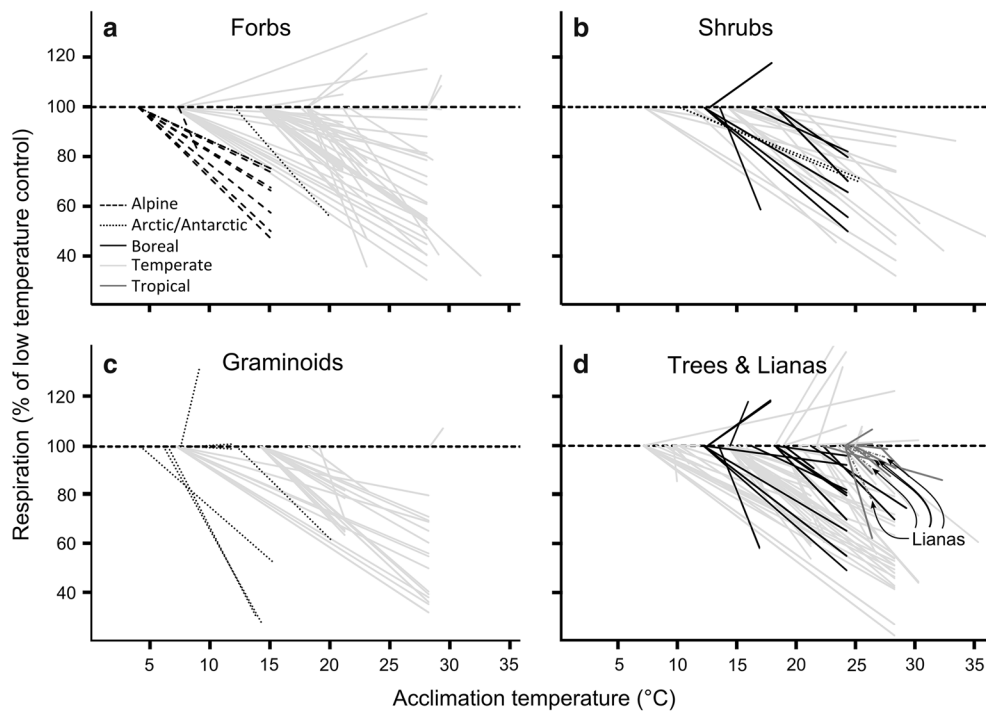
<sup>a</sup> Under all three acclimation scenarios presented in Fig. 1, Acclim<sub>SetTemp</sub> is >1.0, so Acclim<sub>SetTemp</sub> cannot be used to determine whether acclimation results in homeostasis or not. LTR<sub>10</sub>, Acclim<sub>LTR10</sub> and Acclim<sub>Homeo</sub> are all 1.0 under complete homeostasis. LTR<sub>10</sub> >1.0 under partial homeostasis, and <1.0 under overcompensation. Acclim<sub>LTR10</sub> and Acclim<sub>Homeo</sub> are <1.0 under partial homeostasis and >1.0 under overcompensation

variables: biome or climatic region of origin; growth form; temperature difference; duration of exposure; maximum (nighttime) temperature; method (in situ warming above ambient vs. all other methods); leaf developmental status (whether the measured leaves existed prior to exposure to the warmer temperature or whether they developed at the elevated temperature). Leaf habit (evergreen vs. deciduous) was determined for woody species only, so in addition to the above models, we analyzed Acclim<sub>SetTemp</sub> and Acclim<sub>Homeo</sub> of the subset of woody species with models that included leaf habit. We also determined the most parsimonious significant linear regression model of Acclim<sub>SetTemp</sub> and Acclim<sub>Homeo</sub> that revealed a minimal pattern in the residuals using the same candidate predictors as above. All statistical analyses were performed in R version 2.14.1 (R Development Core Team 2011, R Foundation for Statistical Computing, Vienna, Austria).

## Results

Temperature contrasts over which acclimation was determined ranged from 0.3 °C in an in situ infrared heating experiment of *Eucalyptus pauciflora* seedlings (Bruhn et al. 2007) to 21 °C in a growth cabinet study on temperate tree, forb and graminoid species grown in hydroponics (Campbell et al. 2007). Respiratory response to change in temperature ranged from acclimation leading to complete

homeostasis of respiration across the study temperatures to no detectable changes in the instantaneous temperature response curve. Acclimation to warmer temperatures resulted in a downregulation of respiration at a set temperature in 205 of the 229 contrasts for which Acclim<sub>SetTemp</sub> could be calculated. This is indicated in Fig. 2 by the negative slopes of the lines connecting the relative respiration rates at a (contrast-specific) set temperature of the control (which is set to 100 %) and warmed plants plotted at their respective acclimation temperatures, i.e. the control and warming treatment temperature regimes (daily means, or nighttime means, as reported in each study). This downregulation was significant in 41 of the 56 cases for which data were available to determine significance. It is possible that the relationship of respiration at a set temperature and acclimation temperature is not linear, but this distinction requires analysis of temperature series that are unavailable in most studies. Figure 2 further shows that downregulation of respiration at a set temperature occurred for most temperature contrasts regardless of the maximum acclimation temperature to which plants were exposed. Complete homeostasis (Acclim<sub>Homeo</sub> = 1.0) or acclimation leading to overcompensation (Acclim<sub>Homeo</sub> >1.0) were, however, rare, and the mean Acclim<sub>Homeo</sub> value ( $0.79 \pm 0.39$ ; mean  $\pm$  standard deviation) was significantly smaller than 1.0 ( $t$  test,  $t = -5.5$ ,  $P < 0.0001$ ). The tendency for downregulation of respiration in warm-acclimated leaves was consistent across biomes and growth forms (Table 1).



**Fig. 2** Relative change of respiration rate ( $R$ ) at a contrast-specific set temperature for 84 species of forbs (**a**), graminoids (**b**), shrubs (**c**) and trees and lianas (**d**) based on 229 sets of respiration measurements, where the set temperature of measurement varied across studies. Each line connects two points, of which the first point (left end) is the  $R$  of control leaves (scaled to 100 %) plotted against the control temperature, and the second (right end) is the percentage  $R$  of

warmed plants measured at the same set temperature, plotted against the acclimation temperature.  $R$  of warm-acclimated leaves was either taken directly from the published source, or calculated from the  $\text{Acclim}_{\text{SetTemp}}$  value. All contrasts are shown, including those for which the change in respiration at a set temperature was not statistically significant.  $\text{Acclim}_{\text{SetTemp}} = R_{\text{Control}}/R_{\text{Warm}}$ , where  $R_{\text{Control}} = R$  of plants at the control temperature and  $R_{\text{Warm}} = R$  of warmed plants

### Treatment and species effects on acclimation of respiration

Summarizing the data by biome or climatic region appears to suggest lower  $\text{Acclim}_{\text{SetTemp}}$  in the tropics than in cooler ecosystems (Fig. 3). However, this apparent pattern in  $\text{Acclim}_{\text{SetTemp}}$  across biomes could be explained by the average degree of warming used in the experiments: cooler ecosystem studies more often warmed plants by a greater degree than studies from the tropics (Table 1). When the effect of the degree of warming was accounted for, the biome of origin was no longer a significant predictor of either of the acclimation ratios. As indicated above, the maximum nighttime temperature that treatment plants were exposed to also did not affect the acclimation potential of respiration; studies at high temperature (warmest 33 %; mean  $T_{\text{Night Max}} = 26.4$  °C) did not result in lower acclimation ratios than studies done at low temperatures (coldest 33 %; mean  $T_{\text{Night Max}} = 17.4$  °C) (Fig. 3e, f).

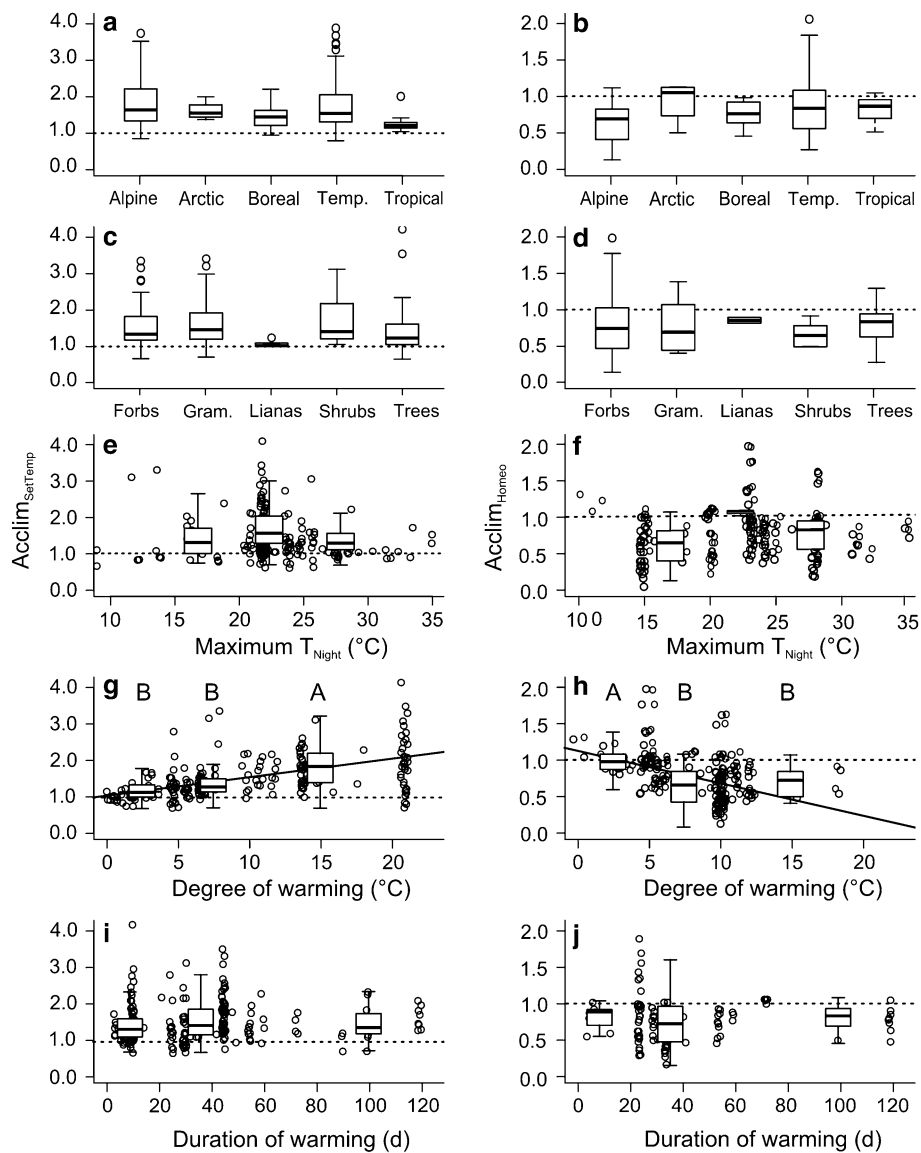
The duration of warming had no effect on  $\text{Acclim}_{\text{SetTemp}}$  (Fig. 3), and the mean  $\text{Acclim}_{\text{SetTemp}}$  of studies exposing leaves to an experimental temperature for <25 days was not significantly different from the categories of warming

25–50 days and warming for >50 days. All three categories had mean  $\text{Acclim}_{\text{SetTemp}}$  values that were significantly greater than 1.0 ( $t$  test,  $P < 0.001$  for all). There were, however, significant and marginally significant interactions between duration of warming and the developmental status of the leaves for both acclimation parameters (Table 3): the longer pre-existing leaves were warmed, the more the respiration rate at a set temperature was down-regulated and the more homeostasis was approached. In contrast, the duration of warming did not affect the acclimation of leaves newly developed at the experimental temperatures.

The developmental status of leaves alone did not affect acclimation. When other factors, such as duration and the degree of warming, were accounted for, leaf developmental status was a significant predictor of  $\text{Acclim}_{\text{SetTemp}}$  (Table 3), with newly developed leaves having greater  $\text{Acclim}_{\text{SetTemp}}$ . When only woody plants were included in the analysis, newly developed leaves achieved greater  $\text{Acclim}_{\text{Homeo}}$  than pre-existing ones.

There were no significant differences in  $\text{Acclim}_{\text{SetTemp}}$  and  $\text{Acclim}_{\text{Homeo}}$  among growth forms, with large variation





**Fig. 3** The  $Acclim_{SetTemp}$  (left panels; higher values indicate greater acclimation) and  $Acclim_{Homeo}$  (ratio of leaf respiration of control and warmed plants at their respective temperatures; right panels; values closer to 1.0 indicate more complete homeostasis) as a function of: **a, b** biome of origin (*Temp.* temperate), **c, d** growth form (*Gram.* graminoids), **e, f** maximum (nighttime,  $T_{Night}$ ) temperature of warmed plants, **g, h** the degree of warming, **i, j** duration of warming. The continuous data in **e–j** (each point is a temperature contrast) were also binned in three groups of similar sample size to summarize in *boxplots* at the median temperature on the *x*-axis. The bins for maximum

$T_{Night}$  (**e, f**) are <20, 20–22, and >22 °C; those for degree of warming (**g, h**) are <5, 5–10, and >10 °C and those for duration of warming (**i, j**) are <25, 25–50, and >50 days. Multi-year warming experiments were omitted from the scatter plot in **i**, but were included in the *boxplot*. Different letters indicate significant difference among groups at  $P < 0.05$  (one-way analysis of variance). The *solid black slanted lines* in **g** and **h** represent significant linear regressions. The *boxplots* indicate the median, 25th and 75th percentile across temperature contrasts; whiskers extend to 1.5 times the interquartile range

existing within each (except for lianas, for which only five contrasts were included, with warming of no more than 3.3 °C) (Fig. 3). When only woody species were included, there was a marginally significant effect of biome on  $Acclim_{Homeo}$ . This was caused by a single shrub species (two temperature contrasts) from the arctic with particularly low  $Acclim_{Homeo}$  values and can thus not be

interpreted as a biologically meaningful systematic biome difference in acclimation potential.

The degree of warming (temperature interval of the contrasts) had a significant effect, such that  $Acclim_{SetTemp}$  increased with the degree of warming, whereas  $Acclim_{Homeo}$  decreased with the degree of warming (Fig. 3). There was a marginally significant interaction between the

**Table 3** *P* values for models of the dependence of  $\text{Acclim}_{\text{SetTemp}}$  and  $\text{Acclim}_{\text{Homeo}}$  on species traits and experimental conditions

| Species' traits and experimental conditions | $\text{Acclim}_{\text{SetTemp}}$ |                    |         | $\text{Acclim}_{\text{Homeo}}$ |                    |         |
|---|----------------------------------|--------------------|---------|--------------------------------|--------------------|---------|
|   | Full model                       | Parsimonious model | 'Woody' | Full model                     | Parsimonious model | 'Woody' |
| Biome                                       | 0.66                             |                    | 0.54    | 0.59                           |                    | 0.05    |
| Growth form                                 | 0.64                             |                    | 0.77    | 0.41                           |                    | 0.12    |
| Leaf habit                                  |                                  |                    | 0.013   |                                |                    | 0.018   |
| Pre-existing                                | 0.03                             |                    | 0.33    | 0.16                           |                    | <0.01   |
| Max $T_{\text{Night}}$                      | 0.44                             |                    | 0.59    | 0.67                           |                    | 0.109   |
| Method                                      | 0.77                             |                    | 0.66    | 0.34                           |                    | 0.28    |
| Duration                                    | 0.13                             |                    | 0.28    | 0.67                           |                    | 0.15    |
| Degree of warming                           | <0.0001                          | <0.0001            | <0.0001 | 0.02                           | <0.0001            | 0.57    |
| Duration × degree of warming                | 0.08                             |                    | 0.23    | 0.40                           |                    | 0.79    |
| Duration × pre-existing                     | <0.05                            |                    | <0.06   | 0.06                           |                    | 0.04    |
| Model $R^2$                                 | 0.37                             | 0.29               | 0.46    | 0.33                           | 0.20               | 0.61    |
| Full model <i>P</i>                         | <0.0001                          | <0.0001            | <0.0001 | 0.003                          | <0.0001            | 0.0058  |

The most parsimonious significant model only included degree of warming. Analysis of variance results are based on Type II sums of squares Biome (arctic/Antarctic, alpine, boreal, temperate, tropical); growth form (forbs, graminoids, shrubs, trees, lianas), leaf habit [evergreen or deciduous (for the subset of 'woody' species)]; pre-existing, leaves developed prior to warming vs. leaves developed at the experimental temperature; max  $T_{\text{Night}}$ , highest nighttime temperature in the experiment; method, the method used in the study (in situ warming above ambient, or all else); duration, duration of exposure to experimental temperature; degree of warming, mean temperature difference between control and warmed leaves

duration and the degree of warming ( $P = 0.08$ ; Table 3) that affected  $\text{Acclim}_{\text{SetTemp}}$ , with  $\text{Acclim}_{\text{SetTemp}}$  increasing more strongly with the degree of warming in leaves that were warmed longer than in leaves warmed for a shorter duration. For both acclimation ratios the most parsimonious significant model only included the degree of warming.

Leaf habit (evergreen vs. deciduous) significantly affected both  $\text{Acclim}_{\text{SetTemp}}$  and  $\text{Acclim}_{\text{Homeo}}$  in the subset of data for which information on leaf habit was available, with deciduousness slightly increasing  $\text{Acclim}_{\text{SetTemp}}$  values, while decreasing  $\text{Acclim}_{\text{Homeo}}$  values compared to evergreens. In a simple one-factorial comparison, evergreen and deciduous leaves did not differ significantly in  $\text{Acclim}_{\text{SetTemp}}$  and evergreen leaves had only marginally significantly higher  $\text{Acclim}_{\text{Homeo}}$  (Fig. 4). Leaf developmental status (pre-existing vs. newly developed leaves) was also a significant predictor in the  $\text{Acclim}_{\text{Homeo}}$  model of the woody taxa (Table 3). Similar to the one-factorial comparison in Fig. 3, newly developed leaves had slightly higher  $\text{Acclim}_{\text{Homeo}}$  values than pre-existing leaves.

#### Acclimation to in situ warming

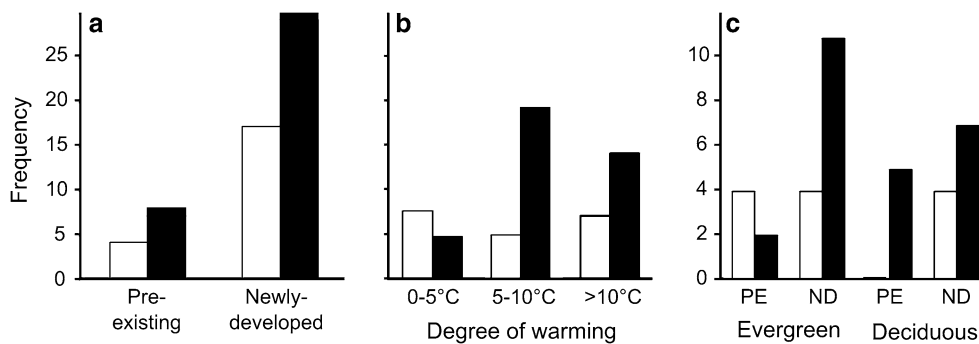
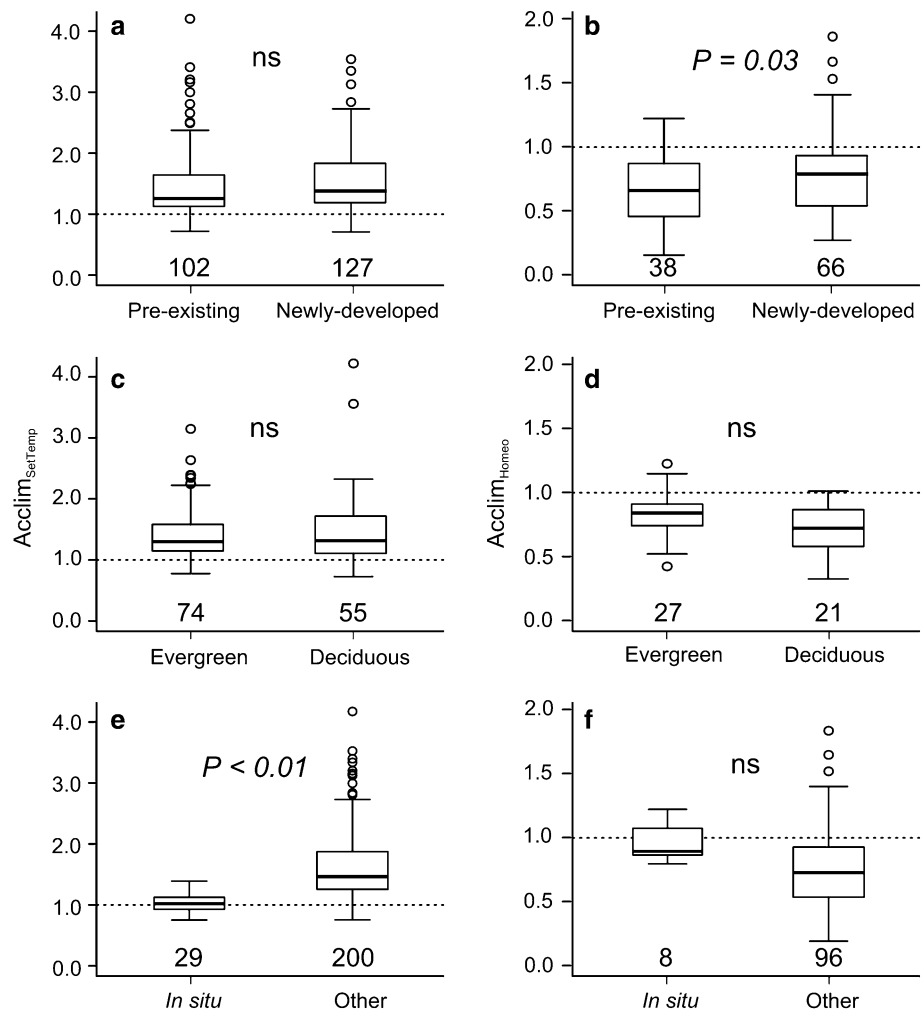
The 12 studies in the field in which the temperature was elevated above ambient temperature warmed leaves by an average of 1.9 °C (median 2.2 °C). This contrasts with a mean temperature difference of 10.8 °C (median 10.0 °C) in the other studies. Median duration of the experimental

warming was the same for the two groups at 30 days, whereas the mean duration was much longer for in situ studies because of two studies that warmed *Pinus sylvestris* trees in Finland for several years (Wang et al. 1995; Zha et al. 2002). Mean  $\text{Acclim}_{\text{SetTemp}}$  with in situ warming was 1.05, which was significantly lower than the mean of the other studies, 1.60 ( $t$  test,  $t = 5.1$ ,  $P < 0.0001$ ) (Fig. 4).  $\text{Acclim}_{\text{Homeo}}$  of in situ warmed leaves was 0.96, which was higher than the mean in other studies, 0.75 ( $t$  test,  $t = -2.0$ ,  $P = 0.03$ ). When the degree of warming was taken into consideration, however, results from the in situ warming studies no longer differed from that of the other studies.

#### Acclimation type

The type of acclimation exhibited by warmed leaves could be determined for 58 temperature contrasts (12 on pre-existing leaves, 46 on leaves developed under the experimental temperature). Both pre-existing and newly developed leaves exhibited Type II acclimation more often than Type I acclimation (Fig. 5a). Evergreen and deciduous species exhibited Type II acclimation in 65 and 75 % of the cases, respectively. Interestingly, four of six contrasts of pre-existing evergreen leaves showed Type I acclimation, whereas all five contrasts of pre-existing deciduous leaves exhibited Type II acclimation (Fig. 5c). Leaves that were warmed by <5 °C exhibited Type I acclimation in the majority of the cases, whereas Type II acclimation

**Fig. 4**  $Acclim_{SetTemp}$  (left panels) and  $Acclim_{Homeo}$  (right panels), in relation to: **a, b** leaf developmental age (pre-existing at the time of warming vs. newly developed under warmed conditions), **c, d** leaf type (evergreen vs. deciduous), **e, f** method of warming (in situ warming above ambient vs. other methods). The number of observations per category is shown below each boxplot. *ns* Not significant. The boxplots indicate the median, 25th and 75th percentile across temperature contrasts; whiskers extend to 1.5 times the interquartile range



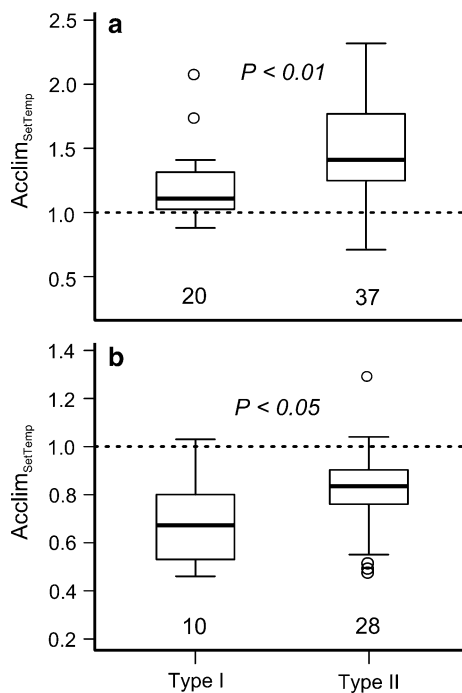
**Fig. 5** Frequency of Type I (open bars) and Type II (filled bars) acclimation of respiration: **a** in leaves present prior to warming (pre-existing) and leaves developed under warmed conditions (newly-developed), **b** in relation to the degree of warming experienced, **c** of

pre-existing (PE) and newly developed (ND) leaves of evergreen and deciduous woody species. In total, 58 sets of observations on 45 species were included in **a** and **b**, and 37 sets of observations on 26 species were included in **c**

was more common in leaves that were warmed by 5–10 °C or by >10 °C (Fig. 5b). Type II acclimation was associated with a greater downregulation of respiration (higher  $Acclim_{SetTemp}$ ) and more homeostatic acclimation than Type I acclimation (Fig. 6).

**Discussion**

Several trends in respiratory acclimation could be identified from our meta-analysis of thermal acclimation data extracted from studies conducted in a wide range of



**Fig. 6**  $Acclim_{SetTemp}$  (a) and  $Acclim_{Homeo}$  (b) under Type I and Type II acclimation of respiration. The number of observations per category is shown below each boxplot. The boxplots indicate the median, 25th and 75th percentile across temperature contrasts; whiskers extend to 1.5 times the interquartile range

climatic regions across the globe. Respiration in warm-acclimated leaves was generally lower than that of control leaves at a set temperature. Importantly, there is no indication that different growth forms and plants from different biomes differ systematically in their thermal acclimation capacity. However, the two acclimation indices that we used gave seemingly conflicting results, which highlights a problem with the quantitative assessment of acclimation. For example, the degree of warming, the strongest predictor of both metrics, increased acclimation according to  $Acclim_{SetTemp}$ , but decreased the completeness acclimation according to  $Acclim_{Homeo}$ . Here, we first discuss the factors we originally hypothesized to affect acclimation and the implications of our results, and then discuss the importance of alternative acclimation metrics.

#### Biome-dependent acclimation potential?

We hypothesized that the biome of origin of plants would affect their acclimation capacity, based on systematic differences across biomes in current ambient temperatures, the seasonality thereof and the proximity to supra-optimal temperatures. Remarkably, after accounting for factors such as the degree of warming and the duration of exposure to warming, the biome of species origin had no effect on

either  $Acclim_{SetTemp}$  or  $Acclim_{Homeo}$  in the current analysis. The relatively low values of  $Acclim_{SetTemp}$  of the tropical species compared to species from mid- and high-latitude biomes were explained by the small degree of warming these plants were exposed to, and do not preclude the possibility for a greater degree of acclimation when warmed more. The absence of biome differences in acclimation means that plants from across wide ranges of current and historical thermal environments have a similar physiological plasticity to warming above their current temperature regimes. In his landmark paper, Janzen (1967) argued that species from a more variable thermal environment (e.g. temperate regions with large seasonal temperature variation) should have evolved a greater capacity to adjust to temperature variation. With respect to the acclimation of respiration to warming, our analysis does not lend simple support for this hypothesis. Respiration is such a vital process for all living organisms that the capacity for acclimation can be expected to be a trait under strong natural selection. Tropical regions do not experience large seasonal temperature fluctuations, but leaf temperatures may vary by 10–20 °C diurnally as sun-exposed leaves may reach temperatures >40 °C in the afternoon (Krause et al. 2013). Respiration of darkened leaves during diurnal temperature fluctuations is by no means homeostatic (Slot et al. 2013), but the diurnal temperature response of respiration varies across species, possibly indicating differences in short-term physiological adjustments across species. It is currently not known to which aspect of diel temperature regime plants may acclimate, but it appears that it is not the daily mean temperature (Atkin et al. 2000). It is possible that diurnal temperature fluctuations may also act as a selective force for the capacity to thermally acclimate in climates with limited seasonal temperature fluctuation, although it remains unknown whether tropical plants can acclimate to much larger degrees of warming beyond the typical warming treatments in the current analysis.

#### Do growth form and leaf habit matter for thermal acclimation?

We found that plants with different growth forms did not differ in their acclimation capacity. Campbell et al. (2007) similarly found no systematic patterns in acclimation across temperate forbs, grasses and trees/shrub. Large ranges of acclimation responses are observed within each growth form, suggesting that there are no growth form-specific constraints on thermal plasticity, just as there appear to be no biome-specific acclimation constraints. After accounting for other factors, we found that deciduousness of leaves was a significant predictor of acclimation in the full model, with evergreen leaves of woody plants achieving a greater degree of homeostasis than deciduous leaves, as previously

reported by Tjoelker et al. (1999). In a given climate, evergreen leaves experience more variable temperature conditions during their lifetime than leaves of deciduous species, and increased acclimation capacity may help to maximize return on investment of these longer lived tissues.

Dynamic global vegetation models characterize vegetation as one of several potential plant functional types per biome, where plant functional types are defined by growth form and leaf habit (e.g. C4 grass, or broadleaf deciduous tree). Our results suggest first of all that these models can be improved by accounting for acclimation, as acclimation appears to be ubiquitous—yet most models currently ignore it (Smith and Dukes 2013)—and second, that acclimation can be addressed without the need to define plant functional type-specific acclimation potential other than distinguishing evergreen from deciduous vegetation.

Pre-existing leaves acclimate over time; newly developed leaves acclimate near-homeostatically directly to development temperature

Longer warming was expected to result in a greater degree of acclimation, even though acclimation may occur as quickly as within a few days. Indeed, pre-existing leaves approached homeostasis more often with a longer duration of warming. In contrast, leaves developed under experimental conditions develop with the enzymatic machinery to achieve greater thermal acclimation than pre-existing leaves (Stitt and Hurry 2002). As such, for these newly developed leaves the duration of warming does not affect the degree of acclimation.

Type I and Type II acclimation in pre-existing and newly-developed leaves

In our meta-analysis, pre-existing leaves exhibited Type II acclimation more frequently than Type I acclimation, even though Type II acclimation has been hypothesized to be associated with newly developed leaves (Atkin et al. 2005). In some species whose pre-existing leaves exhibited Type II acclimation, nitrogen concentrations decreased with increasing temperature (Lee et al. 2005), which suggests downregulation of metabolic capacity. In other species, however, nitrogen concentration did not decrease with warming (Slot et al. 2014a). Clearly, pre-existing leaves can downregulate the respiration capacity at higher temperatures, but the mechanism employed to do so is currently not well understood.

Acclimation and climate warming

As climate continues to warm, plants experience temperature changes from one year to the next that are relatively

small compared to some of the temperature differences included in the current study. Small temperature differences are more likely to result in homeostatic rates of respiration than large temperature differences. Furthermore, newly developed leaves maintain a greater degree of homeostasis than pre-existing leaves. Gradual warming is unlikely to expose leaves to dramatically higher mean annual or mean nighttime temperatures than those experienced during leaf development, especially in conditions where intra-annual temperature variations are small, such as in tropical forests. This suggests that most species are indeed likely to acclimate to a certain degree to warming. However, warming is often not gradual, even if the rise in mean annual temperature change is. Heat waves may occur more frequently, and with increasing intensity, over the current century (Meehl and Tebaldi 2004). Under heat-wave conditions pre-existing leaves will be exposed to temperatures considerably higher than their development temperature and, at best, acclimation will result in limited homeostasis. When the degree of warming was accounted for, we did not find evidence for biome differences in the capacity for acclimation, nor were leaves exposed to high maximum temperatures less likely to exhibit acclimation. However, further study is needed to account for unknown biome-based differences in the response of pre-existing leaves to extreme warming during a heat wave event.

Considerations for quantifying acclimation

When acclimation is simply defined as a change of the short-term temperature response curve of respiration, any significant deviation in elevation or slope indicates that acclimation has occurred. However, assessment of the degree of acclimatory changes requires careful consideration of the most relevant metric. Here, we used two metrics of acclimation, both of which give higher values when more acclimation has occurred. The higher the  $Acclim_{SetTemp}$ , the more respiration is downregulated following acclimation to warming, and thus the greater the degree of acclimation. Similarly, the higher the  $Acclim_{Homeo}$ , the less respiration at ambient temperature increases, and thus the greater the degree of acclimation. However, the degree of warming, the strongest single predictor of both ratios, increases  $Acclim_{SetTemp}$ , while decreasing  $Acclim_{Homeo}$ . Figure 1 illustrates three acclimation scenarios for Type I and Type II acclimation of ‘warm’ and ‘hot’ acclimated leaves. The first scenario is acclimation with partial homeostasis, in which respiration of warm and hot grown leaves is downregulated, but respiration is not perfectly homeostatic across temperatures. A greater degree of warming (i.e. hot > warm) results in a greater  $Acclim_{SetTemp}$  ( $A_2/C_2 > A_2/B_2$ ), but in a smaller  $Acclim_{Homeo}$  value ( $A_1/B_2 > A_1/C_3$ ). Under the scenario of complete homeostasis,  $Acclim_{SetTemp}$  increases

with warming as before, while  $\text{Acclim}_{\text{Homeo}}$  stays the same ( $A_1/B_2 = A_1/C_3 = 1.0$ ). Only in the scenario of overcompensation does  $\text{Acclim}_{\text{Homeo}}$  increase with the degree of warming. Overcompensation requires an enormous degree of downregulation of respiration, corresponding with a very large decrease in  $Q_{10}$  (in case of Type I acclimation) or a considerable downregulation of the respiratory capacity (in case of Type II acclimation). Indeed, overcompensation occurred in only ten cases for which  $\text{Acclim}_{\text{Homeo}}$  could be calculated ( $\text{Acclim}_{\text{Homeo}} > 1.05$ ), whereas 82 contrasts showed partial homeostasis ( $\text{Acclim}_{\text{Homeo}} \leq 0.95$ ), and in 13 cases perfect homeostasis was achieved ( $0.95 \leq \text{Acclim}_{\text{Homeo}} \leq 1.05$ ). Clearly, complete homeostasis requires a considerable alteration of the short-term temperature response, and across wide temperature ranges complete acclimation is often not achieved and overcompensation is even rarer.

So which is the better indicator of the degree of acclimation? When Type I acclimation occurs,  $\text{Acclim}_{\text{SetTemp}}$  is dependent on the temperature at which it is determined ( $A_1/C_1 > A_2/C_2$  in Fig. 1). Therefore, the question when determining acclimation according to the ‘set temperature method’ is: what is the ecologically relevant temperature at which to determine respiration of plants that are grown at contrasting temperature regimes? The choice of reference temperature is often arbitrary and not necessarily ecologically relevant (Bruhn et al. 2007); it is also difficult to standardize the reference temperature across climate regions with contrasting temperature regimes (Vanderwel et al., in preparation). In contrast,  $\text{Acclim}_{\text{Homeo}}$  is not inherently dependent on the measurement temperature, and it only considers environmentally relevant temperatures. Furthermore, the closer acclimation approaches homeostasis, the smaller the temperature-induced increase in leaf respiratory carbon loss, and (considering the lower temperature sensitivity of photosynthesis than of respiration) the smaller the reduction in plant carbon balance. From a plant carbon balance perspective,  $\text{Acclim}_{\text{Homeo}}$  thus appears to be the more useful indicator of acclimation.

On the other hand, estimates of  $\text{Acclim}_{\text{SetTemp}}$  can contribute to improving global carbon flux estimates by implementing the latter in dynamic global vegetation models. In such models, respiration at a given temperature is generally calculated by adjusting a base rate of respiration at an (arbitrary) reference temperature to current temperature by multiplying this rate by a temperature sensitivity parameter (e.g. based on a  $Q_{10}$  value). With information on  $\text{Acclim}_{\text{SetTemp}}$ , the base rate of respiration itself can be made dependent on the acclimation temperature (e.g. temperature in the preceding week). This way, the choice of reference temperature is no longer biologically arbitrary. So, although  $\text{Acclim}_{\text{Homeo}}$  may appear more relevant biologically,  $\text{Acclim}_{\text{SetTemp}}$  may play an important role in improving the quantification of acclimation of respiration in global models.

## Conclusions

We have shown that there is a very strong tendency for thermal acclimation of leaf respiration across biomes, growth forms and temperature ranges. The generality of the acclimation response will simplify the implementation of acclimation algorithms in dynamic global vegetation models, as a single acclimation response can be implemented for all vegetation types and biomes. Hiding behind these general patterns of acclimation, however, there is large variability within each biome and growth form that appears to represent species-specific acclimation capacity. Species differences in thermal acclimation may have consequences for species composition, vegetation dynamics and ecosystem functioning in a warmer world, so it will be important to identify the causes of interspecific variation in the capacity for thermal acclimation. To better understand the mechanistic nature and evolutionary origin of the apparent species-specific thermal acclimation capacity, a valuable future avenue of investigation lies in the identification of functional traits underpinning thermal acclimation within and across species, paired with phylogenetic analysis of acclimation potential. Given the high plant diversity, especially in tropical regions, more data on respiratory acclimation as well as on acclimation of the balance between photosynthesis and maintenance respiration are needed to better predict patterns in warming-induced changes in the carbon flux from vegetation, both within and across biomes.

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