

# Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration

Danielle A. Way · Wataru Yamori

Received: 8 October 2012 / Accepted: 12 June 2013  
© Springer Science+Business Media Dordrecht 2013

**Abstract** While interest in photosynthetic thermal acclimation has been stimulated by climate warming, comparing results across studies requires consistent terminology. We identify five types of photosynthetic adjustments in warming experiments: photosynthesis as measured at the high growth temperature, the growth temperature, and the thermal optimum; the photosynthetic thermal optimum; and leaf-level photosynthetic capacity. Adjustments of any one of these variables need not mean a concurrent adjustment in others, which may resolve apparently contradictory results in papers using different indicators of photosynthetic acclimation. We argue that photosynthetic thermal acclimation (i.e., that benefits a plant in its new growth environment) should include adjustments of both the photosynthetic thermal optimum ( $T_{opt}$ ) and photosynthetic rates at the growth temperature ( $A_{growth}$ ), a combination termed constructive adjustment. However, many species show reduced photosynthesis when grown at elevated temperatures, despite adjustment of some photosynthetic variables, a phenomenon we term detractive adjustment.

**Electronic supplementary material** The online version of this article (doi:10.1007/s11120-013-9873-7) contains supplementary material, which is available to authorized users.

D. A. Way (✉)  
Department of Biology, Western University,  
London, ON, Canada  
e-mail: dway4@uwo.ca

D. A. Way  
Nicholas School of the Environment, Duke University,  
Durham, NC, USA

W. Yamori  
Center for Environment, Health and Field Sciences, Chiba  
University, Kashiwa-no-ha 6-2-1, Kashiwa, Chiba 277-0882,  
Japan

An analysis of 70 studies on 103 species shows that adjustment of  $T_{opt}$  and  $A_{growth}$  are more common than adjustment of other photosynthetic variables, but only half of the data demonstrate constructive adjustment. No systematic differences in these patterns were found between different plant functional groups. We also discuss the importance of thermal acclimation of respiration for net photosynthesis measurements, as respiratory temperature acclimation can generate apparent acclimation of photosynthetic processes, even if photosynthesis is unaltered. We show that while dark respiration is often used to estimate light respiration, the ratio of light to dark respiration shifts in a non-predictable manner with a change in leaf temperature.

**Keywords** Temperature acclimation · Carbon balance · Global change biology · Meta-analysis · Day respiration

## Introduction

Globally, mean air temperatures are expected to increase 3 °C by the year 2100, with warming of up to 6.5 °C at higher latitudes (Christensen et al. 2007). Our ability to predict how this warming might alter terrestrial carbon uptake depends on determining the ability of plants to respond to increasing growth temperatures (Niu et al. 2012). Particularly, we need an improved understanding of how the physiological processes involved in photosynthesis (and respiration) will acclimate to warmer conditions, to provide a clear mechanistic framework for predicting future shifts in carbon fluxes from vegetation. From this standpoint, photosynthetic acclimation will be particularly important in perennial, long-lived plant species that will experience a rise in growing season temperatures over their

lifespan, but that cannot easily migrate (Aitken et al. 2008). Many studies have assessed the strength of thermal acclimation by measuring photosynthetic characteristics of plants that develop at different growth temperatures, but the results are diverse, and at times even appear to be contradictory. Since determining the ability of plant species to thermally acclimate photosynthesis to rising temperatures is particularly relevant in a warming world, we will focus on examples where growth temperatures increase.

In their classic review on temperature acclimation of photosynthesis, Berry and Bjorkman (1980, p. 497) define photosynthetic acclimation as “environmentally induced changes in photosynthetic characteristics that result in an improved performance under the new growth regime”. Much of the early literature on photosynthetic thermal acclimation emphasized the ability of plants to acclimate effectively to a change in temperature, such that the physiological changes induced by the new thermal environment offset the effect of the change in temperature; this type of acclimation results in relatively similar rates of carbon fixation in leaves measured at their own growth temperatures. But plants may demonstrate adjustments in photosynthetic physiology or measured photosynthetic variables that do not appear to improve their performance under the new growth temperature. Thus, there is a need to distinguish between *adjustments in photosynthesis* and *acclimation of photosynthesis*, where the latter is reserved for cases where the photosynthetic adjustments improve (or at least maintain) photosynthetic performance with a shift in growth temperature regime. For example, elevated growth temperatures may alter photosynthetic physiology and leaf anatomy such that photosynthesis is actually reduced in individuals grown at the higher growth temperature compared to individuals from a lower growth temperature (e.g., Ferrar et al. 1989). This paper will focus on the importance of defining what photosynthetic acclimation to increasing temperatures means, look at patterns of different forms of photosynthetic adjustments across studies, and will also briefly explore the importance of considering thermal acclimation of respiration when discussing photosynthetic acclimation to temperature.

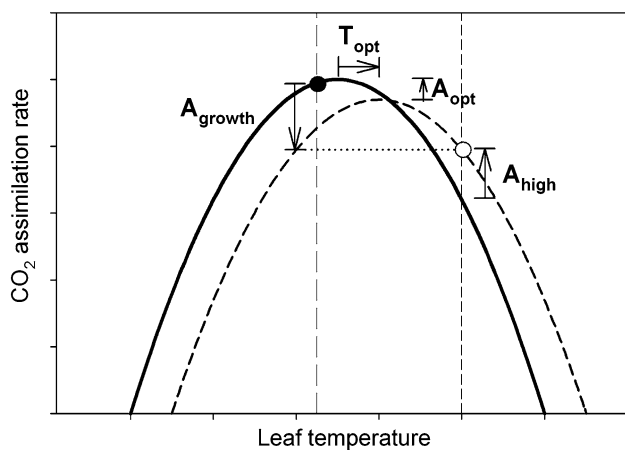
#### Definitions of thermal adjustments of photosynthesis

With regard to global change factors, temperature acclimation of photosynthesis is more complicated to describe than acclimation to rising CO<sub>2</sub> concentrations. Acclimation to elevated CO<sub>2</sub> concentrations is defined in the literature as some degree of down-regulation of photosynthetic capacity, where both the maximum carboxylation rates of Rubisco ( $V_{\text{cmax}}$ ) and the maximum electron transport rates ( $J_{\text{max}}$ ) are reduced in the high CO<sub>2</sub>-grown leaf (Sage 1994).

This photosynthetic down-regulation actually reduces the photosynthetic capacity of an acclimated leaf compared to a leaf that does not acclimate to high CO<sub>2</sub> (and would thus be seen as a photosynthetic adjustment to CO<sub>2</sub> by the definitions used here). However, since the adjustment often improves plant nitrogen use efficiency and can improve overall plant performance (Leakey et al. 2009), when this is demonstrated, the photosynthetic adjustments represent true acclimation. Down-regulation is a common response to high CO<sub>2</sub> concentrations in both pot and field experiments where nutrients supplies are not high, and the mechanisms underlying and limiting down-regulation of photosynthesis are generally understood (recently reviewed in Leakey et al. 2009), giving us some predictive insight into how future vegetation will respond to increasing atmospheric CO<sub>2</sub>. But the response of photosynthesis to an increase in growth temperature is much more diverse than its response to rising CO<sub>2</sub> concentrations and cannot be described in terms of simple up- or down-regulation.

So what do we mean when we use the term thermal acclimation of photosynthesis? In the literature on this subject, researchers use the term “acclimation” for adjustments in a number of photosynthetic variables. An adjustment of any of these variables could increase CO<sub>2</sub> assimilation rates ( $A$ ) or photosynthetic performance in some fashion, but not all of these types of adjustments will necessarily improve the carbon gain of the plant at the new growth temperature. There are at least five photosynthetic variables reported in the literature as indicators of thermal acclimation of photosynthesis, in that adjustments in these variables indicate some improvement of photosynthetic performance in the individual grown at the new, higher temperature compared to an individual from the lower growth temperature (Fig. 1):

- 1)  $A_{\text{high}}$ :  $A$  measured at the new, higher growth temperature ( $A_{\text{high}}$ ) is increased compared to  $A$  at that same temperature in a leaf grown at the reference, lower growth temperature (e.g., Fig. 2a, b). Examples of this are found in *Phaseolus vulgaris* (Cowling and Sage 1998), *Nerium oleander* (Ferrar et al. 1989), *Pisum sativum* (Haldimann and Feller 2005), and *Spinacia oleracea* (Yamori et al. 2005).
- 2)  $A_{\text{growth}}$ :  $A$  measured at the growth temperature ( $A_{\text{growth}}$ ) is increased or maintained in plants grown at the higher growth temperature when compared to the reference, cooler plant (Fig. 2a, b). Here, carbon gain at the respective growth temperature is improved, or at least kept constant. This form of photosynthetic adjustment has been reported in *Solanum tuberosum* (Wolf et al. 1990), *P. vulgaris* (Cowling and Sage 1998), *P. sativum* (Haldimann and Feller 2005), *S. oleracea* (Yamori et al. 2005), *Secale cereale*,



**Fig. 1** Conceptual figure of thermal adjustments of CO<sub>2</sub> assimilation rates ( $A$ ) to an increase in growth temperature, with arrows indicating the degree of adjustment that has occurred in  $A$  at the high growth temperature ( $A_{\text{high}}$ ),  $A$  at the relative growth temperatures ( $A_{\text{growth}}$ ), the thermal optimum for  $A$  ( $T_{\text{opt}}$ ) and  $A$  at  $T_{\text{opt}}$  ( $A_{\text{opt}}$ ). The solid line indicates the control leaf grown at ambient, cooler temperatures, dashed line represent the leaf grown at elevated temperatures; growth temperatures are indicated by vertical lines (long dash for control, short dash for elevated growth temperature) and circles demonstrate performance at the growth temperature (black for control, white for elevated growth temperature)

*Solanum lycopersicum*, *S. tuberosum*, *S. oleracea*, *Triticum aestivum* × *Triticosecale* and *Vicia faba* (Yamori et al. 2009, 2010), and *Zea mays* (Suwa et al. 2010).

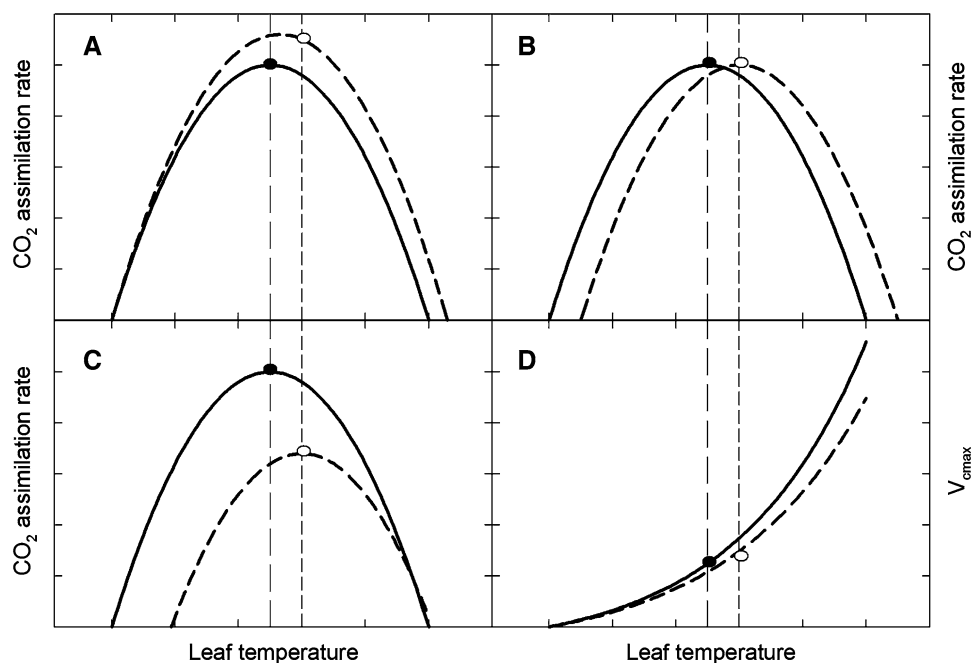
- 3)  $T_{\text{opt}}$  The thermal optimum ( $T_{\text{opt}}$ ) of photosynthesis in a warm-grown leaf has shifted toward the new growth temperature compared to the  $T_{\text{opt}}$  of a reference leaf grown at a cooler temperature (Fig. 2b, c). While this means the thermal optimum is closer to the new growth temperature, it does not necessarily lead to increased  $A_{\text{growth}}$  (compare Fig. 2b where  $A_{\text{growth}}$  is maintained constant between growth temperatures and Fig. 2c where  $A_{\text{high}}$  and  $A_{\text{growth}}$  are both reduced in the warm-grown leaf). Some examples of this include *N. oleander*, *Eucalyptus pauciflora*, *E. incrassata*, and *E. camadulensis* (Ferrar et al. 1989), *S. oleracea* (Yamori et al. 2005), *Picea mariana* (Way and Sage 2008a, b), *Cucumis sativus*, *Nicotiana tabacum*, *Oryza sativa*, *S. cereale*, *S. lycopersicum*, *S. tuberosum*, *S. oleracea*, *T. aestivum* × *Triticosecale*, and *V. faba* (Yamori et al. 2010).
- 4)  $A_{\text{opt}}$ : The photosynthetic rate at  $T_{\text{opt}}$  is increased, or at least maintained, in leaves grown at the higher growth temperature compared to a reference, cool-grown leaf (Fig. 2a, b). Seen in species such as *P. vulgaris* (Cowling and Sage 1998), *Populus deltoides* (Turnbull et al. 2002), and *Quercus rubra* (Gunderson et al. 2010).
- 5) Photosynthetic capacity:  $V_{\text{cmax}}$  and/or  $J_{\text{max}}$  measured at 25 °C (or some other specified and constant

temperature) is altered by the new, higher growth temperature (Fig. 2d). Seen in *E. pauciflora*, *E. incrassata*, *Eucalyptus camadulensis*, *Eucalyptus miniata* (Ferrar et al. 1989), *Eucalyptus regnans* (Warren 2008), and *Helianthemum nummularium* (Stirling et al. 1997).

Note that, numbers 1–4 are points measured on a temperature response curve of photosynthesis (see Fig. 1), while number 5 is a physiological mechanism for generating changes in the shape of a temperature response curve of photosynthesis. Despite this difference, all of these are variables frequently used by authors to describe photosynthetic thermal acclimation in the literature. Although numbers 1–4 are generated by changes in underlying physiological processes, our goal here is to suggest a common framework for reporting experimental results, and a detailed description of these processes is outside the scope of this work, but can be found in our companion paper (Yamori et al. 2013).

The forms of photosynthetic adjustment defined above are based solely on characterization of physiological response curves, rather than the specific conditions experienced by the plants in their environment, but photosynthetic acclimation should be thought of as a process that improves the performance of a plant. From an ecological perspective, if thermal acclimation has occurred (i.e., the photosynthetic performance of a plant at the new growth temperature is enhanced compared to a control plant from a lower growth temperature), there should be both adjustments of both  $T_{\text{opt}}$  (no. 3) and  $A_{\text{growth}}$  (no. 2). The  $T_{\text{opt}}$  adjustment indicates an improvement in the temperature response of  $A$ , while  $A_{\text{growth}}$  adjustment is required to prevent reduced photosynthetic performance in the new thermal environment. This type of dual photosynthetic adjustment can be referred to as *constructive* adjustment (as exemplified in Fig. 2b), and it is likely to help a plant not only cope with a potentially stressful increase in growth temperatures, but maintain or increase its growth compared to the control environment (at least with regard to carbon uptake). Constructive adjustment is therefore consistent with the earlier definition of photosynthetic acclimation. In contrast, *detractive* adjustment can be defined as thermal adjustment in at least one of the photosynthetic variables discussed above, but where  $A_{\text{growth}}$  is reduced in the warm-grown plant compared to a cool-grown, reference individual (see Fig. 2c for an example). These types of adjustments are unlikely to benefit the plant under the new, warmer environment, though there may be benefits to the plant that are not obvious when we focus only on photosynthetic traits (as in the case of down-regulation of photosynthesis to elevated CO<sub>2</sub>).

**Fig. 2** Conceptual figures of how the temperature response curves of **a–c** CO<sub>2</sub> assimilation and **d** the maximum carboxylation capacity of Rubisco ( $V_{\text{cmax}}$ ) can adjust to an increase in growth temperature. *Solid lines* indicate the control leaf grown at ambient, cooler temperatures, *dashed lines* represent the leaf grown at elevated temperatures; growth temperatures are indicated by *vertical lines* (*long dash* for control, *short dash* for elevated growth temperature) and *circles* demonstrate performance at the growth temperature (*black* for control, *white* for elevated growth temperature)



### Why do definitions matter?

Early studies highlighted the ability of plants to effectively acclimate photosynthesis to changes in temperature and improve their performance under new thermal conditions (Berry and Bjorkman 1980), leading later researchers to occasionally comment on the unusual nature of their results when they did not find evidence for thermal acclimation of photosynthesis (e.g., *Eucalyptus regnans*, in Warren 2008). But recent work has tended to emphasize that thermal acclimation of photosynthesis is often weak or nonexistent: for example, there was no evidence for thermal adjustment of photosynthetic capacity across a meta-analysis of data from 36 species from various functional groups (Kattge and Knorr 2007) or in a review of 22 different tree studies (Way and Oren 2010). Is this apparent discrepancy real, or might it be due to a difference in definitions regarding photosynthetic thermal acclimation?

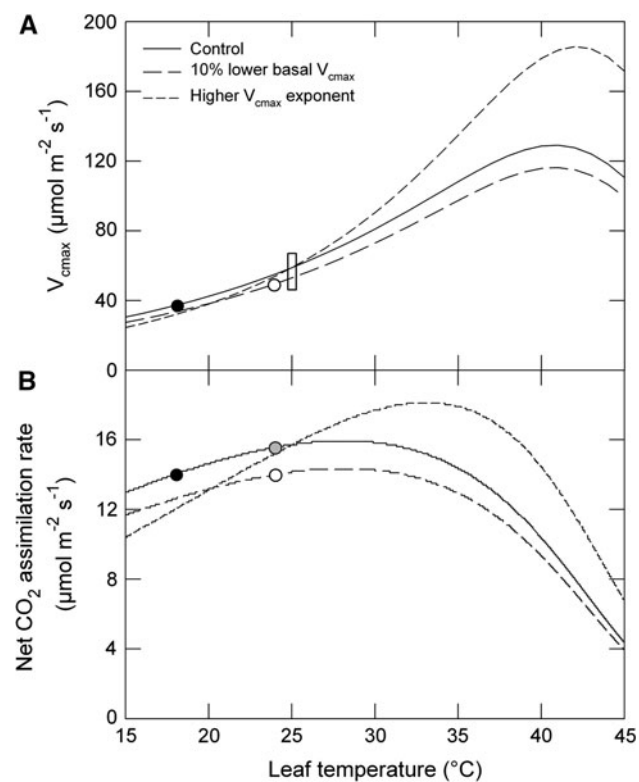
Of the examples shown in the review by Berry and Bjorkman (1980) from controlled growth conditions, increased growth temperatures increased  $T_{\text{opt}}$  (no. 3) in all six cases, but clearly reduced  $A_{\text{high}}$  (no. 1) in two cases, lowered  $A_{\text{growth}}$  (no. 2) in three species, and maintained or increased  $A_{\text{opt}}$  (no. 4) in only two of six cases (Fig. 2 in Berry and Bjorkman 1980). So, there was universal  $T_{\text{opt}}$  adjustment (no. 3), accompanied by  $A_{\text{growth}}$  adjustment (no. 2) in only some cases, demonstrating both constructive and detractive adjustment. While Berry and Bjorkman (1980) explicitly made the point that not all species acclimate photosynthesis equally well, and suggested that what we term detractive adjustment may be more common in

species from cool to temperate environments, the work is most frequently cited for its emphasis on effective acclimation of photosynthesis to changes in temperature.

Studies representing photosynthetic capacity adjustments (no. 4) are not well represented in Berry and Bjorkman (1980), although this is what many recent studies report (e.g., Bauerle et al. 2007; Centritto et al. 2011; Dillaway and Kruger 2010; Dwyer et al. 2007; Ferrar et al. 1989; Ghannoum et al. 2010; Ishikawa et al. 2007; Kositsup et al. 2009; Lewis et al. 2004; Ow et al. 2008a, b; Rilkonen et al. 2009; Shen et al. 2009; Silim et al. 2010; Turnbull et al. 2002; Wang et al. 1996; Warren 2008; Way and Sage 2008a, b; Yamori et al. 2006, 2008). Taken across a wide range of species, basal rates of  $V_{\text{cmax}}$  and  $J_{\text{max}}$  (where “basal rates” indicate any physiological variable measured at 25 °C) generally do not adjust to a change in growth temperature (Kattge and Knorr 2007; Way and Oren 2010). As discussed below, a lack of adjustment of photosynthetic capacity can be entirely consistent with thermal adjustment of  $A_{\text{high}}$ ,  $A_{\text{growth}}$ ,  $T_{\text{opt}}$ , and  $A_{\text{opt}}$ , and thus the difference in variables being measured and reported may itself underlie the differences in how prevalent “thermal acclimation of photosynthesis” is in the literature.

Despite the overall pattern discussed above, there is evidence that plants grown at cooler temperatures often increase their basal  $V_{\text{cmax}}$  and  $J_{\text{max}}$  by increasing photosynthetic enzyme concentrations to compensate for the lower operating temperature (Badger et al. 1982; Yamori et al. 2005; Sage and Kubien 2007). Conversely, a lower enzyme concentration could maintain the same rate of turnover at a higher ambient leaf temperature, implying

that basal  $V_{\text{cmax}}$  and  $J_{\text{max}}$  could be decreased at elevated growth temperatures if a constant photosynthetic capacity was to be achieved across growth temperatures. This type of potential adjustment to warming is shown in Fig. 3. If basal  $V_{\text{cmax}}$  is reduced by 10 % in a leaf grown at 24 °C compared to a control leaf grown at 18 °C (Fig. 3a, box),  $A_{\text{growth}}$  is unchanged (black and white symbols in Fig. 3b); this allows maintenance of a constant  $A_{\text{growth}}$  across different thermal regimes by lowering investment in Rubisco content and therefore reducing  $V_{\text{cmax}}$ . This would be both  $A_{\text{growth}}$  adjustment (no. 2) and photosynthetic capacity adjustment (no. 5). But if the temperature response of  $V_{\text{cmax}}$  is unaltered by changes in growth temperature (i.e., the activation energy of  $V_{\text{cmax}}$  is unaffected, as reported in Kattge and Knorr 2007), then the lack of adjustment in



**Fig. 3** **a** Variation in the temperature response of the maximum carboxylation capacity of Rubisco ( $V_{\text{cmax}}$ ) and **b** the implications for net  $\text{CO}_2$  assimilation rates. *Solid lines* indicate a control leaf; *long dashed lines* show the effect of a 10 % reduction in basal  $V_{\text{cmax}}$  ( $V_{\text{cmax}}$  measured at 25 °C, shown with *box*) from the control leaf; *short dashed lines* represent leaves with the same basal  $V_{\text{cmax}}$  as the control leaf, but a 33 % increased sensitivity of  $V_{\text{cmax}}$  to temperature. Using an 18 °C-grown leaf (*black symbols*) as a reference, *white symbols* show the effect of a 10 % decrease in basal  $V_{\text{cmax}}$  in a leaf grown at 24 °C, and the *grey symbol* indicates the increase in  $A_{\text{net}}$  for a leaf grown at 24 °C if no adjustment in basal  $V_{\text{cmax}}$  or its temperature response occurs with elevated growth temperature (see text for details). Curves were generated with physiological constants and temperature sensitivities taken from Campbell and Norman (1998), except for basal  $V_{\text{cmax}}$ , which was set at  $59 \mu\text{mol m}^{-2} \text{s}^{-1}$  for control runs

basal photosynthetic capacity seen in Kattge and Knorr (2007) and Way and Oren (2010) should increase  $A_{\text{growth}}$  in leaves that develop at, and experience, higher ambient temperatures, at least below an upper heat threshold. For example, we can compare two leaves with the same basal  $V_{\text{cmax}}$  and the same temperature response curve of  $V_{\text{cmax}}$  (i.e., both on the same “Control” curve in Fig. 3a): if one is grown at 18 °C and the other at 24 °C, the inherent increase in  $V_{\text{cmax}}$  across that 6 °C gradient leads to an increase in  $A_{\text{growth}}$  in the warm-grown leaf (Fig. 3b, compare black and grey symbols). Thus, while point measurements of  $A_{\text{growth}}$  would indicate better performance and possible photosynthetic acclimation in the warm-grown leaf, no adjustment of photosynthetic capacity has occurred. Instead, either reciprocal point measurements of  $A$  at the two growth temperatures or a full temperature response curve is required to see that no photosynthetic acclimation has happened.

#### Are some forms of thermal adjustment more common than others?

So, how prevalent are the five different types of thermal adjustment of  $A$ ? And do different plant functional types show different patterns of  $A$  adjustment to increasing temperatures? To investigate this, we compiled 70 studies of 103 species where plants were grown at more than one temperature and the response of at least one of the five types of adjustment described above could be ascertained (Table S1). We emphasized studies that grew plants for months (or longer) at the varied growth temperatures; this is important since pre-existing leaves have less capacity to adjust or acclimate than leaves that develop at the new growth temperature (Campbell et al. 2007), and we sought to capture responses representative of future vegetation that may develop at higher temperatures. We also focused on studies that showed full temperature response curves of photosynthesis to enable us to determine photosynthetic adjustment of as many of our variables as possible.

The temperature response curve of photosynthesis is dependent on the thermal environment of the species, such that the optimal temperature for photosynthesis in a warm-adapted species may severely inhibit photosynthesis in cold climate specialists (e.g., Xiong et al. 2000). Extreme warming treatments, or a mismatch between the treatments and the ecological thermal niche of the species, may therefore expose a species to irreversible heat damage. However, the temperature treatments in our data set were well-matched with the native temperature conditions of the species being studied. Across the studies analyzed here, the low temperature treatment averaged  $17.8 \pm 6.8$  °C and the elevated growth temperature averaged  $28.9 \pm 5.7$  °C

(mean  $\pm$  SD), such that plants in the warming treatments were exposed to moderate, but not extreme, high temperatures. Only one study (on a desert perennial) had an elevated growth temperature over 40 °C, and the five studies with treatment temperatures of 40 °C focused on warm-adapted species, such as *Heliotropium* spp., while the lowest cool growth temperatures of 6–8 °C were used in studies of high latitude and altitude plants, and cool weather crops.

The studies covered a diverse range of functional groups (C3 crops, forbs and grasses, C4 species, deciduous trees, and both broad-leaved and coniferous evergreen shrubs/trees); due to the complexities of measuring CAM photosynthetic temperature response curves, CAM species are not dealt with here (but see Yamori et al. 2013 for more information on thermal acclimation in CAM plants). For every species and growth temperature contrast, we noted the change in daytime growth temperature and the degree to which each of the five types of adjustment had occurred by recording the change in  $A$  between the cool and warm-grown individuals (for  $A_{\text{high}}$ ,  $A_{\text{growth}}$ , and  $A_{\text{opt}}$ ), or the change in the thermal optimum in °C (for  $T_{\text{opt}}$ ). Data were taken from tables when available, but most data were taken digitally from scanned graphs using Data Thief (version 1.5, datathief.org). For studies where more than two growth temperatures were imposed, every individual comparison was made (generating 263 temperature contrasts total); when other experimental conditions were imposed (e.g., elevated CO<sub>2</sub> concentrations, drought, or nutrient stress), only the ambient CO<sub>2</sub>, well-watered or well-fertilized plants were used. Species were broken into four broad functional types (C3 herbaceous, C4, deciduous woody, evergreen woody). Since  $V_{\text{cmax}}$  and  $J_{\text{max}}$  were sometimes measured at a common temperature (usually 25 °C to assess basal rates) and sometimes at the growth temperatures, adjustment of photosynthetic capacity is not as simple to discuss as are the other categories, and thus will be considered separately below.

While responses of  $A$  to short-term changes in leaf temperature are dependent on environmental conditions, such as the measurement and growth photosynthetic photon flux densities (e.g., Pons 2012), light levels were consistent within each study of our analysis, allowing us to focus on the effect of temperature: over 90 % of the contrasts measured temperature responses of light-saturated photosynthesis. Reductions in stomatal conductance, often due to higher VPD at higher temperatures, can also alter photosynthetic temperature responses by lowering intercellular CO<sub>2</sub> concentrations, but few studies provided sufficient stomatal conductance data to evaluate the effect of this phenomenon.

Most combinations of the five adjustment possibilities occur, as can be seen in the full data set in the Supplementary Information (Table S1). Some species, such as *Plantago major* (Atkin et al. 2006), do not show thermal

adjustment of any photosynthetic variable, while others like *P. deltoides* (Turnbull et al. 2002) show every type of thermal adjustment defined here. However, most species show a mix of responses, with the overall trends summarized in Table 1.  $A_{\text{growth}}$  and  $T_{\text{opt}}$  adjustment are more common than  $A_{\text{high}}$  or  $A_{\text{opt}}$  adjustment across the data set, each occurring in over two-thirds of the data, although only 51 % of the data shows constructive adjustment, with both  $T_{\text{opt}}$  and  $A_{\text{growth}}$  adjusting to the new, higher growth temperature. On a binary scale where adjustment either occurs or does not (according to the definitions above), evergreen trees show the least ability to constructively adjust to a change in temperature (consistent with the findings of Yamori et al. 2013), but relatively small sample sizes in the C4, deciduous woody and evergreen woody functional groups preclude more definitive statements (Table 1). Across the dataset, plants that demonstrated any one of  $A_{\text{high}}$ ,  $A_{\text{growth}}$ , or  $A_{\text{opt}}$  adjustment were more likely to show other forms of thermal adjustment of photosynthesis as well ( $p < 0.0001$ ; Table 2), creating a generalized syndrome of temperature adjustment or acclimation (described in Yamori et al. 2010). However, there was no significant relationship between adjustment of  $T_{\text{opt}}$  and adjustment of  $A_{\text{high}}$ ,  $A_{\text{growth}}$ , or  $A_{\text{opt}}$  (Table 2).

We then analyzed the degree of thermal adjustment for each of  $A_{\text{high}}$ ,  $A_{\text{growth}}$ ,  $A_{\text{opt}}$ , and  $T_{\text{opt}}$  with a general linear model, using functional type and the change in day temperature as predictive features (JMP Pro version 10.0.0, SAS Institute, Cary, NC, USA). Data were analyzed in two ways: (1) as absolute changes in  $A$  [using only studies that reported  $A$  on a leaf area basis (i.e.,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ )] for consistency in the units; and (2) in relative terms, where the change in  $A$  was divided by the highest light-saturated  $A$  for that species in that study, to account for differences between species in maximum  $A$  and between studies in the measurement units. When absolute values of  $A$  were used,  $A_{\text{high}}$ ,  $A_{\text{growth}}$ , and  $A_{\text{opt}}$  adjustment appeared to respond differently to changes in temperature between functional groups (Table 3, upper rows); however, this was not seen in the relativized data (Table 3, lower rows) and was therefore due to differences in light-saturated  $A$  between functional groups. Instead, there were no significant patterns in the degree of  $A_{\text{high}}$ ,  $A_{\text{growth}}$ , or  $A_{\text{opt}}$  adjustment based on the daytime temperature change imposed in the studies when  $A$  was relativized. In contrast,  $T_{\text{opt}}$  adjustment increased with an increasing change in day temperature ( $p < 0.0001$ ), and showed a significant difference between functional types ( $p = 0.0025$ ), although all functional groups showed a similar increase in  $T_{\text{opt}}$  as the change in growth temperature increased. For more detailed responses of changes in  $T_{\text{opt}}$ , see Yamori et al. (2013).

While this analysis captures changes in photosynthetic characteristics within a study, we used mostly data that was

**Table 1** The percent of data contrasts from Table S1 that show four types of photosynthetic thermal adjustment ( $A_{\text{high}}$ ,  $A_{\text{growth}}$ ,  $A_{\text{opt}}$  and  $T_{\text{opt}}$ , described in text) and constructive adjustment ( $A_{\text{constructive}}$ , joint  $A_{\text{growth}}$  and  $T_{\text{opt}}$  acclimation); parentheses indicate number of contrasts

	$A_{\text{high}}$	$A_{\text{growth}}$	$T_{\text{opt}}$	$A_{\text{opt}}$	$A_{\text{constructive}}$
All	59 % (90/150)	68 % (115/169)	72 % (163/227)	62 % (118/191)	51 % (76/150)
C3 herb	60 % (56/94)	68 % (70/103)	75 % (78/104)	55 % (56/101)	53 % (51/97)
C4	78 % (14/18)	94 % (17/18)	47 % (9/19)	74 % (14/19)	50 % (9/18)
Deciduous tree	78 % (7/9)	92 % (12/13)	95 % (21/22)	73 % (16/22)	86 % (6/7)
Evergreen tree	45 % (13/29)	46 % (16/35)	67 % (55/82)	65 % (32/49)	36 % (10/28)

Data are broken into categories of plant functional type

**Table 2** Co-occurrence of four different types of photosynthetic thermal adjustment ( $A_{\text{high}}$ ,  $A_{\text{growth}}$ ,  $T_{\text{opt}}$  and  $A_{\text{opt}}$ , as defined in the text), shown as correlation coefficients ( $r^2$ )

	$A_{\text{growth}}$	$T_{\text{opt}}$	$A_{\text{opt}}$
$A_{\text{high}}$	<b>0.177</b>	0.014	<b>0.380</b>
$A_{\text{growth}}$	–	0.001	<b>0.207</b>
$T_{\text{opt}}$	–	–	0.001

Significant  $p$  values (bold, all  $p < 0.001$ ) show where thermal adjustment of one variable co-occurs with thermal adjustment of other variables, forming syndromes of photosynthetic temperature adjustment

**Table 3** Model fits (correlation coefficients,  $r^2$ ) and  $p$  values for general linear models of thermal adjustment of photosynthesis ( $A$ ) for  $A_{\text{high}}$ ,  $A_{\text{growth}}$ ,  $T_{\text{opt}}$ , and  $A_{\text{opt}}$  (defined in the text)

	$A_{\text{high}}$	$A_{\text{growth}}$	$T_{\text{opt}}$	$A_{\text{opt}}$
Absolute values of $A$				
Model $r^2$	0.17	0.49	0.28	0.12
Functional type	<b>0.030</b>	<b>&lt;0.0001</b>	<b>0.0025</b>	<b>0.0093</b>
Temperature difference	0.52	0.29	<b>&lt;0.0001</b>	0.36
Functional type $\times$ temperature difference	<b>0.028</b>	<b>0.048</b>	0.65	0.23
Relative values of $A$				
Model $r^2$	0.07	0.04		0.08
Functional type	0.44	0.14		<b>0.037</b>
Temperature difference	0.28	0.43		0.68
Functional type $\times$ temperature difference	0.26	0.70		0.24

Results for analyses performed with absolute changes in  $A$  (upper rows) and with  $A$  relativized to light-saturated rates of  $A$  for each species (lower rows);  $T_{\text{opt}}$  adjustment was unaffected by the method of evaluating  $A$  and is shown only once. Significant values in bold

expressed on a leaf area basis, as this was the most commonly reported form of data. However, a change in growth temperature generally also changes the specific leaf area (SLA) of leaves that develop at the different temperatures: cooler growth temperatures lead to thicker leaves, that therefore can have much higher concentrations of nitrogen,

photosynthetic proteins and rates of  $A$  per unit leaf area than the thinner leaves that develop at warmer temperatures (e.g., Yamori et al. 2005; Campbell et al. 2007). This temperature-based shift in leaf development can directly lead to a reduction in leaf-area based rates of  $A$  in warm-grown leaves that may not be found when the results expressed on a leaf mass or leaf N basis. In other words, differences in leaf morphology may cause an apparent lack of photosynthetic acclimation on a leaf area basis. Without SLA data to convert our values between area- and mass-based photosynthetic rates (or leaf nitrogen concentrations for an N-based comparison), we cannot assess the extent to which changes in leaf morphology might affect our results. But eight studies on nine species in our data set did express their photosynthetic results on a leaf mass basis (generating 18 temperature contrasts where variables other than  $T_{\text{opt}}$  were assessed), and we can use this subset of data to determine whether mass-based photosynthesis appears to generate a greater degree of photosynthetic adjustment than area-based measures. In total, 55 % of the mass-based contrasts (10/18) showed constructive adjustment, while 72 % had  $A_{\text{high}}$  adjustment, 66 %  $A_{\text{growth}}$  adjustment and 77 %  $A_{\text{opt}}$  adjustment. Given the small size of the data set, we cannot conclude anything definitively, but these patterns are similar to the overall patterns seen in Table 1 for all measurement units, implying that the degree to which leaf morphology changes in response to growth temperature may not fully offset the trends in photosynthetic adjustment reported here.

### Adjustment of photosynthetic capacity

The responses of photosynthetic capacity adjustment (no. 5) are more varied than those of the other four types of photosynthetic adjustment. For simplicity, we will use  $V_{\text{cmax}}$  to represent possible responses of both  $V_{\text{cmax}}$  and  $J_{\text{max}}$ . As mentioned above, adjustment of photosynthetic capacity would involve a change in  $V_{\text{cmax}}$  measured at 25 °C (basal  $V_{\text{cmax}}$ ) in leaves grown at elevated temperature compared to those grown at the control conditions. In

the data, 16 contrasts (41 %) show an increase in basal  $V_{\text{cmax}}$  (or the initial slope of the photosynthetic  $\text{CO}_2$  response curve, used as a proxy for  $V_{\text{cmax}}$ ) and 21 contrasts (54 %) show a decrease in basal  $V_{\text{cmax}}$  (2 contrasts show no change). Either of these can indicate adjustment: if basal rates differ, there is an inherent difference in the photosynthetic capacity of the leaves grown at different temperatures. However, with half of the data showing higher basal  $V_{\text{cmax}}$  and half showing lower basal  $V_{\text{cmax}}$  in warm-grown leaves, there is no clear preferred direction of photosynthetic capacity adjustment, consistent with Kattge and Knorr (2007). Patterns of  $V_{\text{cmax}}$  measured at growth temperature are much clearer: 26 contrasts (76 %) showed an increased  $V_{\text{cmax}}$  in warm-grown leaves, while only 7 contrasts (21 %) had a lower  $V_{\text{cmax}}$  in leaves grown at higher temperatures in comparison with cool-grown leaves. This higher  $V_{\text{cmax}}$  in warm-grown leaves measured at their growth temperature does not, however, necessarily indicate any adjustment of photosynthetic capacity, since this pattern is expected given the inherently exponential increase of  $V_{\text{cmax}}$  in response to increasing measurement temperature (see Fig. 2d).

What about cases where basal  $V_{\text{cmax}}$  does not differ between the growth temperatures (as occurs in two contrasts in Table 1)? While this may indicate that photosynthetic capacity is unaffected by growth temperature, it cannot be used as definitive evidence for a lack of adjustment of photosynthetic capacity to temperature. While there is no overall pattern in how the activation energy of  $V_{\text{cmax}}$  varies with growth temperature (Kattge and Knorr 2007), many studies have shown that thermal acclimation can alter the response of  $V_{\text{cmax}}$  to measurement temperature (Bauerle et al. 2007; Dillaway and Kruger 2010; Dwyer et al. 2007; Ferrar et al. 1989; Ghannoum et al. 2010; Hikosaka et al. 1999; Ishikawa et al. 2007; Kositsup et al. 2009; Shen et al. 2009; Silim et al. 2010; Wang et al. 1996; Warren 2008; Way and Sage 2008b; Yamori et al. 2005, 2006, 2008, 2010). Figure 3 shows the effect of maintaining the same basal  $V_{\text{cmax}}$  as a control leaf (with basal  $V_{\text{cmax}}$  shown in the box in Fig. 3a), but increasing the sensitivity of  $V_{\text{cmax}}$  to temperature in a warm-acclimated leaf (compare the solid and short dashed lines in Fig. 3a). Measurements of basal  $V_{\text{cmax}}$  would show no adjustment between the two growth temperatures; however, the warm-grown leaf with greater  $V_{\text{cmax}}$  thermal sensitivity has a higher  $T_{\text{opt}}$  and higher  $A_{\text{growth}}$  than the control leaf above 25 °C when  $A_{\text{net}}$  responses to temperature are characterized (compare solid and short dashed lines in Fig. 3b). Thus, the exact same plant could be measured by two researchers, and if one was characterizing photosynthetic capacity adjustment (no. 5), they would conclude that there was no thermal acclimation based on basal  $V_{\text{cmax}}$ , while a second researcher who measured the temperature response of  $A_{\text{net}}$

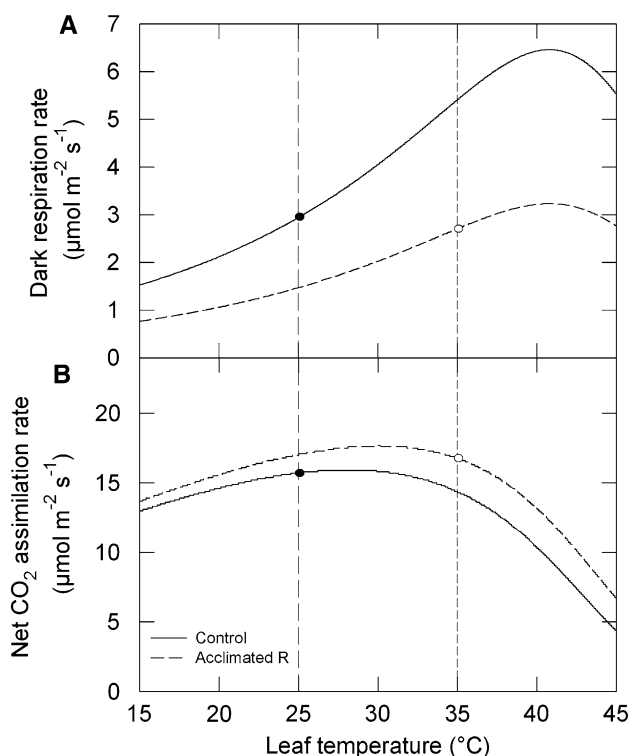
would find significant, constructive adjustment and thermal acclimation based on  $A_{\text{growth}}$  and  $T_{\text{opt}}$  adjustment, provided the elevated growth temperature was above 25 °C.

### The importance of $A_{\text{net}}$ versus $A_{\text{gross}}$

Although photosynthetic acclimation to temperature should by definition deal with photosynthesis, and thus only encompass gross photosynthetic carbon assimilation, studies almost always measure and report  $A_{\text{net}}$ . In Table S1, only four out of 70 papers presented temperature response curves of gross  $\text{CO}_2$  assimilation rates ( $A_{\text{gross}}$ ), truly representing responses of  $A$ , instead of  $A_{\text{net}}$ . In all other cases, a change in the light respiration rate ( $R_{\text{light}}$ , or non-photorespiratory mitochondrial  $\text{CO}_2$  release in the light) will influence our perceived shift in  $A$ , since  $A_{\text{gross}} = A_{\text{net}} + R_{\text{light}}$ . Because  $R_{\text{light}}$  is more difficult to measure than dark respiration ( $R_{\text{dark}}$ ), requiring either photosynthetic light response curve data at low photosynthetic photon flux densities (PPFD) (the Kok method; Kok 1948) or photosynthetic  $\text{CO}_2$  response curves made at multiple light intensities (the Laisk method (Laisk 1977), there are few measurements of how temperature affects  $R_{\text{light}}$  (but see Atkin et al. 2006; Way and Sage 2008b; Zaragoza-Castells et al. 2007; Scafaro et al. 2012). Since the two respiration rates are usually correlated (Atkin et al. 2006; Ayub et al. 2011; Fares et al. 2011), many studies that focus on photosynthetic responses to temperature that also account for thermal acclimation of respiration use approximately half of  $R_{\text{dark}}$  as a proxy for  $R_{\text{light}}$  (e.g., Atkin et al. 2007; Dwyer et al. 2007; Mawson et al. 1986). Both  $R_{\text{light}}$  and  $R_{\text{dark}}$  increase with increasing leaf temperature, with  $R_{\text{dark}}$  generally increasing exponentially with a linear rise in leaf temperature (Fig. 4a), and thus both respiration rates show a very different thermal response than  $A_{\text{gross}}$ . Because of the use of both  $R_{\text{light}}$  and  $R_{\text{dark}}$  to calculate  $A_{\text{gross}}$ , this paper will discuss the two respiration rates under the broader term  $R$  (for respiration), except where a separation of terms is required for clarity.

In almost all cases,  $R$  acclimates more strongly to a change in growth temperature than does  $A$  (Campbell et al. 2007; Ow et al. 2008a, b, 2010; Way and Oren 2010; Way and Sage 2008a, b), although some studies have not found significant acclimation of leaf  $R$  to variation in growth temperature (Bronson and Gower 2010; Wertin et al. 2010). What are the implications of thermal acclimation of  $R$  for photosynthetic thermal acclimation? Figure 4 shows a modeled scenario where photosynthetic characteristics (such as basal  $V_{\text{cmax}}$  and its temperature response) are unchanged between growth temperatures of 25 °C (control plant) and 35 °C (warm-acclimated plant); the only difference in the curves is that while the response of  $R$  to temperature remains unchanged, the basal rate of  $R$  at





**Fig. 4** The effects of **a** thermal acclimation of respiration to elevated temperature on **b** the thermal response of net CO<sub>2</sub> assimilation rates. The control leaf (grown at 25 °C) is indicated by solid lines; dashed lines represent a leaf grown at elevated temperatures of 35 °C with a 50 % reduction in dark respiration. Growth temperatures are indicated by vertical lines (long dash for control, short dash for elevated growth temperature) and circles demonstrate performance at the growth temperature (black for control, white for elevated growth temperature). Curves were generated with physiological constants and temperature sensitivities taken from Campbell and Norman (1998), except for basal  $V_{\text{cmax}}$ , which was set at 59  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for control runs

25 °C is halved in the warm-grown leaf. The acclimation of basal  $R$  allows  $R$  measured at the growth temperatures to remain similar between the plants (Fig. 4a), a not uncommon finding (e.g., Ow et al. 2008a, b; Way and Sage 2008b). However, the leaf grown at higher temperatures also shows  $A_{\text{high}}$ ,  $A_{\text{growth}}$ ,  $T_{\text{opt}}$ , and  $A_{\text{opt}}$  adjustments of  $A_{\text{net}}$ , despite there being absolutely no acclimation of  $A$  itself (Fig. 4b). Separate measurements of  $R$  and its response to temperature are therefore critical in studies of thermal acclimation of  $A$  when: (1) thermal acclimation of  $R$  is significant or; (2) when rates of  $R$  are relatively high compared to rates of  $A$ , such that small changes in  $R$  will affect  $A_{\text{net}}$ . While many studies assume the latter is true in their system, this should be verified.

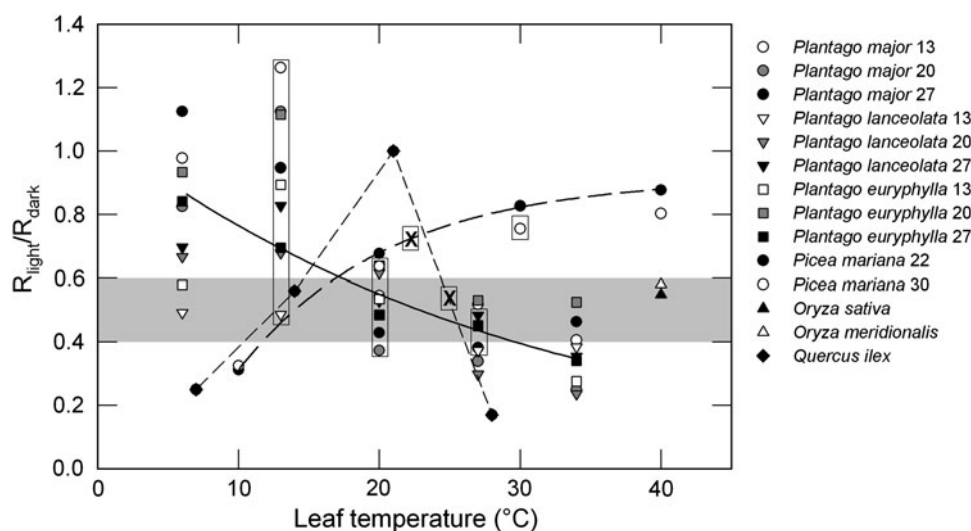
When only  $R_{\text{dark}}$  is measured, can  $R_{\text{light}}$  be calculated? While  $R_{\text{light}}$  is usually lower than  $R_{\text{dark}}$ , with  $R_{\text{light}}$  ranging from 16 to 77 % of  $R_{\text{dark}}$  (Hurry et al. 2005), recent work at a single temperature showed that  $R_{\text{dark}}$  could explain about half of the variation in  $R_{\text{light}}$ , with a slope of 0.7

(i.e.,  $R_{\text{light}}/R_{\text{dark}}$  was  $\sim 0.7$ ) (Ayub et al. 2011). We took data from papers where both the short-term temperature response of  $R_{\text{light}}/R_{\text{dark}}$  could be estimated, as well as the long-term, acclimated ratio of  $R_{\text{light}}/R_{\text{dark}}$  (measured at different growth temperatures). While  $R_{\text{light}}/R_{\text{dark}}$  is near 0.5 at 20 °C in these studies, it is often far from that ratio at other temperatures (Fig. 5). The short-term response of  $R_{\text{light}}/R_{\text{dark}}$  to increasing leaf temperature varies dramatically across the few species for which we found data, including a decrease in the herbaceous C3 species (three *Plantago* species, Atkin et al. 2006), a peaked response in an evergreen broad-leaved tree (*Quercus ilex*, Zaragoza-Castells et al. 2007), and a saturating increase in an evergreen conifer (*P. mariana*, Way and Sage 2008b) (Fig. 5). As well, these studies used different techniques for estimating  $R_{\text{light}}$ , with the Kok method used in Way and Sage (2008b), and the Laisk method used in the other two studies. Even within a single species grown at a single temperature, the irradiance used in estimating  $R_{\text{light}}$  with the Laisk method can alter the response of  $R_{\text{light}}/R_{\text{dark}}$  to rising temperature, switching from a positive correlation in  $R_{\text{light}}/R_{\text{dark}}$  with temperature at low irradiance, to a decrease in  $R_{\text{light}}/R_{\text{dark}}$  with warming at high irradiance (Atkin et al. 2000). Measurements of the temperature response of both  $R_{\text{light}}$  and  $R_{\text{dark}}$  from the same plants are rare, and more data are clearly needed, especially for plants grown at different thermal regimes, before we can make generalizations of the relationship between  $R_{\text{light}}$  and  $R_{\text{dark}}$  under future climate scenarios.

### What should we measure?

If the main goal of our research is to determine how leaf level carbon fluxes respond to warming, measuring thermal adjustments of  $A_{\text{net}}$  may be sufficient. But for many experiments, the goal is instead to determine mechanisms underlying how plants acclimate carbon balance to a change in temperature. In this scenario, separate measurements of  $A_{\text{net}}$  and  $R_{\text{light}}$  are required to calculate and characterize  $A_{\text{gross}}$ . In either case, measurements of CO<sub>2</sub> fluxes should be made on more than one basis (leaf area, leaf mass, leaf nitrogen, chlorophyll concentration), as the preponderance of leaf area-based measurements precludes us from determining the importance of leaf morphology in broad patterns of photosynthetic responses to growth temperature.

As well, we would advocate using clearer definitions when discussing thermal acclimation of photosynthesis, to indicate the variables being measured and their responses to a change in thermal regime. When possible, measurements of both the thermal optimum of photosynthesis ( $T_{\text{opt}}$ ) and photosynthesis at the growth temperature ( $A_{\text{growth}}$ )



**Fig. 5** Short-term response to changes in temperature in the ratio of  $R_{\text{light}}/R_{\text{dark}}$ . Data taken from Atkin et al. (2006) (*Plantago* spp.: solid line represents curve fit to all *Plantago* points), Way and Sage (2008b) (*Picea mariana*: long-dashed line represents curve fit to all *Picea* points), Zaragoza-Castells et al. (2007) (*Quercus ilex*: short-

dashed line connects *Quercus* points). The grey box indicates a ratio of 0.4–0.6, commonly used to convert measured  $R_{\text{dark}}$  to  $R_{\text{light}}$ . Clear boxes indicate range of values measured at growth temperature, representing long-term acclimation to temperature (x marks interpolated points at growth temperature)

should be assessed, allowing us to determine whether constructive thermal adjustment has occurred in response to the new temperature environment.

Lastly, we need to move beyond measuring only the phenomenological responses of photosynthesis to growth temperature, and study the underlying mechanisms that control thermal acclimation of photosynthesis and the adjustments we measure in photosynthetic variables. For example, changes in  $V_{\text{cmax}}$  with growth temperature, or in the thermal responses of  $V_{\text{cmax}}$  (as represented by its activation energy), have been reported in numerous species (Bauerle et al. 2007; Dillaway and Kruger 2010; Dwyer et al. 2007; Ferrar et al. 1989; Ghannoum et al. 2010; Hikosaka et al. 1999; Ishikawa et al. 2007; Kositsup et al. 2009; Shen et al. 2009; Silim et al. 2010; Wang et al. 1996; Warren 2008; Way and Sage 2008b; Yamori et al. 2005, 2006, 2008). However, we have very little understanding of what generates these changes in  $V_{\text{cmax}}$  or its thermal properties: Rubisco is a highly conserved enzyme (Whitney et al. 2011a) and the enzymological changes underpinning thermal acclimation responses in various species are largely unstudied. Thus, while variation in the Rubisco enzyme and its  $V_{\text{cmax}}$  across species and evolutionary time has been addressed (e.g., Whitney et al. 2011a, b), there is still controversy regarding whether Rubisco function can acclimate to changes in growth temperature. Our ability to truly predict how photosynthesis will respond to warmer temperatures increasingly depends on our developing a deeper and more mechanistic understanding of the biochemical, enzymological and regulatory responses underpinning the measurements we make at the leaf-level, which

should set a goal for research into photosynthetic acclimation in coming years.

**Acknowledgments** We thank Gaby Katul, Ram Oren, Sari Palmroth and Andrew Leakey for engaging discussions on earlier versions of the manuscript, and five anonymous reviewers for their thoughtful comments. This study was supported by Grants from NSERC, the US Department of Agriculture, Agriculture and Food Research Initiative (#2011-67003-30222), the US Department of Energy, Terrestrial Ecosystem Sciences (#11-DE-SC-0006967), and the US-Israeli Binational Science Foundation (#2010320) to DAW, and from the Japan Society for the Promotion of Science (Postdoctoral Fellowships) to W.Y.

## References

- Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evol Appl* 1:95–111
- Atkin OK, Evans JR, Ball MC, Lambers H, Pons TL (2000) Leaf respiration of snow gum in the light and dark. Interactions between temperature and irradiance. *Plant Physiol* 122:915–923
- Atkin OK, Scheurwater I, Pons TL (2006) High thermal acclimation potential of both photosynthesis and respiration in two lowland *Plantago* species in contrast to an alpine congener. *Glob Chang Biol* 12:500–515
- Atkin OK, Scheurwater I, Pons TL (2007) Respiration as a percentage of daily photosynthesis in whole plants is homeostatic at moderate, but not high, growth temperatures. *New Phytol* 174: 367–380
- Ayub G, Smith RA, Tissue DT, Atkin OK (2011) Impact of drought on leaf respiration in darkness and light in *Eucalyptus saligna* exposed to industrial age atmospheric growth  $\text{CO}_2$  and temperature. *New Phytol* 190:1003–1018
- Badger MR, Bjorkman O, Armond PA (1982) An analysis of photosynthetic temperature response and adaptation to temperature

- in higher plants: temperature acclimation in the desert evergreen *Nerium oleander* L. *Plant, Cell Environ* 5:85–99
- Bauerle WL, Bowden JD, Wang GG (2007) The influence of temperature on within-canopy acclimation and variation in leaf photosynthesis: spatial acclimation to microclimate gradients among climatically divergent *Acer rubrum* L. genotypes. *J Exp Bot* 58:3285–3298
- Berry J, Bjorkman O (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annu Rev Plant Physiol* 31: 491–543
- Bronson DR, Gower ST (2010) Ecosystem warming does not affect photosynthesis or aboveground autotrophic respiration for boreal black spruce. *Tree Physiol* 30:441–449
- Campbell GS, Norman JM (1998) An introduction to environmental biophysics, 2nd edn. Springer, New York, p 286
- Campbell C, Atkinson L, Zaragoza-Castells J, Lundmark M, Atkin O, Hurry V (2007) Acclimation of photosynthesis and respiration is asynchronous in response to changes in temperature regardless of plant functional type. *New Phytol* 176:375–389
- Centritto M, Brillì F, Fodale R, Loreto F (2011) Different sensitivity of isoprene emission, respiration and photosynthesis to high growth temperature coupled with drought stress in black poplar (*Populus nigra*) saplings. *Tree Physiol* 31:275–286
- Christensen JH, Hewitson B, Busuioac A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon W-T, Laprise R, Magaña Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P (2007) Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge/New York
- Cowling SA, Sage RF (1998) Interactive effects of low atmospheric CO<sub>2</sub> and elevated temperature on growth, photosynthesis and respiration in *Phaseolus vulgaris*. *Plant, Cell Environ* 21:427–435
- Dillaway DN, Kruger EL (2010) Thermal acclimation of photosynthesis: a comparison of boreal and temperate tree species along a latitudinal transect. *Plant, Cell Environ* 33:888–899
- Dwyer SA, Ghannoum O, Nicotra A, von Cammerer S (2007) High temperature acclimation of C<sub>4</sub> photosynthesis is linked to changes in photosynthetic biochemistry. *Plant, Cell Environ* 30:53–66
- Fares S, Mahmood T, Liu S, Loreto F, Centritto M (2011) Influence of growth temperature and measuring temperature on isoprene emission, diffusive limitations of photosynthesis and respiration in hybrid poplars. *Atmos Environ* 45:155–161
- Ferrar PJ, Slatyer RO, Vranjic JA (1989) Photosynthetic temperature acclimation in *Eucalyptus* species from diverse habitats, and a comparison with *Nerium oleander*. *Aust J Plant Physiol* 16: 199–217
- Ghannoum O, Phillips NG, Sears MA, Logan BA, Lewis JD, Conroy JP, Tissue DT (2010) Photosynthetic responses of two eucalypts to industrial-age changes in atmospheric [CO<sub>2</sub>] and temperature. *Plant Cell Environ* 33:1671–1681
- Gunderson CA, O'Hara KH, Champion CM, Walker AV, Edwards NT (2010) Thermal plasticity of photosynthesis: the role of acclimation in forest responses to a warming climate. *Glob Chang Biol* 16:2272–2286
- Haldimann P, Feller U (2005) Growth at moderately elevated temperature alters the physiological response of the photosynthetic apparatus to heat stress in pea (*Pisum sativum* L.) leaves. *Plant Cell Environ* 28:302–317
- Hikosaka K, Murakami A, Hirose T (1999) Balancing carboxylation and regeneration of ribulose-1,5-bisphosphate in leaf photosynthesis: temperature acclimation of an evergreen tree, *Quercus myrsinaefolia*. *Plant Cell Environ* 22:841–849
- Hurry V, Igamberdiev AU, Keerberg O, Parnik T, Atkin OK, Zaragoza-Castells J, Gardestrom P (2005) Respiration in photosynthetic cells: gas exchange components, interactions with photorespiration and the operation of mitochondria in the light. In: Lambers H, Ribas-Carbo M (eds) *Plant respiration: from cell to ecosystem*. Kluwer, Dordrecht
- Ishikawa K, Onoda Y, Hikosaka K (2007) Intraspecific variation in temperature dependence of gas exchange characteristics among *Plantago asiatica* ecotypes from different temperature regimes. *New Phytol* 176:356–364
- Kattge J, Knorr W (2007) Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant, Cell Environ* 30:1176–1190
- Kok B (1948) A critical consideration of the quantum yield of *Chlorella* photosynthesis. *Enzymologia* 13:1–56
- Kositsup B, Montpied P, Kasemsap P, Thaler P, Ameglio T, Dreyer E (2009) Photosynthetic capacity and temperature responses of photosynthesis of rubber trees (*Hevea brasiliensis* Mull. Arg.) acclimate to changes in ambient temperature. *Trees* 23:357–365
- Laisk AK (1977) Kinetics of photosynthesis and photorespiration in C<sub>3</sub> plants. Nauka, Moscow
- Leakey ADB, Ainsworth EA, Bernacchi CJ, Rogers A, Long SP, Ort DR (2009) Elevated CO<sub>2</sub> effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. *J Exp Bot* 60:2859–2876
- Lewis JD, Lucash M, Olszyk DM, Tingey DT (2004) Relationships between needle nitrogen concentration and photosynthetic responses of Douglas-fir seedlings to elevated CO<sub>2</sub> and temperature. *New Phytol* 162:355–364
- Mawson BT, Svoboda J, Cummins RW (1986) Thermal acclimation of photosynthesis by the arctic plant *Saxifraga cernua*. *Can J Bot* 64:71–76
- Niu S, Luo Y, Fei S, Yuan W, Schimel D, Law BE, Ammann C et al (2012) Thermal optimality of net ecosystem exchange of carbon dioxide and underlying mechanisms. *New Phytol* 194:775–783
- Ow LF, Griffin KL, Whitehead D, Walcroft AS, Turnbull MH (2008a) Thermal acclimation of leaf respiration but not photosynthesis in *Populus deltoides* × *nigra*. *New Phytol* 178:123–134
- Ow LF, Whitehead D, Walcroft AS, Turnbull MH (2008b) Thermal acclimation of respiration but not photosynthesis in *Pinus radiata*. *Funct Plant Biol* 35:448–461
- Ow LF, Whitehead D, Walcroft AS, Turnbull MH (2010) Seasonal variation in foliar carbon exchange in *Pinus radiata* and *Populus deltoides*: respiration acclimates fully to changes in temperature but photosynthesis does not. *Glob Chang Biol* 16:288–302
- Pons TL (2012) Interaction of temperature and irradiance effects on photosynthetic acclimation in two accessions of *Arabidopsis thaliana*. *Photosynth Res* 1–3:207–219
- Rilkonen J, Maenpää M, Alavillamo M, Silfver T, Oksanen E (2009) Interactive effect of elevated temperature and O<sub>3</sub> on antioxidant capacity and gas exchange in *Betula pendula* saplings. *Planta* 230:419–427
- Sage RF (1994) Acclimation of photosynthesis to increasing atmospheric CO<sub>2</sub>—the gas exchange perspective. *Photosynth Res* 39: 351–368
- Sage RF, Kubien DS (2007) The temperature response of C<sub>3</sub> and C<sub>4</sub> photosynthesis. *Plant Cell Environ* 30:1086–1106
- Scafaro AP, Yamori W, Carmo-Silva AE, Salvucci ME, von Caemmerer S, Atwell BJ (2012) Rubisco activity is associated with photosynthetic thermotolerance in a wild rice (*Oryza meridionalis*). *Physiol Plant* 146:99–109
- Shen H, Klein JA, Zhao X, Tang Y (2009) Leaf photosynthesis and simulated carbon budget of *Gentiana straminea* from a decade-long warming experiment. *J Plant Ecol* 2:207–216
- Silim SN, Ryan N, Kubien DS (2010) Temperature responses of photosynthesis and respiration in *Populus balsamifera* L.: acclimation versus adaptation. *Photosynth Res* 104:19–30

- Stirling CM, Davey PA, Williams TG, Long SP (1997) Acclimation of photosynthesis to elevated CO<sub>2</sub> and temperature in five British native species of contrasting functional type. *Glob Chang Biol* 3:237–246
- Suwa R, Hakata H, Hara H, El-Shemy HA, Adu-Gyamfi JJ, Nguyen NT, Kanai S, Lightfoot DA, Mohapatra K, Fujita K (2010) High temperature effects on photosynthate partitioning and sugar metabolism during ear expansion in maize (*Zea mays* L.) genotypes. *Plant Physiol Biochem* 48:124–130
- Turnbull MH, Murthy R, Griffin KL (2002) The relative impacts of daytime and night-time warming on photosynthetic capacity in *Populus deltoides*. *Plant Cell Environ* 25:1729–1737
- Wang K-Y, Kellomaki S, Laitinen K (1996) Acclimation of photosynthetic parameters in Scots pine after three years exposure to elevated temperature and CO<sub>2</sub>. *Agric For Meteorol* 82:195–217
- Warren CR (2008) Does growth temperature affect the temperature responses of photosynthesis and internal conductance to CO<sub>2</sub>? A test with *Eucalyptus regnans*. *Tree Physiol* 28:11–19
- Way DA, Oren R (2010) Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. *Tree Physiol* 30:669–688
- Way DA, Sage RF (2008a) Elevated growth temperatures reduce the carbon gain of black spruce (*Picea mariana* (Mill.) B.S.P.). *Glob Chang Biol* 14:624–636
- Way DA, Sage RF (2008b) Thermal acclimation of photosynthesis in black spruce (*Picea mariana* (Mill.) B.S.P.). *Plant Cell Environ* 31:1250–1262
- Wertin TM, McGuire MA, Teskey RO (2010) Higher growth temperatures decreased net carbon assimilation and biomass accumulation of northern red oak seedlings near the southern limit of the species range. *Tree Physiol* 30:1277–1288
- Whitney SM, Houtz RL, Alonso H (2011a) Advancing our understanding and capacity to engineer nature's CO<sub>2</sub>-sequestering enzyme, Rubisco. *Plant Physiol* 155:27–35
- Whitney SM, Sharwood RE, Orr D, White SJ, Alonso H, Galmes J (2011b) Isoleucine 309 acts as a C-4 catalytic switch that increases ribulose-1,5-bisphosphate carboxylase/oxygenase (rubisco) carboxylation rate in *Flaveria*. *Proc Natl Acad Sci USA* 108:14688–14693
- Wolf S, Olesinski AA, Rudich J, Marani A (1990) Effect of high temperature on photosynthesis in potato. *Ann Bot* 65:179–185
- Xiong FS, Mueller EC, Day TA (2000) Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. *Am J Bot* 87:700–710
- Yamori W, Noguchi K, Terashima I (2005) Temperature acclimation of photosynthesis in spinach leaves: analyses of photosynthetic components and temperature dependencies of photosynthetic partial reactions. *Plant, Cell Environ* 28:536–537
- Yamori W, Suzuki K, Noguchi K, Nakai M, Terashima I (2006) Effects of Rubisco kinetics and Rubisco activation state on the temperature dependence of the photosynthetic rate in spinach leaves from contrasting growth temperatures. *Plant Cell Environ* 29:1659–1670
- Yamori W, Noguchi K, Kashino Y, Terashima I (2008) The role of electron transport in determining the temperature dependence of the photosynthetic rate in spinach leaves grown at contrasting temperatures. *Plant Cell Physiol* 49:583–591
- Yamori W, Noguchi K, Hikosaka K, Terashima I (2009) Cold-tolerant crops have greater temperature homeostasis of leaf respiration and photosynthesis than cold-sensitive species. *Plant Cell Physiol* 50:203–215
- Yamori W, Noguchi K, Hikosaka K, Terashima I (2010) Phenotypic plasticity in photosynthetic temperature acclimation among crop species with different cold tolerances. *Plant Physiol* 152:388–399
- Yamori W, Hikosaka K, Way DA (2013) Temperature response of photosynthesis in C3, C4 and CAM plants: temperature acclimation versus temperature adaptation. *Photosynth Res*. doi: [10.1007/s11120-013-9874-6](https://doi.org/10.1007/s11120-013-9874-6)
- Zaragoza-Castells J, Sanchez-Gomez D, Valladares F, Hurry V, Atkin OK (2007) Does growth irradiance affect temperature dependence and thermal acclimation of leaf respiration? Insights from a Mediterranean tree with long-lived leaves. *Plant Cell Environ* 30:820–833