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REVIEW

Temperature response of photosynthesis in C_3, C_4, and CAM plants: temperature acclimation and temperature adaptation

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Abstract Most plants show considerable capacity to adjust their photosynthetic characteristics to their growth temperatures (temperature acclimation). The most typical case is a shift in the optimum temperature for photosynthesis, which can maximize the photosynthetic rate at the growth temperature. These plastic adjustments can allow plants to photosynthesize more efficiently at their new growth temperatures. In this review article, we summarize the basic differences in photosynthetic reactions in C_3, C_4, and CAM plants. We review the current understanding of the temperature responses of C_3, C_4, and CAM photosynthesis, and then discuss the underlying physiological and biochemical mechanisms for temperature acclimation of photosynthesis in each photosynthetic type. Finally, we use the published data to evaluate the extent of photosynthetic temperature acclimation in higher plants, and analyze which plant groups (i.e., photosynthetic types and functional types) have a greater inherent ability for photosynthetic acclimation to temperature than others, since there have been reported interspecific variations in this ability. We found that the inherent ability for temperature acclimation of photosynthesis was different: (1) among C_3, C_4, and CAM species; and (2) among functional types within C_3 plants. C_3 plants generally had a greater ability for temperature acclimation of photosynthesis across a broad temperature range, CAM plants acclimated day and night photosynthetic process differentially to temperature, and C_4 plants was adapted to warm environments. Moreover, within C_3 species, evergreen woody plants and perennial herbaceous plants showed greater temperature homeostasis of photosynthesis (i.e., the photosynthetic rate at high-growth temperature divided by that at low-growth temperature was close to 1.0) than deciduous woody plants and annual herbaceous plants, indicating that photosynthetic acclimation would be particularly important in perennial, long-lived species that would experience a rise in growing season temperatures over their lifespan. Interestingly, across growth temperatures, the extent of temperature homeostasis of photosynthesis was maintained irrespective of the extent of the change in the optimum temperature for photosynthesis (T_{opt}), indicating that some plants achieve greater photosynthesis at the growth temperature by shifting T_{opt}, whereas others can also achieve greater photosynthesis at the growth temperature by changing the shape of the photosynthesis–temperature curve without shifting T_{opt}. It is considered that these differences in the inherent stability of temperature acclimation of photosynthesis would be reflected by differences in the limiting steps of photosynthetic rate.

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Introduction

Global climate change is resulting in increases in the daily, seasonal, and annual mean temperatures experienced by plants. Moreover, climate change will increase the intensity, frequency, and duration of abnormally low and high temperatures (Wagner 1996; Tebaldi et al. 2006; Christensen et al. 2007). Temperature limits plant growth and is also a major determining factor in the distribution of plants across different environments (Mittler 2006). Since plants cannot move from unfavorable to favorable temperature conditions, the ability to withstand and/or acclimate to environmental temperature variation is essential for plant survival. Since photosynthesis has long been recognized as one of the most temperature-sensitive processes in plants, understanding the physiological processes that underlie the temperature response of photosynthesis and its acclimation is important to both agriculture and the environment.

The temperature response of photosynthesis can be described with a parabolic curve having an optimum temperature, and thus photosynthesis is inhibited at both low and high temperatures (Berry and Björkman 1980). Most plants show considerable capacity to adjust their photosynthetic characteristics to their growth temperatures. The most typical phenomenon is a shift in the optimum temperature of photosynthesis as the growth temperature changes or with seasonal temperature shifts, which allows the plant to increase photosynthetic efficiency at their new growth temperature (Berry and Björkman 1980; Yamori et al. 2005, 2006a, 2008, 2010b). From the desert to the arctic, plants also demonstrate extensive physiological and biochemical adaptation to the large environmental range in temperature. The inherent ability for temperature acclimation of photosynthesis can thus be expected to be different among plants utilizing differing photosynthetic pathways [e.g., among C_3, C_4, and crassulacean acid metabolism (CAM) plants]. C_4 plants are often associated with relatively arid regions with high temperatures, such that C_4 plants may have a greater ability for photosynthetic acclimation to high temperature than C_3 plants (e.g., Oberhuber and Edwards 1993; Kubien and Sage 2004; Osborne et al. 2008). Interestingly, even within C_3 plants, interspecific differences in temperature acclimation of photosynthesis have been observed. For example, the inherent ability for temperature acclimation of photosynthesis appears to differ between temperate evergreen species and tropical evergreen species (Hill et al. 1988; Read 1990; Cunningham and Read 2002), between cold sensitive species and cold tolerant species (Yamori et al. 2010b), and even among ecotypes of the same species, depending on their original habitats (Björkman et al. 1975; Pearcy 1977; Slatyer 1977). However, Campbell et al. (2007) found no difference in the level of temperature acclimation of photosynthesis among grasses, forbs, and woody plants. Thus, there is a discrepancy between studies in the inherent ability for photosynthetic temperature acclimation between groups, and we need to understand this phenomenon to predict how changing temperatures will alter plant photosynthetic responses.

In this review article, we first summarize the basic differences in photosynthetic reactions in C_3, C_4, and CAM plants. Second, we show a typical, classic temperature acclimation response of photosynthesis with the proposed mechanisms underlying it. It is now possible to analyze what process limits photosynthesis at various environmental conditions, based on well-tested models of photosynthesis (Farquhar et al. 1980; von Caemmerer 2000). Moreover, developments of molecular biology and transgenic technology have provided a set of powerful tools to identify and then modify the limitations imposed on photosynthesis by the environment. Thus, we then consider the underlying physiological and biochemical mechanisms for temperature acclimation of photosynthesis and discuss what process would be the limiting step of photosynthetic rate at various temperatures. Less research on photosynthetic temperature responses has been done on CAM plants than C_3 and C_4 plants and differences in the temperature response of photosynthesis between day and night have not been clarified in CAM plants with diurnal photosynthetic patterns, although day and night temperatures vary considerably in deserts where many CAM plants are found. We therefore discuss the differences in temperature responses of CO_2 fixation rates at night and chloroplast electron transport rates in the day in two CAM species grown at two different temperature regimes. Finally, we evaluate the extent of photosynthetic temperature acclimation in higher plants from the pool of published data, and describe which plant types (i.e., photosynthetic types and functional types) have the greatest inherent ability for photosynthetic acclimation to temperature.

Photosynthetic reactions in C_3, C_4, and CAM plants

C_3 species represent approximately 85 % of all higher plant species, C_4 species account for about 5 %, and CAM species make up the remaining 10 %. C_4 plants are thought to have originated in relatively arid regions, where high temperatures occur in combination with water stress, whereas desert CAM plants are adapted to drought in arid

regions, where day and night temperatures can show drastic swings (although some CAM species occur in tropical rainforests as epiphytes). Because of adaptation to their respective growth conditions over evolutionary time scales, photosynthetic characteristics greatly differ among C_3, C_4, and CAM plants (Fig. 1). In C_3 plants, CO_2 diffuses through the stomata and the intercellular air spaces, and eventually arrives in the chloroplast. Carbonic anhydrase catalyses the reversible hydration of CO_2 to HCO_3^- in the aqueous phase (i.e., chloroplast, cytosol, and plasma membrane) and is thought to maintain the supply of CO_2 to Rubisco by speeding up the dehydration of HCO_3^-, although the importance of carbonic anhydrase may not be high in C_3 plants (Price et al. 1994). In the chloroplast, Rubisco catalyzes the carboxylation of ribulose-1,5-bisphosphate (RuBP) by CO_2 and produces 3-phosphoglyceric acid (PGA). ATP and NADPH produced by photosynthetic electron transport in the thylakoid membranes are used to produce sugars and starch, as well as the regeneration of RuBP from PGA in the Calvin–Benson cycle.

In contrast, C_4 photosynthesis has a biochemical CO_2 concentrating mechanism that increases CO_2 concentrations by 10–100-fold at the catalytic sites of Rubisco in the bundle sheath compared to ambient air (Furbank and Hatch 1987; Jenkins et al. 1989). In C_4 plants, CO_2 is hydrated to HCO_3^- by carbonic anhydrase and assimilated to oxaloacetate

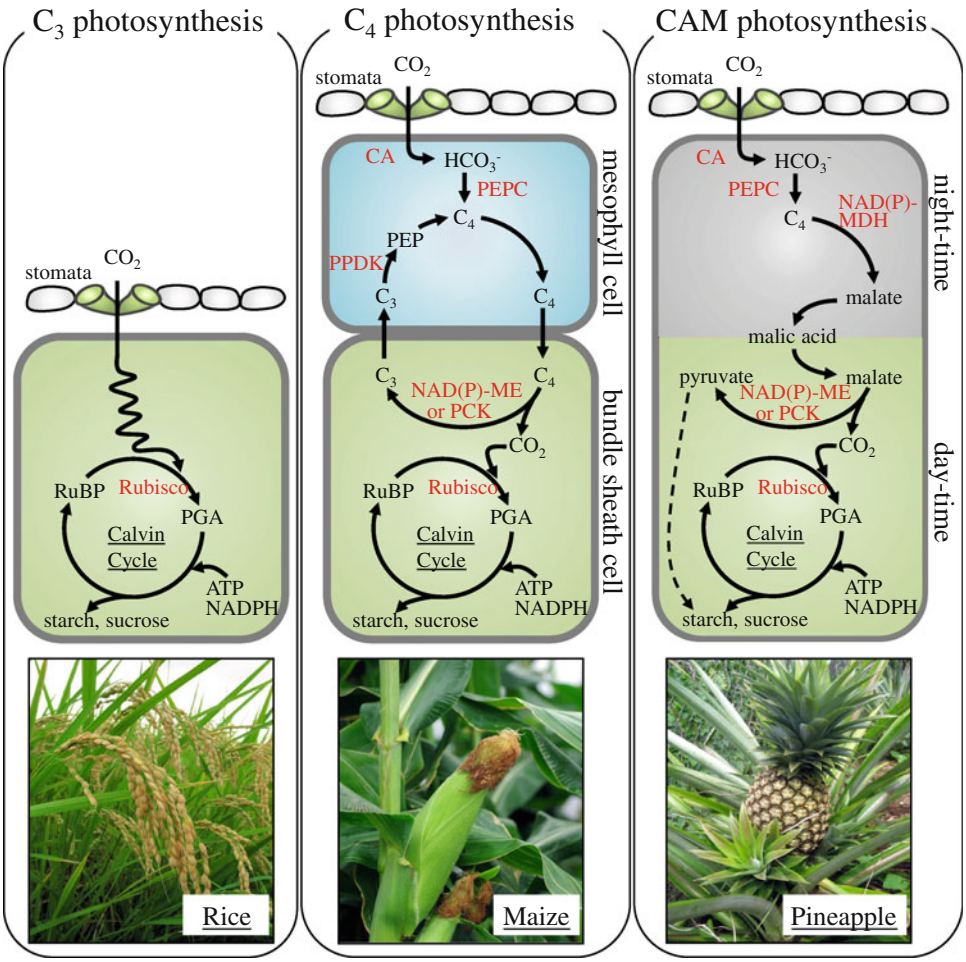

Fig. 1 Photosynthetic reactions in C_3, C_4, and CAM plants. With respect to their photosynthetic pathways, plants are grouped into three categories as C_3, C_4, and CAM. C_3 plants include grain cereals and vegetables such as rice, wheat, spinach, tomato, and trees such as apple, peach, and eucalyptus; C_4 plants include grain cereals and grasses such as maize and sugarcane; CAM plants include pineapple and agave. C_3 plants convert CO_2 into a 3-carbon compound (PGA) with Rubisco. On the other hand, C_4 plants and CAM plants convert CO_2 into a 4-carbon intermediate (OAA) by using PEPC. CAM plants differ from C_4 plants in that CAM plants fix CO_2 at night to store CO_2 as a 4-carbon intermediate (malic acids). Among C_4 plants, there are three subtypes, based on the C_4 acid decarboxylation enzyme, NADP-malic enzyme (NADP-ME) type, NAD-malic enzyme (NAD-ME) type, and phosphoenolpyruvate carboxykinase (PCK) type. Among CAM plants, there are two subtypes, based on the C_4 acid decarboxylation enzyme, NAD(P)-ME type, and PCK type. *CA* carbonic anhydrase, *PGA* phosphoglyceric acid, *RuBP* ribulose-1,5-bisphosphate, *PEP* phosphoenolpyruvate, *Rubisco* ribulose-1,5-bisphosphate carboxylase/oxygenase, *PEPC* phosphoenolpyruvate carboxylase, *NAD(P)-ME* NAD(P)-malic enzyme, *PCK* phosphoenolpyruvate carboxykinase, *PPDK* pyruvate phosphate dikinase, *NAD(P)-MDH* NAD(P)-malate dehydrogenase

(OAA) with substrates of phosphoenolpyruvate (PEP) by phosphoenolpyruvate carboxylase (PEPC) located in the cytosol. PEP is produced from pyruvate and ATP, catalyzed by pyruvate phosphate dikinase (PPDK) located in the chloroplast. OAA is reduced to malate, or alternatively is transaminated to aspartate in a reaction with alanine. Whether malate, aspartate or a mixture of the two are formed, depends on the subtype of the C_4 species. Among C_4 plants, there are three subtypes, based on the C_4 acid decarboxylation enzyme: NADP-malic enzyme (NADP-ME) type, NAD-malic enzyme (NAD-ME) type, and phosphoenolpyruvate carboxykinase (PCK) type. Malate (or aspartate) is transported to the vascular bundle sheath cells and is finally decarboxylated, producing CO_2 and pyruvate. CO_2 is then fixed by Rubisco in the chloroplasts of the bundle sheath cells, which have a normal Calvin cycle, as in C_3 plants.

CAM photosynthesis also has a biochemical CO_2 concentrating mechanism, but it requires a temporal separation of the C_3 and C_4 components, compartmentalized within a common cellular environment. CAM is divided into four distinct phases in a day: (phase I) nocturnal uptake of CO_2 via stomata, CO_2 fixation mediated by PEPC, malate synthesis by NAD(P)-malate dehydrogenase (NAD(P)-MDH) in the cytosol, and accumulation of malic acid in the vacuole of the mesophyll tissue; (phase II) transition when stomata remain open for CO_2 uptake at dawn; (phase III) decarboxylation of malic acid and re-fixation of the regenerated and concentrated CO_2 by Rubisco behind closed stomata; and (phase IV) transition when stomata reopen again for CO_2 uptake at dusk. Two subtypes of CAM plants, NAD(P)-ME type and PCK type, are known, based on the difference in the reaction of decarboxylation of malate during the day (Dittrich et al. 1973, 1976). By opening stomata and incorporating CO_2 at night when evapotranspiration rates are low, CAM plants can achieve high water use efficiencies that are three- to six-fold greater than for C_4 and C_3 species, respectively (Nobel 1996).

Long-term temperature acclimation of photosynthesis to low and high temperature

In many cases, plants grown at low temperature show greater photosynthetic capacity at lower temperatures, whereas plants grown at high temperatures show greater capacity for photosynthesis at higher temperatures (Berry and Björkman 1980; Fig. 2), improving photosynthetic performance at the growth temperature. Figure 2 summarizes a classic example of temperature acclimation of photosynthesis, along with the proposed mechanisms. Generally speaking, photosynthetic acclimation to low temperature involves an increase in the capacity of temperature-limited enzymes, whereas photosynthetic acclimation to high temperature involves increased heat stability of the photosynthetic apparatus. The photosynthesis–temperature curve is often symmetrical or bell-shaped (e.g., Yamori et al. 2010b); however, the curve is more shallow and broad when Rubisco limits photosynthesis and more peaked when electron transport limitations dominate (Sage and Kubien 2007), and there can be a rapid fall-off of photosynthetic rate at high temperatures (Salvucci and Crafts-Brandner 2002).

Photosynthetic acclimation to low temperature

Plants grown at low temperatures have higher amounts of photosynthetic enzymes, such as enzymes of the photosynthetic carbon reduction cycle, including Rubisco, sedoheptulose-1,7-bisphosphatase (SBPase), and stromal fructose-1,6-bisphosphatase (e.g., Holaday et al. 1992; Hurry et al. 1994, 1995; Strand et al. 1997, 1999; Yamori

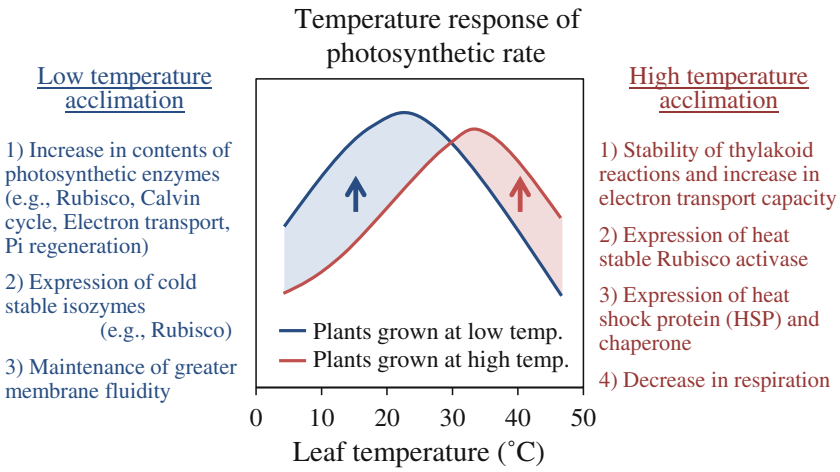

Fig. 2 A classic, idealized diagram of temperature acclimation of the response of photosynthesis to temperature. The proposed mechanisms underlying the temperature acclimation of photosynthesis are summarized

et al. 2005, 2011b), and those of sucrose synthesis, including sucrose phosphate synthase (SPS) and cytosolic fructose-1,6-bisphosphatase (e.g., Guy et al. 1992; Holaday et al. 1992; Hurry et al. 1994, 1995; Strand et al. 1997, 1999). Large amounts of these enzymes would be needed to compensate for decreased activities of the enzymes at low temperatures. Compensation for decreased activities at low temperatures can also be achieved by shifting protein expression to produce isoforms with improved performance at low temperature. For example, Yamori et al. (2006b) showed that the changes in Rubisco kinetics induced by growth temperature contributed to increases in the in vivo photosynthetic capacity of spinach at their respective growth temperatures. This is supported by reports that Rubisco kinetics differed depending on the growth temperature in Puma rye (Huner and Macdowall 1979), and that cold acclimation increased the affinity of SPS for its substrates and decreased the affinity for P_i via expression of new isoforms in potato (Reimholz et al. 1997; Deiting et al. 1998).

The other important process for acclimation to low temperature is an alteration in membrane fatty acid composition, leading to maintenance of cellular function through adjusting membrane fluidity and stabilizing photosynthetic proteins (Falcone et al. 2004). Increasing the ratio of unsaturated to saturated fatty acids is an acclimation response to low temperature, whereas decreasing the ratio facilitates acclimation to higher temperatures (Murata and Los 1997; Murakami et al. 2000; Sung et al. 2003). Since membrane fluidity can affect the conformation of membrane-embedded proteins, changes in membrane fluidity at low-growth temperatures could accelerate interactions between the cytochrome b_6/f complex and plastoquinones or plastocyanin, allowing for increased electron transport capacity in thylakoid membranes.

Photosynthetic acclimation to high temperature

Plants grown at high temperature need greater heat tolerance of thylakoid membranes and photosynthetic enzymes, to enable greater photosynthetic rates at high temperatures. Proton leakiness of the thylakoid membrane has been frequently proposed as a problem at high temperatures, since it could lead to the impairment of the coupling of ATP synthesis to electron transport (Havaux 1996; Pastenes and Horton 1996; Bukhov et al. 1999, 2000). Increases in cyclic electron flow around PSI at high temperature can compensate for thylakoid leakiness, allowing ATP synthesis to continue (Havaux 1996; Bukhov et al. 1999, 2000). Thus, for photosynthetic acclimation to high temperature, greater stability of membrane integrity and increases in electron transport capacity are involved. It should be noted that damage to thylakoid reactions by moderate heat stress is not caused by damage to Photosystem II (PSII) itself, since damage to PSII only occurs at high temperatures, often above 45 °C (Terzaghi et al. 1989; Gombos et al. 1994; Yamane et al. 1998).

In many plant species, the Rubisco activation state decreases at high temperature (e.g., Salvucci and Crafts-Brandner 2004b; Yamori et al. 2006b, 2012; Yamori and von Caemmerer 2009). Mechanistically, it has been proposed that the activity of Rubisco activase is insufficient to keep pace with the faster rates of Rubisco inactivation at these high temperatures (Crafts-Brandner and Salvucci 2000; Salvucci and Crafts-Brandner 2004a; Kurek et al. 2007, Kumar et al. 2009; Yamori et al. 2012). In plants transferred to elevated growth temperatures, a different isoform of Rubisco activase that confers heat stability can be produced by some species, including spinach (Crafts-Brandner et al. 1997), cotton (Law et al. 2001) and wheat (Law and Crafts-Brandner 2001), though not all species seem to have this ability. Thus, maintenance of a high-activation state of Rubisco via expression of heat stable Rubisco activase and/or increases in Rubisco activase contents at high temperature could be important for high-temperature acclimation.

Expression of heat-shock proteins (HSPs)/chaperones at elevated temperatures is an important process for high-temperature acclimation (Vierling 1991). Five major families of HSP/chaperone have been reported: the Hsp70 (DnaK) family; the chaperonins (GroEL and Hsp60); the Hsp90 family; the Hsp100 (Clp) family; and the small Hsp (sHsp) family (Wang et al. 2004). There is some evidence for the significance of chloroplast-localized HSPs for thermotolerance and for linking HSPs and photosynthetic capacity (e.g., Heckathorn et al. 1998, 2002; Barua et al. 2003; Neta-Sharir et al. 2005). The expression of HSP/chaperone molecules is important for protein folding and assembly, stabilization of proteins and membranes, and for cellular homeostasis at high temperature.

The temperature response and thermal acclimation of respiration must also be considered, as mitochondrial respiration can affect net photosynthetic rate, even when photosynthesis is unaltered (Fig. 2). Whereas the optimum temperature of photosynthesis is generally between 20 and 30 °C, the optimum temperature of respiration occurs just below the temperature at which heat inactivation of enzymes occurs (e.g., above 45 °C). Therefore, above the thermal optimum for photosynthesis, photosynthetic rates decrease, but respiration rate continue to increase. Leaves that develop at high temperatures also often acclimate respiration, such that they have lower respiration rates at a common measurement temperature than do leaves grown in colder environments (Atkin and Tjoelker 2003; Atkin et al. 2005; Yamori et al. 2005), and photosynthesis shows less acclimation potential to a change in temperature than dark respiration in mitochondria (Atkin and Tjoelker 2003; Yamori et al. 2005: Campbell et al. 2007; Way and Sage 2008a, b; Ow et al. 2008, 2010; Way and Oren 2010).

While the temperature effects on respiration are outside the scope of this paper, we discuss the interplay between temperature responses of respiration and photosynthesis elsewhere in this issue (Way and Yamori 2013).

Changes in all these factors for low- or high-temperature acclimation could result in an alteration in the temperature response of photosynthesis. Plants exhibit a set of characteristic responses to growth temperature (Yamori et al. 2009, 2010b). For example, plants exhibiting considerable plasticity in a certain parameter also show great plasticity in other parameters. This set of responses has been termed a "syndrome of temperature acclimation" (Yamori et al. 2010b; see also Way and Yamori 2013). Thus, alteration of more than one of these parameters, which are independently regulated, could play an important role in a plant's temperature acclimation.

Limiting step in C_3 and C_4 photosynthesis

A change in the temperature response of photosynthesis depends on the individual temperature responses of the diffusive and biochemical limitations controlling the photosynthetic rate. Understanding the limiting step of photosynthesis at various temperatures leads to understanding the mechanisms of how the temperature response of photosynthesis changes with growth temperature. Both C_3 and C_4 photosynthesis respond to changes in ambient CO_2 concentration, but the CO_2 response of photosynthesis differs between C_3 and C_4 plants. Supplemental Figure S1 summarizes the CO_2 response of the net photosynthetic rate and the candidates for the limiting steps of photosynthesis in C_3 and C_4 plants, respectively.

C_3 photosynthesis

In C_3 species, photosynthesis is classically considered to be limited by the capacities of Rubisco, RuBP regeneration, or P_i regeneration (Farquhar et al. 1980; Supplemental Appendix and Fig. S1). At low CO_2 concentrations, RuBP is saturating and carboxylation of RuBP is the limiting step of photosynthesis. In the process of RuBP carboxylation, CO_2 diffusion (via stomatal conductance and mesophyll conductance) and Rubisco activity (i.e., Rubisco amount, Rubisco kinetics, and Rubisco activation) can affect the photosynthetic rate. On the other hand, at high CO_2 concentrations, RuBP is not saturating and the photosynthetic rate is limited by RuBP regeneration. The RuBP regeneration rate is determined by either the chloroplast electron transport capacity to generate NADPH and ATP (Yamori et al. 2011c) or the activity of Calvin cycle enzymes involved in the regeneration of RuBP (e.g., SBPase: Raines 2006). P_i regeneration limits photosynthesis under some conditions such as high CO_2 concentrations and/or low temperatures (Sage and Sharkey 1987). At current levels of atmospheric CO_2, the control of the temperature response of photosynthesis is typically considered to be a mixture of Rubisco, electron transport, and P_i regeneration limitations (Sage and Kubien 2007). In C_3 plants, concomitant analyses of the CO_2 response of CO_2 assimilation rates and chloroplast electron transport rates estimated from chlorophyll fluorescence can determine the limiting step of CO_2 assimilation at various measurement conditions (Supplemental Appendix and Fig. S2).

At low temperature, the capacity of sucrose synthesis is sometimes observed to be the limiting step over P_i regeneration capacity (Sharkey 1985; Labate and Leegood 1988; Strand et al. 1997, 1999), but this does not always occur and depends on the plant species and growth temperature (Yamori et al. 2010b). The other predominant limitation of photosynthesis at low temperature is RuBP regeneration (Hikosaka et al. 2006; Sage and Kubien 2007; Yamori et al. 2010b). Capacities of both RuBP regeneration and carboxylation generally increase when plants are grown at low temperatures, but plants invest more nitrogen in RuBP regeneration processes than in Rubisco (Hikosaka et al. 1999; Hikosaka 2005; Yamori et al. 2005, 2010b). As a result, the limitation by RuBP regeneration can be alleviated by acclimation to the low-growth temperature, and, in turn, RuBP carboxylation becomes the predominant limitation of photosynthesis. Thus, plants with less ability for temperature acclimation to low temperature remained limited by RuBP regeneration irrespective of growth temperature and do not enhance photosynthetic capacity at low temperatures (Yamori et al. 2010b). The alleviation of limitations by RuBP regeneration at low temperature is proposed to reduce the excess excitation energy by providing a greater sink for photosynthetic electron transport, thereby avoiding photoinhibition in natural habitats where temperature and light intensity vary greatly both daily and seasonally (Hikosaka et al. 2006; Yamori et al. 2010b).

At moderately high temperatures, the mechanisms controlling the response of the photosynthetic rate remain unclear, but several hypotheses have been proposed. The leading hypotheses for photosynthetic limitation above the photosynthetic optimum temperature are heat lability of Rubisco activase and a limitation in electron transport (Salvucci and Crafts-Brandner 2004a, b; Sharkey 2005; Sage and Kubien 2007). Recently, enhanced thermostability of Rubisco activase in *Arabidopsis* has been shown to improve photosynthetic rates and plant growth under heat stress (Kurek et al. 2007; Kumar et al. 2009). Moreover, the overexpression of maize Rubisco activase in rice plants slightly increased Rubisco activation states and photosynthetic rates at high temperature (Yamori et al. 2012). Also, Sage et al. (2008) proposed that Rubisco activase may be

an important factor determining the response of boreal plants to global warming in North America, based on photosynthetic model analyses. These results support the view that a reduction in Rubisco activase activity limits the Rubisco activation state and, therefore, photosynthetic rates at high temperatures. On the other hand, in some plants, the photosynthetic rate at high temperature was limited by electron transport capacity (Schrader et al. 2004; Wise et al. 2004; Cen and Sage 2005). Decreased electron transport rates lower the ATP/ADP ratio and the stromal redox state, resulting in a decreased Rubisco activase activity (since Rubisco activase is regulated by the ATP/ADP ratio and redox state in the chloroplast). Thus, it has been proposed that electron transport is the leading limiting step of photosynthesis at high temperature, and that the decline in Rubisco activation state at high temperature may be a regulated response to a limitation in electron transport capacity, rather than a consequence of a direct effect of heat on the integrity of Rubisco activase (Sharkey 2005; Sage and Kubien 2007). Since the limiting step of photosynthesis at high temperature differs depending on plant species (e.g., cold tolerant vs cold sensitive) and growth condition (e.g., low temperature vs high temperature, low nitrogen availability vs high nitrogen availability) (Yamori et al. 2010a, 2011a), photosynthetic regulation by Rubisco activase or photosynthetic electron transport limitations at high temperature could differ between plant species and growth conditions.

How does the optimum temperature for photosynthesis change with growth temperature? At the optimum temperature, the photosynthetic rate under current atmospheric CO_2 concentrations is often limited by RuBP carboxylation (Sage and Kubien 2007). It has been proposed that the temperature response of RuBP carboxylation controls that of photosynthetic rate at high light under current CO_2 concentrations (Hikosaka et al. 2006), and a literature survey also shows consistent shifts in the optimum temperature of the maximum rate of RuBP carboxylation with growth temperature (Kattge and Knorr 2007). Taken together, alterations of the temperature response of RuBP carboxylation would play an important role in the shift of the optimum temperature of photosynthetic rate at current CO_2 concentrations with growth temperature.

C_4 photosynthesis

C_4 plants exhibit a different pattern of biochemical limitations across a range of temperatures than do C_3 plants (von Caemmerer 2000; Kubien et al. 2003), which should alter the mechanisms underlying temperature acclimation of photosynthesis between C_3 and C_4 plants. The biochemical model of C_4 photosynthesis is more complex than that of C_3 photosynthesis (Fig. S1). At low CO_2 concentrations, the photosynthetic rate in a C_4 plant is determined by CO_2 diffusion (stomatal conductance and mesophyll conductance), carbonic anhydrase activity, and PEPC activity. On the other hand, at high CO_2 concentrations, photosynthetic rate is determined by Rubisco activity (i.e., amount, kinetics, and activation of Rubisco), PEP regeneration via PPDK, and RuBP regeneration (i.e., chloroplast electron transport rate and activity of Calvin cycle enzymes involved in the regeneration of RuBP). Analyses of flux control coefficients in transgenic plants of the C_4 dicot *Flaveria bidentis* suggest that Rubisco and PPDK share control and co-limit C_4 photosynthesis at high light and moderate temperatures (Furbank et al. 1997).

The limiting step of C_4 photosynthesis at high temperature has been examined using antisense Rubisco and Rubisco activase lines of *F. bidentis*. At high temperature, neither Rubisco capacity nor Rubisco activase capacity was a limiting factor for photosynthesis (Kubien et al. 2003; Hendrickson et al. 2008), and it is unclear what process was the principal limitation on photosynthesis. Photosynthetic electron transport rates in the thylakoid membranes or rates of enzymatic PEP or RuBP regeneration are leading possibilities for controlling C_4 photosynthesis at high temperature (von Caemmerer and Furbank 1999; Pittermann and Sage 2001; Sage 2002; Kubien et al. 2003; Dwyer et al. 2007).

C_4 photosynthesis has been suggested to be inherently cold sensitive because C_4 cycle enzymes can be cold-labile (Long 1983). Cold-induced decreases in the photosynthetic rate in C_4 plants have been correlated with decreases in carboxylation efficiency via PEPC (Kingston-Smith et al. 1997; Chinthapalli et al. 2003), capacity for PEP regeneration via PPDK (Du et al. 1999), and Rubisco activity (Kingston-Smith et al. 1997; Du et al. 1999; Pittermann and Sage 2000, 2001; Chinthapalli et al. 2003). Using antisense Rubisco *F. bidentis*, the amount of Rubisco was clearly shown to control the rate of C_4 photosynthesis at low temperatures (Kubien et al. 2003), and C_4 photosynthesis is therefore thought to be most likely limited by Rubisco activity at these conditions (Sage and Kubien 2007). However, it has also been proposed that C_4 photosynthesis at low temperature may instead be limited by PPDK, based on work in *Miscanthus* × *giganteus*, a C_4 species which appears to be exceptional in its ability to maintain high photosynthetic rates at low temperatures (Naidu et al. 2003; Wang et al. 2008). These two studies showed that leaves of *M.* × *giganteus* that developed at low temperature showed greater photosynthetic rates than leaves grown at high temperature, corresponding with increases in PPDK protein content, although Rubisco content remained constant irrespective of growth temperature. Thus, the high sensitivity to low temperature of PPDK may be the main reason why C_4 species have rarely expanded to cooler places (Long 1983; Leegood and Edwards 1996; Naidu et al. 2003; Wang et al. 2008).

This conclusion is supported by the findings that PPDK overexpression transformants of maize maintain greater photosynthetic rates than control lines at low temperature (Ohta et al. 2006).

As with C_3 plants (Yamori et al. 2010b), the limiting step of C_4 photosynthesis may differ depending on the plant species (e.g., cold tolerant vs cold sensitive) and growth condition (low temperature vs high temperature), leading to different conclusions regarding the limiting step of photosynthesis at low temperature. Now, various antisense constructs in *F. bidentis* are available: (1) Rubsico (Furbank et al. 1996); (2) Rubisco activase (von Caemmerer et al. 2005); (3) Carbonic anhydrase (von Caemmerer et al. 2004); (4) NADP-ME (Pengelly et al. 2012); (5) PPDK (Furbank et al. 1997); and (6) NADP-MDH (Furbank et al. 1997). This would therefore be an excellent time to elucidate what limits C_4 photosynthesis at low temperature, as well as high temperature, using *F. bidentis* as a model case, since the temperature response of C_4 photosynthesis in these transgenic plants has not been closely examined.

Different temperature response of photosynthesis at day and night in CAM plants

The difference in temperature responses of photosynthetic reactions during the day and night have not been examined in CAM species. We may expect differential temperature responses of the different phases of CAM photosynthesis in desert CAM plants, since these species often experience a drastic alteration in day and night temperatures during a 24-h period. Thus, we analyzed the temperature responses of nocturnal CO_2 fixation rates (phase I), as well as chloroplast electron transport rates in the day (phase III) in two CAM species (*Kalanchoe daigremontiana* and *K. pinnata*), grown at day/night air temperatures of either 20/10 °C or 30/20 °C. More detailed information on plant growth conditions and photosynthetic measurements is described in Fig. S3.

The temperature response of CO_2 fixation rates at night differed depending on the growth temperature in both species (Fig. 3). CO_2 fixation rates at low temperatures were greater in 20 °C grown plants than in 30 °C grown plants, whereas CO_2 fixation rates at high temperatures were greater in 30 °C grown plants than in 20 °C grown plants. The average optimum temperature for nocturnal CO_2 fixation rates were increased by elevated growth temperatures (*K. daigremontiana*: 16.1 and 21.1 °C and *K. pinnata*: 15.3 and 19.6 °C, in 20 and 30 °C grown plants, respectively). The 30 °C grown plants showed higher optimum temperatures for electron transport rate in the day than 20 °C grown plants in both species, although a clear optimum temperature for daytime electron transport rate could not be obtained. Thus, both CO_2 fixation rates at nighttime and electron transport rates in the daytime acclimated to shifts in growth temperatures.

The temperature response of stomatal conductance at night was also different depending on growth temperature (Fig. S3). The relationship between C_i and CO_2 fixation rate at various leaf temperatures was similar irrespective of growth

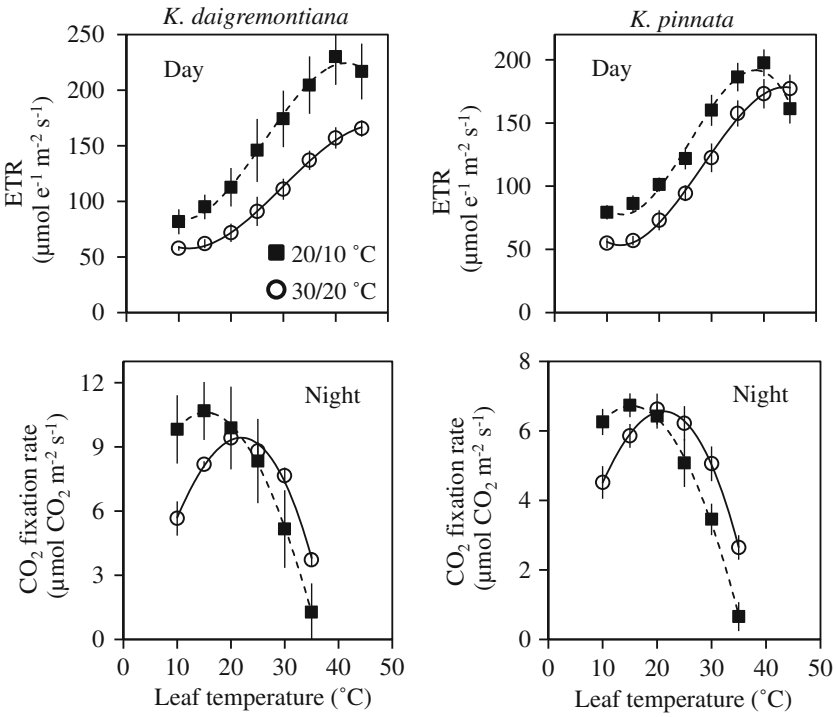

Fig. 3 Temperature responses of CO_2 fixation rate at night as well as chloroplast electron transport rate (ETR) in the day in two CAM species grown at two different temperature regimes. *Kalanchoe daigremontiana* and *K. pinnata* plants were grown at day/night air temperatures of either 20/10 °C or 30/20 °C. CO_2 fixation rate in the dark was measured by gas-exchange (LI-6400; Li-COR), whereas ETR on the thylakoid membranes at high light of 1,500 μmol m^{-2} s^{-1} was analyzed by chlorophyll fluorescence (LI-6400 and LI-6400-40; Li-COR) in a temperature-controlled cabinet. The temperature response of stomatal conductance at night is shown in Supplemental Fig. S3. Data represent mean ± SE, $n = 4$–6

temperature, indicating that the principal limiting step of CO_2 fixation at night was not stomatal conductance or C_i, but other physiological processes. Leaf mass per unit area (LMA) and leaf nitrogen content were greater in both CAM plants grown at 20 °C compared with those from 30 °C (Fig. S3). Temperature acclimation for photosynthesis is related to leaf nitrogen economy, since more than half of leaf nitrogen is in the photosynthetic apparatus, and thus, photosynthetic capacity is strongly related to leaf nitrogen content (Evans 1989; Makino et al. 2003; Hikosaka 2004; Yamori et al. 2010b). Increase in leaf nitrogen content by low-growth temperatures are considered to be a compensatory response to low temperature, which decreases enzyme activity.

The CO_2 fixation rate at night is mainly determined by the rate of CO_2 uptake by PEPC and/or malate formation by NAD(P)-MDH, whereas in the light, it is determined by the decarboxylation rate by NAD(P)-ME, CO_2 assimilation rate by Rubisco, and/or photosynthetic electron transport in the thylakoid membranes. During the daytime, the optimum temperature for the three determining processes would be expected to be adapted to higher daytime temperatures, whereas at night, PEPC and NAD(P)-MDH would be adapted to low temperatures, representative of the cooler nights where they operate. This is partly supported by in vitro studies by Brandon (1967), which indicated that the temperature optimum for decarboxylation by NAD(P)-ME was above 53 °C, and was much higher than that of PEPC and NAD(P)-MDH (i.e., approximately 35 °C). Thus, the different photosynthetic responses to temperature between day and night are likely explained by the temperature responses of enzymatic reactions which are the limiting steps during the respective phases of CAM photosynthesis over the day.

There have been no studies to date analyzing the limiting steps of photosynthetic reactions across a broad temperature range in CAM plants. An efficient and stable transformation in *K. fedtschenko* has been developed as a model CAM system, which makes it possible to manipulate photosynthetic reactions by antisense suppression and/or overexpression of particular genes (for a review, see Borland et al. 2009). Therefore, we can now start to analyze what process limits CAM photosynthesis in the same way as for C_3 and C_4 photosynthesis.

Inherent variations in temperature response of photosynthesis and its acclimation among photosynthetic types and among functional types

Difference among photosynthetic types (C_3, C_4, and CAM plants)

In plant canopies, leaf temperatures can fluctuate rapidly (e.g., Singsaas and Sharkey 1998), mainly due to brief changes in radiation load that are known as sunflecks (recently reviewed by Way and Pearcy 2012). However, the vast majority of our data on temperature acclimation of photosynthesis is derived from temperature response curves of net CO_2 assimilation, where stable rates of photosynthesis can be assessed over a relatively brief time. We therefore drew on this large and rich dataset to compare the inherent ability of photosynthetic temperature acclimation among C_3, C_4, and CAM plants. Temperature responses of photosynthetic rate at high light were pooled from the published data and averaged in C_3, C_4, and CAM plants (Fig. 4). To specify the effect of growth temperature, we selected plants grown under more than two growth temperatures in temperature-controlled growth chambers. It should be noted that, for CAM plants, data for CO_2 fixation at night were pooled, as there have been no studies analyzing temperature responses of CO_2 fixation by Rubisco during the day because of measurement difficulties. C_3 photosynthesis typically exhibits a T_{opt} in the range of 10–35 °C, showing that the potential range of T_{opt} for C_3 photosynthesis is broad. CAM plants generally show low CO_2 fixation rates, which correspond to their relatively slow growth rates; moreover, the T_{opt} is also lower in CAM species than in C_3 or C_4 plants. C_4 plants exhibit a higher T_{opt} and greater maximum photosynthetic rate at T_{opt} than C_3 plants, although, C_4 photosynthesis is sharply depressed at low temperatures.

Each photosynthetic temperature response from the literature was fit with a third-order polynomial, and the T_{opt} and temperatures that realize 80 % of the maximum photosynthetic rate (T_{min} and T_{max}) were obtained from the

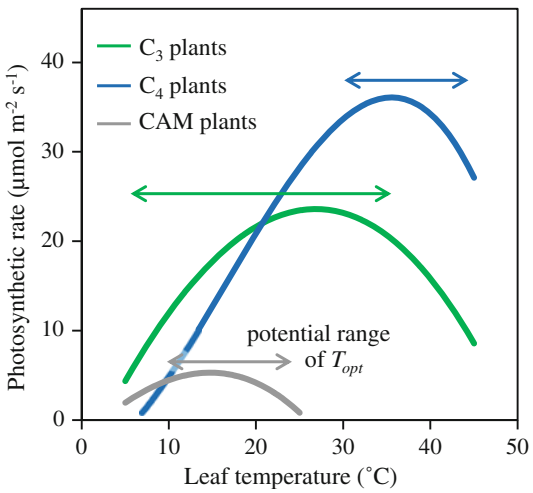

Fig. 4 Typical temperature responses of photosynthesis in C_3, C_4, and CAM plants. Temperature responses of photosynthesis are pooled from the published data and are averaged in C_3, C_4, and CAM plants, respectively (86 C_3 herbaceous plants, 31 C_4 plants, and 27 CAM plants). In CAM plants, data for CO_2 fixation rate at night was pooled. From the pooled data, the potential range of optimum temperature for photosynthesis is indicated in C_3, C_4, and CAM plants, respectively

Table 1 Results of an analysis of variance with a generalized linear model (GLM)

	T_{opt}	T_{min}	T_{max}	*Span*
Comparison between C_3, C_4 and CAM plants				
T_{growth}	316***	186***	280***	2.42^{ns}
Type	96.7***	70.3***	111***	18.2***
T_{growth} × type	3.79*	5.53**	1.55^{ns}	3.59*
Comparison between functional types within C_3 plants				
T_{growth}	213***	160***	235***	3.19^{+}
Type	3.67*	7.95***	16.6***	1.66^{ns}
T_{growth} × type	3.76*	2.32^{+}	8.55***	1.83^{ns}

Variations in temperature response of photosynthesis among photosynthetic types (C_3, C_4 and CAM plants) and among functional types within C_3 plants (annual and perennial herbaceous plants, and deciduous and evergreen woody plants) are assessed

F values with significance are shown. *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, $^{+}$ $P < 0.1$, ^{ns} $P > 0.1$. All the data were pooled for each group. The distribution and link function was "Gaussian" and "identity" in all cases, respectively. Statistical analyses were performed with R (version 2.6.2; R Development Core Team, Vienna, Austria)

curve. Table 1 shows the results of an analysis of variance (ANOVA) with a general linear regression (GLM) analysis of the parameters in relation to growth temperature and photosynthetic type (C_3, C_4, and CAM plants). In all photosynthetic types, T_{opt}, T_{min}, and T_{max} significantly increased with increasing growth temperature (Fig. 5A, Table S1). T_{opt}, T_{min}, and T_{max} were significantly different among photosynthetic types (Table 1). C_4 plants had a higher T_{opt} than species using the other photosynthetic pathways, and the T_{opt} in CAM plants was similar to that in C_3 plants at low-growth temperatures, but tended to be lower at high-growth temperatures. There was a significant interaction of growth temperature and photosynthetic types in T_{opt} and T_{min}, but not in T_{max}. The span of temperature that realizes >80 % of the maximum photosynthetic rate (*Span*) did not depend on growth temperature, but did differ among photosynthetic types: a GLM suggests that the *Span* is greater in C_4 plants and smaller in CAM plants than in C_3 plants (Table S1). However, due to a smaller slope of T_{opt} and T_{min}, C_4 plants had a relatively smaller *Span* at higher growth temperatures. Thus, the smaller *Span* in C_4 than in C_3 species (Fig. 4) partly resulted from higher growth temperatures for C_4 plants.

We also calculated the slope of T_{opt} versus growth temperature in each plant grown at contrasting temperatures (Table 2). The slope of T_{opt} versus growth temperature tended to be lower in C_4 plants than in C_3 and CAM plants (Tables 2 and S1). In C_3 plants, the average of slopes with each species (0.377 °C °C^{-1}) was smaller than the slope across all C_3 species (0.496 °C °C^{-1}), such that the total variation in T_{opt} in C_3 plants is greater than its

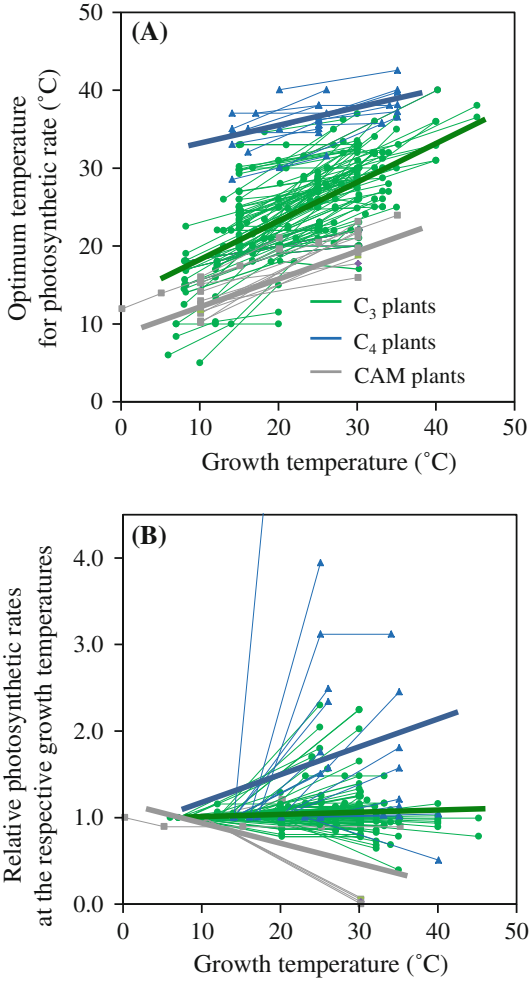

Fig. 5 Effects of growth temperatures on the optimum temperature for photosynthetic rate (**A**). A data set which analyzed the photosynthetic temperature response in plants grown at contrasting temperature regimes in a temperature-controlled growth chamber was divided into C_3 plants, C_4 plants, and CAM plants, respectively. The entire regression line is $y = 0.4964x + 13.066$ ($R^2 = 0.48$) for C_3 plants, $y = 0.2454x + 29.853$ ($R^2 = 0.37$) for C_4 plants, and $y = 0.3408x + 10.369$ ($R^2 = 0.71$) for CAM plants. Effects of growth temperatures on the photosynthetic rates at the respective growth temperatures (relative value to 1.0 at low temperature) (**B**). The entire regression line is $y = 0.0026x + 0.9977$ ($R^2 = 0.01$) for C_3 plants, $y = 0.0189x + 1.2323$ ($R^2 = 0.01$) for C_4 plants, and $y = -0.025x + 1.2168$ ($R^2 = 0.45$) for CAM plants

acclimatory change in each species. The acclimation ability of each species is limited to a certain level, but species differentiation has enabled C_3 species to adapt to a wide range of temperatures. This highlights that not only acclimation, but also evolutionary changes, have played an important role in the ability of C_3 species to inhabit various temperature regimes. On the other hand, in C_4 and CAM plants, the mean of the slopes within each species was similar to the slope across species in each photosynthetic type (Table 2), suggesting a limited differentiation among species in each photosynthetic type and that variation in

T_{opt} can be explained mainly by acclimation within each type.

We evaluated temperature homeostasis of photosynthesis as the ratio of photosynthetic rates at the respective growth temperature (i.e., the photosynthetic rate at high-growth temperature divided by that at low-growth temperature; Table 2). In C_3 plants, it was close to 1, indicating that the photosynthetic rate at the growth temperature was maintained irrespective of growth temperatures (Fig. 5B). In C_4 plants, it was 2.39, indicating that photosynthetic rates were greater at high-growth temperatures. In contrast, CAM plants had a value of 0.47, such that they had lower photosynthetic rates at higher temperatures.

Taken together, the temperature response of photosynthetic traits in each photosynthetic pathway (C_3, C_4, and CAM) likely reflects adaptation to a prevalent temperature regime. There are various C_3 species with different inherent abilities to acclimate photosynthesis to a change in growth temperature, and C_3 plants generally had greater ability of temperature acclimation of photosynthesis across a broad temperature range. At night, CAM plants from desert environments can experience very low temperatures, so CO_2 fixation should be optimized for low night temperatures (Lüttge 2004), although as mentioned earlier, the underlying mechanisms for the temperature response of CO_2 fixation in CAM plants has not been elucidated. In contrast, C_4 plants are generally adapted to warm environments. This could be explained by two possibilities: (1) a high concentration of CO_2 at the site of Rubisco allows high CO_2 assimilation rates at high temperatures, where photorespiration rates are high (Jordan and Ogren 1984); (2) C_4 photosynthetic enzymes are adapted to high temperature. For example, the temperature optimum of PEPC is around 40–45 °C (Chinthapalli et al. 2003), and the maximum rate of RuBP carboxylation (V_{cmax}) as well as electron transport rate (J_{max}) increased exponentially with temperature (Kubien et al. 2003). On the other hand, why do C_4 plants perform poorly at low temperature? As described above, C_4 plants fail at low temperature due to either: (1) enzyme lability in the C_4 cycle (especially at PEP regeneration by PPDK, Naidu et al. 2003; Wang et al. 2008); (2) insufficient Rubisco capacity (Kubien et al. 2003); or (3) low-quantum yield of C_4 photosynthesis relative to C_3 photosynthesis at low temperatures (Ehleringer and Björkman 1977; Ehleringer 1978) where photoinhibition can occur. C_4 photosynthesis is generally considered less plastic than C_3 photosynthesis due to the constraints of regulating an additional biochemical cycle, two cell types, and the rigid positioning of chloroplasts within bundle sheath cells (Sage and McKown 2006).

Difference among functional types (annual and perennial herbaceous plants, and deciduous and evergreen woody plants)

We further assessed variations in the temperature response of photosynthesis among plant functional types within C_3 plants. ANOVA results indicate that T_{opt}, T_{min}, and T_{max} varied among functional types (Table 1). Compared with annual herbaceous plants, perennial herbaceous plants had lower values of T_{opt}, T_{min}, and T_{max}, and evergreen woody species had lower values of T_{min} and T_{max} (Table S2). Perennial herbaceous plants altered their temperature parameters to a change in growth temperature more than annual herbaceous plants. These results suggest that perennial herbaceous and evergreen woody plants are adapted to lower temperatures than annual herbaceous and deciduous woody plants. This could reflect the fact that some perennials and evergreens retain leaves in the winter.

Table 2 Differences in parameters for temperature acclimation of photosynthesis among C_3, C_4, and CAM plants

	C_3 plants	C_4 plants	CAM plants
(1) Alteration in T_{opt} per 1 °C increase in growth temperature across species (°C °C^{-1})	0.496 (282)	0.245 (35)	0.341 (27)
(2) Average of alteration in T_{opt} per 1 °C increase in the growth temperature (°C °C^{-1})	0.377 ± 0.024a (123)	0.249 ± 0.040b (18)	0.393 ± 0.043ab (12)
(3) Temperature homeostasis of photosynthesis (high temp./low temp.)	1.12 ± 0.03a (98)	2.39 ± 0.64b (16)	0.466 ± 0.205c (7)

(1) The alteration in the optimum temperature for photosynthesis (T_{opt}) per 1 °C increase in the growth temperature (T_{growth}) across species in each photosynthetic type was obtained as the slope of the regression of T_{opt} on T_{growth} across species in the photosynthetic type. (2) The alteration in T_{opt} per 1 °C increase in T_{growth} was calculated for each species and averaged in each photosynthetic type. (3) Temperature homeostasis of photosynthetic rate was obtained as the ratio of photosynthetic rate measured at the respective growth temperatures (relative to a value of 1.0 at low temperature). The sample number is shown in parenthesis. Values represent the mean ± SE. Different letters indicate significant differences (Tukey–Kramer multiple comparison test; $P < 0.05$). See Table S1 for the statistical analysis of the slope of the regression of T_{opt} on T_{growth} among photosynthetic types

Alterations in T_{opt} per 1 °C increase in growth temperature, as well as temperature homeostasis of photosynthesis, were also different depending on functional types within C_3 plants (Table 3). Alterations in T_{opt} with a change in growth temperature were similar among annual herbs, perennial herbs, and deciduous woody plants, but were lower in evergreen woody plants. However, in spite of the extent of alterations in T_{opt} depending on growth temperature, evergreen woody species and perennial herbs showed a greater tendency toward temperature homeostasis of photosynthesis than other C_3 groups (Table 3): while photosynthetic rates were not much affected by a change in growth temperature in perennial herbaceous species or evergreen woody plants, annual herbs and deciduous woody plants increased photosynthesis an average of 20–30 % at higher growth temperatures. This indicates that alterations of the temperature response of photosynthesis at low or high temperatures without shifting T_{opt} could lead to more efficient photosynthesis at the growth temperature. It should be noted that plants do not necessarily have to alter T_{opt}, since there are different strategies to improve photosynthetic efficiency at a new growth temperatures (see Way and Yamori 2013). Apparently, temperature homeostasis of photosynthesis was maintained irrespective of the extent of changes in the T_{opt}, especially in C_3 plants (Fig. 6), indicating that some species shift T_{opt} to increase photosynthesis at the growth temperature, whereas others can achieve greater photosynthesis at the growth temperature without shifting T_{opt}. Greater temperature homeostasis of photosynthesis in perennial herbaceous plants and evergreen woody plants indicates that photosynthetic acclimation is particularly important in perennial, long-lived plant species that will experience a rise in growing season temperatures over their lifespan.

The temperature response of photosynthesis differs between temperate evergreen species and tropical evergreen species (Read 1990; Cunningham and Read 2002), and elevated temperatures enhance growth in deciduous species more than in evergreen trees (Carter 1996; Way and Oren 2010), so it is not surprising that functional types show different capacities for acclimating photosynthesis to changes in growth temperature (Table 2). Moreover, similar results have been observed even among ecotypes of the same species depending on their original habitats (e.g., coastal habitat vs desert habitat: Pearcy 1977; Mooney 1980; latitudinal or altitudinal difference; Hill et al. 1988; Read and Busby 1990; Ishikawa et al. 2007). Differences in phenotypic plasticity could be attributed to the extent of the daily and seasonal temperature variations (Hill et al. 1988; Read 1990; Cunningham and Read 2002) or the extent of plant cold tolerance (Yamori et al. 2010b). In addition, variation in the acclimation response caused by species differences may reflect the extent of temperature specialization (Atkin et al. 2006), since specialization for extreme environments may restrict the potential for temperature acclimation. It is still unclear what physiological characteristics are related to

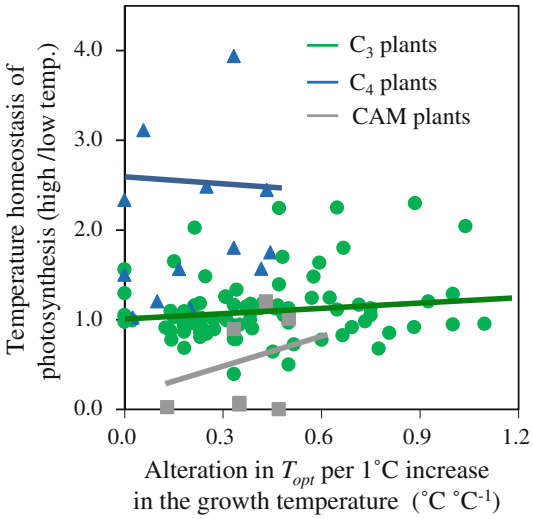

Fig. 6 Relationships between the alteration in T_{opt} per 1 °C increase in the growth temperature and the ratio of photosynthetic rate measured at the respective growth temperatures (relative value to 1:0 at low temperature) as an index of the extent of temperature homeostasis of photosynthesis. The entire regression line is $y = 0.2848x + 1.0077$ ($R^2 = 0.05$) for C_3 plants, $y = -0.2545x + 2.6057$ ($R^2 = 0.01$) for C_4 plants, and $y = 0.9609x + 0.1673$ ($R^2 = 0.05$) for CAM plants

Table 3 Differences in parameters for temperature acclimation of photosynthesis among functional types within C_3 plants

	Annual	Perennial	Deciduous	Evergreen
(1) Alteration in T_{opt} per 1 °C increase in growth temperature across species (°C °C^{-1})	0.525 (73)	0.738 (34)	0.366 (15)	0.433 (141)
(2) Average of alteration in T_{opt} per 1 °C increase in the growth temperature (°C °C^{-1})	0.476 ± 0.048a (34)	0.433 ± 0.085ab (16)	0.497 ± 0.104ab (6)	0.304 ± 0.026bc (67)
(3) Temperature homeostasis of photosynthesis (high temp./low temp.)	1.31 ± 0.07a (33)	1.03 ± 0.07bc (14)	1.19 ± 0.12ac (8)	0.989 ± 0.026bc (43)

Abbreviations are the same as those in Table 2. The sample number is shown in parenthesis. Values represent the mean ± SE. Different letters indicate significant differences (Tukey–Kramer multiple comparison test; $P < 0.05$). See Table S2 for the statistical analysis of the slope of the regression of T_{opt} on T_{growth} among functional types

interspecific variations of photosynthetic temperature acclimation, although, interspecific variation of many leaf traits is related to plant functional type (Wright et al. 2005). Among functional types, the difference in the limiting step of photosynthesis at a given temperature could explain the potential for temperature acclimation of photosynthesis, and also explain the differences in the inherent ability of temperature acclimation of photosynthesis among C_3, C_4, and CAM plants, since these groups exhibit a different pattern of biochemical limitation across a range of temperatures. Further research is necessary to elucidate the mechanisms of the interspecific variation of temperature acclimation of photosynthesis.

Conclusions and future perspective

The earth's climate is predicted to be warm by an average of 1.1–6.4 °C during the next century as a result of the increased greenhouse gases in the atmosphere. High leaf temperatures can reduce plant growth and limit crop yields, with estimates of up to a 17 % decrease in yield per 1.0 °C increase in average growing season temperature (Lobell and Asner 2003). It has been argued that a new "green revolution" is needed in world agriculture to increase crop yields for food demands (Fischer and Edmeades 2010), and enhancing photosynthesis is a promising approach for increasing crop yield. However, to reach this goal, we must understand what process limits photosynthesis under a range of growth conditions, and how well photosynthesis can acclimate to predicted changes in temperature. We found clear differences in the ability to acclimate photosynthesis to increases in growth temperature between species from differing photosynthetic pathways. C_4 species had higher optimum temperatures of photosynthesis, but a reduced ability to acclimate the temperature optimum of photosynthesis to growth temperature, than C_3 species, while C_3 species tended to maintain the same photosynthetic rate at their growth condition across a range of growth temperatures (e.g., had better homeostasis) than C_4 species. We also found that, within C_3 species, evergreen woody plants and perennial herbaceous plants showed greater temperature homeostasis of photosynthesis than deciduous woody plants and annual herbaceous plants. In addition, we found that in CAM plants, the temperature response of CO_2 fixation at night was much different from that of chloroplast electron transport in the day, and that both CO_2 fixation rates and electron transport rates acclimated to shifts in growth temperatures. This could be considered to be an adaptive response since CAM plants from desert environments can experience a drastic alteration in day and night temperatures during a 24-h period.

Advances in plant transformation technology now make it possible to manipulate photosynthesis by overexpressing particular genes for alleviating bottleneck steps of photosynthesis. Thus, understanding the mechanisms of temperature acclimation of photosynthesis via comparisons of species differences and/or changes in growth temperature is of immense importance for identifying a biomolecular target for enhancing leaf photosynthesis. What would be a useful biomolecular target for enhancing leaf photosynthesis? There is no single answer, since the limiting step of photosynthesis differs depending on plants species, and also differs depending on growth and measurement temperatures even in a single plant species (Yamori et al. 2010b). Therefore, the impact on the control of carbon fixation by manipulation of one enzyme would differ depending on the plant species and growth conditions. More attention should be paid to studying differences in the photosynthetic limiting step depending on species and growth conditions, as this might provide opportunities for achieving faster improvements in crop production.

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