

Phenotypic Plasticity in Photosynthetic Temperature Acclimation among Crop Species with Different Cold Tolerances¹[W][OA]

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While interspecific variation in the temperature response of photosynthesis is well documented, the underlying physiological mechanisms remain unknown. Moreover, mechanisms related to species-dependent differences in photosynthetic temperature acclimation are unclear. We compared photosynthetic temperature acclimation in 11 crop species differing in their cold tolerance, which were grown at 15°C or 30°C. Cold-tolerant species exhibited a large decrease in optimum temperature for the photosynthetic rate at 360 $\mu\text{L L}^{-1}$ CO₂ concentration [Opt (A_{360})] when growth temperature decreased from 30°C to 15°C, whereas cold-sensitive species were less plastic in Opt (A_{360}). Analysis using the C₃ photosynthesis model shows that the limiting step of A_{360} at the optimum temperature differed between cold-tolerant and cold-sensitive species; ribulose 1,5-bisphosphate carboxylation rate was limiting in cold-tolerant species, while ribulose 1,5-bisphosphate regeneration rate was limiting in cold-sensitive species. Alterations in parameters related to photosynthetic temperature acclimation, including the limiting step of A_{360} , leaf nitrogen, and Rubisco contents, were more plastic to growth temperature in cold-tolerant species than in cold-sensitive species. These plastic alterations contributed to the noted growth temperature-dependent changes in Opt (A_{360}) in cold-tolerant species. Consequently, cold-tolerant species were able to maintain high A_{360} at 15°C or 30°C, whereas cold-sensitive species were not. We conclude that differences in the plasticity of photosynthetic parameters with respect to growth temperature were responsible for the noted interspecific differences in photosynthetic temperature acclimation between cold-tolerant and cold-sensitive species.

The temperature dependence of leaf photosynthetic rate shows considerable variation between plant species and with growth temperature (Berry and Björkman, 1980; Cunningham and Read, 2002; Hikosaka et al., 2006). Plants native to low-temperature environments and those grown at low temperatures generally exhibit higher photosynthetic rates at low temperatures and lower optimum temperatures, compared with plants native to high-temperature environments and those grown at high temperatures (Mooney and Billings, 1961; Slatyer, 1977; Berry and Björkman, 1980; Sage, 2002; Salvucci and Crafts-Brandner, 2004b). For example, the optimum temperature for photosynthesis differs between temperate evergreen species and tropical evergreen species (Hill et al.,

1988; Read, 1990; Cunningham and Read, 2002). Such differences have been observed even among ecotypes of the same species (Björkman et al., 1975; Pearcy, 1977; Slatyer, 1977).

Temperature dependence of the photosynthetic rate has been analyzed using the biochemical model proposed by Farquhar et al. (1980). This model assumes that the photosynthetic rate (A) is limited by either ribulose 1,5-bisphosphate (RuBP) carboxylation (A_c) or RuBP regeneration (A_r). The optimum temperature for photosynthetic rate in C₃ plants is thus potentially determined by (1) the temperature dependence of A_c , (2) the temperature dependence of A_r , or (3) both, at the colimitation point of A_c and A_r (Fig. 1; Farquhar and von Caemmerer, 1982; Hikosaka et al., 2006).

In many cases, the photosynthetic rate around the optimum temperature is limited by A_c and thus the temperature dependence of A_c determines the optimum temperature for the photosynthetic rate (Hikosaka et al., 1999, 2006; Yamori et al., 2005, 2006a, 2006b, 2008; Sage and Kubien, 2007; Sage et al., 2008). As the temperature increases above the optimum, A_c is decreased by increases in photorespiration (Berry and Björkman, 1980; Jordan and Ogren, 1984; von Caemmerer, 2000). Furthermore, it has been suggested that the heat-induced deactivation of Rubisco is involved in the decrease in A_c at high temperature

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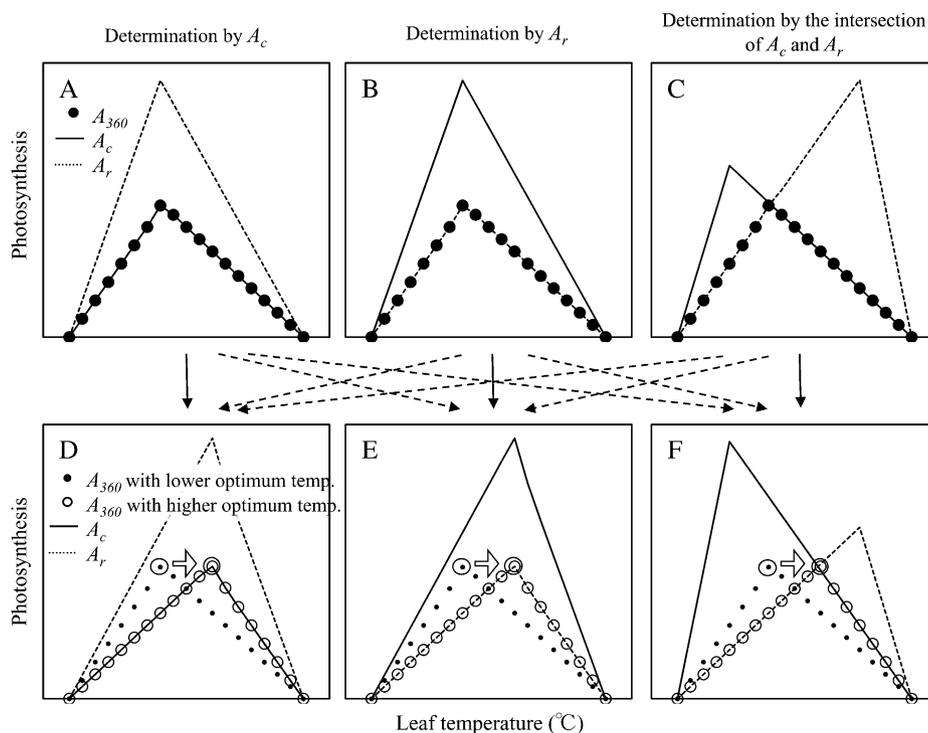


Figure 1. A scheme illustrating the shift in the optimum temperature for photosynthesis depending on growth temperature. Based on the C_3 photosynthesis model, the A_{360} (white and black circles) is limited by A_c (solid line) or A_r (broken line). The optimum temperature for the photosynthetic rate is potentially determined by temperature dependence of A_c (A), temperature dependence of A_r (B), or the intersection of the temperature dependences of A_c and A_r (C). When the optimum temperature for the photosynthetic rate shifts to a higher temperature, there are also three possibilities determining the optimum temperature: temperature dependence of A_c (D), temperature dependence of A_r (E), or the intersection of the temperature dependences of A_c and A_r (F). Especially in the case that the optimum temperature is determined by the intersection of the temperature dependences of A_c and A_r , the optimum temperature can shift by changes in the balance between A_c and A_r , even when the optimum temperatures for these two partial reactions do not change.

(Law and Crafts-Brandner, 1999; Crafts-Brandner and Salvucci, 2000; Salvucci and Crafts-Brandner, 2004a; Yamori et al., 2006b). Numerous previous studies have shown changes in the temperature dependence of A_c with growth temperature (Hikosaka et al., 1999; Bunce, 2000; Yamori et al., 2005). Also, the temperature sensitivity of Rubisco deactivation may differ between plant species (Salvucci and Crafts-Brandner, 2004b) and with growth temperature (Yamori et al., 2006b), which may explain variation in the optimum temperature for photosynthesis (Fig. 1, A and D).

A_r is more responsive to temperature than A_c and often limits photosynthesis at low temperatures (Hikosaka et al., 1999, 2006; Sage and Kubien, 2007; Sage et al., 2008). Recently, several researchers indicated that A_r limits the photosynthetic rate at high temperature (Schrader et al., 2004; Wise et al., 2004; Cen and Sage, 2005; Makino and Sage, 2007). They suggested that the deactivation of Rubisco at high temperatures is not the cause of decreased A_c but a result of limitation by A_r . However, it remains unclear whether limitation by A_r is involved in the variation in the optimum temperature for the photosynthetic rate (Fig. 1, B and E).

A shift in the optimum temperature for photosynthesis can result from changes in the balance between A_r and A_c , even when the optimum temperatures for these two partial reactions do not change (Fig. 1, C and F; Farquhar and von Caemmerer, 1982). The balance between A_r and A_c has been shown to change depending on growth temperature (Hikosaka et al., 1999; Hikosaka, 2005; Onoda et al., 2005a; Yamori et al., 2005) and often brings about a shift in the colimitation temperature of A_r and A_c . Furthermore, recent studies have shown that plasticity in this balance differs among species or ecotypes (Onoda et al., 2005b; Atkin et al., 2006; Ishikawa et al., 2007). Plasticity in this balance could explain interspecific variation in the plasticity of photosynthetic temperature dependence (Farquhar and von Caemmerer, 1982; Hikosaka et al., 2006), although there has been no evidence in the previous studies that the optimum temperature for photosynthesis occurs at the colimitation point of A_r and A_c .

Temperature tolerance differs between species and, with growth temperature, even within species from the same functional group (Long and Woodward, 1989). Bunce (2000) indicated that the temperature

dependences of A_r and A_c to growth temperature were different between species from cool and warm climates and that the balance between A_r and A_c was independent of growth temperature for a given plant species. However, it was not clarified what limited the photosynthetic rate or what parameters were important in temperature acclimation of photosynthesis. Recently, we reported that the extent of temperature homeostasis of leaf respiration and photosynthesis, which is assessed as a ratio of rates measured at their respective growth temperatures, differed depending on the extent of the cold tolerance of the species (Yamori et al., 2009b). Therefore, comparisons of several species with different cold tolerances would provide a new insight into interspecific variation of photosynthetic temperature acclimation and their underlying mechanisms. In this study, we selected 11 herbaceous crop species that differ in their cold tolerance (Yamori et al., 2009b) and grew them at two contrasting temperatures, conducting gas-exchange analyses based on the C_3 photosynthesis model (Farquhar et al., 1980). Based on these results, we addressed the following key questions. (1) Does the plasticity in photosynthetic temperature acclimation differ between cold-sensitive and cold-tolerant species? (2) Does the limiting step of photosynthesis at several leaf temperatures differ between plant species and with growth temperature? (3) What determines the optimum temperature for the photosynthetic rate among A_c , A_r , and the intersection of the temperature dependences of A_c and A_r ?

RESULTS

Temperature Dependence of Photosynthesis

Temperature dependences of dark respiration (R_d) and photosynthesis (A) at high light and $360 \mu\text{L L}^{-1}$ CO_2 (A_{360}) differed between plant species and with growth temperature (Supplemental Fig. S1). When plants were grown at 15°C , the mean optimum temperature for A_{360} [Opt (A_{360})] was significantly lower in cold-tolerant species ($22.3^\circ\text{C} \pm 2.2^\circ\text{C}$) than in cold-sensitive species ($28.3^\circ\text{C} \pm 2.4^\circ\text{C}$; Table I). Conversely, when plants were grown at 30°C , the mean Opt (A_{360}) was similar between cold-tolerant species ($28.4^\circ\text{C} \pm 1.9^\circ\text{C}$) and cold-sensitive species ($31.2^\circ\text{C} \pm 2.2^\circ\text{C}$). All species showed an increase in Opt (A_{360}) with increasing growth temperature, except for *Vicia faba* (Supplemental Table S1). Cold-tolerant species were more responsive to the growth temperatures than cold-sensitive species (Table I).

The temperature dependences of A_c and A_r also differed between plant species and with growth temperature (Supplemental Figs. S1 and S2). When plants were grown at 15°C , the mean Opt (A_c) was lower in cold-tolerant species ($22.6^\circ\text{C} \pm 2.3^\circ\text{C}$) than in cold-sensitive species ($27.6^\circ\text{C} \pm 3.3^\circ\text{C}$; Table I). When plants were grown at 30°C , the mean Opt (A_c) was also lower in cold-tolerant species ($28.1^\circ\text{C} \pm 1.5^\circ\text{C}$) than in cold-

sensitive species ($32.2^\circ\text{C} \pm 3.1^\circ\text{C}$). When plants were grown at 15°C , the mean Opt (A_r) was lower in cold-tolerant species ($26.8^\circ\text{C} \pm 1.9^\circ\text{C}$) than in cold-sensitive species ($28.7^\circ\text{C} \pm 1.8^\circ\text{C}$; Table I). When plants were grown at 30°C , the mean Opt (A_r) was also slightly lower in cold-tolerant species ($30.9^\circ\text{C} \pm 1.3^\circ\text{C}$) than in cold-sensitive species ($32.7^\circ\text{C} \pm 1.1^\circ\text{C}$).

We analyzed the ratio of the chloroplast electron transport rate to the maximum RuBP carboxylation rate ($J_{\text{max}}/V_{\text{cmax}}$) at 25°C , which is a measure of the balance between RuBP regeneration and carboxylation (Table I; Supplemental Table S1). Although the $J_{\text{max}}/V_{\text{cmax}}$ ratio varied depending on measurement temperature, the general trends were not affected by the measurement temperature; the correlation coefficients (r) were 0.77, 0.82, and 0.97 for the relationships between 15°C and 30°C , between 15°C and 25°C , and between 25°C and 30°C , respectively. In cold-sensitive species, the mean $J_{\text{max}}/V_{\text{cmax}}$ ratio was not significantly affected by growth temperature, whereas in cold-tolerant species, the mean $J_{\text{max}}/V_{\text{cmax}}$ ratio increased at low growth temperature. The intercellular CO_2 concentration (C_i) at 25°C was less in 15°C plants than in 30°C plants but was independent of cold tolerance (Table I; for temperature dependence of C_i , see Supplemental Fig. S1).

Limiting Step of the Temperature Dependence of A_{360}

The limiting step of A_{360} was analyzed based on the CO_2 dependence of the photosynthetic rate. Figure 2 shows three typical examples of the limiting step of A_{360} obtained in this study: *Secale cereale* grown at 15°C and *Cucumis sativus* and *Nicotiana tabacum* grown at 30°C (for each species, see Supplemental Fig. S2). Figure 2, A to C, show the ratio of A_{360} to A_{200} . Dotted lines denote the ratio of the A_c at 360 to the A_c at $200 \mu\text{L L}^{-1}$ CO_2 concentration (A_{c360}/A_{c200} ratio), and continuous lines denote the ratio of the A_r at 360 to the A_r at $200 \mu\text{L L}^{-1}$ CO_2 concentration (A_{r360}/A_{r200} ; see "Materials and Methods"). Similarly, the ratios of A_{1500} to A_{360} are shown in Figure 2, D to F. We further analyzed whether of A_c or A_r limited A_{360} using obtained parameter values, based on the C_3 photosynthesis model (Fig. 2, G–I; see "Materials and Methods"). We regarded that A_r (or A_c) limited photosynthesis if the difference between A_r (or A_c) and A_{360} was smaller than 5%.

In *S. cereale* grown at 15°C , the A_{360}/A_{200} ratio was very close to the dotted line (A_{c360}/A_{c200}) at all leaf temperatures (Fig. 2A), whereas the A_{1500}/A_{360} ratio was greater than the continuous line (A_{r1500}/A_{c360}) at all leaf temperatures (Fig. 2D). This indicates that in *S. cereale* grown at 15°C , A_{360} was solely limited by A_c at all leaf temperatures (Fig. 2G). In *C. sativus* at 30°C , A_{360} was colimited by A_c and A_r at low temperature below 25°C , whereas above 25°C , it was limited by A_r (Fig. 2H). In *N. tabacum* grown at 30°C , A_{360} was solely limited by A_r at all leaf temperatures (Fig. 2I). Since the A_{1500}/A_{360} ratio was within 1.0 ± 0.1 at 10°C to 15°C ,

Table 1. $Opt(A_{360})$, $Opt(A_c)$, $Opt(A_r)$, J_{max}/V_{cmax} , and C_i

The data shown are mean values for each species (see Supplemental Table S1 for each species). A repeated-measures ANOVA was used to test for statistical differences. P values from repeated-measures ANOVA are shown for differences between growth temperatures and between plant types and for interactions. NS, Not significant.

Species or Variable	$Opt(A_{360})$ °C	$Opt(A_c)$ °C	$Opt(A_r)$ °C	J_{max}/V_{cmax}	$C_i(25^\circ\text{C})$ $\mu\text{L L}^{-1}$
Cold-sensitive species					
15°C plant	28.3 ± 2.4	27.6 ± 3.3	28.7 ± 1.8	1.48 ± 0.30	277.2 ± 26.9
30°C plant	31.2 ± 2.2	32.2 ± 3.1	32.7 ± 1.1	1.40 ± 0.21	294.8 ± 21.8
Cold-tolerant species					
15°C plant	22.3 ± 2.2	22.6 ± 2.3	26.8 ± 1.9	1.95 ± 0.16	281.5 ± 29.2
30°C plant	28.4 ± 1.9	28.1 ± 1.5	30.9 ± 1.3	1.57 ± 0.16	303.1 ± 18.5
P from repeated-measures ANOVA					
Cold tolerance	<0.001	<0.001	<0.01	<0.001	NS
Growth temperature	<0.001	<0.001	<0.001	<0.001	<0.001
Interaction	<0.01	<0.01	NS	<0.01	NS

A_{360} was limited by inorganic phosphate (Pi) regeneration in *N. tabacum* grown at 30°C. We classified plants into three groups with respect to the limiting step of A_{360} : type 1, A_{360} is limited by A_c at any temperature; type 2, A_{360} is colimited by both A_c and A_r or the limiting step was different depending on measurement temperature; and type 3, A_{360} is limited by A_r at any temperature (Fig. 2).

Figure 3 summarizes the differences in the limiting steps of A_{360} depending on plant species and growth

temperature. In cold-tolerant species, the limiting step of A_{360} varied with growth temperature. Most of the cold-tolerant species grown at 15°C belonged to type 1, whereas all the cold-tolerant species grown at 30°C belonged to type 2. On the other hand, in most of the cold-sensitive species, the limiting step of A_{360} was independent of growth temperature. In most of the cold-sensitive species, A_{360} was limited by A_r across a broad temperature range, irrespective of growth temperatures (type 2 or 3). It is obvious that in plants with

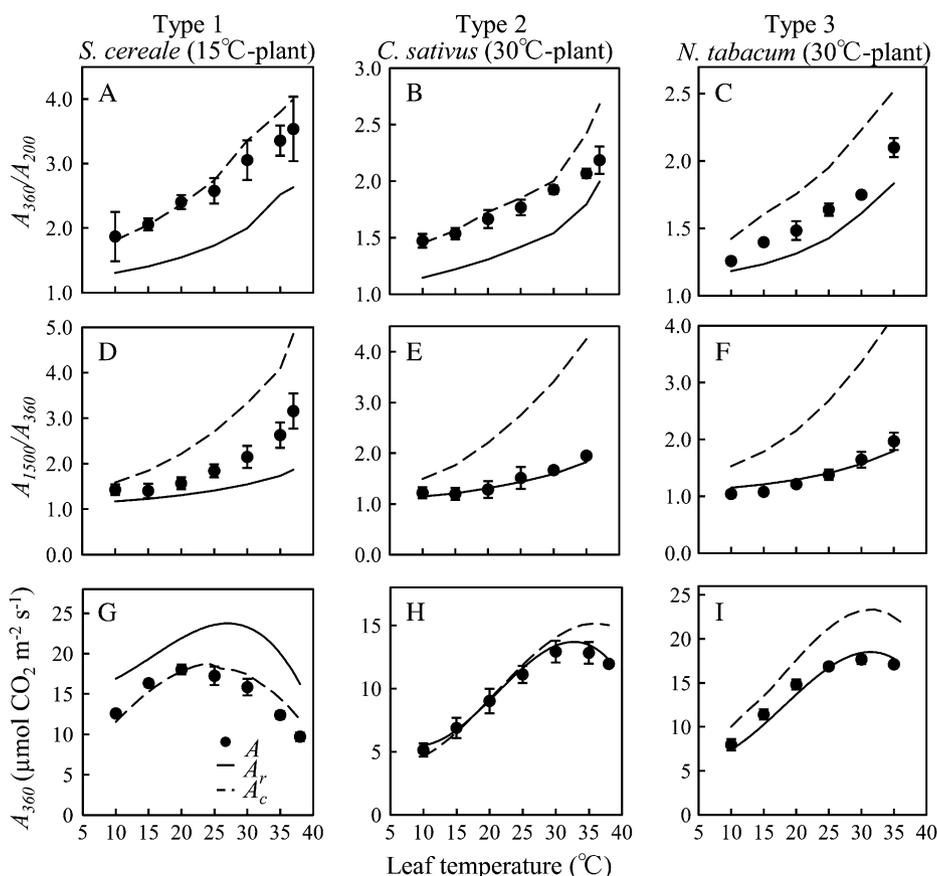


Figure 2. Three examples of limiting steps of the A_{360} . We classified plants into three groups with respect to the limiting step of A_{360} : type 1, A_{360} is limited by A_c at all temperatures in *S. cereale* grown at 15°C (A, D, and G); type 2, A_{360} is limited by both A_c and A_r in *C. sativus* grown at 30°C (B, E, and H); type 3, A_{360} is limited by A_r at all temperatures in *N. tabacum* grown at 30°C (C, F, and I). Black circles with bars denote the mean measured photosynthetic rates with SD. The ratios of A_{360} to A_{200} (A–C) and A_{1500} to A_{360} (D–F) are shown. Lines denote the ratio of the photosynthetic rate assuming the limitation by A_c (dotted lines; see Eq. 2 in Supplemental Appendix S1) or the limitation by A_r (continuous lines; see Eq. 3 in Supplemental Appendix S1). The limiting step of A_{360} was also analyzed by the model of Farquhar et al. (1980) with the obtained parameters (G–I).

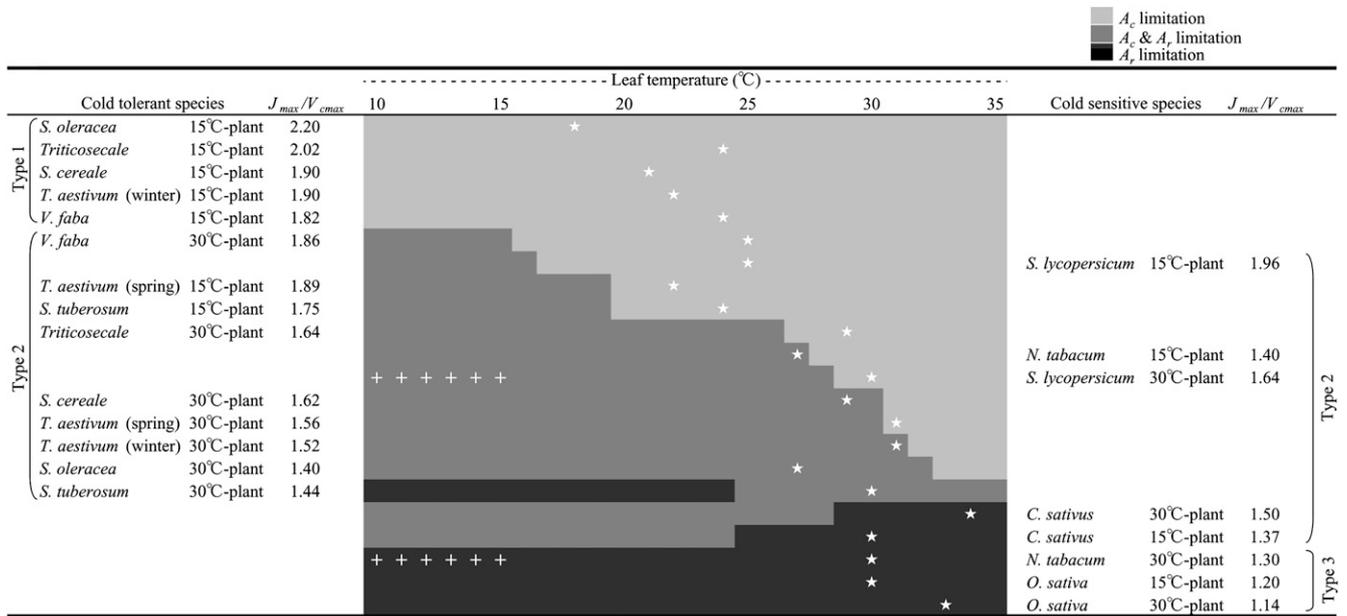


Figure 3. Summary of differences in the limiting step of the temperature dependence of A_{360} by A_c or A_r by plant species and growth temperature. This figure was summarized from Figure 2 and Supplemental Figure S2. The J_{max}/V_{cmax} ratio at 25°C were adopted from Supplemental Table S1. We classified plants into three groups with respect to the limiting step of A_{360} : type 1, A_{360} is limited by A_c at any temperature; type 2, A_{360} is limited by both A_c and A_r ; type 3, A_{360} is limited by A_r at any temperature. White stars indicate the optimum temperature for A_{360} . White crosses indicate that A_{360} was limited by Pi regeneration capacity.

a high J_{max}/V_{cmax} ratio (i.e. cold-tolerant species grown at low temperature), the limitation of A_{360} by A_r was alleviated. In *N. tabacum* and *Solanum lycopersicum* grown at 30°C, A_{360} was limited by Pi regeneration capacity at temperatures below 15°C.

Both in cold-sensitive species grown at 15°C and cold-tolerant species grown at 30°C, A_{360} at the growth temperature was colimited by both A_c and A_r . Conversely, A_{360} at the growth temperature was limited by A_r in two cold-sensitive species (*N. tabacum* and *Oryza sativa*) grown at 30°C and by A_c in most of the cold-tolerant species grown at 15°C.

Determination of the Opt (A_{360})

Opt (A_{360}) strongly correlated both with Opt (A_c) and with Opt (A_r) (Fig. 4, A–C). To judge whether A_r or A_c limits photosynthetic rate at Opt (A_{360}), we calculated A_r and A_c at Opt (A_{360}). A_{360} at Opt (A_{360}) was correlated both with A_{c360} and with A_{r360} at Opt (A_{360}) in both cold-sensitive and cold-tolerant species (Fig. 4, D and E). In cold-sensitive species, A_{360} was lower than A_{c360} but similar to A_{r360} at Opt (A_{360}) (Fig. 4, E and F). On the other hand, in cold-tolerant species, A_{360} was lower than A_{r360} but similar to A_{c360} at Opt (A_{360}) (Fig. 4, D and F). These results indicate that photosynthetic rate at optimum temperature was limited by A_r in cold-sensitive species but by A_c in cold-tolerant species; thus, the determinant of optimum temperature of photosynthesis differed between cold-tolerant and cold-sensitive species.

Syndrome of the Temperature Acclimation of Photosynthesis

In this study, growth temperature caused changes in various physiological characteristics, but the extent of plasticity differed depending on plant species and physiological characteristics. Here, we applied a principal component analysis to the parameters obtained in this study and our previous study (Yamori et al., 2009b). We used differences in Opt (A_{360}) depending on growth temperature [$\Delta\text{Opt} (A_{360})$], the ratio of J_{max}/V_{cmax} at 25°C for 15°C plants to that for 30°C plants (J_{max}/V_{cmax} ratio at 25°C), the ratio of leaf mass per area (LMA) for 15°C plants to that for 30°C plants (LMA), the ratio of nitrogen content per unit area (N_{area}), the ratio of Rubisco content (Rubisco content), the ratio of A_{360} at 15°C for 15°C plants to that at 30°C for 30°C plants (A_{360} at the growth temperature), the ratio of the maximum catalytic turnover rate of Rubisco (k_{cat}) activity (Rubisco k_{cat} at the growth temperature), the ratio of R_d (R_d at the growth temperature), and the ratio of NAD-malic enzyme (ME) activity (NAD-ME at the growth temperature). The first (axis 1) and second (axis 2) axes explained 62.0% and 16.2% of the total variation, respectively (Table II). Eight out of nine parameters were significantly correlated with axis 1, with the relationship between Rubisco k_{cat} at the growth temperature and axis 1 being marginally significant ($P < 0.1$). Axis 2 did not correlate with most parameters except for Rubisco k_{cat} at the growth temperature. Thus, axis 2 reflects mainly Rubisco k_{cat} at the

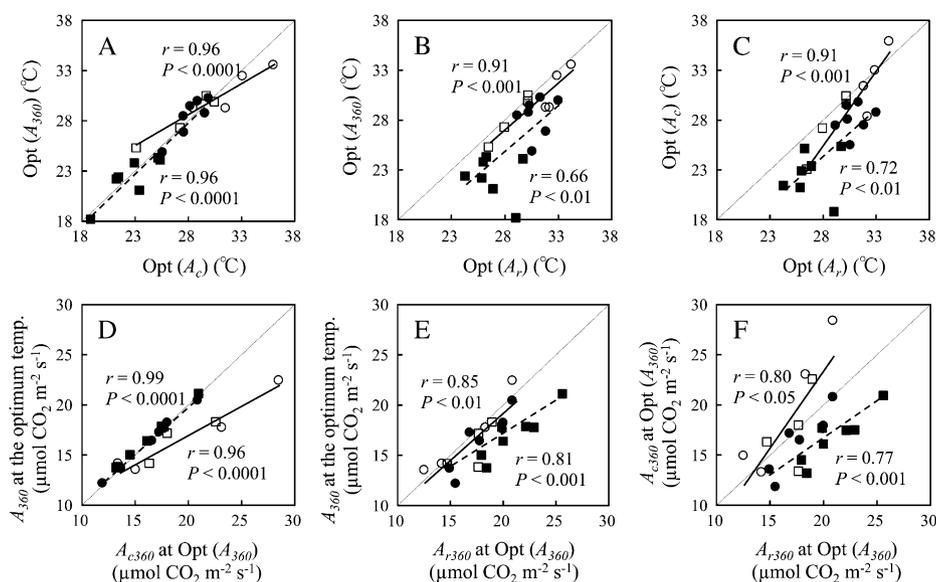


Figure 4. Relationships between Opt (A_{360}) and Opt (A_c) (A), between Opt (A_{360}) and Opt (A_r) (B), between Opt (A_c) and Opt (A_r) (C), between A_{360} at the optimum temperature and A_{c360} at Opt (A_{360}) (D), between A_{360} at the optimum temperature and A_{r360} at Opt (A_{360}) (E), and between A_{r360} at Opt (A_{360}) and A_{c360} at Opt (A_{360}) (F). Cold-sensitive species grown at 30°C (white circles), cold-sensitive species grown at 15°C (white squares), cold-tolerant species grown at 30°C (black circles), and cold-tolerant species grown at 15°C (black squares) are shown. The correlation lines are shown as solid lines for cold-sensitive species and as dashed lines for cold-tolerant species. Values are means; $n = 3$ to 5.

growth temperature, and the trend of interspecific variation in Rubisco k_{cat} at the growth temperature was somewhat different from that in other parameters.

Correlations between the parameters were significant and positive in many cases (Table II). In particular, $\Delta\text{Opt} (A_{360})$ was strongly correlated with $J_{\max}/V_{c\max}$ ratio at 25°C (Fig. 5). Both $\Delta\text{Opt} (A_{360})$ and $J_{\max}/V_{c\max}$ ratio at 25°C were strongly correlated with Rubisco content. Species with a greater $\Delta\text{Opt} (A_{360})$ tended to maintain A_{360} and R_d at the growth temperature. Thus, species with a greater $\Delta\text{Opt} (A_{360})$ tended to have greater change in $J_{\max}/V_{c\max}$ ratio, LMA, N_{area} , Rubisco content, Rubisco k_{cat} , and NAD-ME and consequently more stable A_{360} and R_d at the growth temperature (greater ability of temperature homeostasis).

DISCUSSION

Interspecific Variation in Temperature Acclimation of Photosynthesis

We found significant interspecific variation in photosynthetic temperature acclimation depending on the extent of cold tolerance (Table I; Supplemental Table S1). Inherent ability for photosynthetic acclimation to the high temperature was similar between cold-sensitive and cold-tolerant species, as they all had similar Opt (A_{360}). By contrast, when plants were grown at low temperature, cold-tolerant species exhibited a greater ability to shift Opt (A_{360}) to lower temperatures than cold-sensitive species. Only *S. lycopersicum*, a cold-sensitive species, showed a

Table II. Correlation coefficients and probabilities for plant attributes linked to the first principal components for photosynthetic parameters concerned with temperature acclimation

Variables taken into account are as follows: the differences in Opt (A_{360}) depending on growth temperature [$\Delta\text{Opt} (A_{360})$], the ratio of $J_{\max}/V_{c\max}$ at 25°C for 15°C plants to that at 25°C for 30°C plants ($J_{\max}/V_{c\max}$ ratio at 25°C), the ratio of leaf mass per area for 15°C plants to that for 30°C plants (LMA), the ratio of nitrogen content per unit area for 15°C plants to that for 30°C plants (N_{area}), the ratio of Rubisco content for 15°C plants to that for 30°C plants (Rubisco content), the ratio of A_{360} at 15°C for 15°C plants to that at 30°C for 30°C plants (A_{360} at the growth temperature), the ratio of Rubisco k_{cat} activity at 15°C for 15°C plants to that at 30°C for 30°C plants (Rubisco k_{cat} activity at the growth temperature), the ratio of R_d at 15°C for 15°C plants to that at 30°C for 30°C plants (R_d at the growth temperature), and the ratio of NAD-ME activity at 15°C for 15°C plants to that at 30°C for 30°C plants (NAD-ME activity at the growth temperature). Differences between the mean data for each species were regressed against the scores of Axis 1 and Axis 2. + $P < 0.10$, * $P < 0.05$, ** $P < 0.01$.

Parameter	Axis 1	Axis 2	$J_{\max}/V_{c\max}$	LMA	N_{area}	A_{360}	Rubisco	k_{cat}	R_d	NAD-ME
$\Delta\text{Opt} (A_{360})$	-0.73 *	0.57 +	0.79 *	0.57 +	0.53 +	0.53 +	0.73 *	0.00	0.64 *	0.30
$J_{\max}/V_{c\max}$ ratio at 25°C	-0.82 **	0.19		0.85 **	0.53 +	0.46	0.68 *	0.39	0.47	0.59 +
LMA	-0.88 **	-0.08			0.63 *	0.50	0.79 *	0.57 +	0.40	0.86 **
N_{area}	-0.69 *	0.38				0.42	0.75 *	0.08	0.42	0.48
A_{360} at growth temperature	-0.82 **	-0.17					0.70 *	0.58 +	0.93 **	0.66 *
Rubisco content	-0.91 **	0.23						0.29	0.67 *	0.70 *
k_{cat} at growth temperature	-0.57 +	-0.80 *							0.39	0.85 **
R_d at growth temperature	-0.77 *	0.04								0.51
NAD-ME at growth temperature	-0.84 **	-0.48								
Contribution (%)	62.0	16.2								

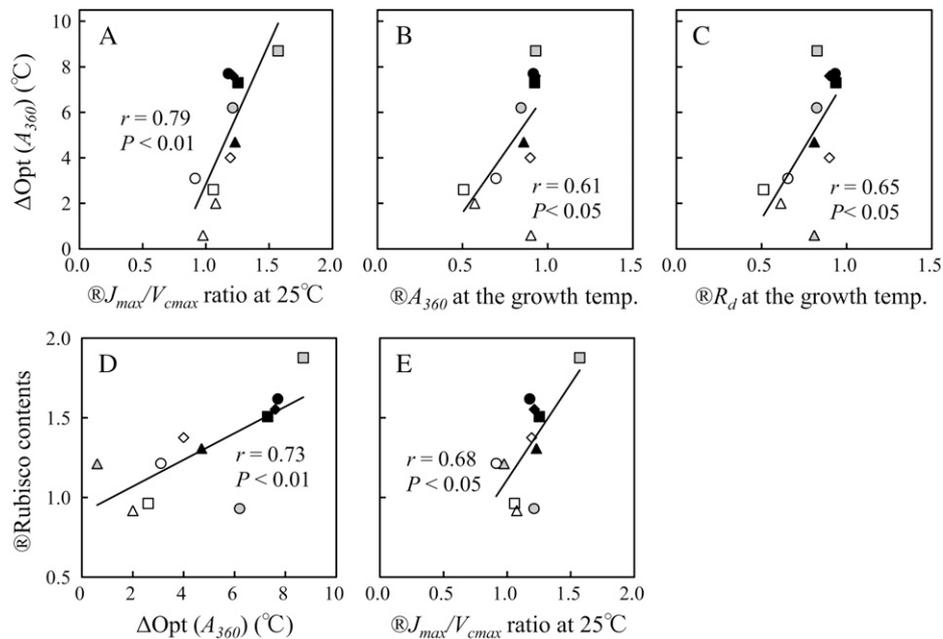


Figure 5. Relationships between $\Delta\text{Opt}(A_{360})$ and $J_{\max}/V_{c\max}$ ratio at 25°C (A), between $\Delta\text{Opt}(A_{360})$ and A_{360} at the growth temperature (B), between $\Delta\text{Opt}(A_{360})$ and R_d at the growth temperature (C), between Rubisco contents and $\Delta\text{Opt}(A_{360})$ (D), and between Rubisco contents and $J_{\max}/V_{c\max}$ ratio at 25°C (E). $\Delta\text{Opt}(A_{360})$ is the difference in the optimum temperature for the Opt (A_{360}) depending on growth temperature, A_{360} (or R_d) at growth temperature is the ratio of A_{360} (or R_d) measured at 15°C in 15°C plants to that measured at 30°C in 30°C plants, $J_{\max}/V_{c\max}$ ratio at 25°C is the ratio of $J_{\max}/V_{c\max}$ for 15°C plants to that for 30°C plants at 25°C, and Rubisco content is the ratio of Rubisco content for 15°C plants to that for 30°C plants. Cold-sensitive species are *C. sativus* (white circles), *N. tabacum* (white triangles), *O. sativa* (white squares), and *S. lycopersicum* (white diamonds); cold-tolerant species are *S. cereale* (black circles), *Solanum tuberosum* (gray circles), *S. oleracea* (gray squares), *T. aestivum* (spring; black squares), *T. aestivum* (winter; black diamonds), *Triticosecale* (black triangles), and *V. faba* (gray triangles). The correlation lines are shown. Values are means; $n = 3$ to 5.

large extent of flexibility in its temperature acclimation of photosynthesis. *S. lycopersicum* is relatively tolerant of low temperature for a cold-sensitive species (Yamori et al., 2009b), but variation in cold tolerance has been reported for a given species (Brüggemann and Linger, 1994; Saruyama and Tanida, 1995; Yu et al., 2002).

Growth temperature-dependent changes in optimum photosynthetic temperature were greater in plants native to desert habitats than in plants native to coastal habitats (Björkman et al., 1975; Pearcy, 1977; Mooney et al., 1978) and were greater in temperate evergreen species than in tropical evergreen species (Hill et al., 1988; Read, 1990; Cunningham and Read, 2002). They suggested that these differences in the phenotypic plasticity were attributed to the extent of the daily and seasonal temperature variations. However, our study clearly shows that the inherent ability of photosynthetic temperature acclimation differed depending on the cold tolerance. Cold-tolerant species were not only able to survive stressful low temperature conditions (i.e. chilling and freezing; Thomashow, 1998, 1999) but were also able to photosynthetically acclimate to low growth temperatures, allowing the plants to perform efficient photosynthesis and maintain their growth.

In this study, we selected two growth temperatures, 15°C/10°C and 30°C/25°C. It may be that cold-sensitive species have a greater capacity for photosynthetic acclimation to growth temperatures higher than 30°C/25°C compared with cold-tolerant species. Further studies are necessary to reveal differences in the inherent capacity for photosynthetic temperature acclimation to high temperatures between cold-sensitive and cold-tolerant species.

What Determines the Temperature Dependence of Photosynthesis?

The limiting step of A_{360} differed depending on plant species and growth temperature (Figs. 2 and 3; Supplemental Fig. S1) and could be classified into three groups: type 1, A_{360} is limited by A_c at all temperatures; type 2, A_{360} is colimited by A_c and A_r or the limiting step changes depending on measurement temperature; and type 3, A_{360} is limited by A_r at all temperatures (Fig. 3). It has been reported that the C_i affects the temperature dependence of A_{360} (Yamori et al., 2006a). Although C_i was slightly lower in 15°C plants than in 30°C plants, the differences in C_i between plant species and between growth temperatures were generally small (Table I; Supplemental Fig. S1).

Differences in the limiting step of A_{360} depending on plant species and growth temperature were attributable to differences in the J_{\max}/V_{cmax} ratio, which may be a result of different nitrogen partitioning within the photosynthetic apparatus. Cold-tolerant species grown at 15°C had much higher J_{\max}/V_{cmax} ratio than cold-sensitive species grown at either 30°C or 15°C (Table I; Fig. 3; Supplemental Table S1), suggesting that they invested more nitrogen in RuBP regeneration processes (electron transport, ATP synthase, and Calvin cycle except for Rubisco) than in Rubisco. As a result, in cold-tolerant species grown at 15°C, A_{360} tended to be limited by A_c at all temperatures, with Opt (A_{360}) determined by its temperature dependence. Additionally, in cold-tolerant species grown at high temperatures, Opt (A_{360}) was also determined by the temperature dependence of A_c . However, in cold-sensitive species, A_{360} tended to be limited by A_r at all temperatures, with Opt (A_{360}) determined by its temperature dependence. In cold-tolerant species, Opt (A_c) greatly altered depending on growth temperature, whereas in cold-sensitive species, Opt (A_r) altered only slightly. Therefore, the differences in the limiting step of A_{360} at the optimum temperature and the plasticity in parameters with respect to growth temperature caused interspecific differences in Opt (A_{360}).

It has been suggested that the shift in Opt (A_{360}) with growth temperature is determined by a shift in the intersection between the temperature dependences of A_c and A_r (Fig. 1, C and F; Farquhar and von Caemmerer, 1982). Although the intersection of A_c and A_r was similar to Opt (A_{360}) in some plant species (Figs. 3 and 4), there was little evidence that the intersection of A_c and A_r determined Opt (A_{360}) at both growth temperatures or that the limiting step of A_{360} at the optimum drastically altered depending on growth temperature (e.g. from A_c to A_r and vice versa). Thus, we conclude that alterations in nitrogen partitioning (i.e. J_{\max}/V_{cmax} ratio) did not contribute to the shift of the Opt (A_{360}) with growth temperature in this study.

Both A_c and A_r have been suggested to limit photosynthetic rate at high temperature; one study indicated that heat-induced Rubisco deactivation limits photosynthesis at high temperature (Salvucci and Crafts-Brandner, 2004a), while another indicated that electron transport limits photosynthesis (Sage and Kubien, 2007). If the limiting step of photosynthesis at a certain temperature were identical among species, every species would have a similar CO_2 dependence of photosynthetic rate. In this study, however, CO_2 dependence differed among species (Fig. 2; Supplemental Fig. S2), suggesting that the limiting step of photosynthesis differs between species, even at high temperatures. Interestingly, our observation that the limiting step differs between cold-sensitive and cold-tolerant species may partly explain the different conclusions between the above-mentioned studies. Previous studies showed that decreases in the photosynthetic rate at high temperature were determined by A_c in cold-

tolerant species, such as *Spinacia oleracea* (Weis, 1981; Yamori et al., 2005, 2006a, 2006b, 2008), *Triticum aestivum* (Kobza and Edwards, 1987; Law and Crafts-Brandner, 1999), and *Deschampsia antarctica* (Salvucci and Crafts-Brandner, 2004b), and by A_r in cold-sensitive species, such as *Gossypium barbadense* (Schrader et al., 2004; Wise et al., 2004), *Ipomoea batatas* (Cen and Sage, 2005), and *O. sativa* (Makino and Sage, 2007). Salvucci and Crafts-Brandner (2004b) showed that the optimum temperature for Rubisco activase activity was 10°C lower in plants from cold regions (*D. antarctica*, *Lysipomia pumila*, and *S. oleracea*) than in plants from warm regions (*Larrea tridentate*, *N. tabacum*, *Simmondsia chinensis*, and *Gossypium hirsutum*). These facts may suggest a generality that the limiting step of photosynthesis at high temperature differs between cold-sensitive and cold-tolerant species.

In this study, we used Rubisco kinetic parameters reported by Bernacchi et al. (2001); however, the possibility that Rubisco kinetic parameters are species specific should be borne in mind. Then, we performed sensitivity analyses of the limiting step of A_{360} (Supplemental Fig. S3) and analyzed the effects of Rubisco kinetic parameters on the limiting step of A_{360} using three different Rubisco kinetic parameters: (1) the Rubisco kinetic parameters obtained from Bernacchi et al. (2001); (2) the Rubisco kinetic parameters multiplied by 1.15; and (3) the Rubisco kinetic parameters multiplied by 0.85. The limiting step of A_{360} showed similar results, irrespective of the Rubisco kinetic parameters used (Supplemental Fig. S3). Moreover, we also analyzed the effects of mesophyll conductance (g_m) on the limiting step of A_{360} under two assumptions: (1) infinite g_m and (2) finite g_m . When we analyzed the limiting step of A_{360} with assumption of infinite g_m , we used Rubisco kinetic parameters from Bernacchi et al. (2001). However, when we took account of g_m , we used Rubisco kinetic parameters and g_m from Bernacchi et al. (2002). The g_m at 25°C was estimated with an assumed relationship between g_m and the photosynthetic rate (A) at 25°C ($g_m = 0.012 \times A$; Evans and von Caemmerer, 1996) and applied it to the temperature dependence (Bernacchi et al., 2002). Although under assumptions with finite g_m A_{360} tended to be limited by A_r at lower temperatures, the limiting step of A_{360} was similar, irrespective of whether an infinite or finite g_m was posited. Therefore, we conclude that our analyses of the limiting step of A_{360} are robust.

At low temperature, Pi regeneration capacity often limits photosynthetic rate (Sharkey, 1985; Sage and Sharkey, 1987; Labate and Leegood, 1988; Cen and Sage, 2005; Sage and Kubien, 2007). When the cold-sensitive species *N. tabacum* and *S. lycopersicum* were grown at 30°C, Pi regeneration capacity limited A_{360} at temperatures below 15°C (Figs. 2 and 3; Supplemental Fig. S2), suggesting that cold-sensitive species tended to be limited by Pi regeneration capacity at low temperature compared with cold-tolerant species but that the limitation by Pi regeneration capacity at low

temperature was not necessarily common even in cold-sensitive species grown at 30°C.

The Balance between RuBP Carboxylation and Regeneration at the Growth Temperature

The limiting step of A_{360} at the growth temperature was different depending on plant species and growth temperature (Figs. 2 and 3; Supplemental Fig. S2). Hikosaka (1997) predicted that the optimal photosynthetic rate at the growth temperature could be achieved under conditions where colimitation by A_c and A_r occurs, since this will allow for the maximally efficient use of nitrogen in the production of photosynthetic proteins. In some of the cold-tolerant species grown at 30°C and the cold-sensitive species grown at 15°C, A_{360} at the growth temperature was colimited by A_c and A_r . However, colimitation of A_c and A_r at the growth temperature was not realized in others. In some of the cold-tolerant species grown at 15°C, A_{360} at the growth temperature was solely limited by A_c , while in some of the cold-sensitive species grown at 30°C, A_{360} was solely limited by A_r . This suggests the existence of constraints on nitrogen partitioning among the photosynthetic apparatus and implies that nitrogen investment may not always be optimal in the natural habitat.

Growth temperature affects nitrogen partitioning in the photosynthetic apparatus (Hikosaka, 2005; Onoda et al., 2005a; Yamori et al., 2005), although these changes are not observed in every species (Onoda et al., 2005b; Atkin et al., 2006; Ishikawa et al., 2007). We found that the J_{\max}/V_{\max} ratio, which is a measure of the balance between A_r and A_c , increased with decreasing growth temperature, and the extent was greater in cold-tolerant species. Rubisco content was also found to significantly increase with decreasing growth temperature (Yamori et al., 2009b). This suggests that with decreasing growth temperature, while Rubisco content increased, proteins related to RuBP regeneration increased to a greater extent. Thus, the process of RuBP regeneration is more responsive to growth temperature than that of RuBP carboxylation. Photoinhibition at low temperature occurs in many species, and the extent of cold-induced photoinhibition differs depending on the cold tolerance (Koroleva et al., 1994; Park et al., 1995; Bertin et al., 1997). A higher J_{\max}/V_{\max} ratio in cold-tolerant species grown at low temperature would reduce excess excitation energy by providing a greater sink for photosynthetic electron transport, thereby avoiding photoinhibition in its natural habitat, where temperature and light intensity vary greatly both daily and seasonally (Hikosaka et al., 2006).

Our results were contrary to those of Bunce (2000), who concluded that the balance between A_r and A_c was roughly constant irrespective of growth temperature and plant species. In cool climate species, the balance seems to change with growth temperature (figure 5 in Bunce, 2000). Therefore, it is fair to say that

the response of the balance between A_r and A_c to growth temperature would be species specific.

Some species have been shown to alter their J_{\max}/V_{\max} ratio in response to growth light intensity (Evans, 1996; Poorter and Evans, 1998; Evans and Poorter, 2001), whereas others did not (Makino et al., 1997; Hikosaka, 2005; Yamori et al., 2009a). It is possible that there is interspecific variation in the response of J_{\max}/V_{\max} to the growth light intensity. In this study, we grew plants in a laboratory environment. Therefore, it will be important to analyze plants grown under natural conditions and analyze seasonal effects in order to clarify photosynthetic responses to growth temperature under natural conditions.

Syndrome of Temperature Acclimation of Photosynthesis

It is known that plants exhibit a set of characteristic responses to growth irradiance. For example, when plants are grown under shade conditions, plants develop longer internodes and petioles, produce broader, thinner leaves, and reduce the chlorophyll *a/b* ratio, photosynthetic capacity, and respiratory capacity (Smith, 1982; Smith and Whitelam, 1997; Kim et al., 2005). In this study, we found that cold-tolerant species that could greatly change Opt (A_{360}) depending on growth temperature exhibited considerable plasticity in other photosynthetic parameters; when the growth temperature decreased from 30°C to 15°C, these species decreased Opt (A_{360}) and increased J_{\max}/V_{\max} ratio, LMA, N_{area} , and Rubisco content, leading to a greater ability for temperature homeostasis of R_d and A_{360} (Fig. 5; Yamori et al., 2009b). Therefore, plants exhibiting considerable plasticity in a certain parameter also showed great plasticity in other parameters. This set of responses may be regarded as a “syndrome” of temperature acclimation. Alteration of all the parameters, which are independently regulated, may play an important role in a plant’s temperature acclimation. Natural selection might favor plasticity in these traits for success in changing environments.

CONCLUSION

We have demonstrated interspecific variation in photosynthetic temperature acclimation among plants with different cold tolerances. Cold-tolerant species drastically altered their Opt (A_{360}) depending on growth temperature, whereas cold-sensitive species were less plastic. There were differences in the limiting step of A_{360} at optimum temperatures and in the plasticity of the photosynthetic limiting step to growth temperature between cold-tolerant and cold-sensitive species. Cold-tolerant plants showed more flexibility in many photosynthetic parameters concerned with temperature acclimation (syndrome of temperature acclimation of photosynthesis). Thus, differences in the extent of plasticity for all of the photosynthetic parameters with respect to growth temperature

caused interspecific differences in photosynthetic temperature acclimation between cold-tolerant and cold-sensitive species.

To facilitate increases in crop yield and to increase tolerance of severe growth environments, genetic manipulation of photosynthesis has become a key target for improvement (Dunwell, 2000; Richards, 2000; Raines, 2006). What determines the maximum photosynthetic rate? Our data indicate that there is no single answer to this question. Even in a single plant species, the limiting step of photosynthesis differed depending on growth and measurement temperatures. Therefore, this study strongly suggests that the impact on the control of carbon fixation by manipulation of one enzyme would differ depending on plant species and growth conditions. More attention should be paid to studying differences in the photosynthesis-limiting step depending on species and growth conditions, as this might provide opportunities for achieving faster improvements in crop production.

MATERIALS AND METHODS

Plant Materials and Growth Conditions

Studies were conducted on 11 herbaceous crop species as described previously (Yamori et al., 2009b). For cold-sensitive species, *Cucumis sativus* (cucumber), *Nicotiana tabacum* (tobacco), *Oryza sativa* (rice), and *Solanum lycopersicum* (tomato) were examined, while for cold-tolerant species, *Secale cereale* (winter rye), *Spinacia oleracea* (spinach), *Solanum tuberosum* (potato), *Triticum aestivum* (spring wheat), *Triticum aestivum* (winter wheat), *Triticosecale* (triticale), and *Vicia faba* (broad bean) were selected. Day and night lengths were 8 and 16 h, respectively. Photosynthetically active photon flux density during the daytime was $250 \mu\text{mol m}^{-2} \text{s}^{-1}$. The day/night air temperatures were either 30°C/25°C or 15°C/10°C, and the relative humidity was 65%. The plants grown at 30°C/25°C and 15°C/10°C are called 30°C plants and 15°C plants, respectively.

Gas-Exchange Measurements

Temperature dependence of the R_d and A at a light intensity of $1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$ was measured at 5°C intervals from 10°C to 35°C and at 38°C using the most recently fully expanded leaves, as described previously (Yamori et al., 2005). The vapor pressure deficit was less than 1.0 kPa at 10°C to 30°C and less than 3.0 kPa at 35°C and 38°C. CO_2 dependence of A was examined based on measurements at CO_2 concentrations in the ambient air (C_a) of 50, 100, 150, 200, 360, and $1,500 \mu\text{L L}^{-1}$ (LI-6400; LI-COR). At each CO_2 concentration, A and C_i were calculated. The optimum temperature for the photosynthetic parameters was derived from cubic curves that were fitted to the data in Excel (Microsoft).

The limiting steps of the photosynthetic rate were analyzed based on their $A-C_i$ curves using the C_3 photosynthesis model (see Supplemental Appendix S1) according to Atkin et al. (2006), Ishikawa et al. (2007), and Makino and Sage (2007). Curve fitting of the $A-C_i$ curve was performed with Kaleidagraph (Synergy Software). The V_{cmax} and A_c were estimated from the photosynthetic rate at low CO_2 concentrations ($<200 \mu\text{L L}^{-1}$), whereas the J_{max} and the A_r were estimated from the photosynthetic rate at $1,500 \mu\text{L L}^{-1}$ (Farquhar et al., 1980; von Caemmerer, 2000). We used the temperature dependence of Rubisco kinetic parameters that were obtained at leaf temperatures of 10°C to 40°C in *N. tabacum* (Bernacchi et al., 2001). We theoretically derived ratios of A_c at 360 $\mu\text{L L}^{-1}$ CO_2 concentration (A_{360}) to A_{200} using Equation 2 in Supplemental Appendix S1. If the measured A_{360}/A_{200} ratio is equal to the A_{c360}/A_{c200} ratio, it indicates that A_{360} is limited by A_c ($A_{360} = A_{c360}$). If the A_{360}/A_{200} ratio is lower than the A_{c360}/A_{c200} ratio, it indicates that A_{360} is limited by A_r (or Pi regeneration limitation). Also, we derived the ratio of A_r at $1,500 \mu\text{L L}^{-1}$ CO_2 concentration (A_{r1500}) to A_{360} using Equation 3 in Supplemental Appendix S1. If the A_{r1500}/A_{360} ratio is equal to the A_{r1500}/A_{360} ratio, it indicates that

A_{360} is limited by A_r ($A_{360} = A_{r360}$), whereas if the A_{r1500}/A_{360} ratio is higher than the A_{r1500}/A_{r360} ratio, it indicates that A_{360} is limited by A_c . If photosynthesis is limited by Pi regeneration (triose phosphate utilization), the A_{1500}/A_{360} ratio becomes 1 (Sage, 1990).

Biochemical Analyses

Immediately after gas-exchange measurements, leaf discs were frozen and stored at -80°C until biochemical analysis. The content of Rubisco was determined by the method of Yamori et al. (2005). The frozen leaf sample was ground in liquid nitrogen and homogenized in an extraction buffer containing 100 mM sodium phosphate buffer (pH 7.0), 1.0% (w/v) polyvinylpyrrolidone, 0.1% (v/v) Triton X-100, 1 mM phenylmethylsulfonyl fluoride, and 1.0% β -mercaptoethanol.

For determinations of enzyme activities of Rubisco and NAD-ME, the frozen leaf sample was rapidly homogenized in a chilled mortar and pestle with extraction buffer containing 100 mM HEPES-KOH (pH 7.8), 10 mM MgCl_2 , 5 mM dithiothreitol, and 1 mM EDTA. The homogenate was centrifuged at $16,000g$ for 30 s at 4°C, and the maximal Rubisco activity of the supernatant was determined by monitoring NADH oxidation at 340 nm, according to the method of Yamori et al. (2006b). After Rubisco was activated for 20 min at 4°C in an activation medium that contained 375 mM HEPES-KOH (pH 7.8), 50 mM MgCl_2 , and 50 mM NaHCO_3 , the total activity was assayed in an assay medium containing 100 mM Bis-Tris-KOH (pH 8.2), 20 mM MgCl_2 , 20 mM NaHCO_3 , 5 mM ATP, 5 mM creatine phosphate, 60 μM NADH, 0.6 mM RuBP, 10 units mL^{-1} creatine kinase, 10 units mL^{-1} 3-phosphoglyceric phosphokinase, and 25 units mL^{-1} glyceraldehyde-3-phosphate dehydrogenase. The k_{cat} was calculated from the Rubisco activity and content. The maximal NAD-ME activity was assayed according to Millar et al. (1998) in a reaction medium consisting of 50 mM MOPS-KOH (pH 6.5), 2 mM NAD^+ , 0.025% (v/v) Triton X-100, 2 mM MnCl_2 , 4 mM dithiothreitol, and 10 mM malate.

The leaf dry mass and nitrogen contents were determined on leaf discs taken after the gas-exchange measurements. The leaf discs were dried at 70°C for at least 7 d, and then leaf nitrogen contents were measured with an NC analyzer (CHNOS Elemental Analyzer, Vario EL III; Elementar).

Statistical Analyses

To evaluate whether the inherent ability of temperature acclimation of photosynthesis is different between cold-sensitive and cold-tolerant species, we used a repeated-measures ANOVA by STATVIEW (version 4.58; SAS Institute). Individual data from each plant species were used.

Principal component analysis was conducted with a program provided at <http://aoki2.si.gunma-u.ac.jp/lecture/stats-by-excel/vba/html/pca.html>.

Supplemental Data

The following materials are available in the online version of this article.

Supplemental Figure S1. Temperature dependence of R_d , A_{360} , and C_i .

Supplemental Figure S2. Analyses of limiting steps of A_{360} .

Supplemental Figure S3. Effects of Rubisco kinetics and mesophyll conductance on the limiting step of A_{360} .

Supplemental Table S1. Opt (A_{360}), Opt (A_c), Opt (A_r), and $J_{\text{max}}/V_{\text{cmax}}$ at 25°C and C_i at 25°C.

Supplemental Appendix S1. C_3 photosynthesis model.

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