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Climatic warming changes plant photosynthesis and its temperature dependence in a temperate steppe of northern China

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Abstract

Warming responses of photosynthesis and its temperature dependence in two C₃ grass (*Agropyron cristatum*, *Stipa krylovii*), one C₄ grass (*Pennisetum centrasiatum*), and two C₃ forb (*Artemisia capillaris*, *Potentilla acaulis*) species in a temperate steppe of northern China were investigated in a field experiment. Experimental warming with infrared heater significantly increased daily mean assimilation rate (*A*) in *P. centrasiatum* and *A. capillaris* by 30 and 43%, respectively, but had no effects on other three species. Seasonal mean *A* was 13, 15, and 19% higher in the warmed than control plants for *P. centrasiatum*, *A. capillaris*, and *S. krylovii*, respectively. The mean assimilation rate in *A. cristatum* and *P. acaulis* was not impacted by experimental warming. All the five species showed photosynthetic acclimation to temperature. The optimum temperature for photosynthesis (*T*_{opt}) and the assimilation rate at *T*_{opt} in the five species increased by 0.33–0.78 °C and 4–27%, respectively, under experimental warming. Elevated temperature tended to increase the maximum rate of ribulose-1,5-bisphosphate (RuBP) carboxylation (*V*_{cm_{max}}) and the RuBP regeneration capacity (*J*_{max}) in the C₃ plants and carboxylation efficiency and the CO₂-saturated photosynthetic rate in the C₄ plant at higher leaf temperature, as well as the optimum temperatures for the four parameters. Our results indicated that photosynthetic responses to warming were species-specific and that most of the species in the temperate steppe of northern China could acclimate to a warmer environment. The changes in the temperature dependence of *V*_{cm_{max}} and *J*_{max}, as well as the balance of these two processes altered the temperature dependence of photosynthesis under climatic warming.

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1. Introduction

Photosynthesis is the fundamental basis for carbon (C) accumulation, growth, and biomass production of plants. Photosynthetic responses to rising global mean temperature of terrestrial plants can potentially alter ecosystem C balance and cycling (Gunderson et al., 2000; Rustad et al., 2001). Previous studies have shown that climatic warming may directly stimulate (Chapin and Shaver, 1996; Apple et al., 2000), restrain indirectly through warming-induced water stress (Callaway et al., 1994; Roden and Ball, 1996; Pearson and Dawson, 2003), or do not impact photosynthesis of plant species (Nijs et al., 1996; Loik et al., 2000; Starr et al., 2000; Llorens et al., 2003, 2004). The inconsistent observations suggest plant photosynthe-

sis in response to climatic warming might be species specific. Differential responses of photosynthesis to rising temperature could change C accumulation, growth, and biomass production of different plant species, which in turn affects their competitive abilities, coverage, and dominance in the community. Therefore, a better understanding of the responses of photosynthesis in different plant species and/or functional types to increased temperature could help predict the potential changes in species composition and ecosystem C cycling under global warming.

Long-term exposure to changes in temperature can result in plant acclimation. Thermal acclimation of photosynthesis refers to the shift in the photosynthesis-temperature relationship of plants under the altered temperature regime (Billings et al., 1971; Berry and Björkman, 1980). By changing the optimum temperature of photosynthesis, plants can keep efficient photosynthesis at the new growth temperature (Berry and Björkman, 1980). Most studies on thermal acclimation of photosynthesis were

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conducted in the laboratory with constant temperature regimes (Gunderson et al., 2000; Xiong et al., 2000; Bolstad et al., 2003; Yamori et al., 2005). However, there are strong seasonal and diurnal variability in the magnitudes of temperature increase under global warming (IPCC, 2007). Therefore, consistent changes in temperature used in the laboratory are obviously unable to simulate the realistic temperature changes under natural conditions (Loik et al., 2000; Llorens et al., 2004).

Various hypotheses have been proposed to clarify the mechanisms of temperature acclimation in photosynthesis (Hikosaka et al., 1999). According to the models of Farquhar et al. (1980) and Farquhar and Von Caemmerer (1982), the balance between carboxylation (V_{cmax}) and regeneration (J_{max}) of ribulose-1,5-bisphosphate (RuBP) determines the temperature dependence of photosynthesis. Experimental evidences have shown that seasonal temperature variations can alter the balance between V_{cmax} and J_{max} (Hikosaka et al., 1999; Bunce, 2000; Wilson et al., 2000; Onoda et al., 2005a,b; Borjigidai et al., 2006). Therefore, we hypothesize that warming will shift the balance between V_{cmax} and J_{max} , which will potentially contribute to the changes in temperature dependence of photosynthesis under climatic warming.

The temperate steppe in northern China represents the regional vegetation in the vast arid and semiarid area across the Eurasian continent and is predicted to be sensitive to climate change (Christensen et al., 2004). This study was conducted to examine warming effect on the photosynthesis and its temperature dependence in the co-existing C_3 and C_4 plants in the temperate steppe of northern China. Two C_3 grass (*Agropyron cristatum*, *Stipa krylovii*), two C_3 forb (*Artemisia capillaris*, *Potentilla acaulis*), and one C_4 grass species (*Pennisetum centrasiatum*) that co-occur in a temperate steppe of northern China were planted under the ambient and elevated temperatures manipulated with an infrared heater in the field. Our specific objectives are to address the following questions: (1) how does climatic warming affect photosynthesis of different plant species in the temperate steppe of northern China? (2) does photosynthesis of different species acclimate to climatic warming and to what extent? (3) what biochemical mechanisms are involved in the changes in temperature dependence of photosynthesis? Given the intrinsic differences in ecophysiology among species, we hypothesize that effects of climatic warming on plant photosynthesis and its temperature dependence are dependent on species identity.

2. Materials and methods

2.1. Study site

The study was carried out in Duolun County ($42^{\circ}2'N$, $116^{\circ}17'E$), a semiarid area located in Inner Mongolia, China. Mean annual precipitation in this area is 385.5 mm, with peaks in July and August. Mean monthly air temperatures ranges from $18.9^{\circ}C$ in July and $-17.5^{\circ}C$ in January, with an annual mean temperature of $2.1^{\circ}C$. The soil could be classified as chestnut soils (Chinese classification) or Calcic-orthic Aridisol in the US Soil Taxonomy classification, with

$62.75 \pm 0.04\%$ sand, $20.3 \pm 0.01\%$ silt, and $16.95 \pm 0.01\%$ clay. Mean bulk density is 1.31 g cm^{-3} and pH value is 6.84 ± 0.07 . The predominant species are *Stipa krylovii*, *Agropyron cristatum*, *Artemisia capillaris*, *Potentilla acaulis*, and *Cleistogenes squarrosa*, which grow in mixture with the mean density of 200–300 individuals/ m^2 .

2.2. Experimental design

Two $3 \text{ m} \times 4 \text{ m}$ plots were dug to a depth of 0.45 m. One plot was heated continuously using the infrared heater and the other was the control. One $1.65 \text{ m} \times 0.15 \text{ m}$ infrared heater (Kalglo Electronics Inc, Bethlehem, Pennsylvania) was suspended 2.25 m above the ground in the warmed plot. Soil temperatures were spatially uniform in the warmed plots in this study and were also reported in a previous study (Wan et al., 2002). In the control plot, one “dummy” heater with the same shape and size as the infrared heater was suspended 2.25 m high to simulate the shading effects of the heater. The distance between the control and the warmed plot was approximately 5 m to avoid heating the control plot by the infrared heater. Soil temperature was measured by a Longstem Thermometer 6310 (Spectrum Technologies Inc., Plainfield, USA) and soil volumetric water moisture was measured by a Diviner 2000 Portable Soil Moisture Probe (Sentek Pty Ltd., Balmain, Australia).

2.3. Plant materials

Two C_3 grass (*Stipa krylovii*, *Agropyron cristatum*), two C_3 forb (*Artemisia capillaris*, *Potentilla acaulis*) and one C_4 grass species (*Pennisetum centrasiatum*) that co-occur in a temperate steppe of northern China were selected. Seedlings with similar size were transplanted from a nearby field to PVC tubes in the middle May 2005. PVC tubes (11 cm in internal diameter and 50 cm in depth) were placed in the two $3 \text{ m} \times 4 \text{ m}$ plots, buried to the depth of 45 cm belowground, and filled with sieved and fully mixed chestnut soil. Two individuals of one species were planted per tube. Twenty tubes were replicated for one species in each plot. All the tubes were placed randomly in both the control and warmed plots. Two weeks after transplanting, the warmed plot was continuously heated (24 h day^{-1}) with an infrared heater till the end of the growing season (late September).

2.4. Photosynthesis and chlorophyll fluorescence measurements

An open gas-exchange system (Li-6400; Li-Cor, Inc., Lincoln, NE, USA) with a 6-cm^2 clamp-on leaf cuvette was used to measure gas exchange. Three tubes per species in each of the treatments were randomly selected for photosynthesis measurement. Two fully expanded leaves were measured in each tube and the two values were averaged as one replicate. Therefore, each data point in the figures represents the mean values of three replicates.

Diurnal patterns of gas exchange were measured from 6:00 to 18:00 with 2-h intervals on clear days in July and August. Air temperature (T_{air}), photosynthetic photo flux density (PPFD), and photosynthetic rate (A) were recorded.

The seasonal changes in assimilation rate were measured between 9:00 and 11:00 (local time) in the morning on clear days (18 June, 28 June, 15 July, 24 July, 3 August, 15 August, and 3 September). At each measuring date, leaf temperature was initially measured. The cuvette was applied to the leaf, and then temperature was held constant at the measured ambient level using the thermoelectric block within the cuvette. To avoid the differences in photosynthesis due to the changing PPFD levels during the growing season, leaves were illuminated at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ using the LED light system at each measuring date. Other environmental conditions within the cuvette were controlled to match the ambient conditions.

The maximum photochemical efficiency of PSII (F_v/F_m) was measured with a Li-6400-40 fluorescence attachment (Li-Cor, Lincoln, NE, USA). Leaves were dark-adapted before the measurement.

2.5. Leaf temperature response curves

The temperature response curves of A were determined by manually setting leaf temperature of the cuvette. Leaf temperature was set at 18°C , and then subsequently increased at 2°C intervals to 36°C with a range $\pm 8^\circ\text{C}$ at the ambient temperature. The cuvette was applied to the leaf and then temperature was held constant at each temperature level using the thermoelectric block within the cuvette. At each temperature, data were recorded only after photosynthetic rate reached a relatively constant level. This method has been used in Borjigidai et al. (2006). Leaves were illuminated at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ using the LED light source.

2.6. CO_2 concentration response curves

The relationship between net assimilation and CO_2 partial pressure ($A-C_i$ curve) was examined over a range of nine external CO_2 partial pressures (C_a) from approximately 50 to 1500 ppm. A constant PPFD of $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ was provided by a LED light source. Three response curves were recorded at 20°C , 28°C and 36°C leaf temperature, respectively. These three temperatures represent the temperature lower than, similar to, and higher than the optimal temperature, respectively. Leaf temperatures were maintained using thermoelectric coolers.

Analysis of $A-C_i$ response curves involved calculation of parameters potentially limiting to photosynthesis: V_{cmax} (maximum carboxylation rate of Rubisco) and J_{max} (RuBP regeneration capacity) in C_3 plant species. This was achieved using Photosynthesis Assistant (v1.1, Dundee Scientific, Dundee, UK) which uses a biochemical model describing photosynthetic rate (Farquhar et al., 1980). For the C_4 species *P. centrasiticum*, the efficiency of the PEP carboxylase CO_2 pump (CE) was determined from the slope of the linear portion of

the $A-C_i$ curve. The CO_2 -saturated assimilation rates (A_{sat}) was determined for *P. centrasiticum* as in Tissue et al. (1995) and Anderson et al. (2001).

2.7. Statistical analysis

Three-way ANOVA was used to examine the main and interactive effects of species, warming, and leaf temperature on temperature dependence of A , $V_{\text{c,max}}$, and J_{max} in the C_3 plants (SPSS 11.0 for windows, USA). The warming effect and its interaction with measuring time (or date) on diurnal A (or seasonal A) were analyzed by repeated measures ANOVA. CE and A_{sat} of the C_4 plants were analyzed by two-way ANOVA to get the warming effect and its interaction with the leaf temperature. Treatment means were compared by least significant difference to determine whether they were significantly different at the 0.05 probability level.

The photosynthesis data from temperature response curves were used to determine the temperature dependence. To estimate optimum temperature for photosynthesis (T_{opt}) and the photosynthetic rate at the optimum temperature (A_{opt}), photosynthesis-temperature response curves were fitted with a quadratic equation:

$$A = aT^2 + bT + c,$$

where A represents the mean net photosynthetic rate at temperature T in $^\circ\text{C}$. a , b , and c are the constants. $T_{\text{opt}} = -b/2a$, $A_{\text{opt}} = (4ac - b^2)/4a$.

3. Results

3.1. Diurnal patterns of assimilation rate (A)

After sunrise at approximately 6:00 am local time, PPFD increased rapidly, peaked between 10:00 and 14:00, and decreased thereafter. Air temperature (T_{air}) increased from morning (6:00), peaked from 12:00 to 14:00 in July and from 10:00 to 16:00 in August, and then declined (Fig. 1k and l).

The five species showed different diurnal patterns of photosynthesis in both July and August (Fig. 1). In July, assimilation rate (A) of the C_4 *Pennisetum centrasiticum* (*P. c*) increased from morning and peaked at 14:00 (Fig. 1a). The four C_3 plant species showed two-peak model with the peak values occurring at 10:00 and 16:00 in *Potentilla acaulis* (*P. a*) (Fig. 1c), *Agropyron cristatum* (*A. c*) (Fig. 1g), and *Artemisia capillaris* (*Ar. c*) (Fig. 1i), and at 10:00 and 14:00 in *Stipa krylovii* (*S. k*) (Fig. 1e). Warming increased peak A in *P. c*, *S. k*, and *Ar. c* and shifted it from 14:00 to 12:00 in *P. c* and from 10:00 to 8:00 in *A. c*. The main effect of warming on A was statistically significant in *P. c* (a 22% increase in daily mean A , $P < 0.05$), but not in other four species ($P > 0.05$).

In August, A of the control plants increased rapidly in the morning, maximized at 10:00 in *P. c*, *P. a*, and *A. c* (Fig. 1b, d and h), 14:00 in *S. k* and *Ar. c* (Fig. 1f and j), then gradually declined till 18:00. Warming increased the peak A in *P. c*, *P. a*, and *Ar. c* and shifted it from 10:00 to 14:00 in *P. a*. Within the diurnal cycle, the main effect of warming on A was significant

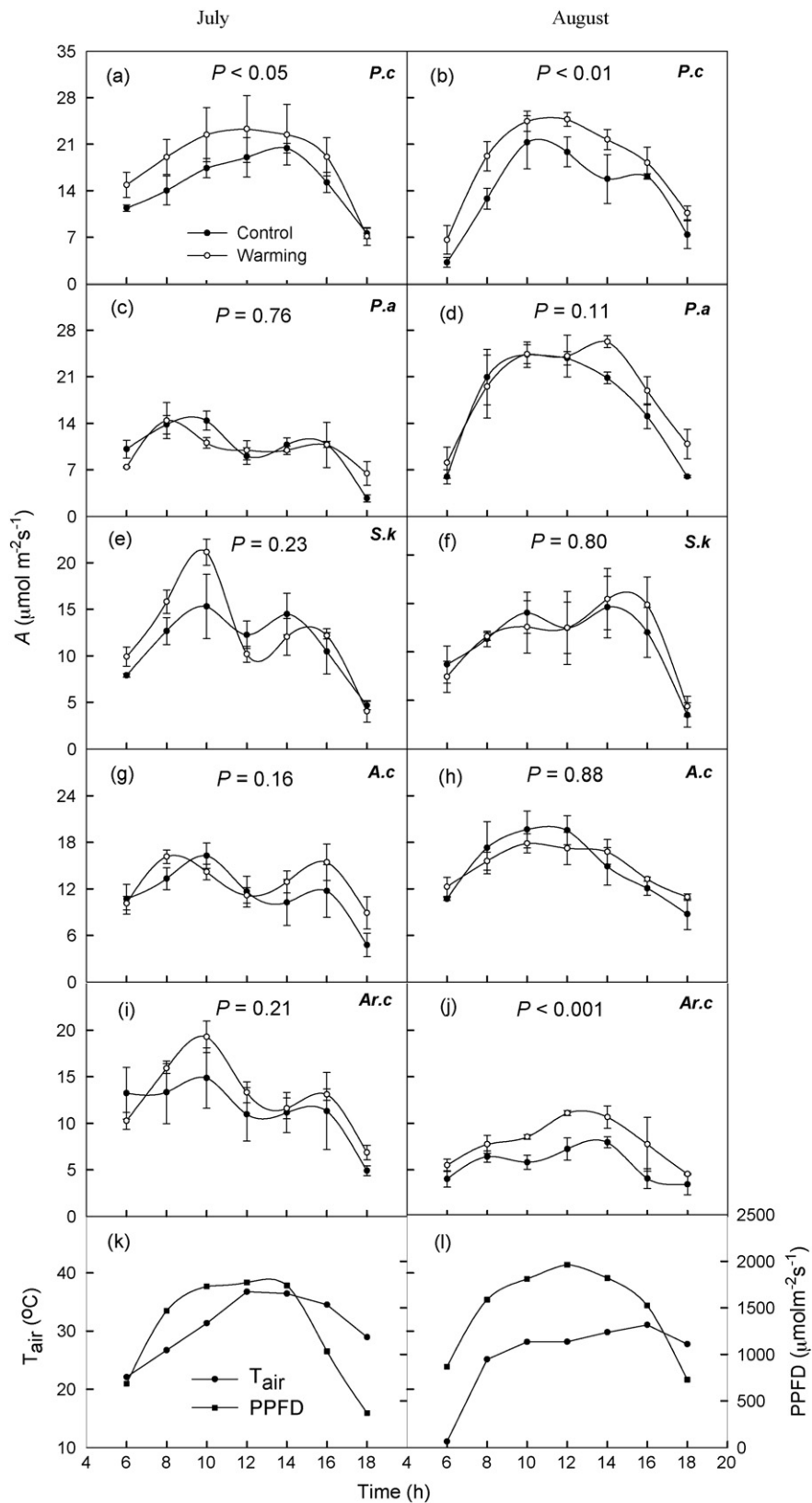


Fig. 1. Diurnal changes in assimilation rate (A) (mean \pm 1 S.E.) in *Pennisetum centrasiticum* (*P. c*) (a and b), *Potentilla acaulis* (*P. a*) (c and d), *Stipa krylovii* (*S. k*) (e and f), *Agropyron cristatum* (*A. c*) (g and h), *Artemisia capillaris* (*Ar. c*) (i and j) under the ambient and elevated temperatures, as well as the air temperature (T_{air}) and photosynthetic photo flux density (PPFD) (k and l) in July (left panels) and August (right panels). P -values represent the significance of warming effects on A in each species.

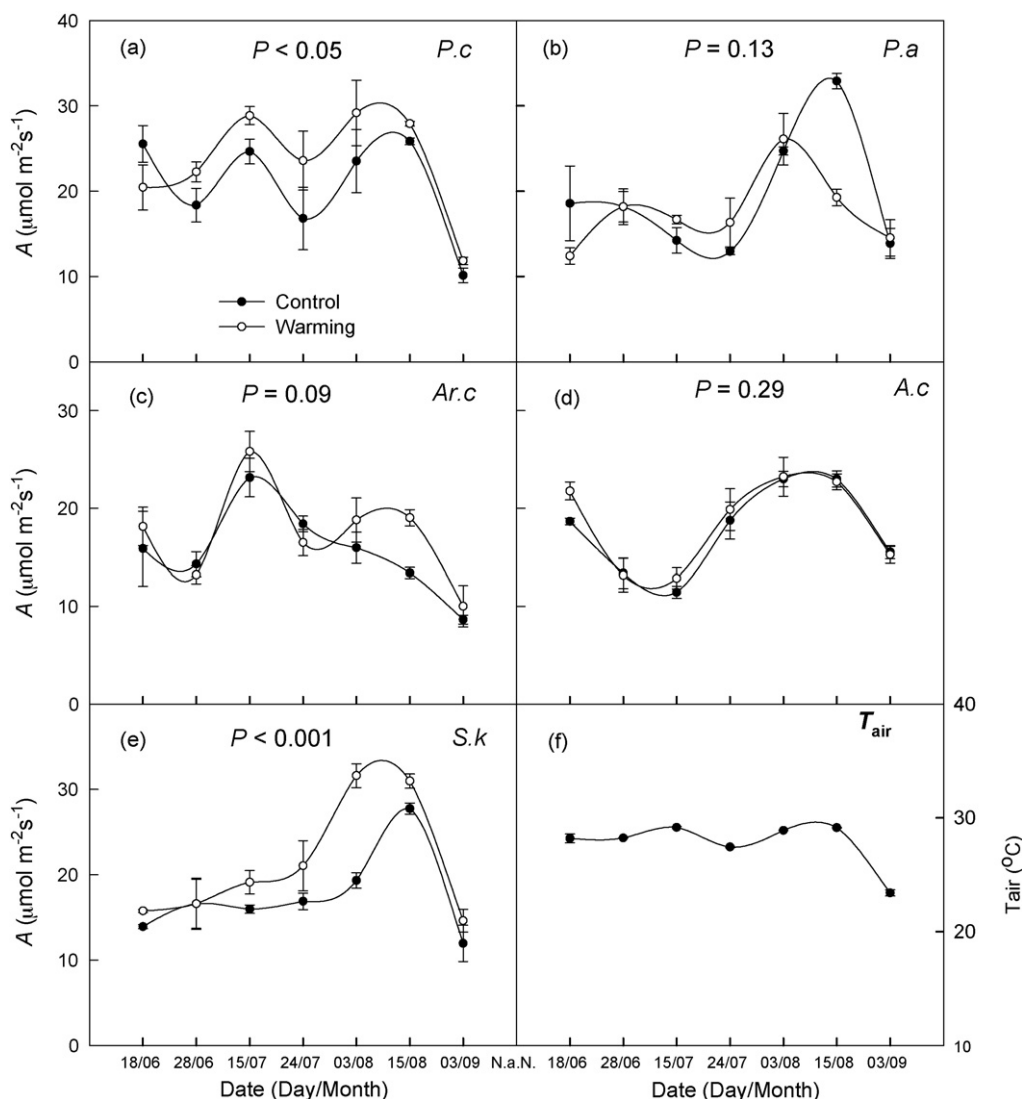


Fig. 2. Seasonal changes in air temperature (f) and assimilation rate (A) (mean \pm 1 S.E.) in *P. c* (a), *P. a* (b), *Ar. c* (c), *A. c* (d), and *S. k* (e) under the ambient and elevated temperatures. See Fig. 1 for species abbreviations. P -values represent the significance of warming effects on A in each species.

for *P. c* and *Ar. c* (Fig. 1b and j), but not for *P. a*, *S. k*, and *A. c* (Fig. 1d, f and h). Infrared heater increased daily mean A by 30 and 43% for *P. c* and *Ar. c*, respectively.

3.2. Seasonal changes in assimilation rate (A)

Over the entire experimental period, the infrared heater increased the mean soil temperature (10 cm) by 1.04 °C ($P < 0.001$), but reduced mean soil moisture (0–10 cm, v/v) by 7% ($P > 0.05$). Assimilation rate of the five species showed different seasonal patterns. Under the ambient temperature, the greater values of A over the growing season were observed on 18 June, 15 July, and 15 August in *P. c* (Fig. 2a), 15 August in *P. a* (Fig. 2b) and *S. k* (Fig. 2e), 15 July in *Ar. c* (Fig. 2c), and 3 August in *A. c* (Fig. 2d). With the lower temperature on 3 September (Fig. 2f), A of all the five species decreased substantially. Warming shifted the peak A to 3 August in *P. a*, and extended it from 3 August to 15 August in *S. k*, whereas the

peak A in the other three species was not affected by experimental warming. The seasonal mean A was 13, 19, and 15% higher in the warmed than control plants for *P. c*, *S. k* (Fig. 2a and e, $P < 0.05$), and *Ar. c* (Fig. 2c, $P = 0.09$), respectively. However, A showed little difference between the two temperature treatments in *P. a* and *A. c* (Fig. 2b and d).

3.3. Temperature response of assimilation rate

Warming and leaf temperature significantly affected A in both the C_3 and C_4 plants ($P < 0.001$, Table 1). Assimilation rate of the five species showed different temperature dependence (Fig. 3). The optimum temperature for A was 32.5 °C in *P. c* and 28.1 to 28.9 °C in other four species under ambient temperature (Table 2, Fig. 3). Warming increased the optimum temperatures (T_{opt}) for photosynthesis in all the five species by 0.14–0.50 °C. A at the optimum temperature (A_{opt}) has also been increased by warming for all the five species. The largest increase in A_{opt}

Table 1
Effects of species, warming, leaf temperature, and their interactions on assimilation rate (A), the maximum rate of RuBP carboxylation (V_{cmax}), and the RuBP regeneration capacity (J_{max}) for the C_3 plants by three-way ANOVA, and effects of warming, leaf temperature, and their interactions on carboxylation efficiency (CE) and the CO_2 -saturated photosynthetic rate (A_{sat}) for the C_4 plant by two-way ANOVA analysis

	A		V_{cmax} (CE)		J_{max} (A_{sat})	
	d.f.	F	d.f.	F	d.f.	F
C_3 plants						
Species	3	10.40***	3	10.09***	3	11.75***
Warming	1	37.79***	1	1.54	1	8.45**
Leaf temperature	11	16.52***	2	10.54***	2	7.72**
Species \times warming	3	1.62	3	0.88	3	0.46
Species \times leaf temperature	33	0.68	6	1.48	6	1.80
Warming \times leaf temperature	11	0.52	2	9.58***	2	3.98*
Species \times warming \times leaf temperature	33	0.39	6	1.12	6	0.72
C_4 plant						
Warming	1	34.44***	1	29.98***	1	8.66*
Leaf temperature	11	6.45***	2	5.74*	2	5.67*
Warming \times leaf temperature	11	0.1	2	0.01	2	1.19

(*), (**), and (***) statistically significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$.

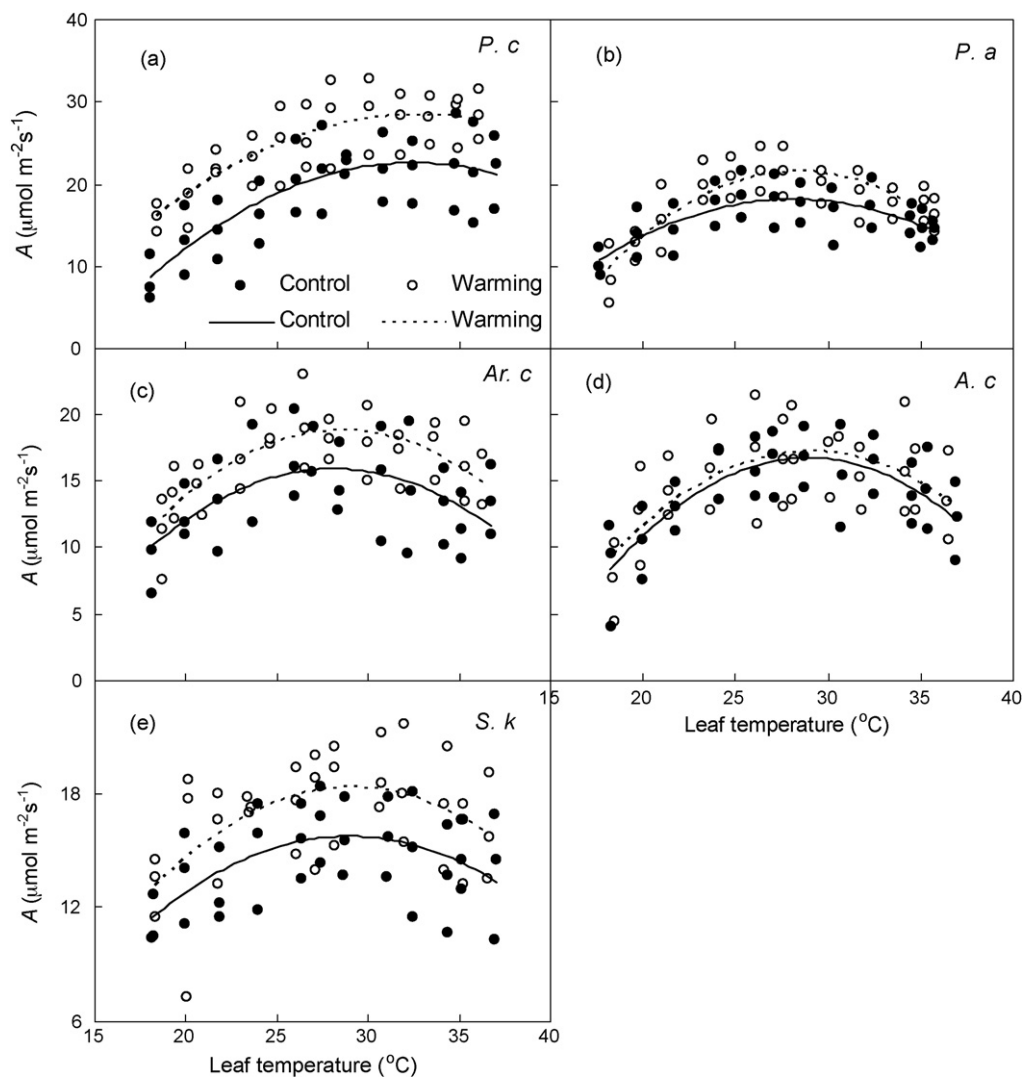


Fig. 3. Temperature responses of assimilation rate (A) (mean \pm I.S.E.) in *P. c* (a), *P. a* (b), *Ar. c* (c), *A. c* (d), and *S. k* (e) under the ambient and elevated temperature. See Fig. 1 for species abbreviations.

Table 2

The optimum temperature for assimilation rate (T_{opt}), the assimilation rate at the optimum leaf temperature (A_{opt}), and the determinant coefficient (r) of the correlation between A and leaf temperature for the five species under the ambient and warmer environment

Species	Treatment	T_{opt} (°C)	A_{opt} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	r
<i>P. c</i>	Control	32.46	22.66	0.77
	Warming	32.86	28.44	0.79
<i>P. a</i>	Control	28.10	18.15	0.68
	Warming	28.42	21.51	0.82
<i>Ar. c</i>	Control	28.10	15.88	0.54
	Warming	28.60	18.79	0.69
<i>A. c</i>	Control	28.95	16.71	0.74
	Warming	29.09	17.20	0.63
<i>S. k</i>	Control	28.95	15.76	0.52
	Warming	29.15	18.29	0.52

Abbreviations for species name: *Pennisetum centrasiticum* (*P. c*), *Potentilla acaulis* (*P. a*), *Artemisia capillaris* (*Ar. c*), *Agropyron cristatum* (*A. c*), and *Stipa krylovii* (*S. k*).

(26%) was observed in *P. c*, while the lowest (3%) was found in *A. c* (Table 2). A_{opt} of *P. a*, *Ar. c*, and *S. k* increased by 16–19% under the elevated comparing to ambient temperature (Table 2, Fig. 3).

3.4. Maximum carboxylation rate (V_{cmax}) and carboxylation efficiency (CE) at different leaf temperatures

The main effects on V_{cmax} of species and leaf temperature as well as the interactive effects of warming \times leaf temperature were all statistically significant in the C_3 plants (Table 1). All the four C_3 plants had the highest V_{cmax} at 20 °C in the control plants, but had the highest value at 28 °C under the elevated temperature (Fig. 4a–d). At 20 °C leaf temperature, V_{cmax} in *A. c*, *P. a*, *Ar. c*, and *S. k* in the warmed plants was lower than or similar with that in the control plants (Fig. 4a–d). By contrast, when measured at 28 °C or 36 °C leaf temperatures, all the species, except for *A. c* at 28 °C, showed 15–59% higher V_{cmax} in the warmed than control plants.

Warming and leaf temperature significantly affected CE in the C_4 plants ($P < 0.05$, Table 1). CE had the highest value at 36 °C leaf temperature in both the control and warmed plants. At 28 °C and 36 °C leaf temperature, CE was increased by 34–39% under the elevated temperature (Fig. 4e).

3.5. RuBP regeneration capacity (J_{max}) and CO_2 -saturated assimilation rate (A_{sat}) at different leaf temperature

Species, warming, leaf temperature, and the interactions of warming \times leaf temperature significantly impacted J_{max} in the C_3 plants (Table 1). Warming changed the temperature response of J_{max} in *A. c*, *P. a*, and *S. k* (Fig. 5a, b and d), but not in *Ar. c* (Fig. 5c). The highest J_{max} in *A. c*, *P. a*, and *S. k* was observed at 20 °C in the control plants but at 28 °C in the warmed plants (Fig. 5a, b and d). At 20 °C leaf temperature, J_{max} in the warmed plants had similar values with the control plants in all the four C_3

plants. Experimental warming increased J_{max} by 12–93% in all the C_3 plants at 28 °C and 36 °C leaf temperatures (Fig. 5a–d).

Warming and leaf temperature also significantly affected A_{sat} in the C_4 plants (Table 1). The highest A_{sat} in *P. c* was observed at 28 °C in the control plants but at 36 °C in the warmed plants. Warming increased A_{sat} in *P. c* by 21 and 31% at 20 °C and 36 °C leaf temperature, respectively (Fig. 5e).

There were positive correlations ($P < 0.05$) between V_{cmax} and J_{max} across the C_3 plants and leaf temperatures under both the ambient and elevated temperatures (Fig. 6). The relative value of $J_{\text{max}}/V_{\text{cmax}}$ (the slope of V_{cmax} vs. J_{max}) was higher in the warmed (5.19) than control plants (2.78).

4. Discussion

4.1. Warming effects on photosynthetic performance in different species

Warming effects on photosynthetic rates remain controversial. Some studies reported no changes in photosynthetic rates (Wookey et al., 1994; Nijs et al., 1996; Loik et al., 2000; Starr et al., 2000; Llorens et al., 2003, 2004) whereas others found decreases (Callaway et al., 1994; Roden and Ball, 1996; He and Dong, 2003) or increases in photosynthetic rates (Huxman et al., 1998; Apple et al., 2000; Shaw et al., 2000). Species-specific responses of photosynthesis to elevated temperature, as observed in our study (Fig. 2), might be largely responsible for the controversy. In addition, the effects of growth temperature on photosynthesis are often influenced by other interacting factors, such as drought, irradiance, and nutrient availability, etc. The different growth conditions might also contribute to the inconsistent results of warming effects among ecosystems. For example, soil water availability might regulate the photosynthetic response to warming. In our study, soil water content under both the temperature treatments was not stressful enough to reduce plant photosynthesis, which was reflected by the high predawn F_v/F_m values (Fig. 7). By contrast, the photosynthesis of *Erigeron speciosus* in a Rocky Mountain meadow under the warming treatment has been constrained by drier soil and lower leaf water potential induced by the increased evaporation and evapotranspiration in the warmed plants (Loik et al., 2000). The species-specific responses of photosynthesis to warming in our study indicate differential changes in growth of plant species, potentially leading to shifts of species dominance and composition, community structure, ecosystem productivity under climatic warming.

4.2. Temperature acclimation of photosynthesis

Temperature acclimation was classified into relative acclimation and absolute acclimation (Xiong et al., 2000). Relative acclimation of photosynthesis refers to the shift in T_{opt} of A when plants are grown under changing temperature (Mooney et al., 1978; Berry and Björkman, 1980). Absolute acclimation refers to the change in A at a new growth temperature (Xiong et al., 2000). Temperature acclimation of photosynthesis was reported for many species in the laboratory experiments (Atkin et al.,

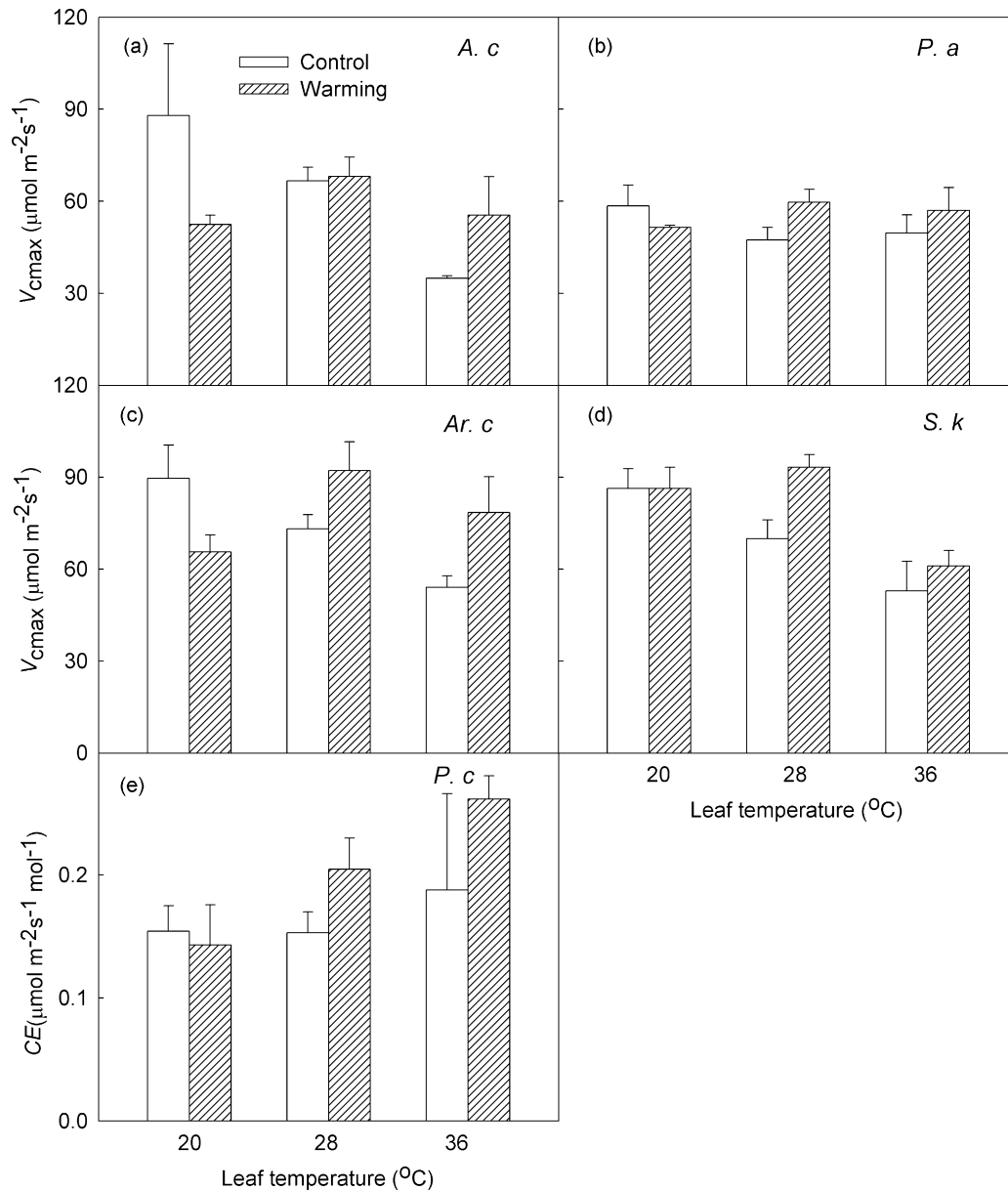


Fig. 4. The maximum rate of RuBP carboxylation (V_{cmax}) in *A. c* (a), *P. a* (b), *Ar. c* (c), *S. k* (d), and the carboxylation efficiency (CE) in *P. c* (e) (mean \pm 1 S.E.) at different leaf temperature under the ambient and elevated temperatures. See Fig. 1 for species abbreviations.

2000a,b; Xiong et al., 2000; Gunderson et al., 2000; Yamori et al., 2005). Our observations showed that all the five species grown under natural conditions in the temperate steppe of northern China acclimated to elevated temperature by increasing both A_{opt} and T_{opt} for photosynthesis (Fig. 3, Table 1). However, the temperature acclimation of photosynthesis was species-specific. The C_4 plants *P. centasiaticum* showed the larger increases in A_{opt} than the four C_3 plants, while the C_3 forbs (*A. capillaris*, *P. acaulis*) increased more in A_{opt} and T_{opt} than the C_3 grasses (*A. cristatum*, *S. krylovii*) (Fig. 3, Table 2). The species-specific temperature acclimation of photosynthesis has been reported by Zhou et al. (2007). Higher optimum temperatures and values of V_{cmax} (or CE) and J_{max} (or A_{sat}) in the warmed over the control plants (Figs. 4 and 5) provided additional evidences for the tem-

perature acclimation of photosynthesis in the plant species in the temperate steppe. Species native to habitats with large temperature variations across the growing season generally display a strong ability to acclimate to temperature for photosynthesis (Xiong et al., 2000). In our study site, the temperature range over the growing season is above 10 °C, which results in a strong temperature acclimation of plant photosynthesis.

The changes in T_{opt} observed in our study (Table 2) were generally within the range of values reported by others. Battaglia et al. (1996) found T_{opt} increased by 0.59 °C in *Eucalyptus globulus* and 0.35 °C in *E. nitens* with 1.0 °C increase in growth temperature. Cunningham and Read (2002) studied eight species and found T_{opt} increased from 0.10 to 0.48 °C depending on species. In our study, infrared heater increased growth temper-

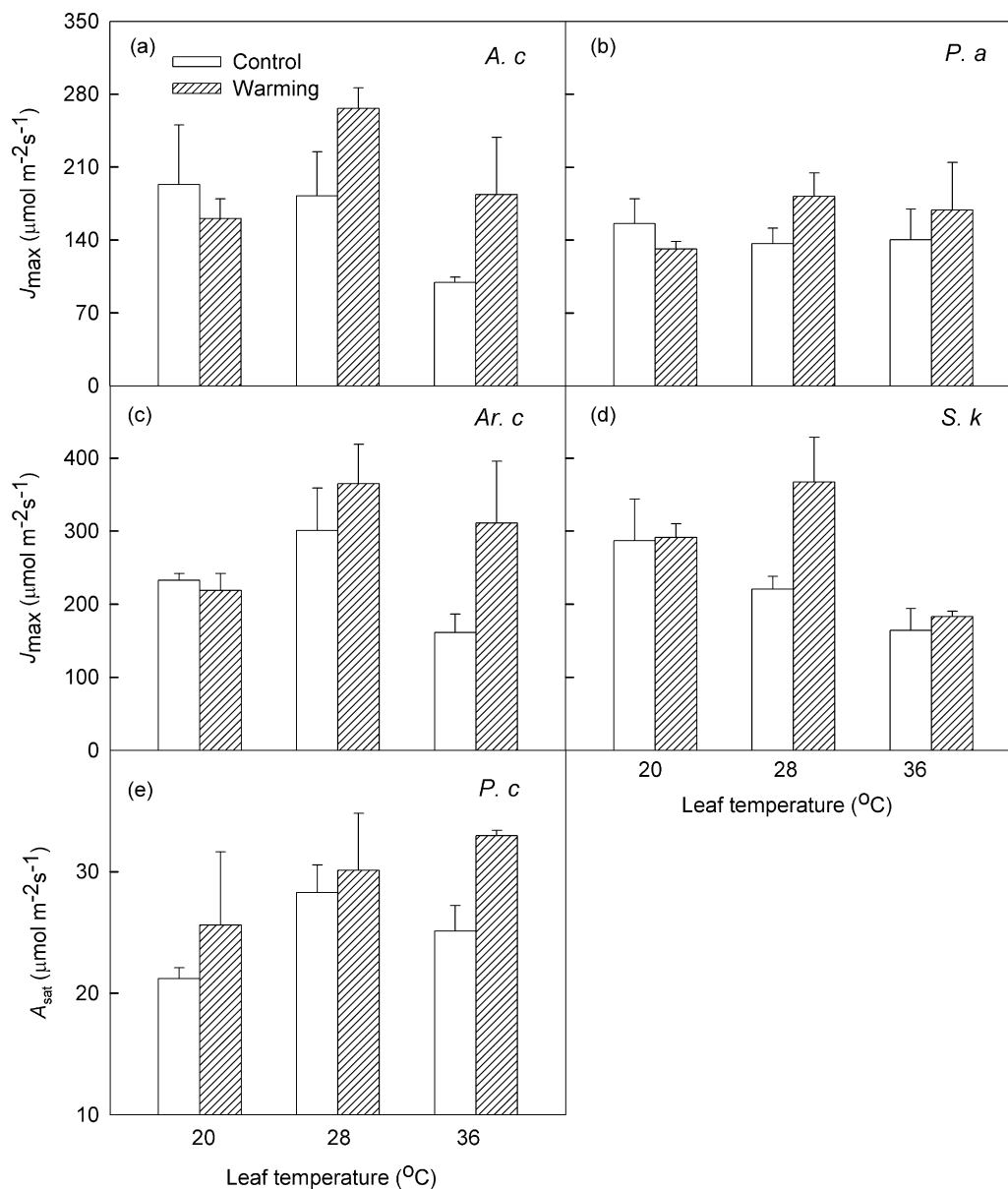


Fig. 5. The maximum rate of RuBP regeneration capacity (J_{max}) in *A. c* (a), *P. a* (b), *Ar. c* (c), *S. k* (d), and the CO_2 -saturated photosynthetic rate (A_{sat}) in *P. c* (e) (mean \pm 1 S.E.) at different leaf temperature under the ambient and elevated temperatures. See Fig. 1 for species abbreviations.

ature by about 1 °C, within which the optimum temperature of the five tested species increased by 0.14–0.5 °C.

4.3. Temperature dependence of V_{cmax} and J_{max}

The acclimation of photosynthesis to climatic warming was consistently reflected by the response of absolute values of V_{cmax} and J_{max} to growth temperature and by variation in the temperature dependencies of V_{cmax} and J_{max} . T_{opt} for V_{cmax} and J_{max} was higher in the warmed than control plants. Warming effects on these parameters varied with leaf temperature (Table 1, Figs. 4 and 5). The non-uniform responses of V_{cmax} and J_{max} to leaf temperature among species and growth temperatures observed in the temperate steppe suggest that species and growth conditions affect the relative temperature sensitivities of

V_{cmax} and J_{max} , leading to changes in the temperature response of photosynthesis.

The temperature dependence of J_{max} was closely parallel to the temperature dependence of V_{cmax} , in which plants grown under elevated temperature had higher optimum temperatures for both J_{max} and V_{cmax} in the four C_3 species (Figs. 4 and 5, Table 2). The similar temperature dependence in J_{max} and V_{cmax} leads to their close relationship under both the ambient and elevated temperatures (Fig. 6). Previous studies have also emphasized the tightness of the linear relationship between J_{max} and V_{cmax} , suggesting that one could be estimated from the other (e.g. Leuning, 1997; Raupach, 1998). In this study, although a constant relationship between J_{max} and V_{cmax} for these species across a range of measuring temperature was observed under both the ambient and elevated temperatures, the relative value

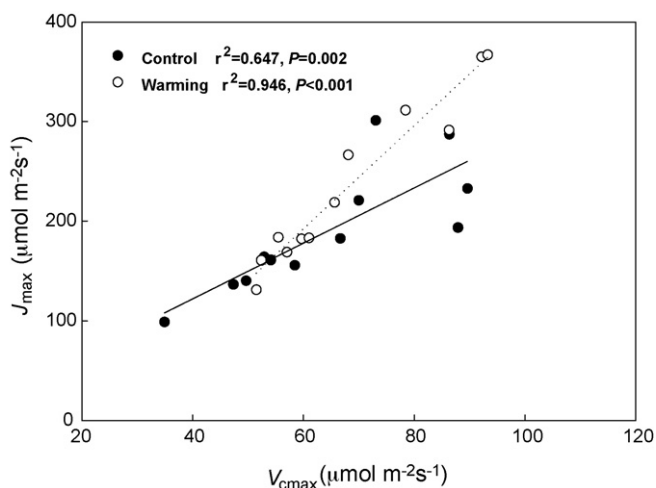


Fig. 6. The relationship between the maximum rate of RuBP carboxylation (V_{cmax}) and RuBP regeneration capacity (J_{max}) across the C_3 plants and measuring temperature under the ambient and elevated temperatures. Regression lines: $J_{max} = 2.78 V_{cmax} + 11.16$ for the control plants; $J_{max} = 5.19 V_{cmax} - 119.15$ for the warmed plants.

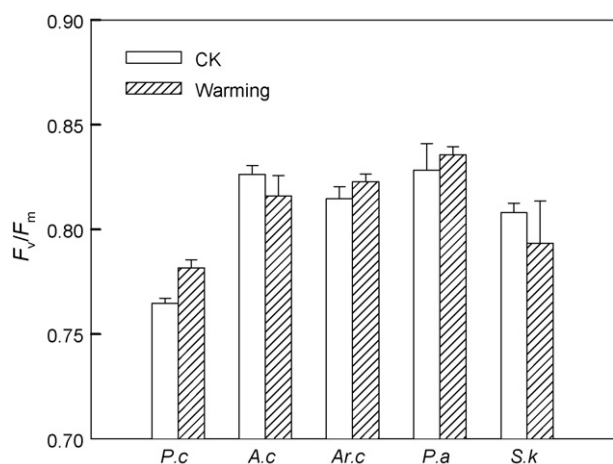


Fig. 7. The maximum photochemical efficiency of PSII (F_v/F_m) in the five species under the ambient and elevated temperatures. See Fig. 1 for species abbreviations.

of J_{max}/V_{cmax} was changed by experimental warming (Fig. 6). According to Farquhar and Von Caemmerer (1982), the variation in the relative values of J_{max} and V_{cmax} are a major source of variation in the optimum temperature of photosynthesis.

The results supported our initial hypothesis that warming differentially affected photosynthesis of the co-existing plant species and plant photosynthesis could acclimate to changing temperature. Shifts in the balance of V_{cmax} and J_{max} contribute to the changes in temperature dependence of photosynthesis under climatic warming. The species-specific photosynthetic response to experimental warming indicate that climatic warming may generally improve the performance of some species while exert no impacts on other species. The different magnitudes of photosynthesis response and temperature acclimation among species and plant functional types could potentially lead to the shifts in species dominance, community structure, and net primary productivity in the temperate steppe of northern China.

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