

Determination of photosynthetic parameters $V_{c_{max}}$ and J_{max} for a C_3 plant (spring hulless barley) at two altitudes on the Tibetan Plateau

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ABSTRACT

On the Tibetan Plateau, the unique alpine climate factors of low air pressure, low CO_2 partial pressure and low air temperature have significant but non-explicit influences on the photosynthetic capacity of plants. To evaluate these influences, we measured the net photosynthetic rates for spring hulless barley leaves at two altitudes of 3688 m (the low altitude) and 4333 m (the high altitude), respectively. Two photosynthetic parameters— $V_{c_{max}}$, the maximum rate of Rubisco carboxylase activity, and J_{max} , the maximum rate of photosynthetic electron transport—were determined. The net photosynthetic rate and the photosynthetic parameters $V_{c_{max}}$ and J_{max} were higher for leaves from plants grown at the high altitude than for those at the low altitude. $V_{c_{max}}$ and J_{max} were approximately 24% and 22% greater, respectively, for leaves from plants grown at the high altitude. The CO_2 and air temperature at the high altitude were lower than those at the low altitude. As a consequence, plants exposed to lower CO_2 partial pressure and lower air temperature have a higher photosynthetic capacity on the Tibetan Plateau. The optimal temperatures for $V_{c_{max}}$ and J_{max} were approximately 6.5% and 3.5% higher, respectively, in leaves from plants grown at the high altitude than those grown at the low altitude, and the ratio of J_{max} to $V_{c_{max}}$ was 12.7% lower at the low altitude. Simulation analyses revealed that the photosynthetic capacities of plants decreased after long-term increases in CO_2 partial pressure and temperature associated with global climate change on the Tibetan Plateau.

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1. Introduction

Two key parameters in Farquhar-type photosynthesis models—the maximum rate of Rubisco carboxylase activity ($V_{c_{max}}$) and the maximum rate of photosynthetic electron transport (J_{max})—accurately describe plant photosynthetic capacity at the leaf level. The correlation between these parameters and photosynthetic capacity has been the subject of extensive research in a wide variety of plants and has been widely applied to other terrestrial ecosystem models (Farquhar et al., 1980; Harley and Tenhunen, 1991a; Harley et al., 1992a; Medlyn et al., 2002a; Sharkey et al., 2007). A retrospective analysis of $V_{c_{max}}$ and J_{max} from 109 C_3 plant species showed considerable differences in $V_{c_{max}}$ and J_{max} between species, except among agricultural crops (Wullschlegel, 1993). That publication is an important reference for species-specific differences in the photosynthetic parameters

$V_{c_{max}}$ and J_{max} . The differences might be closely related to the highly diverse environmental conditions in which plants grown.

CO_2 and temperature are considered two of the primary environmental factors that determine, directly or indirectly, the photosynthetic capacity (Bunce, 2008; Stojanovic, 2008; Kositsup et al., 2009; Possell and Hewitt, 2009). Changes in CO_2 and temperature affect the photosynthetic capacity at the levels of leaf biochemistry, stomata and CO_2 diffusion as well as photosynthetic component activities and CO_2 partial pressure at the carboxylation sites. For plants grown in CO_2 or temperature-controlled growth chambers, researchers have reported that $V_{c_{max}}$ and J_{max} undergo significant changes as a result of changes in either CO_2 partial pressure or temperature (Harley et al., 1992b; Bunce, 2000). For example, $V_{c_{max}}$ for plants grown at a higher CO_2 partial pressure was lower than for those at a lower CO_2 partial pressure, and both $V_{c_{max}}$ and J_{max} were lower for cool-climate plants grown at a warmer temperature. Similar research was conducted on other plants (Hikosaka et al., 2006; Possell and Hewitt, 2009), and these conclusions were verified and compared. Notably, although the changes were general, the trend in and extent of change in $V_{c_{max}}$ and J_{max} were significantly different among plant species. These differences can affect the plant CO_2 absorption pattern in terrestrial ecosystems. Thus, in global carbon budget estimation of the

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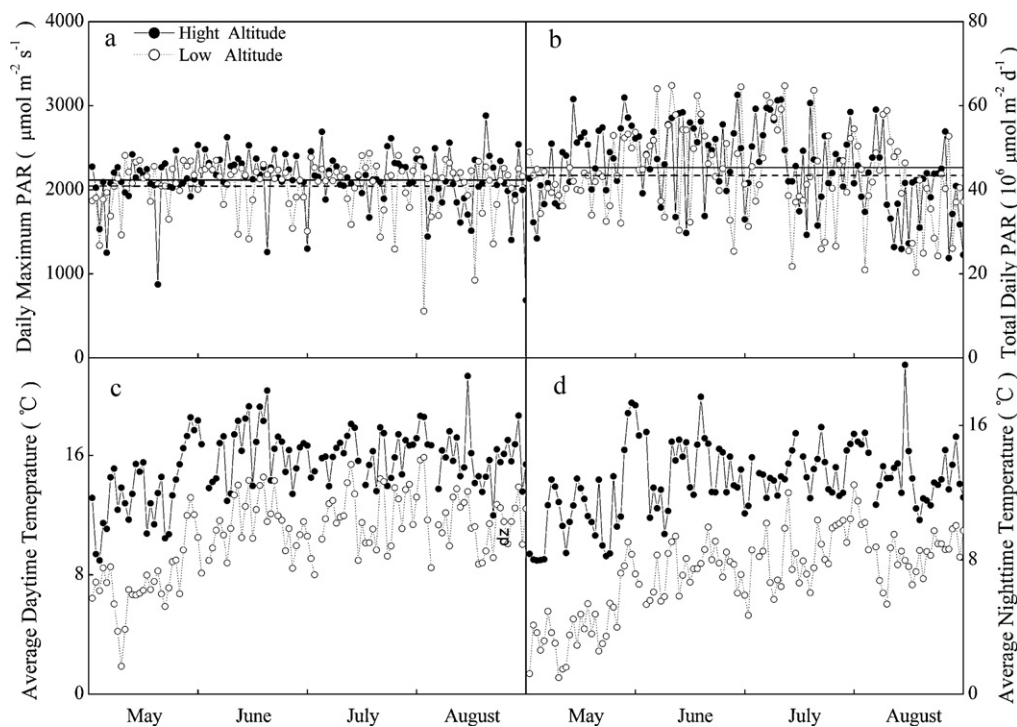


Fig. 1. Meteorological variables at the two sites throughout the research period in 2008. (a) Daily maximum PAR; (b) total daily PAR; (c) average daytime temperature; (d) average nighttime temperature. The lines represent the mean daily maximum PAR (a), $2116.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the high altitude (solid line) and $2043.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ at the low altitude (dashed line), and the mean total daily PAR (b), $45.3 \times 10^6 \mu\text{mol m}^{-2}$ at the high altitude (solid line) and $43.4 \times 10^6 \mu\text{mol m}^{-2}$ at the low altitude (dashed line), respectively.

terrestrial ecosystem, the interspecies differences in changes in V_{cmax} and J_{max} upon alterations in environmental factors will lower the accuracy of these estimation models.

Known as the highest and extensive plateau in the world and the roof of the world, the Tibetan Plateau has an average altitude of more than 4000 m. The high altitude accounts for the low air pressure, low CO_2 partial pressure and low temperature, all of which are known to decline with increasing altitude. Because it is thought to be the world's most climate-sensitive area and one of the "start-up" regions for climate change (Yao et al., 2000; Feng et al., 1998), the response of plant photosynthesis to increased CO_2 and temperature would be expected to be more sensitive on the Tibetan Plateau than on the plain. Therefore, the Tibetan Plateau would likely be a preferred location for research on the photosynthetic performance of plants subjected to global climate change. To date, most research of the photosynthetic responses of alpine plants to changes in either CO_2 partial pressure or temperature has not been concentrated on the photosynthetic model parameters but rather on simple contrast analyses for photosynthetic measurements at extreme altitude (Cabrera et al., 1998; García-Núñez et al., 2004; Zhang et al., 2005; Sakata et al., 2007), especially on the Tibetan Plateau (Liu and Yang, 2001; Liu et al., 1999). Therefore, because V_{cmax} and J_{max} are two key parameters in the photosynthetic model (Farquhar et al., 1980), further research on these parameters should be conducted on plants of the Tibetan Plateau.

The primary purpose of this study was to investigate the photosynthetic parameters V_{cmax} and J_{max} in C_3 alpine plants growing at two different Tibetan Plateau's alpine climates. The CO_2 response curves of photosynthesis for the leaves of spring hulless barley (*Hordeum vulgare* L. subsp. *vulgare*) were measured, and the photosynthetic parameters V_{cmax} and J_{max} are simulated and compared at two altitudes. In addition, to further elucidate V_{cmax} and J_{max} from an enzyme-activation perspective, their temperature dependencies are described using an exponential function.

2. Materials and methods

2.1. Measurement site and experimental treatment

This research was conducted in 2008 at two altitude sites. One site, situated in the Lhasa Agricultural Experiment Station, Chinese Academy of Sciences in Tibet, $29^\circ 40' 40'' \text{N}$, $91^\circ 20' 37'' \text{E}$, has a height above sea level of 3688 m. The other site, situated approximately 1 km from Damxung county, Tibet municipality, China, $30^\circ 25' \text{N}$, $91^\circ 05' \text{E}$, has a height above sea level of 4333 m. In this paper, the conditions at these two sites are referred to as low and high altitude, respectively. Both sites belong to the semi-arid temperate plateau monsoon climate zone. Annual mean precipitation is 425 mm at the low altitude and 475.8 mm at the high altitude. The annual level of solar radiation is 7118.4 MJ m^{-2} at the low altitude and 7527.6 MJ m^{-2} at the high altitude. The atmospheric pressures are 61 kPa at the low altitude and 65 kPa at the high altitude. During the research period, daily maximum photosynthetic active radiation (PAR), total daily PAR, average daytime temperature and average nighttime temperature were monitored continuously (Fig. 1). The differences in daily maximum PAR and total daily PAR were not significant between the two altitudes from May to August in 2008. The average daytime/nighttime temperature ranges differ greatly between the two altitudes.

Hulless barley, a C_3 crop widely cultivated on the Tibetan Plateau, was selected for this study. Seeds were sown in May 2008 at both measurement sites, in pots 20 cm in diameter and 30 cm tall. To minimize the effects of soil properties, shrubby meadow soil was chosen from the 3688 site, which has 2% organic matter content, 0.084–0.103% of total nitrogen and 0.015–0.026% of total phosphorus. Following germination, seedlings were thinned to three per pot, and 20 pots were set up at each study altitude. Plants at both sites were placed in native open habitats. The plants were well watered to a water content of 70–80% field capacity and

fertilized with N and P to ensure that any potential acclimation to the alpine climate was unrelated to water and nutrient stress. As growth rates acclimated to temperature, the emerging time for flag leaves was different between the two altitudes (late June at the low altitude and mid-August at the high altitude). When the youngest flag leaves were 2–3 cm long after 3 days of outgrowth, the well-developed leaves were selected and labeled, thus excluding any influence of flag-leaf age on photosynthetic capacity.

2.2. Gas exchange measurements

Gas exchange was measured using a portable photosynthesis system (LI-6400, LI-COR, Inc., Lincoln, NE, USA) with a 6 cm² leaf chamber. Measurements were conducted on fully expanded flag leaves that had been fully expanded for 6–8 days. Before measurement, the leaves were exposed to sunlight for approximately 50–60 min.

Gas exchange was continually measured from 09:00 to 18:00. For all measurements, PAR was maintained at 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ via red (680 nm) and blue (430 nm) LEDs integrated into the leaf chamber fluorometer (LI6400-40). Leaf temperature was measured using a chromel-constantan thermocouple appressed to the abaxial surface of the leaf, which was simulated synchronously with the ambient air temperature. CO₂ partial pressures were regulated using a 6400-01 CO₂ mixer. Six CO₂ response curves of net photosynthetic rates (P_n) were measured at each temperature of 15 °C, 20 °C, 25 °C, and 30 °C for plants growing at the low altitude and at the altitude, respectively. Twenty-four flag-leaves were measured from different plants at each altitude for four temperatures. From these data, three curves were used to provide parameters for the biochemical model, and three additional curves validated it. During the measurements, to prevent stomatal closure, the vapor pressure deficit surrounding the leaf in the cuvette was maintained between 0.5 and 1.0 kPa. In addition, the relative humidity in the chamber was maintained between 60% and 70%.

2.3. Methods

The P_n versus CO₂ curves of C₃ plants were fitted using the following equations (Farquhar et al., 1980; Harley and Sharkey, 1991b; Medlyn et al., 2002b; Long and Bernacchi, 2003):

$$P_n = V_c - 0.5V_o - R_d = V_c \left(1 - \frac{0.5V_o}{V_c}\right) - R_d \quad (1)$$

$$P_n = \left(1 - \frac{0.5O}{C_i\tau}\right) \min\{W_c, W_j\} - R_d \quad (2)$$

V_c and V_o are the rates of carboxylation and oxygenation for Rubisco, respectively; R_d is the mitochondrial respiratory rate; C_i and O are the intercellular partial pressures for CO₂ and O₂, respectively; W_c is the net RuBP-saturated carboxylation rate; W_j is the net RuBP-limited carboxylation rate; and τ is the Rubisco specificity factor.

At high irradiance and low CO₂ partial pressure (≤ 25 Pa), W_c can be expressed as follows:

$$W_c = \frac{V_{c\max} C_i}{C_i + K_c(1 + O/K_o)} \quad (3)$$

where K_c and K_o are the Michaelis constants for carboxylation and oxygenation, respectively.

At high irradiance and CO₂ partial pressure (> 25 Pa), W_j can be expressed as follows:

$$W_j = \frac{J C_i}{4(C_i + O/\tau)} \quad (4)$$

Table 1

Initial estimates for the parameters used to describe temperature dependence.

Parameter	Units	Temperature parameters	Value	Units
K_c	Pa CO ₂	c	35.79	–
		ΔH_a	80.84	kJ mol ⁻¹
K_o	kPa CO ₂	c	9.59	–
		ΔH_a	14.51	kJ mol ⁻¹
τ	–	c	–3.949	–
		ΔH_a	–28.99	kJ mol ⁻¹

$$J = \frac{\alpha \text{PPFD}}{(1 + (\alpha^2 \text{PPFD}^2 / J_{\max}^2))^{1/2}} \quad (5)$$

where J is the rate of electron transport; α is the efficiency of light energy conversion at an incident light, herein, 0.18 mol electrons mol⁻¹ photon (Wullschlegel, 1993); and PPFD is the incident photosynthetic photon flux density.

Following Harley et al. (1992b), the temperature response for K_c , K_o , τ , J_{\max} and $V_{c\max}$ is described as follows:

$$(K_c, K_o, \tau) = \exp \left[c - \frac{\Delta H_a}{R \cdot T_k} \right] \quad (6)$$

$$(J_{\max}, V_{c\max}) = \frac{\exp[c - \Delta H_a / (R \cdot T_k)]}{1 + \exp[(\Delta S \cdot T_k - \Delta H_d) / (R \cdot T_k)]} \quad (7)$$

Herein, c is a constant, ΔH_a is the activation energy, ΔH_d is the deactivation energy (200 kJ mol⁻¹), R is the gas constant (0.00831 kJ K⁻¹ mol⁻¹), T_k is the leaf temperature (K), and ΔS is the entropy term (0.65 kJ K⁻¹ mol⁻¹). The K_c , K_o and τ values are shown in Table 1 (Harley and Tenhunen, 1991a; Harley et al., 1992b).

$V_{c\max}$ and J_{\max} were estimated by fitting the photosynthetic CO₂ response curves to the biochemical model mentioned above. All such curve fittings were performed using nonlinear least-squares regression via the statistical program OriginLab 8.0 (OriginLab Corporation). A one-way analysis of variance (ANOVA) was the primary statistical procedure applied to demonstrate differences in the net rate of photosynthesis and photosynthetic parameters between plants at the two altitudes.

3. Results

3.1. Characteristics of the net photosynthetic rates

For each temperature measurement at each altitude, three flag-leaf P_n – C_i curves were randomly selected from six curves (Fig. 2). The net photosynthetic rate was higher for hulless barley leaves grown at the high altitude than for those grown at the low altitude in all measurements, and this difference is significant, with $P < 0.05$. However, at both altitudes, all intercellular CO₂ pressures consistently declined from 60–70 Pa at 15 °C to 30–40 Pa at 30 °C. Even though the intercellular CO₂ pressures reached approximately 70 Pa, photosynthetic rates remained sensitive to CO₂. Therefore, no photosynthesis measurements were limited by triose phosphate utilization; instead, they were jointly limited by Rubisco and electron transport at transitions between 20 and 35 Pa at different temperatures.

3.2. $V_{c\max}$ and J_{\max} response to temperature

Altitude affected the $V_{c\max}$ and J_{\max} values for leaves (Fig. 3). Estimates for $V_{c\max}$ increased by approximately 24% for plants grown at the high altitude versus those grown at the low altitude, although the differences in $V_{c\max}$ between the two altitudes were not significant at the 5% probability level, with $P = 0.169$. Estimates for J_{\max} were only approximately 22% higher for plants grown at high altitude, and these differences were significant, with $P = 0.005$.

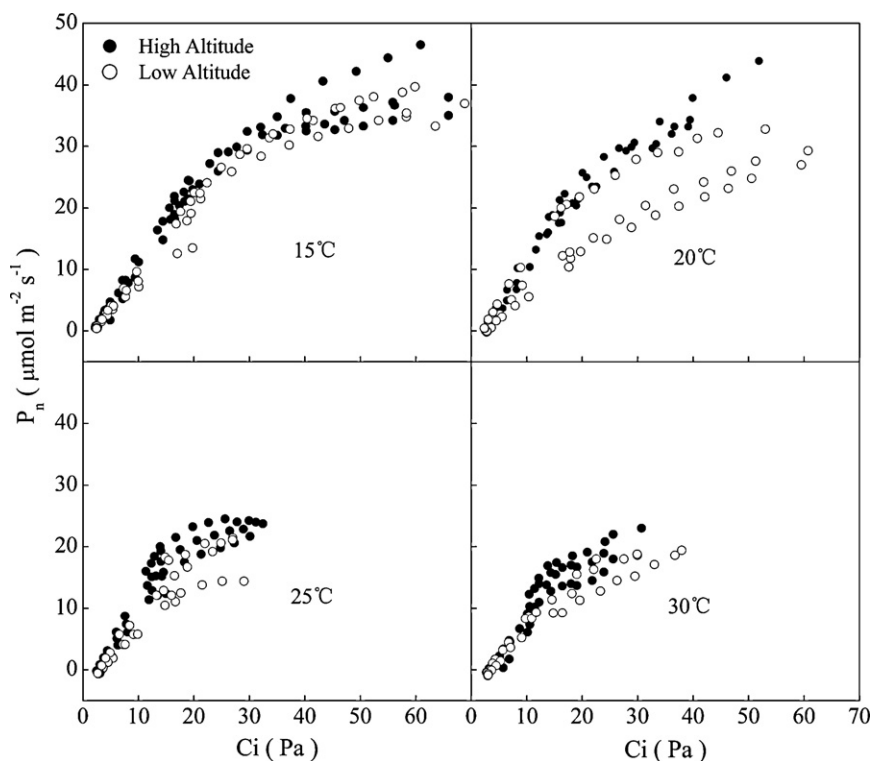


Fig. 2. The net rate of photosynthesis, P_n , as a function of the internal partial pressure of CO_2 , C_i , at various temperatures for leaves of plants grown at two altitudes with different growing environments for alpine plants. Three photosynthetic CO_2 response curves at each temperature were obtained on three individual leaves.

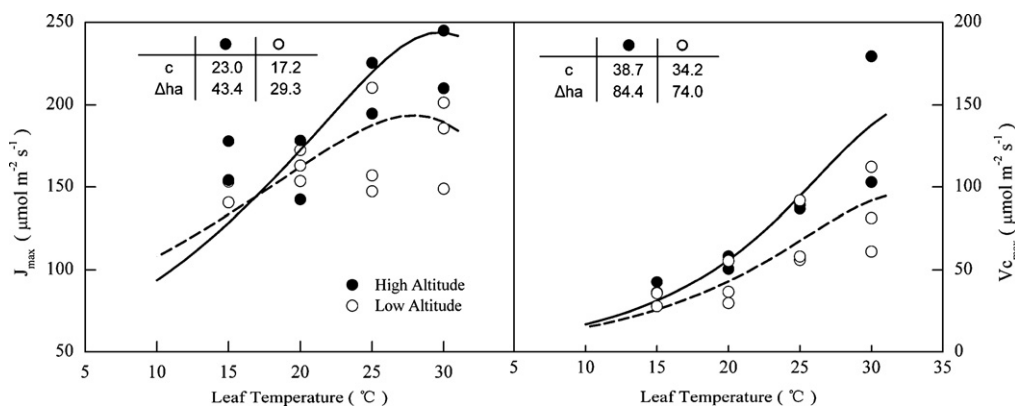


Fig. 3. The temperature dependence of J_{\max} and V_{\max} for leaves of plants grown at two altitudes. J_{\max} and V_{\max} were obtained by non-linear least squares regression. Curves are least-squares fits to Eq. (7) for each altitude treatment, using the parameters shown in the figures.

Given a ΔH_d of 200 kJ mol^{-1} and ΔS of $0.65 \text{ kJ mol}^{-1} \text{ K}^{-1}$, c and ΔH_a for V_{\max} and J_{\max} were estimated (Fig. 3). Using these parameters, the inversion values for V_{\max} and J_{\max} were also estimated using Eq. (7) and were significantly different in leaves at the two altitudes ($P < 0.01$).

Inversion values for V_{\max} and J_{\max} in response to temperature were used to obtain the optimal temperatures for V_{\max} at 33.8°C at the high altitude and 32.6°C at the low altitude as well as for J_{\max} at 29.7°C at the high altitude and 27.9°C at the low altitude. These values were, respectively, approximately 6.5% and 3.5% higher for plants grown at the high altitude than for those at the low altitude. When temperature increased from 15°C to 30°C , V_{\max} displayed continuous increases, but J_{\max} had visible decreases from 25°C to 30°C .

In addition, Fig. 4a shows a marked linear relationship between V_{\max} and J_{\max} . When the temperature increased from 15°C to

30°C , the J_{\max}/V_{\max} ratio plunged from approximately 4.2 to 1.6, and the difference in this ratio increased slightly between leaves at the two altitudes (Fig. 4b). The average ratio was approximately 12.7% higher for plants grown at the high altitude than those at the low altitude.

3.3. Validation of parameters

To confirm the accuracy of the experiment and the model parameters, model validation was performed against an independently measured data set. The results are shown in Fig. 5. The measured net photosynthesis rates for leaves displayed an almost 1:1 linear relationship with the predicted values at the two altitudes. The correlation coefficients were high (>0.98) for these linear relationships, indicating that all the model parameters obtained above are reliable.

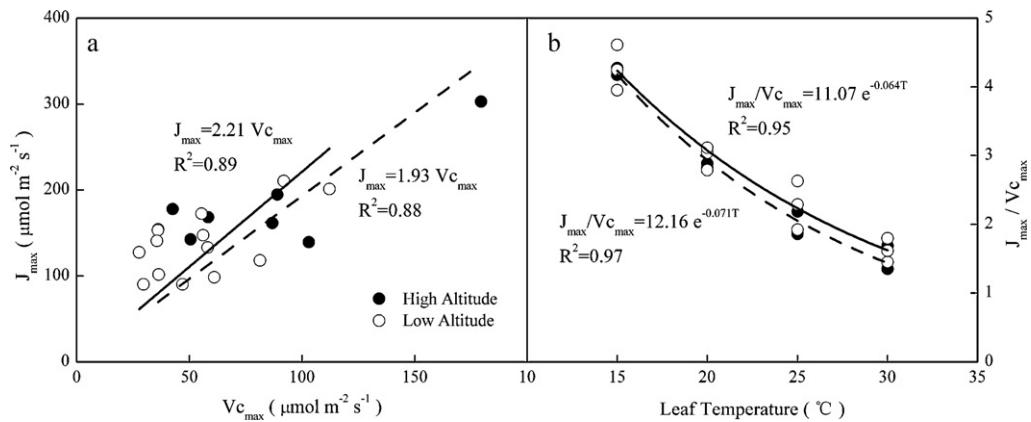


Fig. 4. The temperature dependence of the $J_{\max}/V_{c\max}$ ratio (a) and the relationship between J_{\max} and $V_{c\max}$ (b). The lines represent the index regression of data (a) and the linear regression of data (b). The solid lines represent the relationship for the high-altitude plants, and the dashed lines represent the relationship for the low-altitude plants.

4. Discussion and conclusions

The research reported here shows that the variation in alpine environments with the altitudinal gradient had significant influences on the photosynthetic parameters and the net photosynthetic rate of leaves of plants on the Tibetan Plateau. In alpine environments, there is a wide variety of environmental factors that, if changed, can alter plant photosynthetic performance, such as the physicochemical properties of the soil, water, nitrogen, light intensity, temperature, CO_2 partial pressure and O_2 partial pressure (Farquhar et al., 1980; Sage and Sharkey, 1987; Cabrera et al., 1998; Medlyn et al., 2002b; Sakata and Yokoi, 2002; Bernacchi et al., 2003). In this experiment, except for light intensity, temperature and partial pressure, any differences among the remaining factors were ameliorated by growing the plants in the same soil and using uniform water and fertilizer management at the two altitudes. It was therefore confirmed that differences in the photosynthetic capacity between plants at the two altitudes were caused primarily by changes in light intensity, temperature and CO_2 partial pressures along the altitudinal gradient.

The influence of the light-intensity gradient on plants is reflected primarily in foliar anatomical and biochemical features (Niinemets et al., 1998). As a result of acclimation to the higher growth light environment, the plants had enhanced leaf dry mass per area and leaf nitrogen content per unit leaf dry mass (Yamori et al., 2010; Niinemets and Tenhunen, 1997). Leaf dry mass per area and leaf nitrogen content per unit leaf dry mass have positive relationships with plants' photosynthetic capacity and parameters (Niinemets and Tenhunen, 1997; Zhang and Feng, 2004). In

this study, neither the responsiveness and sensitivity of photosynthetic capacity nor the photosynthetic parameters to changes in light intensity could be determined because of limitations in the experimental facilities and experimental conditions on the Tibetan Plateau. However the light intensity was not significantly different at the two altitudes (Fig. 1a, $P = 0.075$; Fig. 1b, $P = 0.147$), the light intensity could be confirmed to have but only a slight positive effect on the photosynthetic capacity for spring hulless barley grown at the high altitude. Light intensity was not the key reason for the different photosynthetic characteristics at the two altitudes.

Bunce (2000) found that for cool-climate species, the estimated $V_{c\max}$ and J_{\max} were much higher for leaves grown at cooler temperatures than for those grown at warmer temperatures, owing to the acclimation of photosynthesis to temperature. For spring hulless barley on the Tibetan Plateau, the grown temperatures were all below 20°C at two altitudes (Fig. 1c and d). The average estimates of $V_{c\max}$ and J_{\max} at 25°C were, respectively, approximately $87.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $209.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the high-altitude spring barley and $73.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $178.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the low-altitude spring barley. These values were slightly higher than the average estimates of $63.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $167 \mu\text{mol m}^{-2} \text{s}^{-1}$ for $V_{c\max}$ and J_{\max} , respectively, at 25°C in seven cool-climate species (barley and wheat) reported by Wullschlegel (1993), who summarized data from 12 monocots grown at temperatures above 20°C . In addition, ΔH_a can potentially indicate the rate of exponential change for $V_{c\max}$ and J_{\max} with increasing temperature (Farquhar et al., 1980; Harley et al., 1992b; Leuning, 1997; Bernacchi et al., 2003; Kattge and Knorr, 2007). In this study, the higher values of ΔH_a for $V_{c\max}$ and J_{\max} obtained from the

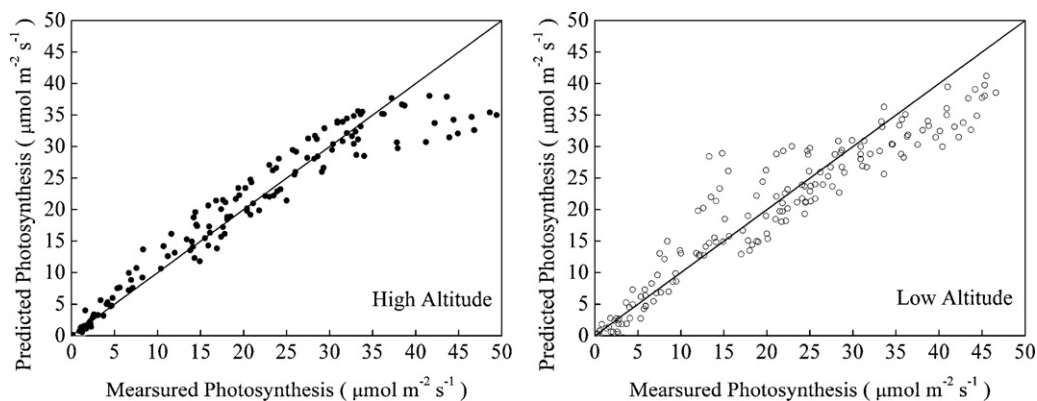


Fig. 5. Comparison of measured net photosynthetic rates with values predicted by the parameterized model, using estimates of $V_{c\max}$ and J_{\max} in Fig. 2 for plants grown at two altitudes. The lines show a 1:1 relationship.

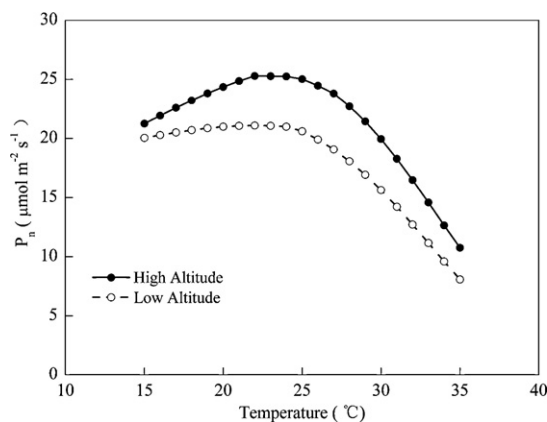


Fig. 6. Model simulations of net photosynthetic rate as a function of temperature, under growth CO_2 partial pressures (23.5 Pa at the high altitude and 24.9 Pa at the low altitude) and O_2 partial pressures (12.7 kPa at the high altitude and 13.5 kPa at the low altitude), and assuming a saturating PPFD ($1600 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and a C_i/C_a ratio of 0.7, using parameterized model for plants grown at the high altitude and at the low altitude, respectively. Parameters are from Table 1 and Fig. 2.

high-altitude plants imply that the values of $V_{c\max}$ and J_{\max} for the high-altitude plants were more affected by temperature increases than were those for the low-altitude plants.

For plants grown at the two altitudes, different temperature dependencies were also observed for net photosynthesis in leaves (Fig. 6). The temperature sensitivity of net photosynthesis was slightly greater for plants grown at the high altitude than for plants grown at the low altitude ($P < 0.5$). The optimal temperature for photosynthesis seemed to decrease as the intercellular CO_2 partial pressure declined with temperature (Hikosaka et al., 2006). The intercellular CO_2 partial pressure significantly declined with temperature (Fig. 2), and in one case it decreased by approximately 50% as the temperature increased from 15 °C to 30 °C. Therefore, for plants at both altitudes on the Tibetan Plateau, the optimal photosynthesis temperature was lower than for plants not subjected to intercellular CO_2 partial pressure declining with temperature, which was 22–23 °C for the former plants and 25 °C for the latter plants (Bunce, 2000; Yamori et al., 2006).

Many recent evidence-based studies have reported that alpine plant specimens at higher altitudes have higher photosynthetic capacities than those at lower altitudes; however, stress from low CO_2 partial pressure was reported not to have an apparent effect (Körner et al., 1986; Körner, 2003; Terashima et al., 1995). The results of the current study are similar to those previously published. Alpine plants have greater leaf nitrogen use efficiency (Terashima et al., 1995) and greater efficiency of CO_2 uptake (Oechel and Vourlitis, 1996), as a consequence of greater leaf and palisade layer thicknesses (Körner et al., 1991), greater leaf nitrogen content per unit leaf area (Körner, 1989), greater leaf dry mass and higher partitioning coefficients for leaf nitrogen in Rubisco and in bioenergetics (Niinemets and Tenhunen, 1997). The positive effects of these factors on photosynthesis at high altitudes compensate for, or even exceed, the negative effect from the decrease in CO_2 partial pressure with increasing altitude (Körner et al., 1991; Sakata et al., 2007).

CO_2 -dependent photosynthesis for plants grown in both altitudes could be predicted if the set of parameters estimated above is adopted (Fig. 7). Given a leaf temperature of 15 °C, PPFD of $1600 \mu\text{mol m}^{-2} \text{ s}^{-1}$, C_i/C_a of 0.7 (Weber et al., 1985; Cannon and Roberts, 1995), and native ambient CO_2 and O_2 partial pressures ($\text{CO}_{2(\text{high altitude})} = 23.5 \text{ Pa}$, $\text{O}_{2(\text{high altitude})} = 12.7 \text{ kPa}$, $\text{CO}_{2(\text{low altitude})} = 24.9 \text{ Pa}$, and $\text{O}_{2(\text{low altitude})} = 13.5 \text{ kPa}$), the P_n value was approximately 9.4% higher in plant leaves grown at the high altitude than in those grown at the low altitude. If exposed for a short time to the low-altitude ambient CO_2 partial pressure, the P_n values for leaves of plants grown at the high altitude increased by 11.5% compared with values for leaves of plants grown at the low altitude. When plants grown at both altitudes were simultaneously allowed short-term exposure to the ambient CO_2 partial pressure ($C_{a(\text{lowland})} = 30.39 \text{ Pa}$), the value of P_n increased by 12.3% in leaves of plants grown at the high altitude versus in leaves of those grown at the low altitude. Thus, short-term exposure to CO_2 enrichment clearly stimulated the photosynthesis of alpine plants, and the sensitivity of photosynthesis to short-term CO_2 enrichment was higher for the high-altitude plants than that for the low-altitude plants.

In this study, the photosynthetic parameters $V_{c\max}$ and J_{\max} for leaves of plants grown at two altitudes on the Tibetan Plateau were estimated, and the response characteristics of leaf-level photosynthesis in C_3 alpine plants to alpine climates were investigated.

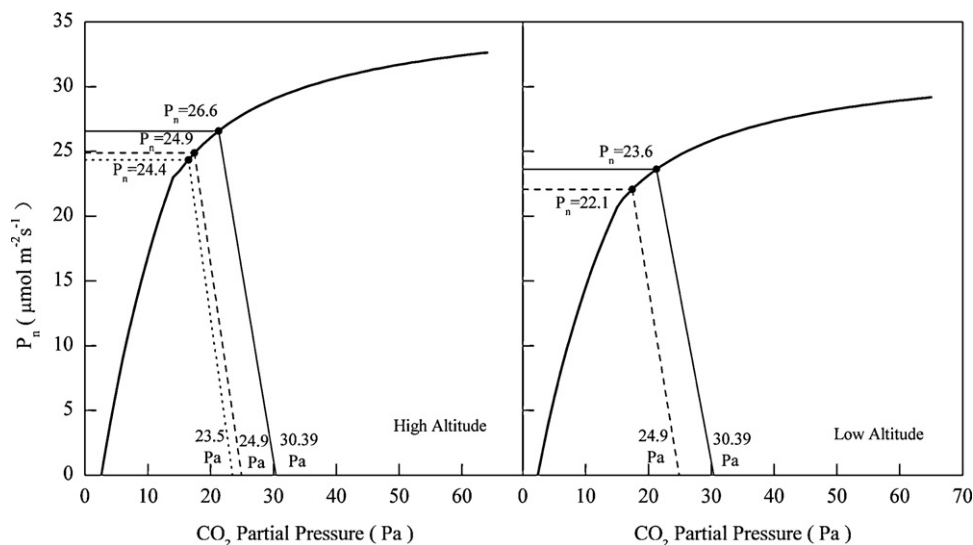


Fig. 7. Model simulations of net photosynthesis as a function of CO_2 partial pressure, under growth O_2 partial pressures (12.7 kPa at the high altitude and 13.5 kPa at the low altitude), 15 °C temperature and saturating PPFD ($1600 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), assuming a C_i/C_a ratio of 0.7, using parameterized models for plants grown at both altitudes. Parameters are from Table 1 and Fig. 2. Model predictions of net photosynthesis (P_n), assuming ambient CO_2 partial pressures of 23.5 Pa, 24.9 Pa or 30.39 Pa at the high altitude and 24.9 Pa or 30.39 Pa at the low altitude, are shown.

According to our results and discussions, the photosynthetic capacity had higher values at the high altitude than at the low altitude, although CO₂ partial pressure and temperature were lower at the high altitude, with values for other additional environmental variables being the same at the two altitudes. During global climate change, CO₂ partial pressure and temperature at high altitude should increase to even higher levels than at low altitudes. Therefore, a long-term increase in CO₂ partial pressure and temperature would likely result in an inevitable decrease in the photosynthetic capacity of alpine plants on the Tibetan Plateau if other environmental conditions are maintained at their current levels. Thus, such a decrease in photosynthetic capacity could potentially influence the net carbon sink function of the terrestrial ecosystem on the Tibetan Plateau. These findings should be considered in further publications.

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