

A comparative analysis of photosynthetic characteristics of hulless barley at two altitudes on the Tibetan Plateau

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Abstract

To determine the photosynthetic characteristics of C₃ plants and their sensitivity to CO₂ at different altitudes on the Tibetan Plateau, hulless barley (*Hordeum vulgare* L. ssp. *vulgare*) was grown at altitudes of 4,333 m and 3,688 m. Using gas-exchange measurements, photosynthetic parameters were simulated, including the maximum net photosynthesis ($P_{\max}$) and the apparent quantum efficiency (α). Plants growing at higher altitude had higher net photosynthetic rates (P_N), photosynthesis parameters ($P_{\max}$ and α) and sensitivities to CO₂ enhancement than plants growing at lower altitude on the Tibetan Plateau. The enhancements of P_N , $P_{\max}$, and α for plants growing at higher altitude, corresponding with 10 $\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}$ increments, were approximately 0.20–0.45%, 0.05–0.20% and 0.12–0.36% greater, respectively, than for plants growing at lower altitude, respectively, where CO₂ levels rose from 10 to 170 $\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}$. Therefore, on the Tibetan Plateau, the changes in the photosynthetic capacities and the photosynthetic sensitivities to CO₂ observed in the C₃ plants grown above 3,688 m are likely to increase with altitude despite the decreasing CO₂ partial pressure.

Additional key words: altitude; apparent quantum efficiency; maximum net photosynthesis; Tibetan Plateau.

Introduction

In general, it has been assumed that a low CO₂ partial pressure has a negative effect on photosynthesis at high altitudes (Tranquillini 1964, Gale 1972, Friend and Woodward 1990, Sakata and Yokoi 2002). However, several observations have suggested that alpine plants have a higher photosynthetic capacity than lowland plants (Billings and Mooney 1968, Körner and Diemer 1987, Körner and Pelaez Menendez-Riedl 1990, Friend and Woodward 1990, Vats 2009). Studying the photosynthetic capacity of plants at different altitudes, Körner *et al.* found that the photosynthetic capacities of plants in the Alps at 2,600 m were 20% higher than those at 600 m (Körner and Diemer 1987, Körner and Pelaez Menendez-Riedl 1990). They suggested that this could be caused by pressure-related changes when the partial pressure of CO₂ decreases. These changes are caused by low-pressure air,

which allows CO₂ to diffuse more quickly through the stomata and intercellular spaces of leaves (Körner and Diemer 1987, Körner 2003). Thus, RuBP oxygenase activity is reduced because of low O₂, which reduces photorespiration (Körner 2003), and this reduction could offset the suppression of photosynthesis due to low CO₂ levels. Therefore, along an altitudinal gradient, some relationship should exist between the difference of the photosynthetic capacities of plants and CO₂ partial pressure. However, these relationships would probably break down in cases where CO₂ partial pressure and temperature change with altitude. To predict the effects on the photosynthetic responses of plants at different altitudes due to changes in CO₂ partial pressure under global climate changes, a comparative study at different altitudes was employed.

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Abbreviations: C_i – intercellular CO₂ concentration; $P_{\max}$ – maximum net photosynthesis; $P_{\max350}$ – maximum net photosynthesis at 350 $\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}$; P_N – net photosynthetic rate; PPFD – incident photosynthetic photon flux density; R_D – day respiration rate; T – leaf temperature; α – apparent quantum efficiency; α_0 – apparent maximum quantum efficiency; τ – CO₂ compensation point in the absence of day respiration; θ – convexity; SD – standard deviation.

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Many scientists have studied characteristics of plant photosynthesis at different altitudes and found that there are significant differences in the photosynthetic characteristics of alpine plants growing at different altitudes (Gale 1972, Kao and Chang 2001, Zhang *et al.* 2005, Castrillo 2006). However, almost all prior studies ignored the differences in the plant species, soil water, soil fertility, and other factors that occurred at different altitudes. These factors would probably influence the effect of CO₂ on plant photosynthesis. Hence, their findings could not adequately determine whether the differences in the photosynthetic characteristics of plants at different altitudes are caused by climatic factors that change with altitude. Furthermore, it is difficult to define photosynthetic sensitivity to CO₂ concentration changes at different altitudes.

The Tibetan Plateau is known as one of the most sensitive regions to global climate change, and it has an average elevation exceeding 4,000 m (Shi *et al.* 2006). Climatic factors present within particular biomes are diverse and complicated along an altitude gradient. Low CO₂ partial pressure due to high altitude is a unique alpine climate characteristic that makes it fundamentally different than the lowland climate, and alpine plants are

more sensitive to climate change (Li and Tang 1988, Shi *et al.* 2006). Therefore, this region provides an ideal experimental situation for comparative research involving photosynthesis along an altitudinal gradient. To determine the characteristics of the photosynthetic responses of alpine plants in relation to alpine climate change, we analyzed the photosynthetic parameters of leaves from hulless barley, which are C₃ plants growing at different altitudes on the Tibetan Plateau, with special attention to the sensitivities of the dependencies of photosynthesis on CO₂ concentrations. Hulless barley was chosen to determine how differences in the dependencies and sensitivities to climatic factors change at different altitudes. The hulless barley was planted in pots at altitudes of 3,688 m and 4,333 m with the same soil and water-fertilizer management regimes. Using the measurements of leaf-level photosynthesis and a model describing light dependencies of leaf-level photosynthesis, two photosynthetic parameters, α and $P_{\max}$, were modelled; comparative P_N , α , and $P_{\max}$ characteristics and their relationships with leaf temperature at two altitudes on the Tibetan Plateau were analyzed. Finally, the sensitivities of these three parameters to CO₂ enrichment were further analyzed.

Materials and methods

Measurement site and experimental treatment: This research was conducted at two altitudes, 3,688 m at the Lhasa River valley (situated on the Lhasa Agricultural Experiment Station, Chinese Academy of Sciences in Tibet, 29°40'40"N, 91°20'37"E) and 4,333 m near the south edge of the Nyainqntanglha Mountains (situated approximately 1 km from Damxung county, Tibet municipality, China, 30°25'N, 91°05'E). Both sites belong to the semiarid temperate plateau monsoon climate zone. The mean daily air temperatures during the growing season and annual mean precipitation are 17°C and 425 mm at 3,688 m, respectively, while they are 15°C and 475.8 mm at 4,333 m. The vegetation is dominated by crops and by *Tipa capillacea*, *Carex montis-everestii* and *Kobresia pygmaea* at 3,688 m and 4,333 m, respectively (Xu *et al.* 2007). The soil types are shrubby meadow soil at the 3,688 m and alpine meadow soil at 4,333 m.

Hulless barley, a C₃ crop cultivated widely on the Tibetan Plateau, was selected for this study. Seeds were sown in May of 2008 at both measurement sites in pots 20 cm in diameter and 30 cm high. Three to four seeds were sown per pot, and 15–20 pots were set up at each study altitude. To minimize the effects of soil properties, the shrubby meadow soil was selected from the 3,688 site, which has a 2% of organic matter content, consisting of 0.084–0.103% total nitrogen and 0.015–0.026% total phosphorus. The plants were well watered to a water content of 70–80% of field capacity and fertilized with N and P [0.471 g(N) and 0.236 g(P₂O₅) per pot during the

experiment] to ensure that possible acclimations to the alpine climate were unrelated to water and nutrient stress. Plants grew in open habitats. Because of the acclimations of growth rates to temperatures, the emerging times for flag leaves were different between the two altitudes (late June at 3,688 m and mid-August at 4,333 m). When the youngest flag leaves were 2–3 cm long after 3-day outgrowth, well developed leaves were selected and marked with labels. These treatments allowed us to avoid the influence of flag leaf age on photosynthetic capacity.

Gas exchange was measured using a portable photosynthesis system (LI-6400, LI-COR, Inc., Lincoln, NE, USA) with a 3 cm × 2 cm (length × width) leaf chamber. Prior to the measurements, photosynthesis was induced by exposing leaves to sunlight for approximately one hour. The measurements were conducted on fully expanded flag leaves. The flag leaves had an age of full expansion on plants of up to 6–8 days, an average length of 7–8 cm. The upper section of each leaf was enclosed in the chamber at a distance of 2.5–3.0 cm away from the blade and measured with a vernier caliper.

The response of CO₂ assimilation to light intensity was measured using the regression of the photosynthetic photon flux density (PPFD) from 2,200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ with an LI-6400-02B red (680 nm)/blue (430 nm) light source in the sensor head, with a native CO₂ concentration of approximately 400 ± 5 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$ at 3,688 m and 375 ± 5 $\mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$ at 4,333 m and leaf temperatures of 15, 20, 25, and 30°C. The leaf

temperature control simulated the ambient air temperature conditions, and temperature anomalies were less than 5°C. To prevent stomatal closure which would decrease photosynthesis, the vapour pressure deficit around the leaf in the chamber was maintained at between 0.5 and 1.0 kPa during measurements.

To determine the differences of the CO₂ dependencies of photosynthetic capacity between altitudes, additional curves were measured in leaves from the CO₂ treatments under conditions of light saturation at 1,600 µmol m⁻² s⁻¹ and a leaf temperature of 20°C. The CO₂ concentration of the chamber air was reduced stepwise from 400 µmol(CO₂) mol⁻¹ to 0 µmol(CO₂) mol⁻¹ and then increased stepwise from 0 µmol(CO₂) mol⁻¹ to 1,300 µmol(CO₂) mol⁻¹ by the injection of CO₂ under the control of an infrared CO₂ analyzer. It usually took 200–300 s for gas-exchange rates to stabilize after changing the light density and CO₂ concentration. Afterward, gas-exchange measurements were recorded.

Such plots of net photosynthetic rates (P_N) as a functions of CO₂ and incident light levels were made continuously on several clear days between 09:00–18:00 and 09:30–10:30 on 4–6 leaves per temperature range at each site. From these data, three curves from each altitude at 15, 20, 25, and 30°C were selected to analyze and simulate the photosynthetic characteristics of hulless barley.

Model description: The nonrectangular hyperbola model that was proposed to describe the relationship between PPFD and the rate of photosynthesis is expressed as (Marshall and Biscoe 1980):

$$P_N = \frac{\alpha \cdot \text{PPFD} + P_{\max} - \sqrt{2(\alpha \cdot \text{PPFD} + P_{\max}) - 4\alpha P_{\max} \theta}}{2\theta} - R_D \quad (1)$$

where $P_{\max}$ and α are the maximum net photosynthesis and the apparent quantum efficiency, respectively. R_D is day respiration rate other than photorespiration, PPFD is

the incident photosynthetic photon flux density, and θ is the apparent convexity at the shoulder of the photosynthetic light-response curve ($0 < \theta < 1$). The two parameters $P_{\max}$ and α can be simulated from the equation of the photosynthetic light responses.

To find the CO₂ dependencies of $P_{\max}$ and α , the two functions proposed by Gaastra *et al.* (1994) and Goudriaan *et al.* (1985) are as follows:

$$\alpha = \alpha_0 \frac{C_i - \tau}{C_i + 2\tau} \quad (2)$$

$$P_{\max 350} = \frac{C_i - \tau}{350 - \tau} \times P_{350} \quad (3)$$

where $P_{\max 350}$ and α_0 are the maximum net photosynthesis at 350 µmol(CO₂) mol⁻¹ and the apparent maximum quantum efficiency, respectively, and τ and C_i are the CO₂ compensation point in the absence of day respiration and the intercellular CO₂ concentration, respectively. P_{350} is the net photosynthesis at 350 µmol(CO₂) mol⁻¹. Factor τ , which varied with leaf temperature (T), was expressed as follows (Brooks and Farquhar 1985):

$$\tau = 42.7 + 1.68 (T - 25) + 0.012 (T - 25)^2 \quad (4)$$

$P_{\max 350}$ and α_0 can be inverted based on Eq. 2, Eq. 3 and Eq. 4, with $P_{\max}$, α , τ , and C_i as inputs, respectively. As parameters of photosynthetic capacity, $P_{\max 350}$ and α_0 should be rather stable for a specific stand independent of temperature and CO₂ concentration. Therefore, it is possible to estimate values for $P_{\max}$ and α at a given CO₂ concentration.

Model-fitting techniques and statistical analysis: The data were processed with *Origin 8.0* software (*OriginLab Corp.*, Northampton, MA, USA). Nonlinear least-squares fitted to Eq. 1, Eq. 2 and Eq. 3 and iterations for $P_{\max}$, α , α_0 , and $P_{\max 350}$ were applied. One-way analysis of variance (ANOVA) was applied to assess differences in the net rates of photosynthesis and photosynthetic parameters between plants at the two altitudes.

Results

Response of photosynthesis to irradiance: Curves relating native P_N to irradiance for fully expanded flag leaves of hulless barley were fit for two altitudes with leaf temperatures set at 15°C, 20°C, 25°C and 30°C and the native CO₂ concentration in the field (Fig. 1). At the two sites, net photosynthesis rapidly increased at a rate of 0–200 µmol m⁻² s⁻¹. Subsequently, the rates slowly increased by 400–1,000 µmol m⁻² s⁻¹ and peaked at approximately 1,500–1,700 µmol m⁻² s⁻¹. The net photosynthetic rates showed significant differences over a range of leaf temperatures, including 15°C, 20°C, 25°C and 30°C, and the nearly optimum temperature was 20°C.

Hulless barley grown at 4,333 m had higher rates of

net photosynthesis than that grown at 3,688 m over all measurements at a given leaf temperature ($p < 0.05$). Plants from 4,333 m exhibited the light-saturated rate of 23 µmol(CO₂) m⁻² s⁻¹, which is approximately 2.5 µmol(CO₂) m⁻² s⁻¹ over the light-saturated rate at 3,688 m under a saturated light intensity of 1,600 µmol m⁻² s⁻¹ and optimum leaf temperature of 20°C.

Parameters of α and $P_{\max}$: To assess the responses of biochemical photosynthetic properties to light, α and $P_{\max}$ were two key parameters used to characterize the status of the leaf photosynthetic apparatus (Marshall and Biscoe 1980). The native parameters of α and $P_{\max}$ for each of

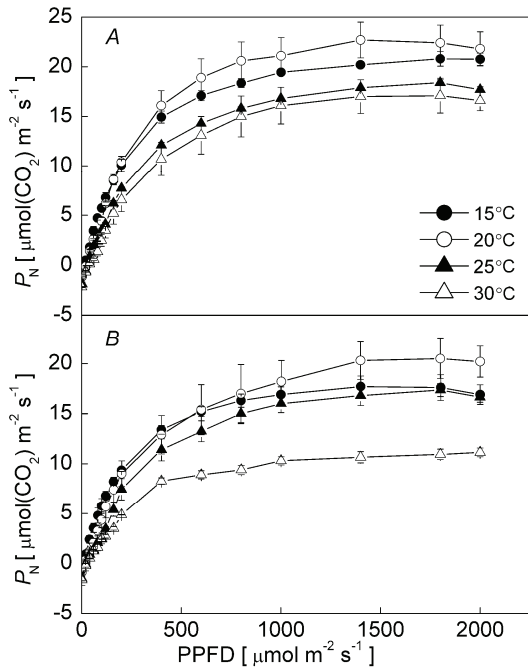


Fig. 1. Net photosynthetic light-response curves for fully expanded flag leaves of hulless barley. The curves were fit from representative hulless barley growing at A: 4,333 m and B: 3,688 m with leaf temperatures of 15°C, 20°C, 25°C and 30°C. Each symbol represents the mean value of three replications and the standard deviation ($\pm$ SD) was also determined.

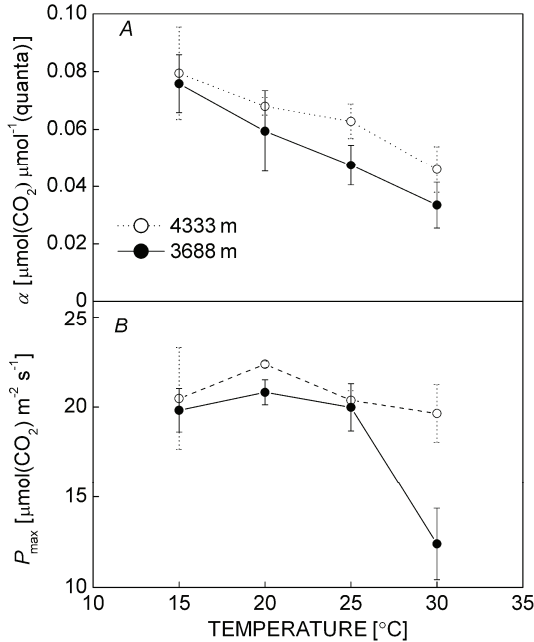


Fig. 2. The relationship between apparent quantum efficiency (α) and A: leaf temperature or B: maximum net photosynthesis ($P_{\max}$) at 4,333 m and 3,688 m. Each symbol represents the mean value of three replications and the standard deviation ($\pm$ SD) was also determined.

the leaves were separately estimated using a nonlinear least-squares method and the photosynthetic light measurements mentioned above to iterate Eq. 1. When the measured P_N and that fitted in Eq. 1 were within $0.01 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$, the iteration was concluded. The values of α and $P_{\max}$ are shown in Fig. 2.

In Fig. 2A, declining trends in α with increasing leaf temperatures were observed for the two altitudinal treatments. The α value declined from 0.0794 to 0.0460 at the altitude of 4,333 m and from 0.0759 to 0.0335 at the altitude of 3,688 m when leaf temperatures increased from 15°C to 30°C. However, there were significant differences in α among the two groups of plants ($p < 0.05$). Higher-altitude plants tended to have higher α values than lower-altitude plants with a mean difference of 17.2% for all leaf temperatures, and the greatest difference was 27.18% at 30°C. To minimize the variation in the photon efficiency in response to leaf temperature, α_0 for the two altitudes was determined using Eq. 2. The α_0 at 4,333 m and 3,688 m was 0.098 and 0.081, respectively, which meant that plants growing at the higher altitude had higher light utilization efficiencies than plants growing at the lower altitude.

From Fig. 2B, we can see that the variation patterns of $P_{\max}$ are highly similar at the two altitudes, as characterized by an initial rise and subsequent decline. They reached a maximum of approximately $22.37 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ at the higher altitude and $20.81 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ at the lower altitude at nearly the same leaf temperature, approximately 20°C. The leaf temperature sensitivities of $P_{\max}$ did not differ significantly between the two altitudes ($p > 0.05$). However, there were slight fluctuations in $P_{\max}$ with an average fluctuation of $1.54 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ per leaf temperature in plants growing at 4,333 m, while the average fluctuation was $3.14 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ in plants growing at 3,688 m. Despite not being significant ($p > 0.05$), the average difference in $P_{\max}$ between the two altitudes was about 11.84%. To avoid the influence of different CO_2 concentrations between the two altitudes on the photosynthetic rate (Barigah *et al* 1994), $P_{\max350}$ values were calculated using Eq. (3). Similar to the previous calculation, $P_{\max350}$ was apparently higher at 4,333 m than at 3,688 m, corresponding to $29.14 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$ and $23.68 \mu\text{mol}(\text{CO}_2) \text{ m}^{-2} \text{ s}^{-1}$, respectively.

Sensitivities of photosynthesis to CO_2 for the two altitudes:

To intuitively describe the sensitivities of photosynthesis to CO_2 in C_3 plants growing at the different altitudes on the Tibetan Plateau, curves relating P_N to C_i were obtained from flag leaves of hulless barley from each altitude treatment under a saturated PPFD of $1,600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ and a leaf temperature of 20°C. The responses of P_N to elevated CO_2 are shown in Fig. 3 for the plants at the two altitudes. P_N for the plants at 4,333 m was higher than for those at 3,688 m under

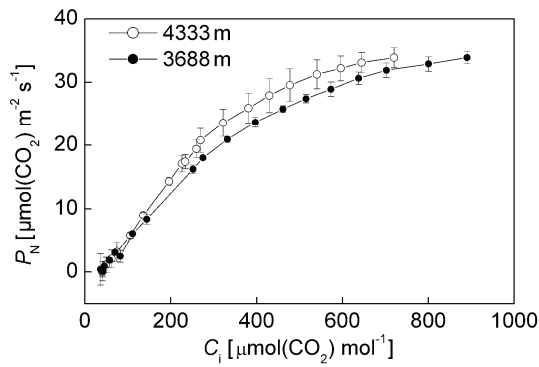


Fig. 3. Correlations between net photosynthetic rate (P_N) vs. intercellular CO_2 concentration (C_i) response measured for native hulless barley at 4,333 m and 3,688 m at an incident photosynthetic photon flux density (PPFD) of $1,600 \mu\text{mol m}^{-2} \text{s}^{-1}$ and leaf temperature of 20°C . Each symbol represents the mean value of three replications and the standard deviation ($\pm$ SD) was also determined.

elevated CO_2 ($p < 0.05$), and the shapes of the P_N/C_i curves were slightly different between the two altitudes. This discrepancy indicated that the sensitivities of photosynthesis to elevated CO_2 were different at the two altitudes.

α , $P_{\max}$, and P_N were calculated using Eq. 2, Eq. 4 and Eq. 1 with $P_{\max 350}$ and α input at a $10 \mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$ progressive enhancement of intercellular CO_2 for both altitudes, a PPFD of $1,600 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a leaf temperature of 20°C . α , $P_{\max}$ and P_N increased with increasing CO_2 by $0.4\sim 1.5\%$, $2.4\sim 4.4\%$ and $2.3\sim 4.6\%$ per $10 \mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$ elevated CO_2 , respectively (Fig. 4). However, α , $P_{\max}$, and P_N for the higher altitude plants were more sensitive to CO_2 treatment, showing levels that were $0.12\sim 0.36\%$, $0.05\sim 0.20\%$ and $0.2\sim 0.45\%$ higher than for the lower altitude plants, respectively. In addition, the percentage of enhancement of α , $P_{\max}$, and P_N decreased with additional CO_2 increments up to $170 \mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$. When CO_2 was above $170 \mu\text{mol}(\text{CO}_2) \text{mol}^{-1}$, the changes and differences between the two altitudes in the percentage of enhancement were small.

Discussion

In this study, we compared the net photosynthetic rate and photosynthetic parameters for flag leaves of hulless barley growing at 3,688 m and 4,333 m on the Tibetan Plateau. Upward regulation of photosynthetic capacity has been characterized in plants with increasing altitudes. This result is consistent with the reported data from Körner *et al.* (2003). However, some studies on altitudinal trends in photosynthetic capacities offered conclusions that contradict our study (Badger 1985, Heber and Walker 1992, Cabrera *et al.* 1998, Kao and Chang 2001, Zhang *et al.* 2005). These contradictions could be explained by a decrease in photosynthesis with

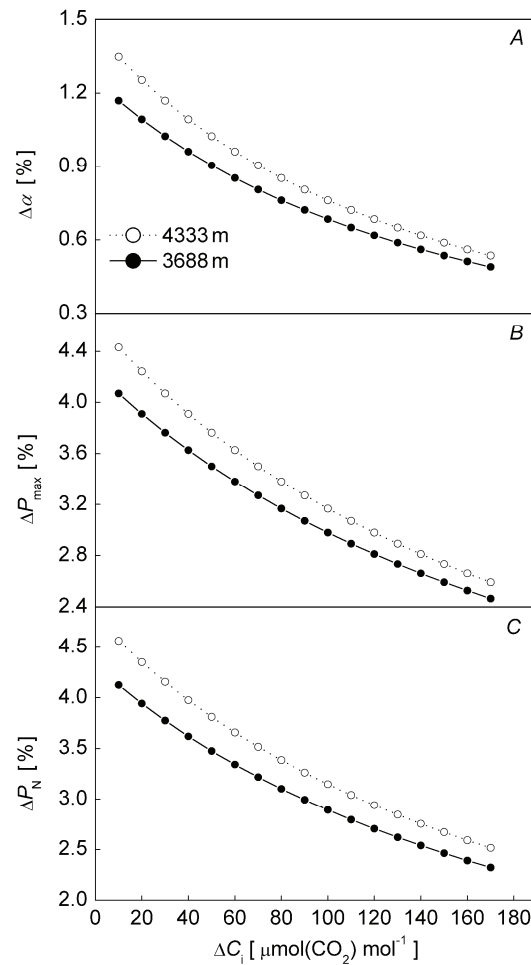


Fig. 4. Estimates of enhancement percentages of apparent quantum efficiency (α), maximum net photosynthesis ($P_{\max}$) and net photosynthetic rate (P_N) plotted as a function of $10 \mu\text{mol mol}^{-1}$ progressive enhancement of intercellular CO_2 from 0 to $170 \mu\text{mol mol}^{-1}$. These parameters were obtained for native hulless barley at 4,333 m and 3,688 m at incident photosynthetic photon flux density (PPFD) of $1,600 \mu\text{mol m}^{-2} \text{s}^{-1}$ and leaf temperature of 20°C .

altitude due to lower leaf N content, water stress and lagging leaf maturity, which are caused by decreasing soil N fertilization, precipitation, and growth temperature with altitude. In our experiment, these constraining factors on photosynthesis were avoided by pot planting, uniform water-fertilizer management and the labeling of flag-leaf ages at the two altitudes. The primary reason for the greater photosynthetic capacity of plants at higher altitude is that the reduction in RuBP carboxylation is less than the reduction in RuBP oxygenation with increasing altitudes, which causes much less of a reduction in photosynthesis compared to that observed

during photorespiration in alpine plants in the alpine environment of the Tibetan Plateau (Terashima *et al.* 1995). In addition, photosynthetic proteins (Körner *et al.* 1989, Morecroft and Woodward 1996, Pyankov *et al.* 1999), stomatal density (Körner *et al.* 1986), rate of gas diffusion (Gale 1972) and the activities of photosynthetic enzymes (Castrillo 2006) in the leaves of alpine plants have been shown to increase with increasing altitudes (Körner *et al.* 1989), all of which correlate with photosynthetic acclimation to the climatic conditions of low air pressure, cool temperature (Körner 2007), and high irradiation (Oguchi *et al.* 2003). Indeed, those positive effects could overcome the negative effect of decreasing CO₂ partial pressure with increasing altitudes in an alpine environment.

For alpine plants, the optimum temperature for photosynthesis decreased with increasing altitudes (Dillaway 2009, Fryer and Ledig 1972, Berry and Björkman 1980, Rada *et al.* 2010). In our study, the optimum photosynthetic temperature was about 20°C, lower than the 25°C optimum that has been measured for lowland plants (Akhkha *et al.* 2001). The photosynthetic capacity decreased as the temperature increased to a level above the optimal value (Lindroth *et al.* 1998). Moreover, the photosynthetic abilities (P_N) of plants growing in cool climates were more sensitive to temperature increases than those of plants growing in warm climates when the temperature was over the optimum (Tranquillini *et al.* 1986). Therefore, the decreases of photosynthetic capacities at high altitude were greater than those at low altitude when temperatures increased up to over 25°C.

Taking this into account, the lower photosynthetic capacities observed for plants at high altitude compared to those at low altitude at 30°C (Zhang *et al.* 1992, Liu *et al.* 2000, Shi *et al.* 2004) may be explained.

Our quantitative estimates of CO₂ sensitivity were modelled according to the light response and CO₂ dependency models of α and P_{max} . These models were proposed on the basis of the physiological characteristics of photosynthesis (Farquhar *et al.* 1980, Marshall and Biscoe 1980, Goudriaan *et al.* 1985) and experimentally confirmed to be reasonable (Moreno-Sotomayo *et al.* 2002, Pons and Anten 2004, Zhou *et al.* 2010). According to the parameters estimated from these models, we were able to determine that plants at the higher altitude had higher photosynthetic sensitivities to CO₂ increases than plants at the lower altitude. It can be predicted that the net photosynthetic rate for hulless barley growing at 4,333 m and 3,688 m would increase by 26.9% and 16.3%, respectively, under the atmospheric CO₂ (C_a) increases of up to 458 $\mu\text{mol}(\text{CO}_2) \text{ mol}^{-1}$ that are predicted for 2050 (McMichael *et al.* 2004), when the constant C_i/C_a ratio is assumed to be 0.7 with a temperature of 20°C (Weber *et al.* 1985, Cannon and Roberts 1995).

In summary, C₃ plants native to an alpine environment and characterized by low atmospheric pressure and low temperature have higher photosynthetic capacities and photosynthetic sensitivities to CO₂ concentration changes at higher altitude than at lower altitude on the Tibetan Plateau, while CO₂ partial pressure decreases with altitude.

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