Leaf Orientation, Incident Sunlight, and Photosynthesis in the Alpine Species Suassurea superba and Gentiana straminea on the Qinghai-Tibet Plateau

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Abstract

The extremely high level of solar radiation on the Qinghai-Tibet Plateau may induce photoinhibition and thus limit leaf carbon gain. To assess the effect of high light, we examined gas exchange and chlorophyll fluorescence for two species differing in light interception: the prostrate *Saussurea superba* and the erect-leaved *Gentiana straminea*. In controlled conditions with favorable water and temperature, neither species showed apparent photoinhibition in gas exchange measurements. In natural environment, however, their photosynthetic rate decreased remarkably at high light. Photosynthesis depression was aggravated under high leaf temperature or soil water stress. Relative stomatal limitation was much higher in *S. superba* than in *G. straminea* and it remarkably increased in the later species at midday when soil was dry. F_v/F_m as an indicator for photoinhibition was generally higher in *S. superba* than in the other species. F_v/F_m decreased significantly under high light at midday in both species, even when soil moisture was high. F_0 linearly elevated with the increment of leaf temperature in *G. straminea*, but remained almost constant in *S. superba*. Electron transport rate (ETR) increased with photosynthetically active photon flux density (PPFD) in *S. superba*, but declined when PPFD was high than about 1000 μmol m^{-2} s^{-1} in *G. straminea*. Compared to favorable environment, the estimated daily leaf carbon gain at PPFD above 800 μmol m^{-2} s^{-1} was reduced by 32% in *S. superba* and by 17% in *G. straminea* when soil was moist, and by 43% and 53%, respectively, when soil was dry. Our results suggest that the high radiation induces photoinhibition and significantly limits photosynthetic carbon gain, and the limitation may further increase at higher temperature and in dry soil.

Introduction

Temperate alpine plants are able to survive harsh environments, such as high radiation, temperature stress, and water stress, which are usually unfavorable for photosynthetic carbon gain of plants On the Qinghai-Tibet Plateau, which contains the largest area of alpine environments in the world, radiation is extremely high in summer in comparison with other alpine environments. Global radiation above the canopy usually approaches, or even surpasses, the solar constant during the plant growth season (Chen and Xu, 2000). The high radiation is frequently accompanied by low temperature and water stresses (Zheng et al., 2000), which tend to induce photoinhibition of photosynthesis, such as often occurs in lowland plants (see reviews in Baker and Bowyer, 1994). However, little evidence is available to assess whether native plants experience photosynthetic photoinhibition under natural alpine environments, and whether there is any limitation of the high radiation on leaf carbon gain.

Different species seem to acclimatize differently to high-radiation environments (Manuel et al., 1999). Some alpine plants acclimatize well to either strong irradiation or the combination of high light and low temperature (Manuel et al., 1999; Germino and Smith, 2000a). Some alpine species are not able to exert photoprotection efficiently enough to escape from photoinhibition during their growing periods (Germino and Smith, 2000a). Severe photoinhibition is also common in the morning in a giant rosette plant (*Lobelia rhynchopetalum*) living at 4000 m in the tropics (Fetene et al., 1997) and for treeline species (Germino and Smith, 2000b).

Environmental stresses other than high radiation may enhance photoinhibition of alpine plants. Water stress, which occurs frequently in alpine environments, can strengthen photoinhibition (Leuschner, 2000). High leaf temperature, which is commonly found in prostrate species in alpine locations, induces photoinhibition by mechanisms differing from those involved in low-temperature inhibition (Yamane et al., 1997; Tsonev et al., 1999). Although much attention has been paid to photoinhibition at low temperatures, little attention has been focused to photoinhibition at high leaf temperatures (Neuner et al., 1999). Germino and Smith (2000a, 2001) reported that plant architecture plays an important role in both light interception and leaf temperature in alpine plants. Steeply inclined broad leaves intercepted more light and warmed up more quickly in the early morning. Light interception and leaf temperature largely determine leaf transpiration potential (Leuschner, 2000), which may also further influence photosynthetic photoinhibition (Liang et al., 1997; Lu and Zhang, 1999). Compared with most other alpine environments, the Qinghai-Tibet Plateau is affected weakly by oceans and receives much lower precipitation (Leuschner, 2000; Zheng et al., 2000). Moreover, grassland deterioration and soil aridification are enhancing water stress there.

The objectives of this study were to determine (1) what strategies plant species with different canopy architectures adopt to cope with the high radiation on the Qinghai-Tibet Plateau; (2) whether the high-radiation environment induces photoinhibition in native grassland species, and (3) if photoinhibition does occur, to what degree it limits leaf carbon gain. To address these questions, we examined two herbaceous species with contrasting architecture: the prostrate *Saussurea superba* (Asteraceae) and the erect-leaved *Gentiana straminea* (Gentianaceae). Both are frequently found in alpine

grassland on the Qinghai-Tibet Plateau, and their occurrence has increased with recent grassland degradation. It is reasonable to suppose that dwarf plants with large prostrate leaves intercept more irradiation than tall plants with small vertical leaves. We therefore hypothesized that the former type would receive higher PPFD and have a higher risk of photoinhibition at noon.

Materials and Methods

STUDY SITE AND PLANT MATERIALS

The field site was an alpine *Kobresia humilis* meadow approximately 1 km from the Haibei Research Station for Alpine Meadow Ecosystems, Chinese Academy of Sciences (lat 37°29′N, long 101°12′E). The station is located at the northeastern edge of the Qinghai-Tibet Plateau. The altitude is about 3250 m. Annual mean air temperature is − 2°C and annual precipitation is 500 mm (Klein et al., 2001).

We studied two common species of forbs: *Saussurea superba* Anth. (Asteraceae) and *Gentiana straminea* Maxim. (Gentianaceae), which differ in stature and leaf inclination. *S. superba* is a dwarf rosette plant with two or three round leaves that expand horizontally. *G. straminea* grows its linear-shaped leaves slantwise from the soil surface to the top of the canopy. Its mature leaves are 20 to 30 cm long. The inclination angle of fully expanded leaves was measured in 20 randomly selected leaves of each species in August 2002. It was 14 ± 8° and 49 ± 9° in *S. superba* and *G. straminea*, respectively. The ratio of length to width was mostly around 1 to 2 in *S. superba* and 4 to 5 in *G. straminea*. Besides, leaves of *G. straminea* were smooth and those of *S. superba* were hairy. Importance value of the two species ranks the fourth and fourteenth for *S. superba* and *G. straminea* in ungrazed areas and tends to increase under overgrazing (Wang et al., 1995).

GAS EXCHANGE

Leaf gas exchange was measured with an LI-6400 portable photosynthesis measurement system (Li-Cor, Inc., Lincoln, NE, USA). Desiccant and soda lime were changed early in the morning before measurement. The instrument was zeroed while we waited for the dew to disappear from the leaves. In diurnal gas exchange measurement, the inlet air was not modified for humidity, temperature, or CO_2 concentration so that these variables and their variation were close to those in ambient environment of measured plants. During the measurement, we kept the leaves in their natural positions as closely as we could. Three or four leaves from different plants of a single species were measured in 4 d.

PHOTOSYNTHETIC RESPONSE TO INTERCELLULAR CO_2 CONCENTRATION AND PPFD

The dependence of photosynthetic rate on intercellular CO_2 concentration (C_i) and PPFD in intact leaves was examined in the field using the LI-6400. Light intensity from an LI-6400-02 LED light source (Li-Cor) was set to 800 μmol m^{-2} s^{-1} in A–C_i curve determination. The CO_2 concentration in the reference chamber of the LI-6400 was kept to 400 μmol mol^{-1}. During this measurement, leaf chamber temperature was controlled using the inside temperature controlling system in LI-6400 so that the air temperature within the chamber was kept to the target value ±1°C . When the relative humidity was higher than 80%, the inlet air was passed through the desiccant tube to reduce the value to 60–70%. In other situations, humidity was not adjusted. Usually A–C_i and A–PPFD curves were measured continuously for one leaf. The complete procedure took

about 2 h for a single leaf. A-PPFD curve was simulated with the following equation (modified from Dewar et al., 1998):

$$\theta(A + R)^2 - (\alpha I + A_{\max} + R) \times (A + R) + \alpha I(A_{\max} + R) = 0 \quad (1)$$

where A is net leaf photosynthesis and $A_{\max}$ is light saturated value of A. R indicates leaf dark respiration. α denotes the quantum yield and θ is dimensionless number determining the shape of the A-PPFD curve. I is the incident PPFD here.

Maximum rate of carboxylation at Rubisco ($V_{c\max}$) is calculated based on the following equation and parameters from Harley et al. (1992).

$$A = \left(1 - \frac{0.5 \times O}{\tau C_i}\right) \times \left(\frac{V_{c\max} C_i}{C_i + K_c(1 + O/K_0)}\right) - R \quad (2)$$

where C_i and O are partial pressures of CO_2 and O_2 in the intercellular air space, respectively. τ is the specificity factor for Rubisco. K_c and K_o are Michaelis constants for carboxylation and oxygenation, respectively.

Relative stomatal limitation (l_s) to photosynthesis was calculated based on A-C_i curves and leaf gas exchange measurements, with sensitivity analysis method according to Jones (1998), as described in detail by Noormets et al. (2001). The equation is:

$$l_s = 100 \times \frac{r_s}{r_s + r^* + r_{bl}} \quad (3)$$

where r_s is stomatal resistance. r^* is the cotangent to the A-C_i curve at operating point, and r_{bl} is boundary resistance, which was calculated from boundary layer conductance (2.84 mol m^{-2} s^{-1}, provided by the software for the LI-6400).

CHLOROPHYLL FLUORESCENCE

While measuring diurnal changes of photosynthesis, we monitored chlorophyll fluorescence concurrently with an LI-6400-06 PAM-2000 adaptor (Li-Cor) and a PAM-2000 chlorophyll fluorometer (Walz, Effeltrich, Germany). Fluorescence emission was recorded hourly in saturation pulse mode. On other days, fluorescence was measured alone. Fluorescence emission in response to light intensity was determined hourly by adjusting leaf orientation. F_0 and F_m were determined once in the early morning after 2 d of precipitation in 2001. We were not able to measure the diurnal changes of F_m and F_0 in 2001 due to lack of leaf dark clips, but did that in 2002. To be comparable with the data of 2001, we conducted the experiment in 2002 by choosing similar light and soil water conditions as in 2001. After steady state (F_t), maximum (F_m'), and minimum (F_0') values of fluorescence under light was measured, maximum (F_m) and minimum (F_0) values of fluorescence was determined after 10-min dark adaptation in leaf clips (Osmond et al., 1999b). Fluorescence parameter calculation was based on the methods of Adams et al. (1999). The quantum efficiency of PSII (F_v'/F_m') and its maximum value (F_v/F_m) were estimated from ($F_m' - F_0$)/F_m' and ($F_m - F_0$)/F_m, respectively. Photochemical quenching (qP) equaled ($F_m' - F_t$)/($F_m' - F_0$). PSII photochemical electron transport rate (ETR) was derived from ($F_m' -F_t$)/$F_m' \times$ PPFD, nonphotochemical quenching (NPQ) was calculated by ($F_m - F_m'$)/F_m'.

ESTIMATION OF CARBON GAIN BUDGET

To calculate stress-induced carbon loss, we plotted diurnal CO_2 uptake rates against PPFD for 6 August (dry conditions), and fitted A–PPFD curves to a fourth-order polynomial for 8 August (wet conditions). Soil water content was 0.23 and 0.30 cm^3 cm^{-3} at 5-cm depth, and RH was 39% and 59% at noon on these 2 d. For 8 August, curves were fitted to the upper profile of data points in the diagram of
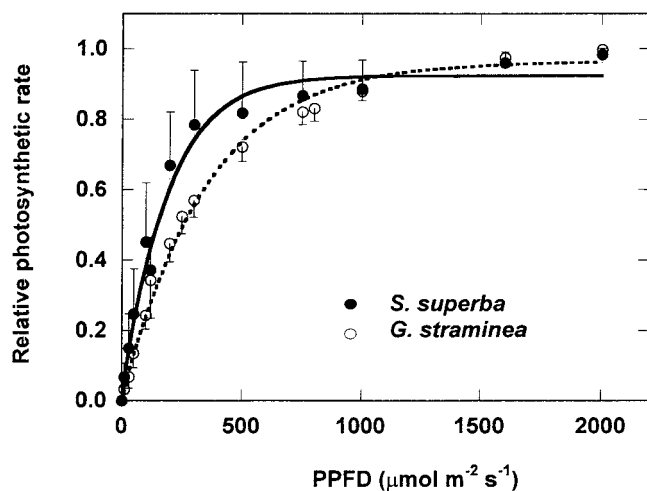
FIGURE 1. CO_2 *uptake response to photosynthetic photon flux density (A-PPFD curve) in leaves of* S. superba *(●) and* G. straminea *(○). Four leaves were measured in each species under controlled* CO_2 *partial pressure (27.7 ± 0.1 Pa). In each leaf, the range of measured photosynthetic rates in the A-PPFD curve was calculated. Relative photosynthetic rate was then got by dividing the difference between the measured photosynthetic rate in each PPFD with the range.*

CO_2 uptake rates against PPFD (see Fig. 2b). As it rained in the afternoon, we used only the morning data. CO_2 uptake rates under assumed favorable conditions were computed on the basis of the A–PPFD curves determined under controlled conditions with favorable soil and air moisture and favorable leaf temperature (see Fig. 1). CO_2 uptake rates and integrated carbon gains were calculated at 15-min intervals from the above curves and from PPFD measured in a horizontal plane 2 m above the ground by a quantum sensor (Li-Cor) from 3 to 30 August 2001. The PPFD was converted to light intensity at the leaf surface from the linear relationship between both, obtained from *in situ* measurement of PPFD in a horizontal plane above the canopy and at the leaf surface of *S. superba* and *G. straminea* over 2 d (unpublished data). Carbon loss was the reduction of daily carbon gain under natural conditions compared with favorable conditions.

Results

GAS EXCHANGE RESPONSE

To characterize the potential photosynthetic response to PPFD in the two alpine species with contrasting architecture, we measured CO_2 uptake under controlled conditions of light, temperature, and CO_2 concentration (Fig. 1). The CO_2 uptake rate became saturated at about 400 to 600 μmol m^{-2} s^{-1} in the erect-leaved *G. straminea* and 800 to 1000 μmol m^{-2} s^{-1} in the prostrate species *S. superba*.

Further measurements of gas exchange were done to clarify leaf carbon gain under changing light and soil water conditions (Fig. 2). Under a relatively dry condition after 8 d with little rainfall, CO_2 uptake rate decreased at a PPFD above 1200 μmol m^{-2} s^{-1} in *G. straminea*, but tended to increase beyond 1200 μmol m^{-2} s^{-1} in *S. superba* (Fig. 2a). The decrease of CO_2 uptake rate in both species occurred at a higher PPFD as moisture improved (Fig. 2b).

Under saturated light, stomatal conductance (g_s) was remarkably lower in *G. straminea* than in *S. superba* (Fig. 3). A marked decrease of CO_2 uptake rate in *G. straminea* was found when g_s were low (Fig. 3a). The intercellular CO_2 concentration increased rapidly with an increase of g_s in *G. straminea*, but tended to be less affected by g_s in *S. superba* in both dry and wet days (Fig. 3b). Relative stomatal
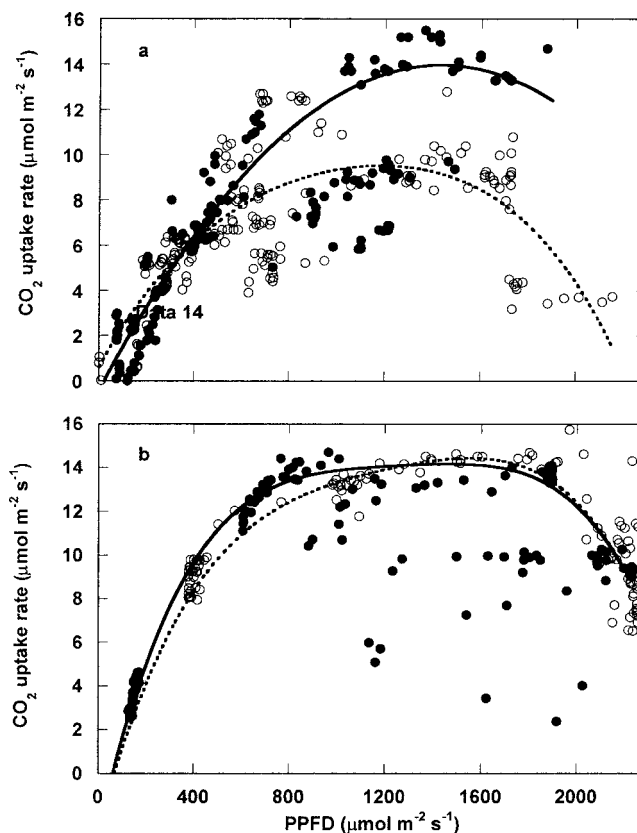

FIGURE 2. *Photosynthetic response to light intensity in* S. superba *(●) and* G. straminea *(○) under field conditions. The measurements were done on a relatively dry day (a: 6 August 2001) and a wet day (b: 8 August 2001) with soil moisture at 5 cm depth of 0.23 and 0.29 cm^3 cm^{-3}, respectively, at 17:30 h in the Haibei alpine meadow. Each data point was the mean of 6 to 12 continuous measurements within 2 to 5 min. Three individual leaves from different plants were sampled and plotted together for each species. Curves were fitted with fourth-order polynomial models.*

limitation (l_s) was much higher in *S. superba* than in *G. straminea* (Fig. 3c). It was remarkably greater in the dry than in the wet day for both species. In the wet day, l_s did not change obviously with stomatal conductance change, while in the dry day, it markedly increased with g_s decrease in both species, in which *G. straminea* was more sensitive than *S. superba*.

At PPFD over 800 μmol m^{-2} s^{-1}, l_s was significantly higher in *S. superba* than in *G. straminea* in both dry and wet conditions, though in the wet day l_s was greatly lower (Fig. 4). The relative stomatal limitation did not change greatly with PPFD in both species. Dramatic elevation of l_s occurred under dry condition at midday, even though PPFD was not high.

To understand the mechanism involved in the decrease of CO_2 uptake at high PPFD under natural conditions, we examined the effect of leaf temperature on photosynthetic gas exchange. A_{max}, which was determined from photosynthetic response to PPFD under controlled conditions, increased with rising leaf temperature, reached a maximum at 18°C (*G. straminea*) or 23°C (*S. superba*), and then decreased as temperature continued to rise (Fig. 5a). The apparent quantum yield decreased markedly as leaf temperature increased in *G. straminea*, but continued to increase in *S. superba* (Fig. 5b). The water vapor pressure deficit in the leaf (VPDL) exponentially increased with leaf temperature (Table 1). g_s decreased at high leaf temperature in both species, but the decreasing rate was fast in *G. straminea* than in *S. superba*. Relative stomatal limitation (l_s) increased more quickly in the dry than in the moist soil condition (Table 1).
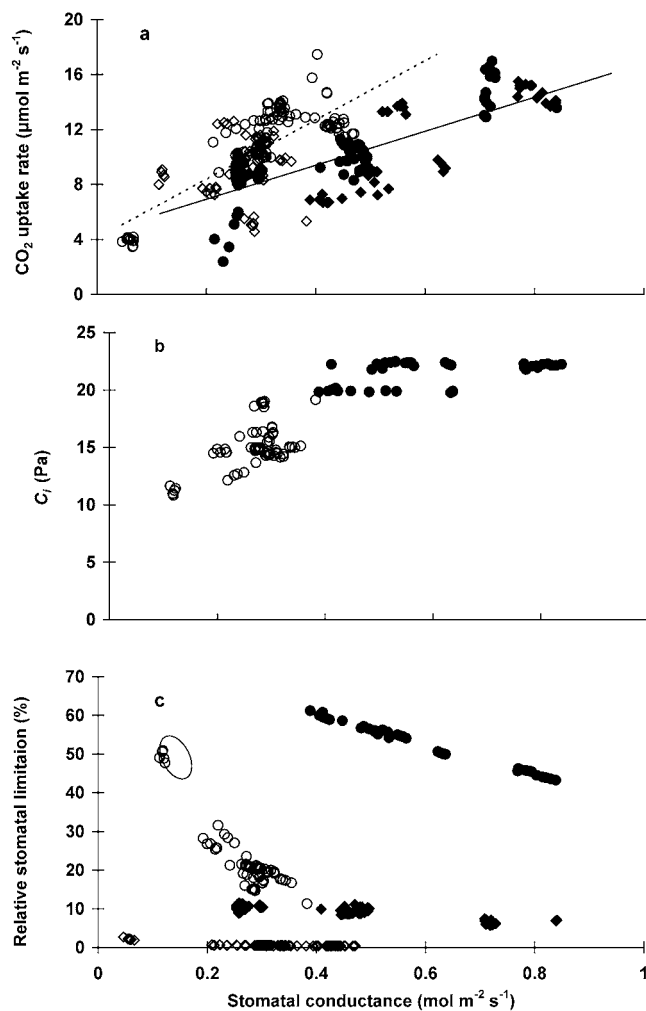
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FIGURE 3. *Relationships between stomatal conductance and (a) CO₂ uptake rate, (b) intercellular CO₂ concentration (C_i), and (c) relative stomatal limitation in* S. superba *(solid symbols, ● and ♦) and* G. straminea *(open symbols, ○ and ◇). Diamond symbols were based on the data in Figure 2a (with dry soil) and circle symbols from Figure 2b (with moist soil), but only those data for PPFD > 800 μmol m⁻² s⁻¹ were plotted here. In Figure 3b, data distribution pattern was similar between wet and dry days. Thus, diamond symbols were omitted to make the diagram clear. Symbols in the ellipse were from data at local noon time.*

FIGURE 4. *Effect of light intensity on relative stomatal limitation in* S. superba *and* G. straminea. *Data sets and the symbols were the same as in Figure 3.*

showed a consistently higher electron transport rate (ETR) at the same light intensity than did *G. straminea*. qP and ETR was also depressed at noon and recovered by 17:00 h in both species, but *G. straminea* showed a greater decline than did *S. superba* (Fig. 8).

We further examined the PSII photochemical ETR, nonphotochemical quenching (NPQ), and F_0 to reveal the influence of temperature on photosynthetic biochemistry (Fig. 9, Table 1). Both ETR and NPQ increased with increasing leaf temperature in *S. superba* (Fig. 9a). NPQ increased markedly with increasing leaf temperature in *G. straminea* (Fig. 9b), but ETR rapidly decreased when leaf temperature exceeded about 30°C. F_0 did not change significantly

The photosynthetic response to different intercellular CO₂ concentrations was similar between species. However, activities of CO₂ fixation enzymes (V_{cmax}) increased as leaf temperature increased in *S. superba* (Fig. 6). V_{cmax} in *G. straminea* reached a maximum at about 32°C and then quickly declined as leaf temperature continued to rise.

CHLOROPHYLL FLUORESCENCE

To understand the physiological mechanisms underlying the gas exchange response in the two species, we measured PSII fluorescence emission in *S. superba* and *G. straminea* throughout the day under field conditions. *S. superba* exhibited a consistently higher level of PSII photochemistry (e.g., qP, F_v'/F_m', F_v/F_m, ETR) than *G. straminea* at all times (Figs. 7, 8). For both species, PSII photochemistry significantly decreased significantly at noon ($P < 0.001$), but recovered by 17:00 h to a value near to that at 10:00. After several days of low soil moisture, F_v/F_m was significantly lower in early morning as compared with that under the high soil moisture ($P < 0.001$, Fig. 7). Similarly, *S. superba*
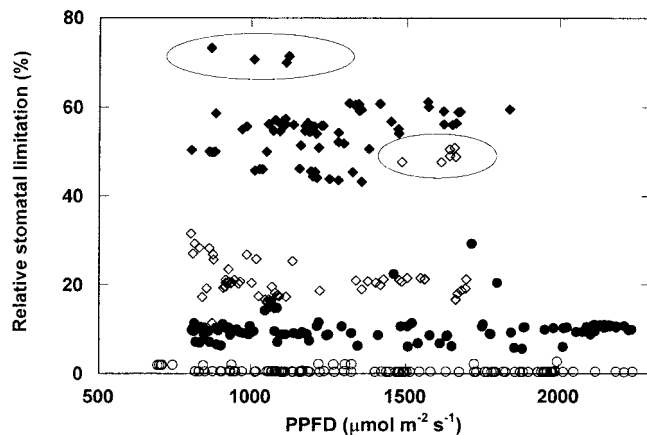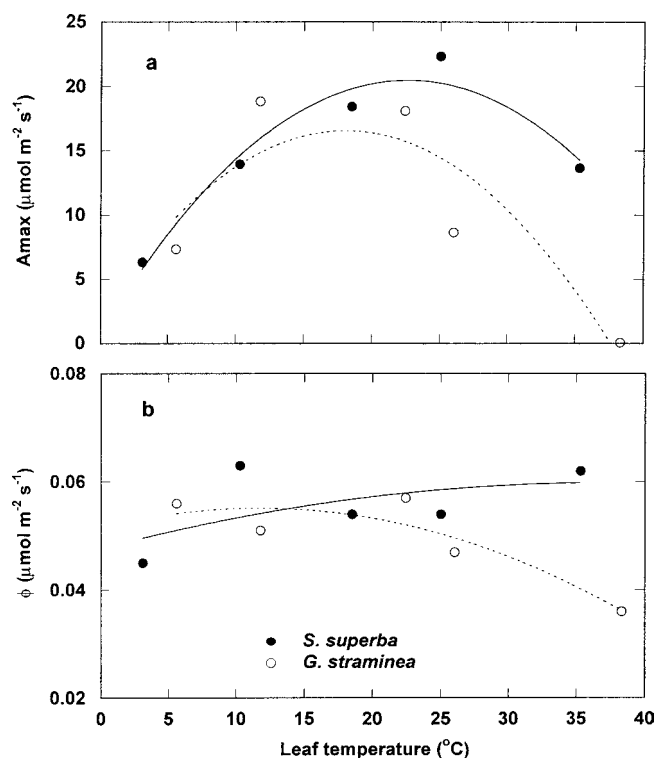

FIGURE 5. *Photosynthetic response (a: maximum CO₂ uptake rate, A_{max}; b: intrinsic quantum yield (Φ) to different leaf temperatures in* S. superba *(●) and* G. straminea *(○). A_{max} and Φ were obtained from A–PPFD response curves measured under natural conditions but with controlled leaf temperature and CO₂ concentration on 3 d with high soil moisture.*

TABLE 1

Dependence of and water vapor pressure deficit in the leaf (VPDL), stomatal conductance (g_s), relative limitation of stomatal conductance on photosynthesis (l_s), maximum quantum efficiency of PSII (F_v/F_m), and minimum fluorescence in darkness (F_0) on leaf temperature in S. superba and G. straminea in the Haibei alpine meadow

Species	Parameters	High soil moisture		Low soil moisture	
		Equation	$R^{2\,b}$	Equation	$R^{2\,b}$
S. superba	VPDL	$Y = 0.130e^{0.0553X}$	0.907***	$Y = 0.0691e^{0.106X}$	0.922***
	$g_s{}^a$	$Y = -0.00287X^2 + 0.127X - 0.804$	0.266***	$Y = -0.00213X^2 + 0.104X - 0.993$	0.372***
	l_s	$Y = -0.0775X^2 + 4.925X - 67.965$	0.579***	$Y = 14.975e^{0.0463X}$	0.466***
	F_v/F_m	$Y = -0.00103X + 0.784$	0.228**	$Y = -0.00501X + 0.928$	0.578***
	F_0	$Y = 0.000204X + 0.249$	0.008	$Y = 0.00121X + 0.212$	0.037
G. straminea	VPDL	$Y = 0.141e^{0.0960X}$	0.991***	$Y = 0.0796e^{0.108X}$	0.947***
	$g_s{}^a$	$Y = -0.00277X^2 + 0.129X - 1.114$	0.643***	$Y = -0.00472X^2 + 0.255X - 2.891$	0.216***
	l_s	$Y = 0.0242X^2 - 1.166X + 14.306$	0.925***	$Y = 1.032e^{0.116X}$	0.674***
	F_v/F_m	$Y = -0.00225X + 0.782$	0.184*	$Y = -0.00561X + 0.891$	0.513***
	F_0	$Y = 0.00164X + 0.252$	0.208***	$Y = 0.0047X + 0.1759$	0.425**

[a] The equations for stomatal conductance and leaf temperature were constructed based on value with leaf temperature above 15°C in order to diminish the effect of very high g_s values observed in early morning.

[b] The marks of * denotes statistical significance of $P < 0.05$, ** of $P < 0.01$, and *** of $P < 0.001$.

with leaf temperature increment in *S. superba* while it increased linearly in *G. straminea*. F_v/F_m declined with leaf temperature linearly in both species. The slope was steeper under the dry than under the wet soil conditions. *G. straminea* showed a slightly higher sensitivity to high temperature than *S. superba* (Table 1).

LEAF CARBON GAIN ESTIMATED FOR DIFFERENT LIGHT CONDITIONS

During the experimental period in August 2001, the estimated daily carbon gain was higher in *S. superba* under favorable (experimentally controlled) and dry conditions but similar in both species under wet conditions (Table 2). The daily carbon gain by both species was much less under natural conditions than under favorable conditions, even when soil moisture was high (Table 2). Most of the reduction occurred under high light conditions, e.g., carbon gain was decreased by 34% in *S. superba* and by 27% in *G. straminea* when PPFD was higher than 1600 µmol m^{-2} s^{-1}. Water stress led to further respective decreases of 12% and 32% in daily carbon gain. Water stress and high light (e.g., >1600 µmol m^{-2} s^{-1}) together induced about 47% carbon gain reduction in *S. superba*, and, more speculatively, 73% in *G. straminea*.

Discussion

HIGH LIGHT DEPRESSED PHOTOSYNTHETIC CARBON GAIN UNDER NATURAL ENVIRONMENTS

Light is the energy source for photosynthesis, but excessive light may induce photoinhibition of photosynthesis and reduction of leaf carbon gain (Osmond et al., 1999a). Many alpine environments are characterized by high levels of irradiation (Körner, 1999). The Qinghai-Tibet Plateau receives significantly more radiation than most other alpine areas in the world (Chen and Xu, 2000). Therefore, avoidance or reduction of photoinhibition should be essential for plant carbon gain, and should give a competitive advantage in such an environment (Osmond et al., 1999a).

CO_2 uptake rate was not depressed even at PPFD > 2000 µmol m^{-2} s^{-1} in both *S. superba* and *G. straminea* when leaves were kept under controlled conditions with favorable soil moisture (Fig. 1). Almost constant values of photochemical fluorescence quenching (qP) under various PPFD in the early morning (Fig. 8a and b) also indicate that high radiation alone was not able to induce significant photo-

inhibition in both the species, as (1 − qP) was recognized as photoinhibition pressure (Osmond et al., 1999a). Species or leaves growing under high radiation are likely to have greater capacity to use or to tolerate high light and thus mitigate photoinhibition than those under low light regimes (Ferrar and Osmond, 1986; Mulky and Pearcy, 1992; Kursar and Coley, 1999; Muraoka et al., 2000). *S. superba* and *G. straminea*, like the species in other alpine areas (Streb et al., 1998; Manuel et al., 1999; Germino and Smith, 2000a), seem to be sun-living species with a high capacity for protection from photoinhibition.

The CO_2 uptake rate decreased, however, at high light in both species under natural conditions (Fig. 2). The diurnal course showed that the decrease always occurred around midday, with a similar pattern as that of maximum variable fluorescence (F_v/F_m, Fig. 7), photochemical fluorescence quenching (qP) and ETR (Fig. 8). Species *S. superba* showed higher photochemical capacity, especially at midday, than *G. straminea* (Figs. 7, 8). The degree of photoinhibition as indicated by F_v/F_m was consistently lower in the former than the latter species (Figs. 7, 8c and d). In *G. straminea*, however, qP was markedly depressed at midday. Consequently, photoinhibition pressure (1 − qP) was built up and F_0 was elevated (Table 1, high temperature appeared simultaneously with high light at midday), indicating
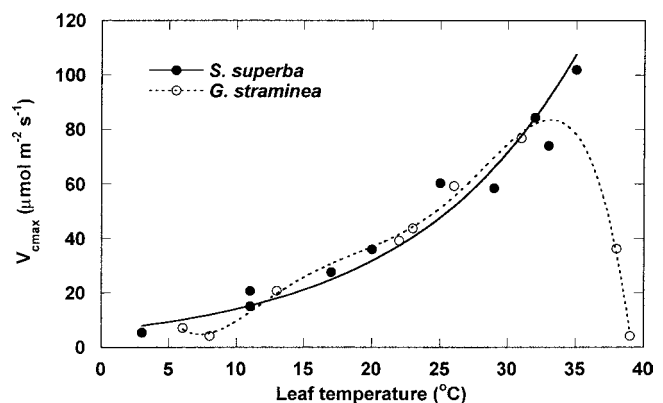

FIGURE 6. *Maximum carboxylation rate (V_{cmax}) under different leaf temperatures in* S. superba *(●) and* G. straminea *(○). V_{cmax} was determined from the A–C_i curves that were constructed at PPFD of 800 µmol m^{-2} s^{-1}. VPDL was between 0.8 and 1.1 kPa during the measurement. Four leaves were used in each species. Relative photosynthetic rate was calculated by the same method in Figure 1.*
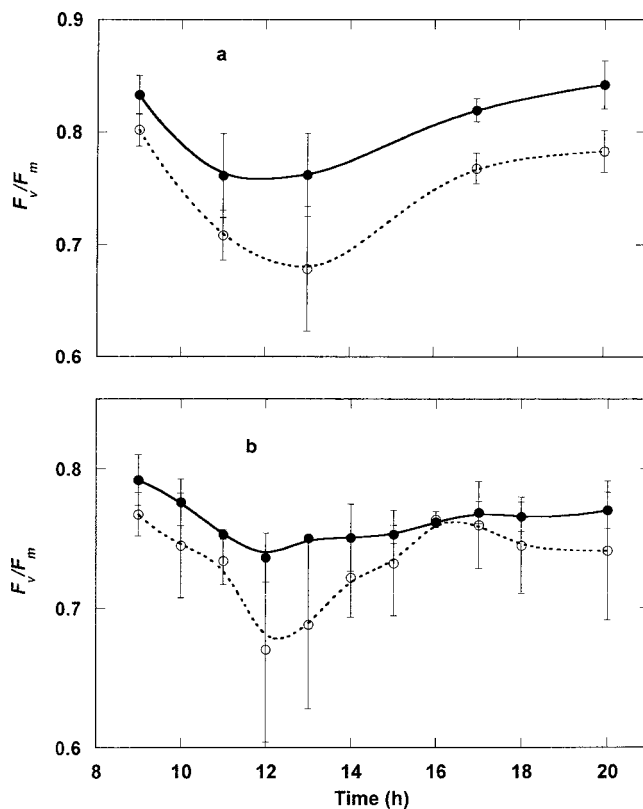
FIGURE 7. *Diurnal change of maximum quantum efficiency of PSII* (F_v/F_m) *in* S. superba *(●) and* G. straminea *(○) under dry (a) and wet (b) soil conditions. Leaves were measured for* F_m *and* F_0 *after dark adaptation in leaf clips for 10 min.* F_v/F_m *was calculated from (*F_m − F_0)/F_m. *Each point was the mean of three to six pieces of leaves.*

significant photoinactivation (Osmond et al., 1999a). A slower recovery of F_v/F_m in later afternoon also showed more serious depression of photochemistry in this species than *S. superba*, in which F_v/F_m almost fully recovered by time of sunset (Figs. 7, 8).

HIGH LEAF TEMPERATURE AND POOR SOIL MOISTURE ACCELERATED THE LIMITATION OF HIGH LIGHT ON PHOTOSYNTHESIS

As mentioned above, high light alone did not induced obvious photoinhibition in these two species, suggesting that these species held effective protective strategies. Chlorophyll fluorescence also showed great stimulation of thermal dissipation of absorbed excitation energy in both species at midday, as demonstrated by quick increase of NPQ in high light and leaf temperature (Fig. 9). Stimulation of thermal dissipation was proposed to be an effective and general way of photoprotection (Warren et al., 1998; Osmond et al., 1999a). Therefore, photoinhibition, as demonstrated by depression of F_v/F_m and ETR (Figs. 7, 8), should be the results of interaction of high light and other factors. Our results showed that high leaf temperature, which generally occurred simultaneously with high light, was an important stressful factor contributing to photoinhibition in natural environment.

Despite of low air temperature in alpine regions, leaf temperature was not necessarily low in local species (Körner, 1999). Leaf temperature was near to 40°C in both species at midday (Fig. 9). In *G. straminea*, F_v/F_m and ETR decreased while F_0 significantly increased at high leaf temperature (Fig. 9, Table 1). In addition to these fluorescence parameters, the reduction of both maximum CO_2 uptake rate and apparent quantum yield at leaf temperatures higher than
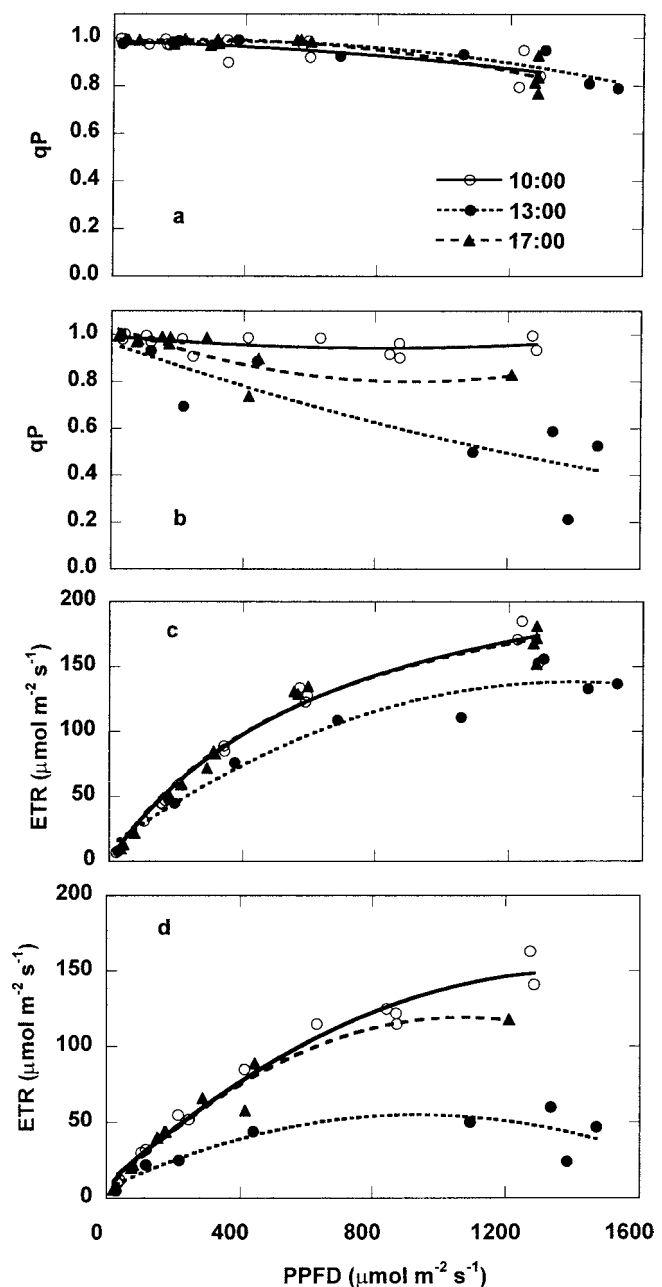

FIGURE 8. *Response of PSII photochemical fluorescence quenching (a − b: qP) and electron transport rate (c − d: ETR) to change in PPFD in* S. superba *(a, c), and* G. straminea *(b, d) in the Haibei alpine meadow. Measurements were taken on 14 August 2001 at 1- to 2-h intervals throughout the day. PPFD was adjusted by either shading plants with polyethylene film or changing leaf orientation.*

20°C indicated that this species suffered from photoinhibition when leaf temperatures was high (Fig. 5; Osmond et al., 1999a). The highly sensitivity of PSII photochemistry to high leaf temperature may be partly induced by dramatically decreased carboxylation enzyme activity (Fig. 6).

S. superba seemed able to cope with much higher radiation than *G. straminea* (Figs. 1, 2a). Nevertheless, high leaf temperature also impaired carbon gain under high light in this species, although to a lesser extent (Figs. 2, 5, 7–9, Table 1). Insensitive of F_0 and ETR to high leaf temperature inferred that photodamage may not occur in this species (Osmond et al., 1999a). Under moderately high light intensity, carboxylation enzyme activity and ETR increased as leaf temperature

increased (Figs. 6, 9). Because net CO_2 uptake rate was saturated or even decreased above a leaf temperature of 23°C (Fig. 5), photorespiration or other electron transportation pathways should be stimulated by an increase in leaf temperature. The rapid decrease of net CO_2 uptake rate (Fig. 2b) and g_s at high PPFD with almost constant relative stomatal limitation (Fig. 4) and C_i (Fig. 3b) also implied that a great stimulation of photorespiration occurred at high leaf temperature. Besides, we observed a linear increase of ETR with light intensity to $>2000\,\mu mol\,m^{-2}\,s^{-1}$ when leaf temperature was around 20°C on the morning of 8 August, when photosynthesis was leveled even below 1000 $\mu mol\,m^{-2}\,s^{-1}$ (Fig. 1). It seems that photorespiration could be promoted by high light intensity to deal with excessive light (Kozaki and Takeba, 1996; Manuel et al., 1999; Streb et al., 1998). Unfortunately, we did not directly measure photorespiration in this experiment because of the technical limitation in the harsh environment.

Water stress promoted the sensitivity of carbon gain to high PPFD in *G. straminea*, and to a less degree, in *S. superba* (Fig. 2a). Mild water stress may not affect PSII photochemical efficiency (Liang and Zhu, 1999). But severe drought or a combination of water deficit and other stresses favored photoinhibition (Masojidek et al., 1991; Giardi et al., 1996; Valladares and Pearcy, 1997; Flexas et al., 1999). Deprivation of CO_2 was thought to be the major reason for depression of photosynthesis in such circumstances (Cornic, 1994; Park et al., 1996). Besides photoinhibition, the following causes make carbon gain by alpine species more sensitive to water stress.

1. High altitude regions had low CO_2 partial pressures. Although air has the same volume concentration of CO_2 at high altitude, the actual partial pressure of CO_2 is much lower. Low CO_2 partial pressure demands higher stomatal conductance to give the same photosynthetic carbon gain as compared with normal CO_2 partial pressure. It was reported that many species in high elevation had higher stomata density and g_s (Hovenden and Brodribb, 2000), though low atmospheric pressure itself may partly compensate for low CO_2 partial pressure in alpine regions (Smith and Knapp, 1990; Terashima et al., 1995; Sakata and Yokoi, 2002).

2. Alpine species tend to have much lower mesophyll conductance than lowland species (Loreto et al., 1992; Kogami et al., 2001). We calculated mesophyll conductance of 0.84 and 1.92 $\mu mol\,m^{-2}\,s^{-1}\,Pa^{-1}$ at 25°C in *S. superba* and *G. straminea* according to Loreto et al. (1992). These values are lower than those reported in other alpine species (Körner and Larcher, 1987; Kogami et al., 2001). Therefore, insufficient CO_2 supply is particularly harmful to carbon gain by alpine species (Fig. 6), especially in species
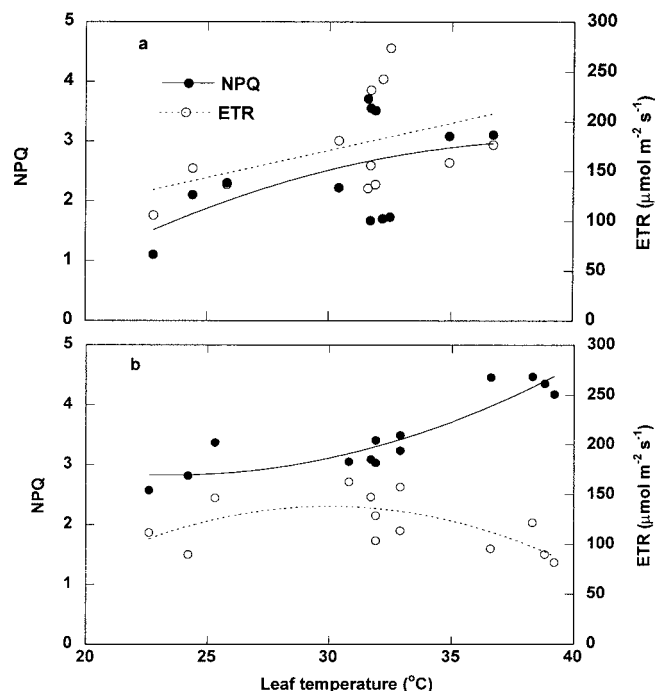

FIGURE 9. *Effect of leaf temperature on PSII photochemical electron transport rate (ETR) and nonphotochemical quenching (NPQ)* S. superba *(a) and* G. straminea *(b) in the Haibei alpine meadow on 14 August 2001. Measurements were taken at 1- to 2-h intervals throughout the day, and PPFD was adjusted by either shading plants with polyethylene film or changing leaf orientation.*

with low stomatal conductance, such as *G. straminea* (Fig. 3a and b, Table 1). The decrease of C_i with decreasing A also indicates a stomatal limitation to photosynthesis (Fig. 3). Photoinhibition in *G. straminea* may be partly caused by stomatal closure at noon under dry conditions (Fig. 3c).

3. Strong radiation induces high leaf temperature and high VPDL (Körner, 1999), which may have a significant effect on photosynthesis (Yong et al., 1997). For instance, in both species the *in situ* leaf temperature reached about 40°C under strong midday radiation (Fig. 9). VPDL increased rapidly with leaf temperature elevation, particularly under the dry soil conditions (Table 1). Low g_s, by impairing transpirational cooling, may further promote leaf temperature and then

TABLE 2

Leaf carbon gain estimated for S. superba *and* G. straminea. *Daily carbon gain was estimated by integrating instantaneous CO_2 uptake at 15-min intervals from 06:30 to 20:00 h. Instantaneous CO_2 uptake was calculated from A–PPFD curves experimentally obtained in the study. Carbon gain assumed for favorable (experimentally controlled) conditions was estimated from the A–PPFD curve fitted for the data in Figure 1 by a hyperbolic model (Dewar et al., 1998). Carbon gain for leaves under natural conditions was estimated from fourth-order polynomial models that were fitted to the measured data on 6 and 8 August (dry and wet conditions, respectively)*

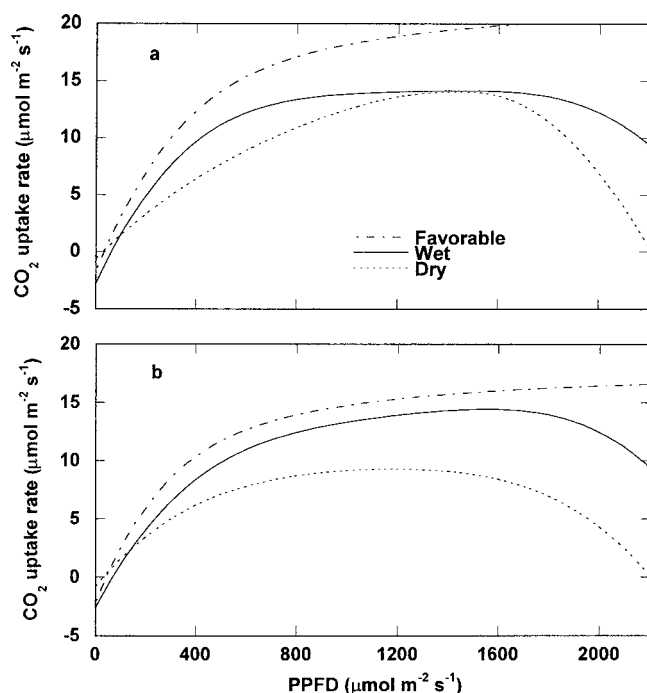|	*S. superba*			*G. straminea*		
	Experimentally controlled condition	Natural environment		Experimentally controlled condition	Natural environment	
		High soil water	Low soil water		High soil water	Low soil water
Total daily CO_2 uptake (mol m^{-2} day^{-1})	0.56	0.41	0.34	0.48	0.38	0.23
Daily contribution of CO_2 uptake by PPFD ≥ 800 $\mu mol\,m^{-2}\,s^{-1}$ (%)	66	65	69	71	72	63
Daily contribution of CO_2 uptake by PPFD ≥ 1600 $\mu mol\,m^{-2}\,s^{-1}$ (%)	28	26	25	37	33	21

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FIGURE 10. *Comparison of CO_2 uptake rates under different conditions to determine carbon budget under high light and water stress in* S. superba *(a) and* G. straminea *(b) in the Haibei alpine meadow. Fourth-order polynomial models were fitted to the measured data on 6 and 8 August (Fig. 2), which represent "dry" and "wet" conditions, respectively. The A–PPFD curves measured under controlled conditions were fitted by hyperbolic models (Dewar et al., 1998) to indicate favorable conditions (same curves as in Fig. 1).*

stimulate VPDL. Such feedforward effect seems more harmful to *G. straminea*, which had lower g_s than *S. superba*, as indicated by quick decrease of C_i when g_s declined (Fig. 3b). Leaf with low C_i was more prone to photoinhibition under high light (Park et al., 1996). In *S. superba*, C_i did not decrease with g_s declination (Fig. 3b and c), probably due to the stimulated photorespiration. As a result, in both species, CO_2 uptake rate suddenly dropped (Fig. 2) at PPFD around 1800 μmol m^{-2} s^{-1} was accompanied by a rapid increase of leaf temperature and VPDL, though soil and air moisture was almost constant during the daytime.

It seemed that high PPFD alone did not change the relative relationship between stomatal and nonstomatal limitation in both species (Fig. 4). The abrupt increase of l_s at midday when soil was dry supposed be the direct result of low g_s (Fig. 3c) induced by high leaf temperature and VPDL (Table 1). In *G. straminea*, nonstomatal limitation always dominated. Nevertheless, the rapid increase of l_s at midday when PPFD, leaf temperature and VPDL were high (Figs. 3c, 4) inferred that, besides photoinhibition, reduction of g_s further damaged CO_2 uptake, especially in dry days.

PLANT ARCHITECTURE CONTRIBUTED TO THE DIVERGENCE OF PHOTOINHIBITION

The divergent sensitivity of carbon gain to strong light, high leaf temperature, and water stress in the two species was directly related to their leaf architecture. Leaves of *S. superba* lie prostrate on the ground and so intercept high radiation (unpublished data), and have a thick boundary layer (Rosenberg et al., 1983). Consequently, the leaf

temperature was high. As photorespiration rate increased with leaf temperature, photoinhibition was efficiently avoided by high photochemical fluorescence quenching, despite of the lower NPQ, as compared with *G. straminea* (Fig. 9). Furthermore, although g_s was high, large water loss was avoided because the low boundary layer conductance directly controlled transpiration (Rosenberg et al., 1983). Even under mild water stress, C_i did not decrease greatly (Fig. 3b), and CO_2 assimilation rate was maintained (Fig. 2a and b). On the other hand, high boundary layer resistance led to higher relative stomatal limitation than nonstomatal limitation under dry conditions (Fig. 4). Furthermore, photoprotection by elevated photorespiration directly reduced net CO_2 uptake rate (Fig. 10, Table 2).

The leaves of *G. straminea* stretch up into the air, in contrast to those of *S. superba*. Therefore, they intercept less light and have better air circulation than *S. superba*. Hence, thermal dissipation and leaf transpirational cooling was faster and leaf temperature was lower. It is not surprising that this species uses thermal dissipation of absorbed excitation energy as the main way of photoprotection (Fig. 9b). Yet it seems that NPQ was not sufficient to avoid photoinhibition under strong light (Figs. 7, 8). To avoid large water loss, stomatal conductance is low (Fig. 3). Stomatal conductance was low and relative stomatal limitation was high at high leaf temperatures (data not shown). Carboxylation activity was also markedly inhibited by high leaf temperatures (Fig. 6). Consequently, photochemistry was depressed and ETR declined.

Contrary to *S. superba*, transpiration was determined by g_s in *G. Straminea*. Stomatal conductance was lower and responded faster to leaf temperature and VPDL (Table 1), so as to avoid vast water loss thought transpiration. Despite of the lower stomatal conductance and of the higher sensitivity of CO_2 uptake rate to g_s decrease in *G. straminea*, the relative stomatal limitation was much lower in this species than in *S. superba* (Figs. 3c, 4), which denoted that nonstomatal factors generally limited carbon gain at PPFD high than 800 μmol m^{-2} s^{-1}. This was consistent with the lower light saturation point (Fig. 1) and photochemical activities (Fig. 8) as well as higher sensitivity of enzyme activities to high leaf temperature (Figs. 5, 7).

Since photochemistry almost fully recovered in the late afternoon (Figs. 7, 8), photoinhibition was not chronic in both species. However, substantial carbon loss was expected, because PPFD was greater than 800 μmol m^{-2} s^{-1} for more than half of the daytime, accounting for more than 70% of total PPFD in the area in August 2001 (unpublished data). These figures did not change significantly for the whole growth season, as calculated by the models of Jones (1992). Our rough estimation demonstrates that substantial carbon gain is lost under natural conditions, even when soil water content is high (Table 1). Photoinhibition may be a major cause of carbon loss in *G. straminea*, but photoprotection by photorespiration also led to marked loss of carbon gain in *S. superba*. High light intensity induced the greatest reduction of carbon fixation, and the reduction was aggravated by water stress (Table 1). *Gentiana. straminea* was more sensitive to water stress, or to water stress plus strong radiation. Our calculation was based on the PPFD measured in a horizontal plane above the canopy, and so tended to overestimate the reduction of carbon gain. Nevertheless, this may be partly offset by neglect of the prolonged depression of photosynthesis after midday photoinhibition (as shown by the very low values of CO_2 uptake at lower PPFDs in Fig. 2b). Because normal conditions can be both drier and wetter than those on the days we used in our calculations, and we compared leaf architecture in a simple manner, detailed models should be developed to distinguish the effects of architecture, biochemistry, and photoinhibition in the carbon budget of alpine ecosystems (Ninemets and Tenhunen, 1997). Nevertheless, our rough estimation suggests that carbon gain and biomass production of forbs in this alpine grassland are limited by high light intensity, and that the limitation can be exacerbated by high leaf temperatures and water stress.

Acknowledgments

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