Photosynthetic depression in relation to plant architecture in two alpine herbaceous species

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Abstract

The Qinghai-Tibet Plateau is characterized by extremely high radiation, which may induce down-regulation of photosynthesis in plants living in this alpine ecosystem. To clarify whether photoinhibition occurs in the alpine environment and to discern its underlying mechanisms, we examined photosynthetic gas exchange and fluorescence emission in response to the changes in photosynthetic photon flux density (PPFD) and leaf temperature under natural regimes for two herbaceous species: prostrate *Saussurea superba* and erect-leaved *Saussurea katochaete* from altitude 3250 m on the Qinghai-Tibet Plateau. *S. superba* intercepted a higher maximum PPFD and experienced much higher leaf temperature than the erect-leaved *S. katochaete*. *S. superba* exhibited a much higher light saturation point for photosynthesis than *S. katochaete*. Under controlled conditions, the former species had higher CO_2 uptake rates and neither species showed obvious photosynthetic down-regulation at high PPFD. Under natural environmental conditions, however, apparent photoinhibition, indicated by reduced electron transport rate (ETR), was evident at high PPFD for both species. After a night frost, the photochemistry of *S. katochaete* was depressed markedly in the early morning and recovered by mid-day. After a frost-free night, it was high in the morning and low at noon due to high radiation. *S. superba* did not respond to the night frost in terms of daytime photochemical pattern. In both species, photochemical depression was aggravated by high leaf temperature and the erect species was more sensitive to high temperature. This study suggests that the high radiation on the Qinghai-Tibet Plateau is likely to induce rapidly reversible photoinhibition, which is related closely to plant architecture. Photochemistry in the prostrate species seems able to tolerate higher PPFD, without obvious suppression, than the erect species.
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1. Introduction

Exposure of plants to excessive light energy generally induces photoinhibition, including dynamic photoinhibition or photoprotection, and chronic photoinhibition or photoinactivation (Chow, 1994; Long et al., 1994; Osmond and Grace, 1995; Osmond et al., 1999). Under natural conditions, however, photoinhibition can occur even under moderately high irradiation when other environmental stresses exist (Streb et al., 1997; Osmond et al., 1999). Several authors have suggested that low temperature, which may lead to reduction of photosynthetic activity, induces photoinhibition in the field (Streb et al., 1997; Germino and Smith, 2000a,b); however, the low Fv/Fm (maximum quantum efficiency) on cold days may be due to effective photoprotection in some cases (Osmond et al., 1999). Water stress is likely to increase photoinhibition (Flexas et al., 1999), and high temperature promotes the sensitivity of PSII to strong light stress (Yamane et al., 1997; Misra et al., 1998). However, the effects of these factors on photoinhibition in various studies have been inconsistent, partly due to the complexity of their interactions (Watling et al., 1997; Lu and Zhang, 1999; Manuel et al., 1999).

Alpine areas are characterized by high radiation, which generally co-occurs with low temperature and/or water stress; these conditions are unfavorable for photosynthesis and other physiological processes in plants (Körner, 1999). Such a combination of climatic conditions often may induce photosynthetic photoinhibition in lowland plants (see reviews in Baker and Bowyer, 1994). However, previous studies showed that alpine species seem to acclimate well to either strong irradiation or the combination of strong irradiation and low temperature (Manuel et al., 1999; Germino and Smith, 2000a). Local species in the Qinghai-Tibet grasslands were more resistant to the above stresses than crops, especially those cultivated in the lowlands (Zhang et al., 1995). The suggested mechanisms include delays in greening (Lütz, 1996), increases in antioxidants (Wildi and Lütz, 1996; Streb et al., 1997), elevation of cyclic electron transport (Manuel et al., 1999), and high rates of photorespiration (Heber et al., 1996; Streb et al., 1998; Manuel et al., 1999).

On the other hand, some studies have shown that alpine plants cannot exert photoprotection sufficiently to avoid photoinhibition during their growing period (Germino and Smith, 2000a). *Eriophorum angustifolium*, in which greening is delayed, was damaged by the strong irradiation that followed a frost once its leaves turned green, even in the presence of high concentrations of protective zeaxanthin (Lütz, 1996). Severe photoinhibition was also common in the morning for a tropical alpine giant rosette plant living at 4000 m (Fetene et al., 1997) and tree-line species (Germino and Smith, 2000b).

On Qinghai-Tibet Plateau, global radiation above the canopy usually approaches, or even surpasses, the solar constant during the plant growth season (Chen and Xu, 2000). In summer, intense light sometimes follows a night frost and it is accompanied by marked variations in temperature and/or water stress on clear days (Zheng et al., 2000). The objectives of this study were to determine: (1) whether photoinhibition occurs in local species in their natural environments, and if so, (2) whether, and if so how, plant architecture influences the degree of photoinhibition, because changes in plant architecture may result in variations in light interception and, or, temperature of leaves. To address these questions, we used two species from an altitude of 3250 m. Both species were in the family Asteraceae, *Saussurea superba* and *Saussurea katochaete*, which are found commonly in the alpine grasslands on the Qinghai-Tibet Plateau. These species differ in their architecture with respect to plant height, leaf size and leaf inclination. Dwarf plants with prostrate and large leaves, like *S. superba*, are thought to accept more irradiation than the tall plants with vertical and small leaves, like *S. katochaete*. We hypothesized that the former species intercepts higher photosynthetic photon flux density (PPFD) and tends to have a higher risk of photoinhibition at noon and that the latter experiences photoinhibition induced by low temperature in the morning.

2. Materials and methods

2.1. Study site and plant materials

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

Two commonly found herbaceous species that differ in plant stature and leaf inclination, *S. superba* Anth. (Asteraceae) and *S. katochaete* Maxim. (Asteraceae), were studied. *S. superba* is a dwarf rosette plant with two or three-round leaves that expand horizontally on the soil surface. *S. katochaete* usually has two to four small vertical leaves that are extended to the upper canopy of the community by long petioles. The fully expanded leaves in *S. superba* are three to four times larger than those in *S. katochaete*. The two species co-exist in the alpine meadow and their dominance tends to increase under overgrazing.

2.2. Temperature and light interception measurement

Three plants from each species were selected within an area of about 1 m^2 for leaf temperature measurement. A copper–constantan thermocouple was attached to the abaxial side of a fully expanded leaf on each plant. Air temperature was measured with a sensor just above the canopy. A photodiode (G1118, Hamamatsu, Japan) was placed close to the leaves to which the thermocouples had been attached, with the light-sensitive surface of the sensor was in the same plane as the adaxial surface of the leaf. The azimuth angle of the selected leaves for temperature and light incidence measurement was between 140 and 180°. The inclination angle was between 10 and 20° in *S. superba* and 75 and 85° in *S. katochaete*. Two light sensors were set horizontally above the canopy and on the soil surface, to determine the light intensity above and below the canopy. All the sensors were connected to a data-logger (Thermo-dac E, Eto Denki, Japan) to record the signals at 1-min intervals. The theoretical calculation of light intercepted by leaves with different orientation and inclination angles was based on the method of Jones (1992).

2.3. Photosynthetic response to intercellular CO$_2$ concentration and PPFD

The dependence of photosynthetic rate on intercellular CO$_2$ concentration (C_i) and PPFD was examined with intact leaves using an infrared gas analyzer (LI-6400; Li-Cor, Inc., Lincoln, NE, USA). For $A-C_i$ curve determinations, the light intensity was 800 μmol m^{-2} s^{-1} with an artificial light source. The CO$_2$ concentration in the reference chamber was kept at 400 μmol mol^{-1}. During the measurement, leaf temperature was controlled to the target temperature ±1 °C. When the relative humidity of the air exceeded 80%, the inlet air was passed through a desiccating tube and the humidity reduced to 60–70%. In other situations, the relative humidity was not adjusted. $A-C_i$ and $A-$PPFD curves were fitted according to Harley et al. (1992) and Dewar et al. (1998), respectively.

2.4. Chlorophyll fluorescence

Chlorophyll fluorescence was monitored using a chlorophyll fluorometer (PAM-2000; Walz, Effeltrich, Germany). Lasting time and intensity of saturation pulse light was pre-tested to ensure fully reduction of PSII reaction centers even under high light in field measurement. Fluorescence emission was recorded hourly in saturation pulse mode. Fluorescence emission in response to light intensity was determined hourly by adjusting the leaf orientation or shading the leaf with polyethylene film. F_o and F_m were determined in the early morning. The parameters were calculated as described by Adams et al. (1999).

2.5. Data analysis

One-way ANOVA method was used to compare the results with software SPSS for WINDOWS (SPSS Inc., 1997, Chicago, USA).

3. Results

3.1. Light interception and leaf temperature

To assess the light regime and leaf temperature, we examined the PPFD incidence on leaves with different inclination and the diurnal variation of

leaf temperature. *S. superba* received higher maximal PPFD than *S. katochaete* (Fig. 1). PPFD, which exceeded 1600 μmol m^{-2} s^{-1}, accounted for more than 60% of daily total PPFD interception in *S. superba* but less than 20% in *S. katochaete*, on typical bright days in August 2001 (Fig. 2). Theoretical calculations, as shown in Fig. 3, yielded similar diurnal patterns of PPFD incidence to those measured (Fig. 1).

The leaf temperature was much higher in *S. superba* than *S. katochaete* on clear days, with daily maximums of 43.5 and 30.5 °C, respectively (Fig. 1). *S. katochaete* began to intercept strong light when leaf temperature was low in early morning, while *S. superba* received high PPFD later with high leaf temperature.

3.2. Photosynthetic response to intercellular CO$_2$ concentration and PPFD

To characterize the potential photosynthetic response to PPFD in the two alpine species with contrasting architecture, we measured CO$_2$ uptake under controlled light and temperature conditions and at controlled CO$_2$ concentrations (Fig. 4a). Under favorable leaf temperature and soil water conditions, the CO$_2$ uptake rate saturated at about 600 μmol m^{-2} s^{-1} in *S. katochaete* and at about 1000 μmol m^{-2} s^{-1} in *S. superba*. The light-
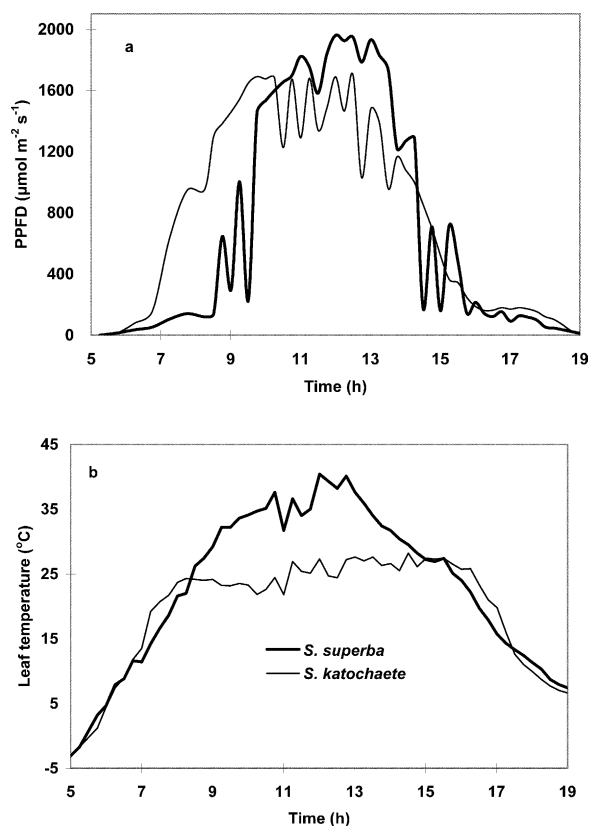

Fig. 1. Diurnal change of PPFD interception (a) and temperature (b) in leaves of *S. superba* (thick line) and *S. katochaete* (thin line) on a clear day in August 2001. The azimuth angles of the selected leaves for temperature and light incidence measurements were from 140 to 180°. The inclination angle was between 0 and 20° in *S. superba* and 70 and 85° in *S. katochaete*.
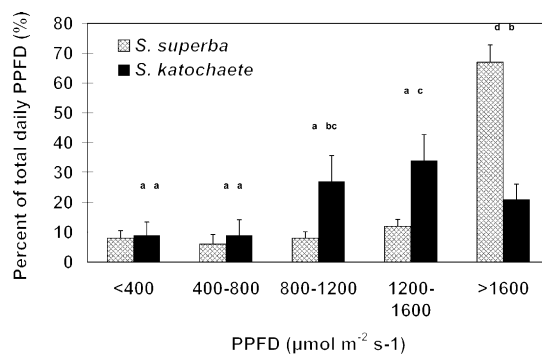

Fig. 2. Frequency distribution of PPFD incidence on leaves of *S. superba*, *S. katochaete*, on a typical clear day in August 2001. Data from three separate sensors for each species were averaged and standard errors were represented. Different letters indicate significant differences ($P < 0.05$).
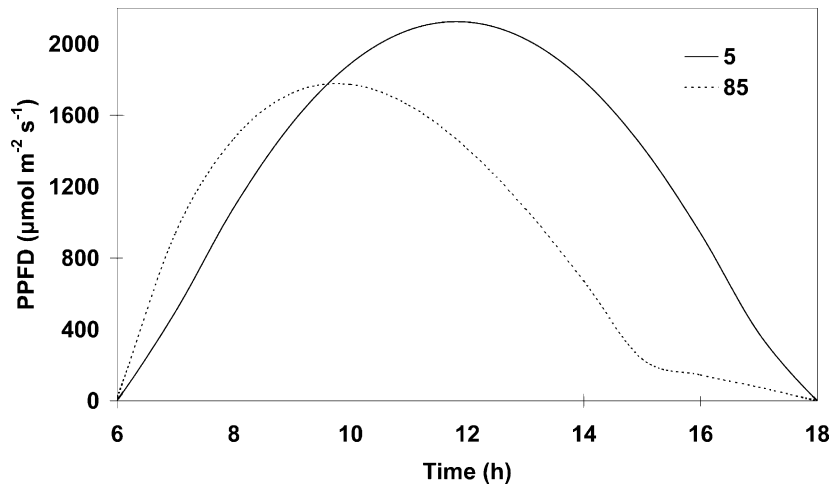
Fig. 3. Modeled diurnal change of PPFD intercepted by leaves with inclination angle of 5° (simulation of *S. superba*) and 85° (simulation of *S. katochaete*), respectively. The orientation angle of the modeled leaves was 150°, similar to that of the leaves we measured in the field (see. Fig. 1). The calculation was performed according to Jones (1992).

saturated CO_2 uptake rate (A_{max}) in the prostrate *S. superba* was nearly twice that in the erect-leafed species *S. katochaete*.

The photosynthetic response to intercellular CO_2 concentration ($A-C_i$ curves) demonstrated that *S. superba* had a markedly higher CO_2 uptake rate than *S. katochaete* under the same ambient CO_2 partial pressure (Fig. 4b).

We also examined the effect of leaf temperature on photosynthetic gas exchange. A_{max} changed in a parabolic manner with leaf temperature; it peaked at about 20–25 °C in both species, whereas slightly lower in *S. katochaete* than in *S. superba* (Fig. 5a). The apparent quantum yield decreased linearly with increasing leaf temperature in *S. katochaete* but did not change significantly in *S. superba* (Fig. 5b).

The carboxylation efficiency peaked at about 20 and 25 °C in *S. katochaete* and *S. superba*, respectively (Fig. 5c), it decreased more quickly with increasing leaf temperature in the former species. The maximal carboxylation velocity of the CO_2 fixation enzyme (Vcmax) increased with leaf temperature increment in *S. superba* (Fig. 5d), whereas it declined in *S. katochaete* at high leaf temperature.

3.3. PSII fluorescence

To understand the physiological mechanisms underlying the gas exchange response in these two contrasting species, we measured PSII fluorescence emission in *S. superba* and *S. katochaete* throughout the day under field conditions. On 14 August 2001, after leaf temperatures had fallen to approximately −5 °C in the early morning (Fig. 1), *S. superba* exhibited a markedly higher level of PSII photochemical activity than *S. katochaete* at any PPFD in the morning, as shown by Fv'/Fm' (PSII photochemical efficiency, Fig. 6a), qP (photochemical fluorescence quenching, Fig. 6b), and ETR (PSII photochemical electron transport rate, Fig. 6c). At this time, non-photochemical fluorescence quenching (NPQ) was markedly higher in *S. katochaete*, which saturated at a PPFD of 800 $\mu mol\ m^{-2}\ s^{-1}$. qP declined linearly with PPFD increments (Fig. 6b). However, all of these variables were similar for the two species at noon (Fig. 6). On 19 August, there had been no frost at last night. PPFD incidence on leaf surface was similar to that on 14 August in both species. The relationship between photochemical activity and PPFD maintained within the whole day in both species
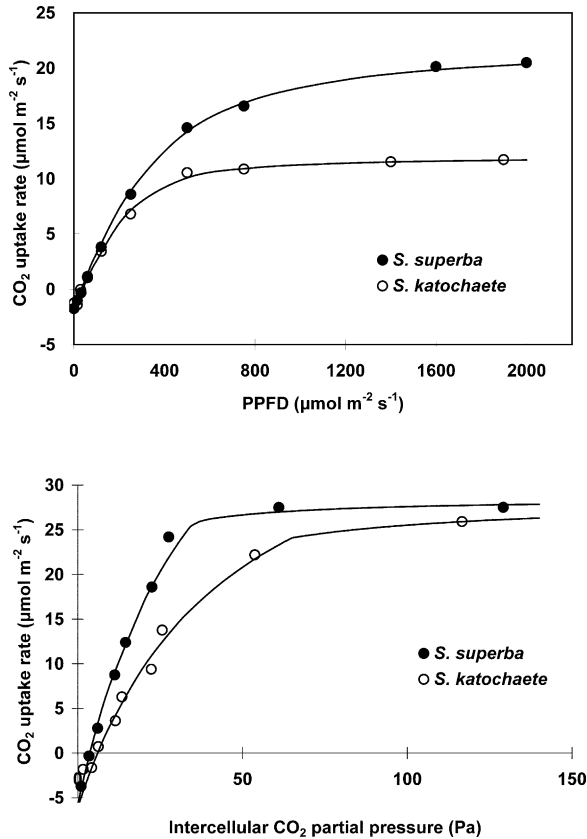
Fig. 4. CO_2 uptake rate response to PPFD (a, A–PPFD curves) and intercellular concentration (b, A–C_i curves) in leaves of *S. superba* (●) and *S. katochaete* (○) under controlled leaf temperature (24 ± 1 °C) and VPD (0.8–1.1 kPa). In A–PPFD curve determination, the CO_2 partial pressure in the reference cell was 27.7 ± 0.1 Pa and during A–C_i curve measurement the PPFD was set to 800 μmol m^{-2} s^{-1}.

(Fig. 7). Obvious down-regulation of ETR occurred under high light in *S. katochaete*.

4. Discussion

4.1. Plant architecture and combination of leaf light incidence and leaf temperature

The environmental conditions for alpine plants are usually characterized by high radiation (Körner, 1999), which sometime approaches or even exceeds solar constant during plant growing season on Qinghai-Tibet Plateau (Chen and Xu,

2000). The PPFD measured in August 2001 was consistent with these observations (Fig. 2). However, species with diverse architectures, such as *S. superba* and *S. katochaete* that we studied, differed substantially in both the maximal daily PPFD and the proportion of high light intercepted by their photosynthetic organs (Figs. 1–3). Consequently, the combination of leaf temperature and light differed remarkably (Fig. 1). The prostrate species had a higher daily maximum PPFD and leaf temperature than the erect species, which received high light early in the morning when its leaf temperature was low (Fig. 1). However, the prostrate species intercepted strong irradiation later, when the leaf temperature was high; the maximum PPFD incidence on the leaf co-occurred with the maximum leaf temperature, at noon. The difference in light interception patterns between the two species was due mainly to leaf morphology and orientation, as demonstrated by the theoretical calculations (Fig. 3).

On the Qinghai-Tibet Plateau, frost may occur during the whole growing season (Zheng et al., 2000). Both species seemed unable to avoid night frost efficiently since their leaf temperature dropped as low as -5 °C even in August (Fig. 1). This was consistent with other observations (Körner, 1999; Neuner et al., 1999). However, Germino and Smith (2001) found higher leaf temperatures in erect-leafed species. Because there was a thick boundary layer on the broad and prostrate leaves of *S. superba*, which was located deeply in the canopy, leaf temperature was prone to more rapid increases (Rosenberg et al., 1983). The leaves of the erect *S. katochaete*, however, coupled well with the atmosphere so as to prevent high leaf temperature. We attribute the difference in PPFD between our study and that of Germino and Smith (2001) mainly to leaf morphology and orientation, as demonstrated by our theoretical calculations (Fig. 3).

4.2. Influence of leaf temperature on photoinhibition

Apparent photoinhibition, as indicated by the fall in ETR, was recognized at PPFD over 800–1000 μmol m^{-2} s^{-1} in *S. katochaete* (Figs. 6 and
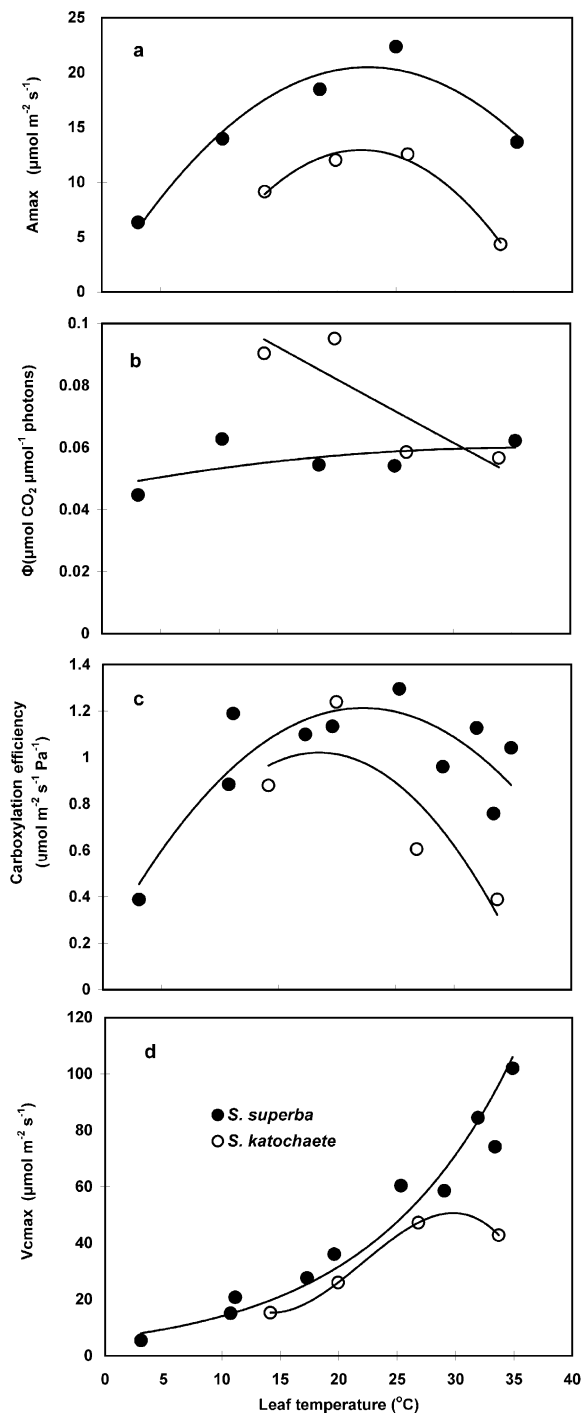
Fig. 5

7). Consistent with higher light saturation point and CO_2 uptake rate under high light (Fig. 4a), the prostrate species *S. superba* did not show obvious decrease of ETR and Fv'/Fm' at high PPFD, even at noon (Figs. 6 and 7).

Leaf temperature played a fundamental role in photoinhibition; it is well known that low temperature may induce photoinhibition (Adams et al., 1995). We found a close relationship between photoinhibition and leaf inclination. Photosynthetic enzyme activity and light utilization were sensitive to low leaf temperature in the two species (Fig. 5), but the prostrate species seemed to have a higher optimal leaf temperature for CO_2 uptake. At low leaf temperatures, the A_{max} of the erect species decreased but Φ was unchanged, probably because of reversible photoinhibition.

Under natural conditions, *S. katochaete* became photo-inhibited in the morning under high PPFD and low temperature after a night frost (Figs. 1 and 6). The almost optimal leaf temperature for photochemical activity during the rest of the day (Figs. 1 and 5) permitted steady recovery of Fv'/Fm' and ETR (Fig. 6a, d). The favorable temperature helped the recovery from stress-induced photoinhibition (Teicher et al., 2000). However, the prostrate species avoided photoinhibition in the early morning, due to favorable leaf temperature upon incipience of strong light interception (Figs. 1 and 6). The fairly high leaf temperature also protected the two species from photoinhibition in the early morning on 19 August (Fig. 7). Some alpine species can tolerate strong light without obvious photo-damage at air temperatures well below 0 °C (Warren et al., 1998); the Fv/Fm decline in the early morning might have been due to photoprotection rather than photo-inactivation (Osmond et al., 1999). The quick recovery

Fig. 5. Photosynthetic responses to different leaf temperatures in *S. superba* (●) and *S. katochaete* (○). (a) Maximum CO_2 uptake rate, A_{max}; (b) apparent quantum yield, Φ; (c) carboxylation efficiency; and (d) maximum carboxylation rate, Vcmax. A_{max} and C_i were obtained from A–PPFD response curves and carboxylation efficiency and Vcmax were from the A–C_i curves, which were measured over 3 days with high soil moisture as described in Fig. 4, except for leaf temperature varied.

of photochemical efficiency observed in this study suggested a rapidly reversible photoinhibition in *S. katochaete* in the early morning (Fig. 6).
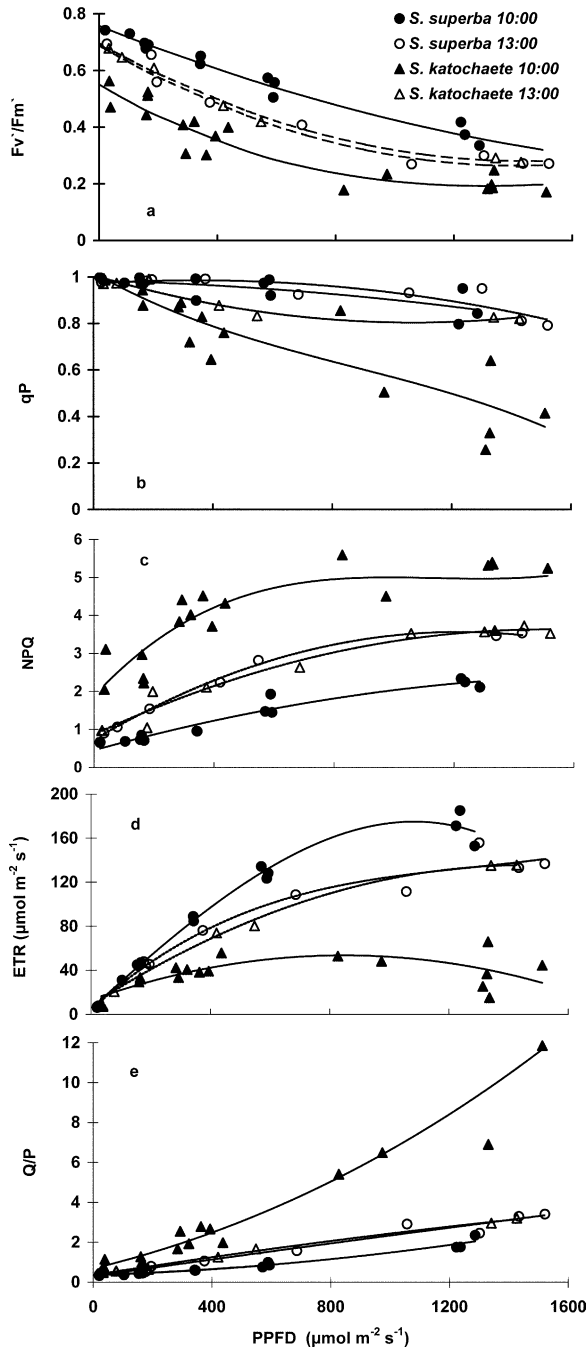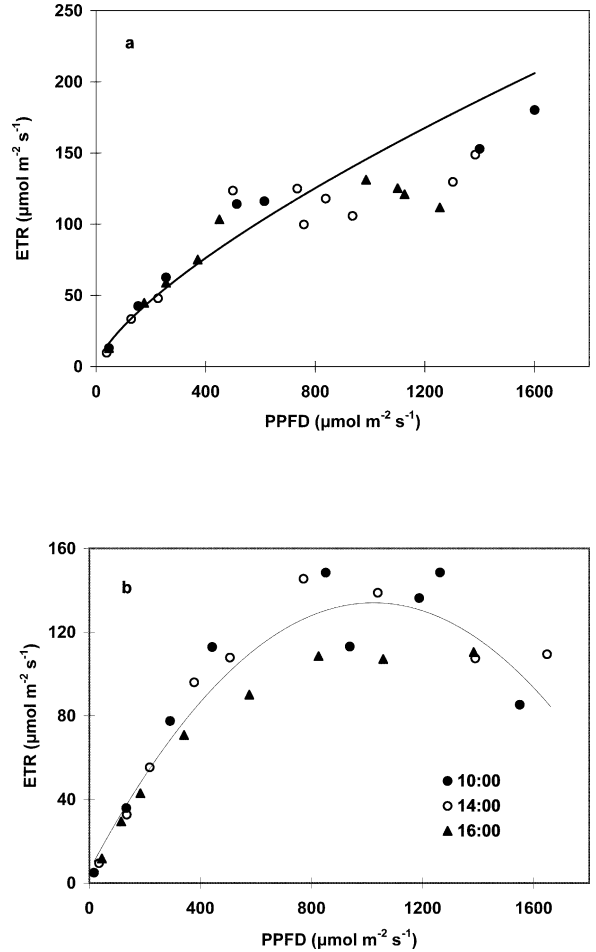

Fig. 6

Fig. 7. Response of ETR to change of PPFD in *S. superba* (a) and *S. katochaete* (b) in a Haibei alpine meadow on 19 August 2001. Measurements were the same as described in Fig. 6. Different symbols indicated the time of measurements. The simulated lines were based on the bulk data.

Fig. 6. Response of PSII photochemistry to change of PPFD in *S. superba* (circles) and *S. katochaete* (triangles) in a Haibei alpine meadow. Measurements were made on 14 August 2001, throughout the day at 1–2-h intervals. (a) Photochemical efficiency (Fv'/Fm'); (b) photochemical fluorescence quenching efficiency (qP); (c) non-photochemical fluorescence quenching (NPQ); (d) ETR of PSII photochemistry; (e) proportion of thermal dissipation to photochemical activity (Q/P). PPFD was adjusted by either shading plants with polyethylene film or changing leaf orientation.

High temperature and strong light have been shown to have additive effects on photoinhibition (Srivastava and Strasser, 1996). The erect species showed rapid declination in both $A_{\max}$ and Φ at supra-optimal leaf temperature (Fig. 5), indicating photoinactivation (Osmond et al., 1999). *S. superba* adapted to higher temperatures in photosynthesis (Fig. 5). However, under natural conditions, the down-regulation of ETR at noon implied that high leaf temperature (e.g. above 40 °C, Fig. 1) aggravated strong light-induced declination in photochemical activity (Figs. 6 and 7).

4.3. Integrating plant architecture and physiological acclimation

Plants adapt to different stresses through both physiological and morphological adjustment (Rundel et al., 1998). Several biochemical and physiological processes are essential for strong light acclimation (Germino and Smith, 2000a; Manuel et al., 1999; Streb et al., 1997, 1998; Wildi and Lütz, 1996). Because plant architecture directly affected light interception and, consequently, the temperature of photosynthetic organs, it was reasonable to assume that plant architecture may play some role in high-light adaptation by alpine species (Germino and Smith, 2000b, 2001).

The two species in this study differed greatly in architecture and, consequently, light incidence and leaf temperature (Figs. 1 and 2). The horizontally spreading leaves of *S. superba* received higher PPFD than the erect leaves of *S. katochaete*. Consistently, photochemical activity (such as ETR, qP, and Fv'/Fm') and photosynthesis were generally more effective in *S. superba* under strong light and favorable leaf temperature (Figs. 4, 6 and 7). Under natural conditions, *S. superba* did not show obvious photoinhibition by short-term strong light, which was demonstrated by the high photochemical activity in the early morning (Figs. 6 and 7). However, the erect species was sensitive to strong radiation in local environments (Figs. 6 and 7).

The erect leaves were also likely to receive strong light early in the morning when the leaf temperature was low (Figs. 1 and 3). To mitigate photoinhibition, this species dissipated a high proportion of absorbed light thermally in the early morning when the air temperature was low (Fig. 6c, e), which may have effect on rapid increase of leaf temperature. Since metabolic sinks rarely accounted for more than 20–30% of photoprotection at light saturation (Osmond et al., 1999), saturation of NPQ above 800 µmol m^{-2} s^{-1} may lead to an elevation of the other two components of non-photochemical fluorescence quenching, including photoinhibition (Vavilin et al., 1995). The co-occurrence of a rapid increase in photoinhibition pressure, as measured by $1-qP$ (Germino and Smith, 2000a), and a decrease in ETR suggested insufficient photoprotection by thermal dissipation and photoinactivation of PSII in *S. katochaete* (Ishida et al., 1999).

As mentioned earlier, the temperature of *S. superba* leaves that lay deep in the canopy tended to increase quickly in the morning when light intensity was still low. Photoinhibition was avoided in the morning when its leaf temperature was favorable before strong light exposure (Fig. 1). On the other hand, the combination of extremely strong light and high leaf temperature at noon might have caused down-regulation of photochemical activity (Fig. 6a, d, Fig. 7). Leaf cooling was difficult for this species because it has a thick boundary layer; therefore, thermal dissipation played an essential role in photoprotection only when the leaf temperature was low (Fig. 6). At higher leaf temperatures, photorespiration played a more prominent role (Heber et al., 1996; Park et al., 1996; Streb et al., 1998; Manuel et al., 1999; Sage and Monson, 1999). We did not directly measure photorespiration in this experiment because of technical limitation. However, more than two-thirds of the photochemical energy was estimated to flow through the photorespiration pathway at a PPFD above 1800 µmol m^{-2} s^{-1} if there were no other significant electron acceptors. In *S. katochaete*, ETR saturated at the approximate light saturation point (Fig. 4a, Fig. 6d), which might have prevented any increase in photorespiration.

Photosynthesis of both species in our study seemed to acclimate well to the high light regime.

For example, there was no significant indication of any photoinhibition under controlled conditions (Fig. 4) and the Fv/Fm was normal in early morning. Nevertheless, either insufficient thermal dissipation in *S. katochaete* or enhanced photorespiration in *S. superba* resulted in the downregulation of CO_2 uptake. The effects of these findings on species fitness and community production remain to be determined.

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