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Response of effective quantum yield of photosystem 2 to *in situ* temperature in three alpine plants

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Abstract

The response of effective quantum yield of photosystem 2 (ΔF/F$_m$') to temperature was investigated under field conditions (1 950 m a.s.l.) in three alpine plant species with contrasting leaf temperature climates. The *in situ* temperature response did not follow an optimum curve but under saturating irradiances [PPFD >800 μmol(photon) m^{-2} s^{-1}] highest ΔF/F$_m$' occurred at leaf temperatures below 10 °C. This was comparable to the temperature response of antarctic vascular plants. Leaf temperatures between 0 and 15 °C were the most frequently (41 to 56 %) experienced by the investigated species. At these temperatures, ΔF/F$_m$' was highest in all species (data from all irradiation classes included) but the species differed in the temperature at which ΔF/F$_m$' dropped below 50 % (*Soldanella pusilla* >20 °C, *Loiseleuria procumbens* >25 °C, and *Saxifraga paniculata* >40 °C). The *in situ* response of ΔF/F$_m$' showed significantly higher ΔF/F$_m$' values at saturating PPFD for the species growing in full sunlight (*S. paniculata* and *L. procumbens*) than for *S. pusilla* growing under more moderate PPFD. The effect of increasing PPFD on ΔF/F$_m$', for a given leaf temperature, was most pronounced in *S. pusilla*. Despite the broad diurnal leaf temperature amplitude of alpine environments, only in *S. paniculata* did saturating PPFD occur over a broad range of leaf temperatures (43 K). In the other two species it was half of that (around 20 K). This indicates that the setting of environmental scenarios (leaf temperature×PPFD) in laboratory experiments often likely exceeds the actual environmental demand in the field.

Additional key words: chlorophyll fluorescence induction; heat; *Loiseleuria procumbens*; photoinhibition; *Saxifraga paniculata*; *Soldanella pusilla*; temperature optimum.

Introduction

The effective quantum yield of photosystem 2 (ΔF/F$_m$') is considered a good eco-physiological indicator of how plants respond to environmental stress (Rascher *et al.* 2000). Deviations of ΔF/F$_m$' from the control usually reveal a reversible down regulation of photosystem 2 (PS2) photochemistry rather than irreversible damage to photosynthetic apparatus (see Demmig-Adams *et al.* 1996). Leaf temperatures have a significant effect on ΔF/F$_m$'. The temperature response of ΔF/F$_m$' has mainly been determined *ex situ* under constant irradiation (Niinemets *et al.* 1999, Xiong *et al.* 1999, Kitao *et al.* 2000, Yamasaki *et al.* 2002). Field studies of the temperature response of ΔF/F$_m$' are rare (Gratani *et al.* 2000, Larcher 2000). In these studies temperature responses were compiled using data from different seasons, as in most environments it is difficult to obtain field data at saturating photosynthetic photon flux density (PPFD) under a broad range of temperatures within one season. A peculiar feature of alpine environments is that diurnal leaf temperature amplitudes of up to 50 K can occur (see Körner and Larcher 1988). Within the course of a single clear day freezing temperatures can occur in the morning and high leaf temperatures critical to survival can occur in the middle of the day (Braun *et al.* 2002, Buchner and Neuner 2003). At high altitudes these temperature extremes occur at altitudinally increased PPFD (Körner 1999). This unusual environmental combination offers the opportunity to measure the response of ΔF/F$_m$' to a broad range of temperatures under field conditions. In a recent study we investigated the variability of high temperature thresholds for heat inactivation of PS 2 in alpine plant species (Braun *et al.* 2002). Here we report on the temperature

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Abbreviations: ΔF/F$_m$' = effective quantum yield of PS2; LT$_{50}$ = temperature at which 50 % of the leaf tissue is heat damaged; PPFD = photosynthetic photon flux density; PS2 = photosystem 2.

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response of $\Delta F/F_m$' under alpine field conditions. The data was obtained by monitoring plants under a wide range of naturally occurring leaf temperature and irradiance combinations.

An additional feature of alpine environments is that leaf temperatures of plants that grow in close proximity differ greatly as a result of differences in micro-exposure and plant stature (see Cernusca 1976, Körner 1999). This allows to investigate the temperature response of $\Delta F/F_m$' in plant species with contrasting leaf temperature climates but under similar macroclimatic field conditions. The second aim of this study was thus to investigate the influence of naturally occurring leaf temperature and PPFD combinations on $\Delta F/F_m$' in alpine plant species with contrasting microenvironments.

Materials and methods

Experimental site and plant species: The experimental site is situated at the alpine timberline (1 950 m a.s.l.) on the NNW-exposed slope of the summit of Mt. Patscherkofel south of Innsbruck, Austria (47°12'N, 11°27'E). *Loiseleuria procumbens* (L.) Desv., *Soldanella pusilla* Baumg., and *Saxifraga paniculata* Mill. grow extensively within the experimental site. It was expected that these species would differ greatly with respect to leaf temperature climate as they prefer contrasting microsites and differ with respect to plant stature. The dwarf shrub *L. procumbens* prefers sun and wind exposed ridges. Rosettes of *S. pusilla* grow on shaded mainly north-facing microsites with permanently moist soils. Cushions of *S. paniculata* grow on sites with shallow substrates that can dry out quickly and that often experience high temperatures (Neuner *et al.* 1999).

Microclimate measurements: At all three sites, microclimate was recorded with a data logger (*CR10X Micrologger*, *Campbell Scientific*, Logan, USA). PPFD and air temperature (the sensors were mounted inside unaspirated radiation shields; *URS1*, *Campbell Scientific*, Logan, USA) were measured 2 m above ground. Leaf temperatures were measured with type *T* 0.2 mm copper constantan, fine-wire thermocouples. PPFD and temperature data was sampled every 30 s and averages were calculated and stored every 30 min.

Chlorophyll fluorescence measurements were conducted *in situ* on leaves of the three investigated species during the growing periods of two different years (1996 and 1998). The effective quantum yield of PS2 ($\Delta F/F_m$') was determined according to Genty *et al.* (1989) with *PAM* (pulse-amplitude-modulated) fluorometers. For parallel measurements on different plant species all types of *PAM* fluorometers available in the laboratory in Innsbruck (*Mini-PAM* and *PAM-2000*, *H. Walz*, Effeltrich, Germany) were employed. $\Delta F/F_m$' was calculated as (F_m' – F)/F_m'. F is the fluorescence yield of the irradiation-adapted sample and F_m' is the maximum irradiation-adapted fluorescence yield when a saturating pulse of 800 ms duration is superimposed upon the prevailing natural PPFD (Schreiber and Bilger 1993).

***In situ* temperature response of $\Delta F/F_m$'**: Fluorescence and concomitant leaf temperature and PPFD measurements were conducted using leaf clip holders or the optional micro quantum/temperature sensor (*Walz*, Effeltrich, Germany). The fibre optic was placed between 6 and 16 mm from the investigated leaves. Differences in plant status, and in leaf shape, size, and arrangement made a species-specific positioning of the *PAM* fibre optic necessary. For *S. paniculata* the fibre optic was centred above a whole leaf rosette, for *S. pusilla* one leaf was placed within the leaf clip holder, and for *L. procumbens* the fibre optic was placed above the leaf canopy surface. $\Delta F/F_m$', leaf temperature, and PPFD were determined automatically at 10-min intervals from morning until evening. To yield an *in situ* temperature response for $\Delta F/F_m$' from field data, mean values of $\Delta F/F_m$' were calculated from values measured within 5 °C leaf temperature classes for each of the following PPFD classes: low PPFD [0–99 µmol(photon) m^{-2} s^{-1}], moderate PPFD [100–799 µmol(photon) m^{-2} s^{-1}], and saturating PPFD [>800 µmol(photon) m^{-2} s^{-1}]. This last irradiance range saturates photosynthesis in the investigated species (Grabherr 1977, Körner and Diemer 1987).

PPFD response of $\Delta F/F_m$': The field data were also used to compile an *in situ* PPFD response curve for $\Delta F/F_m$'. For this, mean values of $\Delta F/F_m$' from all values within 200 µmol(photon) m^{-2} s^{-1} classes were calculated. PPFD response curves for $\Delta F/F_m$' were also measured under controlled temperature. Leaves of *S. pusilla* were fixed on a temperature controlled heating plate that was preset either to 20 or 40 °C. For leaves of *S. pusilla* leaf temperatures of 40 °C are not yet critical for the functioning of PS2 since these temperatures are lower than the minimum thermotolerance of PS2 (44.0 °C) measured for this species (Braun *et al.* 2002) and leaf tissue is not heat damaged at less than 44.4 °C (Buchner and Neuner 2003). Leaf temperatures were measured with type *T* 0.2 mm copper constantan, fine-wire thermocouples that were mounted to the lower leaf surface. Temperatures were recorded with a data logger (*CR10X Micrologger*, *Campbell Scientific*, Logan, USA). Measurements of the PPFD response of $\Delta F/F_m$' began after leaves had been pre-darkened for 30 min at either 20 or 40 °C. Halogen lamps were used as an "actinic light" source. PPFD was increased from darkness in 100 µmol(photon) m^{-2} s^{-1} steps at 30-min intervals. At the end of each 30-min exposure to a certain PPFD, $\Delta F/F_m$' was determined.

Statistical data analysis: The significance of differences between means of ΔF/F$_m$' for the three species in various PPFD classes was tested by analysis of variance and the Bonferroni test (p<0.01) (*SPSS*, Chicago, USA). The significance of differences between two groups of means of ΔF/F$_m$' was measured with the Student's *t*-test (p<0.01) (*SPSS*, Chicago, USA).

Results

Two contrasting daily time courses of ΔF/F$_m$' measured on *S. paniculata* leaves are presented in Fig. 1. Despite similar PPFD conditions with maximum around 1 800 μmol(photon) m^{-2} s^{-1} during the middle of the day (Fig. 1*A*) leaf temperatures differed significantly (Fig. 1*B*) between these two summer days. While on 9 August 1996 leaf temperatures did not exceed 34.7 °C, they remained above 35 °C for 7 h on 19 July 1996 and even increased to a daily maximum of 49.7 °C. Such high leaf temperatures potentially damage leaves of *S. paniculata* [47.2–57.5 °C (LT$_{50}$); Buchner and Neuner 2003]. The difference in leaf temperature can be explained by a difference in precipitation patterns. In 1996, July was a dry month whereas the 9th August was one day without precipitation within a rainy period. On 19 July a significant reduction in ΔF/F$_m$' was observed during the middle of the day (Fig. 2*A*). This reduction in ΔF/F$_m$' was induced by high leaf temperatures as it coincided with an increase in leaf temperature beyond 35 °C during exposure to a constant, saturating PPFD (Fig. 2*B*). The reduction in ΔF/F$_m$' remained evident throughout the whole afternoon but was completely reversed over night (data not shown).

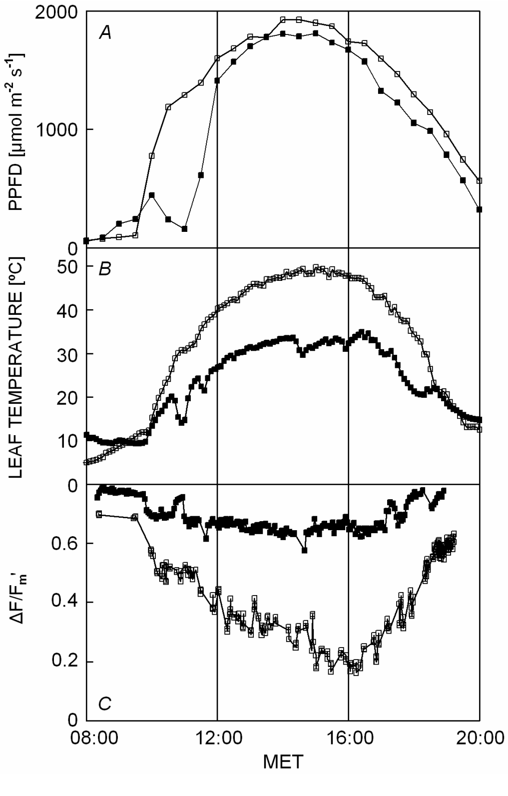

Fig. 1. Daily time courses of (*A*) photosynthetic photon flux density, PPFD [μmol(photon) m^{-2} s^{-1}], (*B*) leaf temperature [°C], and (*C*) effective quantum yield of photosystem 2, ΔF/F$_m$' measured on leaves of *S. paniculata* at 1 960 m a.s.l. on Mt. Patscherkofel on two summer days (*open symbols:* 19 July 1996; *closed symbols*: 9 August 1996).

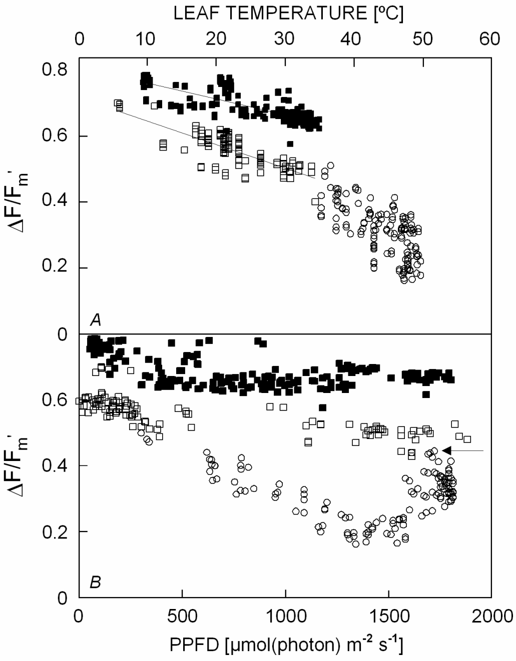

Fig. 2. Effective quantum yield of PS2 (ΔF/F$_m$') measured on leaves of *S. paniculata* at 1 960 m (a.s.l.) on Mt. Patscherkofel in response to leaf temperature (*A*) and PPFD (*B*) on two summer days (*open symbols:* 19 July 1996; *closed symbols*: 9 August 1996). *Circles* indicate leaf temperatures >35 °C, *squares* indicate leaf temperatures <35 °C. *The arrow* in *B* highlights the change to leaf temperatures higher than 35 °C.

PPFD response curves of ΔF/F$_m$' measured under controlled, constant leaf temperatures of either 20 or 40 °C confirmed the negative effect of high leaf temperatures on ΔF/F$_m$' found under field conditions. For leaves of *S. pusilla* (Fig. 3) ΔF/F$_m$' measured at 40 °C was significantly (p<0.01) lower than when measured at 20 °C when PPFD was less than 600 μmol(photon) m^{-2} s^{-1}. This difference was found for all investigated plant species.

Plotting all ΔF/F$_m$' values obtained during *in situ* daily time courses (including all PPFD classes) against leaf temperature reveals a successive decrease in ΔF/F$_m$' above threshold temperatures (Fig. 4). Leaf temperatures of 0–15 °C had no effect on ΔF/F$_m$' in all species as means in these temperature classes were not significantly (p<0.01) different from each other. Leaf temperatures between 10 and 15 °C were the most frequently experienced by the investigated species during summer at the investigation sites. They occurred at a relative frequency between 41–56 % depending on the species. However, there was a species-specific response to further increase in leaf temperature. A reduction in $\Delta F/F_m'$ to values below 50 % was observed at leaf temperatures higher than 20 °C in *S. pusilla*. For leaves of *L. procumbens* similar low $\Delta F/F_m'$ values were only measured when leaf temperatures increased above 25 °C and in leaves of *S. paniculata* above 40 °C. These differences in the temperature response evidently mirror differences in the overall leaf temperature climate between species. Leaf temperatures at which major reductions in $\Delta F/F_m'$ (<50 %) occurred were measured in all species at a similarly low frequency (15 % in leaves of *S. pusilla*, 18 % in leaves of *L. procumbens*, and 4 % in leaf rosettes of *S. paniculata*) despite significant differences in the overall leaf temperature climate between the investigated species.

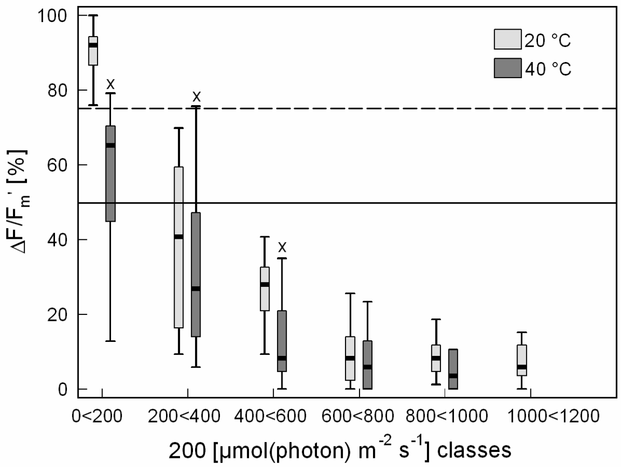

Fig. 3. PPFD-response curves of $\Delta F/F_m'$ measured on detached leaves of *S. pusilla* exposed to 20 °C (*light grey*) and 40 °C (*dark grey*). *The box plots* show the median (*line inside the box*), 75 and 25 % (*margins of boxes*), and *the whisker* extends over the range of the 10 and 90 %. *The dashed line* indicates a 25 % reduction in $\Delta F/F_m'$; *the continuous line* a 50 % reduction in $\Delta F/F_m'$. *Asterisks* indicate significant differences (p<0.01) between values for 20 and 40 °C, respectively.

As both rising leaf temperatures and rising PPFD can cause a reduction in $\Delta F/F_m'$, the temperature response of $\Delta F/F_m'$ at three different PPFD (low, moderate, and saturating) is shown in Fig. 5*A*. Under saturating PPFD a significant reduction in $\Delta F/F_m'$ to below 50 % occurred at 20 °C in *S. pusilla*, at 25 °C in *L. procumbens*, and at 40 °C in *S. paniculata*. Saturating PPFD occurred at a frequency of more than 35 % over the measurement period and was combined with different ranges of leaf temperature in the tested species. While in *S. paniculata* the range of leaf temperatures at saturating PPFD was broad (5.2–48.3 °C) it was distinctly narrower in the other two species (*L. procumbens* 16.1–38.2 °C, *S. pusilla* 12.3–33.5 °C). In none of the species was a distinct temperature optimum deducible from the field data. Rather it appeared that $\Delta F/F_m'$ dropped successively with increasing leaf temperatures indicating a temperature optimum lower than 10 °C in *S. paniculata*, 20 °C in *L. procumbens*, and 15 °C in *S. pusilla*. At similar leaf temperatures, higher PPFD reduced $\Delta F/F_m'$ in all three species (Fig. 5*B*). The species growing in full sunlight, *i.e. S. paniculata* and *L. procumbens*, showed significantly higher $\Delta F/F_m'$ at moderate and saturating PPFD combined with leaf temperatures higher than 20 °C than *S. pusilla*.

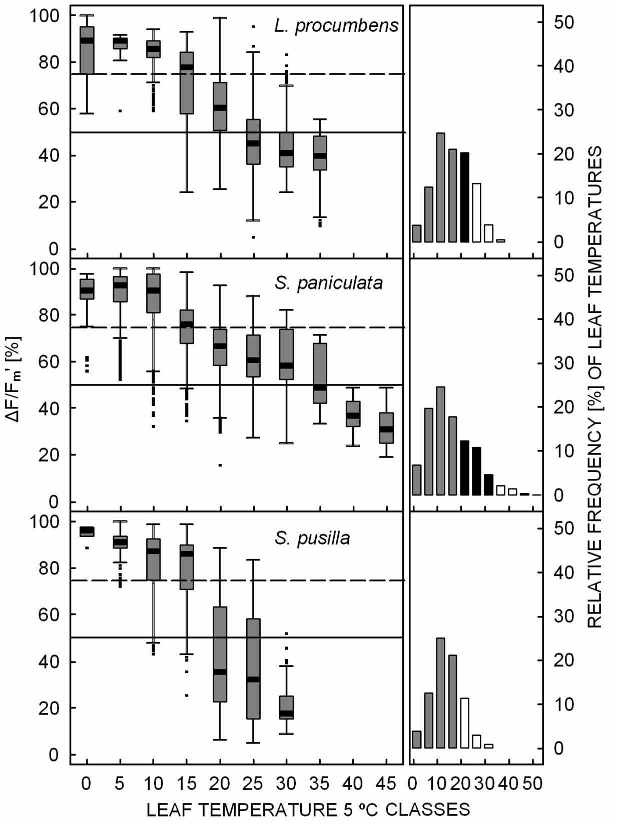

Fig. 4. *Left graphs*: $\Delta F/F_m'$ [% of maximum] measured on leaves of *L. procumbens*, *S. paniculata*, and *S. pusilla* in response to leaf temperature (5 °C temperature classes). *The box plots* show the median (*line inside the box*), 75 and 25 % (*margins of boxes*), and *the whisker* extends over the range of 10 and 90 %. *The scattered points above and below the whiskers* are extreme values. *The dashed line* indicates a 25 % reduction in $\Delta F/F_m'$, the continuous line a 50 % reduction in $\Delta F/F_m'$. *Right graphs*: Relative frequency [%] of leaf temperatures measured during daytime [PPFD >30 µmol(photon) m^{-2} s^{-1}] at the investigation site on leaves of *L. procumbens*, *S. paniculata*, and *S. pusilla*. *Grey bars* indicate leaf temperatures at which $\Delta F/F_m'$ is higher than 75 %, *black bars* indicate leaf temperatures at which $\Delta F/F_m'$ is between 75 and 50 %, and *white bars* indicate leaf temperatures at which $\Delta F/F_m'$ is lower than 50 %.

The *in situ* PPFD response of $\Delta F/F_m$' differed between the investigated plant species (Fig. 6). At all PPFD values, $\Delta F/F_m$' measured on leaf rosettes of *S. paniculata* was significantly (p<0.01) higher than in leaves of *S. pusilla* and *L. procumbens*. A 50 % reduction in $\Delta F/F_m$' was recorded for leaf rosettes of *S. paniculata* at PPFD higher than 800 µmol(photon) m^{-2} s^{-1} and for leaves of *S. pusilla* at PPFD higher than 400 µmol (photon) m^{-2} s^{-1}.

Discussion

The temperature response of $\Delta F/F_m$' obtained from field data under saturating PPFD was not an optimum curve despite being determined under a broad range of leaf temperatures, particularly for *S. paniculata* (5.2–48.3 °C). In this species highest $\Delta F/F_m$' values were recorded at leaf temperatures below 10 °C suggesting a low temperature optimum. A comparably low temperature optimum for $\Delta F/F_m$' is also reported for the two antarctic vascular plants, *Deschampsia antartica* (7 °C) and *Colobanthus quitensis* (9 °C) (Xiong *et al.* 1999) corroborating our results for *S. paniculata.* The temperature optimum for $\Delta F/F_m$' varies greatly between plant species from different temperature environments. While in our results and for antarctic vascular plants (Xiong *et al.* 1999) optimum temperatures for $\Delta F/F_m$' are between 5 and 10 °C, in the temperate deciduous tree *Populus tremula* (Niinemets *et al.* 1999) and in the tropical dipterocarp tree *Shorea platyclados* (Kitao *et al.* 2000) an optimum temperature for $\Delta F/F_m$' of around 40 °C is reported. The temperature optimum for $\Delta F/F_m$' of other plant species ranges from 15 to 35 °C (*Tilia cordata* Niinemets *et al.* 1999; *Triticum aestivum* Yamasaki *et al.* 2002; other dipterocarp tree species Kitao *et al.* 2000).

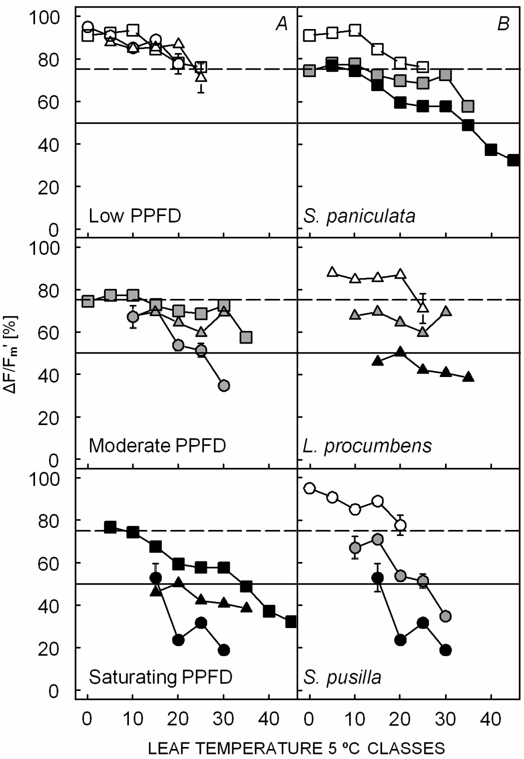

Fig. 5. $\Delta F/F_m$' [% of maximum] measured on leaves of *L. procumbens* (*triangles*), *S. paniculata* (*squares*), and *S. pusilla* (*circles*) in response to leaf temperature (5 °C temperature classes) at three different PPFD classes: (*open symbols*) low PPFD [0–99 µmol(photon) m^{-2} s^{-1}], (*grey symbols*) moderate PPFD [100–799 µmol(photon) m^{-2} s^{-1}], and (*black symbols*) saturating PPFD [>800 µmol(photon) m^{-2} s^{-1}]. *The dashed line* indicates a 25 % reduction in $\Delta F/F_m$', the continuous line a 50 % reduction in $\Delta F/F_m$'. *A*: Comparison of the species within a PPFD class. *B*: Comparison of the different PPFD classes within one species.

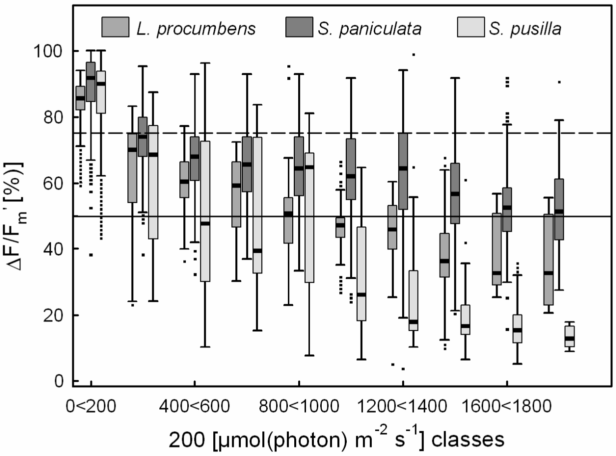

Fig. 6. PPFD-response of $\Delta F/F_m$' [% of maximum] measured during daily time courses for leaf rosettes of *S. paniculata* and leaves of *S. pusilla* and *L. procumbens* [classes of 200 µmol(photon) m^{-2} s^{-1}]. *The box plots* show the median (*line inside the box*), 75 and 25 % (*margins of boxes*), and *the whisker* extends over the range of the 10 and 90 %. *The scattered points above and below the whiskers* are extreme values. *The dashed line* indicates a 25 % reduction in $\Delta F/F_m$', *the continuous line* a 50 % reduction in $\Delta F/F_m$'.

For *S. pusilla* and *L. procumbens* the leaf temperature at which $\Delta F/F_m$' was reduced to below 50 % is distinctly lower (20–24 K) than the thermotolerance of PS2 (*S. pusilla* 44.0–49.3 °C, *L. procumbens* 44.6–53.8 °C; Braun *et al.* 2002). For *S. paniculata* there is no information about the thermotolerance of PS2 but minimum tissue heat tolerance usually corresponds well with thermotolerance of PS2 (Bilger *et al.* 1984), *i.e.* 47.2 °C (LT_{50}; Buchner and Neuner 2003). Minimum tissue heat tolerance was only 7 K higher than the leaf temperature at which $\Delta F/F_m$' was reduced to below 50 %. This indicates a distinctly better PS2 performance under high leaf temperatures than the other two investigated species.

The only previous report of an *in situ* temperature response for $\Delta F/F_m$' is for *Quercus ilex* with an optimum temperature of 20–35 °C. However, the results are only to a limited extent comparable to our results as they were obtained from data measured the whole year round (Gratani *et al.* 2000, Larcher 2000). Under laboratory conditions, optimum temperatures for $\Delta F/F_m$' are usually determined by exposing leaves to a series of leaf temperatures, from low to high under constant PPFD. Alpine plants are typically exposed to high diurnal leaf temperature amplitudes of up to 50 K (Körner and Larcher 1988). Our results show that in the field saturating irradiation naturally occurs at a broad range of leaf temperatures (43 K) in *S. paniculata* leaves. However, in the two other species, *S. pusilla* and *L. procumbens*, this range is much smaller (around 20 K) despite high naturally occurring diurnal leaf temperature amplitude (1998: *L. procumbens* 33 K; *S. pusilla* 30 K). Hence, our results indicate that the setting of environmental factors in laboratory experiments to determine the potential performance of a plant under various leaf temperature×PPFD combinations is likely to exceed the actual environmental demand in the field. This may be even more important for species from (with respect to diurnal temperature amplitude) more moderate temperature environments than the alpine environment.

The *in situ* PPFD responses of $\Delta F/F_m$' for the three species investigated mirror the environment peculiar to their natural microhabitat. Both *S. paniculata* and *L. procumbens* grow on sun-exposed sites. The PPFD responses of $\Delta F/F_m$' are within the range of responses typically observed in sun plants, *i.e.* higher $\Delta F/F_m$' at saturating PPFD than shade adapted plants (Björkman and Demmig-Adams 1994, Franco *et al.* 1999, Strong *et al.* 2000, Franco and Lüttge 2002, Kitao *et al.* 2003, Lüttge *et al.* 2003, Einhorn *et al.* 2004). In contrast, *S. pusilla* shows a PPFD response for $\Delta F/F_m$' similar to shade adapted plants (Strong *et al.* 2000, Franco and Lüttge 2002, Kitao *et al.* 2003, Einhorn *et al.* 2004). *S. pusilla* usually inhabits sites with a more moderate irradiation than the two other species. The effect of irradiation at a given leaf temperature was most distinct in *S. pusilla* indicating a greater readiness to respond to increasing irradiation of PS2 than the two sun adapted plants *S. paniculata* and *L. procumbens*.

In alpine environments the leaf energy budget is mainly directed by photon input (Körner and Larcher 1988) with differences in PPFD climate resulting in large differences in leaf temperature. Despite these differences in leaf temperature between micro-sites, at all three sites the leaf temperatures most frequently experienced matched optimum temperatures for $\Delta F/F_m$'. This accordance indicates that for the three plant species investigated, PS2 is very well adapted to the microclimate of their habitat. This is also reflected in different responses and critical thresholds with respect to PPFD and leaf temperature.

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