



Photosynthetic activity in three vascular species of Spitsbergen vegetation during summer season in response to microclimate

Miloš BARTÁK, Peter VÁCZI and Josef HÁJEK

*Department of Plant Physiology, Institute of Experimental Biology, Masaryk University,
Kotlářská 2, 61137 Brno, Czech Republic
corresponding author: <mbartak@sci.muni.cz>*

Abstract: Diurnal measurements of photosynthetic processes, effective quantum yield of photosystem II (Φ_{PSII}), photosynthetic electron transport rate (ETR) were done in three dominant species of Arctic tundra (*Silene acaulis*, *Dryas octopetala*, *Salix polaris*) in Petunia-bukta, Spitsbergen. Daily courses of net photosynthesis (P_N) were calculated from chlorophyll fluorescence data and daily photosynthesis evaluated. The short-term field measurements were carried out in summer 2009, and 2010. Fluorometric parameters (Φ_{PSII} and ETR) were measured each 5 minutes as well as microclimate characteristics of the site for 10 (2009) and 8 days (2010), respectively. In all species photosynthetic ETR was well related to incident photosynthetically active radiation and leaf temperature. In general, *D. octopetala* exhibited slightly lower ETR than the other two species. Estimated maximum photosynthetic rate (P_{Nmax}) reached 17.6, 21.4, and 22.9 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *S. polaris*, *S. acaulis*, and *D. octopetala*, respectively. Daily photosynthesis reached comparable values in all species, *D. octopetala*, however, exhibited slightly lower values than the other two species both for overcast and fully sunny days (3.9 and 13.4 $\text{mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$, respectively). The range of daily photosynthesis for *S. polaris* and *S. acaulis* studied, reached the ranges of 4.6–6.9 and 14.6–15.2 $\text{mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ for overcast and fully sunny day, respectively.

Key words: Arctic, Svalbard, vascular plants, plant ecophysiology, net photosynthesis, chlorophyll fluorescence.

Introduction

Thanks to numerous long-term field projects carried out in several Arctic regions of the Earth within last decades, a lot of data exist on daily and seasonal net ecosystem CO_2 exchange rate (NEE). NEE was measured in Svalbard (Lloyd 2001), Greenland (Nordstroem *et al.* 2001; Marchand *et al.* 2005), European Arctic (Laurila *et al.* 2001), Canadian Arctic (Welker *et al.* 2004), and Siberian tundra

(Parmentier *et al.* 2011). These studies typically applied the approach of transparent measuring chamber placed over vegetation cover composed of several plant, moss and lichen species. In such studies, photosynthetic CO₂ fixation of all autotrophic species present inside the chamber was accompanied by simultaneous respiration of the species and soil respiration, including bacterial CO₂ release respectively. Therefore, it was not possible to derive diurnal measurements of net photosynthesis for individual plant species and calculate their particular contribution to net community and/or ecosystem CO₂ exchange.

In Antarctica, the first measurements of diurnals of photosynthetic processes exploiting *in situ* chlorophyll fluorescence records were made on lichens. Kappen *et al.* (1998) used simultaneous gasometric and fluorometric measurements in foliose lichen species *Umbilicaria aprina*. Since that time many studies focusing diurnals of Antarctic lichens and mosses (Schlensog and Schroeter 2001; Schroeter *et al.* 2011; Pannowitz *et al.* 2005) have been performed. Some of them (*e.g.* Schroeter *et al.* 2011; Barták *et al.* 2009) reported even several years-lasting continuous measurements of effective quantum yield of photosynthetic processes (Φ_{PSII}). Such measurements enabled to evaluate the duration of periods of cold-, and dark period-induced dormancy and limitations of photosynthetic activity of these poikilohydric organisms. All the above-mentioned studies showed that there is a need for both short- and long-term field measurements using the chlorophyll fluorescence approach in plants and other photosynthesising organisms in polar regions in order to evaluate the limiting factors of photosynthesis for individual species, locations and weather situations. In plants abundant in polar regions of the Northern Hemisphere numerous field measurements of photosynthesis have been performed for individual plants. However, only a few attempts have been made to measure daily photosynthesis using a chlorophyll fluorescence approach. These studies, however, did not apply continuous measurements of an effective quantum yield of photosystem II (Φ_{PSII}) and were time limited (Jones and Demmers-Derks 1999). One of the Arctic regions where the diurnal measurements of photosynthesis are unknown is Svalbard. This is an important region as currently it is especially vulnerable to climate change, especially global warming and episodic events (*e.g.* manipulated warming, Bokhorst *et al.* 2010). The majority of studies of the dominant species of Svalbard vegetation used gasometric measurements (*e.g.* Uchida *et al.* 2010 – *Salix polaris*) sometimes combined with the chlorophyll fluorescence technique (Muraoka *et al.* 2008). Therefore, information on diurnal courses of photosynthetic processes in species dominating Svalbard vegetation is still insufficient.

In this study we measured photosynthetic processes in three dominant vascular plant species at Svalbard in relation to environmental factors, especially daily courses of photosynthetically active radiation, during a short-term period of Arctic summer. For the study, *Silene acaulis*, *Dryas octopetala*, and *Salix polaris* were chosen, because they were most abundant species at the place. We hypothesised that there would be interspecific differences of the efficiency of photosystem II be-

cause of different leaf anatomy and morphology (McGraw 1985), growth form of individual plants and their cushions (Antonsson *et al.* 2009), growth rates of plants forming Arctic vegetation cover (Benedict 1989). In the above-specified three species we expected specific values of effective quantum yield of photosynthetic processes in photosystem II (Φ_{PSII}) and their changes induced by varying environmental factors during the daytime. We hypothesised that diurnal measurements of Φ_{PSII} taken for the three species growing in the same habitat could be used for calculation of their photosynthetic rates when data on incident photosynthetically active radiation, quantum yield of CO_2 fixation (Φ_{CO_2}) are available (for review see *e.g.* Singaas *et al.* 2001). In our study, we used chlorophyll fluorescence data, daily courses of Φ_{PSII} in particular, for estimation of net photosynthetic rate and calculations of daily totals of their photosynthesis expressed per leaf area unit. Such information, *i.e.* daily photosynthetic courses and daily carbon fixation for leaves and/or green above-ground parts is reported only very rarely for vascular polar plants (*e.g.* Gerasimenko *et al.* 1996). In our study we hypothesised that continuous recording of fluorometric data (Φ_{PSII}) on three species for several days would point out inter-specific differences not only in maximum net photosynthesis reached at sunny days but also in daily photosynthesis for particular species, sunny, and overcast days, respectively.

Material and methods

Study site. — Study site is located in Petuniabukta (Spitsbergen, Billefjorden, 78°41'01 N, 16°26'49 E). The site has midnight sun from the middle of April until the end of August. An overview of general climatic conditions of Petuniabukta is given by Láska *et al.* (2012) for the last several seasons. Study site was located 300 m N of Petunia hut in a shallow depression formed by several small streams. The depression is located 100 m from the coastal line, slightly inclined to E, facing Petunia Bay. The study site is supplied by water from melting snowfields for a majority of the summer season; however, in July, water limitation may occur since the streams disappear.

Species selection. — For the study of photosynthesis we selected three species that dominate tundra vegetation in Petuniabukta, Spitsbergen: (1) *Silene acaulis*, (2) *Salix polaris* and (3) *Dryas octopetala* (Figs 1 to 3). *Silene acaulis* is a 2–5 cm high plant that forms compact, hemispherical or flat cushions up to 50 cm in diameter. The small leaves (about 10 mm long) are distributed along the stems. The compact cushions provide protection from winds. Spatial arrangement of leaves within the cushions maximizes leaf surface area available for photosynthesis. *Dryas octopetala* is an Arctic-alpine plant forming dwarf-shrub clumps. *D. octopetala* has a wide range of distribution. The species is quite abundant in Svalbard where it represents one of the most frequent species. *Salix polaris* is a woody plant



Fig. 1. *Silene acaulis* at study site, Petuniabukta.

widely distributed in Svalbard and dominant in semi-desert areas of Ny-Ålesund (*e.g.*, Robinson *et al.* 1998). It is a dwarf shrub with a short stem and small round-shaped leaves. The stems are connected by stolons below ground. At the study site the three species formed a pattern of clumps of individual plants and polycormones, *S. acaulis* grew on slightly drier places while *S. polaris* and *D. octopetala* were abundant close to water stream margins.

Field measurements of chlorophyll fluorescence. — Within the two summer expeditions (Svalbard 2009, 2010), researchers from the Masaryk University Brno, Czech Republic carried out short-term comparative measurements of photosynthetic processes in three species of vascular plants. Two different fluorometers were used to measure diurnal patterns of Φ_{PSII} : (1) a multichannel monitoring fluorometer Moni-PAM (Heinz Walz, Germany) in 2009 – see Fig. 4, and (2) a portable FP-100 fluorometer (Photon Systems Instruments, Czech Republic) in 2010. Since the Moni-PAM, which uses an automatic data collection regime, was not available for the 2010 summer expedition, a hand-operated FP-100 fluorometer was used instead.

General technical description of the Moni-PAM system and its operation under field conditions is given by Porcar-Castell *et al.* (2008). The Moni-PAM



Fig. 2. *Salix polaris* at study site, Petuniabukta.



Fig. 3. *Dryas octopetala* at study site, Petuniabukta.



Fig. 4. Measuring head of the fluorometric system Moni-PAM (Walz, Germany).

fluorometric system was installed from 8 to 17 July 2009 in close vicinity of Petunia hut located at Petunia Bay. The measuring apparatus consisted of three monitoring fluorometric probes linked to a controlling and data storing unit (Moni-DA, Heinz Walz, Germany). The whole measuring apparatus was supplied by a high-capacity gel accumulator and a voltage convertor. In our field experiment we used 3 monitoring heads connected to a data-collecting unit (Fig. 5). Such a set up allowed us to use the repetitive saturation pulse method. The pulses of light (1.0 sec, $3\,000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ incident on upper surface of a leaf) were applied each five minutes in the actual light-adapted physiological state of a plant. Light-adapted state reflected the actual amount of incident photosynthetically active radiation. In this way the quantum yield of photosynthetic processes in photosystem II (effec-

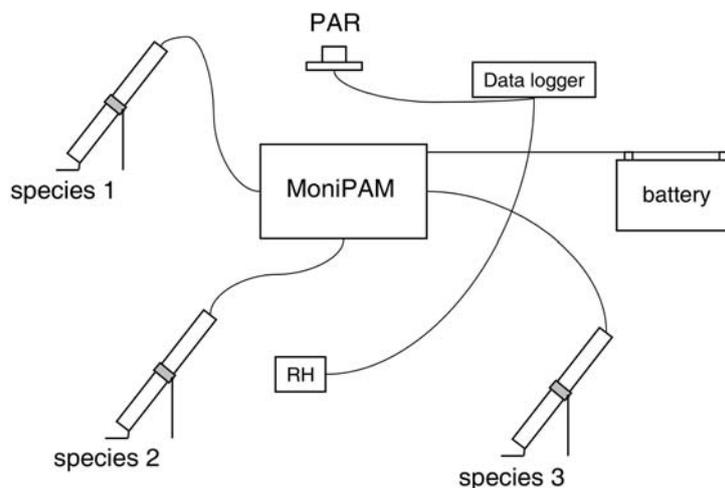


Fig. 5. Schematic view of instrumental set up used in measurements of chlorophyll fluorescence parameters in Petuniabukta in 2009.

tive quantum yield: Φ_{PSII}) was measured. From the chlorophyll fluorescence signal reached during the pulse (F_M'), an effective quantum yield of photosynthetic processes in photosystem II (Φ_{PSII}) was calculated using the following equation:

$$\Phi_{\text{PSII}} = (F_M' - F_S) / F_M' \quad (1)$$

where (F_S) denotes values of steady state chlorophyll fluorescence, and F_M' denotes maximum chlorophyll fluorescence in the light adapted state (for nomenclature of chlorophyll fluorescence parameters see *e.g.* Roháček *et al.* 2008). In this way, Φ_{PSII} was evaluated and recorded every 5 minutes. Relative electron transport rate (ETR) of photosynthetic processes was then calculated by WinControl-3 (Heinz Walz, Germany) as

$$\text{ETR} = \Phi_{\text{PSII}} * \text{PAR} * a * 0.5 \quad (2)$$

where PAR is photosynthetically active radiation (for measurements see Microclimate measurements) and a is an absorption coefficient. The values of 0.83 (*Salix polaris*) and 0.84 (*Silene acaulis*, *Dryas octopetala*) were used. The coefficient of 0.5 used in the equation reflected the assumption that absorbed light energy is distributed equally between PS II and PS I.

Diurnal measurements of photosynthetic activity. — Estimation of net photosynthetic rate (P_N) was made according to the Equation 3, where Φ_{PSII} is effective quantum yield of photosynthetic processes in PS II (measured in the field, see Field measurements of chlorophyll fluorescence), C is a coefficient evaluating the relation between quantum yield of CO_2 fixation and photosynthetic PSII activity (*i.e.* $\Phi_{\text{CO}_2}/\Phi_{\text{PSII}}$ ratio), a is leaf absorption coefficient for photosynthetically active radiation (PAR), and PAR is the value of photosynthetically active radiation

Table 1
 Relationship between measured actual quantum yield (Φ_{PSII}) and particular microclimatic factors (air temperature, leaf temperature, relative air humidity – RH, photosynthetically active radiation – PAR) expressed by Spearman's nonparametric correlation coefficients. Asterisks denote statistical significance at $p < 0.05$.

	Spearman's nonparametric correlation coefficients					
	Φ_{PSII} (<i>Salix polaris</i>)		Φ_{PSII} (<i>Silene acaulis</i>)		Φ_{PSII} (<i>Dryas octopetala</i>)	
Year 2009						
Air temperature	-0.533	*	-0.532	*	-0.415	*
Leaf temperature	-0.669	*	-0.695	*	-0.561	*
RH [%]	0.514	*	0.656	*	0.479	*
PAR	-0.845	*	-0.776	*	-0.872	*
Year 2010						
Air temperature	-0.426	*	-0.732	*	-0.553	*
Leaf temperature	-0.459	*	-0.795	*	-0.745	*
Rh [%]	0.335	*	0.537	*	0.338	*
PAR	-0.272	*	-0.838	*	-0.412	*

Table 2
 Photosynthetic characteristics calculated from chlorophyll fluorescence data. Coefficient C (the range and particular equations) evaluating the relation between quantum yield of CO_2 fixation and photosynthetic PSII activity, maximal net photosynthetic rate (P_{Nmax}) and daily net photosynthesis (Daily P_{N}) calculated for *Salix polaris*, *Silene acaulis* and *Dryas octopetala* plants.

	C ($\Phi_{\text{CO}_2}/\Phi_{\text{PSII}}$)		P_{Nmax} [$\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$]	Daily P_{N} [$\text{mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$]	
	range	equation		min	max
<i>Salix polaris</i>	0.030–0.085	$y = 0.0280 + 0.0618 * e^{-0.0023 * \text{PAR}}$	17.6	min max mean	6.917 14.648 10.117
<i>Silene acaulis</i>	0.041		21.4	min max mean	4.591 15.170 8.713
<i>Dryas octopetala</i>	0.047–0.056	$y = 0.0469 + 0.0103 * e^{-0.0029 * \text{PAR}}$	22.9	min max mean	3.961 13.432 7.216

measured in the field (see Microclimate measurements). For each species, Φ_{CO_2} (sensu operational Φ_{CO_2} – Singsass *et al.* 2001) was estimated from individual photosynthetic light-response curves available in literature (see the references below) using the Equation 4, where P_{N} is net photosynthetic rate derived from a curve for particular light, a is absorption coefficient, and PAR^* is photosynthetically active radiation derived from the curve (PAR^* used only in Equation 4). In such a way, relation between Φ_{CO_2} and PAR^* was calculated (see the equation in Table 2).

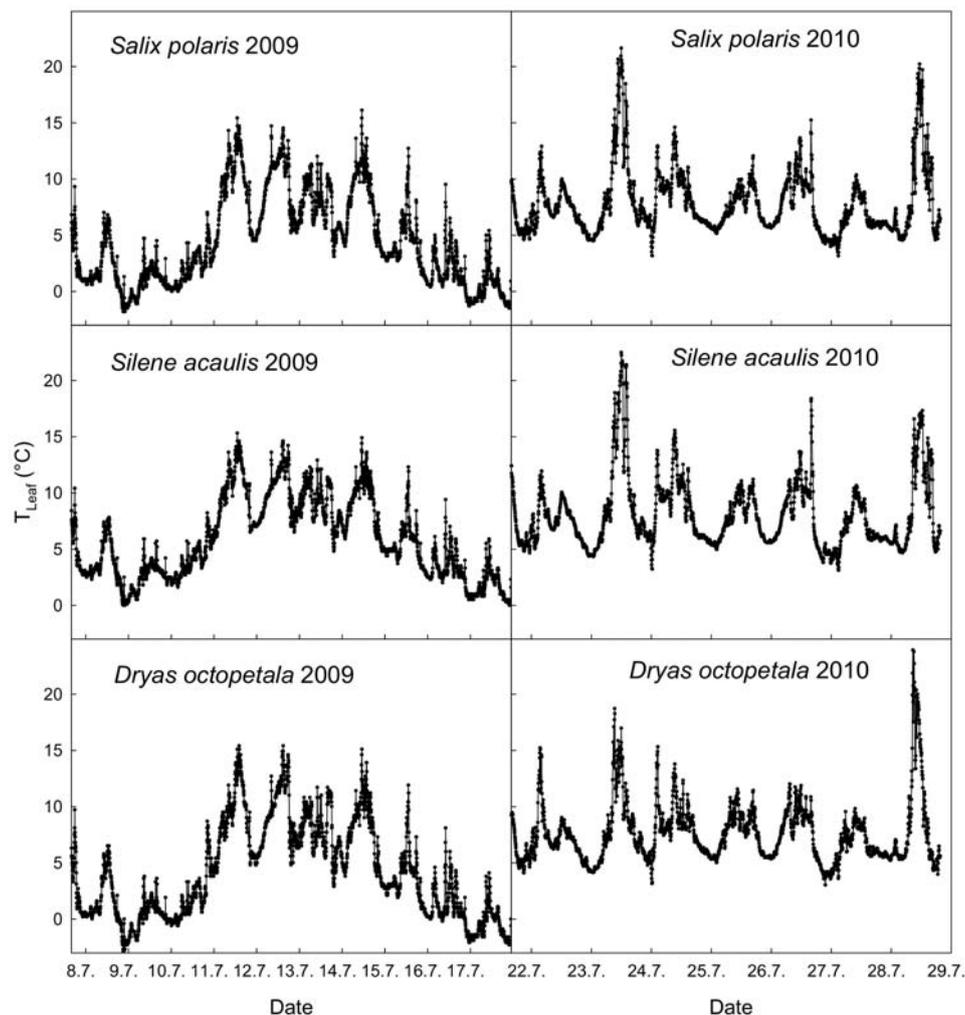


Fig. 6. Diurnal courses of leaf temperature (T_{Leaf}) measured on plants during the periods of 8–17 July 2009 (left) and 21–28 July 2010 (right).

Resulting Φ_{CO_2} values were used for P_N evaluation (Equation 3) using the values of measured PAR. In Equation 4, only P_N but not respiration was considered because no literature data were available on photorespiration of the three experimental species as dependent on light.

$$P_N = \Phi_{PSII} * C * a * PAR \quad (3)$$

$$\Phi_{CO_2} = P_N / (a * PAR) \quad (4)$$

Numerical value of C is species- and light-dependent (Oberhuber *et al.* 1993). It was, therefore, evaluated for individual species using data published by several au-

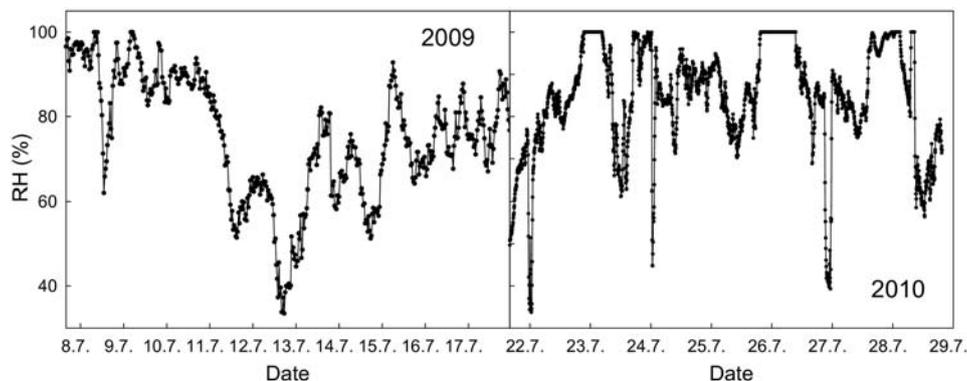


Fig. 7. Diurnal courses of relative air humidity (RH) measured 5 cm above vegetation cover at study site during the periods of July 8–17 July 2009 (left) and 21–28 July 2010 (right).

thors who measured photosynthetic light-response curves in the field. For *S. polaris*, the value of C was estimated 0.030–0.085 (see Table 2). For $\Phi_{\text{CO}_2}/\Phi_{\text{PSII}}$ calculation, particular Φ_{CO_2} values were taken from Muraoka *et al.* (2002), and Φ_{PSII} ones from Muraoka *et al.* (2008), respectively. For *D. octopetala* the C value was estimated 0.047–0.056 and based on data of Muraoka *et al.* (2008) and Wookey *et al.* (1995). For *S. acaulis*, the value of C was estimated 0.041 using data presented by Laporte and Delph (1996) and by McKiernan and Baker (2006). Leaf absorption coefficients are species-specific and dependent on optical properties of particular leaves, prevailing light regimen (Davis *et al.* 2011), leaf water status and chlorophyll concentrations (Bauerle *et al.* 2004). Therefore, specific numeric values of a were taken into the Equation 3 for each species after compilation of available literature data (*see sources in brackets*): *Salix polaris* ($a = 0.83$; Ehleringer 1988; Ehleringer and Comstock 1987; Hjelm and Ögren 2004), *Dryas octopetala*, *Silene acaulis* ($a = 0.84$). After P_N calculations, diurnals of P_N were constructed and daily totals of photosynthetic fixation of carbon for particular days and species calculated.

Microclimate measurements. — Simultaneously with the fluorometric parameters of the three plant species, ecophysiological data on (1) leaf temperature, and (2) relative leaf irradiance were recorded in 5 minute intervals. Moreover, measurements of absolute values of incident photosynthetically active radiation (PAR) were taken by a EMS-12 radiometer and stored in a Minikin (EMS Brno, Czech Republic) datalogger. In 2010, PAR data for 21–28 July were recorded as mentioned above. Leaf temperature was measured by CuCo thermocouples and recorded to a V8 datalogger (EMS Brno, Czech Republic) while relative air humidity at the research plot was measured by a Minikin (EMS Brno, Czech Republic).

Statistical analysis. — We analyzed the data using Spearman's nonparametric correlation parameters to determine the main environmental factor affecting quantum yield of photosynthetic processes in photosystem II (Φ_{PSII}). For each plant spe-

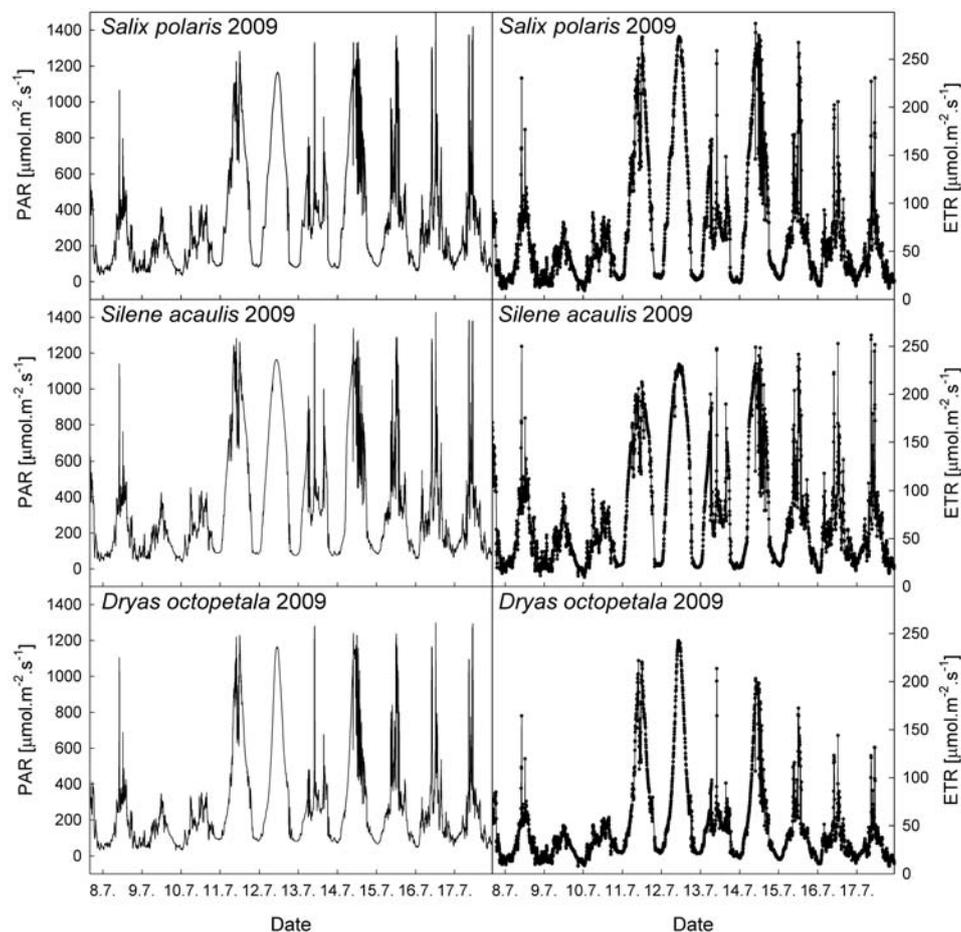


Fig. 8. Diurnal courses of incident photosynthetic active radiation (PAR, left) and electron transport rate (ETR, right) measured on plants during the period of 8–17 July 2009.

cies we identified relationships between Φ_{PSII} and PAR, air temperature (T), leaf temperature (T_{Leaf}), and relative air humidity (RH), respectively. STATISTICA version 9.1. (StatSoft, Inc., Tulsa, USA) was used for the statistical analyses.

Results

Microclimate. — Measurements of leaf temperature, RH and PAR (Figs 6, 7 and 8, respectively) taken in 2009 showed that, within the measuring periods, there were three basic weather types: (a) overcast days (8–10 July 2009), (b) partly cloudy days (15–17 July), and (c) fully sunny days (11–14 July). In the July 2010 measuring period two days were classified as fully sunny (23 and 28 July) while the rest of the

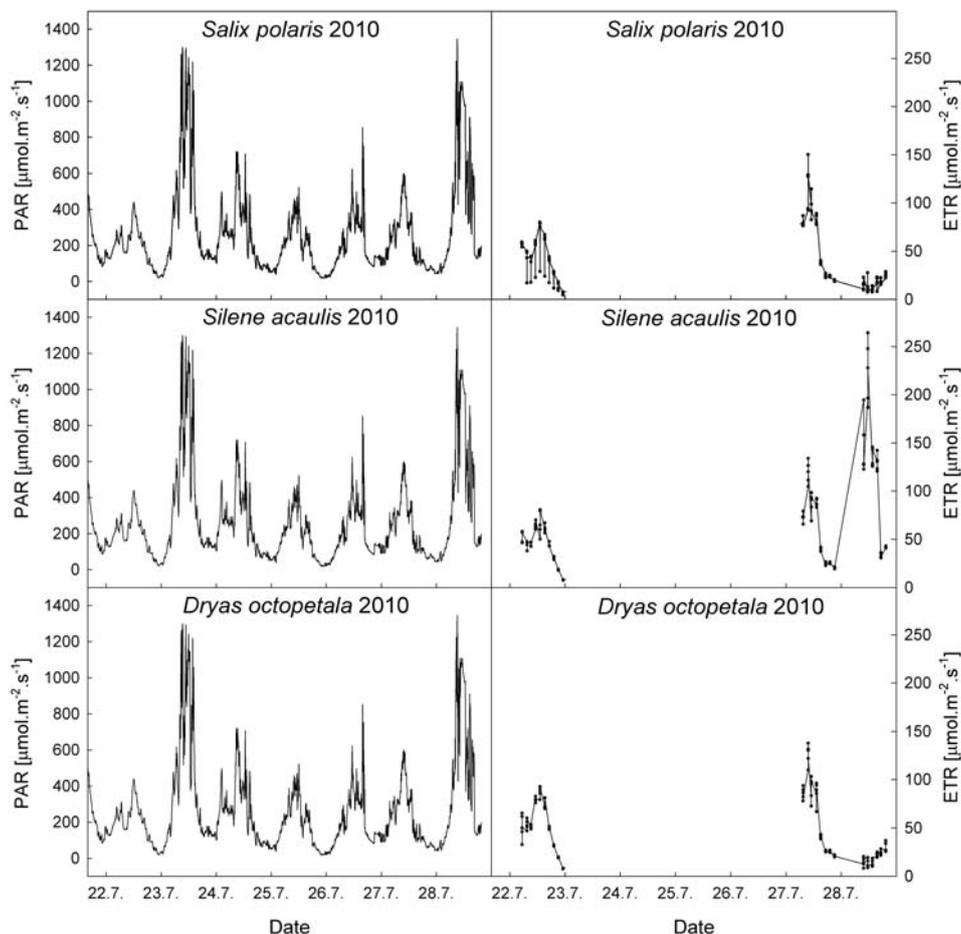


Fig. 9. Diurnal courses of incident photosynthetic active radiation (PAR, left) and electron transport rate (ETR, right) measured on plants during the period of 21–28 July 2010.

days were considered overcast (Fig. 9). Instantaneous PAR values ranged from 80 to 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for fully sunny days and from 35 to 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for overcast days. Direct sunlight strongly determined the daily courses of leaf/air temperatures. During sunny days leaf temperature reached up to 20°C whereas it did not exceed 10.0°C on overcast days. In 2009, leaf temperature reached a minimum of -2.3°C and maximum of 16.1°C, while in the 2010 measuring period, a minimum of 2.4°C and maximum of 23.9°C were recorded. There were differences in leaf temperature between species in both measuring periods, however, they were rather small and statistically insignificant ($P = 0.05$). Relative air humidity differed within the ranges of 35–100% (2009), and 75–100% (2010). The RH changes reflected mainly precipitation events. Typical was a rise in RH due to common morning precipitation, especially in the 2010 measuring period.

Photosynthesis in response to light. — Diurnal measurements of the relative electron transport rate (ETR) of photosynthetic processes recorded by a fluorometer running in automatic mode are given in Fig. 8. In all experimental species, ETR courses for the 2009 measuring period were similar in shape to PAR daily courses. ETR reflected the PAR daily courses and ranged from 15 to 250 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during sunny and semicloudy days, but did not exceed 100 during overcast days. Maxima of ETR reached values above 220 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during midday hours of fully sunny days, when the sun elevation angle was the highest. On a semicloudy day (14 July), maximum ETR was, however, reached in *S. polaris* during a short-term period of full sunshine passing through a large gap between clouds. For *S. acaulis*, maximum ETR was reached under similar circumstances on 17 July. In contrast to the above two species, maximum ETR was reached on a fully sunny day in *D. octopetala*. The maximum ETR values for particular days were somewhat lower in *D. octopetala* than in the other two species. ETR values never reached zero since there was still substantial PAR available (PAR range from 50–100 $\mu\text{mol m}^{-2} \text{s}^{-1}$) during night time when the elevation angle of the sun reached its minimum above the horizon.

Due to nonavailability of an automatic fluorometer in the 2010 measuring period, we were able to measure only three diurnals of ETR for each species. On 22 July, patterns of ETR diurnal measurements followed PAR courses, similar to all ETR records taken in the 2009 measuring period. On 28 July, however, ETR values for *S. polaris* and *D. octopetala* remained low throughout the day and did not relate to the PAR course. In spite of the fact that ETR reached a maximum of about 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ on the previous day with PAR reaching only 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, ETR did not exceed 30 on 23 July when much higher values of PAR were available throughout the day. It was apparent that ETR was inhibited in *S. polaris* and *D. octopetala* and did not reflect daily variations of PAR on 28 July (Fig. 10). Inhibition of ETR was even more apparent when ETR diurnal rates were compared for two days (of 2009 and 2010 season) with similar weather typified by fluctuating PAR (see Fig. 8). Statistical data analyses showed that the Φ_{PSII} decrease on 28 July 2010 for *S. polaris* and *D. octopetala* was associated with air and leaf temperature, but not with relative air humidity and photosynthetically active radiation (see Table 1). These results may indicate temperature-induced limitation of photosynthetic processes (ETR, Φ_{PSII}) in *S. polaris* and *D. octopetala*. No such ETR inhibition was seen in the data from the 2009 measuring period. In 2009, diurnal changes of Φ_{PSII} were strongly related to daily PAR courses (see Table 1) throughout the whole measuring period. The other factors (air temperature, leaf temperature, and relative air humidity) played less important role. In 2010, however, leaf temperature was most dominant factor that affected Φ_{PSII} in *S. polaris*, and *D. octopetala*, while PAR was the main factor affecting Φ_{PSII} in *S. acaulis*.

Diurnal measurements of calculated values of P_N for the period of 8–18 July 2009 are shown in Fig. 11. They are of similar shape as ETR. P_N maxima ($P_{N\text{max}}$)

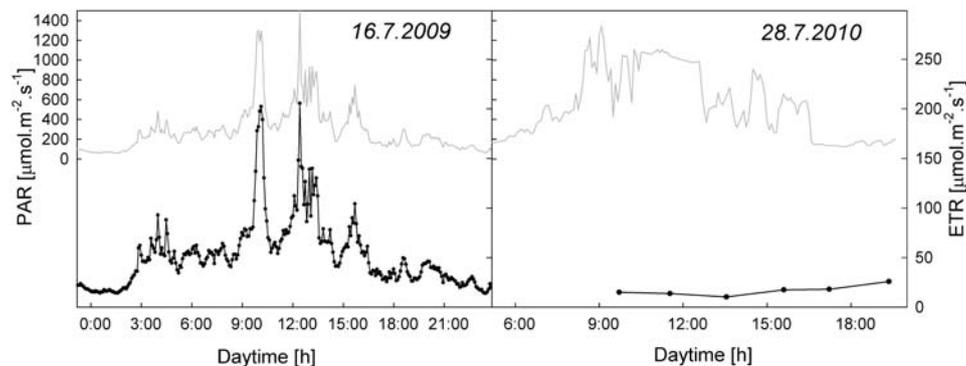


Fig. 10. Diurnal courses of photosynthetic active radiation (PAR; grey line) and electron transport rate (ETR; black line) measured on *Salix polaris* in 2 selected days in 2009 (left) and 2010 (right).

are showed in Table 2. Maximum P_N was reached for individual species at midday on fully sunny days and the days with partial cloudy weather in the time when clouds did not cover sun disc. In *S. polaris*, the daily P_N maxima peaks ranged 18–20 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. In *S. acaulis* and *D. octopetala* the P_N ranges were 23–27, and 18–24 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively. On fully overcast days (9–10 July 2009 in Fig. 11), daily maxima of P_N were much lower. They were about 18–24 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for *S. polaris* and *S. acaulis*, while P_N maximum reached only about 6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ in *D. octopetala*. Daily totals of P_N are summarized in Table 2. For all three species maximum daily total of P_N was calculated for fully sunny day, *i.e.* 12 July 2009. In all species $P_{N\text{max}}$ reached comparable values, *i.e.* 14.6, 15.2, and 13.4 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ for *S. polaris*, *S. acaulis* and *D. octopetala*, respectively. Daily totals of P_N for overcast days were much lower (see Table 2), however, slight interspecific difference was still apparent.

Discussion

In the 2009 measuring period, the highest values of photosynthetic electron transport rate (ETR) were found in midday when direct sunshine was available. This is well documented for 4 July, a typical fully sunny day. Absolute maxima of ETR, however, were reached in *S. polaris* and *S. acaulis* during a partly cloudy day, when a few clouds acted as additional sources of reflected radiation. For limited short-term periods of time (couple of minutes), PAR incident on vegetation consisted of direct solar radiation and radiation reflected from several individual clouds resulting in absolute maxima of about 1 200–1 400 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Under such conditions ETR in *S. polaris* and *S. acaulis* reached values of about 250 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. The same PAR, however, caused substantially lower ETR in *D. octopetala*. Since lower ETR was found in *D. octopetala* (compared to *S. polaris* and *S.*

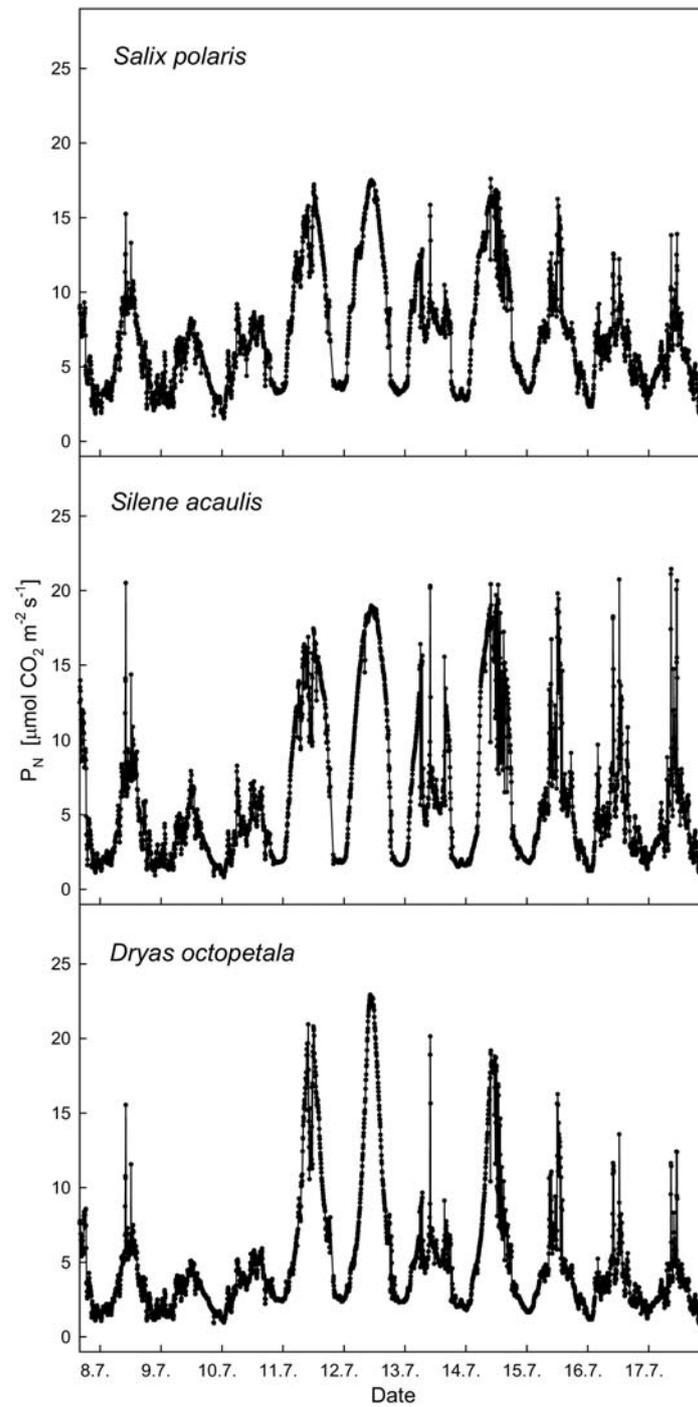


Fig. 11. Diurnal courses of net photosynthesis (P_N) measured on plants during the period of 8–17 July 2009.

acaulis) for the whole range of PAR, it may be concluded that *D. octopetala* exhibits lower effectivity of energy conversion in photosystem II and resulting reduction in electron transport in thylakoid membrane of chloroplast than the other two species. This finding is in accordance with the light-response curves of ETR measured by Muraoka *et al.* (2008) who reported lower ETR in *D. octopetala* (by 20%) than in *S. polaris*. Our ETR data integrated for the whole 2009 measuring period (data not shown) indicated interspecific differences in ETR expressed as a relative value: *S. polaris* (96.3%), *S. acaulis* (100%), and *D. octopetala* (66.9%). High photosynthetic rate of *S. polaris* was supported also by the gasometric measurements of Muraoka *et al.* (2002) on leaves during the early summer season. The same authors, however, reported an age-dependent decrease in photosynthesis in *S. polaris* attributed to reduction in stomatal conductance for water vapour. Thus, *S. polaris* exhibits a high photosynthetic rate only when well supplied with water. If there is water limitation in a particular period of the growing season, the photosynthetic rate may decrease rapidly. In spite of the fact that *D. octopetala* showed the lowest photosynthetic ETR among the studied species, it seemed to be very efficient in photosynthesis if expressed on a ground area basis. Due to a high leaf area index (Muraoka *et al.* 2008) and effective distribution of leaf inclination angles within the clump that optimizes PAR interception and photosynthetic production (Herbert 2003), photosynthetic production per ground and area unit is higher than in the species with lower leaf area index.

In 2009, photosynthetic process (Φ_{PSII}) in all species was related most closely to PAR (Table 1). In 2010, Φ_{PSII} values were related to PAR only in *S. acaulis*. The other two species showed their Φ_{PSII} values dependent rather on leaf temperature (see Table 1) than PAR. The most apparent discrepancy between PAR and photosynthesis courses in *S. polaris* and *D. octopetala* was apparent on 28 July 2010, when ETR courses for *S. polaris* and *D. octopetala* showed different shapes (reduced values) than PAR for the particular day. Such a reduction in ETR may indicate limitation of photosynthetic processes rather by air and leaf temperature (see also high coefficient values for T_{Leaf} in Table 1) than PAR.

Maximum P_{N} (P_{Nmax} – Table 2) derived from diurnals are comparable to the values reported by other authors who measured photosynthesis in tundra/polar plants gasometrically. For *Salix* sp. Oberbauer and Oechel (1989) reported the range of 8–14 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Starr *et al.* (2008) measured seasonal P_{Nmax} means for three consecutive years in *Salix pulchra* and reported the range of 10.0–12.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. The same authors recorded a single-day absolute maximum of P_{Nmax} as 20.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. Our data on P_{Nmax} for *S. polaris* fit well to the above-mentioned literature data: both P_{Nmax} (17.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and P_{N} values calculated from Φ_{PSII} for 11.00–14.00 h. of local time (15.8–17.6 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for the period 11–15 July 2009. Compared to our data, somewhat lower P_{Nmax} values are reported for *D. octopetala* (14.0/20.0 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for untreated control, and phosphorus-treated plants, respectively) by Baddeley *et al.* (1994). Our

P_{Nmax} reached $22.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for June 12, 2009 and the range of $19.2\text{--}22.9 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ for the period of 11–14 July 2009. The higher P_{Nmax} values, however, might be attributed to different geographical locations and particular *D. octopetala* populations. For *S. acaulis*, only few photosynthetic studies focused on temperature effects on particular photosynthetic processes has been published (e.g. Neuner *et al.* 2000; Buchner *et al.* 2007). Unfortunately, they do not bring any data on P_N , P_{Nmax} , respectively. Therefore, it is not possible to compare our finding ($P_{Nmax} = 21.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) with relevant data. Oberbauer and Oechel (1989) reported that majority of tundra plant species had their P_{Nmax} within the range of $10\text{--}20 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$. We may, therefore expect that our chlorophyll fluorescence-derived values of P_N , and P_{Nmax} , respectively, were slightly overestimated. To evaluate the likely overestimation, simultaneous *in situ* measurements of photosynthetic CO_2 exchange on leaf and/or plant level and chlorophyll fluorescence are necessary. Moreover, supplemental laboratory measurements of Φ_{CO_2} under controlled light (Barták *et al.* 1997), temperature, atmospheric and limited oxygen concentration (Krall and Edwards 1992) is required for accurate estimation of photorespiration as dependent on physical factors. In this way, precise value of $\Phi_{\text{CO}_2}/\Phi_{\text{PSII}}$ relevant for respiratory and non-respiratory conditions, might be calculated (Oberhuber *et al.* 1993).

Due to the lack of literature data on species-specific daily net photosynthesis our estimates of daily photosynthetic CO_2 fixation (see Table 2) for *S. polaris*, *S. acaulis*, and *D. octopetala* could be compared only with net ecosystem CO_2 exchange rates (NEE) that are reported for tundra ecosystems, e.g. Laurila *et al.* (2001), Welker *et al.* (2004), and Uchida *et al.* (2010). In these studies soil respiration represents major negative component of ecosystem CO_2 exchange. In our study, only leaf photorespiration, that ranges 10–30% of gross photosynthesis in majority of plants, is a negative component of leaf CO_2 exchange. However, when recalculated for individual species, our daily P_N data give daily means of $0.32\text{--}0.45 \text{ mg CO}_2 \text{ m}^{-2} \text{ d}^{-1}$. This is comparable to the values reported by Welker *et al.* (2004), i.e. $0.3 \text{ mg CO}_2 \text{ m}^{-2} \text{ d}^{-1}$ evaluated for wet plots of high Arctic ecosystems. Reasonable agreement is reached also with daily NEE of *S. polaris*-dominated ecosystem in Ny-Ålesund (Uchida *et al.* 2010). Our daily photosynthetic CO_2 fixation ranged $13.2\text{--}18.5 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$ (recalculated from Table 2). They reached lower part of the NEE interval reported by Uchida *et al.* (2010) for July ($5.8\text{--}58.1 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) and were comparable to the maximum values of NEE range reported for August, September (about $13.0 \text{ mg CO}_2 \text{ m}^{-2} \text{ h}^{-1}$), respectively.

Acknowledgements. — The authors are grateful to Dr. K. Láska (Masaryk University, Brno) for providing part of the climatological data. Technical support of J. Hazdrová M.Sc. (Masaryk University, Brno) during manuscript preparation is also acknowledged. The research reported in this paper was supported by grants INGO LA341 and LM2010009 Project Czech Polar (Czech Ministry of Education) and EHP No. B/CZ0046/3/0013 from Iceland, Lichtenstein and Norway within the frame of the EEA/Norwegian financial mechanism.

References

- ANTONSSON H., BJÖRK R.G. and MOLAU U. 2009. Nurse plant effect of the cushion plant *Silene acaulis* (L.) Jacq. in an alpine environment in the subarctic Scandes, Sweden. *Plant Ecology & Diversity* 2: 17–25.
- BADDELEY J.A., WOODIN S.J. and ALEXANDER I.J. 1994. Effects of increased nitrogen and phosphorus availability on the photosynthesis and nutrient relations of three arctic dwarf shrubs from Svalbard. *Functional Ecology* 8: 676–685.
- BARTÁK M., LÁSKA K., PROŠEK P., HÁJEK J. and VÁCZI P. 2009. Long-term study on vegetation responses to manipulated warming using open top chambers installed in three contrasting Antarctic habitats. In: M. Barták, J. Hájek, and P. Váczi (eds) *Structure and Function of Antarctic Terrestrial Ecosystems*. Book of Abstracts and Contributed Papers. Conference, Brno, October 22th–23th, 2009. Masaryk University, Brno, Czech Republic: 48–51.
- BARTÁK M., NIJS I. and IMPENS I. 1997. Relation between photosynthetic CO₂ fixation and photosystem II activity in perennial ryegrass grown at doubled atmospheric CO₂ and elevated air temperature. *Abstracta Botanica* 21: 317–322.
- BAUERLE W.L., WESTON D.J., BOWDEN J.D., DUDLEY J.B. and TOLER J.E. 2004. Leaf absorptance of photosynthetically active radiation in relation to chlorophyll meter estimates among woody plant species. *Scientia Horticulturae* 101: 169–178.
- BENEDICT J.B. 1989. Use of *Silene acaulis* for dating: The relationship of cushion diameter to age. *Arctic and Alpine Research* 21: 91–96.
- BOKHORST S., BJERKE J.W., DAVEY M., TAULAVUORI K., TAULAVUORI E., LAINE K., CALLAGHAN T.V. and PHOENIX G.K. 2010. Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. *Physiologia Plantarum* 140: 128–140.
- BUCHNER O., HOLZINGER A. and LÜTZ C. 2007. Effects of temperature and light on the formation of chloroplast protrusions in leaf mesophyll cells of high alpine plants. *Plant, Cell and Environment* 30: 1347–1356.
- DAVIS P.A., CAYLOR S., WHIPPO C.W. and HANGARTER R.P. 2011. Changes in leaf optical properties associated with light-dependent chloroplast movements. *Plant, Cell and Environment* 34: 2047–2059.
- EHLERINGER J.R. 1988. Changes in leaf characteristics of species along elevational gradients in the Wasatch Front, Utah. *American Journal of Botany* 75: 680–689.
- EHLERINGER J.R. and COMSTOCK J. 1987. Leaf absorptance and leaf angle: Mechanisms for stress avoidance. In: J.D. Tenhunen, F.M. Catarino, O.L. Lange, and W.C. Oechel (eds) *Plant response to stress. Functional analysis in Mediterranean ecosystems*. Springer-Verlag, New York: 55–76.
- GERASIMENKO T.V., KAIPIAINEN E.L., FILATOVA N.I. and CHUPAKHINA N.I. 1996. CO₂ exchange in some vascular plants inhabiting the polar urals. *Russian Journal of Plant Physiology* 43: 331–341.
- HERBERT T.J. 2003. A latitudinal cline in leaf inclination of *Dryas octopetala* and implications for maximization of whole plant photosynthesis. *Photosynthetica* 41: 631–633.
- HJELM U. and ÖGREN E. 2004. Photosynthetic responses to short-term and long-term light variation in *Pinus sylvestris* and *Salix dasyclados*. *Trees – Structure and Function* 18: 622–629.
- JONES H.G. and DEMMERS-DERKS H.W.M. 1999. Photoinhibition as a factor in altitudinal or latitudinal limits of species. *Phyton, Annales Rei Botanicae, Horn*. Special Issue: *Eurosilva* 39: 91–97.
- KAPPEN L., SCHROETER B., GREEN T.G.A. and SEPPELT R.D. 1998. Chlorophyll *a* fluorescence and CO₂ exchange of *Umbilicaria aprina* under extreme light stress in the cold. *Oecologia* 113: 325–331.
- KRALL J.P. and EDWARDS G.E. 1992. Relationship between photosystem II activity and CO₂ fixation in leaves. *Physiologia Plantarum* 86: 180–187.

- LAPORTE M.M. and DELPH L.F. 1996. Sex-specific physiology and source-sink relations in the dioecious plant *Silene latifolia*. *Oecologia* 106: 63–72.
- LÁSKA K., WITOSZOVÁ D. and PROŠEK P. 2012. Weather patterns of the coastal zone of Petuniabukta, central Spitsbergen in the period 2008–2010. *Polish Polar Research* 33 (4): 297–318.
- LAURILA T., SOEGAARD H., LLOYD C.R., AURELA M., TUOVINEN J.P. and NORDSTROEM C. 2001. Seasonal variations of net CO₂ exchange in European Arctic ecosystems. *Theoretical and Applied Climatology* 70: 183–201.
- LLOYD C.R. 2001. The measurement and modelling of the carbon dioxide exchange at a high Arctic site in Svalbard. *Global Change Biology* 7: 405–426.
- MARCHAND F.L., MERTENS S., KOCKELBERGH F., BEYENS L. and NIJS I. 2005. Performance of High Arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology* 11: 2078–2089.
- MCGRAW J.B. 1985. Experimental ecology of *Dryas octopetala* ecotypes: Relative response to competitors. *New Phytologist* 100: 233–241.
- MCKIERNAN M. and BAKER N.R. 2006. Adaptation to shade of the light-harvesting apparatus in *Silene dioica*. *Plant, Cell and Environment* 14: 205–212.
- MURAOKA H., NODA H., UCHIDA M., OHTSUKA T., KOIZUMI H. and NAKATSUBO T. 2008. Photosynthetic characteristics and biomass distribution of the dominant vascular plant species in a high Arctic tundra ecosystem, Ny-Ålesund, Svalbard: implications for their role in ecosystem carbon gain. *Journal of Plant Research* 121: 137–145.
- MURAOKA H., UCHIDA M., MISHIO M., NAKATSUBO T., KANDA H. and KOIZUMI H. 2002. Leaf photosynthetic characteristics and net primary production of the polar willow (*Salix polaris*) in a high Arctic polar semi-desert, Ny-Ålesund, Svalbard. *Canadian Journal of Botany* 80: 1193–1202.
- NEUNER G., BUCHNER O. and BRAUN V. 2000. Short-Term Changes in Heat Tolerance in the Alpine Cushion Plant *Silene acaulis* ssp. *excava* [All.] J. Braun at Different Altitudes. *Plant Biology* 2: 677–683.
- NORDSTROEM C., SOEGAARD H., CHRISTENSEN T.R., FRIBORG T. and HANSEN B.U. 2001. Seasonal carbon dioxide balance and respiration of a high-arctic fen ecosystem in NE-Greenland. *Theoretical and Applied Climatology* 70: 149–166.
- OBERBAUER S.F. and OECHEL W.C. 1989. Maximum CO₂-assimilation rates of vascular plants on an Alaskan arctic tundra slope. *Holarctic Ecology* 12: 312–316.
- OBERHUBER W., DAI Z.-Y. and EDWARDS G.E. 1993. Light dependence of quantum yields of photosystem II and CO₂ fixation in C₃ and C₄ plants. *Photosynthesis Research* 35: 265–274.
- PANNEWITZ S., GREEN T.G.A., MAYSEK K., SCHLENSOG M., SEPPELT R., SANCHO L.G., TÜRK R. and SCHROETER B. 2005. Photosynthetic responses of three common mosses from continental Antarctica. *Antarctic Science* 17: 341–352.
- PARMENTIER F.J.W., VAN DER MOLEN M.K., VAN HUISSTEDEN J., KARSANAEV S.A., KONONOV A.V., SUZDALOV D.A., MAXIMOV T.C. and DOLMAN A.J. 2011. Longer growing seasons do not increase net carbon uptake in the Northeastern Siberian tundra. *Journal of Geophysical Research* 116: G04013, 11 pp.
- PORCAR-CASTELL A., PFÜNDEL E., KORHONEN J.F.J. and JUUROLA E. 2008. A new monitoring PAM fluorometer (MONI-PAM) to study the short- and long-term acclimation of photosystem II in field conditions. *Photosynthesis Research* 96: 173–179.
- ROBINSON C.H., WOOKEY P.A., LEE J.A., CALLAGHAN T.V. and PRESS M.C. 1998. Plant community responses to simulated environmental change at a high Arctic polar semi-desert. *Ecology* 79: 856–866.
- ROHÁČEK K., SOUKUPOVÁ J. and BARTÁK M. 2008. Chlorophyll fluorescence: A wonderful tool to study plant physiology and plant stress. In: B. Schoefs (ed.) *Plant Cell Compartments – Selected Topics*. Research Signpost, Kerala, India: 41–104.

- SCHLENSOG M. and SCHROETER B. 2001. A new method for the accurate *in situ* monitoring of chlorophyll *a* fluorescence in lichens and bryophytes. *Lichenologist* 33: 443–452.
- SCHROETER B., GREEN T.G.A., PANNEWITZ S., SCHLENSOG M. and SANCHO L.G. 2011. Summer variability, winter dormancy: lichen activity over 3 years at Botany Bay, 77°S latitude, continental Antarctica. *Polar Biology* 34: 13–22.
- SINGSAAS E.L., ORT D.R. and DELUCIA E.H. 2001. Variation in measured values of photosynthetic quantum yield in ecophysiological studies. *Oecologia* 128: 15–23.
- STARR G., OBERBAUER S.F. and AHLQUIST L.E. 2008. The photosynthetic response of alaskan tundra plants to increased season length and soil warming. *Arctic, Antarctic, and Alpine Research* 40: 181–191.
- UCHIDA M., KISHIMOTO A., MURAOKA H., NAKATSUBO T., KANDA H. and KOIZUMI H. 2010. Seasonal shift in factors controlling net ecosystem production in a high Arctic terrestrial ecosystem. *Journal of Plant Research* 123: 79–85.
- WELKER J.M., FAHNESTOCK J.T., HENRY G.H.R., O'DEA K.W. and CHIMNER R.A. 2004. CO₂ exchange in three Canadian High Arctic ecosystems: response to long-term experimental warming. *Global Change Biology* 10: 1981–1995.
- WOOKEY P.A., ROBINSON C.H., PARSONS A.N., WELKER J.M., PRESS M.C., CALLAGHAN T.V. and LEE J.A. 1995. Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high Arctic polar semi-desert, Svalbard. *Oecologia* 102: 478–489.

Received 28 June 2011

Accepted 5 July 2012