Rapid photosynthetic recovery of a snow-covered feather moss and *Peltigera* lichen during sub-Arctic midwinter warming

Jarle W. Bjerke[a], Stef Bokhorst[b], Terry V. Callaghan[c,d], Matthias Zielke[e] and Gareth K. Phoenix[c]

[a]*Norwegian Institute for Nature Research (NINA), FRAM – High North Research Centre on Climate and the Environment, NO-9296 Tromsø, Norway;* [b]*Department of Forest Ecology and Management, Swedish University of Agricultural Sciences, SE-90183 Umeå, Sweden;* [c]*Department of Animal and Plant Sciences, University of Sheffield, Western Bank, Sheffield S10 2TN, UK;* [d]*Royal Swedish Academy of Sciences, Lilla Frescativägen 4A, SE-114 18, Stockholm, Sweden;* [e]*Norwegian Institute for Agricultural and Environmental Research (Bioforsk), Arctic Agriculture and Land Use Division, NO-9269 Tromsø, Norway*

[*]Corresponding author. Email: jarle.werner.bjerke@nina.no.

Running headline: Sub-Arctic moss and lichen photosynthesis during midwinter warming

Bjerke, Jarle Werner; Bokhorst, Stef; Callaghan, Terry V.; Zielke, Matthias; Phoenix, Gareth K..
Rapid photosynthetic recovery of a snow-covered feather moss and Peltigera lichen during sub-Arctic midwinter warming. Plant Ecology & Diversity 2013 ;Volum 6.(3-4) s. 383-392 DOI 10.1080/17550874.2013.771712

Abstract

Background: Arctic lichens and mosses are covered by snow for more than half the year and are generally considered as being dormant for most of this period. However, enhanced frequency of winter warming events due to climate change can cause increased disturbance of their protective subnivean environment.

Aim: To further understand cryptogamic responses to mid-winter warming we compared the ecophysiological performance of one lichen and one moss species during a simulated warming event.

Methods: We measured photosynthesis and dark respiration in samples of the moss *Hylocomium splendens* and the lichen *Peltigera aphthosa* removed from under snow, and on natural refreezing after the warming event, which was simulated by using infrared heaters suspended above the ground.

Results: The moss exposed to light at +5 °C immediately after removal from their subnivean environment and from warmed plots showed positive net gas exchange within 332 s; the lichen required 1238 s. Photosynthesis and nitrogen fixation rates were equal to that, or higher than, during the preceding growing season. Upon refreezing after the event, moss photosynthesis declined considerably.

Conclusions: The moss, and to a lesser extent the lichen, may contribute to subnivean midwinter ecosystem respiration, and both are opportunistic, and can take advantage of warmer winter phases for photosynthesis and growth. This ought to be taken into account in vegetation change projections of cryptogam-rich ecosystems.

Keywords: carbon flux; climate change; cryptogams; dormancy; gas exchange; nitrogen fixation; reactivation; snow melt; subnivean environment; winter warming

39

Introduction

Drying and freezing may induce anabiosis in lichens and bryophytes. While the effects of rehydration and desiccation of bryophytes and lichens have received much attention (e.g., Smith and Molesworth 1973; Lange et al. 2006; Proctor et al. 2007), their freezing-induced anabiosis and reactivation – and cryobiology in general – are far less understood. The most cryotolerant lichens have detectable photosynthetic activity down to –24 °C (Lange 1965), but for most lichens, activity ceases at milder subfreezing temperatures (Kappen 1993). For bryophytes, photosynthesis has been reported down to –8 °C (Kappen et al. 1989). Low winter temperatures have been considered to halt functioning of cryptogams during the winter period (Phoenix and Lee 2004; Schlensog et al. 2004). However, considerable wintertime respiration suggests that many arctic, sub-arctic and alpine ecosystems are not at all dormant during winter (Zimov et al. 1993; Brooks et al. 1997; Grogan et al. 2001; Grogan and Jonasson 2006; Nobrega and Grogan 2007). Mid-winter temperatures in the interface between snowpack and soil can be close to 0 °C, despite severe freezing temperatures above the snowpack (Grogan and Jonasson 2006; Bokhorst et al. 2010a), enabling subnivean metabolic respiration, especially by microbial soil organisms (Mikan et al. 2002).

Climate change in the Arctic is not only projected to lead to increases in mean wintertime temperatures, but also increased frequency of extreme warming events, which can result in rapid snow melt and loss of the insulating snow layer (Putkonen and Roe 2003; Christensen et al. 2007; Bokhorst et al. 2009; Callaghan et al. 2010, 2011a, 2011b). Both simulated and natural sub-arctic winter warming events have recently been shown to cause considerable damage to plants (Bokhorst et al. 2008, 2009, 2010b, 2011, 2012). The most likely cause of such damage is the initiation of premature spring-like development, which is interrupted by return to normal winter temperatures, exposing the vegetation to freezing temperatures in the absence of an insulating snow cover (Crawford 2008; Bokhorst et al. 2010b). Lichens and bryophytes are important components of many arctic and sub-arctic vegetation types. In a recent winter warming simulation experiment (Bokhorst

et al. 2008, 2011), it has been shown that the dominant lichen and bryophyte species had contrasting sensitivities to winter warming events; the feather moss *Hylocomium splendens* (Hedw.) Schimp. experienced severely reduced photosynthesis and growth rates during the following growing seasons, whereas the lichen *Peltigera aphthosa* (L.) Willd. remained unaffected (Bjerke et al. 2011). It was shown that the severe freezing following the warming events damaged vulnerable bryophyte tissues whose development was stimulated during the warming events (Bjerke et al. 2011), a similar mechanism as that seen to result in considerable damage to the vascular plants in the same experiment (Bokhorst et al. 2010b, 2011). These differences between the moss and the lichen in response to extreme winter warming indicate contrasting vulnerability to winter frost damage. Whether this is due to differences in ecophysiological activity is, however, not known, but there are indications of different recovery time after winter anabiosis for mosses and lichens (Schlensog et al 2004). Continental Antarctic bryophytes need more time to recover from winter anabiosis than lichens (Schlensog et al. 2004).

This paper originates from a winter warming manipulation experiment that was undertaken in the Swedish sub-Arctic. While the previous studies from this experiment focused on vascular plant and summertime cryptogamic responses to winter warming, this study focuses on wintertime responses of the dominant moss and lichen in this ecosystem. To explore mid-winter reactivation rates of *H. splendens* and *P. aphthosa* and their associated cyanobacteria we measured ecophysiological activity of specimens that became gradually exposed during snow melt from a simulated extreme winter warming event, and of specimens removed directly from their subnivean environment. To the best of our knowledge, midwinter carbon flux measurements of sub-Arctic feather mosses and lichens and the nitrogen fixation activity of their associated cyanobacteria have not been reported previously. The results presented here therefore provide novel insight into the midwinter ecology of these cryptogams and their reactivation rates to winter warming events. Assuming that sub-Arctic and continental Antarctic bryophytes and lichens respond similarly, we hypothesised that the lichen would be reactivated more rapidly than the bryophyte in our study. We also hypothesised that the

specimens that were gradually exposed would reach higher photosynthetic rates than the specimens removed directly from their subnivean environment, as the former group had more time to adapt to light. Finally, we expected that refreezing following the warming event would negatively affect photosynthetic capacity of the moss, as its hardening mechanisms were reduced during the warming event.

Materials and methods

Study area and species

This study was carried out in a sub-Arctic heathland close to the Abisko Scientific Research Station in northern Sweden (68° 21' N, 18° 49' E). The sub-Arctic heathland is dominated by evergreen dwarf shrubs (Bokhorst et al. 2008), but the most abundant lichen, *Peltigera aphthosa*, and bryophyte, the feather moss *Hylocomium splendens*, also have a high ground cover (Bjerke et al. 2011). In the study area, these two cryptogams are most abundant in mesic heath vegetation that under normal winter conditions are covered by snow for about 8 months (ca. October-May).

The warming treatment

Three discrete winter warming events were simulated, at the beginning of March (period of maximum snow depth in this region (Kohler et al. 2006)) in 2007, 2008 and 2009 by using infrared heating lamps to thaw the snow (for details see Bokhorst et al. 2008, 2009). The experiment consisted of 18 plots of 2.1 m × 1.0 m; six control plots and six of each of two warming treatments: canopy warming and canopy with soil warming. In the two warming treatments, four infrared heating lamps (Kalglo Electronics Co., Bethlehem, PA, USA) were suspended (70 cm apart) in parallel from wooden frames. The canopy with soil warming plots were further warmed by soil heating cables at 5 cm soil depth and running parallel at 20 cm distance from each other. Soil warming cables were switched on two days after the lamps to simulate the delay in soil thaw during a real event. Control plots received no warming treatment and remained insulated under the natural winter snow cover. Snow depth varied between 40 and 50 cm, and the soil surface temperature was around -3 °C (Bokhorst et al. 2010a). For this study, to avoid disturbing the control plots that served as control for the main experiment with the complete suite of species, we established new control plots for our measurements. Before snow fall in autumn 2008, sites with the two species close to the warming experiment were marked for use as control plots and revisited at the beginning of March in

2009. Temperatures were recorded by a data logger at 6-h intervals using thermistors placed in each plot at dwarf shrub canopy height (which was under snow prior to warming), at the soil surface and at 5 cm depth.

Each warming event lasted 7 d during which the lamps were kept at a constant distance of 50 cm from the snow surface, i.e. they were lowered as the snow depth decreased. This approach ensured a gradual snow thaw, taking 2 to 3 d to thaw the full depth of snow in each plot. As vegetation became exposed, lamps were kept at 50 to 70 cm above the soil surface to maintain canopy warming (lower lamp heights were needed during higher wind speeds and lower ambient temperatures). Temperatures from the thermistors were monitored to ensure warming was realistic and within the bounds of temperatures recorded for real events. The aim was to raise temperature to 5 °C (Bokhorst et al. 2008), and for most of the time temperature was close to 5 °C; temperature at canopy height fluctuated between 0.9 and 7.0 °C during the warming events. Thermocouple measurements of vegetation surface temperatures were also made to ensure that leaves did not overheat. Incident light (photosynthetic photon flux density; PPFD) was measured with quantum sensors (SKP215, Campbell Scientific, Shepshed, UK) placed at the ground (snow-covered in March) and at 1.5 m above ground (not covered by snow and with minimal shading from trees). The irradiance measurements at 1.5 m above ground, representative also for the incident light to warmed plots after snow melt, reached daily maxima of between 166 and 290 μmol m^{-2} s^{-1} PPFD during the warming events in 2008 and 2009. Irradiance measurements on the ground under snow showed no light transmittance through the snowpack.

Sampling and ecophysiological measurements

During the third winter warming simulation event in March 2009 (i.e. of single events simulated in three consecutive years), metabolic activity in the lichen and bryophyte was measured by using a portable gas exchange and fluorescence system (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany). Samples from the 12 warmed plots (both warming treatments) were measured 2-4 h after first

147 emergence from under snow and exposure to warming treatment temperature while they still were
148 moist from the melted snow. These samples were compared with those taken from below the snow
149 in the control plots. The snow was carefully removed from the vegetation. Samples were collected
150 one at a time, placed in dark bags and immediately brought to the GFS-3000 for measurements of
151 dark respiration and photosynthesis. These samples henceforth are termed 'subnivean'. The
152 temperature at the soil-snowpack interface at the time of sampling was around –3 °C (figure 1 in
153 Bokhorst et al. 2010a). The time from sampling to the start of the gas exchange measurements was
154 3-4 minutes.

155 Samples were not artificially moistened; the melting snow and ice on their surfaces and within the
156 thalli, and the relative humidity (RH) in the air were the only water sources for the subnivean
157 samples, while the samples from the warming treatments were moist from the snow thawed by the
158 heating lamps. The objective with not adding extra moisture was to test activity under natural
159 thawing conditions. Samples were dried completely and weighed after measurements. Weights of
160 naturally moist and dried samples showed that water content was within the range suitable for
161 optimal photosynthetic rates (140 to 220 % of dry weight). Only first-year and second-year segments
162 of the feather moss were used. Each sample consisted of ca. five shoots. Lichen samples consisted of
163 one ellipsoid lobe without apothecia, ca. 2.5 cm wide and 4 cm long.

164 While subnivean samples were naturally dark-adapted, warmed plot samples exposed to light were
165 dark pre-treated for 1 h before sampling. The analytical run consisted of a short period of instrument
166 calibration in darkness (1 min), followed by measurements of dark respiration (DR) and maximal
167 quantum efficiency of photosystem II (PSII), i.e. F_v/F_m (Maxwell and Johnson 2000), before the light
168 was switched on. A saturating but not photoinhibiting (cf. Lange et al. 1996) PPFD of 400 μmol m^{-2} s^{-1}
169 was used during measurements of NP. CO_2 concentration was set to 380 ppm, cuvette humidity to
170 7000 ppm H_2O, and temperature to 5 °C. This temperature was selected because it approximated
171 the average canopy air temperature in the warming treatments after full snow melt (see figure 1 in

Bokhorst et al. 2010b). During the light treatment, the quantum yield of PSII, Φ_{PSII} (Genty et al. 1989; Maxwell and Johnson 2000) and fluorescence quenching parameters were measured continuously (quenching data not reported here). Carbon assimilation curves flattened out after 5 to 45 min of light treatment (not to horizontal which would have needed more time for most samples, but until the steep, almost exponential rise in assimilation was passed). All samples were measured for at least 30 min in light. Assimilation rates were used to quantify the time taken from light exposure until positive net photosynthetic rates were reached, and to derive maximum net photosynthesis (NP) rates (within the time limits and environmental conditions given; i.e. longer light treatments and/or higher temperatures would probably have rendered higher NP). DR (with negative values) and NP were used to calculate gross photosynthesis (GP), where GP = NP – DR. Values for NP, DR and GP were expressed on a dry weight basis. Comparisons with NP rates from the preceding growing season (reported in Bjerke et al. 2011) were used to check the potential of winter gas exchange; rates close to or higher than during summer would indicate high potentials.

To test how 1 day of freezing after the warming event would affect the photosynthesis and respiration (i.e. 12-18 h after) warming was turned off and before the first snowfall, samples of *H. splendens* moistened by wind-blown snow were collected from the warming treatments and measured using the same procedure as for the other samples. It took a full day to obtain a full data set. These samples are referred to as 'refreezing'. Capacity constraints on the GFS-3000 led to that only the moss could be analysed the first day after turning off the heat. The second day the warmed plots had been completely re-covered by newly fallen and wind-blown snow. Our principle was not to manipulate snow cover after the warming event. Hence, we could not dig for more samples, and the lichen was therefore not analysed after refreezing.

The leaf photosynthesis system used is supplied with a temperature sensor for measuring leaf temperature, but when using the cuvette specially designed for loose samples of cryptogams, this

196 sensor is not in direct contact with the cryptogam. Thus, we cannot report exact thallus surface
197 temperatures from the ecophysiological measurements.

198 Nitrogen fixation rates of cyanobacteria associated with *H. splendens* and *P. aphthosa* were
199 measured during the second winter warming event in March 2008. Samples for nitrogen fixation
200 measurements were randomly selected and carefully removed from the plots. They consisted of
201 whole, cleaned thalli or tufts of ca. 25 cm^2 which were measured using the acetylene reduction assay
202 (Stewart et al. 1967). No measurements on subnivean samples were taken. Samples were wetted
203 and kept moist overnight. They were placed in air-tight chambers outdoors and incubated with 10%
204 (v:v) acetylene for ca. 2 h (exact incubation time noted for every sample). Mean chamber
205 temperatures (1-3 °C higher than ambient) and PPFD during incubation were 6.8 °C and 207 µmol m^{-2}
206 s^{-1}. Gas samples were measured according to Zielke et al. (2002). Nitrogen fixation activity during
207 the event was compared with growing season fixation rates from the same plots reported in the
208 electronic supplement of Bjerke et al. (2011).

209 *Data analyses*

210 Relationships between time of exposure to light and carbon assimilation rates were curve-fitted by
211 using the sigmoidal Morgan-Mercer-Flodin model, which, for all relationships provided better fits
212 than other models, both sigmoidal and non-sigmoidal. Differences between the two warming
213 treatments were first tested with a series of Student's *t*-tests. As there were no significant
214 differences between the two treatments for any of the measured parameters (lowest *P*-value was
215 0.11; most *P*-values were above 0.50), the two types of warming treatment data could be pooled
216 (canopy only, and canopy plus soil warming), here called 'warming'. The pooled warming data were
217 compared against subnivean samples, and, for *H. splendens*, also against refrozen samples. Separate
218 repeated-measures ANOVAs of warming vs. refreezing data rendered the same significance effects
219 as when refreezing was considered a separate treatment in a one-way ANOVA. Thus, for being able
220 to combine subnivean, warming and refreezing data in the same significance test, the results

221 presented are based on one-way ANOVA with refreezing as a separate treatment. Post-hoc multiple
222 comparisons of these data were analysed by using the Tukey-Kramer HSD test. A two-way ANOVA
223 was used to test for significant species × treatment interactions on response rates. Student's *t*-tests
224 were used to compare subnivean and warming data of *P. aphthosa*, and a paired Student's *t*-test
225 was used to compare warming treatment NP from March 2009 and July 2008.

226 Data sets were tested for heterogeneity using Levene's test. In cases where this test was significant,
227 suggesting lack of homogeneity, the data were also analysed by using non-parametric tests (the
228 Kruskal-Wallis and Mann-Whitney-*U* tests). Changing from parametric to non-parametric tests did
229 not affect significance in any of the cases, i.e., in cases where *P*-values were below 0.05 using
230 ANOVA, significance levels were below 0.05 also with the non-parametric tests, and vice versa. All
231 tests were carried out by using the PASW Statistics 18 package (SPSS Inc., Chicago, IL, USA), except
232 for the curve fitting, which was made in Microsoft Excel by using the add-on XLfit ver. 5.3.1.3 (ID
233 Business Solutions Ltd., Guildford, UK).

Results

Response times to light exposure

Positive photosynthetic rates of *Hylocomium splendens* were reached within an average of 332 s. The three sample types of *H. splendens*, i.e. samples from the subnivean environment, the warming plots and upon refreezing 1 d after warming, showed similar time responses to light exposure (Figure 1; $F_{2,23}$ = 0.06, P = 0.94). *Peltigera aphthosa* showed a large variation in response times, with samples from the subnivean environment being on average nearly eight times slower than samples from the warming treatment (Figure 1; lack of homogeneity; Mann-Whitney *U*-test, P = 0.005). Subnivean samples of *P. aphthosa* needed on average 1238 s to reach positive photosynthetic rates. Samples of the lichen and the moss from the warming treatment had similar response times to light exposure, while subnivean samples of the lichen had significantly longer response times than subnivean samples of the moss (Figure 1, upper-case letters at the columns, interaction species × treatment: $F_{2,24}$ = 12.04, P = 0.002).

Typical response curves of photosynthetic rates as a function of time since first light (Figure 2) show that the fittest samples of *H. splendens* reached positive rates after 60 s of light exposure (Figure 2a; canopy warming example). After refreezing, a few samples tended to respond more slowly to the light treatment (example with open squares in Figure 2a); albeit without having an effect on mean response times for this group (Figure 1). The distinctive differences in response times between lichen samples from the warming treatment and from the subnivean environment is exemplified by three samples in Figure 2b. The samples with the fastest response reached maximal NP within ca. 600 s, as seen from the curve flattening of the canopy and soil warming example in Figure 2b.

Ecophysiological performance

Overall, ecophysiological performance of *H. splendens* was identical in the subnivean and winter warming samples, but refreezing samples differed (Figure 3, left panels). In *H. splendens* DR in the subnivean, warming, and refreezing samples was variable and there were no differences among the

three treatments (Figure 3a; $F_{2,23}$ = 0.14, P = 0.87). Upon refreezing large declines were found in NP and Φ_{PSII}. NP in refrozen samples was 59 % lower (Figure 3b; $F_{2,23}$ = 6.01, P = 0.009) and Φ_{PSII} was 2.5 times higher (Figure 3d; $F_{2,23}$ = 8.99, P = 0.002) compared to subnivean samples. . Mean F_v/F_m was 14.5 % lower upon refreezing than during the warming event (Figure 3c; lack of homogeneity; Kruskal-Wallis, P = 0.069). Mean NP of *H. splendens* during the winter warming event in 2009 did not differ from growing season NP (paired t_7 = 1.05, P = 0.33).

DR of *Peltigera aphthosa* was 1.7 times higher in subnivean samples compared to the winter warming treatment (Figure 3a; $F_{1,12}$ = 10.09, P = 0.009), and chlorophyll fluorescence was 35 % lower compared to the winter warming treatment (Figure 3c; lack of homogeneity, Mann-Whitney U-test, P = 0.009). Mean NP was 57% lower in the subnivean samples compared to the winter warming treatment, but due to high variability not significantly so (Figure 3b; $F_{1,12}$ = 3.23, P = 0.1), and the same applies to Φ_{PSII} which was 37% higher in the subnivean samples (Figure 3d; $F_{1,12}$ = 3.78, P = 0.078). NP of *P. aphthosa* during the winter warming event in 2009 was on average 4.3 times higher than during the preceding growing season (paired t_6 = -3.78, P = 0.009).

GP of the two species did not differ among the treatments (*H. splendens*: $F_{2,23}$ = 1.43, P = 0.26, *P. aphthosa*: $F_{1,12}$ = 0.88, P = 0.37; data not shown). Nitrogen fixation activity was high during the second winter warming event, with mean values of 1.26 and 2.23 mmol C_2H_4 h^{-1} g^{-1} for *H. splendens* and *P. aphthosa*, respectively (no differences between groups, data not shown), for both species being more than twice as high as the activity measured in July the preceding year (all treatments pooled; *H. splendens*: t_{29} = -2.23, P = 0.034; *P. aphthosa*: t_{23} = -4.04, P = 0.001).

Discussion

Our results suggested that on exposure to light and temperatures above freezing the moss responded nearly four times faster than the lichen to gain positive NP following a number of months of darkness under snow. This is in contrast to what we expected, as Schlensog et al. (2004) found that bryophytes were slower to recover than lichens in continental Antarctica. The physiological measurements suggest that sub-Arctic bryophytes and lichens can contribute significantly to winter ecosystem respiration and assimilation, as also recently suggested by Street et al. (2012) based on primary productivity analyses during late winter and spring of the two bryophytes *Polytrichum piliferum* Hedw. and *Sphagnum fuscum* (Schimp.) H. Klinggr.

The average response time of 332 s by *H. splendens* was particularly rapid, but the response by *Peltigera* at 1238 s was also rapid in comparison with the Antarctic bryophyte *Bryum subrotundifolium* A. Jaeger which needed 16 h from first re-activation after overwintering under a 30 cm deep snowpack before positive net photosynthesis was gained (Schlensog et al. 2004). While the temperature of the subnivean Antarctic environment at -15 °C (Schlensog et al. 2004) was too low for any significant cryptogamic metabolic activity (Kappen 1993), the sub-arctic subnivean environment in this study had a temperature of -3 °C which is above the lower limit for metabolic activity. This difference in the degree of dormancy is the most likely cause for the contrasting response times between the Antarctic and the sub-Arctic sites.

The lack of difference in NP, DR, F_v/F_m and Φ_{PSII} between the subnivean control and the warming treatments demonstrated that *H. splendens* was not at all dormant in its subnivean environment. As the subnivean microclimate in the sub-Arctic is suitable for high water potentials (Zimov et al. 1993; Mikan et al. 2002; Grogan and Jonasson 2006; Nobrega and Grogan 2007), this suggests that subnivean bryophytes may significantly contribute to wintertime CO_2 respiration rates. This contrasts with the situation in continental Antarctica where persistently low winter temperatures

304 make wintertime water potentials very low, even at high subnivean RH, leading to extensive
305 desiccation at the cellular level (Schroeter et al. 1994; Schroeter and Scheidegger 1995).

306 ### *Differences between* H. splendens *and P.* aphthosa

307 High DR rates of subnivean *P. aphthosa* (Figure 3a) indicate that the lichen also has the potential of
308 subnivean respiration when temperatures are close to 0 °C and may therefore contribute to
309 wintertime ecosystem respiration, depending on the temperature course. Several lichens show
310 detectable DR under mild subfreezing conditions (e.g. Gannutz 1970; Lange and Green 2005). Mild
311 subnivean conditions are in fact suggested as a primary reason why terricolous, fruticose lichens are
312 very sparse in oceanic areas of the Arctic and sub-Arctic, because such dark and mild conditions over
313 several months may cause severe respiratory loss that can ultimately kill the lichen (Bjerke 2011).
314 These lichens are often more abundant in continental areas with lower subnivean temperatures,
315 where they make up an important part of the winter forage for reindeer (e.g., Tømmervik et al.
316 2012).

317 Lichens tend to rapidly release a burst of non-metabolic CO_2 the first 15 min during a temperature
318 increase (Sundberg et al. 1999). The lichens from the subnivean environment experienced a rapid
319 temperature increase of 8 °C (from –3 °C to +5 °C) while being transported from the field to the gas
320 exchange chamber, whereas the samples from the warmed plots had been at 5 °C for some hours
321 prior to gas exchange measurements. The temperature increase that the subnivean samples were
322 exposed to certainly led to a burst of CO_2 release and this explains why DR of *P. aphthosa* was higher
323 in the subnivean samples than in the samples from the warmed plots (Figure 3a), which had its burst
324 release of CO_2 while being heated up in the plots a few hours before gas exchange measurements.

325 We suspect that the longer response times of the lichen compared to the moss were due to their
326 large differences in surface area-to-volume ratios. Thick, broad-lobed foliose lichens such as *P.*
327 *aphthosa* have much lower ratios than feather mosses, and this leads to higher water retention
328 which, in turn, slows down the thawing rate. Thus, the moss probably reached positive thallus

329 temperatures much faster than the lichen when they were moved from their subnivean
330 environment at around –3 °C to the cuvette temperature at +5 °C. Street et al. (2012) also used
331 differences in water retention capacity to explain why *Sphagnum fuscum* has lower photosynthetic
332 rates than *Polytrichum piliferum* in late winter, as large amounts of frozen water within capillary
333 spaces of *S. fuscum* melt slowly and restrict CO_2 diffusion. The longer response time and the reduced
334 subnivean F_v/F_m (Figure 3c) of *Peltigera aphthosa* as compared to *H. splendens* indicate that the high
335 water retention of the lichen slowed down the reactivation rate after light exposure. Subnivean
336 samples of an Antarctic liverwort have also been reported to have had much lower chlorophyll
337 fluorescence than adjacent samples that were free of snow (Snell et al. 2007). Nevertheless, the
338 short time required to reach positive NP shows that *P. aphthosa* can take advantage of winter
339 thawing events for photosynthesis and growth, and lichens with higher surface area-to-volume
340 ratios, e.g. fruticose reindeer lichens (*Cladonia* spp.), may thaw more rapidly and be more similar to
341 *H. splendens* than to *P. aphthosa* in terms of response time.

342 *Comparison with growing season activity*

343 NP and nitrogen fixation rates of *H. splendens* and *P. aphthosa* during the growing season in the
344 study area are variable (Bjerke et al. 2011). NP rates of *P. aphthosa* and N fixation rates of both
345 species during the winter warming event were 2 to 4.3 times higher than the range of rates during
346 the preceding growing season, suggesting that the winter warming events rendered optimal
347 temperature and humidity conditions for ecophysiological activity. In fact, it has been suggested that
348 many sub-arctic cryptogams have the highest photosynthetic activity during late winter, spring and
349 autumn, because thalli stay moist for longer periods of time during these seasons due to water from
350 snowmelt, higher precipitation rates and slower drying rates than during summer (e.g., Sonesson
351 1989, 2001; Rikkinen 1995; Moore et al. 2002; Bjerke et al. 2005). This may be especially true for
352 continental parts of the circumpolar region which can be very dry and warm in summer. For
353 example, the maximum photosynthesis rates of the feather moss *Pleurozium schreberi* (Brid.) Mitt.
354 from Finland were much higher in spring and autumn than in summer (Kallio and Saarnio 1986),

whereas the epiphytic lichens *Melanohalea olivacea* (L.) O. Blanco et al. and *Parmeliopsis ambigua* (Wulfen) Nyl. from the Abisko area showed much higher growth rates in spring than in summer and autumn (Sonesson et al. 2011). Also, in warmer and wetter regions, for example the British Isles, the cold seasons are considered an important period for cryptogamic growth, due to continuously moist conditions (Bates et al. 2005). Our results indicate that *P. aphthosa* and cyanobacteria may also be more active in autumn and spring, rather than during summer, but to confirm this, year-round monitoring of carbon exchange would need to be carried out, as was done with the temperate lichen *Lecanora muralis* (Schreber) Rabenh., whose carbon assimilation was almost completely dependent on momentary hydration conditions (Lange 2003). NP in *Hylocomium splendens* was not different from NP during the preceding summer, and this contrasts to the results for NP in *P. aphthosa* and N fixation in the cyanobacteria. This may be due to the fact that the mosses in the warmed plots were damaged by the winter warming events of 2007 and 2008 (Bjerke et al. 2011), and therefore the subnivean moss samples required more time to reach maximum NP rates.

Refreezing

High ecophysiological activity and spring-like development generally lead to de-hardening (e.g., Rütten and Santarius 1992; Ögren 1996; Bokhorst et al. 2010b), and the lichen and moss therefore run a risk of damage by refreezing, a risk which is higher for mosses due to their freeze-susceptible organs (Clausen 1964; Hudson and Brustkern 1965; Kennedy 1993; Bjerke et al. 2011). Refreezing led to a reduction of the photosynthetic performance of *H. splendens*; NP was reduced by 52 %, F_v/F_m was near-significantly reduced, and Φ_{PSII} was 1.5 times higher than during the event (Figure 3). Φ_{PSII} measures the proportion of light absorbed by chlorophyll associated with PSII that is used in photochemistry, and it often shows an inverse correlation with the efficiency of carbon fixation (Genty et al. 1989; Maxwell and Johnson 2000). Thus, the higher refreezing values of Φ_{PSII} indicate reduced efficiency, as also demonstrated by the reduced NP. Moreover, NP after refreezing was lower and Φ_{PSII} higher than the subnivean values, suggesting that refreezing imposed stress causing stronger reductions than seen after the down-regulation of activity during winter dormancy. Bjerke

et al. (2011) hypothesised that the high sensitivity to extreme winter warming by *H. splendens* seen during the following growing seasons was because of initiation during the warming events of growth of young, freeze-susceptible shoot apices, which were damaged on refreezing after the warming event. The ecophysiological data presented here confirm that the moss was active during the warming events and that freeze-induced stress immediately after the warming events caused severe reductions in ecophysiological performance. However, new growth during the warming event could not be observed visually. Therefore, to clearly confirm that growth was initiated during extreme winter warming events, it would have been necessary to assay biochemical responses related to growth, as was made for vascular plants in the same warming simulation (Bokhorst et al. 2010b).

Our data showed that the lichen *P. aphthosa* was highly active during the winter warming event, but, presumably, as this lichen does not have any freeze-susceptible organs, it could withstand the sudden post-warming refreezing without being damaged (Bjerke et al. 2011). Nevertheless, it would be relevant to test if *P. aphthosa* also experiences a sudden reduction in photosynthetic performance upon refreezing.

Conclusion

The results presented here provide increased insight to the winter ecology of heath cryptogams in the sub-Arctic. Their moist and relatively mild subnivean environment prevents full dormancy, at least for parts of the winter season. Instead, they probably have some more or less continuous respiratory activity while staying ready to take advantage of solar radiation as soon as light transmittance through snow is above the light compensation point for photosynthetic activity, which for cryptogams are generally reached at 17-30 μmol m^{-2} s^{-1} PPFD (Kappen 1993; Lange et al. 1996; Sommerkorn 2000; Pannewitz et al. 2003; Street et al. 2012). Thus, their role in wintertime carbon fluxes may have been underestimated. Full snow melt and increases in temperature to a few degrees above freezing, as experienced during the winter warming events, are shown to render good conditions for ecophysiological activity, leading to NP and nitrogen fixation rates similar to or

406 larger than typical rates observed during the growing season. Winter climate change with increasing
407 frequency of extreme warming events therefore may have large consequences for summer growth
408 of lichens and mosses. It may affect their competitive potential against vascular plants which are
409 known to be highly sensitive to winter warming events (Bokhorst et al. 2008, 2009, 2010b, 2011,
410 2012; Callaghan et al. 2010, 2011a, 2011b; Crawford 2008). This suggests that winter processes may
411 reduce the rate of increasing dominance of vascular plants over cryptogams resulting from summer
412 processes which stimulate vascular plant growth (Cornelissen et al. 2001; Keuper et al. 2011).
413 Actually, the balance between winter and summer processes is unknown and is a major topic for
414 future research. Enhanced knowledge of the winter ecology of cryptogams is in this context crucial
415 for the understanding of the full impacts of climate change in polar regions. We have here shown
416 that sub-arctic lichens and mosses are not as dormant in mid-winter as previously assumed. This
417 implies that increased opportunities for growth by cryptogams during the cold seasons, due to
418 increased frequency of warming events, must be taken into account when modelling future
419 vegetation composition changes in the sub-Arctic.

420

Acknowledgements

This research was supported by two grants from the Research Council of Norway (grant nos. 171542/V10 and 216434/E10) awarded to J.W.B., by a Leverhulme Trust (UK) grant to G.K.P. and T.V.C. (grant F/00 118/AV), by ATANS grants (EU Transnational Access Program, FP6 Contract no. 506004) to J.W.B., S.B., M.Z. and G.K.P., by the Norwegian Institute for Nature Research, and by FRAM – High North Research Centre on Climate and the Environment through its terrestrial flagship programme. We would like to thank staff of the Abisko Scientific Research Station for their assistance. Infrastructure and equipment support were supplied by the Royal Swedish Academy of Sciences and Jerry Melillo and Francis Bowles from the Ecosystems Center at the Marine Biological Laboratory, USA. We also thank the University Centre in Svalbard for access to gas chromatography facilities, and three anonymous reviewers and the editor-in-chief for their constructive comments.

Notes on contributors

Jarle W. Bjerke is a senior researcher. His research interests include the impacts of climate change and land-use on vegetation and terrestrial ecosystems of cold biomes.

Stef Bokhorst is a postdoctoral researcher. His research interests include the above and belowground response of Polar ecosystems to climate change. Especially the changes in winter climate and the impacts of extreme weather events for dwarf shrubs, soil arthropods and decomposition are of great interest.

Terry V. Callaghan is a Distinguished Research Professor , Professor of Arctic Ecology and visiting Professor at Tomsk State University, Russia. He specialises in arctic ecology and global change impacts on Arctic ecosystems.

Matthias Zielke is a researcher. He works with research questions related to microbial ecology in Arctic soils, especially on climate change impacts on biological nitrogen fixation.

Gareth K. Phoenix is a senior lecturer. His research interests include the impacts of global change (summer and winter warming, snow regime change, precipitation, UV-B radiation) on arctic ecosystems and the consequences for biogeochemical cycling.

References

Bates JW, Thompson K, Grime JP. 2005. Effects of simulated long-term climatic change on the bryophytes of a limestone grassland community. Global Change Biology 11:757-769.

Bjerke JW. 2011. Winter climate change: ice encapsulation at mild subfreezing temperatures kills freeze-tolerant lichens. Environmental and Experimental Botany 72:404–408.

Bjerke JW, Elvebakk A, Domínguez E, Dahlback A. 2005. Seasonal trends in usnic acid concentrations of arctic, alpine and Patagonian populations of the lichen *Flavocetraria nivalis*. Phytochemistry 66:337–344.

Bjerke JW, Bokhorst S, Zielke M, Callaghan TV, Phoenix GK. 2011. Contrasting sensitivity to extreme winter warming events of dominant sub-Arctic heathland bryophyte and lichen species. Journal of Ecology 99:1481–1488.

Bokhorst S, Bjerke JW, Callaghan T V, Melillo J, Bowles F, Phoenix G K. 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf-shrub heathland. Global Change Biology 14:2603–2612.

Bokhorst SF, Bjerke JW, Tømmervik H, Callaghan TV, Phoenix GK. 2009. Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event. Journal of Ecology 97:1408–1415.

Bokhorst S, Bjerke JW, Melillo J, Callaghan TV, Phoenix GK. 2010a. Impacts of extreme winter warming events on litter decomposition in a sub-Arctic heathland. Soil Biology & Biochemistry 42:611–617.

Bokhorst S, Bjerke JW, Davey MP, Taulavuori K, Taulavuori E, Laine K, Callaghan TV, Phoenix GK. 2010b. Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. Physiologia Plantarum 140:128–140.

472 Bokhorst S, Bjerke JW, Street LE, Callaghan TV, Phoenix GK. 2011. Impacts of multiple extreme
473 winter warming events on sub-Arctic heathland: phenology, reproduction, growth, and CO_2 flux
474 responses. Global Change Biology 17:2817–2830.

475 Bokhorst S, Tømmervik H, Callaghan TV, Phoenix GK, Bjerke JW. 2012. Vegetation recovery following
476 extreme winter warming events in the sub-Arctic estimated using NDVI from remote sensing and
477 handheld passive proximal sensors. Environmental and Experimental Botany 81:18–25.

478 Brooks PD, Schmidt SK, Williams MW. 1997. Winter production of CO_2 and N_2O from alpine tundra:
479 environmental controls and relationship to inter-system C and N fluxes. Oecologia 110:403–413.

480 Callaghan TV, Bergholm F, Christensen TR, Jonasson C, Kokfelt U, Johansson M 2010. A new climate
481 era in the sub-Arctic: accelerating climate changes and multiple impacts. Geophysical Research
482 Letters 37:L14705.

483 Callaghan TV, Johansson M, Brown RD, Groisman PY, Labba N, Radionov V, Barry RG, Bulygina ON,
484 Essery RLH, Frolov DM, Golubev VN, Grenfell TC, Petrushina MN, Razuvaev VN, Robinson DA,
485 Romanov P, Shindell D, Shmakin AB, Sokratov SA, Warren S, Yang D. 2011a. The changing face of
486 Arctic snow cover: a synthesis of observed and projected changes. Ambio 40:17–31.

487 Callaghan TV, Johansson M, Brown RD, Groisman PY, Labba N, Radionov V, Bradley RS, Blangy S,
488 Bulygina ON, Christensen TR, Colman JE, Essery RLH, Forbes BC, Forchhammer MC, Golubev VN,
489 Honrath RE, Juday GP, Meshcherskaya AV, Phoenix GK, Pomeroy J, Rautio A, Robinson DA,
490 Schmidt NM, Serreze MC, Shevchenko VP, Shiklomanov AI, Shmakin AB, Sköld P, Sturm M, Woo
491 M, Wood EF. 2011b. Multiple effects of changes in Arctic snow cover. Ambio 40:32–45.

492 Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon WT, Laprise R,
493 Magaña Rueda V, Mearns L, Menéndez CG, Räisänen J, Rinke A, Sarr A, Whetton P. 2007.
494 Regional climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB,
495 Tignor M, Miller HL, editors. Climate change 2007: the physical science basis. Contribution of

496 working Group I to the fourth assessment report of the Intergovernmental Panel on Climate
497 Change. Cambridge: Cambridge University Press. p. 847–940.

498 Clausen E. 1964. The tolerance of hepatics to desiccation and temperature. Bryologist 67:411–417.

499 Cornelissen, JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DA, Hobbie SE,
500 Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Jones DG, Jonasson S, Chapin FS,
501 Molau U, Neill C, Lee JA, Melillo JM, Sveinbjörnsson B, Aerts R. 2001. Global change and Arctic
502 ecosystems: is lichen decline a function of increases in vascular plant biomass? Journal of
503 Ecology 89:984–994.

504 Crawford RMM. 2008. Cold climate plants in a warmer world. Plant Ecology & Diversity 1:285–297.

505 Gannutz T. 1970. Photosynthesis and respiration of plants in the Antarctic Peninsula Area. Antarctic
506 Journal of the U.S. 5:49–52.

507 Genty B, Briantais JM, Baker NR. 1989. The relationship between the quantum yield of
508 photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochimica et
509 Biophysica Acta 990:87–92.

510 Grogan P, Jonasson S. 2006. Ecosystem CO_2 production during winter in a Swedish subarctic region:
511 the relative importance of climate and vegetation type. Global Change Biology 12:1479-1495.

512 Grogan P, Illeris L, Michelsen A, Jonasson S. 2001. Respiration of recently-fixed plant carbon
513 dominates mid-winter ecosystem CO_2 production in sub-Arctic heath tundra. Climatic Change
514 50:129–42.

515 Hudson MA, Brustkern P. 1965. Resistance of young and mature leaves of *Mnium undulatum* L. to
516 frost. Planta 66:135–155.

517 Kallio P, Saarnio E. 1986. The effect on mosses of transplantation to different latitudes. Journal of
518 Bryology 14:159-178.

519 Kappen L. 1993. Plant activity under snow and ice, with particular reference to lichens. Arctic
520 46:297–302.

521 Kappen L, Smith RIL, Meyer M. 1989. Carbon dioxide exchange of two ecodemes of *Schistidium*
522 *antarctici* in continental Antarctica. Polar Biology 9:415–422.

523 Kennedy AD. 1993. Photosynthetic response of the Antarctic moss *Polytrichum alpestre* Hoppe to
524 low temperatures and freeze-thaw stress. Polar Biology 13:271–279.

525 Keuper F, Dorrepaal E, van Bodegom PM, Aerts R, van Logtestijn RSP, Callaghan TV, Cornelissen JHC.
526 2011. A Race for Space? How *Sphagnum fuscum* stabilizes vegetation composition during long-
527 term climate manipulations. Global Change Biology 17:2162–2171.

528 Kohler J, Brandt O, Johansson M, Callaghan TV. 2006. A long-term Arctic snow depth record from
529 Abisko, northern Sweden, 1913-2004. Polar Research 25:91–113.

530 Lange OL. 1965. Der CO_2-Gaswechsel von Flechten bei tiefen Temperaturen. Planta 64:1–19.

531 Lange OL. 2003. Photosynthetic productivity of the epilithic lichen *Lecanora muralis*: long-term field
532 monitoring of CO_2 exchange and its physiological interpretation. III. Diel, seasonal, and annual
533 carbon budgets. Flora 198:277-292.

534 Lange OL, Green TGA. 2005. Lichens show that fungi can acclimate their respiration to seasonal
535 changes in temperature. Oecologia 142:11–19.

536 Lange OL, Green T GA, Melzer B, Meyer A, Zellner H. 2006. Water relations and CO_2 exchange of the
537 terrestrial lichen *Teloschistes capensis* in the Namib fog desert: measurements during two
538 seasons in the field and under controlled conditions. Flora 201:268–280.

539 Lange OL, Hahn SC, Müller G, Meyer A, Tenhuhnen JD. 1996. Upland tundra in the foothills of the
540 Brooks Range, Alaska: influence of light, water content and temperature on CO_2 exchange of
541 characteristic lichen species. Flora 191:67–83.

542 Maxwell K, Johnson GN. 2000. Chlorophyll fluorescence – a practical guide. Journal of Experimental
543 Botany 51:659–668.

544 Mikan CJ, Schimel JP, Doyle AP. 2002. Temperature controls of microbial respiration in Arctic tundra
545 soils above and below freezing. Soil Biology and Biochemistry 34:1785–1795.

546 Moore TR, Bubier JL, Frolking SE, Lafleur PM, Roulet NT. 2002. Plant biomass and production and
547 CO_2 exchange in an ombrotrophic bog. Journal of Ecology 90:25–36.

548 Nobrega S, Grogan P. 2007. Deeper snow enhances winter respiration from both plant-associated
549 and bulk soil carbon pools in birch hummock tundra. Ecosystems 10:419–431.

550 Ögren E. 1996. Premature dehardening in *Vaccinium myrtillus* during a mild winter: a cause for
551 winter dieback? Functional Ecology 10:724–732.

552 Pannewitz S, Schlensog M, Green TGA, Sancho LG, Schroeter B. 2003. Are lichens active under snow
553 in continental Antarctica? Oecologia 135:30–38.

554 Phoenix GK, Lee JA. 2004. Predicting impacts of Arctic climate change: past lessons and future
555 challenges. Ecological Research 19:65–74.

556 Proctor MCF, Oliver MJ, Wood AJ, Alpert P, Stark LR, Cleavitt NC, Mishler BD. 2007. Desiccation-
557 tolerance in bryophytes: a review. Bryologist 110:595–621.

558 Putkonen J, Roe G. 2003. Rain-on-snow events impacts soil temperatures and affect ungulate
559 survival. Geophysical Research Letters 30:1188.

560 Rikkinen J. 1995. What's behind the pretty colours. A study on the photobiology of lichens.
561 Bryobrothera 4:1–239.

562 Rütten D, Santarius KA. 1992. Relationship between frost tolerance and sugar concentration of
563 various bryophytes in summer and winter. Oecologia 91:260–265.

564 Schlensog M, Pannewitz S, Green TGA, Schroeter B. 2004. Metabolic recovery of continental
565 Antarctic cryptogams after winter. Polar Biology 27:399–408.

566 Schroeter B, Scheidegger C. 1995. Water relations in lichens at subzero temperatures: structural
567 changes and carbon dioxide exchange in the lichen *Umbilicaria aprina* from continental
568 Antarctica. New Phytologist 131:273–285.

569 Schroeter B, Green TGA, Kappen L, Seppelt RD. 1994. Carbon dioxide exchange at subzero
570 temperatures. Field measurements on *Umbilicaria aprina* in Antarctica. Cryptogamic Botany
571 4:233–241.

572 Smith DC, Molesworth S. 1973. Lichen physiology. XIII. Effects of rewetting dry lichens. New
573 Phytologist 72:525–533.

574 Snell KRS, Convey P, Newsham KK. 2007. Metabolic recovery of the Antarctic liverwort *Cephaloziella*
575 *varians* during spring snowmelt. Polar Biology 30:1115–1122.

576 Sommerkorn M. 2000. The ability of lichens to benefit from natural CO_2 enrichment under a spring
577 snow-cover: a study with two Arctic-alpine species from contrasting habitats. Bibliotheca
578 Lichenologica 75:365–380.

579 Sonesson M. 1989: Water, light and temperature relations of the epiphytic lichens *Parmelia olivacea*
580 and *Parmeliopsis ambigua* in northern Swedish Lapland. Oikos 56:402–415.

581 Sonesson M. 2001. Ecology of some epiphytic lichens on the mountain birch. In: Wielgolaski FE
582 editor. Nordic mountain birch ecosystems. New York, London: The Parthenon Publishing Group.
583 p. 63–70.

584 Sonesson M, Sveinbjörnsson B, Tehler A, Carlsson BÅ. 2011. Seasonal variation in concentrations of
585 carbohydrates and lipids in two epiphytic lichens with contrasting, snow-depth related
586 distribution on subarctic birch trees. Bryologist 114:443-452.

587 Stewart WDP, Fitzgerald GP, Burris RH. 1967. In situ studies on N_2 fixation using acetylene reduction
588 technique. Proceedings of the National Academy of Sciences, USA 58:2071–2078.

589 Street LE, Stoy PC, Sommerkorn M, Fletcher BJ, Sloan VJ, Hill TC, Williams M. 2012. Seasonal
590 bryophyte productivity in the sub-Arctic: a comparison with vascular plants. Functional Ecology
591 26:365–378.

592 Sundberg B, Ekblad A, Näsholm T, Palmqvist K. 1999. Lichen respiration in relation to active time,
593 temperature, nitrogen and ergosterol concentrations. Functional Ecology 13:119–125.

594 Tømmervik H, Bjerke JW, Gaare E, Johansen B, Thannheiser D. 2012. Rapid recovery of recently
595 overexploited winter grazing pastures for reindeer in northern Norway. Fungal Ecology 5:3–15.

596 Zielke M, Ekker AS, Olsen RA, Spjelkavik S, Solheim B. 2002. The influence of abiotic factors on
597 biological nitrogen fixation in different types of vegetation in the High Arctic. Arctic, Antarctic
598 and Alpine Research 34:293–299.

599 Zimov SA, Zimova GM, Daviodov SP, Daviodova AI, Voropaev YV, Voropaeva ZV, Prosiannikov SF,
600 Prosiannikova OV, Semiletova IV, Semiletov IP. 1993. Winter biotic activity and production of
601 CO_2 in Siberian soils – a factor in the greenhouse-effect. Journal of Geophysical Research -
602 Atmospheres 98:5017–5023.

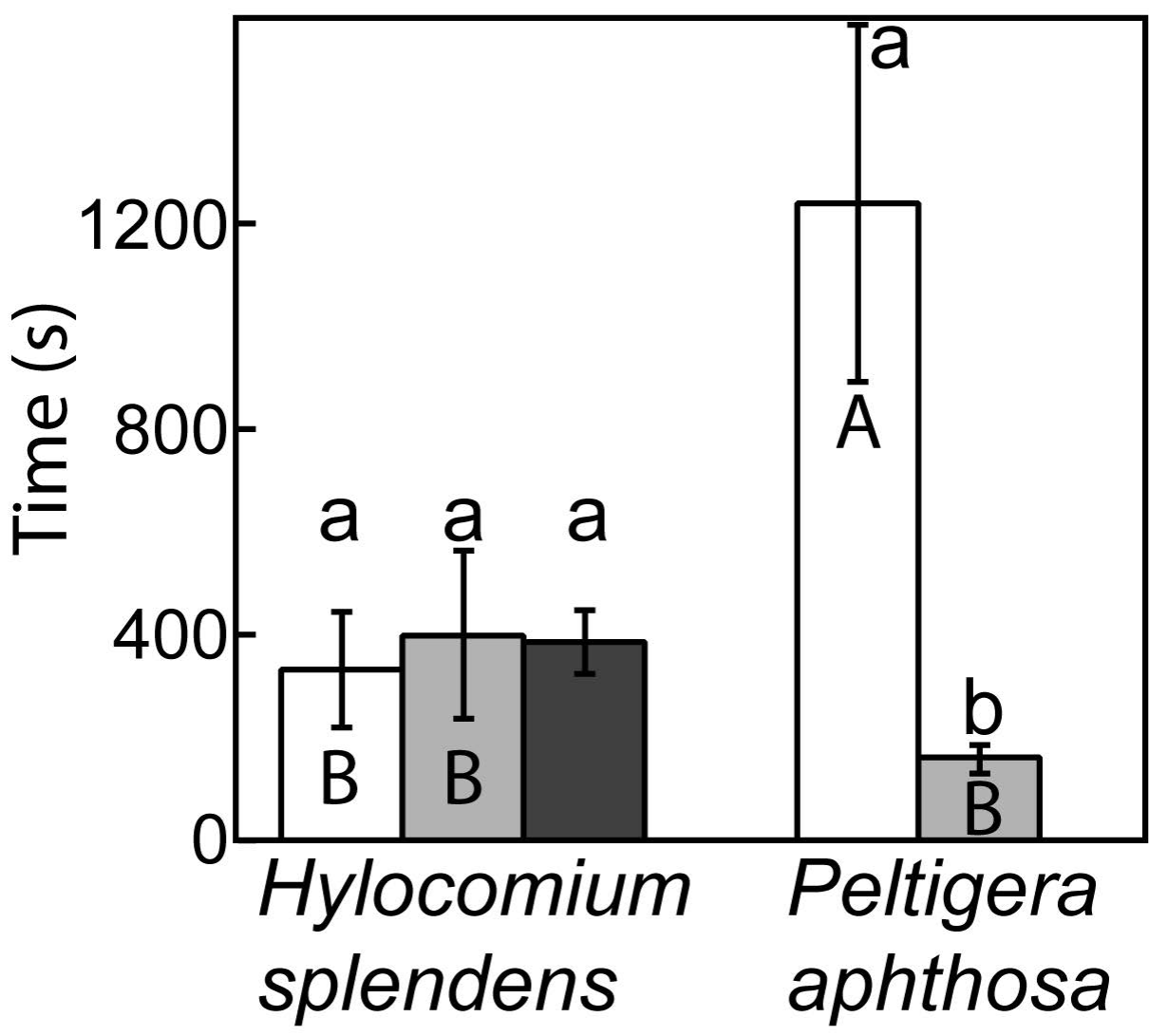
603

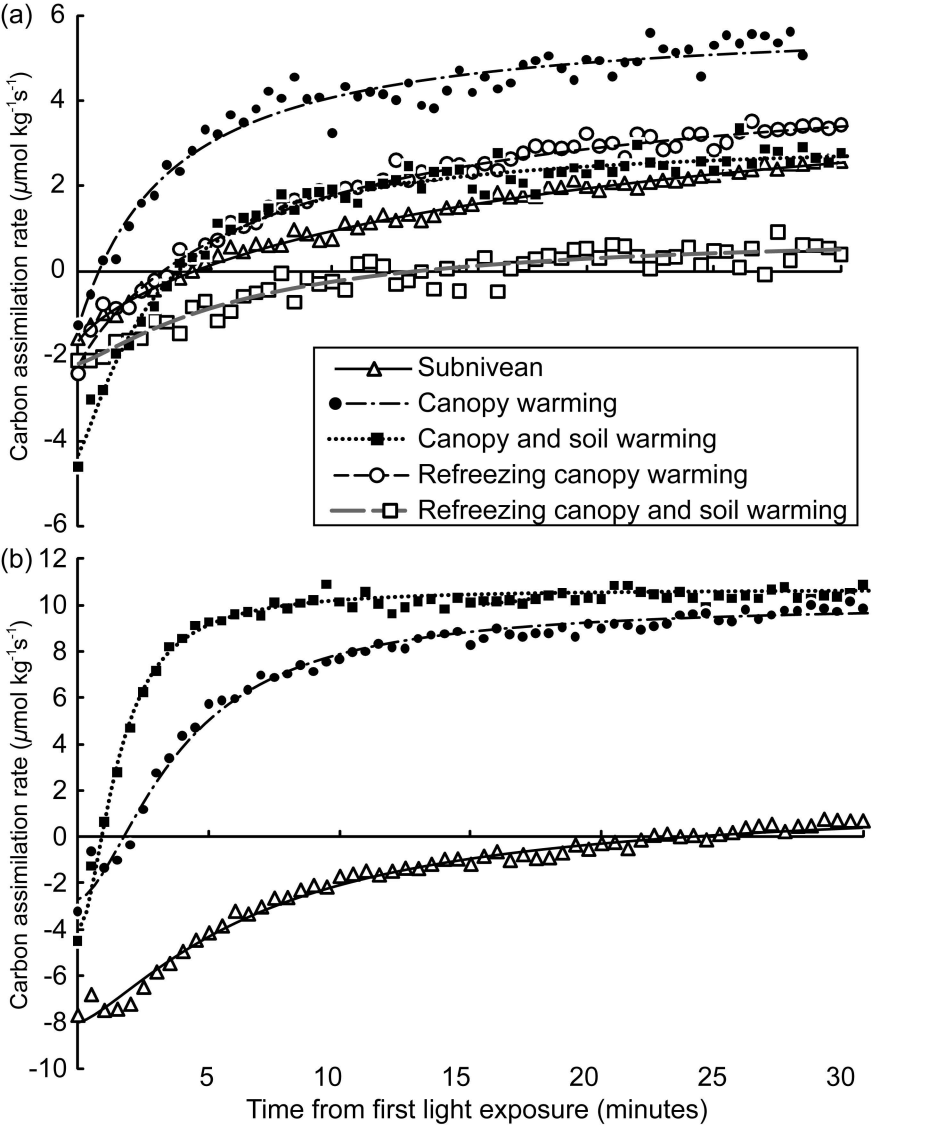
Figures

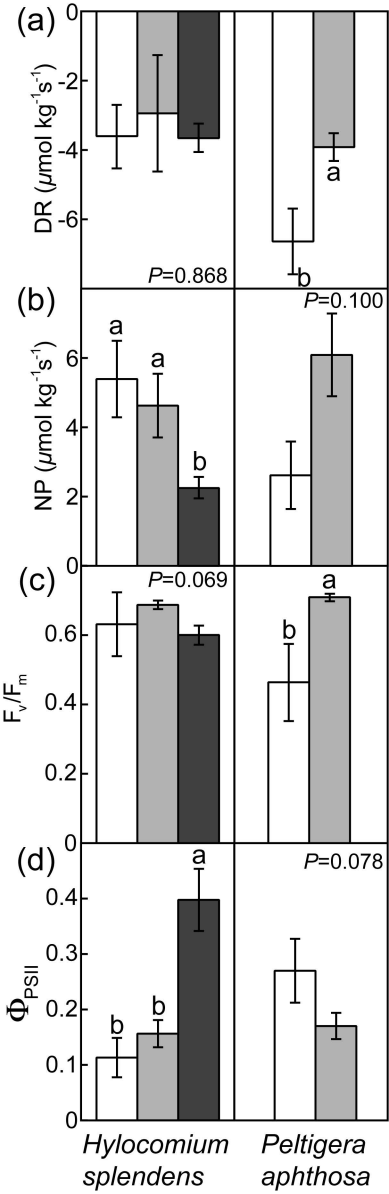
Figure 1. Time from start of light exposure (400 μmol m^{-2} s^{-1} PPFD) until positive photosynthetic rates were reached for *Hylocomium splendens* and *Peltigera aphthosa* at 5 °C during a winter warming event in March 2009 (light grey bars), upon refreezing 1 d after warming (only *H. splendens*; dark grey bar) and of samples dug out from under snow (subnivean control; unfilled bars). Error bars are ± SE. Lower-case letters above the columns indicate significant differences among means from the same species, whereas upper-case letters in the columns indicate significant interspecific differences among means from the same sample type.

Figure 2. Examples of typical response curves for individual thalli of *Hylocomium splendens* (a) and *Peltigera aphthosa* (b) during the first 30 min of exposure to light (400 μmol m^{-2} s^{-1} PPFD). Only *H. splendens* was measured after refreezing. Correlation coefficients (R^2) are between 0.96 and 0.98 for the fitted sigmoidal regression curves, except for the refreezing canopy and soil warming curve (R^2 = 0.90).

Figure 3. Ecophysiological performance of *Hylocomium splendens* (left) and *Peltigera aphthosa* (right) at 5 °C during the winter warming event in March 2009 (light grey bars), upon refreezing after warming (only *H. splendens*; dark grey bar) and of samples dug out from under snow (subnivean; unfilled bars). (a) DR; (b) NP; (c) F_v/F_m; (d) Φ_{PSII}. Error bars are ± SE. Different letters indicate significant differences ($P < 0.05$) between means. The exact *P*-levels are given for cases without significant differences.


Time (s)
1200
800
400
0
a
A
b
B
a
a
a
B
B
Hylocomium splendens
Peltigera aphthosa


(a)
(b)
Carbon assimilation rate (μmol kg-1s-1)
Time from first light exposure (minutes)
Subnivean
Canopy warming
Canopy and soil warming
Refreezing canopy warming
Refreezing canopy and soil warming


(a)
DR (μmol kg-1s-1)
0
-2
-4
-6
P=0.868
a
b
(b)
NP (μmol kg-1s-1)
P=0.100
a
a
b
6
4
2
0
(c)
Fv/Fm
P=0.069
a
b
0.6
0.4
0.2
0
(d)
ΦPSII
P=0.078
a
b
b
0.4
0.3
0.2
0.1
0
Hylocomium splendens
Peltigera aphthosa