Polar Biol (2017) 40:853–862
DOI 10.1007/s00300-016-2010-2

ORIGINAL PAPER

Factors affecting water availability for high Arctic lichens

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Received: 24 April 2015 / Revised: 11 July 2016 / Accepted: 14 July 2016 / Published online: 22 July 2016

Abstract Lichen symbiosis is a successful nutritional strategy that drives lichen distributions in high Arctic ecosystems. However, the in situ effects of fungal partners (mycobionts) on water availability for the photosynthetic partners (photobionts) and their necessity for survival remain unclear. We investigated the factors creating differences in water availability in high Arctic lichen assemblages using observational and experimental analyses of substrates and thallus morphology in the high Arctic, near Ny-Ålesund, Svalbard (79°N) during the snow-free season. We used five lichen species found on five substrate types: moss litter, vascular plant litter, mixed litter, biological soil crust (BSC) and gravel. BSC had significantly higher water content than the other substrates; although it had high levels of surface evaporation, BSC took up more ground water. Moreover, the structure of BSC supported greater water retention than the four other substrates in our study, providing the moistest environment for lichens. In fact, 60 % of the surface area of the crustose lichen *Ochrolechia frigida*, which was mainly distributed on BSC, was in contact with the substrate. In contrast, the four fruticose lichens had larger surface areas than *Och frig* and roughly 90 % air exposure. Initial rates of absorption and evaporation increased with greater thallus surface area, suggesting that water availability for photobionts is strongly affected by both morphological characteristics and substrate water properties, both of which depend on mycobionts. We conclude that lichens show preferences for both morphologies and substrates that promote autotrophic nutrition in the water-limited glacier foreland of the high Arctic region.

Keywords Lichen · High Arctic · Water availability · Substrate · Surface area

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Introduction

Lichens are a symbiosis of nutritionally specialized fungi and photosynthetic partners (photobionts) that provide fixed carbon for the fungi (mycobionts) upon hydration (Honegger 1991; Ahmadjian 1993). Mycobionts, in turn, control water conditions and photosynthetic activity of photobionts through the morphology and texture of the poikilohydric lichen thalli (Honegger 1985, 2009; Ahmadjian 1993), which are built by the mycobionts. Because water status varies passively with environmental conditions, water availability is of primary importance for lichen metabolism, photosynthesis and survival (Walter 1973; Green and Lange 1995). This symbiosis is a successful nutritional strategy that limits lichen distributions to the physiological limits of vascular plants in high alpine, Arctic, Antarctic and desert ecosystems (Longton 1988; Kappen 2000; Nash 2008). The in situ contribution of mycobionts to water availability for photobionts, however, remains unclear.

Lichens are often dominant organisms in polar regions and play important roles in carbon flux (Longton 1988; Ahmadjian 1995; Kappen 2000). Some lichens can perform photosynthesis and respiration in freezing temperatures

(Kappen et al. 1996; Pannewitz et al. 2003). In high Arctic regions, however, low solar elevation and snow cover during the cold season further decrease the availability of solar radiation; here, lichen photosynthetic production occurs mainly during the short snow-free summer. Yet, even in the summer photosynthesis can be limited by low water availability, which occurs mainly during the desiccation period (Longton 1988; Uchida et al. 2006; Inoue et al. 2014). Lichens dominating these areas often have morphological and distributional adaptations that provide resistance to desiccation, enabling photosynthesis.

Previous studies have shown that green algal lichens can photosynthesize using atmospheric moisture. In high Arctic regions, daily wetting and drying cycles can provide a critical water source for lichens in the absence of rain (e.g. Lange et al. 1986; Lange 1988; Green and Lange 1995; Lange et al. 2001; Green et al. 2002; Reiter et al. 2008; Inoue et al. 2014). Substrate moisture also affects the ecology of high Arctic lichens, where distribution patterns vary with substrate moisture, which depends both on substrate texture and composition and on topographic factors (Brodo 1973; Smith 1993; Wynn-Williams 1993; van der Wal et al. 2001; Cannone et al. 2004; Holt et al. 2007; Vittoz et al. 2010). However, the direct effects of substrate moisture on lichen photosynthesis have only been examined by Harris (1971). Knowledge of photosynthetic performance and ecological success of high Arctic lichens requires studies of water availability and in situ photosynthesis of various lichen species under ambient conditions. Using field observations and experimental analyses of substrates and thallus morphologies of high Arctic lichens, we identified factors causing differences in water availability and photosynthesis.

Materials and methods

Study area

Field studies were performed on the glacier foreland of Austre Brøggerbreen (78°55′N, 11°50′E), 2 km southwest of Ny-Ålesund in the Svalbard archipelago (Fig. 1) during 15–21 July 2010. From 2001 to 2008, the annual mean air temperature was 4.2 °C, the mean annual precipitation was 433 mm, and the snow-free period was roughly 2 months (July–August; Uchida et al. 2010). Field measurements and sampling were performed in the same site as in previous studies (Inoue et al. 2011, 2014).

Lichen species distributions on different substrates

Lichens in the sampling site were found primarily on five substrate types: moss litter, vascular plant litter, mixed litter, biological soil crust (BSC, 0.5- to 1.0-cm layer consisting of cyanobacteria, bryophytes, algae and cyanobacterial lichens) (Belnap and Lange 2001; Yoshitake et al. 2010) and gravel. Ten 30 × 30 cm quadrats were placed randomly on each substrate type. Lichens that covered more than 1 % of the substrate by visual estimates were collected and taxonomically identified. Rates of appearance (F) on each substrate were then calculated for each species according to the number of quadrats containing that species (Qn) relative to the total number of quadrats ($Qt = 10$):

$$F = Qn/Qt \quad (1)$$

Rates of appearance were ranked according to Braun-Blanquet (1964) as follows: V (>80 %), IV (60–80 %), III (40–60 %), II (20–30 %) and I (20–10 %).

Substrate water retention properties

To determine the water-holding capacity (WHC, g cm^{-3}) and solid-phase density (SPD, g cm^{-3}) of the five substrate types, five samples of each substrate were collected using a cylindrical core sampler (c. 3.24π; height = 1 cm). Filter paper was used to prevent loss of material from the bottom of the corer after sampling, and the core was soaked with water from the bottom. Cores were then placed in containers and kept for 24 h at 24 °C under laboratory conditions. Cores were then allowed to drain by gravity, after which the saturated weight (SW, g) was measured. Cores were then dried to constant weight (DW_{sub}, g) at 80 °C for 12–98 h in an electric oven. WHC and SPD of each substrate were calculated as follows:

$$\mathrm{WHC} = (\mathrm{SW} - \mathrm{DW_{sub}})/3.24\pi \quad (2)$$

$$\mathrm{SPD} = \mathrm{DW_{sub}}/3.24\pi \quad (3)$$

Water balance measurements

To estimate the water balance of the litter, BSC and gravel substrates, five samples of each substrate were collected using the previously described core sampler on 15, 17, 19 and 21 July 2010. The water retention abilities of the three litter substrates were considered equivalent according to the water retention properties measured. The fresh weight (FW_{date}, g) of each sediment sample was measured immediately after collection, and samples from 15 to 19 July were transferred into cylindrical plastic cups of the same dimension to prevent water exchange between the substrate and the ground. These samples remained at the collection site for 2 days, after which each fresh weight was remeasured ($FW_{2\ days}$). Samples were then dried to constant weight (DW, g) at 80 °C for 12–98 h in an electric

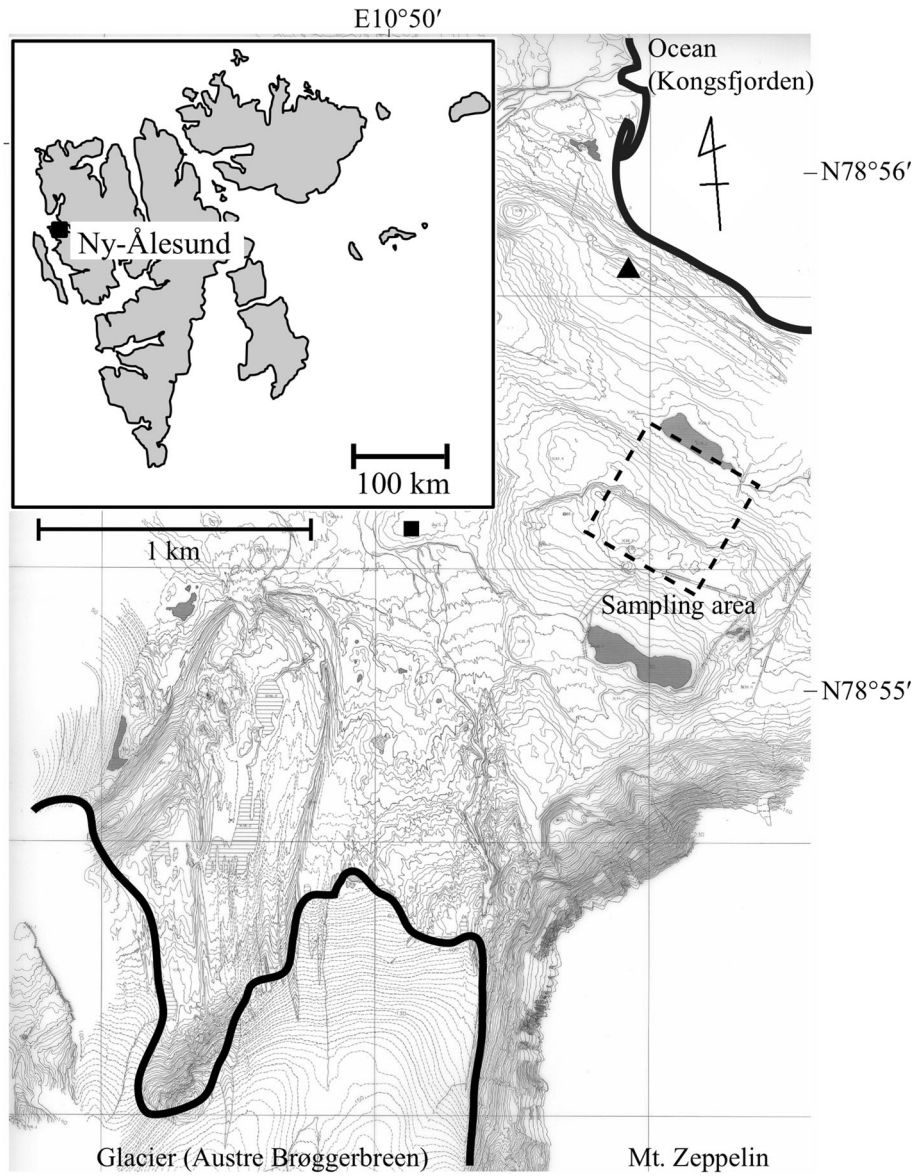

Fig. 1 Map showing the study areas in the Austre Brøggerbreen glacier foreland, southwest of Ny-Ålesund in the Svalbard archipelago. The contour interval is 2 m; *triangle* indicates Ny-Ålesund Airport and Japanese station; *square* indicates locations where precipitation was recorded; the *dashed square* delimits the sampling area

oven. The volumetric water content (VWC, g cm^{-3}) of each substrate was calculated using the FW_{date}, DW and sample volume as follows:

$$VWC = (FW_{date} - DW)/3.24\pi \quad (4)$$

Changes in fresh weight per volume of those samples kept in cups for 2 days represent the water balance between the air and the substrate (WB_{a-s}, g cm^{-3}) during the measurement period and were calculated as follows:

$$WB_{a-s} = (FW_{2\ days} - FW_{date})/3.24\pi \quad (5)$$

The water balance between the substrate and the ground (WB_{g-s}, g cm^{-3}) was calculated using the 2-day change in fresh weight under natural conditions (FW_{change}, g) and WB_{a-s} as follows:

$$WB_{g-s} = FW_{change}/3.24\pi - WB_{a-s} \quad (6)$$

Estimation of lichen surface areas

We selected the five lichen species *Cetrariella delisei*, *Flavocetraria nivalis*, *Cladonia arbuscula* ssp. *mitis*, *Cladonia pleurota* and *Ochrolechia frigida*, all of which are common in the Arctic (Elvebakk and Hertel 1996), and abbreviated according to the British Lichen Society (BLS). Five specimens of each species were soaked in water for 1 h, lightly blotted dry with paper and placed between slide glasses with a 1-cm^2 grid sheet. Digital photographs (Powershot A640, Canon, Tokyo, Japan) were taken from the lateral (slide glasses), upper (e.g. hole of podetium cup in *Clad pleu*) and lower (that in contact with the substrate) sides of the thalli, and thallus surface area was measured by analysing images using Photoshop CS6 Extended Software (Adobe Systems Inc., San Jose, CA). Samples were then

dried at 80 °C for 12 h in an electric oven, and dry weights ($DW_{thallus}$, g) were measured. The surface area in contact with the air (SA_{air}, cm^2) and with the substrate (SA_{sub}, cm^2) was determined separately and was expressed relative to the $DW_{thallus}$ (cm^2 g^{-1}).

Properties of absorption/evaporation of lichen thalli

Three thalli of each of the five lichen species were air-dried for 3–4 days, and air-dried weights (ADW, g) were determined. Samples were then fully hydrated in sealed plastic containers containing 100 ml water, and change in weight (W_{time}, g) was determined at 10, 30, 60, 100, 150 and 210 min and at 12 h to estimate the moisture absorption properties of each sample. Samples were kept in 100 % humidity for 12 h, and, assuming a moisture-saturated state, thallus weights were expressed as MSW (g). To allow comparison among samples, weight-specific absorbed water volume from moist air (AV, g g^{-1}) was calculated using the initial air-dried weight (ADW, g) as follows:

$$AV = (W_{time} - ADW)/ADW \quad (7)$$

Saturated samples were again placed in a sealed container containing 100 ml of glycerol-water to maintain relative humidity at 80 % (Solomon 1951; White and Zar 1968), and changes in weight were recorded at 10-min intervals for 1 h to estimate evaporative properties in dry air. Weight-specific evaporated water volume at <80 % humidity (EV, g g^{-1}) was also normalized by initial MSW:

$$EV = (MSW - W_{time})/MSW \quad (8)$$

Following these treatments, the relative humidity in the sealed containers was continuously monitored using a temperature–moisture metre (TR-72, T&D Co., Matsumoto, Japan). No substantial changes in humidity were observed in either the 80 or 100 % treatment. Both AV and EV were plotted against time (AV_t, EV_t), and the initial rates of absorption (α) and evaporation (β) were calculated using a saturation curve-fitting method (Thornley 1976; Uchida et al. 2006) in KaleidaGraph software v.3.6 (Synergy Software Co., Reading, PA) according to the following formulae:

$$AV_t = \alpha t + AV_{max} - \left\{(\alpha t + AV_{max})^2 - 4\alpha\theta t AV_{max}\right\}/2\theta \quad (9)$$

$$EV_t = \beta t + EV_{max} - \left\{(\beta t + EV_{max})^2 - 4\beta\theta t EV_{max}\right\}/2\theta \quad (10)$$

where AV_{max} and EV_{max} are the asymptotic values of AV and EV, and θ is a dimensionless constant (0.8). Calculated values of AV and EV were used to estimate thallus water content (WC, %) and water potential (WP, MPa) as WC_{AV}, WC_{EV}, WP_{AV} and WP_{EV} following Inoue et al. (2014).

Samples were then placed between water-saturated wiping papers for 12 h, and the fully hydrated mass (WM, g) was measured to determine the thallus liquid water content. Samples were then dried at 80 °C for 12 h, and dry weights were measured (DW).

Air-dried water content ($WC_{air\text{-}dried}$, %), maximum water content under saturated conditions ($WC_{max\text{-}water}$, %) and maximum water content from moist air ($WC_{max\text{-}moist}$, %) were calculated for each thallus as follows:

$$WC_{air-dried} = (ADW - DW)/DW \times 100 \quad (11)$$

$$WC_{max-water} = (WM - DW)/DW \times 100 \quad (12)$$

$$WC_{max-moist} = (WM - DW)/DW \times 100 \quad (13)$$

Statistics

Differences in variables among substrates and lichens were analysed using analysis of variance (ANOVA) with *Tukey–Kramer* post hoc *tests* in KaleidaGraph (Synergy Software Co.). *Paired t tests* were then performed to assess the relationships between initial rates of absorption/evaporation and lichen surface area. Differences were considered significant at $P < 0.05$.

Results

Lichen distributions among substrates

Flavocetraria nivalis, Cladonia arbuscula ssp. *mitis* and *Cladonia pleurota* showed rates of appearance of 60–80 % on vascular plant litter, moss litter and biological soil crust (BSC), respectively (Table 1). Rates of appearance of *Cetrariel deli* and *Och frig* were more than 40 % for all substrates, although the most frequently inhabited substrate differed between the two species. Rates of appearance of *Cetrariel deli* were significantly higher on the three litter and gravel substrates, whereas the rate of appearance of *Och frig* was significantly greater on BSC (Table 1).

Substrate water properties

Water-holding capacities (WHC) of the three litter substrates and BSC were similar (7–9 × 10^{-1} g cm^{-3}), whereas that of gravel (1.4 × 10^{-1} g cm^{-3}) was significantly lower (Table 2). Solid densities of the three litter types were similar, whereas those of BSC (69.1 × 10^{-2} g cm^{-3}) and gravel (114.1 × 10^{-2} g cm^{-3}) were significantly higher (Table 2).

Table 1 Lichen species distributions among substrates

	Moss litter	Vascular plant litter	Mixed litter	Biological soil crust	Gravel
Cetrariel delisei	V	V	V	III	V
Flavocet nivalis		IV			
Cladonia arbuscula spp. *mitis*	IV				
Cladonia pleurota				IV	
Ochrolechia frigida	III	III	IV	V	III

Lichens in the study site were found primarily on five substrate types: moss litter, vascular plant litter, mixed litter, biological soil crust and gravel. Rates of appearance on each substrate were ranked as: V (>80 %), IV (60–80 %), III (40–60 %), II (20–30 %) and I (20–10 %) following Braun-Blanquet (1964)

Only 1.1 mm and 2.4 mm of rainfall were recorded in the sampling area during the study period (19 and 20 August 2010, respectively; Fig. 2a). The volumetric water content (VWC) of BSC was highest among the substrates and stayed at roughly 0.3 g cm^{-3} during the observation period (Fig. 2a). Gravel had the lowest VWC, with a maximum of only 0.04 g cm^{-3} (19 August). VWC of moss litter was low at 0.05 g cm^{-3} between 15 and 17 August, but recovered to 0.1 g cm^{-3} with the rain between 19 and 21 August.

The air–substrate water balance ($WB_{a–s}$) of BSC was negative during the observation period, indicating greater evaporation from BSC than water absorption from the air (Fig. 2b). In contrast, the $WB_{a–s}$ of moss litter and gravel was positive (<0.1 g cm^{-3}) between 17 and 19 August, indicating higher water transfer from the air to the substrate than evaporation during this period (Fig. 2b).

The substrate–ground water balance ($WB_{g–s}$) was positive for all substrates throughout the observation period, indicating that water was transferred from the ground to the substrates (Fig. 2c). The $WB_{g–s}$ of BSC in particular was significantly higher than those of the other substrates, except for moss litter during 17–19 and 19–21 August, when both had a $WB_{g–s}$ of ~0.1 g cm^{-3}. The $WB_{g–s}$ of gravel was negligible throughout the observation period (Fig. 2c).

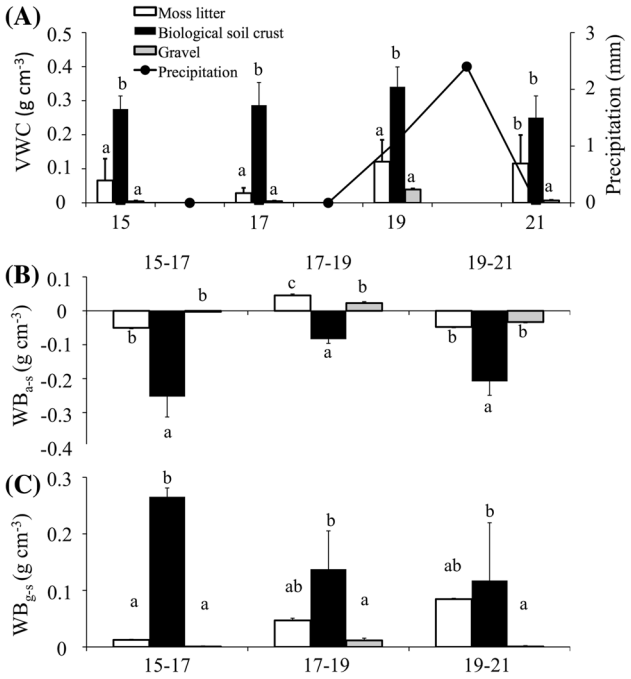

Fig. 2 Means and standard deviations (±SD) of the **a** volumetric water content and precipitation, **b** water balance between air and substrate ($WB_{a–s}$) and **c** water balance between substrate and ground ($WB_{g–s}$) for each substrate type during the observation period (15–21 July 2010). Values with different *letters* (*a*, *b*, *c*) differ significantly among the three substrates (Tukey test, $P < 0.05$)

Lichen morphological characteristics

The fruticose lichens *Cetrariel deli*, *Flavocet niva, Clad arbu miti* and *Cladonia pleu* are attached to the substrate only by the holdfast (Table 3), whereas the crustose lichen *Och frig* is fully adhered to substrate via hyphae (Table 3).

Surface area exposed to the air (SA_{air}) was more than 100 cm^2 g^{-1} for all four fruticose species (Table 3) and

Table 2 Substrate water capacities and solid-phase densities

Substrate type	Water-holding capacity (g/cm^{-3})	Solid-phase density (g/cm^{-3})
Moss litter	$8.6 \times 10^{-1} \pm 1.6 \times 10^{-1}$bc	$7.0 \times 10^{-2} \pm 1.7 \times 10^{-2}$a
Vascular plant litter	$6.7 \times 10^{-1} \pm 1.0 \times 10^{-1}$b	$9.9 \times 10^{-2} \pm 2.1 \times 10^{-2}$a
Mixed litter	$9.7 \times 10^{-1} \pm 1.0 \times 10^{-1}$c	$9.1 \times 10^{-2} \pm 2.0 \times 10^{-2}$a
Biological soil crust	$7.0 \times 10^{-1} \pm 1.0 \times 10^{-1}$bc	$69.1 \times 10^{-2} \pm 19.8 \times 10^{-2}$b
Gravel	$1.4 \times 10^{-1} \pm 1.0 \times 10^{-1}$a	$144.1 \times 10^{-2} \pm 26.7 \times 10^{-2}$b

Data are presented as means and standard deviations (±SD) of five different experiments (five samples of each substrate). Values with different letters (a, b, c) are significantly different (Tukey test, $P < 0.05$)

significantly higher in *Cetrariel deli* and *Flavocet niva* (200 cm^2 g^{-1}) than the other species. The SA_{air} of *Och frig* was significantly lower at roughly 40 cm^2 g^{-1} (Table 3). In contrast, the surface area in contact with the substrate (SA_{sub}) was significantly lower in *Cetrariel deli* and *Cladonia pleu* (~8 cm^2 g^{-1}) than in the other species (Table 3).

Moisture absorbance and evaporation

Water content and water potential caused by absorption from moist air (WC_{AV} and WP_{AV}) increased rapidly across species, with WC_{AV} at roughly 40 and 20 % after 100 min for the fruticose lichens and *Och frig*, respectively. WC_{AV} did not increase significantly after 100 min (Fig. 3a). WP_{AV} was at roughly −20 and −30 MPa in the fruticose lichens and in *Och frig* after 30 min, respectively (Fig. 3b).

Thallus water content after 30 min in evaporative conditions at 80 % humidity (WC_{EV}) was about 40–60 and 20 % in the fruticose lichens and in *Och frig*, respectively. All lichens were air-dried within 50 min (Fig. 3c). In all lichens, the water potential decreased to −30 MPa after 30 min in evaporative conditions (WP_{EV}; Fig. 3d).

Initial rates of absorption and evaporation (g g^{-1} min^{-1}) were significantly higher in *Flavocet niva* than in the other four species, while those of *Och frig* were lowest (Table 4). Neither air-dried water content ($WC_{air\text{-}dried}$) nor maximum water content of saturated thalli ($WC_{max\text{-}water}$) differed significantly among species. In contrast, maximum water content of thalli kept in moist air ($WC_{max\text{-}moist}$) was significantly lower in *Och frig* than in the four fruticose lichens (Table 4). Finally, initial rates of absorption and evaporation were positively correlated to surface area to weight ratios ($P > 0.05$; Fig. 4).

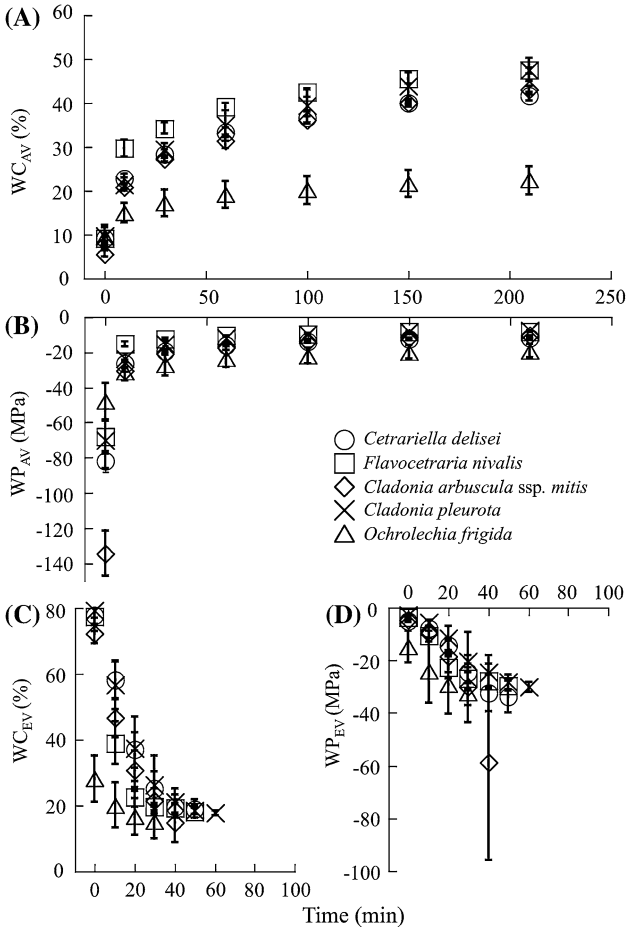

Fig. 3 Temporal changes in **a**, **b** absorption from moist air and **c**, **d** evaporation under 80 % humidity in each lichen species. Water content (WC_{AV}, WC_{EV}) and water potential (WP_{AV}, WP_{EV}) are plotted against sampling time. Data are presented as mean ± SD of three different experiments

Discussion

As poikilohydric organisms, lichens' water status varies passively with surrounding environmental conditions (Nash 2008). Lichens are often restricted to a narrowly defined substrate that is species-specific (Barkman 1958; Brodo 1973). There were five dominant substrate types in the present study area. Three of the fruticose lichens (*Flavocet niva*, *Clad arbu mitis* and *Clad pleu*) had high rates of appearance (>50 %) on each species' respective preferred substrate (Table 1), suggesting a relatively high substrate specificity that is likely to drive patterns of distribution. In contrast, the fruticose lichen *Cetrariel deli* and the crustose lichen *Och frig* had lower substrate specificity,

Table 3 Lichen morphology and surface areas exposed to air and in contact with the substrate

	Water-holding capacity (g/cm^3)	Solid-phase density (g/cm^3)
Moss litter	$8.6 \times 10^{-1} \pm 1.6 \times 10^{-1}$bc	$7.0 \times 10^{-2} \pm 1.7 \times 10^{-2}$a
Vascular plant litter	$6.7 \times 10^{-1} \pm 1.0 \times 10^{-1}$b	$9.9 \times 10^{-2} \pm 2.1 \times 10^{-2}$a
Mixed litter	$9.7 \times 10^{-1} \pm 1.0 \times 10^{-1}$c	$9.1 \times 10^{-2} \pm 2.0 \times 10^{-2}$a
Biological soil crust	$7.0 \times 10^{-1} \pm 1.0 \times 10^{-1}$bc	$69.1 \times 10^{-2} \pm 19.8 \times 10^{-2}$b
Gravel	$1.4 \times 10^{-1} \pm 1.0 \times 10^{-1}$a	$144.1 \times 10^{-2} \pm 26.7 \times 10^{-2}$b

Data are presented as means and standard deviations (±SD) of five different experiments. Values with different letters (a, b, c) differ significantly between species (Tukey test, $P < 0.05$)

Table 4 Initial rates of absorption and evaporation, air-dried water content ($WC_{air\text{-}dried}$), maximum water content of saturated thalli ($WC_{max\text{-}water}$) and maximum water content of thalli in moist air ($WC_{max\text{-}moist}$)

	Initial rates (g/g min)		$WC_{air\text{-}dried}$ (%)	$WC_{max\text{-}water}$ (%)	$WC_{max\text{-}moist}$ (%)
	Absorption	Evaporation			
Cetrariel deli	$0.8 \times 10^{-2} \pm 0.1 \times 10^{-2}$b	$1.4 \times 10^{-2} \pm 0.1 \times 10^{-2}$b	9.1 ± 0.5a	215 ± 75a	77 ± 3a
Flavocet niva	$1.9 \times 10^{-2} \pm 0.4 \times 10^{-2}$a	$3.0 \times 10^{-2} \pm 0.4 \times 10^{-2}$a	9.2 ± 1.1a	411 ± 22a	75 ± 4a
Clad arbu miti	$0.8 \times 10^{-2} \pm 0.1 \times 10^{-2}$b	$1.6 \times 10^{-2} \pm 0.2 \times 10^{-2}$b	5.7 ± 0.8a	353 ± 69a	83 ± 2a
Clad pleu	$0.6 \times 10^{-2} \pm 0.1 \times 10^{-2}$b	$1.6 \times 10^{-2} \pm 0.6 \times 10^{-2}$b	9.6 ± 2.1a	389 ± 66a	88 ± 6a
Och frig	$0.3 \times 10^{-2} \pm 0.1 \times 10^{-2}$b	$0.9 \times 10^{-2} \pm 0.3 \times 10^{-2}$b	9.6 ± 2.7a	356 ± 69a	45 ± 4b

Data are presented as mean ± SD of five different experiments. Values with different letters (a, b, c) differ significantly between species (Tukey test, $P < 0.05$)

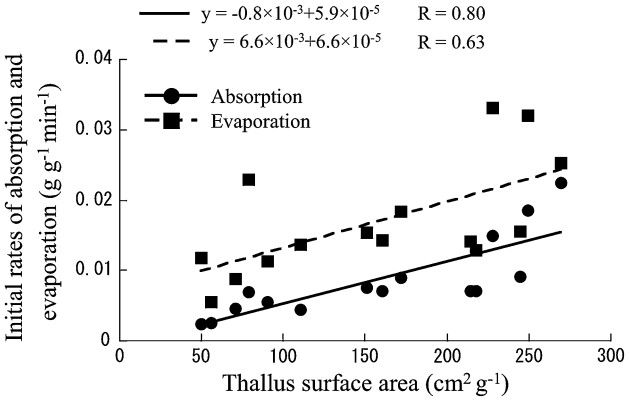

Fig. 4 Relationships between thallus surface area and initial rates of absorption and evaporation in the five lichen species

with high rates of appearance on all five substrates (Table 1). Substrate specificity may be defined by metabolitic requirements and tolerance of various substrate properties such as texture, water and chemicals (Brodo 1973). Water conditions during the snow-free season in high Arctic terrestrial ecosystems are a major limiting factor for plant growth (Kappen 1973; Longton 1988; Uchida et al. 2006; Inoue et al. 2014); thus, the distribution of these lichen species may reflect the characteristics of differing substrates and thallus morphologies that affect thallus water status.

Previous studies suggest both that lichen distributions reflect water conditions and that substrate water capacities vary with texture and composition (Barkman 1958; Brodo 1973; Kappen 1973; Smith 1993; Wynn-Williams 1993; van der Wal et al. 2001; Cannone et al. 2004). In the present study, measurements of the in situ water balance clearly indicated differences among substrates in water movement to/from the ground and the air. For example, BSC released large quantities of water ($\sim$0.1–0.3 g cm^{-3}) from the substrate surface (Fig. 2b), but also absorbed more water from the ground (Fig. 2c). Therefore, moisture content remained greater in BSC than in the other substrates (moss litter and gravel) throughout the observation period (Fig. 2a). Although the water capacity of BSC did not differ from that of the three litter substrates, the higher density of BSC resulted in higher water retention (Table 2). Soils with numerous small pore spaces and large surface areas or mass can absorb more water from the surface and retain the water in pore spaces with little loss due to surface tension (Jury and Horton 2004). Thus, it is likely that the structure of BSC, which was the moistest substrate tested, led to its greater water retention capacity.

Thallus morphology may also significantly influence water availability (Larson and Kershaw 1976; Larson 1981; Sancho and Kappen 1989) and resulting lichen distributions (Bergamini et al. 2005; Spribille et al. 2008; Vittoz et al. 2010; Rodnikova 2012). Air-dried and maximum water contents of saturated thalli did not differ significantly among lichen species (Table 4). Lichens did, however, exhibit differing water status, reflecting differences in surface areas in contact with air or substrate. The crustose lichen *Och frig* had 60 % contact with the substrate, four times more than that of the fruticose lichens (Table 3). Gaßmann and Ott (2000) suggested that the spinules of *Och frig* may improve water supply by increasing contact with the substrate. Our previous work also indicated that *Och frig* gains twice as much water from BSC than does *Cetrariel deli* (Inoue et al. 2014). Thus, interspecific differences in thallus–substrate water movement may reflect substrate preferences.

In contrast with *Och frig*, most of the surface area (>100 cm^2 g^{-1}, $\sim$90 %) of the fruticose lichens was directly exposed to air. Similarly to previous studies (Larson and Kershaw 1976; Larson 1981; Sancho and Kappen 1989), these lichens have been shown to capture 2–3 times more water from the air than *Och frig* in field (Inoue et al. 2014) and laboratory conditions (maximum water content obtained from moist air, Table 4). Laboratory studies evaluating the relationships between thallus water conditions and photosynthetic activity have suggested that *Cetrariel deli, F. nivalis* and *Clad arbu mitis* cease to photosynthesize when water content or potential

drops below 20–40 % (Lechowicz and Adams 1973; Schipperges 1992; Uchida et al. 2006) or −30 to −40 MPa (Barták et al. 2005, 2015). The fructose lichens studied achieved the water content and potential necessary for photosynthesis after 10 min in moist conditions (Fig. 3a, b). Thus, expansive thallus contact with air facilitates water capture from moist air and may suggest that these lichens depend on water from air for photosynthesis.

Thallus surface area, which has been previously correlated with absorptive and evaporative rates (Larson and Kershaw 1976; Larson 1981), also showed positive correlations with initial rates of absorption and evaporation in the present study (Fig. 4). Using a packing bead method that estimates microscopic external features of lichens (e.g. lobe, hole of podetium cup, scyphus), Larson and Kershaw (1976) and Larson (1981) reported thallus surface areas of 370 and 150 $cm^2\ g^{-1}$ in *F. nivalis* and *Cladonia chlorophaea*, respectively. The surface areas measured in the present study tended to be smaller (Table 3), which may have resulted from underestimation in analysis of the macroscopic photographs. Nonetheless, similar trends between surface area and rates of absorption/evaporation suggest that interspecific differences in thallus–air water movement reflect differences in aerial surface areas.

Green algal lichens have been shown to resume photosynthesis after exposure to humidity (Lange et al. 1986; Lange 1988; Green and Lange 1995; Lange et al. 2001; Green et al. 2002; Reiter et al. 2008; Inoue et al. 2014). We previously demonstrated that photosynthetic production in the four fruticose lichens studied was optimal in shady conditions around 500 $\mu mol\ m^{-2}\ s^{-1}$ PAR when water vapour can be obtained from humid air (Inoue et al. 2014). Moreover, all of the studied lichens contain green algal photobionts. Hence, these lichens may depend on the sequestration of water vapour from the air (Table 3; Fig. 4). Morphologically advanced lichens that grow above the substrate, such as fruticose forms, may compete for aboveground space to control water conditions and photobiont activities (Honegger 1995, 2009). The thalli of *Cetrariel deli*, however, have little contact with the substrate and thus are unlikely to receive much water from the substrate (Table 3), although thalli of *Cetrariel deli* were observed to absorb some water from BSC under strong light conditions (Inoue et al. 2014). Similarly, this water movement can activate photosynthesis, but may also cause photoinhibition (Lange et al. 1970; Demmig-Adams et al. 1990, Inoue et al. 2014). Moreover, lichen suprasaturation increased resistance to CO_2 diffusion, leading to a depression of photosynthetic production (Lange et al. 1970, 2001). Thus, *Cetrariel deli* and other lichens that exhibit optimal photosynthesis in shady conditions may grow poorly on moist substrates such as BSC (Table 1). Yet the fruticose lichen *Clad pleu*, which also exhibits maximal photosynthesis under shady conditions, had high rates of appearance on BSC. The twofold thallus that *Clad pleu* develops (vertical fruticose and horizontal crustose-squamulose; Büdel and Scheidegger 2008) may affect the external and internal structure and/or the placement of photobionts, potentially altering water availability and photosynthesis compared with other fruticose lichens. Furthermore, lichen growth is also dependent on other substrate factors such as temperature, texture, nutrients and chemical composition (Brodo 1973).

The crustose lichen *Och frig* has been shown to exhibit a sun-adapted pattern of photosynthesis with no strong light inhibition (PAR >1000 $\mu mol\ m^{-2}\ s^{-1}$) and a photosystem that remains active under conditions of strong direct sunlight (Inoue et al. 2014). In accordance with a broad area of contact with the substrate, growth of *Och frig* was more strongly influenced by substrate water content than by water vapour, and it acquired water from BSC according to the water potential gradient. Hence, while photosynthesis ceased around noon in the fruticose lichen, *Och frig* retained water and continued to perform photosynthesis. These characteristics likely underlie the high rates of appearance of *Och frig* on most moist substrates in the water-limited glacier foreland.

Substrate specificity represents a significant physiological restriction for lichens, and mycobiont preferences for substrate nutrients, texture and temperature act as significant factors. Moreover, thallus morphological characteristics are also dependent on mycobionts (Brodo 1973; Ahmadjian 1993; Honegger 2009). The present data suggest that water availability for lichens is highly dependent on both morphological characteristics (surface area contact with the surrounding environment) and substrate water properties, and we conclude that these two mycobiont-dependent factors are essential for autotrophic nutrition of lichens and their photobionts in the water-limited glacier foreland of the high Arctic region.

Acknowledgments This study was supported by a Grant-in-Aid for Scientific Research from the Japan Society for the Promotion of Science (No. 19255003) and the National Institute of Polar Research through General Collaboration Projects (No. KP-11) of The Graduate University for Advanced Studies (Sokendai).

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