




Standard Paper

The globally threatened epiphytic cyanolichen *Erioderma pedicellatum* depends on a rare combination of habitat factors

Alexander R. Nilsson , Knut Asbjørn Solhaug  and Yngvar Gauslaa 

Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

Abstract

Lichen extinction occurs at rapid rates as a result of human activity, although species could potentially be rescued by conservation management based on ecophysiological knowledge. The boreal old forest cyanolichen *Erioderma pedicellatum* currently occurs in few sites worldwide. To protect it from extinction, it is essential to learn more about it. The last remaining good European site is a canyon with a waterfall, in a low-rainfall region of Norway. Here, a spatially restricted population of 1500–2000 thalli dominates the epiphytic vegetation of a small number of *Picea abies* canopies. We were able to document that 1) *E. pedicellatum* grew on thin branches with higher bark pH than is normal for *P. abies* in a canyon that provided an unusual combination of very high light, high air humidity, and cool temperatures in the growing season. However, the species did not inhabit the main waterfall spray zone. 2) *Erioderma pedicellatum* had a high light saturation point, high CO₂ uptake at high light ($\geq 600 \mu\text{mol m}^{-2} \text{s}^{-1}$) and cool temperatures (5–20 °C), and experienced strong suprasaturation depression of photosynthesis when fully hydrated. 3) It showed good tolerance of desiccation and high light; it was slightly more tolerant than the morphologically similar, but more common cyanolichen *Pectenia plumbea*. 4) The European population in its sunny habitat had higher water holding capacity than previously recorded in slightly shaded rainforest populations in Newfoundland, consistent with acclimation to compensate for high evaporative demands. Understanding the ecological niche and responses to critical environmental factors is essential for action plans to avoid extinction of *E. pedicellatum*. Methods used in this study could also be applicable for ecological understanding of other threatened lichen species.

Key words: bark pH, CO₂ uptake, desiccation tolerance, ecophysiology, hydration traits, *Pectenia plumbea*

(Accepted 22 November 2021)

Introduction

Lichens, being intricate symbiotic associations between algae and fungi (Spribille 2018), represent an important biodiversity component in many ecosystems. They often dominate habitats where plants are less successful and are important for ecosystem functioning at high latitudes and elevations (Asplund & Wardle 2017). Lichens occur in most terrestrial ecosystems and often tolerate extreme desiccation and temperatures (Büdel *et al.* 1997; Lange *et al.* 1998, 2000; Sancho *et al.* 2007; Colesie *et al.* 2016). Yet they are vulnerable to environmental change, particularly to changes in climate (Cornelissen *et al.* 2001; Elmendorf *et al.* 2012; Lang *et al.* 2012) and land use (Stofer *et al.* 2006).

Lichens interact with their environment by various functional traits and thereby increase functional diversity (Ellis *et al.* 2021). Some functional traits relate to water uptake that allows them to utilize hydration sources such as rain, dew, and humid air (Lange *et al.* 1986; Gauslaa 2014; Phinney *et al.* 2019). Light is essential for photosynthesis and growth, but only when lichens are moist (Palmqvist 2000). However, light affects hydration levels, as solar

radiation drives desiccation rate (Lange 1969; Gauslaa *et al.* 2017). Furthermore, high light often damages the photosynthetic apparatus in dry lichens (Gauslaa & Solhaug 1996; Gauslaa *et al.* 2012) and causes oxidative stress (Beckett *et al.* 2021). Thus, the interaction of high light and lasting desiccation can threaten various forest lichens. The pH of the substratum is another important factor. It influences nutrient availability (Richardson *et al.* 2004; Penn & Camberato 2019) and thus shapes the distribution of many lichens (Gauslaa *et al.* 2020). Some species, such as cyano- and cephalolichens forming the epiphytic *Lobarion* community, require a substratum with higher pH than the many acidophytic chlorolichens (Gauslaa 1985, 1995; Gauslaa & Holien 1998; Gauslaa *et al.* 2021). Bark pH is shaped by the chemical characteristics of air-borne depositions, local soils and elemental uptake by the tree itself (Barkman 1958). Due to tree species-specific bark pH, tree species often host different lichen communities (Rose 1988).

Many lichens are red listed, some close to extinction (IUCN 2021). Endangered lichens, such as the critically endangered cyanolichen *Erioderma pedicellatum* (Hue) P. M. Jørg. (*Pannariaceae*) (Scheidegger 2003), are often thought to be facilitated by the partly shaded and humid environment created by old forests. *Erioderma pedicellatum* was first described by Hue in 1911 from New Brunswick, Canada (Jørgensen 2000), and was reported as new to Europe from Norway in 1938 and Sweden in 1941 (Ahlner 1948). The known Norwegian population consisted of a small number of

Author for correspondence: Yngvar Gauslaa. E-mail: yngvar.gauslaa@nmbu.no

Cite this article: Nilsson AR, Solhaug KA and Gauslaa Y (2022) The globally threatened epiphytic cyanolichen *Erioderma pedicellatum* depends on a rare combination of habitat factors. *Lichenologist* 54, 123–136. <https://doi.org/10.1017/S002428292200007X>

specimens only, whereas the population in Sweden was greater (Ahlner 1948). Shortly afterwards the species was considered extinct due to logging in all known European sites (Ahlner 1954; Jørgensen 1990) and had declined elsewhere (Scheidegger 2003). The decline has been related to land-use changes such as logging (Cameron *et al.* 2013b; Tagirdzhanova *et al.* 2019) and air pollution (Richardson & Cameron 2004), but wildfire (Tagirdzhanova *et al.* 2019) and gastropod grazing (Cameron 2009) are important local threats. After new populations in Alaska and Kamchatka were discovered, the situation improved, but was still considered critical (Cameron *et al.* 2013a; Stehn *et al.* 2013; Holien 2015; Tagirdzhanova *et al.* 2019). After being considered extinct for < 50 years in Europe, two thalli were found in the Norwegian boreal rainforest (Tønberg *et al.* 1996). Later, a population was discovered in a canyon in Rendalen, south-eastern Norway (Reiso & Hofton 2006), estimated to host 1500–2000 thalli (Björn Nordén, personal communication); this therefore currently comprises the largest European *E. pedicellatum* population. This population on thin dead *Picea abies* branches produces a litter of healthy specimens (A. R. Nilsson, personal observation 2019, 2020) available for experiments.

Our overall aim was to use newly fallen thalli to gain basic eco-physiological knowledge about this rare species, which may improve the success of future reintroductions to new sites. Without new knowledge, effective conservation for this globally threatened lichen is challenging, and conservation management is left with few other options than creating nature reserves. More specifically, we aim to 1) report microclimate (light, temperature, relative humidity) and bark pH in the best European site for *E. pedicellatum*. Another aim is to 2) quantify basic hydration traits for Norwegian *E. pedicellatum* and to compare them with recently assessed traits for a population on slightly shaded trunks of *Abies balsamea* in Newfoundland rainforests (Gauslaa & Arsenault 2020). In the macro-climatically dry Norwegian site, it occurs on sun-exposed thin *Picea abies* branches enriched by humid air from a waterfall, a situation known to support oceanic lichens in inland sites (Björk *et al.* 2009). We hypothesize that the sun-exposed Norwegian population has a higher water holding capacity (WHC) to compensate for higher evaporative demands than the more protected Newfoundland population on trunks. Furthermore, because *E. pedicellatum* is restricted to humid or rainy sites, we aim to 3) quantify its desiccation and high light tolerance (Gauslaa *et al.* 2012), since light in the dry state can be detrimental for poikilohydric organisms (as reviewed by Beckett *et al.* (2021)). The morphologically similar *Pannariaceae* species, *Pectenium plumbeum* (Light.) P. M. Jørg. & P. James, was included to test the hypothesis that the rare *E. pedicellatum* is more intolerant to desiccation and light than the common *P. plumbeum*. Since measurements of CO₂ uptake along environmental gradients can identify optimal conditions for lichen growth, we finally aim to 4) quantify photosynthetic responses of *E. pedicellatum* to light, temperature and desiccation. We hypothesize that this boreal lichen is most efficient at low light and cool temperatures, and that its optimal water content for photosynthesis is close to the internal water holding capacity (WHC_{internal}) as shown for chloro- and cephalolichens (Solhaug *et al.* 2021).

Materials and Methods

Field site

The best European *E. pedicellatum* site is in Rendalen (c. 61°52'N, 10°51'E, 460 m a.s.l., eastern part of southern Norway), c. 40 m

from a 25 m tall waterfall in a small river. The catchment area for the waterfall is 89 km², of which > 90% is situated above the timberline, creating a rather constant water flow in the growing season (Reiso & Hofton 2006; NVE 2020). The macroclimate is slightly continental with precipitation c. 500 mm y⁻¹. July and August receive most rain (Moen 1999; NVE 2020). Normal annual temperature at the nearest meteorological station in Alvdal (28 km away) is 2.2 °C; –8 °C in December and 13.8 °C in July. The vegetation is middle boreal (Moen 1999). From the waterfall, the canyon continues for 300 m before the landscape flattens (Fig. 1A). The canyon hosts some *Picea abies*, whereas *Pinus sylvestris* forms the open dry forest above the canyon. *Erioderma pedicellatum* grew only on thin, mainly dead branches (Fig. 1D) of some *P. abies* facing the waterfall up on the opposite side of the canyon, outside the waterfall spray zone during most of the year. The branches with most specimens were south-west-facing and sun-exposed (Fig. 1C).

Four small trees in one cluster hosted c. 90% of the *E. pedicellatum* population that dominated the epiphytic vegetation on the most sun-exposed branches. In addition, there were c. 10 nearby trees with some thalli on each. This strong spatial aggregation differs from its distribution pattern elsewhere (Cameron *et al.* 2013a; Stehn *et al.* 2013; Holien 2015; Tagirdzhanova *et al.* 2019). The lower part of the canyon represents a unique environment with epiphytes and microclimate resembling those in open patches of the Norwegian boreal rainforest (Holien & Tønberg 1996), differing from the surrounding dry low-productive pine forest.

The spruce forest in the canyon is not old, but moss-loaded dwarf trees suppressed by excess humidity closer to the fall may have functioned as continuity carriers. The surrounding pine forest originated on former clear-cuts, and is aged < 100 y. Surrounding mountain ranges have protected the area against the most acidic rain; pH in the precipitation is c. 4.9 (Tørseth & Manø 1996).

Lichen material

Healthy *E. pedicellatum* thalli found on dead, newly fallen branches on the ground were collected during visits (September 2019, April, May and October 2020, May 2021). For comparison, thalli of *Pectenium plumbeum* were collected on *Quercus petraea* in Kristiansand (58°7'50"N, 8°8'7"E), southern Norway, in July 2020. After collection, lichens were air-dried at 20 °C and stored at –18 °C in the laboratory for 2–12 months, before experiments started. Lichen performance should not be affected by such treatment (Honegger 2003).

Microclimatic measurements

A hemispherical photograph (Fig. 1B) was taken in October 2020 close to the branches dominated by *E. pedicellatum* with a Pentax K-5II SLR camera using a Sigma 4.5 mm fisheye lens. The camera was placed horizontally with the true north direction indicated and positioned at a similar height above ground as the branches with most *E. pedicellatum*. The photograph was analyzed by Hemisfer v. 3.0 (www.schleppi.ch/patrick/hemisfer/) to estimate the duration of direct sunlight through the year under clear sky conditions.

Two HOBO Micro Station Data Loggers with a 12-bit Temperature/Relative Humidity Smart Sensor and a quantum sensor (model S-LIA-M003) monitored with HOBOware Pro v. 2.2.1 (Onset, Bourne, MA, USA) were installed for the 2020 growth season (18 April–4 October). Light, temperature and



Fig. 1. A, canyon with the waterfall in Rendalen. The best site for *Erioderma pedicellatum* was on a cluster of small *Picea abies* on the steep, rocky SW-facing slope slightly downstream from the larger spruce trees seen to the left in the photograph. This cluster of trees faced, unobstructed, the waterfall on the opposite side of the canyon (photograph: Sigve Haugland). B, fisheye photograph, positioned horizontally, taken in October 2020 close to the SW-facing spruce branches with the densest population of *E. pedicellatum*. The upper part of the waterfall on the opposite side of the canyon can be seen in the lowermost part of the photograph close to the south direction. The dark cluster of dead, lichen-covered outer branches near the centre of the photograph (arrow) is where *E. pedicellatum* occurs most abundantly (see Fig. 1C). The gridlines show the annual sun tracks over the sky, dividing the year into 6 sectors and the day into 24 sectors (photograph: K. A. Solhaug). C, branches visible as the dark cluster facing the sky in Fig. 1B were totally dominated by *E. pedicellatum*, exposing their light lower side along marginal lobes. D, *E. pedicellatum* thallus showing the numerous brown apothecia (C & D photographs: Y. Gauslaa). In colour online.

relative humidity were recorded every 5 min. One microclimate station was placed close to the main population (± 1 m), the other one next to a host tree (± 2 m) with only a couple of *E. pedicellatum* thalli, c. 50 m north-west of the main population, to differentiate between an optimal and suboptimal site. Both microclimate stations were placed c. 1 m above ground, and as close to the host trees as possible.

pH measurement

In May 2020, branches were collected from three categories of *P. abies* based on their epiphytic vegetation: 1) dominance of *E. pedicellatum* ($n = 7$); 2) dominance of other *Lobaria* species (cephalo- and cyanolichens; $n = 10$); 3) only chlorolichens in the *Parmeliaceae* (*Parmelion*; $n = 10$). Branches were brought to the laboratory and

analyzed 2 d after collection. Each branch was cleaned (epiphytes removed), cut into a 6 cm long segment and put in a small glass vial with 6 ml 25 mM KCl and repeatedly shaken for 1.5 h. Thereafter, branches were removed and pH was measured in the solution with a calibrated pH-meter (see Gauslaa & Holien 1998).

Additionally, conductivity and pH were measured in six water samples from the waterfall. Conductivity was measured in the field with a portable conductivity meter (Mettler-Toledo International Ltd, Singapore), whereas the pH of water samples kept in closed bottles were measured in the laboratory within 24 h.

Hydration traits

A randomly selected batch of *E. pedicellatum* thalli was used to measure water holding capacity (WHC) and specific thallus

mass (STM). First, air-dry mass (± 0.1 mg) was measured for lichens kept dry at 20 °C for 24 h. Then wet mass (WM_{shaking}) was recorded by weighing sprayed and fully water-saturated thalli that had been gently shaken; and blotting mass (WM_{blotting}) after removing surface water by gently blotting the lichens with filter paper. Each hydrated lichen was placed under a plate of glass to flatten it on a transilluminator to optimize the photographs (Pentax K-5II SLR camera with a Sigma 70 mm macro lens). We used ImageJ 1.48 (Rasband 2014) for calculating thallus area (A). Oven-dry mass (DM) was weighed in five additional thalli after 24 h drying at 70 °C, and the DM/air-dry mass-ratio was used to calculate DM for all experimental thalli. Specific thallus mass ($STM = DM/A$), total ($WHC_{\text{total}} = WHC_{\text{shaking}} = (WM_{\text{shaking}} - DM)/A$), internal ($WHC_{\text{internal}} = WHC_{\text{blotting}} = (WM_{\text{blotting}} - DM)/A$) and external water holding capacity ($WHC_{\text{external}} = WHC_{\text{shaking}} - WHC_{\text{blotting}}$) were computed.

Light and desiccation tolerance experiment

Randomly selected thalli were first acclimated in the moist state at low light ($10\text{--}15 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ from white fluorescent bulbs) for 24 h. When air-dry, five *E. pedicellatum* and four *P. plumbea* thalli were randomly placed on nets above saturated salt solutions (Greenspan 1977) inside each of 16 boxes sealed with cling film across four relative humidity levels (0% [silica gel], 35% [MgCl_2], 55% [$\text{Mg}(\text{NO}_3)_2$], 75% [NaCl]) and two light treatments (0 and $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ of equal levels of red, blue and green light from an SL-3500 LED panel). Each of the eight combinations of humidity and light was thus replicated in two boxes (see Gauslaa et al. 2012). The number of replicates for each of the eight treatments was 10 for *E. pedicellatum* and 8 for *P. plumbea*. Boxes were rotated daily to reduce the effects of small heterogeneities in light. On the 7th day, lichens were removed from the sealed boxes, hydrated, and placed under low light ($10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ from white fluorescent bulbs). Recovery kinetics of maximal PSII efficiency (F_w/F_m) was measured at 15 °C after 0.5 h, 2 h, 6 h, 24 h and 48 h using ImagingPam (red-LED IMAGING-PAM M-series, Walz Effeltrich, Germany).

Photosynthetic responses to light and temperature

All measurements of photosynthetic CO_2 uptake in this paper used a portable infrared gas-analyzer (LI-6400XT, LiCor, Lincoln, NE, USA) with a LiCor 6400-24 bryophyte chamber and a LI-6400-18 RGB LED light source. Light response curves for six thalli were recorded at 10 and 20 °C with white light (equal amounts of red, green and blue light) and 410 ppm CO_2 and analyzed using Photosyn Assistant v. 1.1 (Parsons and Ogston, Dundee Scientific, Dundee, UK). To keep the humidity inside the cuvette at c. 70%, all water was removed from the incoming air when measuring large thalli. Before measuring light response curves, thalli were lightly blotted with drying paper to remove external water. After inserting a thallus into the cuvette, the first measurement was taken when photosynthesis was stable at $800 \mu\text{mol photons m}^{-2} \text{s}^{-1}$. The light was then reduced to 400, 200, 100, 50, 25 and 0 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ in 2-min steps and CO_2 uptake was recorded at the end of each step. For each measurement, we checked that lichens had an optimal water content for photosynthesis (Solhaug et al. 2021) during the entire light response curve.

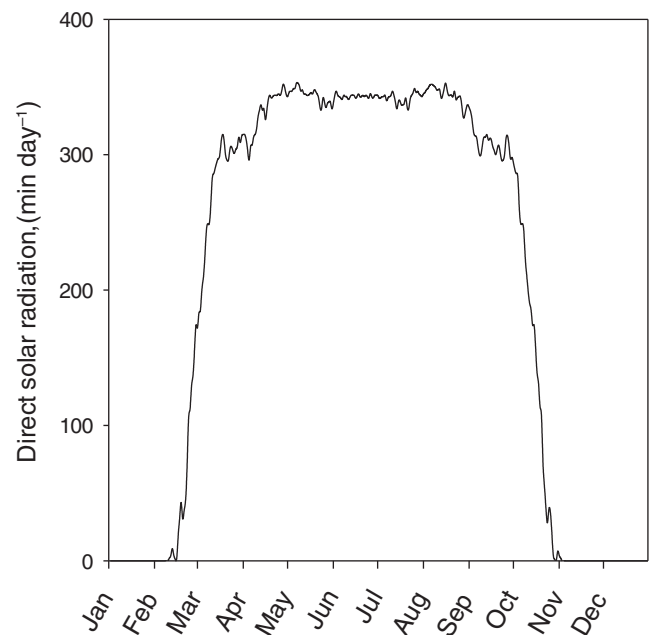


Fig. 2. Annual course of estimated duration of direct sunlight (minutes per day) near the *Picea abies* branches with the highest dominance of *Erioderma pedicellatum*, assuming clear sky conditions. Data were estimated from the hemispherical photograph in Fig. 1B using Hemisfer v. 3.0 (www.schleppi.ch/patrick/hemisfer/).

To quantify temperature responses, CO_2 uptake was measured in 15 thalli at 5, 10, 15, 20 and 25 °C, respectively, at 410 ppm CO_2 and $400 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ red light, after removing external water by blotting. Firstly, moist lichens were acclimated to the selected temperature for 24 h at $10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, completing all measurements at one temperature in one day. Afterwards, lichens were acclimated for another 24 h at the next temperature before measurements at the second temperature, and likewise for each of the remaining temperatures.

CO_2 uptake during desiccation cycles

Eighteen thalli were hydrated before their area was recorded with a leaf area meter (Li-3100 Area Meter, Li-cor, Lincoln, NE, USA). One by one, they were placed in the gas analyzer cuvette while fully water-saturated (WM_{shaking} , corresponding to WHC_{total}), at 410 ppm CO_2 , $400 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ red light, and 20 °C. The thallus was taken out for weighing every 5 min until the lichen became air-dry and inactive.

Statistical analyses

Data were log-transformed to meet test assumptions when needed. Simple linear regressions tested the relationships between hydration traits of interest and surveyed relationships of interest in the desiccation experiment. Paired *t*-tests were conducted to test differences between parameters of interest for the microclimatic data.

One-way ANOVAs investigated differences between the categories for bark pH measurements and for CO_2 uptake at different temperatures, combined with post-hoc analyses. Thalli were tested for as a random effect when the same thalli were repeatedly measured during an experiment, by using linear mixed models where assumptions were met.

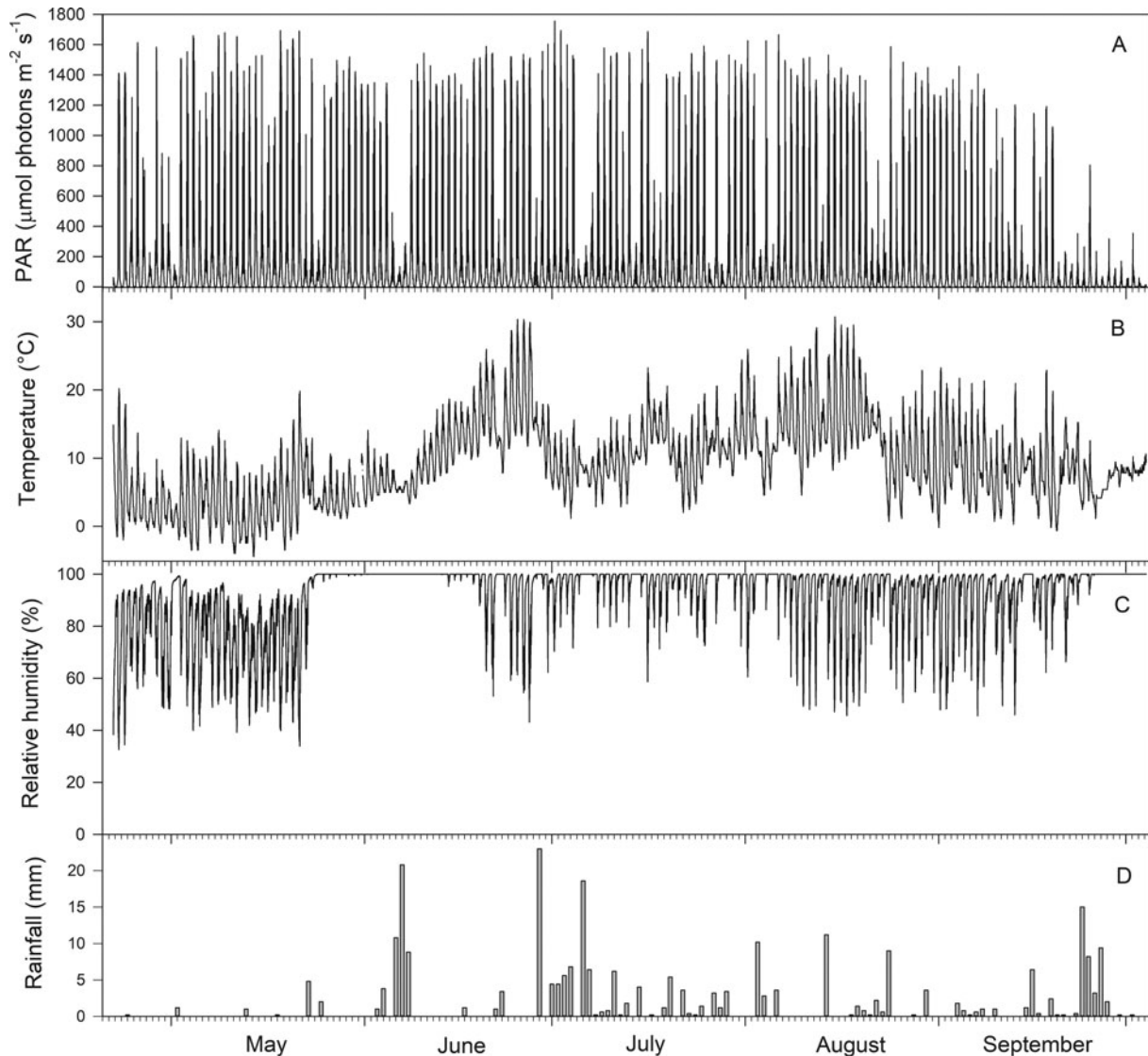


Fig. 3. Microclimate measurements from the *Erioderma pedicellatum* site in Rendalen, Norway. A, photosynthetic active radiation (PAR). B, air temperature (°C). C, relative humidity (RH%). PAR and temperature were recorded for the main population, RH data were from the suboptimal population due to a longer period of missing data for the main population. D, rainfall (mm) records from the Alvdal meteorological station. All recordings started 18 April 2020 and ended 4 October 2020.

In the light and desiccation tolerance experiment, a three-way linear mixed model was run for F_v/F_m after 48 h recovery with species, light and relative humidity as fixed factors, and box (i.e. the container that the samples were in) as a random factor. Assumptions for the model were met.

A small number of specimens of *E. pedicellatum* were excluded as outliers from some analyses due to very low responses, or errors during measurements with the gas analyzer. Since all specimens of *E. pedicellatum* were collected from fallen branches, it was expected that some individuals could be impaired by low vitality. Means \pm 1 SE are given in the text. Statistical analyses were run using Jamovi v. 1.2 (www.jamovi.org/).

Results

Microclimate

The estimated daily direct sunlight on clear days lasted continuously for > 5 h around noon from early April to late August

(Fig. 2). From late October to early March, lichens received no direct sunlight due to shading landscape elements. The largest European *Erioderma pedicellatum* population thus experienced much direct sunlight in summer and a total lack of sun exposure in winter.

The relative humidity (RH) reached 100% almost every night between 24 May–4 October (Fig. 3C). Before 24 May, when nocturnal temperature often dropped below 0 °C and minimized snow melt (Fig. 3B) (and thus the flow rate in the river), RH never reached 100%. From 24 May to 19 June, RH was 100% day and night (Fig. 3C), but after 19 June higher air temperatures reduced RH during the daytime. Overcast and rainy days (Fig. 3D) with little light and small diurnal temperature amplitudes were associated with only minor daily reductions in RH. This was clearest during late September/early October before measurements ended (Fig. 3). High light (> 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) frequently occurred between April–August (Fig. 3A).

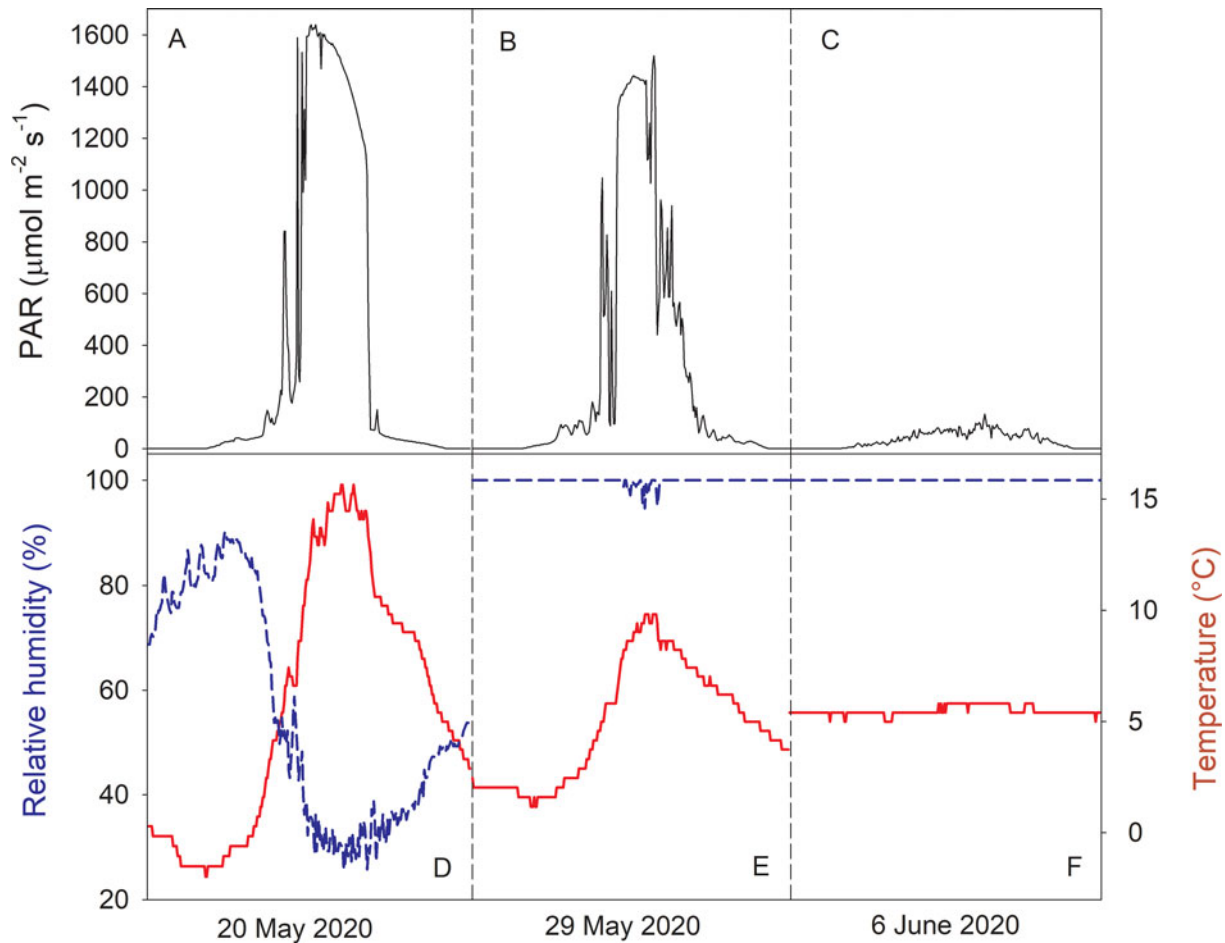


Fig. 4. A–C, diurnal variation in photosynthetic active radiation (PAR). D–F, relative humidity (RH%, dashed line) and temperature (°C, solid line). Data show three selected days with different weather conditions (see text). All data were from the microclimate station at the site of the main population. In colour online.

Strong links between light, air temperature and RH occurred on sunny days (e.g. 20 May; Fig. 4A & D). While RH gradually increased at night, increasing solar radiation in the morning heated the air with a rapid and strong concurrent decline in RH. However, after the marked seasonal shift in RH from 24 May (Fig. 3C), RH was rather unaffected by increases in light and temperature on clear days (Fig. 4B & E). On cloudy and rainy days, light hardly exceeded $100 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Fig. 4C), with no diurnal variation in RH and air temperature (Fig. 4F).

The optimal site had higher mean light (167 ± 2 vs $136 \pm 1 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$, $P < 0.001$) and temperature (9.21 ± 0.03 vs $8.67 \pm 0.02 \text{ }^\circ\text{C}$, $P < 0.001$) than the suboptimal site, but lower RH (85.3 ± 0.1 vs $92.2 \pm 0.1\%$, $P < 0.001$).

Bark pH

Bark pH differed significantly between sampled categories of *Picea abies* branches ($P < 0.001$; Fig. 5). Branches with chlorolichens (*Parmelion*) were acidic ($\text{pH} = 3.98 \pm 0.11$), followed by the less acidic *Lobarion* branches with *Lobaria* and *Nephroma* species but without *E. pedicellatum* ($\text{pH} = 4.48 \pm 0.23$), whereas branches with a dominance of *E. pedicellatum* had the least acidic bark ($\text{pH} = 4.98 \pm 0.18$).

The water in the waterfall had a pH of 7.3 and a conductivity of $8.3 \mu\text{S cm}^{-1}$.

Hydration traits

Mean specific thallus mass (STM), a proxy of thallus thickness, of *E. pedicellatum* was $23.6 \pm 0.8 \text{ mg cm}^{-2}$. Internal ($\text{WHC}_{\text{internal}} = 58.1 \pm 2.3 \text{ mg H}_2\text{O cm}^{-2}$), external ($\text{WHC}_{\text{external}} = 60.1 \pm 2.1$), and total water holding capacity ($\text{WHC}_{\text{total}} = 118.2 \pm 3.5$) were highly significantly correlated to STM (Fig. 6A–C); the strongest regression was found for $\text{WHC}_{\text{internal}}$, the weakest for $\text{WHC}_{\text{external}}$. The thicker the thallus, the more water it held. Thallus dry mass (DM) was strongly related to thallus size ($0.4\text{--}10.7 \text{ cm}^2$; Fig. 6F). $\text{WHC}_{\text{external}}/\text{WHC}_{\text{internal}}$ -ratio ($0.4\text{--}3.3$) decreased with size (Fig. 6D), whereas STM, a proxy of thallus thickness, increased (Fig. 6E). Due to the connection between WHC and STM, $\text{WHC}_{\text{internal}}$ and $\text{WHC}_{\text{total}}$ were also strongly size-dependent.

Desiccation and light tolerance

Before the start of the experiment, F_v/F_m (dotted lines in Fig. 7) was higher in *Pectenium plumbea* than in *E. pedicellatum* ($P < 0.001$, one-way ANOVA). After the desiccation treatment in darkness, the subsequent hydration caused rapid recovery of F_v/F_m to the starting values in both species, although *P. plumbea* initially responded more slowly than *E. pedicellatum* (Fig. 7A & B). The medium light used during desiccation severely aggravated the photoinhibition, evidenced by the strong depression in F_v/F_m and

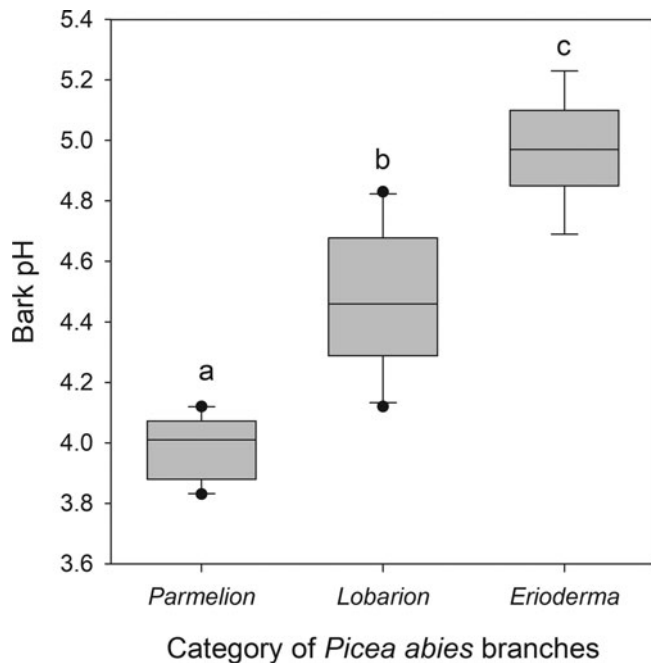


Fig. 5. Boxplot of bark pH in three categories of *Picea abies* branches classified due to their epiphytic vegetation: 1) *Parmelion* dominated by chlorolichens in the *Parmeliaceae* ($n=10$); 2) *Lobarion* dominated by cyano- and cephalolichens other than *Erioderma pedicellatum* ($n=10$); 3) *Erioderma*, epiphytic vegetation dominated by *E. pedicellatum* ($n=7$). Means with different letters significantly differed at $P < 0.05$ (Tukey HSD test); the one-way ANOVA showed a significant difference, $r_{\text{adj}}^2 = 0.829$, $P < 0.001$.

delayed recovery of both species (Fig. 7C & D). F_v/F_m after 48 h recovery, representing more lasting effects, was analyzed in a linear mixed model (Table 1; with estimates of fixed parameters given in Table 2). Box (i.e. sample container) was tested for as a random effect, and the full model including fixed and random factors accounted for slightly higher variation in F_v/F_m ($r_{\text{conditional}}^2 = 0.759$) than the fixed factors alone ($r_{\text{marginal}}^2 = 0.694$; Table 1). Nevertheless, after 48 h recovery, both light and humidity highly significantly affected F_v/F_m . The two species did not differ, but there was a weakly significant species \times light interaction ($P = 0.012$; Table 1), implying a slightly stronger adverse effect of light in *P. plumbea*. The highly significant light \times humidity interaction occurred because the hardest desiccation (0% relative humidity) had a much stronger impact in light than in darkness (Fig. 7, Table 1).

Photosynthetic responses to light and temperature

The CO_2 uptake for *E. pedicellatum* was high and became light saturated at 400 (10°C) and 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (20°C ; Fig. 8A). The light compensation point was 28 ± 3 and 63 ± 9 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, and dark respiration was 1.14 ± 0.08 and 1.49 ± 0.08 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$ at 10 and 20°C , respectively. There was no significant relationship between CO_2 uptake and thallus area ($4.45\text{--}12.5 \text{ cm}^2$). According to a repeated measures ANOVA (data not shown), temperature alone did not affect the CO_2 uptake. However, light and the light \times temperature interaction were highly significant, as was the random factor thallus ID.

Erioderma pedicellatum had a broad temperature optimum for photosynthesis (Fig. 8B). Only at 25°C was the CO_2 uptake significantly lower than at other studied temperatures. At 5°C , differences between individual responses were large, even after removing two

outliers. As the same thalli were measured at all temperatures, thallus ID was included as a random factor ($P = 0.021$) in a mixed effects model with temperature as a fixed factor ($r_{\text{adj}}^2 = 0.707$, $P < 0.001$).

CO_2 uptake during desiccation cycles

The desiccation cycles (Fig. 9) started at a hydration level of $98.5 \pm 7.0 \text{ mg H}_2\text{O cm}^{-2}$, slightly below $\text{WHC}_{\text{total}}$, implying substantial amounts of external water. At this stage, the CO_2 uptake was depressed to $35 \pm 2\%$ (total range 22–49%) of maximal levels. Optimal photosynthesis occurred at a water content of $51.3 \pm 3.1 \text{ mg H}_2\text{O cm}^{-2}$ ($\approx \text{WHC}_{\text{internal}}$, or at 280% water) that was reached after 39 ± 4 min of desiccation. The rather narrow phase of optimal water content peaked at slightly lower water contents than $\text{WHC}_{\text{internal}}$. The desiccation time needed for a fully saturated thallus to reach the optimal water content per thallus area (WC_A) for photosynthesis strongly increased with thallus size (Fig. 9, insert; $r_{\text{adj}}^2 = 0.815$, $P < 0.001$), indirectly evidenced by a shift of the curves (Fig. 9) to higher water contents from smaller to larger thalli. There was also a highly significant positive regression between the $\text{WHC}_{\text{internal}}$ and the optimal area-based water content for photosynthesis ($\text{WC}_A = 17.169 + 0.499 \times \text{WHC}_{\text{internal}}$; $r_{\text{adj}}^2 = 0.648$, $P < 0.001$). After maximal photosynthesis, CO_2 uptake rapidly declined with decreasing water content. When lichens had reached a water content of $7.9 \pm 0.8 \text{ mg H}_2\text{O cm}^{-2}$ (corresponding to $66 \pm 5\%$), CO_2 uptake was no longer measurable, and individual curves converged (Fig. 9) after a slower decline in CO_2 uptake in larger than in smaller thalli.

Discussion

Microclimate

Studied canopies dominated by *Erioderma pedicellatum* occurred in a unique habitat that combined strong solar radiation with high humidity after vernal snow melt raised the waterfall flow rate. This microclimatic shift ended the early dry spring during which ground inhabiting bryophytes were often dry, even in the morning. The following long period with c. 100% RH even during sunny days probably occurred because the higher water flow formed aerosols that crossed the canyon and partly reached the cluster of small trees with *E. pedicellatum* up on the steep slope opposite the waterfall. When the snow later disappeared, RH during the daytime declined on clear days and became more driven by solar radiation and temperature. However, the water flow appeared sufficient to saturate the air humidity almost every night and kept RH during the day higher in summer than in spring.

The higher humidity at the suboptimal compared to the optimal site suggests that water can be too much, even for hygrophilous cyanolichens, consistent with the observed bryophyte dominance on trees within the waterfall spray zone and with data showing that river regulations reducing the discharge of water can result in a great decrease in hygrophilous bryophytes and an increase in lichens (Odland *et al.* 1991). It is also consistent with the strong suprasaturation depression in *E. pedicellatum* (Fig. 9). The higher light at the optimal site probably improves CO_2 uptake by reducing external water and enables high photosynthetic rates in a species with high light compensation point and light saturation (Fig. 8A). The higher mean temperature at the optimal site during the growth season is closer to the presented temperature optimum for carbon gain in *E. pedicellatum* (c. $10\text{--}15^\circ\text{C}$) than the temperature at the suboptimal site.

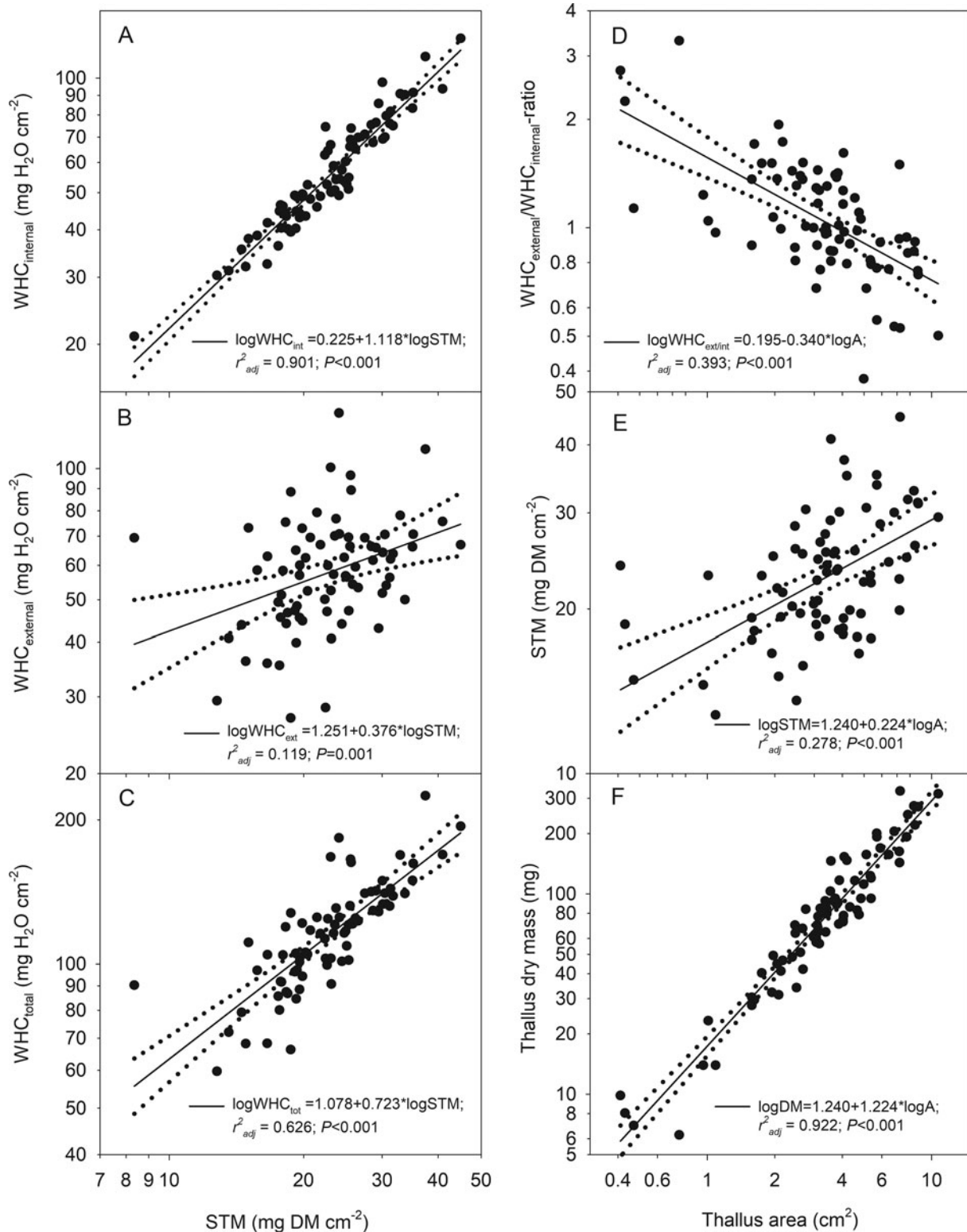


Fig. 6. Relationships between measures of water holding capacity (A, $WHC_{internal}$; B, $WHC_{external}$; C, WHC_{total} versus specific thallus mass (STM) and the size-dependency of $WHC_{external}/WHC_{internal}$ (D), STM (E), and thallus dry mass (F) in *Erioderma pedicellatum*. All axes are log-transformed. Regression equations (solid lines) with corresponding r^2_{adj} and P -level are given. Dotted lines indicate 95% confidence intervals.

Bark pH

Erioderma pedicellatum grew on branches with higher bark pH (4.98 ± 0.18) than usual for *P. abies* (pH = 3.9–4.2; Gauslaa &

Holien 1998). Conifer bark has been considered too acidic for *Lobarion* in parts of Europe previously influenced by acid rain (Rose 1988). *Lobarion* grows on *P. abies* branches with higher

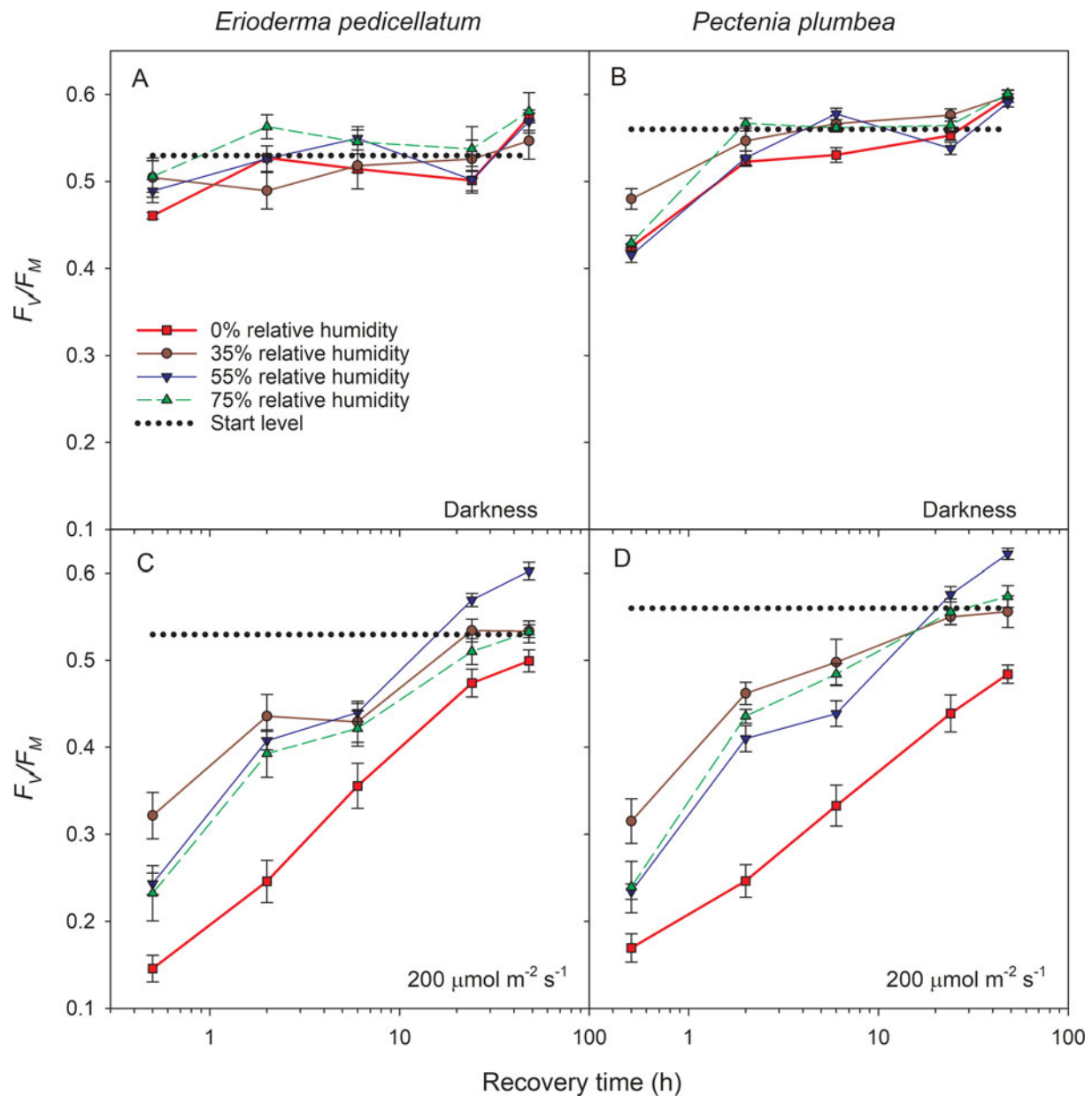


Fig. 7. Maximal PSII efficiency (F_v/F_m) kinetics during recovery (h) after 7 d exposure to four levels of relative humidity and two light levels (0 and $200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). Dotted lines represent the mean start level. Vertical bars indicate ± 1 standard error; *Erioderma pedicellatum* $n = 10$, *Pectenota plumbea* $n = 8$. In colour online.

pH than does *Parmelion*, a ubiquitous epiphytic community dominated by members of the *Parmeliaceae*, as shown in Norway (Gauslaa & Holien 1998) and British Columbia (Gauslaa & Goward 2012; Gauslaa *et al.* 2020). More specifically, bark supporting the *Lobarion* community is higher in base cations (Ca, Mg, K) and lower in Mn (Hauck & Spribille 2002; Gauslaa *et al.* 2021), and local factors such as soil pH and drip-zones from some tree species can modify the bark pH of *P. abies* (Gauslaa & Holien 1998; Goward & Arsenault 2000; Gauslaa *et al.* 2020). Faster growth in *Lobarion* species is associated with higher bark pH and base-cation availability (Gauslaa & Goward 2012, 2020; Bidussi *et al.* 2013b). Larsen & Rasmussen (2021) recently showed the importance of high bark pH for ascospore germination in the sexually reproducing *Xanthoria parietina*, which may also be the case for *E. pedicellatum* spores (Cornejo *et al.* 2016).

In Europe, *E. pedicellatum* was first found in boreal rainforests (Ahlner 1948) little affected by acidification, with a rainfall pH of 5.2 (Tørseth & Manø 1996). In North America, air pollution is considered a threat to *E. pedicellatum* (Richardson & Cameron 2004; Cameron *et al.* 2013a). In the past, acid rain threatened *Lobarion* communities by substantially reducing bark pH (Gauslaa 1995), and it has probably reduced suitable habitats for *E. pedicellatum* by depleting soils of cations, implying that bark and soil pH do not easily recover to preindustrial levels (Falkengren-Grerup 1986; Nilsson & Tyler 1995). Measured pH of *E. pedicellatum* branches (4.98) corresponds to the present rainfall pH (4.9) in Rendalen (Tørseth & Manø 1996).

It is not clear why epiphytic vegetation and associated bark pH varied within the site. Tree species associated with high bark pH were absent, such as *Populus tremula*, which could have enriched the local canopy throughfall in base cations (Goward & Arsenault

Table 1. Fixed effect omnibus tests computed by the linear mixed model for maximal PSII efficiency (F_w/F_m) measured after 48 h recovery in *Erioderma pedicellatum* and *Pectenium plumbea* after exposure to two light treatments (0 and 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) and four relative humidity treatments (0, 35, 55 and 75%). Box, that is containers of subsets of thalli during exposure, was treated as a random factor. Original data shown in Fig. 7.

	F	df	P
Species (S)	0.289	1, 103	0.592
Light (L)	30.093	1, 103	< 0.001
Humidity (H)	26.666	3, 104	< 0.001
S * L	6.578	1, 103	0.012
S * H	1.608	3, 103	0.192
L * H	22.216	3, 106	< 0.001

The full model including fixed and random factors accounted for slightly higher variation in F_w/F_m ($r^2_{\text{conditional}} = 0.759$) than the fixed factors alone ($r^2_{\text{marginal}} = 0.694$). The non-significant 3-way interaction was excluded. Three extreme outliers had been removed (standard residuals higher than 4.0 or lower than -4.0). Note: Satterthwaite method for degrees of freedom (the df column is as follows: df of the factor, df of the error).

2000; Gauslaa et al. 2020). Bark pH was possibly enriched by aerosols from the waterfall (pH = 7.3). However, the low conductivity in the river suggests low buffering capacity, and *Lobarion* branches on mossy trees in the waterfall spray zone had lower pH than host trees of *E. pedicellatum*. Local soil chemistry is important (Gauslaa et al. 2021); the steep rock shelf with the best host trees is likely to be a source of newly weathered minerals and temporarily upwelling groundwater.

Hydration traits

The strong regression between $\text{WHC}_{\text{internal}}$ versus STM confirms that thicker thalli hold more water as in other cyanolichens (Gauslaa & Solhaug 1998; Gauslaa & Coxson 2011; Gauslaa &

Arsenault 2020). The positive relationship between STM and size implies that growth and aging lead to increased thickness. Because STM is a strong predictor of $\text{WHC}_{\text{internal}}$ in lichens with a given photobiont group (Gauslaa & Coxson 2011), STM can be used to compare hydration traits among cyanolichens. A comparison of our size-dependent data for *E. pedicellatum* with those from Newfoundland (Gauslaa & Arsenault 2020) showed that our population had significantly higher STM (Fig. 10) and thus thicker thalli across all thallus sizes, evidenced by the non-overlapping 95% confidence intervals. The mean STM of Norwegian *E. pedicellatum* ($23.6 \pm 1.8 \text{ mg cm}^{-2}$) was 1.5 times higher than the values from Newfoundland (Gauslaa & Arsenault 2020), despite the slightly smaller mean thallus sizes in Rendalen. The STM of the Norwegian *E. pedicellatum* population was as high as that of *Pectenium plumbea* (Gauslaa & Solhaug 1998), evidenced by overlapping 95% confidence intervals for regression lines for STM versus area (data not shown). The *Pannariaceae* species (*Erioderma*, *Pectenium*) studied here have thereby significantly higher STM and thus higher water storage than previously examined cyanolichen members (*Lobaria scrobiculata*, *Pseudocyphellaria citrina*) of the *Lobariaceae* (Merinero et al. 2014).

Erioderma pedicellatum in Rendalen exclusively dominated branches (Reiso & Hofton 2006; Holien 2015) facing the sun in summer. With such high evaporative demands, dry mass should increase more than area (Bidussi et al. 2013a; Alam et al. 2015). By contrast, specimens on vertical trunks beneath a protecting canopy in Atlantic Canadian rainforests with frequent rain (Gauslaa & Arsenault 2020) probably experience longer periods with full turgor pressure that would promote hyphal elongation and thus area expansion. The high STM and corresponding $\text{WHC}_{\text{internal}}$ in the sun-exposed habitat can be considered an acclimation to maximize water storage and thus prolong hydration in sunny places, consistent with findings from the chlorolichen *Ramalina capitata* (Pintado et al. 1997).

Table 2. Fixed effects parameter estimates computed by the linear mixed model for maximal PSII efficiency (F_w/F_m) given in Table 1 for *Erioderma pedicellatum* and *Pectenium plumbea* after exposure to two light treatments, 0 (L0) and 200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (L1) and four relative humidity treatments (H; 0, 35, 55 and 75%).

Parameter	Effect	Estimate	SE	95% confidence interval		df	t	P
				Lower	Upper			
(Intercept)	(Intercept)	0.5738	0.0071	0.5599	0.5877	3.0	80.77	< 0.001
Species (S)	<i>Pectenium plumbea</i> (P) <i>Erioderma pedicellatum</i> (E)	0.0032	0.0060	-0.0085	0.0150	102.9	0.54	0.592
Light (L)	1-0	-0.0379	0.0069	-0.0514	-0.0243	102.6	-5.49	< 0.001
Humidity (H1)	35-0	0.0213	0.0060	0.0095	0.0332	102.9	3.53	< 0.001
Humidity (H2)	55-0	0.0640	0.0082	0.0480	0.0801	104.5	7.83	< 0.001
Humidity (H3)	75-0	0.0564	0.0079	0.0408	0.0719	102.9	7.10	< 0.001
S * L	P - E * 1-0	-0.0310	0.0121	-0.0547	-0.0073	102.9	-2.57	0.012
S * H1	P - E * 35-0	0.0157	0.0121	-0.0081	0.0394	102.9	1.30	0.198
S * H2	P - E * 55-0	0.0026	0.0156	-0.0281	0.0332	102.9	0.17	0.869
S * H3	P - E * 75-0	-0.0186	0.0159	-0.0497	0.0125	102.9	-1.17	0.244
L * H1	1-0 * 35-0	0.0468	0.0120	0.0195	0.0742	103.8	3.36	0.001
L * H2	1-0 * 55-0	0.1381	0.0171	0.1046	0.1717	104.7	8.06	< 0.001
L * H3	1-0 * 75-0	0.0786	0.0176	0.0441	0.1130	105.8	4.47	< 0.001

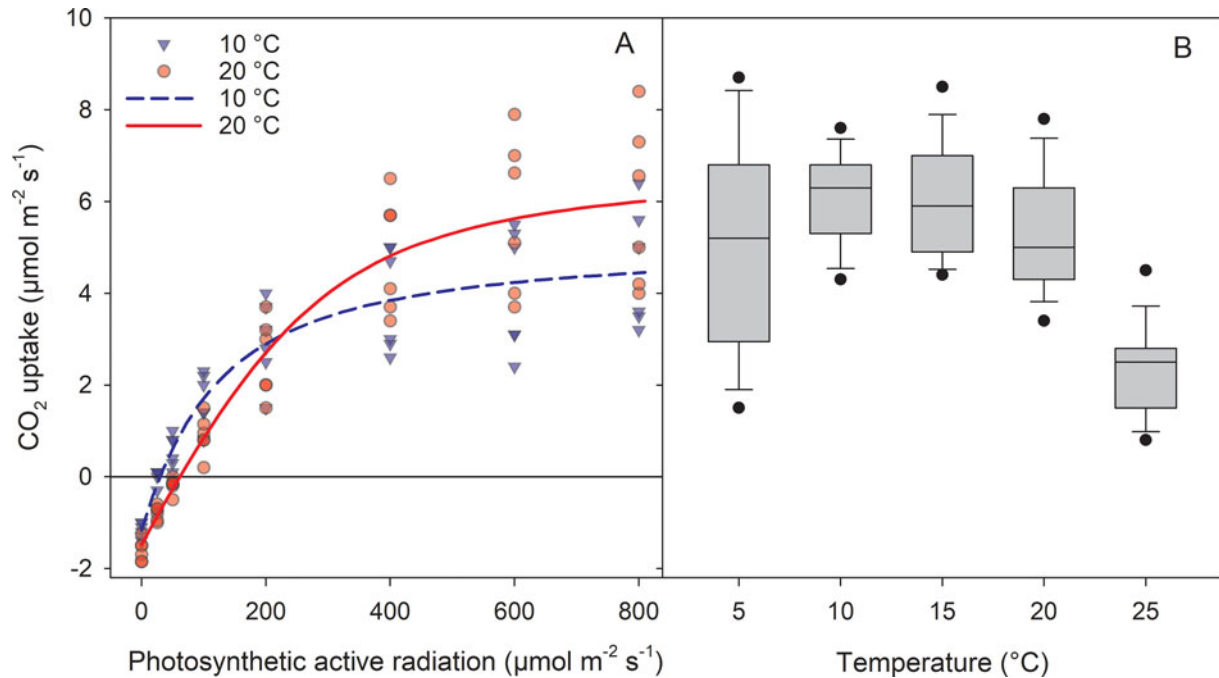


Fig. 8. A, light response curve of CO_2 uptake ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) at 10 and 20 °C and at increasing light levels ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) in six thalli of *Erioderma pedicellatum*. The lines represent mean CO_2 uptake at the two respective temperatures. Curves are estimated using Photosyn Assistant v. 1.1 (Parsons and Ogston, Dundee Scientific, Dundee, UK). Darker symbols represent overlapping values for more than one specimen. B, CO_2 uptake response to temperature treatments at 410 ppm CO_2 and 400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Only the mean at 25 °C significantly differed from the other means ($P < 0.05$; Tukey HSD test). $n = 15$, except for the 5 °C group ($n = 13$). In colour online.

Cyanolichens depend on liquid water for activation of photosynthesis (Lange & Kilian 1985; Lange *et al.* 1986). Nevertheless, continuous humid air over consecutive days slowly activates cyanolichen photosynthesis (Schlensog *et al.* 2000). Such conditions rarely occur in the field because drying normally occurs during a day without rain. Therefore, Schlensog *et al.* (2000) did not question the dependency of cyanolichens on liquid water as a general statement. However, the unique Rendalen habitat probably has sufficiently long humid periods to allow cyanolichen activation in humid air.

Desiccation and light tolerance

High light is an important stressor in many lichens, as reviewed by Beckett *et al.* (2021). Many lichens with green algae (cephalo- and chlorolichens) rapidly activate in humid air (Phinney *et al.* 2018; Ås Hovind *et al.* 2020) and are susceptible to longer exposures to high light when desiccated (Gauslaa & Solhaug 1996; Färber *et al.* 2014). Severe photoinhibition in light is often avoided in nature by cephalo- and chlorolichens because such lichens activate every humid morning (Lange 2003) when they can repair photoinhibitory damage that otherwise would accumulate. By contrast, cyanolichens tolerate a long-lasting combination of light and desiccation (Gauslaa *et al.* 2012), which is required due to their dependency on rarer occurrences of rain for activation (Lange *et al.* 1986). The rare *E. pedicellatum* seems to be no exception and follows other high light and desiccation tolerant old-forest cyanolichens such as *Lobaria scrobiculata*, *L. hallii*, *L. anomala* and *L. retigera* (Gauslaa *et al.* 2012). In contrast to our hypothesis, it even has a slightly higher tolerance to light and desiccation than the more common *P. plumbea*. The dry and sunny spring before snow melt starts lasted longer than the

seven days used in our experiment, and certainly implies a need for high light and desiccation tolerance.

In winter, *E. pedicellatum* was continuously shaded from direct sun, which may be important for reducing the potential of accumulation of reactive oxygen species during conditions with low photosynthesis due to desiccation or too low temperatures (Kranner *et al.* 2008; Beckett *et al.* 2021).

Photosynthetic responses to light and temperature

Erioderma pedicellatum has a broad optimum for carbon gain (5–20 °C), but a high light compensation point (28 and 63 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ at 10 and 20 °C, respectively). These high values, consistent with a Q_{10} for respiration of *c.* 2 (for example, see Lambers & Oliveira 2019), imply that the species is poorly adapted to shaded environments, in which respiration may consume much of the gained C. The clear reduction in light compensation at low temperatures probably contributes to its strong association with cool forests, consistent with its boreal distribution (Cameron *et al.* 2013a; Stehn *et al.* 2013; Holien 2015; Tagirdzhanova *et al.* 2019) and with a recorded mean temperature of 9.2 °C in Rendalen in the main growing season from late April to early October.

CO_2 uptake during desiccation cycles

Like other rainforest lichens (Lange *et al.* 1993), *E. pedicellatum* suffered substantially from suprasaturation when water-saturated, although not as severely as *P. plumbea* that had no net photosynthesis at maximal hydration (Gauslaa & Solhaug 1998). At high levels of water content, the CO_2 uptake of *E. pedicellatum* was 1/3 of maximal rates, attributed to blockage of CO_2 diffusive

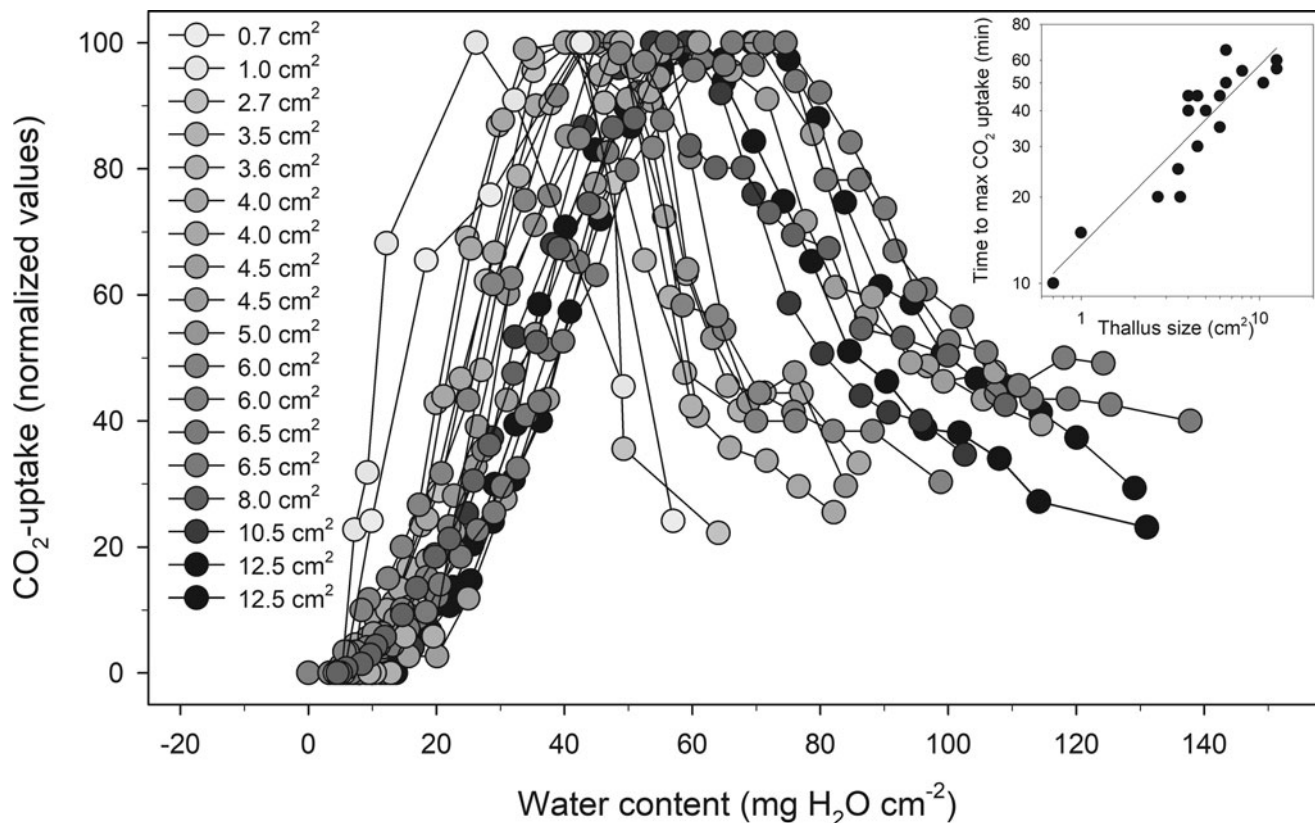


Fig. 9. CO₂ uptake (normalized values) versus water content per thallus area during desiccation cycles for 18 thalli of *Erioderma pedicellatum*, starting with shaken wet thalli. Insert: the relationship between thallus size and the time needed for a fully saturated thallus to reach the hydration that provides maximal CO₂ uptake rate; $\log(\text{time}) = 1.132 + 0.628 \times \log(\text{thallus area})$; $r_{\text{adj}}^2 = 0.815$, $P < 0.001$.

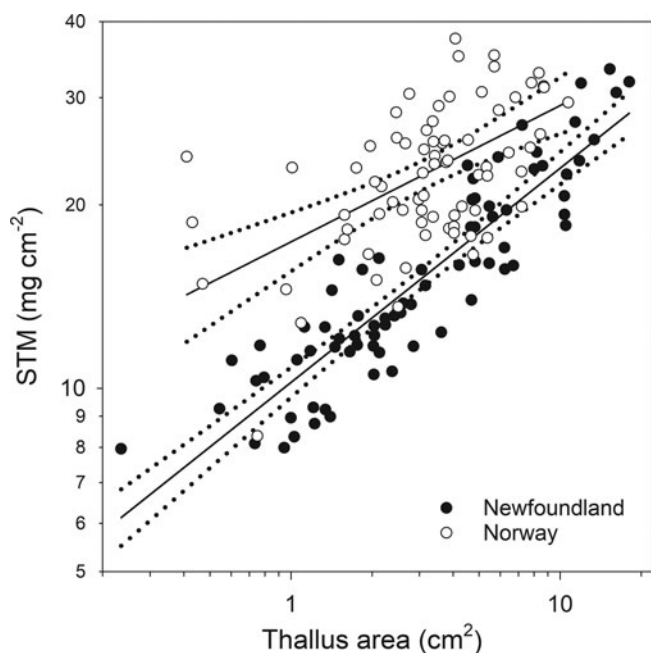


Fig. 10. The relationship between specific thallus mass (STM) and thallus area in *Erioderma pedicellatum* from Newfoundland ($\log(\text{STM}) = 1.010 + 0.3519 \times \log(\text{area})$; $r_{\text{adj}}^2 = 0.806$, $P < 0.001$; Gauslaa & Arsenault 2020) and Norway ($\log(\text{STM}) = 1.240 + 0.224 \times \log(\text{area})$; $r_{\text{adj}}^2 = 0.278$, $P < 0.001$), respectively. Solid lines show regressions and dotted lines indicate 95% confidence intervals.


pathways by excess water (Lange *et al.* 1996). Long-lasting excess hydration could be disadvantageous for *E. pedicellatum*, consistent with the sparser population at the wetter (suboptimal) site and the total lack of *E. pedicellatum* in trees within the main waterfall spray zone. Nevertheless, *E. pedicellatum*, unlike *P. plumbea*, had a positive CO₂ uptake when fully water-saturated, so it should not experience carbon loss when fully water-saturated *in situ*. Its optimal water content for CO₂ uptake (*c.* 280%) was higher than in *P. plumbea* (200%; Gauslaa & Solhaug 1998). There seems to be large internal population dynamics with new regeneration and simultaneous loss of broken branches with *E. pedicellatum*. The growth rate of *E. pedicellatum* is therefore likely to be high, suggesting that there are long hydration periods without suprasaturation.

Maximum photosynthesis in *E. pedicellatum* occurs at a $\text{WC}_A \approx \text{WHC}_{\text{internal}}$, consistent with documented patterns in chloro- and cephalolichens (Solhaug *et al.* 2021), and probably represents a general pattern in foliose lichens. Thalli with large $\text{WHC}_{\text{internal}}$ thus need more water to reach maximum photosynthesis, implying a trade-off between robust thalli with large $\text{WHC}_{\text{internal}}$ versus small flexible thalli with low $\text{WHC}_{\text{internal}}$.

Conclusion

Even with access to only a restricted number of experimental thalli, this study has provided new and important knowledge about the threatened *Erioderma pedicellatum*. The studied Norwegian *E. pedicellatum* population on sun-exposed branches

has higher WHC and STM than rainforest populations on trunks in Newfoundland, emphasizing the acclimation potential. The species not only depends on high light, high relative humidity and cool temperatures, but also tolerates well a rather extreme combination of desiccation and light. Since it also grows on *P. abies* branches with exceptionally high bark pH for this tree species, considerations of various unrelated habitat characteristics are important in management plans. CO₂ uptake was high, consistent with fast growth and pioneer-like occurrences on outer fragile portions of thin and dead spruce branches. The unusual combination of habitat characteristics may explain the rareness of the species despite its flexible hydration traits. The new knowledge gained, in combination with that established previously, should form a basis for successful conservation and for selecting suitable habitat for restoration and reintroduction by transplantation to secure the future survival of this critically endangered lichen.

Author ORCIDs.  Alexander R. Nilsson, 0000-0001-9282-8427; Knut Asbjørn Solhaug, 0000-0003-3368-5205; Yngvar Gauslaa, 0000-0003-2630-9682.

Competing Interests. The authors declare none.

References

- Ahlner S (1948) Utbredningstyper bland Nordiska barrträds-lav. *Acta Phytogeographica Suecica* **22**, 1–257.
- Ahlner S (1954) Värmlands märkligaste lav. In Magnusson NH and Curry-Lindahl K (eds), *Natur i Värmland*. Stockholm: Bokförlaget Svensk Natur, pp. 99–102.
- Alam MA, Gauslaa Y and Solhaug KA (2015) Soluble carbohydrates and relative growth rates in chloro-, cyano- and cephalolichens: effects of temperature and nocturnal hydration. *New Phytologist* **208**, 750–762.
- Asplund J and Wardle DA (2017) How lichens impact on terrestrial community and ecosystem properties. *Biological Reviews* **92**, 1720–1738.
- Barkman JJ (1958) *Phytosociology and Ecology of Cryptogamic Epiphytes*. Assen: van Gorcum.
- Beckett RP, Minibayeva F, Solhaug KA and Roach T (2021) Photoprotection in lichens: adaptations of photobionts to high light. *Lichenologist* **53**, 21–33.
- Bidussi M, Gauslaa Y and Solhaug KA (2013a) Prolonging the hydration and active metabolism from light periods into nights substantially enhances lichen growth. *Planta* **237**, 1359–1366.
- Bidussi M, Goward T and Gauslaa Y (2013b) Growth and secondary compound investments in the epiphytic lichens *Lobaria pulmonaria* and *Hypogymnia occidentalis* transplanted along an altitudinal gradient in British Columbia. *Botany* **91**, 621–630.
- Björk CR, Goward T and Spribille T (2009) New records and range extensions of rare lichens from waterfalls and sprayzones in inland British Columbia, Canada. *Evansia* **26**, 219–224.
- Büdel B, Becker U, Porembski S and Barthlott W (1997) Cyanobacteria and cyanobacterial lichens from inselbergs of the Ivory Coast, Africa. *Botanica Acta* **110**, 458–465.
- Cameron R (2009) Are non-native gastropods a threat to endangered lichens? *Canadian Field-Naturalist* **123**, 169–171.
- Cameron R, Goudie I and Richardson D (2013a) Habitat loss exceeds habitat regeneration for an IUCN flagship lichen epiphyte: *Erioderma pedicellatum*. *Canadian Journal of Forest Research (Revue Canadienne de Recherche Forestière)* **43**, 1075–1080.
- Cameron RP, Neily T and Clapp H (2013b) Forest harvesting impacts on mortality of an endangered lichen at the landscape and stand scales. *Canadian Journal of Forest Research (Revue Canadienne de Recherche Forestière)* **43**, 507–511.
- Colesie C, Green TGA, Raggio J and Büdel B (2016) Summer activity patterns of Antarctic and high alpine lichen-dominated biological soil crusts – similar but different? *Arctic, Antarctic and Alpine Research* **48**, 449–460.
- Cornejo C, Nelson PR, Stepanchikova I, Himelbrant D, Jørgensen PM and Scheidegger C (2016) Contrasting pattern of photobiont diversity in the Atlantic and Pacific populations of *Erioderma pedicellatum* (Pannariaceae). *Lichenologist* **48**, 275–291.
- Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* **89**, 984–994.
- Ellis CJ, Asplund J, Benesperi R, Branquinho C, Di Nuzzo L, Hurtado P, Martínez I, Matos P, Nascimbene J, Pinho P, *et al.* (2021) Functional traits in lichen ecology: a review of challenge and opportunity. *Microorganisms* **9**, 766.
- Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Bjorkman AD, Callaghan TV, Collier LS, Cooper EJ, Cornelissen JHC, Day TA, *et al.* (2012) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* **15**, 164–175.
- Falkengren-Grerup U (1986) Soil acidification and vegetational changes in deciduous forest in southern Sweden. *Oecologia* **70**, 339–347.
- Färber L, Solhaug KA, Esseen P-A, Bilger W and Gauslaa Y (2014) Sunscreening fungal pigments influence the vertical gradient of pendulous lichens in boreal forest canopies. *Ecology* **95**, 1464–1471.
- Gauslaa Y (1985) The ecology of *Lobaria pulmonaria* and *Parmelion caperatae* in *Quercus* dominated forests in south-west Norway. *Lichenologist* **17**, 117–140.
- Gauslaa Y (1995) The *Lobaria*, an epiphytic community of ancient forests threatened by acid rain. *Lichenologist* **27**, 59–76.
- Gauslaa Y (2014) Rain, dew, and humid air as drivers of lichen morphology, function and spatial distribution in epiphytic lichens. *Lichenologist* **46**, 1–16.
- Gauslaa Y and Arsenault A (2020) The cyanolichens *Erioderma pedicellatum* and *Coccocarpia palmicola* need much more than a dewfall to fill their water holding capacity. *Flora* **269**, 151648.
- Gauslaa Y and Coxson D (2011) Interspecific and intraspecific variations in water storage in epiphytic old forest foliose lichens. *Botany* **89**, 787–798.
- Gauslaa Y and Goward T (2012) Relative growth rates of two epiphytic lichens, *Lobaria pulmonaria* and *Hypogymnia occidentalis*, transplanted within and outside of *Populus* dripzones. *Botany* **90**, 954–965.
- Gauslaa Y and Goward T (2020) Melanic pigments and canopy-specific elemental concentration shape growth rates of the lichen *Lobaria pulmonaria* in unmanaged mixed forest. *Fungal Ecology* **47**, 100984.
- Gauslaa Y and Holien H (1998) Acidity of boreal *Picea abies*-canopy lichens and their substratum, modified by local soils and airborne acidic depositions. *Flora* **193**, 249–257.
- Gauslaa Y and Solhaug KA (1996) Differences in the susceptibility to light stress between epiphytic lichens of ancient and young boreal forest stands. *Functional Ecology* **10**, 344–354.
- Gauslaa Y and Solhaug KA (1998) The significance of thallus size for the water economy of the cyanobacterial old-forest lichen *Degelia plumbea*. *Oecologia* **116**, 76–84.
- Gauslaa Y, Coxson DS and Solhaug KA (2012) The paradox of higher light tolerance during desiccation in rare old forest cyanolichens than in more widespread co-occurring chloro- and cephalolichens. *New Phytologist* **195**, 812–822.
- Gauslaa Y, Solhaug KA and Longinotti S (2017) Functional traits prolonging photosynthetically active periods in epiphytic cephalolichens during desiccation. *Environmental and Experimental Botany* **141**, 83–91.
- Gauslaa Y, Goward T and Pypker T (2020) Canopy settings shape elemental composition of the epiphytic lichen *Lobaria pulmonaria* in unmanaged conifer forests. *Ecological Indicators* **113**, 106294.
- Gauslaa Y, Goward T and Asplund J (2021) Canopy throughfall links canopy epiphytes to terrestrial vegetation in pristine conifer forests. *Fungal Ecology* **52**, 101075.
- Goward T and Arsenault A (2000) Cyanolichen distribution in young unmanaged forests: a dripzone effect? *Bryologist* **103**, 28–37.
- Greenspan L (1977) Humidity fixed points of binary saturated aqueous solutions. *Journal of Research of the National Bureau of Standards – A, Physics and Chemistry* **81**, 89–96.
- Hauck M and Spribille T (2002) The Mn/Ca and Mn/Mg ratios in bark as possible causes for the occurrence of *Lobaria* lichens on conifers in the dripzone of *Populus* in western North America. *Lichenologist* **34**, 527–532.

- Holien H** (2015) Fagrunnlag til handlingsplan for fire lavarter i boreal regnskog. *Høgskolen i Nord-Trøndelag Utredning* **177**, 1–59.
- Holien H and Tønsberg T** (1996) Boreal regnskog i Norge - habitater for trøndelagselementets lavarter. *Blyttia* **54**, 157–177.
- Honegger R** (2003) The impact of different long-term storage conditions on the viability of lichen-forming ascomycetes and their green algal photobiont, *Trebouxia* spp. *Plant Biology* **5**, 324–330.
- IUCN** (2021) *The IUCN Red List of Threatened Species*. Version 2021-1. [WWW resource] URL <https://www.iucnredlist.org/> [Accessed 8 April 2021].
- Jørgensen PM** (1990) Trønderlav (*Erioderma pedicellatum*) – Norges mest gåtefulle plante? *Blyttia* **48**, 119–123.
- Jørgensen PM** (2000) Survey of the lichen family *Pannariaceae* on the American continent, north of Mexico. *Bryologist* **103**, 670–704.
- Kranner I, Beckett RP, Hochman A and Nash TH, III** (2008) Desiccation-tolerance in lichens: a review. *Bryologist* **111**, 576–593.
- Lambers H, Oliveira RS** (2019) Photosynthesis, respiration, and long-distance transport: respiration. In *Plant Physiological Ecology*. Cham, Switzerland: Springer International, pp. 115–172.
- Lang SI, Cornelissen JHC, Shaver GR, Ahrens M, Callaghan TV, Molau U, ter Braak CJF, Hölzer A and Aerts R** (2012) Arctic warming on two continents has consistent negative effects on lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology* **18**, 1096–1107.
- Lange OL** (1969) Die funktionellen Anpassungen der Flechten an die ökologischen Bedingungen arider Gebiete. *Berichte der Deutschen Botanischen Gesellschaft* **82**, 3–22.
- Lange OL** (2003) Photosynthetic productivity of the epilithic lichen *Lecanora muralis*: long-term field monitoring of CO₂ exchange and its physiological interpretation: III. Diel, seasonal, and annual carbon budgets. *Flora* **198**, 277–292.
- Lange OL and Kilian E** (1985) Reaktivering der Photosynthese trockener Flechten durch Wasserdampfaufnahme aus dem Luftraum: Artsspezifisch unterschiedliches Verhalten. *Flora* **176**, 7–23.
- Lange OL, Kilian E and Ziegler H** (1986) Water vapor uptake and photosynthesis in lichens: performance differences in species with green and blue-green algae as photobionts. *Oecologia* **71**, 104–110.
- Lange OL, Büdel B, Heber U, Meyer A, Zellner H and Green TGA** (1993) Temperate rainforest lichens in New Zealand: high thallus water content can severely limit photosynthetic CO₂ exchange. *Oecologia* **95**, 303–313.
- Lange OL, Green TGA, Reichenberger H and Meyer A** (1996) Photosynthetic depression at high thallus water content in lichens: concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal *Peltigera* species. *Botanica Acta* **109**, 43–50.
- Lange OL, Belnap J and Reichenberger H** (1998) Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO₂ exchange. *Functional Ecology* **12**, 195–202.
- Lange OL, Büdel B, Meyer A, Zellner H and Zotz G** (2000) Lichen carbon gain under tropical conditions: water relations and CO₂ exchange of three *Leptogium* species of a lower montane rainforest in Panama. *Flora* **195**, 172–190.
- Larsen HME and Rasmussen HN** (2021) Bark extract influence on spore germination in corticolous lichen *Xanthoria parietina* in vitro. *Mycological Progress* **20**, 313–323.
- Merinero S, Hilmo O and Gauslaa Y** (2014) Size is a main driver for hydration traits in cyano- and cephalolichens of boreal rainforest canopies. *Fungal Ecology* **7**, 59–66.
- Moen A** (1999) *National Atlas of Norway: Vegetation*. Hønefoss: Norwegian Mapping Authority.
- Nilsson SI and Tyler G** (1995) Acidification-induced chemical changes of forest soils during recent decades – a review. *Ecological Bulletins* **44**, 54–64.
- NVE** (2020) *Tegninga*. [WWW resource] URL <https://www.nve.no/vann-og-vassdrag/vassdragsforvaltning/verneplan-for-vassdrag/innlandet/002-22-tegninga/> [Accessed 16 November 2021].
- Odland A, Birks HH, Botnen A, Tønsberg T and Vevle O** (1991) Vegetation change in the spray zone of a waterfall following river regulation in Aurland, Western Norway. *Regulated Rivers: Research and Management* **6**, 147–162.
- Palmqvist K** (2000) Carbon economy in lichens. *New Phytologist* **148**, 11–36.
- Penn CJ and Camberato JJ** (2019) A critical review on soil chemical processes that control how soil pH affects phosphorus availability to plants. *Agriculture* **9**, 120.
- Phinney NH, Solhaug KA and Gauslaa Y** (2018) Rapid resurrection of chlorolichens in humid air: specific thallus mass drives rehydration and reactivation kinetics. *Environmental and Experimental Botany* **148**, 184–191.
- Phinney NH, Solhaug KA and Gauslaa Y** (2019) Photobiont-dependent humidity threshold for chlorolichen photosystem II activation. *Planta* **250**, 2023–2031.
- Pintado A, Valladares F and Sancho LG** (1997) Exploring phenotypic plasticity in the lichen *Ramalina capitata*: morphology, water relations and chlorophyll content in north- and south-facing populations. *Annals of Botany* **80**, 345–353.
- Rasband WS** (2014) *ImageJ*. US National Institutes of Health. [WWW resource] URL <http://imagej.nih.gov/ij/>
- Reiso S and Hofton TH** (2006) Trønderlav *Erioderma pedicellatum* og fossefjelllav *Fuscopannaria confusa* funnet i Hedmark. *Blyttia* **64**, 83–88.
- Richardson DHS and Cameron RP** (2004) Cyanolichens: their response to pollution and possible management strategies for their conservation in northeastern North America. *Northeastern Naturalist* **11**, 1–22.
- Richardson SJ, Peltzer DA, Allen RB, McGlone MS and Parfitt RL** (2004) Rapid development of phosphorus limitation in temperate rainforest along the Franz Josef soil chronosequence. *Oecologia* **139**, 267–276.
- Rose F** (1988) Phytogeographical and ecological aspects of *Lobaria* communities in Europe. *Botanical Journal of the Linnean Society* **96**, 69–79.
- Sancho LG, de la Torre R, Horneck G, Ascaso C, de los Rios A, Pintado A, Wierzbos J and Schuster M** (2007) Lichens survive in space: results from the 2005 LICHENS experiment. *Astrobiology* **7**, 443–454.
- Scheidegger C (Lichen Specialist Group)** (2003) *Erioderma pedicellatum*. *The IUCN Red List of Threatened Species*. eT43995A10839336 [WWW resource] URL <http://dx.doi.org/10.2305/IUCN.UK.2003.RLTS.T43995A10839336.en>
- Schlenog M, Schroeter B and Green TGA** (2000) Water dependent photosynthetic activity of lichens from New Zealand: differences in the green algal and the cyanobacterial thallus parts of photosymbiodemes. *Bibliotheca Lichenologica* **75**, 149–160.
- Solhaug KA, Asplund J and Gauslaa Y** (2021) Apparent electron transport rate – a non-invasive proxy of photosynthetic CO₂ uptake in lichens. *Planta* **253**, 14.
- Spruille T** (2018) Relative symbiont input and the lichen symbiotic outcome. *Current Opinion in Plant Biology* **44**, 57–63.
- Stehn SE, Nelson PR, Roland CA and Jones JR** (2013) Patterns in the occupancy and abundance of the globally rare lichen *Erioderma pedicellatum* in Denali National Park and Preserve, Alaska. *Bryologist* **116**, 2–14.
- Stofer S, Bergamini A, Aragón G, Carvalho P, Coppins BJ, Davey S, Dietrich M, Farkas E, Kärkkäinen K, Keller C, et al.** (2006) Species richness of lichen functional groups in relation to land use intensity. *Lichenologist* **38**, 331–353.
- Tagirdzhanova G, Stepanchikova IS, Himelbrant DE, Vyatkina MP, Dyomina AV, Dirksen VG and Scheidegger C** (2019) Distribution and assessment of the conservation status of *Erioderma pedicellatum* in Asia. *Lichenologist* **51**, 575–585.
- Tønsberg T, Gauslaa Y, Haugan R, Holien H and Timdal E** (1996) The threatened macrolichens of Norway – 1995. *Sommerfeltia* **23**, 1–283.
- Tørseth K and Manø S** (1996) *Overvåkning av langtransportert forurenset luft og nedbør. Atmosfærisk tilførsel*, 1996. NILU OR 33/97. Kjeller: Norwegian Institute of Air Research.
- Ås Hovind AB, Phinney NH and Gauslaa Y** (2020) Functional trade-off of hydration strategies in old forest epiphytic cephalolichens. *Fungal Biology* **124**, 903–913.