Norwegian University
of Life Sciences

**Master's Thesis 2021 60 ECTS**
The Department of Ecology and Natural Resource

# *Erioderma pedicellatum*: An ecophysiological study of a globally threatened pioneer lichen on thin spruce branches in old forests

Alexander Ruhs Nilsson
Master of Science in Natural Resource Management

**Acknowledgements**

I would like to thank Yngvar Gauslaa and Knut Asbjørn Solhaug for great guidance through this thesis. It has been a true pleasure and a privilege to work with them. I would also like to thank Björn Nordén for originally initiating the project. Thanks to Vinay Nannuru for statistical advice and thanks to Inga Haugdahl Solberg for reading trough the final version of the thesis and to Erlend Ekeland for help with general technical issues. Thanks to Vemund Opedal, Anders Gunnar Helle and Kåre Lye for help with the field work at Tegningfallet.

Ås, April 30th 2021

Alexander Ruhs Nilsson

**Abstract**

Lichen extinction occurs at a fast rate due to human activity, and species yet to be discovered are likely go extinct every year. Many species close to extinction may still be rescued by conservation management based on an understanding of species-specific habitat requirements and physiological responses. *Erioderma pedicellatum* is close to extinction and only known at a few sites world-wide. To prevent this species from going extinct, we need to know its ecophysiological responses and why it is rare. At its last remaining site in Europe, Tegningfallet in Norway, a spatially restricted population of 1500-2000 thalli dominate the epiphytic vegetation in a few *Picea abies* trees in a canyon with a waterfall. Microclimatic conditions at the site show that *E. pedicellatum* demands high-light conditions in combination with high relative humidity and relatively cool temperatures. It further requires unusually high pH branches of *Picea abies*. *Erioderma pedicellatum* has a high $CO_2$ and $O_2$-uptake under suitable conditions, experiences suprasaturation depression of photosynthesis at high water contents, and its growth rate was reduced with increasing thallus size. Too humid conditions appeared harmful for the species. *Erioderma pedicellatum* tolerates desiccation in combination with light well, but the population at Tegningfallet is shaded from direct sun light during the entire winter. Optimum temperature range for photosynthesis occurred at 10-15 °C, temperatures ≥25 °C significantly reduced carbon gain. Morphology and functional hydration traits significantly differed between the Tegningfallet and Newfoundland populations, in line with the different hydration sources in these two habitats. Understanding why and how *E. pedicellatum* can exist at a site such as Tegningfallet is essential for understanding how we can prevent this species from going extinct, and the presented results should encourage new management action plans and further research at the other remaining sites of the species. Methods used in this thesis could also be applicable for ecological understanding of other lichen species at risk of extinction.

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# 1. Introduction

Lichens, the intricate symbiotic association between algae and fungi (Spribille, 2018), represent a large part of biodiversity in many terrestrial ecosystems. Lichens are able to colonise habitats and fill niches in which plants are less successful (Chen et al., 2000). They are particularly important for biodiversity and ecosystem functioning at high latitudes and elevations. Lichens are found in most terrestrial ecosystems on Earth, and often in what we consider extreme environments. Many lichens tolerate more extreme desiccation and temperatures than other organisms (Sancho et al., 2007; Shukla et al., 2017). On the other hand, lichens are rather vulnerable to environmental changes, and the one threat above all is shown to be human-induced area change and expansion (Stofer et al., 2006), which may lead to large losses of both species and functional diversity.

Lichens respond to their environment with a wide range of functional traits and increase by that the functional diversity in terrestrial ecosystems (Ellis et al., 2021). Several of these functional traits relate to water uptake. Hydrology and humidity are highly variable in terrestrial ecosystems depending on temporal and spatial scales affected by landscape, topography and climate (Gauslaa, 2014). Traits related to water uptake differentiate lichens from higher plants, by lacking organs for water uptake regulation such as roots and stomata. This opens up for utilization of a broad spectrum of water sources such as rain, dew and humid air (Gauslaa, 2014). By utilizing this broad spectrum of water sources, lichens can colonize sites inaccessible for higher plants. Some lichens are capable of colonising Earth's most extreme sites when it comes to water availability, from the driest deserts to the most humid rain forests (Lange et al., 1991; 1993b; 1994; 1998; 2000). Other diversity-driving factors include light, temperature, nutrient availability, and substratum pH.

Light affects water storage in lichens, as strong light increases the desiccation rate in contrast to low light levels (Gaulsaa et al., 2017). Light can also cause irreversible damage to lichens, especially high solar radiation in combination with drought (Gauslaa & Solhaug, 1996, 1999; Kranner et al., 2008; Gauslaa et al., 2012). However, light is also essential for photosynthesis and thus carbon balance and growth, but only when the lichen is wet (Palmqvist, 2000). Carbon balance is again affected by internal physiological processes responding to for instance temperature. Higher temperatures increase metabolic rates but increase respiration more than $CO_2$-uptake (Lange & Green, 2006). Conversely, lower temperatures are known to reduce

respiratory rates, and temperature is by that an important explanatory factor for lichen species distribution (Lange et al., 1994; Zotz et al., 1998).

Nevertheless, Bidussi et al. (2013b) interestingly found evidence suggesting that pH was a stronger predictor for lichen growth than temperature. pH is an important factor because the availability of nutrients to a large degree follows pH (Richardson et al., 2004). It is well documented that some lichen species require substrates with higher pH than others (Gauslaa, 1985; Rose, 1988; Gauslaa & Holien, 1998). pH is largely determined by environmental factors such as air-borne depositions, geology, and topography, but bark pH is also known to differ among tree species. Due to large tree species-specific differences in bark pH, tree species often host distinctly different lichen communities (Rose, 1988).

Interacting factors affecting lichen ecology often complicate the understanding of species distribution. The symbiotic association of lichens further complicates the picture, as lichens can contain either green algae (chlorolichens), cyanobacteria (cyanolichens), or a combination of both (cephalolichens) as their photobiont. Within these major groups, specific photobiont families again respond differently to e.g., humid air (Phinney et al., 2019), which further illustrates the great functional diversity within lichens. After decades of ecological and physiological lichen research, we can now at least to some extent explain larger distribution patterns for some groups of lichens (Phinney et al., 2021). However, there are still knowledge-gaps, making conservation of rare species challenging. Many lichens are today red-listed on the global red list of species and close to extinction (IUCN, 2021). Several endangered species are old forest associated, and one of the flagship species for lichens is the critically endangered *Erioderma pedicellatum* (Hue) P.M. Jørg. (Pannariaceae) (Scheidegger, 2003).

**Fig. 1** Dry thalli of *Erioderma pedicellatum* on sun-exposed branches of Norway Spruce at Tegningfallet, Rendalen, Eastern Norway 18.05.2020.

*Erioderma pedicellatum* is restricted to a few sites in four boreal areas of the world (Alaska, Atlantic Canada, Scandinavia, and Kamchatka; Fig. 2). This foliose cyanolichen was first described by Hue in 1911 in New Brunswick, Canada (Jørgensen, 2000). Ahlner (1948) reported it as new to Europe from a few sites in Nord Trøndelag (Norway) in the summer of 1938, and later from Värmland in Sweden in 1941. The populations in Trøndelag consisted of a few specimens only, whereas the Värmland population was described as rich (Ahlner, 1948). The populations of Scandinavia have until recent years been considered extinct (Holien, 2016), and it has also been reported a strong decline in other known populations of the world (Scheidegger, 2003). Population decline has been explained by land-use change by human activities such as logging (Cameron et al., 2013b; Tagirdzhanova et al., 2019) and air pollution (Richardson & Cameron, 2004), but forest fires (Tagirdzhanova et al., 2019) and gastropod grazing (Cameron, 2009) have also been mentioned as adverse factors. However, as new populations recently have been discovered in northwestern America and northeastern Asia the situation has now improved, yet is still considered critical (Stehn et al., 2013; Cameron et al., 2013a; Holien, 2016; Tagirdzhanova et al., 2019; Gauslaa & Arsenault, 2020).

In Europe, a new population was recently found in Rendalen (southeastern Norway), in a canyon with the waterfall Tegningfallet (Reiso, 2015). This population was at first assumed to only contain a couple thalli (Reiso, 2015), but during later visits to the site, it was estimated to host approximately 1500-2000 thalli (Björn Nordén, pers. communication), and thus represents the main currently known European population (Holien, 2016). However, the ecology of the species is still poorly known, and physiological studies are lacking, except Gauslaa & Arsenault (2020) which quantified its water-storage traits in Newfoundland. Effective conservation is therefore still challenging, and conservation management is left with few other options than creating nature reserves and conserving the populations from human activity. *Erioderma pedicellatum* is a species highly relevant for transplantation where populations are rich, as at Tegningfallet. However, we have not enough knowledge about the species requirements to identify suitable habitats for transplantation.

**Fig. 2** Global distribution of *Erioderma pedicellatum* per. 23.04.2021. Map downloaded from GBIF. The Asian population (Tagirdzhanova et al., 2019) was added to the map as it was missing in GBIF.

With the high risk of extinction and the large knowledge-gaps regarding *E. pedicellatum*, the aim of this thesis is to gain new knowledge about this species that has received little experimental attention. The rareness of the species has hardly allowed collection for experiments. However, at Tegningfallet, branches with many thalli fall to the ground every year from the large epiphytic population (A. R. Nilsson; pers. observation, 2019, 2020). The seasonal litter supplies of healthy specimens allow for collection without reducing the population size in the canopy. *Pectenia plumbea* (Light.) P.M. Jørg. & P. James, is another old forest associated cyanolichen with known large demands for humidity. In contrast to the boreal *E. pedicellatum*, *P. plumbea* is a frequent and more temperate Pannariaceae species that was collected as a

common reference species in some experiments as a contrast to the markedly rarer yet morphologically rather similar *E. pedicellatum*.

Through physiological experiments, basal data can be gained on ecological preferences, and in recent decades there has been a rapid development of both methods and technology within the field of lichen ecophysiology. Gas analysers with custom cuvettes for lichen and mosses now allow for non-destructive carbon flux measurements at different light, temperatures, and $CO_2$ levels (Sancho et al., 2020). Chlorophyll fluorescence imaging is another powerful method that enables interesting experimental setups and allows for rapid measurements of the same thalli at different times (Phinney et al., 2018; Ås Hovind et al., 2020). Growth chambers were recently shown to be useful tools for ecophysiological lichen experiments, as they give reliable and strong data, as well as the opportunity to study how various functional traits affect growth rate, which is a good proxy for ecological fitness (Bidussi et al., 2013a; Alam et al., 2015; Gauslaa et al., 2016). Portable climate stations and software analysing hemispherical photos have also opened for detailed data recording of microclimatic conditions (Bidussi et al., 2015).

Few studies aim to survey a broad spectrum of ecological traits for a species. However, to gain a better picture of a species' ecology, knowledge about diverse functional traits is essential. Sancho et al. (2020) showed that such data gain was achievable, and such studies are highly valuable for conservation management. With this, I aim to survey water-storage traits, growth rates, pH requirements, desiccation tolerance for *E. pedicellatum* and report microclimatic conditions for its habitat at Tegningfallet. The aim of this thesis is to investigate the ecophysiology of *E. pedicellatum* and to survey how the species can exist at Tegningfallet, a site very different from the other known *E. pedicellatum* sites of the world. In the following paragraphs, I will present some background for the study.

As Gauslaa & Arsenault (2020) already quantified water-storage traits such as specific thallus mass (STM) and water holding capacity (WHC) for the Newfoundland population of *E. pedicellatum,* it is of interest to compare these traits with those for the Tegningfallet population due to their different growth substrata and habitats. The Newfoundland population grow on trunks of Balsam Fir in rain forests, while at Tegningfallet, *E. pedicellatum* exclusively grow on Norway Spruce branches in a dry macroclimate, but with local humidity supplies from a waterfall. More specifically, I want to test if the hydration traits WHC and STM differ between thalli in a rain-influenced site and thalli in a site with high humidity, but few large water droplets. Such traits indicate water storage capacity and may point to whether and to what degree a lichen specimen relies on rain, fog or humid air as water source, as reviewed by

Gauslaa (2014). As WHC corresponds to mm $H_2O$, WHC indicates how much $H_2O$ is required to fill the water storage of the studied organism, and is therefore highly useful when studying how a species utilizes water sources in the environment (Gauslaa, 2014).

Furthermore, photosynthetic light response curves are useful for determining optimal light conditions for a species and can efficiently be gained through lab experiments with gas analysers and oxygen-electrodes. Specifically, I want to test if *E. pedicellatum* has a high photosynthesis under high-light conditions, as at Tegningfallet which is highly light exposed. Temperature dependency of photosynthesis together with measurements during a full desiccation cycle will also be tested. The hypothesis is that an optimum temperature range for photosynthesis should be below 20 °C and that an optimum water content for photosynthesis should be close to $WC_{blotting}$.

Being a member of the Pannariaceae family, *E. pedicellatum* should belong to the Lobarion community dominated by cyano- and cephalolichens, which depends on substrates with relatively high pH (Gauslaa, 1985) and as *E. pedicellatum* habitat descriptions are often characterised with a rich flora dominated by larger herbs and grasses (Holien, 2016), a demand for a high pH is expected. I therefore hypothesise that *E. pedicellatum* demands spruce twigs with higher pH than usual.

Because *E. pedicellatum* is rare and apparently restricted to very humid sites, a desiccation tolerance experiment is designed to test its tolerance of exposure to low relative humidities in combination with light, an often devastating combination for old forest lichens (Gauslaa et al., 2012). On the other hand, as previously shown by Gauslaa & Solhaug (1996), cyanolichens are rather desiccation tolerate. *Pectenia plumbea* will be included in the latter experiment to compare responses between the two species. The hypothesis is that *E. pedicellatum* is rather desiccation tolerant at Tegningfallet, as its growth site is drought exposed.

At last, a growth chamber experiment in different temperature regimes will be conducted to test growth responses at different temperature treatments. This to test if *E. pedicellatum* successfully grows in the lab, to find an optimum temperature range for carbon gain and to compare results from the carbon uptake and $O_2$-evolution experiments. Whether a species has a rapid or slow growth rate is also useful information for management actions. Since *E. pedicellatum* exclusively grow on dead twigs, I hypothesise that it has a high growth rate, since the downfall rate will be high, and fast recruitment and growth therefore necessary. Finally, I also hypothesise that temperatures above 20 °C will reduce carbon gain and growth rate.

An overall aim is to contribute to new knowledge about a poorly studied species at a globally high risk of extinction and to encourage further research, as well as to form the basis for management actions to prevent this species from going extinct. The results will extend previous findings on lichen ecophysiology, and hopefully show that through a combination of different methods and experiments, it is possible to gain a more detailed picture of a lichen species' ecological requirements.

# 2. Materials and methods

### 2.1 Field site

Tegningfallet (61°52'41''N, 10°51'0.6''E) is a 25 m tall waterfall in the river Tegninga, located in Rendalen municipality, in the eastern part of southern Norway. Rendalen has a slightly continental climate, with only approximately 500 mm of precipitation a year. July and August receive most precipitation (Moen, 1998; NVE, 2020). Mean annual temperature is 0-1 °C, and the vegetation zone is middle boreal (Moen, 1998). Tegningfallet is in a steep canyon, shaped by the river and waterfall, which has eroded the dominating bedrock (sandstone). Lower parts of the canyon are dominated by Norway Spruce (*Picea abies*), whereas the forest above the canyon is Scotch Pine (*Pinus sylvestris*) dominated. *Erioderma pedicellatum* was only found on thin, mainly dead branches of a couple of spruce trees facing the waterfall on the opposite side of the canyon. The branches with most specimens were sun-exposed and facing southwest (Fig. 3).

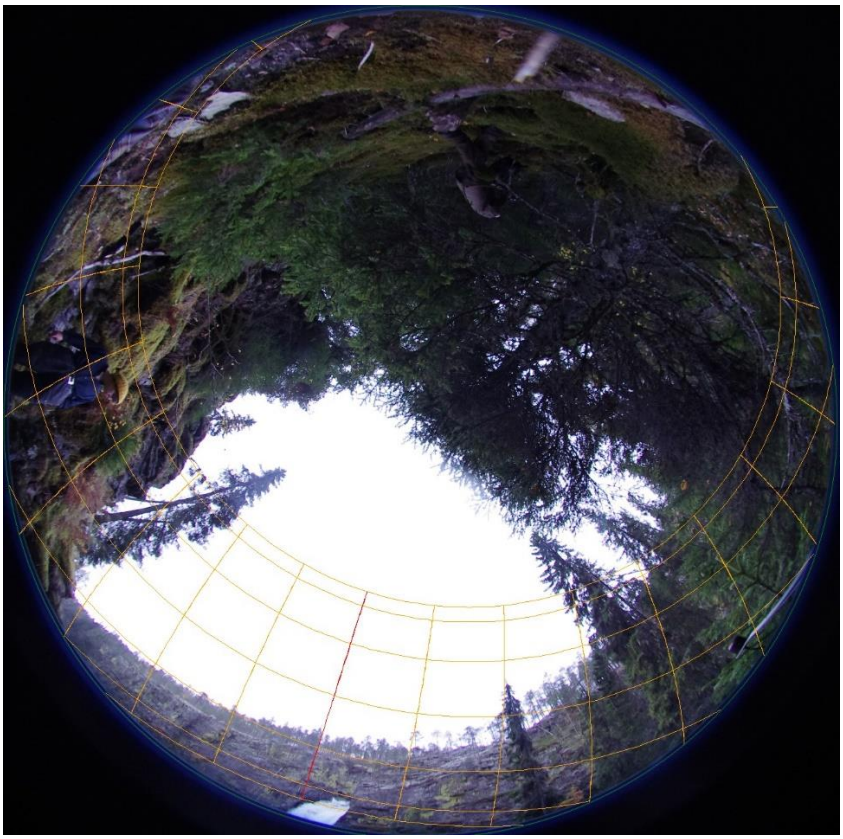

**Fig. 3** Fisheye photo taken close to the SW-facing spruce branches with the densest population of *E. pedicellatum* at Tegningfallet. The waterfall on the eastern side of the canyon can be seen in the bottom of the photo. The dark-coloured cluster of dead twigs near the centre of the photo, is where *E. pedicellatum* occurs most abundantly, filling most spaces between the thin branches. The photo is taken at noon in a rainy day in early October 2020. The yellow lines show the suntrack over the sky throughout the year dividing the year into 6 sectors and the day into 24 sectors. The red line indicates south.

There were four small trees in one cluster with 1500-2000 thalli of *E. pedicellatum* comprising ≈ 90% of the population at the site. In addition, there were approximately ten nearby trees with a couple of thalli on each tree. This strong spatial aggregation of thalli differs from its distribution pattern elsewhere (Stehn et al., 2013; Cameron et al., 2013a; Holien, 2016; Tagirdzhanova et al., 2019; Gauslaa & Arsenault, 2020). The lower part of the canyon facing the waterfall represents a very different environment than the surrounding dry low-productive pine forest. The unique habitat influenced by the waterfall resembles boreal rainforest (Holien & Tønsberg, 1996; Reiso, 2015) due to its extreme humidity and low temperatures. From the waterfall, the canyon continues for about 300 meters, before the landscape flattens (Fig. 4). The catchment area of Tegninga is relatively large (89 $km^2$) creating a rather constant stream of water in the waterfall (Reiso, 2015; NVE, 2020).

**Fig. 4** Picture of Tegningfallet. *Erioderma pedicellatum* occurs in the lower part of the canyon, facing towards the spray-zone of the waterfall. Photo: Sigve Haugland.

The spruce forest in the canyon is not very old, but there are some small moss-loaded trees suppressed by excess humidity ("dwarf-spruces") that seem rather old, and that might have functioned as continuity carriers. The surrounding pine forest has apparently originated on a former clear-cut area less than 100 years old. The site is shielded by mountain ranges against acid rain (Tørseth & Manø, 1996). pH in precipitation at this site is now around 4.9, but was historically somewhat higher (Tørseth & Manø, 1996).

## 2.2 Lichen material

All thalli of *E. pedicellatum* were collected from dead, fallen branches on the ground below the trees at Tegningfallet, Norway (61°52'41''N, 10°51'0.6''E). Such fallen samples that appeared healthy were collected during every visit at the site; first in September 2019, then April and May 2020, and finally in October 2020. Field observations revealed that branches break and fall to the ground in all seasons. Thalli of *P. plumbea* were collected on oak trunks in Kristiansand (58°7'50''N, 8°8'7''E) in southern Norway, July 2020.

After collection, lichens were air-dried at 20 °C and stored at -18 °C in the lab for 2-12 months, before experiments took place. Lichen performance in experiments should not be affected by such treatment (Honegger, 2003).

## 2.3 Water-storage traits

A randomly selected batch of collected *E. pedicellatum* thalli was used to measure WHC and STM for the Tegningfallet population. First, air-dry mass was measured for lichens that were 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 to remove waterdrops (shaking wet). Blotting mass ($WM_{blotting}$) was measured after removing excessive water by gently blotting the lichens with dry filter paper. Then, hydrated lichens were placed under a Pentax K-5II SLR camera with a Sigma 70 mm macro lens, mounted on an adjustable pole facing downwards, approximately one meter above the lichens, with glass placed upon the lichens, holding the lobes spread out on a transilluminator, allowing photos optimized for calculation of the thallus area, using ImageJ (J 1.48). Oven dry mass (DM) was weighed in five additional thalli after 24 h drying at 70 °C, and the oven dry/air-dry mass-ratio was used to calculate DM for all experimental thalli. Water holding capacity (WHC) was calculated as WHC = (WM-DM)/A. STM was calculated as STM=DM/A. In addition, a separation between ($WHC_{shaking} = WHC_{total}$) and ($WHC_{blotting}=WHC_{internal}$) was done. Internal water holding capacity ($WHC_{internal}$) = ($WM_{blotting}$-DM)/A, and external water holding capacity ($WHC_{external}$) = $WHC_{shaking} - WHC_{blotting}$. All mass measurements were done using Sartorius analytical scale (±0.1 mg). Methods follow Gauslaa & Arsenault (2020).

## 2.4 Microclimatic measurements in the field

A hemispherical photo was taken close to the branches with most *E. pedicellatum* at Tegningfallet with Pentax K-5II SLR camera with Sigma 4.5 mm circular fisheye lens (Fig. 3).

North direction was set by a compass, and the camera was placed horizontally with the true north direction indicated. A camera stand positioned the camera at a similar height above ground as the branches with *E. pedicellatum*. The picture was analysed in the software Hemisfer (3.0) to estimate light through the year under clear sky conditions. The suntrack over the sky was estimated and illustrated by dividing the year into 12 periods (2x6) and the day into 24 hours (Fig. 3).

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 v2.2.1 (Onset, Bourne, MA, USA) were installed at the location 18.4.2020 and collected 4.10.2020, comprising the growth season. They recorded light, temperature, and relative humidity. One climate station was put right next to the main population (± 1m), and the other one next to a host tree (±2m) with only a couple thalli of *E. pedicellatum*, approximately 50 meters north-west of the main population to differentiate between an optimal and suboptimal site. Both climate stations were placed approximately 50 cm above ground, and as close to the host trees as possible, without shading or disturbing the lichen.

### 2.5 pH- measurement

While visiting the field site in May 2020, spruce branches were collected from three categories of spruce trees based on their epiphytic vegetation. 1: seven branches on trees dominated by *E. pedicellatum* thalli, 2: ten branches on trees only supporting other Lobarion species (cephalo- and cyanolichens), and 3: seven branches on trees with only chlorolichens in the Parmeliaceae (non-Lobarion; which is the abundant epiphytic vegetation on spruce branches). Branches were brought to the lab and analysed within two days after collection. Each branch was cleaned (epiphytes removed), cut into a 6 cm long piece and put into a small glass vial with 6 ml 25 mM KCl-solution and repeatedly shaken. The branches were submerged in the solution for 1.5 h. Thereafter, branches were removed, and pH was measured in the KCl-solution with a calibrated pH-meter. Method follows as in Gauslaa & Holien (1998).

As a supplement, conductivity and pH were measured in six water samples from the river Tegninga. Conductivity was measured at the site with a portable conductivity meter (Mettler-Toledo International Ltd, Singapore), whereas water samples were brought in closed bottles to the lab for measurement of pH within 24 h.

### 2.6 Light response curves of $O_2$-evolution

$O_2$-evolution was measured with a leaf-disc electrode (Model LD2, Hansatech, King's Lynn, Norfolk, UK) at 18 °C and 5% $CO_2$ using $NaHCO_3$ as $CO_2$ source. Measurements were repeatedly done with increasing light levels, starting at 25 followed by 50, 100, 200, 400 and 600 µmol photons $m^{-2}$ $s^{-1}$ from a LED light source panel using equal levels of red, green and blue light (Model SL-3500, Photon System Instruments, Drasov, Czech Republic). Estimates of mean $O_2$-evolution was conducted with the Photosyn Assistant ver. 1.1.2 software.

### 2.7 $CO_2$ uptake at different temperatures

The gas analyser (LI-64000XT) was placed in a temperature-controlled room to ensure constant temperature during acclimation and subsequent measurements. Here 15 lichen thalli were weighed on a scale (± 0.1mg) and $CO_2$ uptake was measured at 5, 10, 15, 20 and 25 °C, respectively at 410 ppm $CO_2$ and 400 µmol photons $m^{-2}$ $s^{-1}$. First, moist lichens were acclimated to the selected measurement temperature for 24 h in low light (50-100 µmol photons $m^{-2}$ $s^{-1}$). This allowed for completing the measurements at one temperature a day. Afterwards, all lichens were acclimated another 24 h at the next temperature. Measurements were done at a water content ($WC_A$) corresponding to blotting weight, the optimal hydration level for $CO_2$ uptake (Solhaug et al., 2021). This was accomplished by gently pressing fully hydrated lichens with dry filter paper to remove excessive waterdrops, and then weighing them.

### 2.8 $CO_2$ uptake during desiccation cycles

$CO_2$-uptake was measured with a gas analyser (LI-6400XT Portable Photosynthesis System) with a cuvette (6400-24 Bryophyte Chamber) and a LED panel (6400-18A RGB Light Source) (Li-Cor, Lincoln, NE, USA). Lichens were hydrated with de-ionized water before their thallus area was measured with a leaf-area meter (Li-3100 Area Meter, Li-cor, Lincoln, NE, USA). They were then placed in the gas analyser cuvette while fully water-saturated ($WM_{shaking}$), with a $CO_2$ concentration of 410 ppm, at 400 µmol photons $m^{-2}$ $s^{-1}$ red light and 20 °C. Lichens were taken out of the gas analyser to be weighed every fifth minute, and then put back into the gas analyser. Measurements continued until the lichen was air-dry. This was done for 18 *E. pedicellatum* thalli.

### 2.9 Light and desiccation tolerance experiment

Lichens were placed on nets above different salt-solutions inside sixteen small boxes of transparent plastic (Table 1). Boxes were sealed with cling film. Five thalli of *E. pedicellatum* and four thalli of *Pectenia plumbea* were placed inside each box. Eight boxes were exposed to light (200 µmol photons $m^{-2}$ $s^{-1}$ composed of equal levels of red, blue and green light from the SL-3500 LED panel), the remaining eight stayed in darkness. Four relative humidity treatments were used, 0%, 35%, 55% and 75% for each of the two light treatments (Table 1), replicated in two boxes. Before being placed in the boxes, all lichens had been acclimated in low light (100-150 µmol photons $m^{-2}$ $s^{-1}$ red light from the SL-3500 LED panel) and kept moist for 24 h.

**Table 1** The saturated salt solutions in sealed boxes and associated relative humidity.

| Relative humidity | Salt |
|---|---|
| 0 % | Silica gel |
| 35% | $MgCl_2$ |
| 55% | $Mg(NO_3)_2$ |
| 75% | NaCl |

Boxes were rotated daily to avoid box-dependency due to small heterogeneities in light treatment. At the end of the seventh day, all lichens were removed from the sealed boxes. They were hydrated and kept in low light (10 µmol photons $m^{-2}$ $s^{-1}$ light) to record recovery kinetics at 15 °C. Fv/Fm was measured at 0,5 h, 2 h, 6 h, 24 h and 48 h after hydration. ImagingPam (red-LED IMAGING-PAM M-series, Walz Effeltrich, Germany) was used to measure maximum PSII efficiency (Fv/Fm). Methods follow Gauslaa et al. (2012).

### 2.10 Growth experiment

Sixteen thalli were randomly selected for each of the four temperature treatments in a growth experiment using two growth chambers (SANYO MLR-351, Sanyo electrics, Japan). Treatments were 6/1, 12/7, 18/13 and 24/19 °C (day/night temperature), with 12 h day at 150 µmol photons $m^{-2}$ $s^{-1}$ (fluorescent lamps, Mitsubishi/Osram FL 40SS W/37) and 12 h night (darkness). All thalli were sprayed with de-ionized water in the morning and evening (12 h interval). Thalli were placed on nets mounted on top of open Petri dishes with filter-papers in the bottom that was kept constantly wet, to enhance air humidity and retard desiccation.

Humidity in the growth chambers was enhanced by moist newspapers placed at the top and bottom shelves. The aim was to keep all thalli hydrated for approximately 12 h in between sprayings yet allowing them to desiccate before the start of night to maximize growth.

Each treatment lasted for fourteen days and a rotation of Petri dishes ensured as similar conditions for all thalli as possible. Before start, photos of each thallus were taken, as described in 2.3. Air-dry mass was recorded before and after the experiments and corrected to oven-dry mass by using a correction factor as described in 2.3. The experimental design was based upon previous growth experiments with lichens (Bidussi et al., 2013a; Alam et al., 2015; Gauslaa et al., 2016).

Chlorophyll fluorescence was measured with Imaging-PAM MAXI-version. Measurements of maximal PSII efficiency (Fv/Fm) were done for each thallus, using a strong saturating pulse on dark adapted thalli.

### 2.11 Statistical analyses

For the water-storage traits, simple linear regressions were computed to test various relationships between parameters of interest. The data was log-transformed to meet test assumptions when needed. For comparisons between populations in the discussion, unpaired two-sample t-test was used. Paired t-tests were conducted to test differences between parameters of interest within the microclimatic data.

One-way ANOVAs were computed to investigate differences between the tested groups in the pH measurements and in the experiment with $CO_2$-uptake at different temperatures, combined with post-hoc analyses to test where the differences between groups could be found. Thalli were tested for as a random effect when the same thalli were measured several times during an experiment, this using linear mixed models where assumptions were met. Simple linear regressions were conducted to survey relationships in the desiccation cycle experiment.

For analysis of the light and desiccation tolerance experiment, a three-way repeated measures ANOVA with Fv/Fm as response was performed. This allowed to include all variables and to check for interactions, at the same time as the repeated measures of the response was included. Box was added as random effect, to test for box-dependency in the light treatment. All assumptions were met before the model was performed.

The RGR-data from the growth experiment was analysed using a general linear model, using temperature as factor and Fv/Fm and thallus area as covariates. An ANOVA omnibus tests was run, together with fixed effects parameter estimates and a post-hoc test, to test where the significance could be found. Assumption checks were done with histogram plot, Shapiro test of normality and Q-Q plot.

Statistical analyses were conducted in R studio (Version 1.2.5033) and Jamovi (Version 1.2). The results were plotted in R studio (Version 1.2.5033) with the "ggplot2"-package and SigmaPlot v14.0 (Systat Software, San Jose, CA).

A few specimens of *E. pedicellatum* were excluded as outliers from the analyses in the following experiments: 1) $CO_2$ uptake during desiccation cycle in gas analyser, 2) $CO_2$ uptake at different temperatures in gas analyser, and 3) Growth experiment. This was done due to either very low photosynthetic response, or errors during measurements with the gas analyser. As all specimens of *E. pedicellatum* used were collected from fallen branches, it was expected that some individuals would be removed as outliers due to low vitality.

# 3. Results

### 3.1 Water-storage traits

Mean specific thallus mass (STM), a proxy of thallus thickness, of *Erioderma pedicellatum* from Tegningfallet was 8.1 ± 1.8 mg $cm^{-2}$. Thallus dry mass and area were strongly coupled (Fig. 5A), and STM highly significantly increased with thallus area (Fig. 5B). $WHC_{internal}$, $WHC_{external}$ and $WHC_{total}$ were all significantly related to STM, the strongest regression was found for $WHC_{internal}$ (Fig. 6A-C). Thalli of all sizes followed the same trend, and the thicker the thallus was, the more water it held. Mean $WHC_{internal}$, $WHC_{external}$ and $WHC_{total}$ were 20 ± 1.0, 20 ± 0.7 and 40 ± 1.5 $H_2O$ $cm^{-2}$, respectively, meaning that the internal and external water storages were equally large.

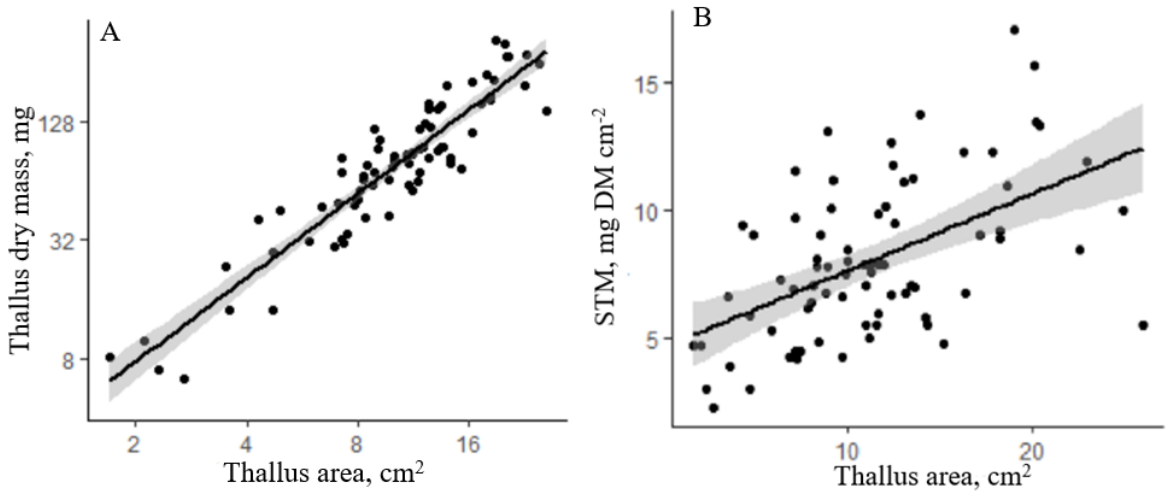


**Fig. 5** (A) The relationship between thallus dry mass and thallus area mass in *E. pedicellatum* from Tegningfallet. Axes are log-transformed. $R^2 = 0.852$, P < 2.2e-16. (B) The relationship between specific thallus mass (STM) and thallus area. $R^2 = 0.2818$, P < 8.08e-07. Regression lines (solid lines) and 95% confidence intervals (grey areas) are given.

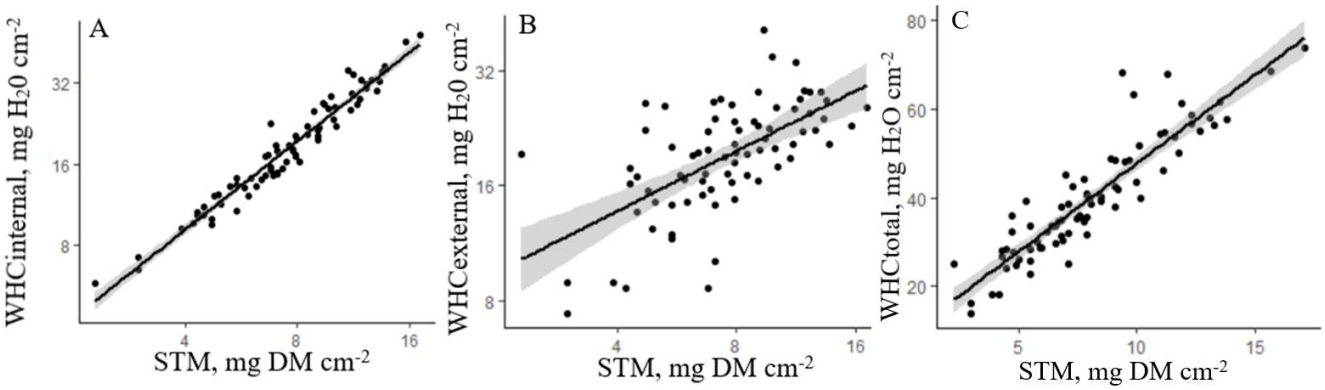


**Fig. 6** (A) The relationship between internal water holding capacity ($WHC_{internal}$) and specific thallus mass (STM) in *E. pedicellatum* from Tegningfallet. Axes are log-transformed. $R^2 = 0.947$, P: < 2.2e-16. (B) The relationship between external water holding capacity ($WHC_{external}$) and specific thallus mass (STM). Axes are log-transformed. $R^2 = 0.3329$, P < 4.89e-08. (C) The relationship between total water holding capacity ($WHC_{total}$) and STM. $R^2 = 0.8252$, P < 2.2e-16. Regression lines (solid lines) and 95% confidence intervals (grey areas) are given.

### 3.2 Microclimate

The estimated amount of light reaching the densest population of *E. pedicellatum* on outer branch portions in the absence of clouds followed a clear pattern (Fig. 7A-B), shaped by the local landscape and latitude. The presented data are estimates of maximum possible sunlight during a day, with the assumption that all days had a clear sky. *Erioderma pedicellatum* received no direct sunlight during the winter and very much in summer (Fig. 7A-B). There was no direct sunlight from late October until March 1 (Fig. 7A) due to shading landscape elements, but from approximately the last week of February, direct sunlight increased substantially from day to day until mid-March when direct sunlight lasted for 300-350 min during each clear day

until the end of August (Fig. 7B and 3). The habitat of the largest *E. pedicellatum* population at Tegningfallet is thus exposed to much direct sunlight in summer but protected against it in winter.

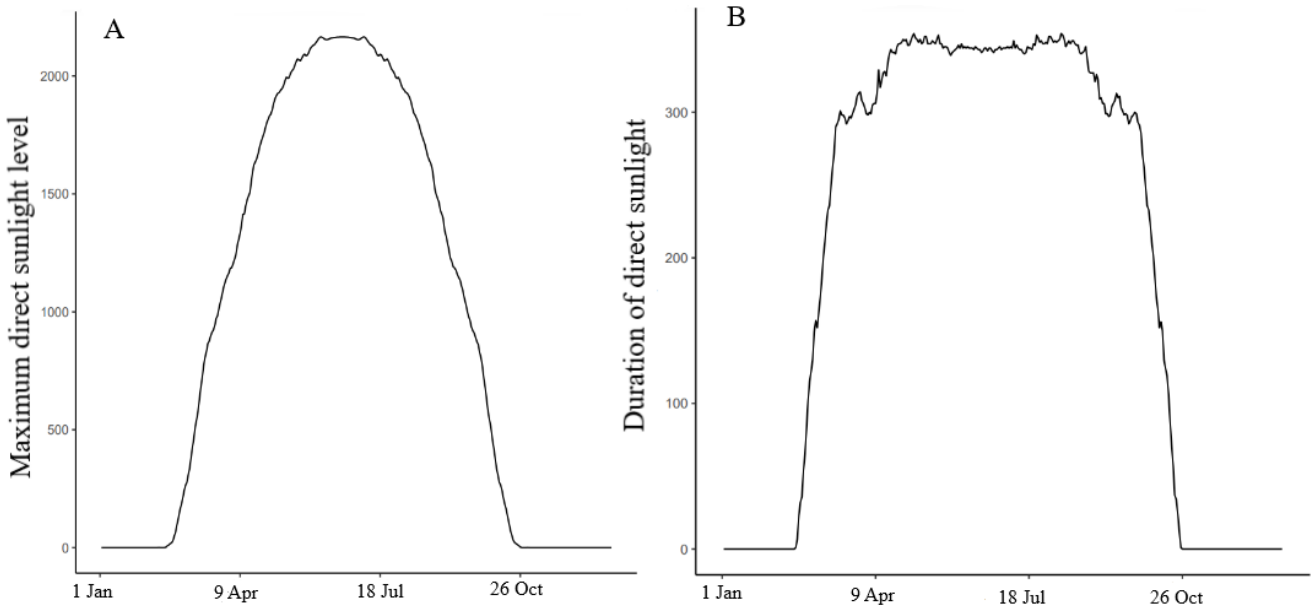


**Fig. 7** (A) Maximum direct sunlight level (µmol photons $m^{-2}$ $s^{-1}$) in a cloudless day (y-axis) versus date of the year (x-axis). (B) Duration of direct sunlight (minutes, x-axis) per day (y-axis), assuming clear sky versus date on the x-axis. Data was generated with Hemisfer 3.0. (As described in 2.4).

Recordings of relative humidity (RH) at the *E. pedicellatum* site from April 18 until October 4 showed that RH reached 100% almost every night from May 24 until October 4 (Fig. 8C). May 24 represented a clear shift in RH at the site, since RH never reached 100% before this day. In the days before this shift, temperatures below 0 °C ceased, and temperatures generally rose. From May 24 until June 19 RH remained 100% almost constantly (Fig. 8C). Light, temperature and RH seemed tightly connected, and after June 19 higher temperatures seemed to impact RH to a larger degree resulting in reduced RH during daytime. Days with little light caused only small reductions in RH during daytime. When light levels where low, temperature amplitude between day and night where lower, which again affected RH. This can be seen most clearly in Fig. 8 during end of September/start of October right before measurements ended.

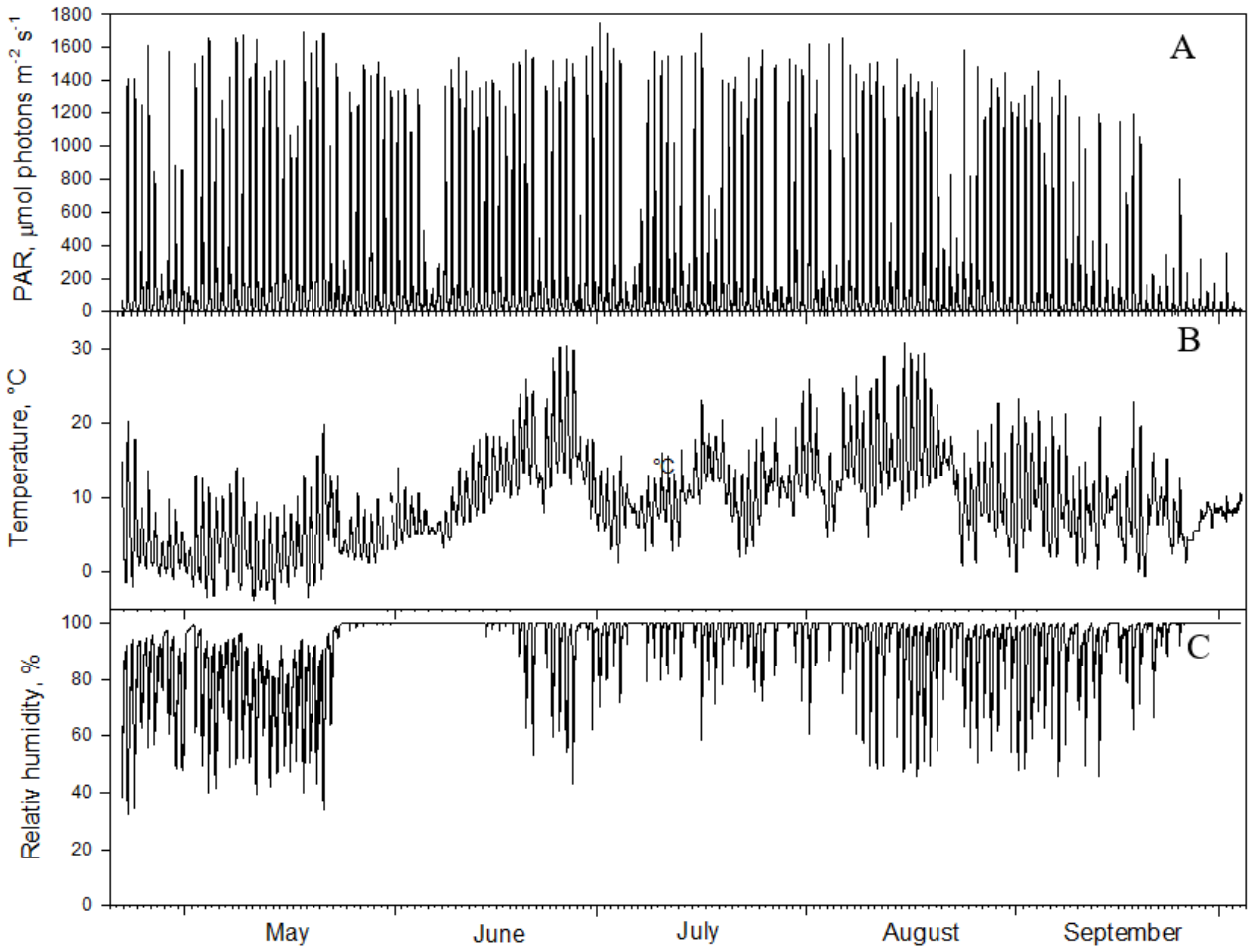


**Fig. 8** (A) Recordings of photosynthetic active radiation (PAR), (B) temperature (°C) and (C) relative humidity (RH%), respectively. Recordings of PAR and temperature are data from the climate station placed by the main population whereas RH data are from the climate station by the subpopulation, this due to some missing data of RH recordings at the main population. Recordings started April 18 2020 and ended October 4 2020, at Tegningfallet, Norway.

The close relationship between light, temperature and RH can be seen clearly in Fig. 9 on May 20, the day with the longest duration of strong light. An increase in light increased temperature, which further resulted in reduced RH. However, after the shift in RH from May 24 until June 19, RH was less affected by both increases in light and temperature. On June 6 (Fig. 9), assumingly a rainy day due to very low light levels, RH seemed unaffected by both light and temperature increase, as these values are rather low and stable. Fig. 9 further illustrates the importance of light for diurnal temperature amplitude at Tegningfallet.

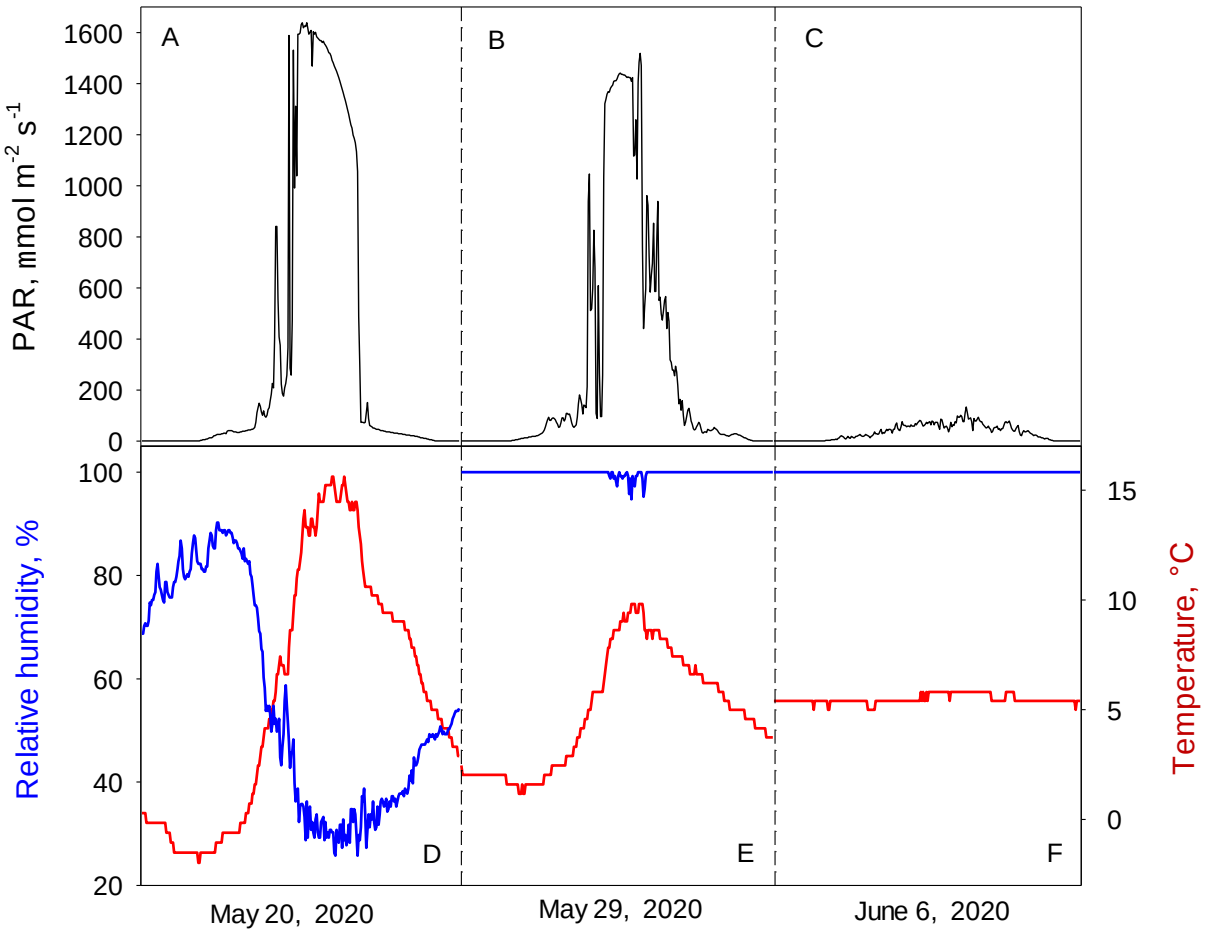


**Fig. 9** Recordings of photosynthetic active radiation (PAR), relative humidity (RH) and temperature (C°) for May 20 2020, May 29 2020 and June 6 2020, respectively. All data are from the climate station by the main population.

There were clear significant differences for light, temperature and relative humidity between the optimal and suboptimal site of *E. pedicellatum* at Tegningfallet (Fig. 10). The optimal site had generally higher light levels ($P < 0.001$) and temperature ($P < 0.001$) than the suboptimal site, but lower RH ($P < 0.001$). Climatic conditions at the optimal site were: RH 85.30 ± 0.09%, temperature 9.21 ± 0.03 °C and PAR 167.01 ± 1.50 µmol photons $m^{-2}$ $s^{-1}$, and the suboptimal site: RH 92.20 ± 0.06%, temperature 8.67 ± 0.02 °C and PAR 136.04 ± 1.30 µmol photons $m^{-2}$ $s^{-1}$.

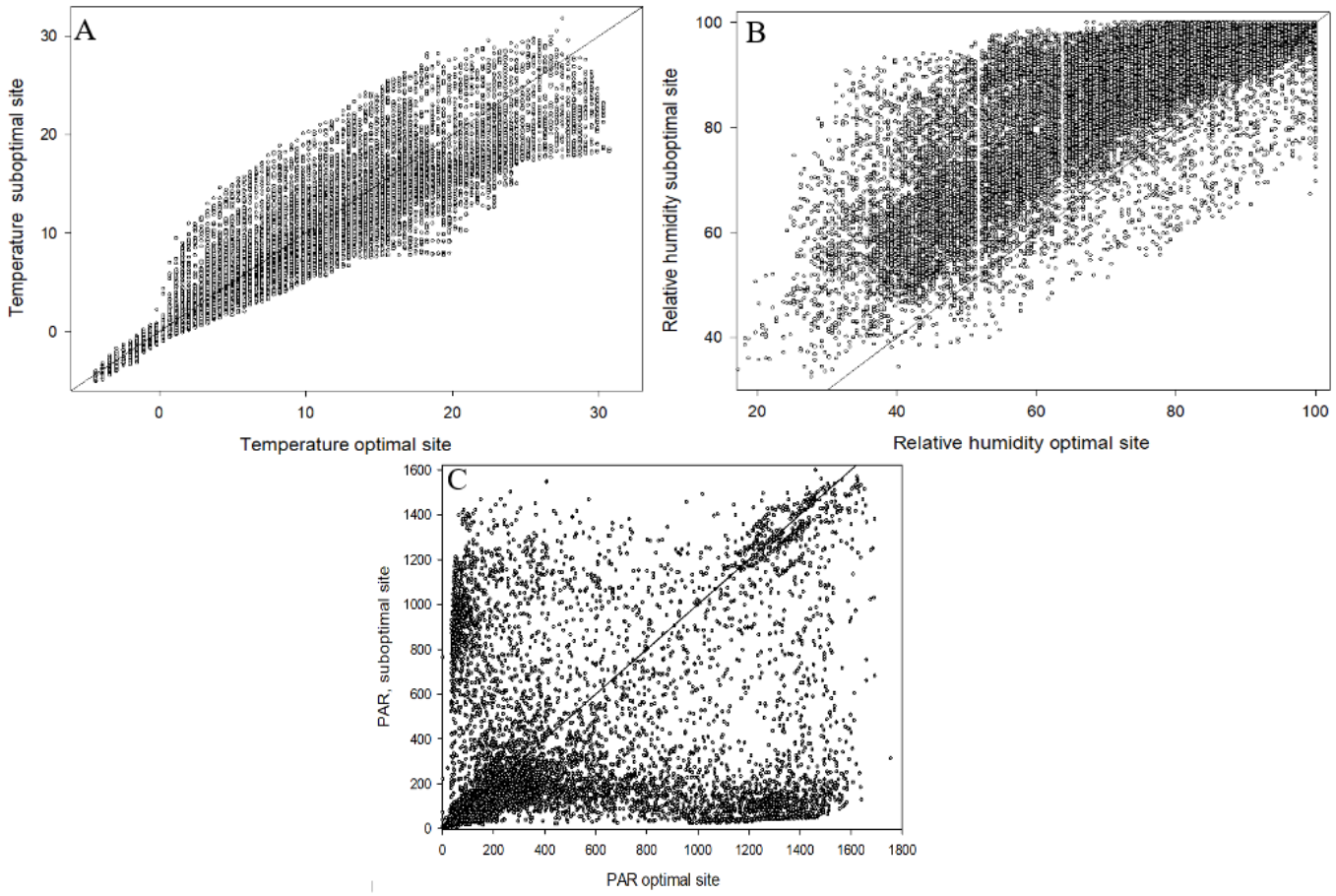


**Fig. 10** (A) Temperature (°C), (B) relative humidity (RH, %) and (C) photosynthetic active radiation (PAR, µmol photons $m^{-2}$ $s^{-1}$) for both the optimal and suboptimal site of *E. pedicellatum* at Tegningfallet, respectively, plotted against each other. A line showing equal values are shown.

### 3.3 Bark pH of spruce branches

Bark pH of *Picea abies* significantly differed between the three tested categories of branches ($P < 0.001$). Branches with Lobarion (pH=4.48 ± 0.23) and non-Lobarion (pH=3.98 ± 0.11) had significantly ($P < 0.001$) lower pH than branches with *E. pedicellatum* (pH=4.98 ± 0.18).

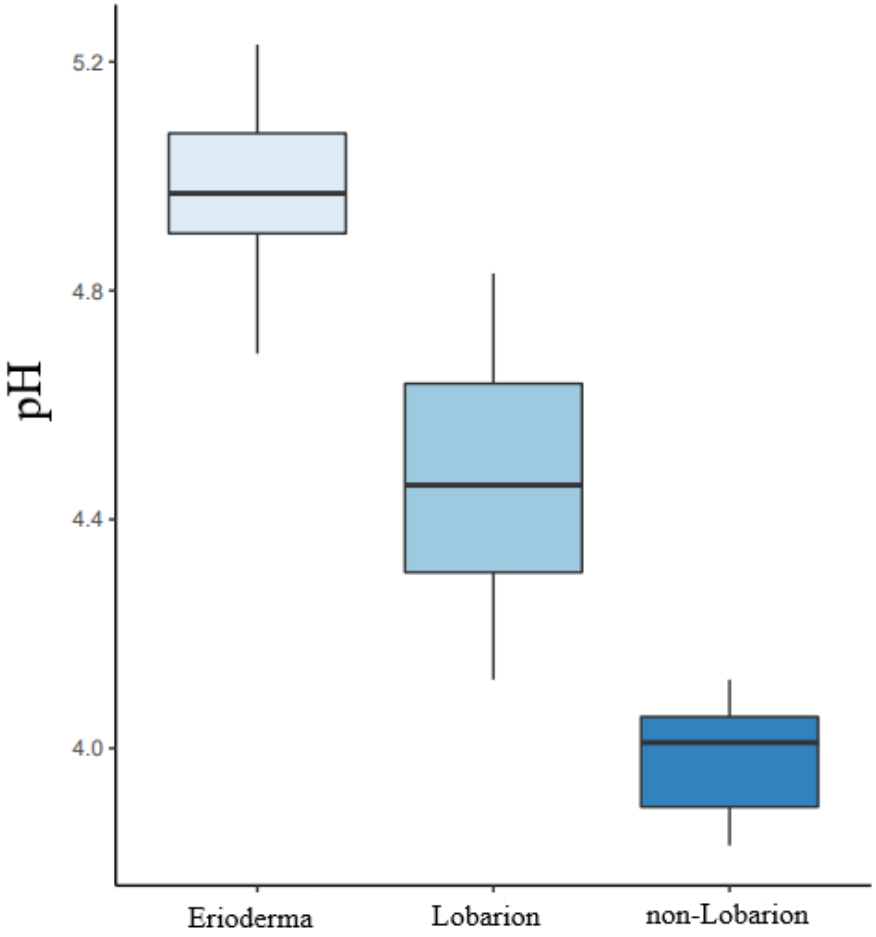


**Fig. 11** Boxplot of bark pH of three categories of *Picea abies* branches based on their epiphytic vegetation: 1) epiphytic vegetation dominated by *E. pedicellatum* (*Erioderma*; n=7), 2) dominated by other Lobarion species (Lobarion; n=10), 3) dominated by chlorolichens in the Parmeliaceae (non-Lobarion; n=10). According to a TukeyHSD test, the three branch categories had significantly different bark pH ($P < 0.001$).

### 3.4 Light response curves of $O_2$-evolution

The $O_2$-evolution for *E. pedicellatum* increased to the highest measured light levels, although at slower rates (Fig. 12). In darkness (0 µmol photons $m^{-2}$ $s^{-1}$), photosynthesis was negative, implying that there was an $O_2$ uptake as dark respiration. At 25 µmol photons $m^{-2}$ $s^{-1}$, the average photosynthesis was close to the compensation point, although most individuals still had negative photosynthesis at this point. At 50 µmol photons $m^{-2}$ $s^{-1}$ all individuals had positive photosynthesis, and from there to 200 µmol photons $m^{-2}$ $s^{-1}$, photosynthesis rapidly increased (Fig. 12). The increase from 400 to 600 µmol photons $m^{-2}$ $s^{-1}$ suggested that light saturation is rather high. Linear mixed model was used to test for thalli ID as random effect, but this was insignificant.

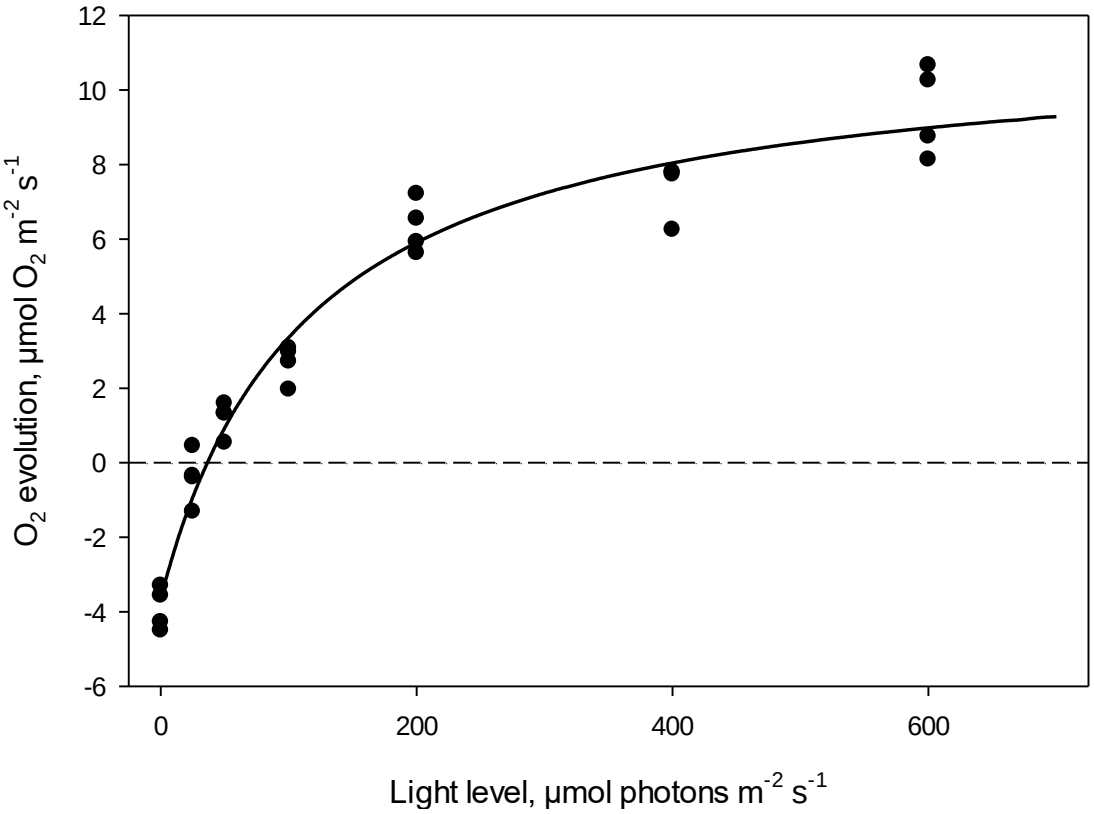


**Fig. 12** Light response curve of $O_2$-evolution (µmol $O_2$ $m^{-2}$ $s^{-1}$) with increasing light level (µmol photons $m^{-2}$ $s^{-1}$) in four thalli of *E. pedicellatum*. Dots represent actual values, whereas the line represents the mean $O_2$-evolution. The line is estimated with the Photosyn Assistant ver. 1.1.2 software. Dotted horizontal line represents light compensation point.

### 3.5 The temperature-dependency of $CO_2$-uptake

*Erioderma pedicellatum* had a broad temperature optimum for photosynthesis (Fig. 13). Only at 25 °C was the $CO_2$-uptake significantly lower than at other studied temperatures. Measurements at 5 and 20 °C, respectively, appeared slightly lower than those in between (10 and 15 °C), but this was not significant. At 5 °C, there were large differences between individual responses. Even after removing outliers, the variance was large and several thalli had a low C-uptake at this temperature. The highest mean C-uptake occurred at 10 °C, suggesting that cool temperatures are optimal for carbon gain in *E. pedicellatum*. As the same thalli were measured at all temperatures, thallus ID was included as a random factor in a linear mixed model, but was insignificant.

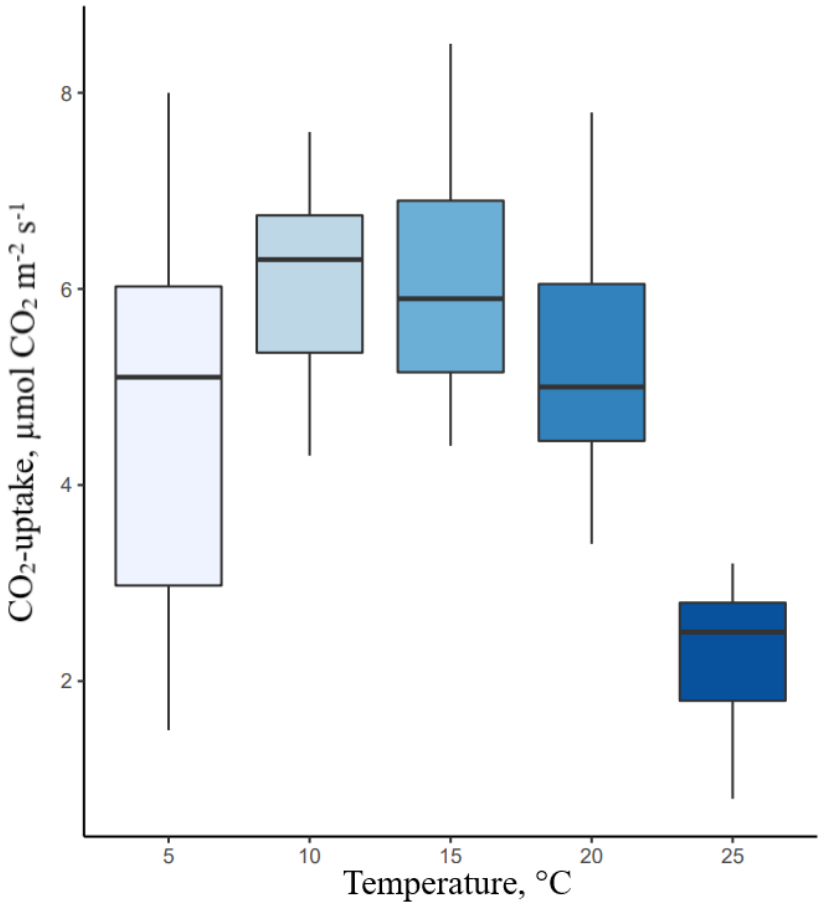


**Fig. 13** Photosynthesis as response of temperature treatments measured with $CO_2$ gas analyser. Only the 25 °C treatment resulted in significantly reduced photosynthesis ($P<0.001$; Tukey HSD-test; n=13). (n=15, except the 5 °C group with n=13).

### 3.6 $CO_2$-uptake during desiccation cycles

The desiccation cycles started with depressed photosynthesis at the highest water contents, but gradually increased and reached maximal photosynthesis when the lichen had reached a hydration level close to blotting weight, with dry mass-based water contents ($WC_{DM}$) around 200% (Fig. 14). Maximum photosynthesis was found at an average $WC_{DM}$ of 206%. When max. photosynthesis was reached, one could observe a colour change in the lichen, from deep blue to somewhat greyer. After the top was reached, photosynthesis decreased slowly until it became inactivated by desiccation. Eventually, when the lichen was close to air-dry ($WC_{DM} \approx 20\%$), there was no longer any measurable photosynthesis (Fig. 14). Differences in both desiccation time and $CO_2$-uptake between thalli were large and showed great variance between individuals (Fig. 14). The largest thallus (12.5 $cm^2$) was photosynthetically active for approximately 120 minutes, whereas the smallest thallus (0.7 $cm^2$) was dry ($WC_{DM} \approx 20\%$) with no positive photosynthesis already after 35 minutes. The thallus with the longest desiccation time was

photosynthetically active for 155 minutes. Photosynthetic active period was significantly related to $WHC_{total}$ (Fig. 15A) and thallus area (Fig. 15B), meaning that larger thalli and thalli with higher $WHC_{total}$ stayed photosynthetically active for longer time. A significant positive relationship was found between $WC_A$ at maximum photosynthesis and $WHC_{internal}$ (Fig. 16), meaning that the higher $WHC_{internal}$ a thallus had, the higher $WC_A$ was needed to obtain maximum photosynthesis.

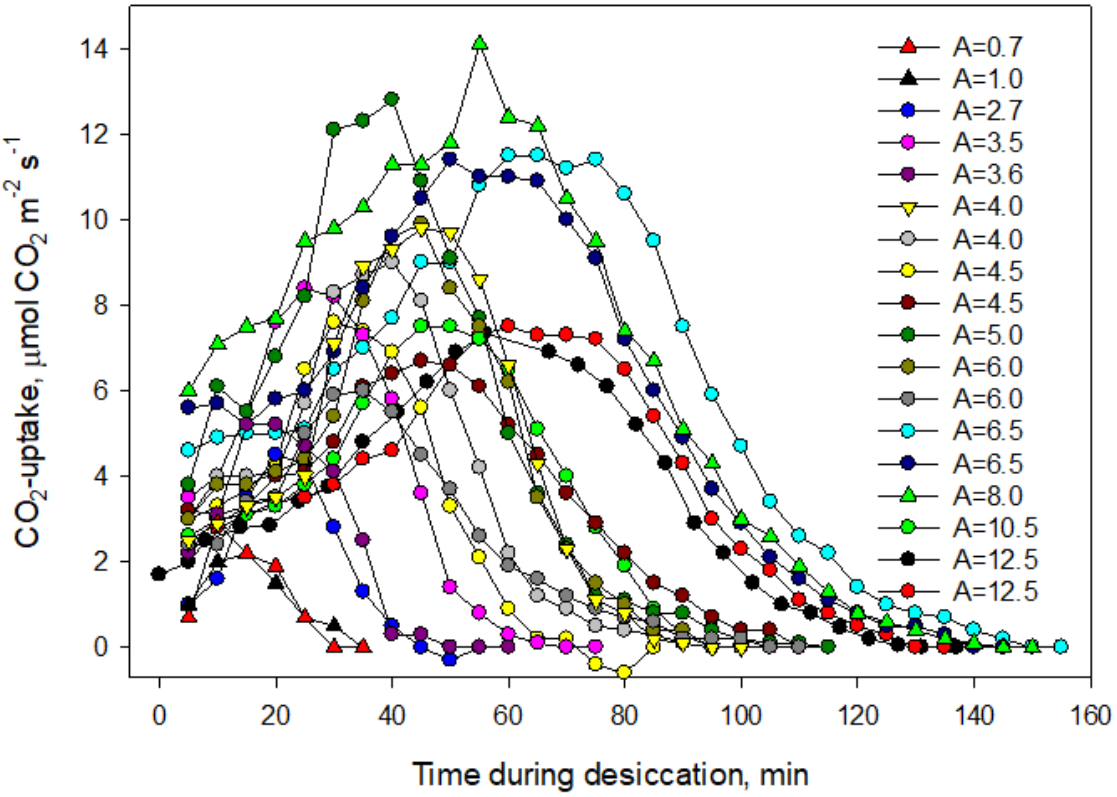


**Fig. 14** $CO_2$-uptake (µmol $CO_2$ $m^{-2}$ $s^{-1}$) during a desiccation cycle for *E. pedicellatum* (n=18), with time during desiccation in minutes on x-axis. Legends show thallus area ($cm^2$) for each thallus, represented with colour/shape.

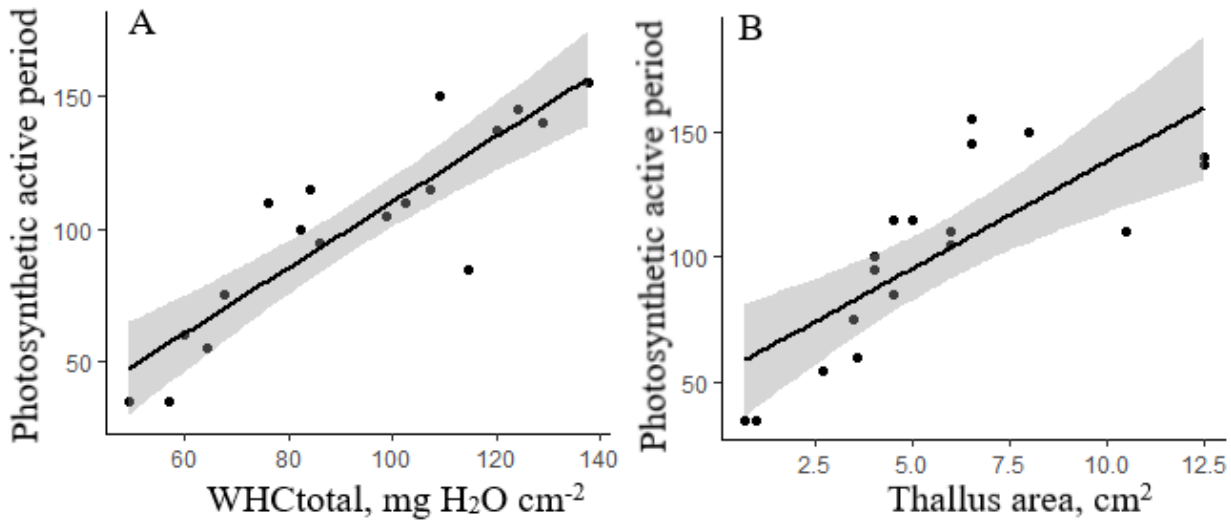


**Fig. 15** (A) The relationship between photosynthetic active period (minutes) and total water holding capacity ($WHC_{total}$) for *E. pedicellatum* (n=18), $R^2$adj= 0.771, P < 0.001. (B) The relationship between photosynthetic active period (minutes) and thallus area ($cm^2$), $R^2$adj=0.565, P<0.001. Regression lines (solid lines) and 95% confidence intervals (grey areas) are given.

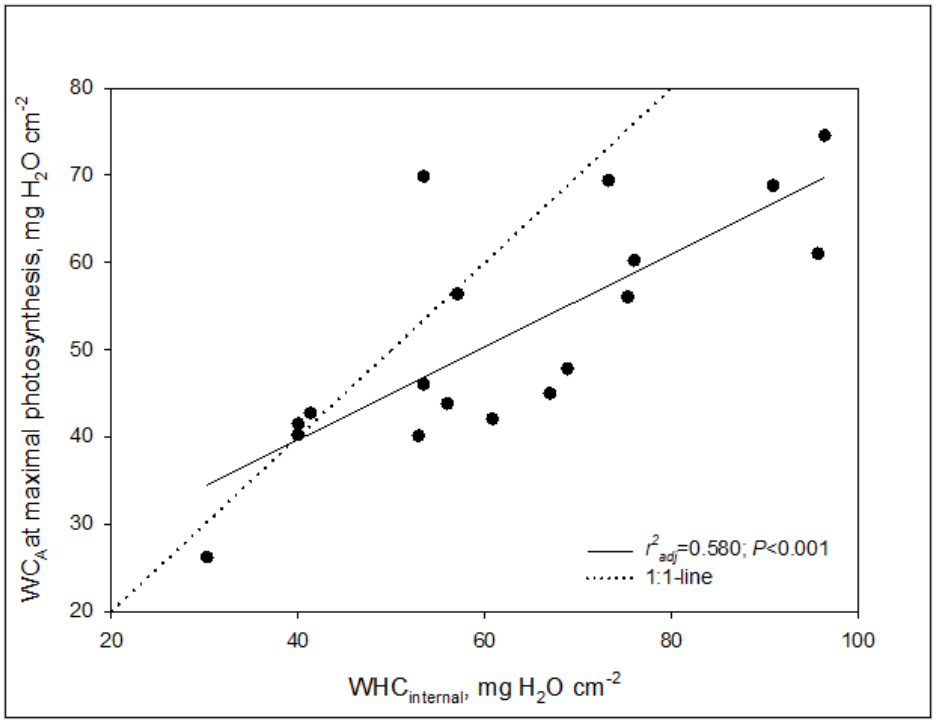


**Fig. 16** The relationship between water content ($WC_A$) at maximal photosynthesis and internal water holding capacity ($WHC_{internal}$). Regression line (solid line) and 1:1 line (dotted line) is shown.

### 3.7 Desiccation and light tolerance

Desiccation tolerance in darkness was significantly different between the two species ($P < 0.001$), where *E. pedicellatum* was the least affected (Fig. 17). Both recovered fully after 48 h of hydration, but *P. plumbea* at a slower rate. As both Fig. 17 and Table 2 shows, light was clearly the most significant factor for Fv/Fm reduction, as it delayed recovery substantially for both species. Nevertheless, both *E. pedicellatum* and *P. plumbea* recovered to normal Fv/Fm levels after seven days of exposure to light in the air-dry state, except at the hardest drying regime at 0% relative humidity (Fig. 17). At 0% relative humidity and 200 µmol photons $m^{-2}$ $s^{-1}$, both species had delayed recovery, and none of them recovered to normal values even after 48 h. As the repeated measures ANOVA confirms, the two species had a rather similar desiccation tolerance, as the interaction species, light, humidity and time were insignificant (Table 2). The repeated measures ANOVA further emphasizes the importance of time and humidity (Table 2). Box was tested for as a random effect, and was slightly significant (P=0.02). For both species in light, Fv/Fm did not decline with decreasing RH during the drought part of the experiment, except at 0% RH as mentioned. RH of 35% gave the least Fv/Fm reduction when exposed to light at the first measuring time after hydration 0,5 h, whereas after 48 h, RH of 55% humidity clearly gave the best recovery in Fv/Fm for both species (Fig. 17). Fv/Fm recovery in darkness was less affected by the differences in RH during drought (Fig. 17).

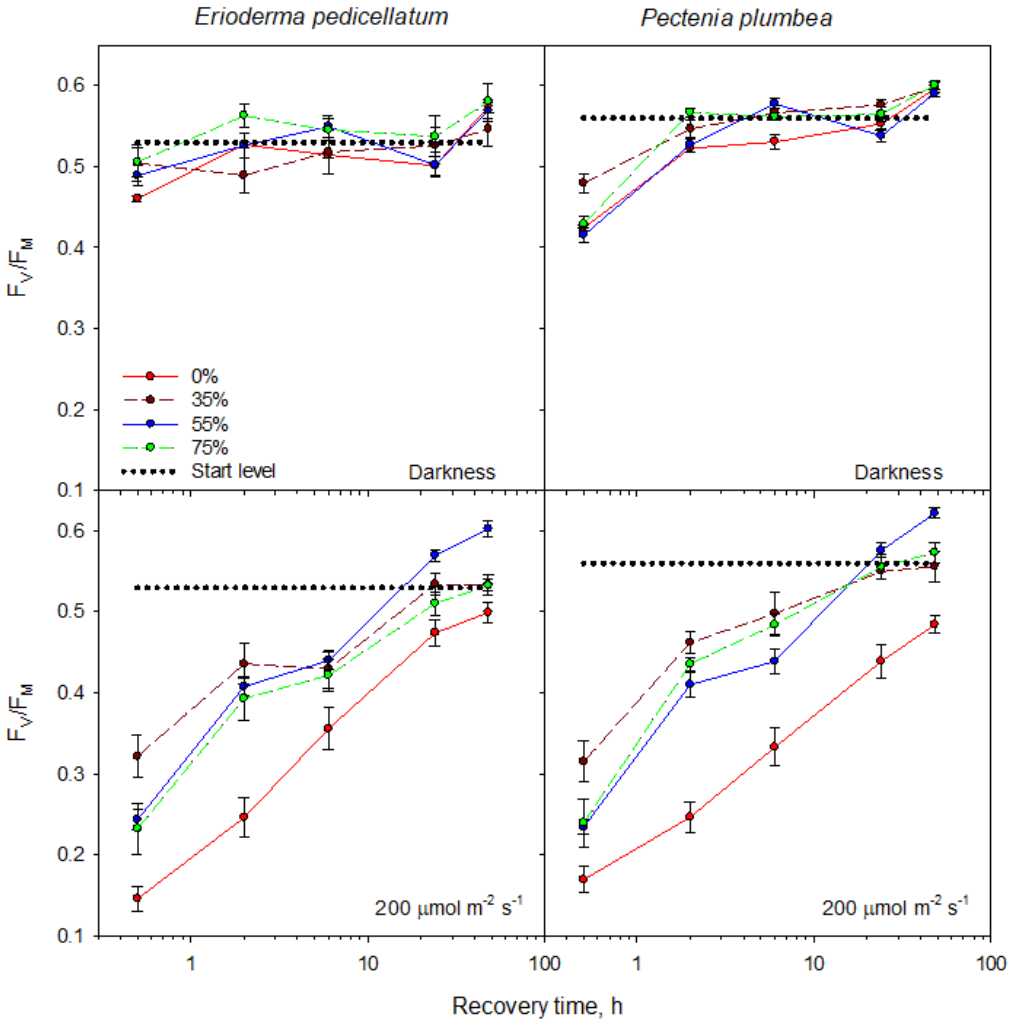


**Fig. 17** Fv/Fm kinetics during recovery (h) after 7 d exposure to four levels of relative humidity and two light levels (0 and 200 µmol photons $m^{-2}$ $s^{-1}$), x-axis is log-scale, and dotted lines represent mean start level. Vertical bars show ±1 standard error. (*E. pedicellatum* n=80, *P. plumbea* n=64)

**Table 2** Repeated measures ANOVA for Fv/Fm in *E. pedicellatum* and *P. plumbea* exposed for 7 d to four relative humidities, two light levels (0 and 200 µmol photons $m^{-2}$ $s^{-1}$) with box as random effect. Data are shown in Fig. 17.

| | Df | F value | Pr(>F) |
|---|---|---|---|
| Species | 1 | 25.98 | 0.000 |
| Light | 1 | 1841.09 | 0.000 |
| Humidity | 3 | 159.98 | 0.000 |
| Thallus.id | 80 | 11.20 | 0.000 |
| Time | 5 | 670.42 | 0.000 |
| Box | 1 | 5.33 | 0.02 |
| Humidity:Time | 12 | 10.90 | 0.000 |
| Light:Time | 4 | 251.24 | 0.000 |
| Species:Time | 4 | 13.69 | 0.000 |
| Time:Box | 4 | 0.62 | 0.64 |
| Light:Humidity | 3 | 22.42 | 0.000 |
| Species:Humidity | 3 | 5.44 | 0.001 |
| Humidity:Box | 3 | 15.17 | 0.000 |

| | | | |
|---|---|---|---|
| Species:Light | 1 | 5.18 | 0.02 |
| Light:Box | 1 | 6.54 | 0.01 |
| Light:Humidity:Time | 12 | 8.33 | 0.000 |
| Species:Humidity:Time | 12 | 1.56 | 0.1 |
| Humidity:Time:Box | 12 | 6.46 | 0.000 |
| Species:Light:Time | 4 | 8.41 | 0.000 |
| Light:Time:Box | 4 | 2.06 | 0.08 |
| Species:Light:Humidity | 2 | 3.98 | 0.01 |
| Light:Humidity:Box | 2 | 1.29 | 0.27 |
| Species:Light:Humidity:Time | 12 | 0.46 | 0.45 |
| Light:Humidity:Time:Box | 12 | 1.26 | 0.24 |
| Residuals | 516 | 0.589 | 0.001 |

### 3.8 Growth rates

Temperature influenced the relative growth rate (RGR) of *E. pedicellatum* (Fig. 18). Temperature, thallus area and Fv/Fm explained 41% of the variation in RGR (General linear model). At the highest temperature treatment, 24/19 °C, *E. pedicellatum* had slightly significantly lower RGR (0.26 ± 1.12 mg $g^{-1}$ $day^{-1}$) than at the 6/1 °C (0.75 ± 0.60 mg $g^{-1}$ $day^{-1}$) and 18/13°C temperatures (2.70 ± 0.72 mg $g^{-1}$ $day^{-1}$), respectively (Fig. 18). In general, thalli grown at 18/13 °C had the highest RGR. RGR at the 12/7 °C treatment was 0.86 ± 1.07 mg $g^{-1}$ $day^{-1}$. Mean dry mass growth in percentage were as follows: 6/1 °C =1.11 %, 12/7 °C = 1.35%, 18/13 °C= 3.92%, 24/19°C= 0.55%. RGR significantly ($P < 0.001$) declined with increase in thallus size (Fig. 19A), whereas it slightly significantly ($P = 0.002$) increased with increase in Fv/Fm performance after ended experiment (Fig. 19B). The thallus with the highest RGR (10.9 mg $g^{-1}$ $day^{-1}$) was grown at 18/13 °C, and the temperature treatment with most thalli with negative RGR was 24/19 °C. In this group, 7 out of 16 thalli had negative RGR, which indicates a trend of high loss of biomass in warm temperatures for *E. pedicellatum*. The smallest difference was between the 6/1 °C and 12/7 °C groups respectively, and the largest difference was between the 18/13 °C and the 24/19 °C group.

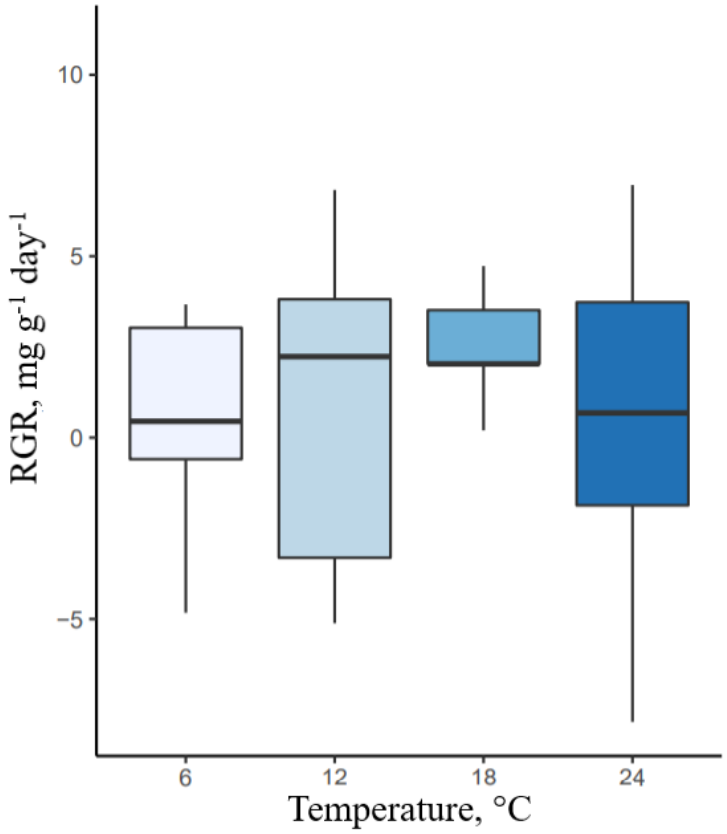


**Fig. 18** Boxplot of relative growth rate (RGR) for *E. pedicellatum* at the different temperature treatments (night + day temperature). According to a TukeyHSD test, weak significance was found in RGR between the 6/1°C – 24/19 °C groups (P =0.028) and 18/13 °C- 24/19 °C (P = 0.038).

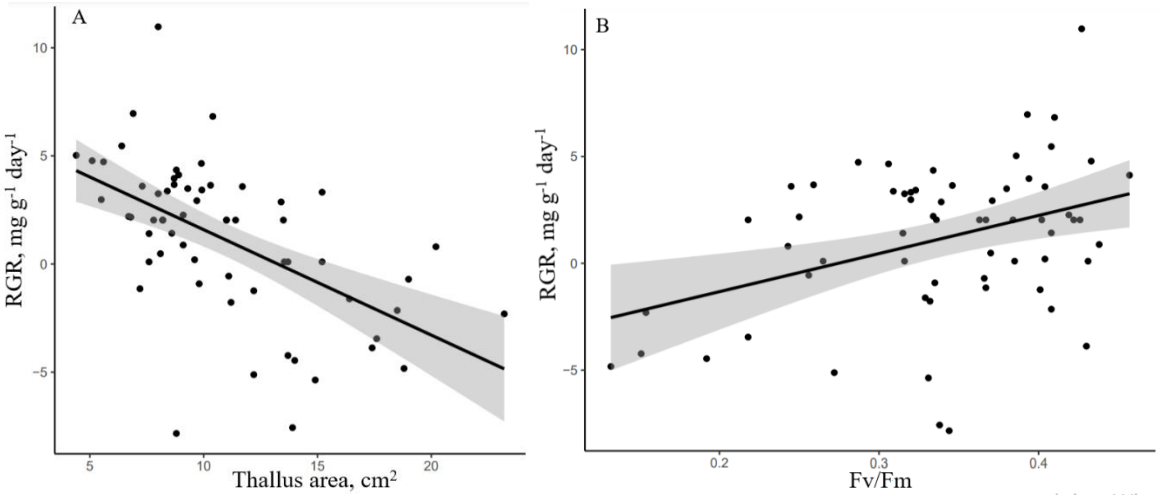


**Fig. 19** (A) Relationship between relative growth rate (RGR) and thallus area for *E. pedicellatum*, $R^2$adj = 0.297, P < 0.001. (B) The relationship between relative growth rate (RGR) and Fv/Fm, $R^2$adj =0.129, P=0.002. Regression lines (solid lines) and 95% confidence intervals (grey areas) are given.

# 4. Discussion

## 4.1 Microclimate

Local landscape elements and latitude shape the diurnal and seasonal light courses that drive RH and temperature at Tegningfallet (Fig. 7-9) and are thus important factors for *E. pedicellatum* (presented results). The clear shift in RH on May 24 concurred with the cease of night temperatures below 0 °C, which assumingly accelerated snow melting. This likely increased water in the waterfall, which assumingly to a large degree explains the sudden rise in RH. During the long and rather continuous period of 100% RH during both day and night from May 24 until June 19, light levels and diurnal temperature amplitude were relatively low. However, during this period RH was high even at high light levels and increased temperatures (Fig. 9), emphasizing the powerful effect of the waterfall on the microclimate. As water supplement from snow melting assumingly decreases after a relatively long period of warm temperatures above 0 °C, RH became more variable and more strongly affected by light and temperature after June 19 (Fig. 9).

The significantly different microclimatic conditions (Fig. 10) at the optimal and suboptimal site provide information on the ecological niche of *E. pedicellatum*. The lower RH at the optimal compared to the suboptimal site coincides with the findings from the desiccation cycles, as *E. pedicellatum* clearly suffers from suprasaturation when fully water saturated (Fig. 14). Sites closer to the waterfall or with higher RH should therefore be less suitable and too humid for a sustained high photosynthesis. The higher light levels at the optimal site are important for reducing RH, but also for enabling high photosynthetic rates, in line with the rather high light saturation in *E. pedicellatum* (Fig. 12). The higher mean temperature at the optimal site during the growth season is also closer to the presented temperature optimum for carbon gain for *E. pedicellatum*, ranging from ≈10-15 °C (Fig. 13). The microclimatic conditions at the optimal site and the lichen's responses to such factors combined with a dominance of *E. pedicellatum* suggest that this site represents optimal conditions for the species. The presented findings confirm the species' demands for large amounts of strong light during the growing season, in combination with high, but not too high, water access, combined with relatively cool temperatures.

### 4.2 Water-storage traits

The high correlations between STM and $WHC_{internal}$ (Fig. 6A-C) confirm that thicker thalli hold more water. This is by now well documented across lichen species and populations (Gauslaa & Coxson, 2011; Gauslaa & Arsenault, 2020). The lower $R^2_{adj}$ between $WHC_{external}$ and STM than $WHC_{internal}$ and STM indicates that water storage on the surface of the lichen thallus is less related to the thickness of the thallus, than water storage within the thallus. Furthermore, accurate determination of $WC_{shaking}$ is more challenging than $WC_{blotting}$, which may explain the weaker regression for $WHC_{external}$ and thus the different strength of the relationship between $WHC_{total}$ and $WHC_{internal}$ versus STM. The strong relationship between STM and thallus area implies that area expansion follows increased thickness, as the lichen grows, supported by the strong regression of thallus dry mass and thallus area mass. However, while dry mass normally increases with area, an increase in STM with thallus area certainly indicates thickness increase.

A comparison of WHC and STM between populations from two different continents, the Tegningfallet population and the Newfoundland population (Gauslaa & Arsenault, 2020), was conducted, and there was a significant difference between them, as hypothesized ($P < 0.001$; Fig. 20). Compared to the Tegningfallet population, the Newfoundland population has higher STM and $WHC_{internal}$, regardless of size (Fig. 21). Because STM is a strong predictor for $WHC_{internal}$, it is a useful trait for comparison of populations. Comparison of STM between groups is however not recommended due to group-specific effects caused by the photobiont (Gauslaa & Coxson, 2011; Gauslaa & Arsenault, 2020).

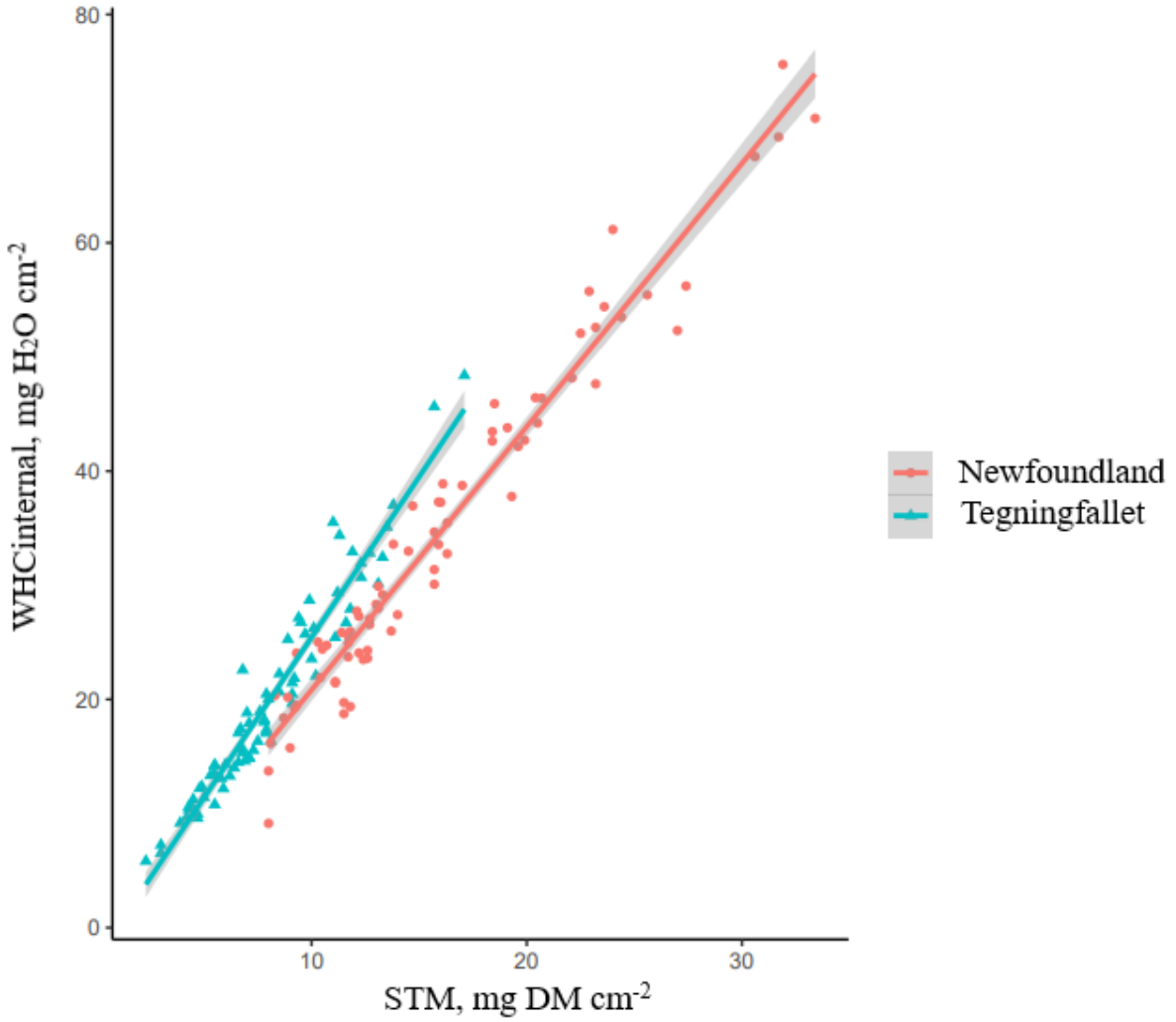


**Fig. 20** The relationship between internal water holding capacity ($WHC_{internal}$) and specific thallus mass (STM) for the Newfoundland ($R^2_{adj}$ = 0.956, P < 2.2e-16) and Tegningfallet ($R^2_{adj}$ = 0.935, P < 2.2e-16) populations, respectively. (Circles represent Newfoundland, Canada; triangles represent Tegningfallet, Norway.) Regression equations: Tegningfallet: $WHC_{internal}$ = - 2.678 + 2.812 * STM; Newfoundland: $WHC_{internal}$ = -2.227 + 2.306 * STM. Regression lines (solid lines) and 95% confidence intervals (grey areas) are given.

Mean STM of *E. pedicellatum* at Tegningfallet 8.1 ± 1.8 mg $cm^{-2}$ was half the STM of *E. pedicellatum* in Newfoundland 16.0 ± 0.7 mg $cm^{-2}$ (Gauslaa & Arsenault, 2020). STM of *E. pedicellatum* at Tegningfallet was rather similar to other old forest associated cyanolichens like *Lobaria scrobiculata 8.6 ± 0.2* mg $cm^{-2}$ and *Pseudocyphellaria citrina* 7.3 ± 0.1 mg $cm^{-2}$ (Merinero et al., 2014).

The Newfoundland population of *E. pedicellatum* grew on trunks (Gauslaa & Arsenault, 2020), whereas in Norway it has exclusively been found on thin branches (Reiso, 2015; Holien, 2016) and are thus more exposed to humidity than prostrate thalli on thicker trunks. This distinct

difference between the two populations may have large implications for their exposure to various hydration sources (Gauslaa & Coxson, 2011). *Erioderma pedicellatum* in Newfoundland experiences an average yearly precipitation of 1283 mm $y^{-1}$ (Gauslaa & Arsenault, 2020), whereas the yearly precipitation at Tegningfallet is just 500 mm $y^{-1}$, which may to a large extent explain the difference in both STM and WHC between the two populations.

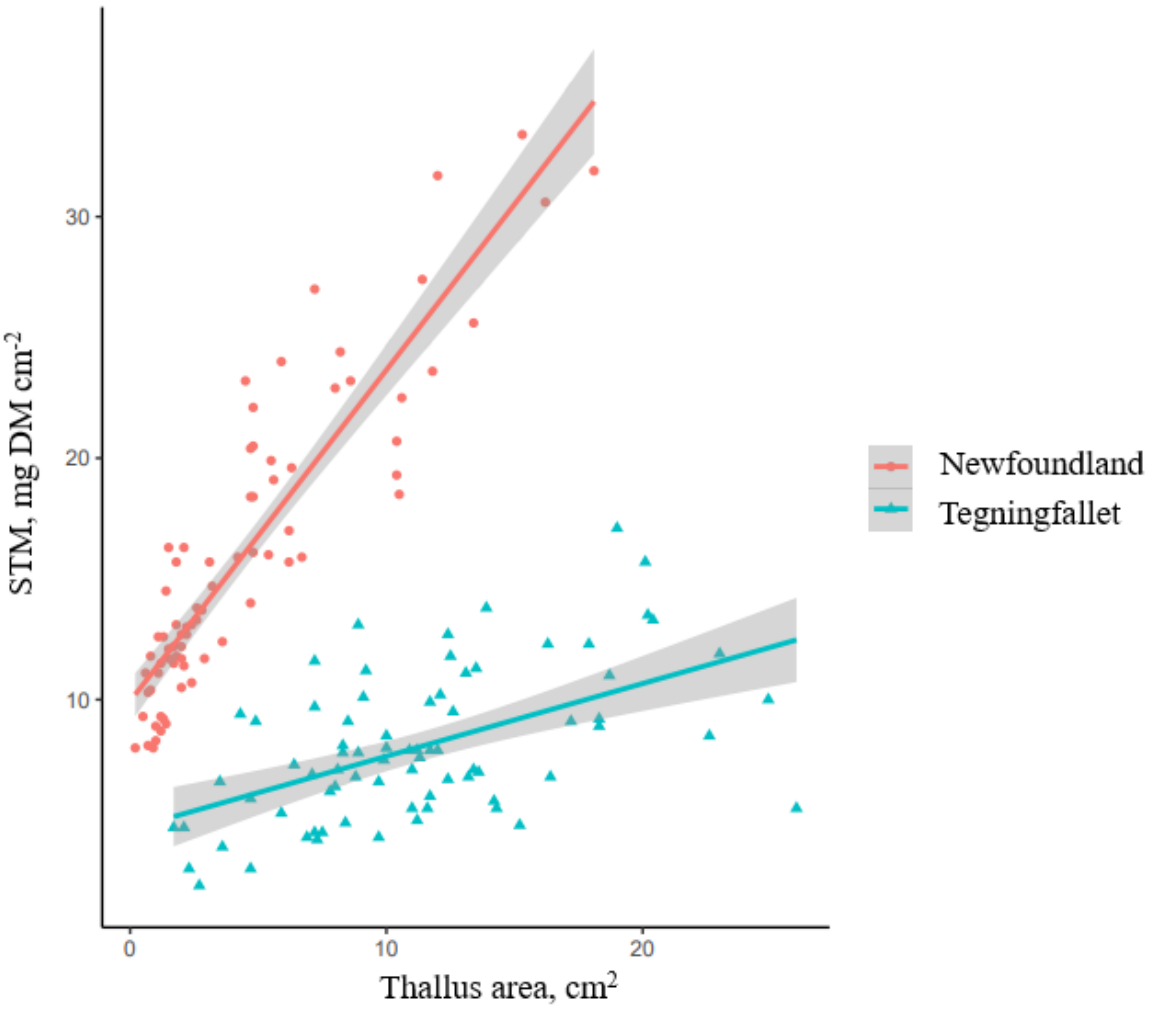


**Fig. 21** The relationship between specific thallus mass (STM) and thallus area in *E. pedicellatum* from Newfoundland ($R^2$adj = 0.8105, P < 2.2e-16) and Tegningfallet ($R^2$adj = 0.2818, P < 8.08e-07), respectively. (Circles represent Newfoundland, Canada; triangles represent Tegningfallet, Norway.) Regression lines (solid lines) and 95% confidence intervals (grey areas) are given. Regression equations: Tegningfallet: STM = 4.641 + 0.301 * thallus area; Newfoundland: STM = 9.932 + 1.372 * thallus area.

Lichens with low STM more rapidly fill their water storage in humid air, and may therefore be less dependent on frequent precipitation (Phinney et al., 2018; Ås Hovind et al., 2020). Reduced

thickness implies reduced water storage capacity (Gauslaa & Coxson, 2011), creating a trade-off between water uptake and water loss (Phinney et al., 2018). For lichens depending on rainwater, as the Newfoundland population (Gauslaa & Arsenault, 2020), thickness prolongs photosynthetically active periods and thus improves carbon uptake rates. At Tegningfallet, where precipitation is less frequent, reduction of thickness facilitates utilization of other hydration sources (Gauslaa & Coxson, 2011).

The waterfall at Tegningfallet is likely essential for *E. pedicellatum's* success, and its relatively low STM and WHC could be an adaption to utilize water in humid air and temporal, small fog droplets from the waterfall. From various visits at different times, *E. pedicellatum* appeared relatively dry at noon unless it had rained within few hours (A.R Nilsson, Pers. obs.). If the water droplets from the waterfall reaches all the way to the host trees of *E. pedicellatum,* yearly precipitation should be considered significantly higher. Field observations and hydration state of lichens before May 24 indicated that the droplets did not reach the host trees. The recorded air humidity changed after May 24, possibly because melting snow enlarged the spray zone around the waterfall enhanced the RH. Nevertheless, at the host trees of the main population, all branches facing the waterfall were loaded with *E. pedicellatum*, emphasizing the importance of the waterfall.

Furthermore, humid air or fog can maximally contribute 0.2 mm = 20 mg $H_2O/cm^{-2}$ (Jacobs et al., 2002, 2006; Xiao et al., 2013), which corresponds to the mean $WHC_{internal}$ for *E. pedicellatum* at Tegningfallet, and gives a strong indication that the morphology of *E. pedicellatum* at Tegningfallet is adapted to utilize these hydration sources. By contrast, the mean $WHC_{internal}$ of 34.7 ± 1.7 mg $H_2O$ $cm^{-2}$ of the Newfoundland population cannot be filled by even a heavy dewfall (Gauslaa & Arsenault, 2020). However, dewfall alone cannot fill the water storage of larger *E. pedicellatum* thalli at Tegningfallet, whereas it may fill the water storage of smaller thalli. The $WHC_{total}$ recorded for *E. pedicellatum* at Tegningfallet implies that dew fall might even fill the $WHC_{total}$ for small thalli, whereas larger thalli should depend on liquid water to fill their water storage.

Even in larger thalli, long-lasting exposure of some days of humid air close to 100% RH may slowly activate cyanolichen photosynthesis (Schlensog et al., 2000), despite the fact that liquid water has earlier been claimed essential for photosynthetic activation of cyanolichens (Lange et al., 1986, 1993a). Since larger thalli at Tegningfallet have a $WHC_{internal}$ more than twice the amount that one nocturnal dewfall can contribute with, precipitation as rain or water droplets should play an important role for *E. pedicellatum*'s water economy at the site. The relatively

low precipitation levels at Tegningfallet would again imply that larger thalli have very few days with the $WC_A$ needed for maximum photosynthesis (Fig. 16), which again strengthens the assumption that the waterfall contributes with liquid water, at least during parts of the growth season.

### 4.3 Bark pH of spruce branches

*Erioderma pedicellatum* grew on branches with unusually high bark pH 4.98 ± 0.18 compared to normal levels for spruce in Norway. Lobarion's requirements for higher pH on spruce than Pseudevernion is previously shown by Gauslaa & Holien (1998). pH measurements show that *E. pedicellatum* has even higher demand for pH than other Lobarion species at Tegningfallet (Fig. 11), consistent with my hypothesis, and strongly suggests that spruce bark has to be enriched by base cations to become a suitable substrate for *E. pedicellatum*. Spruce bark is generally rather acidic (Nihlgård, 1971; Gauslaa & Holien, 1998), and has been considered too acidic for Lobarion in parts of Europe earlier influenced by acid rain (Rose, 1988). However, local factors are known to be able to modify the pH of spruce twigs (Gauslaa & Holien, 1998; Goward & Arsenault, 2000; Gauslaa et al., 2020).

Why Lobarion and *E. pedicellatum* demand high pH might partly be related to spore germination, particularly since *E. pedicellatum* exclusively spreads by ascospores (Cornejo et al., 2016), but also in achieving high growth rates, as growth increases with both pH and Ca availability (Gauslaa & Goward, 2012, 2020; Bidussi et al., 2013b). Larsen & Rasmussen (2021) recently discovered the importance of bark pH for spore germination in the nitrophytic *Xanthoria parietina*, showing that spores did not germinate if pH was too low. These findings likely explain why pH is of such high importance for lichen distribution, even on a small scale such as at Tegningfallet, where small-scale variations in spruce bark pH seem to constrain the ecological niche of *E. pedicellatum*.

A location where spruce is known to have a higher pH is in the boreal rainforest of Norway, in Trøndelag, known as one of the least air-polluted areas in Europe, with pH in precipitation around 5.2 (Tørseth & Manø, 1996). This was also the first site where *E. pedicellatum* was found in Norway (Ahlner, 1948). Air pollution is considered a threat for *E. pedicellatum* in North America (Cameron et al., 2013a; Richardson & Cameron, 2004), and as a general threat to Lobarion communities as acid rain previously reduced bark pH substantially (Gauslaa, 1995; Gauslaa & Holien, 1998). It is likely that acid rain in the past has reduced suitable habitat for

*E. pedicellatum* drastically, and acid rain may have depleted the soils for cations, implying that despite the efficient control of acid rain, bark and soil pH seems not to have recovered to preindustrial levels (Falkengren-Grerup, 1986; Nilsson & Tylor, 1995).

The pH of branches with *E. pedicellatum* (4.98 ± 0.18) coincides with present pH (4.9) in the precipitation at Tegningfallet (Tørseth & Manø, 1996). However, spruce branches with the widespread acidophytic epiphyte vegetation were more acidic (Fig. 11), likely because *Picea abies* acidificates its own environment and soil (Nihlgård, 1971). There are probably other factors affecting the pH of the branches, since spruce branches with *E. pedicellatum* had significantly higher pH than those of surrounding trees with Lobarion and Pseudovernion, respectively. There were no surrounding tree species with high bark pH, such as *Populus tremula*, that could have modified pH by base cation-rich canopy throughfall (Goward & Arsenault, 2000; Gauslaa et al., 2020). Such characteristics indicate that the pH of the spruce trees should have been rather low. The bark pH was possibly enriched by air borne water droplets from the waterfall with recorded conductivity of 8.3 and pH of 7.3. By constant addition of cation-rich water droplets, accumulation of cations may occur and enhance the pH of the spruce branches. However, branches on trees closer to the waterfall had lower pH than the optimal host trees of *E. pedicellatum*. At last, soil might be an important, and the rock shelf where the best host trees grew might have locally enriched soils. Soil samples should give further indications of why the trees of *E. pedicellatum* had branches with enriched pH.

### 4.4 Light-response curves of $0_2$ evolution

*E. pedicellatum* has a rather high $O_2$-evolution compared to other foliose lichens (Demmig-Adams et al., 1990; Gauslaa & Solhaug, 1996; Solhaug et al., 2014), as hypothesized. When measuring $O_2$-evolution in lichens with a leaf-disc electrode (Model LD2, Hansatech, King's Lynn, Norfolk, UK), the lichen thallus is $CO_2$-saturated by lying in bicarbonate, and it seems that *E. pedicellatum* responds well to high amounts of $CO_2$. As $O_2$-evolution is recognised as a good proxy for photosynthesis and thus carbon uptake, the presented results suggest that *E. pedicellatum* has rapid growth rates under suitable conditions. Based on the light response curves, *E. pedicellatum* could be considered a fast-growing species in high light. $O_2$ uptake above 10 µmol $O_2$ $m^{-2}$ $s^{-1}$ is very high for a lichen (Demmig-Adams et al., 1990; Gauslaa & Solhaug, 1996; Solhaug et al., 2014), and has to my knowledge not been recorded before. As all thalli used in this experiment were collected from downfallen branches, overestimates seem unlikely.

### 4.5 The temperature-dependency of $CO_2$-uptake

*Erioderma pedicellatum* has its highest carbon gain at 10 to 15 °C (Fig. 13). This fits well with its boreal distribution, and with a recorded mean temperature of 9.21 ± 0.03 °C at the optimal site at Tegningfallet from late April to early October, which roughly represents the growing season. Carbon uptake was reduced at 5 °C (Fig. 13). However, photosynthetic measurements at this temperature were challenging due to high air humidity in the temperature-controlled room that sometimes caused condensation inside the cuvette, which had an impact on the gas analyser and resulted in the removal of two outliers in the 5 °C treatment. Air humidity decreased with increasing temperatures, giving more robust readings. Low carbon gain at 5 °C is likely caused by a temperature reduction of enzymatic activity related to photochemical processes of the symbiotic photobiont (Lines et al., 1989; Smallwood & Bowels, 2002). That being said, $CO_2$-uptake at 5 °C was not significantly lower than at other temperatures, except at 25 °C. The trend may have been significant if a higher number of healthy thalli had been tested. As hypothesised, carbon gain was significantly reduced at 25 °C, due to increased dark respiration. This is consistent with *E. pedicellatum*'s restriction to cool boreal areas (Stehn et al., 2013; Cameron et al., 2013a; Tagirdzhanova et al., 2019; Holien, 2016; Gauslaa & Arsenault, 2020). Lichens can acclimate respiratory rates to different temperatures (Lange & Green, 2005). Increasing temperatures due to climate change should be considered a possible treat for *E. pedicellatum* at Tegningfallet, as dark respiration at 25 °C significantly reduces net photosynthesis.

### 4.6 $CO_2$ uptake during desiccation cycles

As previously shown for *P. plumbea* (Gauslaa & Solhaug, 1998) and other lichens (Larson, 1984; Hestmark et al., 1997; Pérez, 1997), the duration of photosynthetic active period increases with thallus size also for *E. pedicellatum* (Fig. 15B). Larger thalli, requiring more water, should thus have longer periods of active photosynthesis after a hydration event. This implies that smaller thalli have shorter periods of active photosynthesis, which underlines the importance of size for poikilohydric organisms. On the other hand, small thalli can utilize even small amounts of water for photosynthesis, thus allowing more flexible use of various hydration sources. This is supported by the finding that maximum photosynthesis occurs at a $WC_A$ similar to $WHC_{internal}$ (Fig. 16), meaning that thalli with larger $WHC_{internal}$ need more water to obtain maximum photosynthesis, whereas this is gained at a lower $WC_A$ for thalli with lower

$WHC_{internal}$. This is in line with the findings of Solhaug et al. (2021) for some chloro- and cephalolichens, now also shown for the cyanolichen *E. pedicellatum*, and apparently represents a universal pattern for foliose lichens. $WHC_{internal}$ therefore creates a trade-off, where thalli with larger WHC are more robust, versus thalli with lower $WHC_{internal}$ that are more flexible.

Measurements of $CO_2$-uptake during a full desiccation cycle (Fig. 14) showed that also the rain forest-associated lichen *E. pedicellatum* suffered from suprasaturation (Lange et al., 1993b; Lange & Green, 1996) when fully water saturated. At high water contents, its $CO_2$-uptake was depressed due to blockage of diffusive pathways of $CO_2$ (Lange et al., 1996), which further implies that long-lasting excess hydration could be a disadvantage for *E. pedicellatum*. This is further supported by the low number of thalli at the suboptimal site at Tegningfallet, and by the spruce trees closer to the waterfall lacking *E. pedicellatum* but hosting dense bryophyte carpets and other cyanolichens. Nevertheless, *E. pedicellatum* had a positive $CO_2$-uptake when fully water saturated, so it should not experience carbon loss when fully water saturated *in situ.*

Interestingly, Gauslaa & Solhaug (1998) reported max $CO_2$-uptake in *P. plumbea* to occur at $WC_{DM} \approx 200\%$, similar with reported values for *E. pedicellatum*. At this optimal water content for photosynthesis, excess water blocking diffusive $CO_2$ pathways should have evaporated (Solhaug et al., 2021). At Tegningfallet, there seems to be a large internal population dynamic with both regeneration and loss of broken branches with *E. pedicellatum* (A.R Nilsson, pers. obs.). The species totally dominated the four trees hosting the main population, and several new thalli were found on the ground during every visit at the site. The growth rate of *E. pedicellatum* at Tegningfallet is therefore likely high under these environmental conditions.

### 4.7 Desiccation and light tolerance

Desiccation in combination with light can damage both *E. pedicellatum* and *P. plumbea* (Fig. 17). They fully recovered after 7 d of desiccation but at a delayed rate at all drying treatments except for the hardest desiccation at 0% RH. Their ability to recover after environmentally relevant drying regimes is consistent with the view that old forest cyanolichens are rather tolerant to periods of drought in combination with light (Gauslaa et al., 2012). As recovery from damages caused by light during desiccation requires activation by hydration, cyanolichens need a higher resistance than chloro- and cephalolichens that can be activated every night by humid air.

At Tegningfallet, continuous drought periods can be longer than the 7 d used in this experiment. While visiting the site during the long dry period in May 2020, all individuals of *E. pedicellatum* were dry. I also observed that bryophytes even on the ground closer to the waterfall than the trees with *E. pedicellatum* were fully desiccated in the morning. This drought period lasted over twenty days, when RH never exceeded 95%, an important threshold for cyanolichens, as they require long-lasting RH above 95% for activation of photosynthesis (Schlensog et al., 2000). Such observation supports the presented finding that *E. pedicellatum* has a high desiccation tolerance and confirms that *E. pedicellatum* tolerates periods up to several weeks at most, without precipitation combined with a relatively low RH.

Interestingly, the responses in Fv/Fm were rather similar for the two species. The rare *E. pedicellatum*, believed to experience most damage from the drought treatments, actually tolerated drought in darkness slightly better than the much more common *P. plumbea*. *Pectenia plumbea* is an abundant species in wet coastal deciduous forests in Norway (Artsdatabanken, 2020), but a large difference between the two could not be found in desiccation tolerance.

Light was a strong explanatory variable (Table 2) for the response in Fv/Fm for both species. As Fig. 7A-B show, the main *E. pedicellatum* population was continuously shaded from direct sun from the end of October until March 1, and this might be important for reducing chances 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). The exposure of the four trees hosting the main part of the population to light and mist from the waterfall, together with the unique bark pH for spruce bark (as previously mentioned in 4.3) may explain the strong spatial distribution of specimens at the site.

### 4.8 Growth rates

*E. pedicellatum* was more challenging to grow in a growth chamber than expected. As the growth experiment was performed after measuring high $CO_2$ uptake and $O_2$-evolution, a high growth rate was expected. Unexpectedly, several thalli had negative RGR, indicating that carbon loss was higher than carbon gain. The limited pool of available specimens only allowed for n=16 thalli at each temperature regime, and as several thalli lost biomass, trends in temperature response were hard to detect. Only weakly significantly lower RGR was shown at the highest temperature, likely due to high respiratory rates (Lange & Green, 2006). The optimum temperature of this experiment 18/13 °C fits well with the optimum temperature found

in the experiment of temperature-controlled $CO_2$ uptake. Another similarity between the gas exchange and growth results was the lower carbon gain at the coldest temperature.

Growth chamber experiments have previously shown that cyanolichens can achieve an RGR of 10 mg $g^{-1}$ $day^{-1}$ during a 14-day growth experiment under similar conditions (Bidussi et al., 2013a). This corresponded to the RGR recorded for the most fast-growing specimen of *E. pedicellatum*. At the same time, these earlier measured Lobarion species had a reported $CO_2$-uptake about four-five times smaller than *E. pedicellatum* (Bidussi et al., 2013a). This raises the question of whether the experimental set up (Gauslaa et al., 2016) was less optimal for the assumingly demanding *E. pedicellatum*. Some of the Petri-dishes tended to be filled up with water that soaked the lichen, likely causing suprasaturation. However, when this was observed, dishes where emptied, and this possible cause of error was checked for more carefully watering the rest of the time. Even if suprasaturation frequently occurred, *E. pedicellatum* should still have had positive $CO_2$-uptake, as the experiment with $CO_2$ uptake during desiccation cycles shows (Fig. 14), and this alone should therefore not explain the negative RGR in several thalli. On the other hand, almost all thalli had low Fv/Fm values at the end of the experiment, indicating some damage during the experiment. In the general linear model (3.8), Fv/Fm reduction did to some extent explain the low RGR levels in damaged thalli. Another possible source of error was a leaching of carbohydrates due to overwatering (Alam et al., 2015), however, a different experimental setup is needed to check for this. It is also possible that some thalli were already damaged before the start of the experiment, as they were collected from fallen branches. It should be mentioned that for all experiments, available lichen material was highly restricted due to the rareness of the species, and for several experiments, sample size (n) was not as large as ideal.

The relatively low RGRs of *E. pedicellatum* from this experiment should also be discussed in a life cycle perspective, as the same experimental setup as the one used here has achieved high RGR for several Lobarion species (Bidussi et al., 2013a). Compared to for instance the fast-growing *Lobaria pulmonaria* which is known to have a generation time of more than 17 years, with investments in growth mostly at early life stages (Larsson & Gauslaa, 2011), *E. pedicellatum* appears fertile already with thallus size as small as 2-3 $cm^2$ (Gauslaa & Arsenault, 2020; Pers. observation). *Erioderma pedicellatum* thus appears to use a r-strategy (Grime, 1977), with large investments in reproduction at early life stages, which may lead to large maintenance costs and thus less carbon allocation to growth when larger. This is supported by the significant decrease in RGR with increasing thallus area (Fig. 19A). Species such as *L.*

*pulmonaria* which can be considered k-strategists, mostly invest in growth at early life stages (Gauslaa & Goward, 2012). There is trade-off between growth and reproduction in lichens (Gauslaa, 2006), which may to some degree contribute to *E. pedicellatum*'s relatively low growth rate in this experiment. That being said, *E. pedicellatum's* choice of substratum at Tegningfallet requires a high growth rate, as the branches it grows on fall down at such a high rate. It is therefore expected that RGR would have been markedly higher if all thalli included in the experiment consisted of healthy thalli, and if the experiment had been performed without further damaging thalli by overwatering.

# Concluding remarks

Even with access to a highly restricted number of thalli for experiments, this thesis has provided much new knowledge about the ecophysiology of *E. pedicellatum*. The studied Norwegian population of *E. pedicellatum* has a lower WHC and STM than the Newfoundland population, which further has implications for water-storage and water uptake. The species depends on unusually high bark pH for spruce at Tegningfallet, in combination with high light, high relative humidity and cool temperature conditions. Its $CO_2$ and $O_2$-uptake were high, indicating that the species has a rapid growth rate at Tegningfallet. However, the growth rate recorded in growth cabinets was shown low, assumingly due to high maintenance costs combined with too humid conditions. *Erioderma pedicellatum* shared the high desiccation tolerance with other cyanolichens, but experienced some permanent damage when exposed to the hardest desiccation treatment in combination with light. The findings may explain the rareness of the species, as it assumingly demands a combination of condition that is rare in nature. The knowledge gained in this thesis should be used in combination with persisting knowledge about lichen conservation actively to create suitable habitat by restauration, and consider transplantation trials to better the situation of this critically endangered lichen species.

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# Supplementary material

**Table 1** Water-storage traits data with thallus area ($cm^2$), specific thallus mass (mg DM $cm^{-2}$), total water holding capacity (mg $H_2O$ $cm^{-2}$), internal water holding capacity (mg $H_2O$ $cm^{-2}$), external water holding capacity (mg $H_2O$ $cm^{-2}$) and external/internal water holding capacity (mg $H_2O$ $cm^{-2}$) for *E. pedicellatum* from Tegningfallet, Norway.

| Thallus | Area | STM | $WHC_{total}$ | $WHC_{internal}$ | $WHC_{external}$ | $WHC_{ext/int}$ |
|---|---|---|---|---|---|---|
| 1 | 16.4 | 6.8 | 31.2 | 22.6 | 8.6 | 0.4 |
| 2 | 12.4 | 12.7 | 55.1 | 32.8 | 22.3 | 0.7 |
| 3 | 12.1 | 10.2 | 40.0 | 22.1 | 17.9 | 0.8 |
| 4 | 8.9 | 7.8 | 34.5 | 18.2 | 16.3 | 0.9 |
| 5 | 11.7 | 6.0 | 28.8 | 14.3 | 14.5 | 1.0 |
| 6 | 17.2 | 9.1 | 37.9 | 21.5 | 16.5 | 0.8 |
| 7 | 20.1 | 15.7 | 68.5 | 45.6 | 22.9 | 0.5 |
| 8 | 12.4 | 6.7 | 34.5 | 17.4 | 17.1 | 1.0 |
| 9 | 24.9 | 10.0 | 43.6 | 23.6 | 20.0 | 0.9 |
| 10 | 7.2 | 11.6 | 53.7 | 26.7 | 26.9 | 1.0 |
| 11 | 26.0 | 5.5 | 33.7 | 13.5 | 20.2 | 1.5 |
| 12 | 8.9 | 13.1 | 58.1 | 30.1 | 28.0 | 0.9 |
| 13 | 12.5 | 11.8 | 50.1 | 27.9 | 22.2 | 0.8 |
| 14 | 17.9 | 12.3 | 58.7 | 30.7 | 28.0 | 0.9 |
| 15 | 10.0 | 8.5 | 39.2 | 22.2 | 17.0 | 0.8 |
| 16 | 11.6 | 5.5 | 25.8 | 14.3 | 11.6 | 0.8 |
| 17 | 4.7 | 3.0 | 16.2 | 7.2 | 8.9 | 1.2 |
| 18 | 3.6 | 3.9 | 18.1 | 9.2 | 8.9 | 1.0 |
| 19 | 2.3 | 3.0 | 13.9 | 6.5 | 7.4 | 1.1 |
| 20 | 1.7 | 4.7 | 32.3 | 10.0 | 22.4 | 2.2 |
| 21 | 12.6 | 9.5 | 48.1 | 26.8 | 21.3 | 0.8 |
| 22 | 20.2 | 13.5 | 61.7 | 35.1 | 26.6 | 0.8 |
| 23 | 9.7 | 4.3 | 26.7 | 10.6 | 16.1 | 1.5 |
| 24 | 8.8 | 6.8 | 35.1 | 15.3 | 19.8 | 1.3 |
| 25 | 7.8 | 6.2 | 32.4 | 13.3 | 19.1 | 1.4 |
| 26 | 11.2 | 5.0 | 25.9 | 11.4 | 14.5 | 1.3 |
| 27 | 14.2 | 5.8 | 30.1 | 13.1 | 17.0 | 1.3 |
| 28 | 6.4 | 7.3 | 42.4 | 15.5 | 26.9 | 1.7 |
| 29 | 11.7 | 7.9 | 31.8 | 17.1 | 14.7 | 0.9 |
| 30 | 10.0 | 8.0 | 39.5 | 20.0 | 19.5 | 1.0 |
| 31 | 9.9 | 7.5 | 35.3 | 16.3 | 19.0 | 1.2 |
| 32 | 20.4 | 13.3 | 56.5 | 32.5 | 24.0 | 0.7 |
| 33 | 7.5 | 4.5 | 24.0 | 10.4 | 13.6 | 1.3 |
| 34 | 18.3 | 9.2 | 41.7 | 21.9 | 19.9 | 0.9 |
| 35 | 11.7 | 9.9 | 63.4 | 28.7 | 34.7 | 1.2 |
| 36 | 16.3 | 12.3 | 56.6 | 31.9 | 24.7 | 0.8 |
| 37 | 9.2 | 11.2 | 54.7 | 29.4 | 25.3 | 0.9 |
| 38 | 13.1 | 11.1 | 46.0 | 25.4 | 20.5 | 0.8 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 39 | 9.7 | 6.6 | 33.5 | 17.1 | 16.4 | 1.0 |
| 40 | 18.7 | 11.0 | 54.4 | 35.5 | 18.9 | 0.5 |
| 41 | 19.0 | 17.1 | 73.9 | 48.4 | 25.5 | 0.5 |
| 42 | 11.0 | 5.5 | 28.4 | 14.2 | 14.2 | 1.0 |
| 43 | 11.0 | 7.1 | 38.7 | 14.8 | 23.9 | 1.6 |
| 44 | 13.9 | 13.8 | 57.5 | 37.0 | 20.5 | 0.6 |
| 45 | 8.4 | 4.9 | 24.6 | 12.4 | 12.3 | 1.0 |
| 46 | 7.2 | 9.7 | 48.4 | 25.7 | 22.6 | 0.9 |
| 47 | 13.4 | 7.1 | 32.1 | 17.9 | 14.2 | 0.8 |
| 48 | 7.1 | 6.9 | 30.3 | 14.6 | 15.6 | 1.1 |
| 49 | 7.2 | 4.5 | 28.2 | 11.2 | 16.9 | 1.5 |
| 50 | 2.7 | 2.3 | 25.1 | 5.8 | 19.3 | 3.3 |
| 51 | 2.1 | 4.7 | 35.8 | 9.6 | 26.2 | 2.7 |
| 52 | 11.2 | 7.9 | 40.7 | 17.1 | 23.6 | 1.4 |
| 53 | 14.3 | 5.5 | 22.7 | 10.8 | 11.9 | 1.1 |
| 54 | 13.6 | 7.0 | 45.2 | 18.8 | 26.4 | 1.4 |
| 55 | 8.1 | 7.1 | 25.0 | 14.9 | 10.1 | 0.7 |
| 56 | 13.2 | 6.8 | 37.9 | 15.7 | 22.2 | 1.4 |
| 57 | 8.0 | 6.4 | 33.5 | 14.0 | 19.5 | 1.4 |
| 58 | 4.3 | 9.4 | 68.1 | 27.1 | 40.9 | 1.5 |
| 59 | 12.0 | 7.9 | 35.7 | 17.3 | 18.3 | 1.1 |
| 60 | 8.3 | 7.8 | 44.0 | 18.0 | 26.0 | 1.4 |
| 61 | 4.7 | 5.9 | 28.8 | 12.2 | 16.6 | 1.4 |
| 62 | 22.6 | 8.5 | 40.1 | 20.6 | 19.4 | 0.9 |
| 63 | 23.0 | 11.9 | 61.2 | 32.9 | 28.3 | 0.9 |
| 64 | 18.3 | 8.9 | 48.8 | 25.3 | 23.5 | 0.9 |
| 65 | 15.2 | 4.8 | 27.7 | 12.2 | 15.5 | 1.3 |
| 66 | 9.1 | 10.1 | 51.9 | 26.2 | 25.6 | 1.0 |
| 67 | 11.3 | 7.6 | 36.0 | 18.9 | 17.1 | 0.9 |
| 68 | 6.9 | 4.3 | 28.0 | 10.4 | 17.7 | 1.7 |
| 69 | 8.5 | 9.1 | 42.6 | 19.7 | 22.9 | 1.2 |
| 70 | 10.9 | 7.9 | 41.0 | 20.5 | 20.6 | 1.0 |
| 71 | 3.5 | 6.6 | 29.6 | 14.5 | 15.1 | 1.0 |
| 72 | 13.5 | 11.3 | 67.9 | 34.4 | 33.5 | 1.0 |
| 73 | 8.3 | 8.1 | 38.7 | 16.4 | 22.3 | 1.4 |
| 74 | 5.9 | 5.3 | 39.1 | 13.3 | 25.8 | 1.9 |
| 75 | 4.9 | 9.1 | 48.4 | 20.5 | 28.0 | 1.4 |
| 76 | 7.3 | 4.2 | 18.3 | 9.7 | 8.6 | 0.9 |

**Table 2** $CO_2$-uptake during desiccation cycle data, with thallus area ($cm^2$), wet mass blotting (mg), wet mass shaking (mg), dry mass (mg), desiccation time (minutes) and maximum recorded net $CO_2$-uptake ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$).

| Thallus | Area | WMb | WMs | DM | Desiccation time | Max C-uptake |
|---|---|---|---|---|---|---|
| 1 | 12.5 | 1233 | 1982 | 480 | 137 | 7.35 |
| 2 | 12.5 | 1442 | 2188 | 574.3 | 140 | 7.5 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 3 | 10.5 | 927 | 1384 | 307 | 110 | 7.5 |
| 4 | 4.5 | 465 | 666 | 150.6 | 85 | 7.6 |
| 5 | 2.7 | 179 | 240 | 67 | 55 | 4.5 |
| 7 | 3.5 | 212 | 307 | 71.2 | 75 | 8.4 |
| 8 | 4 | 249 | 417 | 88.5 | 100 | 9.8 |
| 9 | 6.5 | 674 | 1106 | 210.2 | 155 | 11.5 |
| 10 | 4 | 251 | 427 | 82.8 | 95 | 9 |
| 11 | 4.5 | 426 | 634 | 151.4 | 115 | 6.7 |
| 12 | 5 | 330 | 525 | 105.1 | 115 | 12.8 |
| 14 | 6 | 436 | 742 | 149 | 105 | 9.9 |
| 15 | 6.5 | 694 | 1017 | 209.4 | 145 | 11.4 |
| 16 | 3.6 | 226 | 265 | 49.7 | 60 | 5.2 |
| 17 | 6 | 358 | 552 | 95.2 | 110 | 6 |
| 18 | 1 | 51 | 74 | 24.8 | 35 | 2.2 |
| 19 | 0.7 | 44 | 54 | 14.1 | 35 | 2.9 |
| 20 | 8 | 623 | 1046 | 174.6 | 150 | 14.1 |

**Table 3** Growth experiment data, with thallus area ($cm^2$), temperature (°C), Fv/Fm after experiment ended, change in dry mass weight (mg) and relative growth rate (mg $g^{-1}$ $day^{-1}$).

| Thallus | Area | Temp | Fv/Fm | ± weight | RGR |
|---|---|---|---|---|---|
| 1 | 19 | 1+6 | 0.366 | -1.580 | -0.703 |
| 2 | 10.3 | 1+6 | 0.346 | 2.782 | 3.642 |
| 3 | 13.54 | 1+6 | 0.431 | 0.107 | 0.100 |
| 4 | 9.92 | 1+6 | 0.323 | 1.858 | 3.423 |
| 5 | 23.2 | 1+6 | 0.154 | -8.645 | -2.306 |
| 7 | 12.2 | 1+6 | 0.401 | -0.835 | -1.236 |
| 8 | 20.2 | 1+6 | 0.243 | 2.061 | 0.800 |
| 9 | 13.7 | 1+6 | 0.316 | 0.121 | 0.100 |
| 10 | 6.8 | 1+6 | 0.25 | 0.945 | 2.170 |
| 11 | 8.7 | 1+6 | 0.259 | 1.854 | 3.672 |
| 12 | 15.2 | 1+6 | 0.32 | 2.789 | 3.323 |
| 14 | 7.6 | 1+6 | 0.315 | 0.970 | 1.410 |
| 15 | 7.6 | 1+6 | 0.265 | 0.045 | 0.100 |
| 16 | 11.1 | 1+6 | 0.256 | -0.765 | -0.559 |
| 17 | 18.8 | 1+6 | 0.132 | -15.022 | -4.828 |
| 18 | 9.7 | 1+6 | 0.371 | 3.735 | 2.929 |
| 19 | 9.9 | 7+12 | 0.306 | 4.608 | 4.651 |
| 20 | 8.7 | 7+12 | 0.394 | 3.701 | 3.962 |
| 22 | 8.4 | 7+12 | 0.309 | 2.788 | 3.372 |
| 23 | 9.1 | 7+12 | 0.419 | 1.887 | 2.264 |
| 24 | 13.4 | 7+12 | 0.339 | 6.541 | 2.870 |
| 25 | 17.4 | 7+12 | 0.43 | -14.948 | -3.876 |
| 26 | 14 | 7+12 | 0.192 | -10.586 | -4.461 |
| 27 | 4.4 | 7+12 | 0.386 | 1.840 | 5.028 |
| 28 | 16.4 | 7+12 | 0.329 | -4.247 | -1.613 |
| 30 | 13.7 | 7+12 | 0.151 | -10.574 | -4.231 |
| 31 | 15.2 | 7+12 | 0.385 | 0.749 | 0.100 |

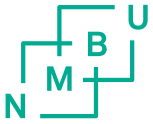
| | | | | | |
|---|---|---|---|---|---|
| 32 | 6.7 | 7+12 | 0.334 | 1.889 | 2.201 |
| 33 | 10.4 | 7+12 | 0.41 | 7.322 | 6.827 |
| 34 | 12.2 | 7+12 | 0.272 | -4.423 | -5.116 |
| 35 | 8.2 | 13+18 | 0.426 | 1.275 | 2.032 |
| 36 | 8 | 13+18 | 0.427 | 8.979 | 10.973 |
| 38 | 5.6 | 13+18 | 0.287 | 3.207 | 4.728 |
| 39 | 11 | 13+18 | 0.402 | 2.159 | 2.032 |
| 40 | 8.2 | 13+18 | 0.384 | 1.171 | 2.032 |
| 41 | 11.4 | 13+18 | 0.422 | 4.292 | 2.032 |
| 42 | 9.3 | 13+18 | 0.38 | 4.378 | 3.490 |
| 43 | 9.6 | 13+18 | 0.404 | 0.401 | 0.201 |
| 44 | 13.5 | 13+18 | 0.336 | 3.408 | 2.032 |
| 46 | 17.6 | 13+18 | 0.218 | -17.257 | -3.451 |
| 47 | 5.5 | 13+18 | 0.32 | 2.878 | 2.979 |
| 48 | 7.8 | 13+18 | 0.367 | 2.159 | 2.032 |
| 49 | 11.7 | 13+18 | 0.404 | 4.222 | 3.585 |
| 50 | 8.2 | 13+18 | 0.218 | 2.471 | 2.032 |
| 51 | 8.8 | 13+18 | 0.334 | 5.149 | 4.349 |
| 52 | 11 | 13+18 | 0.363 | 4.318 | 2.032 |
| 54 | 14.9 | 19+24 | 0.331 | -11.931 | -5.363 |
| 55 | 9.1 | 19+24 | 0.438 | 1.397 | 0.880 |
| 56 | 18.5 | 19+24 | 0.408 | -9.389 | -2.146 |
| 57 | 7.3 | 19+24 | 0.245 | 2.098 | 3.602 |
| 58 | 6.4 | 19+24 | 0.408 | 4.369 | 5.462 |
| 59 | 8.6 | 19+24 | 0.408 | 2.142 | 1.425 |
| 60 | 8 | 19+24 | 0.316 | 2.436 | 3.253 |
| 62 | 8.9 | 19+24 | 0.457 | 5.409 | 4.123 |
| 63 | 8.8 | 19+24 | 0.344 | -14.514 | -7.835 |
| 64 | 8.1 | 19+24 | 0.37 | 0.565 | 0.480 |
| 65 | 6.9 | 19+24 | 0.393 | 6.458 | 6.961 |
| 66 | 5.1 | 19+24 | 0.433 | 3.181 | 4.780 |
| 67 | 7.2 | 19+24 | 0.367 | -0.987 | -1.143 |
| 69 | 9.8 | 19+24 | 0.335 | -1.134 | -0.913 |
| 70 | 11.2 | 19+24 | 0.332 | -4.685 | -1.773 |
| 71 | 13.9 | 19+24 | 0.338 | -15.129 | -7.567 |

**Table 4** Temperature dependent $CO_2$-uptake data, with thallus area ($cm^2$), temperature (°C) and net $CO_2$-uptake (µmol $CO_2$ $m^{-2}$ $s^{-1}$).

| Thallus | Area | Temperature | Net C-uptake |
|---|---|---|---|
| 1 | 3.8 | 5 | 2.5 |
| 2 | 2.5 | 5 | 1.5 |
| 3 | 4.3 | 5 | 5.5 |
| 5 | 3.2 | 5 | 2.9 |

| | | | |
|---|---|---|---|
| 6 | 8.9 | 5 | 6.9 |
| 7 | 8.2 | 5 | 5.2 |
| 8 | 4.7 | 5 | 5 |
| 10 | 7.4 | 5 | 6.7 |
| 12 | 3.6 | 5 | 3 |
| 13 | 5 | 5 | 4.3 |
| 14 | 7.1 | 5 | 5.8 |
| 15 | 5.9 | 5 | 8 |
| 1 | 3.8 | 10 | 4.7 |
| 2 | 2.5 | 10 | 5.4 |
| 3 | 4.3 | 10 | 6.3 |
| 4 | 12.3 | 10 | 6.8 |
| 5 | 3.2 | 10 | 6.7 |
| 6 | 8.9 | 10 | 5.3 |
| 7 | 8.2 | 10 | 5.5 |
| 8 | 4.7 | 10 | 6.6 |
| 9 | 7.6 | 10 | 7.2 |
| 10 | 7.4 | 10 | 6.9 |
| 11 | 8.9 | 10 | 7.6 |
| 12 | 3.6 | 10 | 4.3 |
| 13 | 5 | 10 | 4.9 |
| 14 | 7.1 | 10 | 5.7 |
| 15 | 5.9 | 10 | 6.6 |
| 1 | 3.8 | 15 | 4.6 |
| 2 | 2.5 | 15 | 4.8 |
| 3 | 4.3 | 15 | 6.8 |
| 4 | 12.3 | 15 | 6.6 |
| 5 | 3.2 | 15 | 5.9 |
| 6 | 8.9 | 15 | 5.7 |
| 7 | 8.2 | 15 | 5.4 |
| 8 | 4.7 | 15 | 7.5 |
| 9 | 7.6 | 15 | 7 |
| 10 | 7.4 | 15 | 6.1 |
| 11 | 8.9 | 15 | 8.5 |
| 12 | 3.6 | 15 | 4.4 |

| | | | |
|---|---|---|---|
| 13 | 5 | 15 | 5.7 |
| 14 | 7.1 | 15 | 4.9 |
| 15 | 5.9 | 15 | 7.2 |
| 1 | 3.8 | 20 | 4.8 |
| 2 | 2.5 | 20 | 5.3 |
| 3 | 4.3 | 20 | 6.3 |
| 4 | 12.3 | 20 | 4.3 |
| 5 | 3.2 | 20 | 5 |
| 6 | 8.9 | 20 | 4.3 |
| 7 | 8.2 | 20 | 5.3 |
| 8 | 4.7 | 20 | 6.8 |
| 9 | 7.6 | 20 | 5.8 |
| 10 | 7.4 | 20 | 4.9 |
| 11 | 8.9 | 20 | 7.1 |
| 12 | 3.6 | 20 | 4.1 |
| 13 | 5 | 20 | 4.6 |
| 14 | 7.1 | 20 | 3.4 |
| 15 | 5.9 | 20 | 7.8 |
| 1 | 3.8 | 25 | 2.5 |
| 2 | 2.5 | 25 | 1.5 |
| 3 | 4.3 | 25 | 3.1 |
| 4 | 12.3 | 25 | 2.5 |
| 5 | 3.2 | 25 | 2.1 |
| 6 | 8.9 | 25 | 2.8 |
| 7 | 8.2 | 25 | 1.4 |
| 8 | 4.7 | 25 | 3.2 |
| 9 | 7.6 | 25 | 2.5 |
| 10 | 7.4 | 25 | 2.1 |
| 11 | 8.9 | 25 | 4.5 |
| 12 | 3.6 | 25 | 1.1 |
| 13 | 5 | 25 | 0.8 |
| 14 | 7.1 | 25 | 2.8 |
| 15 | 5.9 | 25 | 2.3 |




**Norges miljø- og biovitenskapelige universitet**
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway