Size is a main driver for hydration traits in cyano- and cephalolichens of boreal rainforest canopies

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ABSTRACT
We measured the water holding capacity per area (WHCA; mg H2O cm⁻²), and thus the saturating rainfall (mm), for sympatric cyano- (Lobaria scrobiculata and Pseudocyphellaria crocata) and cephalolichens (Lobaria pulmonaria) along canopy height gradients in boreal rainforests, to quantify the importance of specimen size, photobiont type and branch height as WHCA drivers. Size increased WHCA by a factor of four. Cyanolichens had z 1.5 times higher WHCA than cephalolichens. Finally, branch height significantly increased WHCA for the Lobaria species. Reported responses are consistent with higher optimal rainfall requirements for reproducing versus juvenile specimens, and for cyanolichens versus those with green algal photobionts. Increased WHCA with height in the canopy is consistent with acclimation to stronger evaporative demands. The results highlight the link between rainfall patterns and maximal sizes realized for a given lichen species and habitat, and extend our understanding of why the cyanolichen/green algal lichen-ratio increases in forests with increasing rainfall.

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Introduction
Poikilohydric organisms like lichens depend on hydration events to resume metabolic processes and grow (e.g. Palmqvist & Sundberg, 2000). While humid air alone can activate photosynthesis in chloro- and cephalolichens with green algae as the only or major photobiont, respectively (e.g. Jonsson Cabrajic et al., 2010; Lidén et al., 2010), cyanolichens entirely depend on liquid water for positive carbon gain (Lange et al., 1986). These two hydration traits associate with morphological adaptation and/or acclimation: Many lichens, chlorolichens in particular, are thin and rapidly resume
photosynthesis in humid air, whereas thick lichens need a longer time (Larson & Kershaw, 1976; Larson, 1981; Lange & Kilian, 1985), or remain inactive (cyanolichens). To compensate for the longer time needed to fill the water storage of thick lichens with water from humid air, thick lichens retain water for longer periods after hydration events. Water holding capacity (WHCₐ, expressed as mass of water at saturation per thallus area) is an often ignored, but important, lichen trait that equates to mm rainfall needed for saturation. It determines the duration of hydration periods and influences the ecological niche (as reviewed by Gauslaa, 2014). Specific thallus mass (STM; dry mass per thallus area) drives the WHCₐ at intra- and interspecific levels (Gauslaa & Coxson, 2011). STM is the inverse equivalent of the frequently used parameter specific leaf area, SLA, in plant science, connected to the resource use economy (e.g. Reich et al., 1998; Wright et al., 2004). In adult lichen life stages, STM increases with size (Dahlman et al., 2002; Gauslaa et al., 2009; MacDonald & Coxson, 2013). However, the size-dependency of WHCₐ from early juvenile to late reproductive stages is not known. Because small juvenile thalli are likely particularly influenced by their ability to retain moisture, they may represent a more critical stage in the lichen life cycle than buffered mature thalli (Gauslaa & Solhaug, 1998).

Epiphytic lichens representing a threatened biodiversity component show strong vertical gradients in tree canopies (McCune, 1993; McCune et al., 1997; Gauslaa, 1997; Coxson & Coyle, 2003; Gauslaa et al., 2008; Rambo, 2010; Marmor et al., 2013). However, regulating factors for such gradients are insufficiently known. We will search for vertical gradients in STM and WHCₐ for the cephalolichens Lobaria pulmonaria and for the cyanolichens Pseudocyphellaria crocata and Lobaria scrobiculata in boreal Picea abies-dominated rainforests in Norway recognized as hot spot areas for epiphyte diversity (Holien & Tønsberg, 1996; Rolstad et al., 2001). The canopy height gradient is complex because spruce drains the water away from the inner and lower canopy (see Stoutjesdijk & Barkman, 1987; Goward, 2003). Availability of liquid water may thus decline with increasing distance from tree tops, whereas air humidity tends to be highest in sheltered lower canopy, at least during the day (Geiger, 1950). Wind and light often increase with height, leading to increasing evaporative demands. In such canopy gradients, WHCₐ of cyanolichens that depends on liquid water may respond differently than the WHCₐ of lichens with green algae capable also of using humid air.

By focusing on STM and WHCₐ, we add information to a recent trend in quantifying lichen traits (e.g. Asplund & Wardle, 2013; Lang et al. 2009). We will quantify these two traits across size classes for each of three sympatric study species sampled on branches from different height levels in Picea abies-dominated old rainforests. Our aim is to test the following hypotheses: (1) Thallus size drives WHCₐ in a similar way across size classes – consistent with the view that reproduction per se does not have major effects on hydration requirements. (2) WHCₐ is shaped by STM in species-specific ways – consistent with species-specific water storage traits; and/or (3) The photobiont influences the size-dependency of WHCₐ in lichens – consistent with a trade-off between rapid and frequent uptake of humidity in thin green algal lichens versus more water conserving strategies in cyanolichens that depend on liquid water. (4) WHCₐ increases with height in the canopy – consistent with acclimation tuning these traits to ambient hydration sources. Finally, we discuss how measured traits influence the ecology of our species.

### Material and methods

#### Site

We studied lichens on Picea abies in old ravine forests in Foss, Nord-Trøndelag, Norway (64°47'800''N, 12°00'079''E, 50–100 m a.s.l.). The stand age, estimated from cores of 27 trees, was 120 yr (Table 1). The site, classified as boreal rainforest (Della-Sala et al., 2011), is located in the markedly oceanic section of the southern boreal vegetation zone with 240 rainy days a year (Moen, 1999). Mean annual precipitation is 1375 mm, varying from 59 mm (May) to 154 mm (Oct.). Rainfall was frequent; 128 d of 214 d in total were rainy for Mar.-Sep. averaged for 2010–2012, but gentle (52 d ≤ 1 mm; 106 d ≤ 10 mm d⁻¹). Rainfall data were obtained from the Norwegian Meteorological Institute, eiklima.met.no., Overhalla.

We randomly collected 37 entire intact branches from 23 trees, as a subset of a larger lichen population study (Hilmo et al., 2013). Trees had to be alive, >50 cm in circumference.
at breast height, and the tree top should not be broken. We established a canopy height gradient from 2 to 14 m above the ground, comprising >2 branches per m height level (tree and branch variables; see Table 1). Sampled branches were dried at room temperature and stored 13 months at −20 °C before sampling of lichens.

**Lichen material**

Studied lichens were *L. pulmonaria* with green algal primary photobiont with Nostoc in internal cephalodia, versus *L. scrobiculata* and *P. crocata* with Nostoc only. *Lobaria scrobiculata* was the most abundant species, followed by *P. crocata*, and then *L. pulmonaria* (Hilmo et al., 2013). We randomly gathered a numerically representative sample of healthy and intact thalli of each species, including the smallest and largest on every branch to widen the size distribution (Table 1; 1 178 thalli in total). Each thallus was stored after debris had been removed.

**Functional traits**

Lichens were hydrated by repeated sprayings with deionized water until full saturation. Photographs were taken of fully hydrated thalli placed on a white light transilluminator (Model TW-43 White light, UVP, Upland, CA 91786 USA) and flattened below a piece of glass (Nikon D300 camera; Nikon AF-S Micro Nikkor 105 mm lens). Area (A) was recorded by analyzing photographs in ImageJ 1.46f version (Wayne Rasband, National Institutes of Health, USA). Shortly after taking the photographs, thalli were again fully moistened, and then gently blotted with filter paper to remove excess surface water before wet mass (WM) was measured. After 2 hr of air-drying at room temperature, thalli were oven-dried for 24 hr at 70 °C and reweighed to obtain dry mass (DM). Mass was measured to the nearest 10 µg, or 0.1 mg, depending on thallus size. Based on A and DM values, specific thallus mass (STM), was calculated as STM = DM/A. The water holding capacity (WHCA) was calculated as WHCA = (WM – DM)/A. The percent water at saturation was calculated as % water = [(WM – DM) *100]/DM. Lichen mass per area at full hydration is thus STM + WHCA.

**Statistical analyses**

Distributions of studied variables were not normal. Therefore, Kruskal–Wallis and Dunn’s methods were used to test differences among species. For simple and multiple regressions, all variables were log-transformed to improve normality and linearity. Multiple regressions were done in SigmaPlot 11.0 (Systat Software Inc., San Jose, CA); other analyses were done in Minitab 16 (Minitab Inc., State College, PA). We analyzed the effect of canopy height on WHCA by using best subset multiple regression analyses for each species separately. In order not to use strongly correlated independent variables, we used the mass of water (WM – DM) at saturation (dependent variable) instead of WHCA, and the independent variables used were thallus area and branch height. However, for comparison, we also ran the best subset regression models for species-specific WHCA by adding STM.

**Results**

STM was a main driver of WHCA in each of the three species (Fig 1; r^2_adj = 0.842–0.878). The more biomass the lichen invested per thallus area, the higher was its WHCA.

| Table 2 – Mean values ± SE for thallus size (minimum – maximum is given), specific thallus mass (STM), water holding capacity (WHCA) and percentage water at saturation for sampled thalli of studied species |
|-----------------|-----------------|-----------------|-----------------|-----------------|
|                 | **n**           | **Size (mm²)**  | **STM (mg DM cm⁻²)** | **WHCA (mg H₂O cm⁻²)** | **% Water at saturation** |
| Lobaria pulmonaria | 223             | 853 ± 140⁸ (3.2–12 450) | 8.6 ± 0.2b | 12.7 ± 0.3a | 146 ± 1⁸ |
| Lobaria scrobiculata | 567             | 468 ± 49⁷ (2.3–16 630) | 9.7 ± 0.1c | 18.0 ± 0.2b | 187 ± 1c |
| Pseudocyphellaria crocata | 388           | 242 ± 20° (2.4–3 126) | 7.3 ± 0.1a | 12.8 ± 0.2a | 176 ± 1b |

Among species, means sharing the same letter are not statistically different from each other (all pairwise multiple procedures: Dunn’s; p < 0.05).
particularly in cyanolichens. Across the entire STM range, *L. pulmonaria* had the lowest and *L. scrobiculata* the highest WHC. *L. scrobiculata* had a WHC/STM-ratio of 1.86 versus 1.75 in *P. crocata*, and 1.48 in *L. pulmonaria* as computed from overall means (Table 2).

STM as well as WHC highly significantly increased with thallus size in all species (Fig 2). *P. crocata* had the lowest STM (7.3 ± 0.1 mg DM cm⁻²), followed by *L. pulmonaria* (8.6 ± 0.2 mg DM cm⁻²) and *L. scrobiculata* (9.7 ± 0.1 mg DM cm⁻²; Table 2). The WHCA in *P. crocata* (12.8 ± 0.2 mg H₂O cm⁻²) matched the WHCA in *L. pulmonaria* (12.7 ± 0.3 mg H₂O cm⁻²) despite its significantly lower STM. These two species had lower WHC than *L. scrobiculata* (18.0 ± 0.2 mg H₂O cm⁻²; Fig 2D). The slope of all regression lines (Fig 2A–C) were similar in the log–log plot, summarized in Fig 2D, implying that the increase in WHCA with size in plots with linear scales would have been significantly steeper in the two cyanolichens than in the cephalolichen. The two cyanolichens had significantly higher percent water at saturation than the cephalolichen, and among the cyanolichens, *L. scrobiculata* contained most water (Table 2).

WHCA directly translates to the minimum mm rainfall needed to saturate a lichen specimen with water (10 mg H₂O cm⁻² = 0.1 mm rain). The minimum rainfall needed for full photosynthetic activation depended on size, but was in the range of 0.05–0.4 mm for studied thalli (Fig 3). Relatively large (100 cm²) thalli needed 3.6 times (*L. scrobiculata*) to 4.7 times (*P. crocata*) higher rainfall for activation than small ones (1 mm²). At all the low intensity rainfall levels shown in Fig 3, approximately 10 times larger thalli were fully hydrated for *L. pulmonaria* than for *L. scrobiculata*. For example, 0.2 mm rain only saturates *L. scrobiculata* up to a size of 3.3 cm², but fully hydrates 10 times larger *L. pulmonaria* (35 cm²) and six times larger *P. crocata* (20 cm²; see Fig 3).

The species distribution along the height gradient differed between the species (Table 1). *L. pulmonaria* (2–10 m) and *P. crocata* (2–9 m) grew in a narrower canopy height range (<10 m) than *L. scrobiculata*, (2–14 m; Table 1). In the best subset multiple regression analysis (Table 3), increasing canopy height was highly significantly associated with larger water storage for both *Lobaria* species. However, in *P. crocata* with most thalli found on the lower branches, water storage slightly, but significantly (p = 0.026) decreased with increasing canopy height. Adding STM to the species-specific model given in Table 3 (data not shown), branch height became slightly more significant; size and STM both gave highly significantly positive contributions to the WHC. These models should be treated with some caution due to intercorrelation between size and STM (VIF = 2.4–4.4).

![Fig 2](image-url)

**Fig 2** – The thallus size (area) dependency of specific thallus mass (STM) and water holding capacity (WHC) in (A) *Lobaria scrobiculata*, (B) *L. pulmonaria* and (C) *Pseudocyphellaria crocata* sampled on branches of *Picea abies* in boreal rainforests. (D) Regression lines for all species (see A–C) with corresponding 95% confidence intervals are given. Regression equations: *L. scrobiculata*: log(WHC) = 0.954 + 0.138 log(area); r²_adj = 0.693; p < 0.001, log(STM) = 0.688 + 0.136 log(area); r²_adj = 0.701, p < 0.001. *L. pulmonaria*: log(WHC) = 0.759 + 0.153 log(area); r²_adj = 0.769; p < 0.001, log(STM) = 0.643 + 0.131 log(area); r²_adj = 0.763; p < 0.001. *P. crocata*: log(WHC) = 0.75 + 0.167 log(area); r²_adj = 0.630; p < 0.001, log(STM) = 0.543 + 0.15 log(area); r²_adj = 0.583; p < 0.001. Closed symbols: STM; open symbols: WHCₐ.
Percent water at saturation did not significantly relate to size (data not shown). There were weak, but highly significant positive regressions between percent water at saturation and size at similar rates throughout all life stage classes from juvenile to old ages (Fig 2). Within the main growing season for lichens in our study area (Larsson & Gauslaa, 2011), as many as 2/3 of the 128 rainy days had <0.6 mm rain (Fig 3; inset). The other source of liquid water, dewfall, is often <0.2 mm (Richards, 2002; Jacobs et al., 2002, 2006; Hao et al., 2012), but may occasionally extend to 0.3–0.5 mm (Garratt & Segal, 1988; Xiao et al., 2013). Because the variation in WHCA in our species equates to a range of 0.04–0.40 mm rain corresponding to common rainfall intensities in the study area (see Fig 2), many low rainfall events influence hydration and growth in a strongly size-dependent way.

Small thalli with green algae are opportunistic as they do not depend only on major rainfalls, which is also the situation for thin lichen thalli (Larson & Kershaw, 1976; Larson, 1981; Lange & Kilian, 1985). For example, the thin Lecanora muralis depends more on dew than on rain for its annual carbon gain (Lange, 2002, 2003b, a). With increasing size, lichens should become more dependent on lasting rain, and benefit more from canopy drainage water flushing the lichens, particularly because overlying branches trap the first rain in a tree canopy. Drainage water probably allows the lichens we studied to form much larger thalli on trunks of deciduous trees than on spruce branches. Growth rate (Armstrong & Bradwell, 2011) and mature size (Jackson et al., 2006) of a given lichen species vary substantially between its habitats. Variation in water availability likely influences habitat-specific mature sizes of a given lichen species.

Size influences lichen growth, survival and reproduction (Armstrong & Bradwell, 2011; Larsson & Gauslaa, 2011; Hilmo et al., 2013). As large specimens stay moist and active for longer periods than small ones, they should grow faster or

### Discussion

#### Size dependency

Large lichen specimens store more water per thallus area than small ones (Gauslaa & Solhaug, 1998; Fos et al., 1999). Nevertheless, our study is the first to show that WHCA, and thus the mm rain needed to fill the lichen water storage, also increase with size at similar rates throughout all life stage classes from juvenile to old ages (Fig 2). Within the main growing season for lichens in our study area (Larsson & Gauslaa, 2011), as many as 2/3 of the 128 rainy days had <0.6 mm rain (Fig 3; inset). The other source of liquid water, dewfall, is often <0.2 mm (Richards, 2002; Jacobs et al., 2002, 2006; Hao et al., 2012), but may occasionally extend to 0.3–0.5 mm (Garratt & Segal, 1988; Xiao et al., 2013). Because the variation in WHCA in our species equates to a range of 0.04–0.40 mm rain corresponding to common rainfall intensities in the study area (see Fig 2), many low rainfall events influence hydration and growth in a strongly size-dependent way.

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### Table 3 – Best subset multiple regression models for the mass of water, log(WM – DM), in Lobaria pulmonaria, L. scrobiculata and Pseudocyphellaria crocata sampled on branches of Picea abies in boreal rainforests

<table>
<thead>
<tr>
<th>Variable</th>
<th>Coef. ± std. error</th>
<th>t</th>
<th>P</th>
<th>VIF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lobaria pulmonaria ($r^2_{adj} = 0.995$; $p &lt; 0.001$; n = 223)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>0.998 ± 0.0197</td>
<td>50.68</td>
<td>&lt;0.001</td>
<td>0.000</td>
</tr>
<tr>
<td>Log(thallus size)</td>
<td>1.156 ± 0.0056</td>
<td>208.21</td>
<td>&lt;0.001</td>
<td>1.023</td>
</tr>
<tr>
<td>Log(branch height)</td>
<td>0.104 ± 0.0293</td>
<td>3.54</td>
<td>&lt;0.001</td>
<td>1.023</td>
</tr>
<tr>
<td>Lobaria scrobiculata ($r^2_{adj} = 0.986; p &lt; 0.001; n = 567$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>1.260 ± 0.0096</td>
<td>130.92</td>
<td>&lt;0.001</td>
<td>0.000</td>
</tr>
<tr>
<td>Log(thallus size)</td>
<td>1.031 ± 0.0053</td>
<td>194.93</td>
<td>&lt;0.001</td>
<td>1.033</td>
</tr>
<tr>
<td>Log(branch height)</td>
<td>0.0536 ± 0.0120</td>
<td>4.468</td>
<td>&lt;0.001</td>
<td>1.033</td>
</tr>
<tr>
<td>Pseudocyphellaria crocata ($r^2_{adj} = 0.988; p &lt; 0.001; n = 388$)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Constant</td>
<td>1.100 ± 0.0081</td>
<td>136.65</td>
<td>&lt;0.001</td>
<td>0.000</td>
</tr>
<tr>
<td>Log(thallus size)</td>
<td>1.168 ± 0.0065</td>
<td>180.10</td>
<td>&lt;0.001</td>
<td>1.003</td>
</tr>
<tr>
<td>Log(branch height)</td>
<td>-0.035 ± 0.0016</td>
<td>-2.23</td>
<td>0.026</td>
<td>1.003</td>
</tr>
</tbody>
</table>

VIF: Variation Inflation Factor.
reproduce more. Significant increases in chlorophyll content per thallus area with increasing size in *L. pulmonaria* (Asplund & Gauslaa, 2007) may also imply higher growth potential with increasing size. However, large and/or thick thalli require more water, and their high biomass per area necessarily implies higher maintenance costs than for small ones, as is the case for leaves of most plants (e.g., Milla & Reich, 2007). Investments in carbon-based secondary compounds increase with size (Asplund & Gauslaa, 2007). Also reproductive effort increases with size, and reproduction reduces growth rates (Gauslaa, 2006). In general, growth rates decline with size even in juvenile stages (Larsson & Gauslaa, 2011), and likely reflect more rapidly increasing costs than benefits. Also in plants, growth is reduced with increasing specific leaf mass, or with decreasing specific leaf area using plant biology terms (e.g., Poorter & Remkes, 1990). Thereby, increasing size, and thus higher WHCₐ and chlorophyll contents, may just be the way growing lichens maintain the status quo.

**Species-specific differences**

In addition to strong size-dependencies of STM and WHCₐ, there were significant differences between sympatric lichen species (Fig 2). *L. scrobiculata* needs much higher hydration levels to become photosynthetically active than the thinner *L. pulmonaria* with rapid water uptake/loss (MacKenzie & Campbell, 2001), but the former species has longer periods of carbon fixation (Campbell, 2001), but the former species has longer periods of carbon fixation (MacKenzie & Campbell, 2001). In general, growth rates decline with size even in juvenile stages (Larsson & Gauslaa, 2011), and likely reflect more rapidly increasing costs than benefits. Also in plants, growth is reduced with increasing specific leaf mass, or with decreasing specific leaf area using plant biology terms (e.g., Poorter & Remkes, 1990). Thereby, increasing size, and thus higher WHCₐ and chlorophyll contents, may just be the way growing lichens maintain the status quo.

**Habitat-specific differences**

In addition to size- and species-specific differences, there is still some environmental regulation of STM and WHCₐ. After 3 months transplantation to shaded young stands darker than source stands, STM in *L. pulmonaria* decreased, whereas it increased in clear-cuts (Gauslaa et al., 2006). Across all sizes, *L. pulmonaria* had higher STM when growing on the light-demanding *Alnus incana* than on nearby shade-tolerant *Abies lasiocarpa* (MacDonald & Coxson, 2013). Likewise, STM in *Lobaria* species increased in sunny dry seasons and decreased in wet seasons (Larsson et al., 2012). Thus, STM increases with increasing light and/or evaporative demands. Here, WHCₐ and STM in *L. pulmonaria* and *L. scrobiculata* increased with height in the canopy. High WHCₐ may improve lichen functioning in dry upper canopies, and we see this as acclimation to increased light and/or evaporative demands (Hilmo, 2002; Gaio-Oliveira et al., 2004; Gauslaa & Goward, 2012). However, *P. crocata* did not respond in this way, which may contribute to its rarity in upper canopies (Hilmo et al., 2013), as well as explain its absence outside Atlantic forests in Europe (Holien & Tønsberg, 1996). The low WHCₐ of this and other thin cyanolichen members of *Pseudocyphellaria*, like *Pseudocyphellaria anomala* (Gauslaa & Coxson, 2011) and *Pseudocyphellaria dis-similis* (Snellgr & Green, 1981), probably constrains their ecological niche to very humid sites (Green & Lange, 1991), whereas the *Lobaria* species benefitting from humid air (*L. pulmonaria*) or from large water storage (*L. scrobiculata*) have wider ecological amplitudes.

In conclusion, WHCₐ strongly increases with increasing size, consistent with partly different ecological niches for small and large specimens. Secondly, species respond differently, consistent with photobiont-specific water storage traits. Finally, the two *Lobaria* species acclimate by increasing WHCₐ with increasing height in canopy gradients, consistent with acclimation to increasing evaporative demands.

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