



Externally held water – a key factor for hair lichens in boreal forest canopies



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ABSTRACT

Lichens hold water inside (internal pool) and outside their body (external pool). Yet, external pool size is not known in hair lichens dominating boreal forest canopies. Here we quantify morphological traits and internal/external water in two widespread *Bryoria* species along *Picea abies* canopy-height gradients: *Bryoria fuscescens* at 5–20 m and *Bryoria capillaris* at 15–20 m. Dry mass and specific thallus mass (STM) of intact *B. fuscescens* increased with height, while STM of individual branches did not. Maximum water holding capacity ($\text{mg H}_2\text{O cm}^{-2}$) increased with height, but did not differ between the species. *Bryoria* had much larger external (79–84% of total) than internal water pools, trapping water by dense clusters of thin, overlapping branches. They thus increase water storage in boreal forest canopies and influence hydrology. High external water storage extends hydration periods and improves lichen performance in upper canopies, and thereby contributes to the success of these hair lichens.

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1. Introduction

Physiological activity in lichens and other poikilohydric organisms, including carbon gain, depends on hydration, whereas uptake, storage and loss of water are physical processes (Palmqvist, 2000; Proctor and Tuba, 2002). Depending on the availability of different water sources, lichens have evolved a suite of anatomical and morphological traits that passively influence their hydration status (Lakatos, 2011; Gauslaa, 2014). Water content is usually expressed as a percentage of dry mass (WC), while water holding capacity relating water content to thallus area (WHC, $\text{mg H}_2\text{O cm}^{-2}$) is a measure of mm rain needed to fill a lichen's water storage spaces. Lichens store water both inside their body (internal pool) and on their surface (external pool; Rundel, 1988; Hartard et al., 2009). Their maximal water content including internal and external pools is often recorded after shaking a fully hydrated thallus ($\text{WHC}_{\text{total}}$), while the internal pool ($\text{WHC}_{\text{internal}}$) is usually

determined after gentle blotting has removed the surface water (Blum, 1973; Kershaw, 1985). The external pool ($\text{WHC}_{\text{external}} = \text{WHC}_{\text{total}} - \text{WHC}_{\text{internal}}$) is ecologically important because it extends the duration of time spent hydrated and thus the metabolic activity. However, external water often causes substantial suprasaturation depression of photosynthesis (Lange et al., 1993, 2001; Green et al., 2011) while internal water likely causes less depression. Yet, few studies quantify both internal and external water in lichens (Green et al., 1985; Green and Lange, 1991; Gauslaa, 2014). The $\text{WHC}_{\text{total}} : \text{WHC}_{\text{internal}}$ ratio varies between 1.4 and 2.3 in the few foliose lichens that have been measured (Gauslaa, 2014); this ratio has so far not been measured for fruticose lichens. In lichens, there is often a trade-off between fast uptake of water vapor and high storage capacity (Rundel, 1988).

Epiphytic lichens show vertical niche separation in forest canopies (McCune, 1993; Coxson and Coyle, 2003; Ellis, 2012), but mechanisms are not well understood. For example, Antoine and McCune (2004) showed that vertical distribution patterns of lichens (realized niche) did not always correspond to their growth rate patterns along a canopy height gradient (fundamental niche). This gradient is complex with multiple interacting factors,

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including light, moisture, temperature, wind, nutrients, disturbance as well as substratum availability, quality and age (Sillett and Antoine, 2004; Ellis, 2012). All these factors may influence lichen establishment, growth, reproduction and mortality. Various hypotheses have been proposed for vertical niche differentiation in lichens, including moisture and stand age gradients (McCune, 1993), vapor pressure deficit (Rambo, 2010), light availability (McCune et al., 1997), herbivory (Asplund et al., 2010) and sun-screening pigments (Färber et al., 2014). Water relations likely play a role in vertical stratification because rain, water vapor, dew, snow and subsequent patterns of lichen hydration vary with canopy height, particularly in tall forests (Campbell and Coxson, 2001; Sillett and Antoine, 2004). Lichens in the upper canopy receive water mainly from precipitation while those in lower canopy depend more on humid air, due to interception of rain in the upper canopy (Link et al., 2004). Even in periods without rain, canopy lichens significantly influence diurnal latent heat fluxes in the forest by their diurnal uptake and loss of water (Pypker et al., 2017). Yet, little is known about how water storage traits influence the vertical distribution of lichens in forest canopies (but see Merinero et al., 2014, 2015).

Filamentous 'hair' lichens in the genus *Bryoria* are abundant in forest canopies in cool and cold climates and perform important ecological functions (Brodo and Hawksworth, 1977; Esseen et al., 1996, 2016; Asplund and Wardle, 2017). Ecological studies have often treated intermixed *Bryoria* species collectively because they are difficult to identify (Myllys et al., 2016). However, already Ahlner (1948) recognized species-specific habitat preferences, while Edwards et al. (1960) and Arseneau et al. (1997) documented vertical niche differentiation in forest canopies. *Bryoria* species may occur over the entire canopy height gradient, but are often most abundant in the upper canopies (Arseneau et al., 1997; Campbell and Coxson, 2001; Benson and Coxson, 2002) because of their inability to withstand prolonged hydration in lower canopies (Coxson and Coyle, 2003). By contrast, *Alectoria* and *Usnea* mainly dominate lower canopies of most boreal forests (Ahlner, 1948; Campbell and Coxson, 2001; Benson and Coxson, 2002), probably due to their less protective sun-screen (Färber et al., 2014).

Goward (2003) recognized three vertical zones in forest canopies in British Columbia, differing in *Bryoria* abundance and morphology. The upper canopy supported maximum biomass and densely branched thalli, while *Bryoria* was scarce and less branched in the lower canopy. Goward (2003) suggested that snow depth and ventilation shaped the zones, based on observed high mortality on lower branches after long-lasting rain (Goward, 1998).

In a study restricted to the lower canopy, we showed that *Bryoria* has low capacity to store internal water (Esseen et al., 2015). Here we quantify morphology and internal as well as external water storage in two widespread *Bryoria* species along canopy height gradients in a boreal forest to test the following hypotheses: (1) External water storage in these thin hair lichens is significantly higher than internal storage. (2) Water storage capacity increases with height in the canopy. (3) Species-specific differences in water storage can explain vertical niche separation between *Bryoria capillaris* and *Bryoria fuscescens*.

2. Material and methods

2.1. Study area

We collected *Bryoria* in Vindeln Experimental Forest, 50 km northwest of Umeå, northeastern Sweden. The site (64°13'58"N, 19°49'37"E; 200 m a.s.l.) had old, mesic-moist *Picea abies*-dominated boreal forest with emergent *Pinus sylvestris*. The stand originated after a fire in 1779 and most *Picea* were 160–230 yr old

(Esseen, P.-A., unpublished data). The open forest had a canopy cover of 50% and a basal area of 24 m² ha⁻¹ (80% *Picea* and 19% *Pinus*). *Picea* had a mean height of 18.4 m (maximum 25 m). The climate is cold-temperate humid. Mean annual temperature is 2.0 °C; monthly mean temperature is –10 °C in January, 15 °C in July (1961–2014; data from the Swedish Meteorological and Hydrological Institute, <http://luftweb.smhi.se/>). Mean annual precipitation is 672 mm; 65% rain and 35% snow.

Hair lichens showed a clear vertical zonation. In the lower canopy (<10 m), *Alectoria sarmentosa* dominated the epiphytic vegetation, followed by *Bryoria* and *Usnea* species. *Bryoria* constituted 17% of total hair lichen biomass at 3–4 m height and increased to 27% at 6–7 m (P.-A. Esseen, unpublished data). There was a rapid shift to full *Bryoria* dominance in upper canopy (Fig. 1A). The pale *B. capillaris* (Fig. 1B) dominated the tree tops. About 2–3 m down, the dark *B. fuscescens* (Fig. 1C, D) took over the dominance, while dark *Bryoria fremontii* mainly occurred below c. 15 m. All *Bryoria* species occurred in lower canopy, but *B. capillaris* was very sparse.

2.2. Lichen collection

Lichens were collected in November–December 2013 on eight recently windthrown *P. abies* trees. Four trees grew in undisturbed forest while four grew in stands thinned in 2009. Mean diameter of sample trees was 28.5 cm (range 18–38 cm) and mean height was 20.8 m (range 15.7–24.3 m). We sampled lichens from branches at four height intervals: 5–7, 10–12, 15–16 and 20–23 m, hereafter referred as 5, 10, 15 and 20 m. We selected thalli representing the variability in morphology at each height interval, but excluded thalli enveloping twigs. Only specimens without or with minimal ingrowth of other species were sampled. The thalli were carefully separated from the substratum to preserve intact morphology. They were dried 24 h at room temperature and stored 2–4 months at –18 °C until measurements were performed. Sixteen thalli per species were selected from each height interval: 5–20 m for *B. fuscescens*, but only 15 and 20 m for *B. capillaris*, due to insufficient material in the lower canopy. We checked the identity of all specimens by the KOH spot test (Velmalá et al., 2014).

2.3. Determination of STM and water storage in whole thalli

Methods followed Esseen et al. (2015) with minor modifications. Each thallus, placed on a plastic garden grid (mesh size of 1 cm), was repeatedly sprayed with deionized water until full hydration (≥ 10 min). Then we placed another grid on top of the thallus and removed excess surface water by gently shaking the lichen three times before turning the grids upside-down and repeating three shakings. The water saturated thallus was weighed (WM_{shaking}), then gently blotted twice between filter papers to remove all external water. The thallus was reweighed (WM_{blotting}) and then placed between two 18 cm × 24 cm × 0.2 cm glass plates on a light panel (Dörr LP-400, LED light). Images were taken with a Nikon D800E camera (36 megapixel sensor) and Nikon 105 mm macro lens with a resolution of 0.02 mm/pixel at 61 cm focal distance.

Lichens were dried for 24 h at room temperature and weighed. Ten random thalli per species were dried at 70 °C for 24 h and their oven-dry mass (DM) was recorded. DM was calculated for all thalli by multiplying their air-dry masses with the mean species-specific correction factor (DM/air-dry mass-ratio).

2.4. Determination of morphological traits in dry subsamples

Specific thallus mass for individual branches (STM-branch_{dry}, a proxy of branch thickness; see below) and thallus area overlap

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