



Morphology influences water storage in hair lichens from boreal forest canopies



Per-Anders Esseen^{a,*}, Therese Olsson^a, Darwyn Coxson^b, Yngvar Gauslaa^c

^a Department of Ecology and Environmental Science, Umeå University, SE 901 87 Umeå, Sweden

^b University of Northern British Columbia, Ecosystem Science and Management Program, 3333 University Way, Prince George, BC, V2N 4Z9, Canada

^c Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway

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ABSTRACT

Hair lichens (*Alectoria*, *Bryoria*, *Usnea*) with high surface-area-to-mass ratios rapidly trap moisture. By photography and scanning we examined how internal water storage depended on morphological traits in five species. Specific thallus mass (STM, mg DM cm⁻²) and water holding capacity (WHC, mg H₂O cm⁻²) after shaking and blotting a fully hydrated thallus increased with thallus area. STM was ≈50% higher in *Alectoria* and *Usnea* thalli than in *Bryoria*. WHC was highest in *Alectoria* while percent water content of freshly blotted thalli was lowest in *Usnea*. Thallus area overlap ratio (TAO), assessing branch density of the thallus, was highest in the two thinnest *Bryoria*; lower in the thicker *Usnea*. Within species, hair lichens increased their water storage by increasing branch density rather than branch diameter. The taxonomically related genera *Alectoria* and *Bryoria* shared water storage characteristics, and differed from *Usnea*. Hair lichens in lower canopies have among the lowest water storage capacity reported in lichens.

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1. Introduction

With their poikilohydric way of life, lichens do not actively regulate uptake, storage and loss of water (Rundel, 1988; Green et al., 2011). Instead they use morphological traits facilitating uptake and retention of water from different sources (rain, humid air, dew), such as thickness of certain tissues (Gauslaa and Coxson, 2011), special structures like hypothallus (Gauslaa and Solhaug, 1998), and extracellular sheaths holding water around cyanobacterial photobionts (Honegger et al., 1996) to prolong photosynthetic periods. The maximal water held in a lichen includes both internal water of a fully hydrated thallus and external water on its surfaces. The utilization of external water sources separates poikilohydric lichens and bryophytes from homoiohydric vascular plants (Proctor and Tuba, 2002). Surface water is ecologically relevant, but here we quantify the internal water component only. With a 'saturated' thallus we refer to the water content left after shaking

and blotting a fully hydrated thallus. Water holding capacity (WHC), given in mg H₂O cm⁻², is an important functional parameter (reviewed in Gauslaa, 2014) that can be translated to mm rainfall, a unit often used in gas exchange studies of crustose lichens that cannot easily be weighed (Lange et al., 1998; Lakatos et al., 2012). Water content, after lightly blotting surface water films from saturated thalli, refers to the combined water held within biont tissue itself and the water held in free spaces within the thallus, e.g. as between mesophyll cells (WHC_{blotting}). Here, we use the term WHC as a short abbreviation for WHC_{blotting}. Specific thallus mass (STM, mg DM cm⁻²), a simple proxy of thickness, is a main driver of WHC in foliose (Gauslaa and Coxson, 2011) and fruticose lichens (Gauslaa, 2014). Morphological parameters like STM and WHC are shaped by evolutionary processes, evidenced by species-specific traits, and by acclimation to environmental conditions (Merinero et al., 2015). Such traits are coupled to the spatial and temporal variability of water sources as summarized by Gauslaa (2014). However, as STM and WHC depend on size (Merinero et al., 2014), size must be taken into account in any comparison among species.

Both uptake and loss of water are physical processes in lichens

* Corresponding author.

E-mail address: per-anders.esseen@umu.se (P.-A. Esseen).

in which hydration kinetics vary among species depending on water storage capacity, morphology, anatomy and colour (Palmqvist, 2000). For example, the exchange of water is normally faster in fruticose lichens than in foliose ones (Kershaw, 1985; Hartard et al., 2009). The models developed by Jonsson et al. (2008), Jonsson Čabrajč et al. (2010) and Lidén et al. (2010) are tools to predict not only hydration status, desiccation and hydration kinetics, but also productivity in foliose and fruticose lichens from biophysical data. Yet, interactions between morphological traits and water storage are not well understood in filamentous fruticose lichens. 'Hair' lichens (alectorioids) in genera like *Alectoria*, *Bryoria* and *Usnea*, have high surface-area-to-mass ratios (Larson and Kershaw, 1976; Larson, 1981; Kershaw, 1985). Their green-algal bionts can activate photosynthesis in humid air; by contrast cyanolichens require liquid water (Lange et al., 2001). The growth form of thin morphotypes of hair lichens, e.g. in *Ramalina menziesii* and *Ramalina thrausta*, is regarded as an adaptation for rapid uptake of moisture from humid air (Lange et al., 1986). Thin thalli enable rapid hydration by any kinds of water source. Yet, we do not know how internal factors like thickness (branch diameter), structure (cortex, medulla and central cord, if present), as well as the 3D branching structure and density shape their water storage capacity. Here we use the term 'branch' for both 'main' (if present) and side branches following Brodo and Hawksworth (1977) and Thell and Moberg (2011).

The species-rich *Usnea* genus has worldwide distribution, while *Alectoria* and *Bryoria* mostly occur in cool climates. Hair lichens vary widely in habitat requirements, but are particularly dominant in old boreal forest canopies, where they perform important ecosystem functions (Esseen et al., 1996; Hauck, 2011). They are key species in food webs (Pettersson et al., 1995; Kinley et al., 2006), contributing to the interception of water and nutrients (Stevenson and Coxson, 2003; Campbell et al., 2010), and may improve the water use of their hosts (Stanton et al., 2014). In the boreal zone, *Bryoria* is most abundant in open drier forests, while *Alectoria/Usnea* tend to dominate more shaded, humid and/or warmer forests (Ahlner, 1948; Thell and Moberg, 2011). Whereas *Bryoria* dominates upper canopies, *Alectoria/Usnea* are more abundant in lower canopies (Campbell and Coxson, 2001), but can dominate upper canopies in moist forests (Benson and Coxson, 2002; Antoine and McCune, 2004).

Studying morphology and water storage in hair lichens is challenging. First, accurate area estimation is difficult in thin branches (<1 mm in diameter). Leaf area meters (e.g. LI3100 Licor; Lincoln. Nebr., USA) have insufficient resolution to capture such thin branches. Second, the three-dimensional structure of hair lichens cannot easily be projected in two dimensions, a task complicated by large thallus sizes. Third, hydrated hair lichen area must be measured quickly because of rapid evaporation. Finally, their colour varies from light grey to dark brown, which complicates classification of images.

These limitations point to the need for improved techniques for studying hair lichens. Here, we describe the morphology and water storage in hair lichens using photography and scanning in combination with image analysis. By such methods, we compare water storage parameters and their dependency on morphological traits in five boreal members of the genera *Alectoria*, *Bryoria* and *Usnea*, and test the following hypotheses: (1) STM and WHC in hair lichens are size dependent and follow the 1:1 relationship reported for foliose (Gauslaa and Coxson, 2011) and fruticose chlorolichens (Gauslaa, 2014). Such knowledge may facilitate comparison and understanding of lichen functioning across functional groups. (2) *Alectoria* and *Usnea*, occupying the lower canopy, share water storage parameters (WHC, percent water at saturation) and morphological traits (STM, branch diameter, branch overlap), but

differ from *Bryoria* dominating the upper canopy. (3) Hair lichens increase water storage by increasing branch density (area overlap) rather than by increasing branch diameter.

2. Material and methods

2.1. Study species

Five widespread boreal hair lichens were studied: *Alectoria sarmentosa*, *Bryoria capillaris*, *Bryoria fremontii*, *Bryoria fuscescens* and *Usnea dasypoga* (Thell and Moberg, 2011). *B. fremontii* prefers open pine forests in Fennoscandia, *B. capillaris* occurs in mesic-humid forests and prefers spruce where it often inhabits the rain shadow in lower canopy, while *B. fuscescens* has the widest niche. However, it should be noted that *Bryoria* is regarded a difficult genus (Myllys et al., 2011; Thell and Moberg, 2011; Velmala et al., 2014); species distribution and taxonomy is incompletely understood. The lower canopy is the only height where all study species co-occur. To facilitate comparisons of species-specific traits, all lichens were consistently sampled from branches 2–4 m above ground. Healthy and intact thalli representing single 'individuals' were collected, without ingrowth from other species. Sampled thalli, representing a range of size classes, were free-hanging; thalli intermingled in twigs and needles were excluded. Precautions were taken to maintain their 3D morphology during sampling and transportation. Lichens were collected in August–October 2012 and stored at -18°C until measurements were performed a few weeks later.

2.2. Study area

Lichens were collected in the sites used by Färber et al. (2014) in Vindel'n's Experimental Forest, c. 60 km northwest of Umeå, north-eastern Sweden at 175–200 m a.s.l. The climate is cold-temperate humid. Mean annual temperature is 2°C ; monthly mean temperature is -11°C in January, 14°C in July (Raab and Vedin, 1995). Mean annual precipitation: ≈ 600 mm; 65% is rain and 35% is snow (November–April). *B. capillaris* was collected in a mesic, open mixed *Picea abies* and *Pinus sylvestris* stand ($64^{\circ}13'58''\text{N}$, $19^{\circ}49'37''\text{E}$). *B. fuscescens*, *B. fremontii* ($64^{\circ}13'47''\text{N}$, $19^{\circ}46'57''\text{E}$) and *A. sarmentosa* ($64^{\circ}14'23''\text{N}$, $19^{\circ}47'46''\text{E}$) were from mesic, semi-open stands with *P. abies* and *P. sylvestris*, while *U. dasypoga* was from a moist-wet, closed canopy *P. abies* stand ($64^{\circ}14'13''\text{N}$, $19^{\circ}47'29''\text{E}$) along a small stream. Lichens were sampled mainly from *P. abies* but also from *P. sylvestris*.

2.3. Estimation of thallus area

The hydrated thallus area (A_{wet}) is an important functional lichen parameter. For methodological reasons (see below), only dry thallus area (A_{dry}) can be accurately measured for individual branches in subsections of thin hair lichens. Thallus area (A_{wet} and/or A_{dry}) was expressed as the vertically projected area of a 'gently' compressed thallus laying on a flat surface. Pilot studies examined whether a flatbed scanner or a digital camera was best suited for area estimation of hydrated thalli. Both hydrated and dry thalli (10–25 cm) of *Alectoria* and *Bryoria* were scanned and photographed after placement between two $18\text{ cm} \times 24\text{ cm} \times 0.2\text{ cm}$ glass plates. The upper plate added sufficient pressure to flatten the branched specimen to optimize focus. Pass-through light was used for both the scanner and the camera to minimize shadows.

2.3.1. Scanning

The scanner (Epson Perfection 4990 Photo) had a maximum optical resolution of 4800 dpi. The software was Epson scan and the

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