



Morphology drives water storage traits in the globally widespread lichen genus *Usnea*

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ABSTRACT

Links between lichen morphology, internal/external water storage and distribution patterns are poorly known. We compared mass- (WC, % H₂O) and area-based (WHC, mg H₂O cm⁻²) hydration traits in seven pendent or shrubby *Usnea* species from oceanic to continental climates. All species held more external than internal water. Internal WHC and WC increased with specific thallus mass (STM, mg cm⁻²), while external WC decreased. Shrubby species had higher STM and total WHC than pendent ones. The continental *Usnea hirta* (shrubby) had the highest total and external storage; the suboceanic *Usnea longissima* (pendent) had the lowest internal storage. Morphology drives hydration traits and explains distributions of some *Usnea* species, but such traits did not distinguish oceanic from widespread species. Shrubby species maximize water storage and thus prolong hydration after rainfall events and/or hydration by dew. The low internal WHC in pendent species is likely an adaptation to frequent hydration in humid air.

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1. Introduction

Lichens inhabit most terrestrial ecosystems and contribute to ecosystem function and biodiversity (Nash, 2008; Porada et al., 2013; Asplund and Wardle, 2017). Environmental and anthropogenic factors (reviewed by Nash, 2008; Ellis, 2012) shape the distribution of species at global, regional and local scales (Leavitt and Lumbsch, 2016). At the same time, hydration regime, i.e. the spatial and temporal availability of rain, humid air, fog, dew and/or snow, plays fundamental roles in driving carbon gain and lichen distributions (e.g. Lange, 2000b, 2003a; Palmqvist, 2000; Green et al., 2011; Gauslaa, 2014). Lichens are poikilohydric, and their uptake, storage and loss of water are physical processes determined by ambient humidity (Rundel, 1988). However, anatomical and morphological traits also influence their hydration status. For example, thin fruticose lichens activate almost instantaneously in humid air (Phinney et al., 2018) and efficiently absorb moisture (Lakatos, 2011; Esseen et al., 2015), even fog in deserts (Stanton and

Horn, 2013), whereas thick hypothalli capture substantial rain and stemflow in some cyanolichens (Gauslaa and Solhaug, 1998). Better knowledge on how hydration traits shape lichen distributions across climates may improve our understanding of lichens' responses to the hydric environment at various spatial scales.

Hydration status in lichens is usually expressed as dry mass-based water contents (WC, %) and/or area-based water contents of a hydrated thallus, also denoted by water-holding capacity (WHC, mg H₂O cm⁻²). The latter represents mm rain needed to fill a lichen with water. Hydration status can also be studied with physiological traits such as apoplastic water content and corresponding water potential (Ψ) (Beckett, 1995, 2002; Nardini et al., 2013). Lichens store water inside as well as on the outer surfaces of their tissues. Both internal and external water influence hydration periods and hence carbon gain. Excess external water often causes substantial suprasaturation depression of photosynthesis due to the inherently slower diffusion of CO₂ in water as compared to air (Lange et al., 1993, 2001; Green et al., 2011). So far, few studies have separated internal and external water in lichens (Green et al., 1985; Green and Lange, 1991; Gauslaa, 2014) and related such characteristics to their morphological traits. However, recent studies have shown that fruticose *Bryoria* spp. have a much larger

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external water storage than foliose *Lobaria* spp. (Esseen et al., 2017; Longinotti et al., 2017).

Usnea, a hyperdiverse fruticose lichen genus (≈ 350 spp.), distributed from polar to tropical areas (Walker, 1985; Stevens, 1991; Truong and Clerc, 2016), is the largest fruticose genus within the Parmeliaceae (Thell et al., 2012; Lücking et al., 2016). The genus has large inter- and intraspecific variability in anatomy and morphology (Clerc, 1998, 2011; Randlane et al., 2009) and is suitable for analysing links between hydration traits and broad-scale distribution in lichens. The thallus is erect (shrubby) or pendent. All species have an elastic, cartilaginous central axis providing mechanical strength. The branches are cylindrical to irregular, with or without fibrils, papillae, tubercles, fiberclcs, soralia, isidiomorphs and isidiofibrils (Clerc, 1998, 2011) that likely affect the capacity to hold water externally by increasing the thallus surface area. Also the thickness and type of the cortex, medulla and axis are important taxonomic characters in this genus (Clerc, 1998), that have been shown to influence storage of water in foliose lichens (Gauslaa and Coxson, 2011).

The genus *Usnea* is most diverse in temperate and tropical forests, particularly in montane rainforests (Thell et al., 2012; Truong et al., 2013; Truong and Clerc, 2016). *Usnea* is also abundant in many boreal forests, with important ecosystem functions, e.g. food and habitat for animals (Hauck, 2011; Esseen and Coxson, 2015; Asplund and Wardle, 2017). Thirty-two *Usnea* species have been recorded in Europe (Randlane et al., 2009), 17 of which occur in Norway and Sweden (Clerc, 2011). Some are restricted to oceanic, high-rainfall forests (e.g. *Usnea cornuta*, *Usnea flammea*), while others are widespread (e.g. *Usnea dasopoga*, *Usnea subfloridana*). The iconic *Usnea longissima* – the world's longest lichen – has become threatened in Europe due to logging and air pollution (Esseen et al., 1981; Rolstad and Rolstad, 2008; Storaunet et al., 2008; Nascimbene and Tretiach, 2009). The largest European populations of *U. longissima* occur in Fennoscandia, where it is mainly associated with humid, old *Picea abies* forests (Ahlner, 1948). To implement effective conservation measures, we need to understand how its hydration traits are linked to both macro- and microclimate.

For the dominant hair lichen genera in boreal forests (i.e. *Alectoria*, *Bryoria*, *Usnea*), climate, nutrients, forest structure and air pollution are key factors shaping their distribution (Bruteig, 1993; Esseen et al., 2016). The genus *Usnea* is more common in the temperate zone and southern parts of the boreal zone (Clerc, 2011), and high biomass is often associated with productive, humid forests. Water storage has been quantified in some *Usnea* spp. (e.g. Blum, 1973; Lange et al., 1993; Hartard et al., 2009; Gauslaa, 2014), but comparisons of species from different climates are lacking. Esseen et al. (2015) showed that the pendent *U. dasopoga* had lower internal water content than sympatric *Alectoria sarmentosa* and *Bryoria* spp. However, we do not know if internal and external water storage differ between pendent and shrubby *Usnea* species, or between species in continental and oceanic climates.

In this study, we have compared the mass (WC) and area-based (WHC) hydration traits in seven epiphytic *Usnea* species to search for links between these functional traits, morphology, and their broad-scale distributions. We test the following hypotheses: (1) Internal water storage increases with specific thallus mass (STM), a proxy of lichen thickness at intra- and interspecific levels. (2) External water relates to thallus morphology; thin, pendent species with high surface-area-to-mass ratios (low STM) can hold more external water than thick shrubby species. (3) Shrubby species have higher maximal water storage than pendent species. (4) Hydration traits differ between oceanic and continental species.

2. Material and methods

2.1. Study species

We selected seven *Usnea* species (Fig. 1) to maximize variability in growth form, morphology, anatomy, and distribution from oceanic to continental areas. Two species were pendent: *U. dasopoga* (widespread) and *U. longissima* (syn. *Dolichousnea longissima*, suboceanic); five were shrubby: *U. cornuta* (oceanic), *U. flammea* (oceanic), *Usnea florida* (southern), *Usnea hirta* (continental tendency) and *U. subfloridana* (widespread).

Lichens were collected in optimal habitats supporting large populations in southern Norway and northern Sweden in August 2015. Thalli of a range of sizes for each species were sampled 0.5–4.0 m above ground from 10 to 15 trees per site. *U. cornuta*, *U. flammea* and *U. subfloridana* were collected from two nearby coastal hills in Spindanger, south-west Norway (58°2'N, 6°50'E; elevation c. 70 m a.s.l.). The climate was oceanic with a mean annual rainfall of 1745 mm and a mean annual temperature of 6.9 °C (<https://www.yr.no>; Lyngdal site). Both sites were temperate, oak-dominated forest on mesic soils in a previously grazed, wooded landscape. *U. cornuta* and *U. flammea* were only present on lower trunks of *Quercus petraea*, *Betula pubescens* and *Populus tremula* beneath a relatively continuous canopy, while *U. subfloridana* occurred on branches of *Q. petraea* in open, low forest. *U. florida* was collected from *Quercus robur/petraea* branches in Svarttjennheia, south-east Norway (58°78'N, 9°3'E; 90 m a.s.l.) in a gentle S-facing slope with open, mixed, oak-dominated forest on thin, mesotrophic soils. The climate was suboceanic with mean annual precipitation of 1230 mm and annual temperature of 5.3 °C (<https://www.yr.no>; Nelaug site). *U. longissima* was collected from *P. abies* in a steep N-facing slope in an old, humid and open boreal forest in Totenåsen, Oppland, eastern Norway (60°35'N, 11°02'E; 720 m a.s.l.). The annual precipitation was 1000 mm; mean annual temperature (0–2 °C). All thalli lacked a holdfast, and had thus resulted from natural fragmentation, the normal type of dispersal for this species (Esseen, 1985; Gauslaa, 1997). *U. hirta* was collected from *Pinus sylvestris* in Norrmjöle, NE Sweden (63°39'N, 20°7'E; 10 m a.s.l.) in a dry-mesic, open and low-productive, old coniferous boreal forest near the Baltic Sea. The precipitation was 639 mm/year; mean annual temperature 3.7 °C (<http://luftweb.smhi.se/>). Finally, *U. dasopoga* was collected from *P. abies* in an old, mixed coniferous boreal forest at Stor-Skogberget, NE Sweden (64°1'N, 20°34'E; 75 m a.s.l.). The forest was humid and semi-open with tall trees. The annual precipitation was 759 mm; mean annual temperature was 2.9 °C. Collected lichens were dried at room temperature for 24 h and stored 1–3 months at –18 °C until measurements.

2.2. Determination of morphological and water storage traits

Methods follow Esseen et al. (2015, 2017), but we sprayed the thalli for 60 min (see below) to ensure full hydration, including the compact central axis. We selected 36 thalli of each species, varying in size and morphology. The thalli were kept at room temperature for 24 h and weighed (DM_{air} ; ± 0.1 mg). Oven dry mass (DM) after 24 h in 70 °C was determined for five additional random thalli per species and used as a correction factor (DM/DM_{air}) to calculate oven-dry DM for all thalli. Experimental thalli were then placed on a net (mesh size 3 mm \times 3 mm), and sprayed with deionized water at 5 min intervals during 60 min. Each thallus was subsequently placed between two plastic nets (mesh size 14 mm \times 14 mm), and shaken three times. The nets were then turned upside down and shaken three additional times, and wet mass ($WM_{shaking}$) was recorded. Thereafter, each thallus was placed between two filter

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