

Hydration traits in cephalolichen members of the epiphytic old forest genus *Lobaria* (s. lat.)

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Abstract: This study aims to quantify the size-dependency of important hydration traits in *Lobaria amplissima*, *L. pulmonaria* and *L. virens* sampled in sympatric populations on deciduous tree trunks in southern Norway, and to discuss possible implications of species-specific traits for the ecological niches of these old forest cephalolichens. Traits measured were thallus size (area and mass), specific thallus mass (STM), internal (WHC_{internal}) and external water-holding capacity (WHC_{external}), and water content (WC) after shaking and after blotting. *Lobaria amplissima* had the highest WHC_{internal}, 2–6 times higher than *L. pulmonaria* with the lowest WHC_{internal}. WHC_{internal} driven by STM, strongly depended on size. WHC_{external} was 28% (*L. virens*) to 47% (*L. pulmonaria*) of the WHC_{internal}. Unlike WHC_{internal}, WHC_{external} did not depend on thallus area, meaning that WHC_{external} is proportionally higher for smaller compared with larger thalli. The most widespread species, *L. pulmonaria*, benefits from a flexible hydration strategy due to low STM, facilitating the use of more diverse water sources than the other two species that depend more on rain, particularly *L. amplissima* with the highest STM and thus relatively high WHC_{internal}. For *L. virens*, a combination of less specialized hydration traits and a low tolerance to higher light intensity probably jeopardizes its survival outside rainforest habitats.

Key words: *Lobaria amplissima*, *Lobaria pulmonaria*, *Lobaria virens*, specific thallus mass, water-holding capacity, water storage

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Introduction

A lichen is a symbiotic association in which a mycobiont provides water, mineral nutrients, shelter and chemical defence for its photosynthetic partners living inside a fungus-made growth cabinet (but see Spribille *et al.* (2016) reporting additional basidiomycete yeasts in most lichen cortices). In return, autotrophic partners provide the fungal host(s) with fixed carbon derived from photosynthesis. Lichens play important functional roles (Asplund & Wardle 2016); they participate in water and nutrient cycles (Ellis 2012) by increasing canopy interception of precipitation and trapping airborne nutrients (Van Stan & Pypker 2015). Lichens with cyanobacteria as their only or secondary photobiont also fix atmospheric nitrogen (e.g. Green *et al.* 1980;

Antoine 2004), with benefits for their ecosystems. Moreover, epiphytic lichens constitute fodder for microfauna and, by facilitating large arthropods, they improve the foraging habitat quality for birds (Pettersson *et al.* 1995). Finally, lichens serve as indicators to monitor environmental factors, such as ecological continuity in forests (Rose 1976; Nordén & Appelqvist 2001) and ambient hydration sources (e.g. Gauslaa 2014; Giordani *et al.* 2014; Matos *et al.* 2015).

Lichens, as poikilohydric organisms, lack active regulation of water uptake and loss (Kranter *et al.* 2008; Green *et al.* 2011). Thus, external factors drive their desiccation and rehydration cycles (Lakatos 2011), although morphological modifications can be important (see below). Most lichens with green algae as their only or main photobiont (chloro- and cephalolichens, respectively) can reactivate photosynthesis in humid air, whereas cyanolichens require liquid water such as rain or dew (Lange *et al.* 1986; Schlensoeg *et al.* 2000). A poikilohydric

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strategy enables the majority of lichens to survive long dry periods and to recover quickly upon rehydration (Lakatos 2011), and thus to dominate habitats characterized by severe environmental stresses such as Arctic and alpine regions, upper tree canopies and rocks.

Although enhancing survival, a poikilohydric strategy comes with a price. For instance, prolonged exposure to light while desiccated can cause lasting photoinhibitory damage (Gauslaa *et al.* 2012). The longer the period of desiccation, the longer the time lichens need to re-establish normal carbon fixation rates (as reviewed by Kranner *et al.* 2008). Moreover, desiccation entails increased ROS (i.e. reactive oxygen species) formation. Therefore resources have to be devoted to defence mechanisms, such as antioxidants (Kranner *et al.* 2008) and energy dissipating mechanisms (Heber *et al.* 2010). Most damage occurs when drought occurs at higher light intensities (Gauslaa *et al.* 2012; Färber *et al.* 2014), despite drying reducing cortical light transmittance (Gauslaa & Solhaug 2001) and inducing the curling of lobes which reduces light exposure (Barták *et al.* 2006). Such processes are not always sufficient to prevent high light-induced damage in desiccated lichens (Gauslaa *et al.* 2012), particularly in shade-adapted old forest species (Gauslaa & Solhaug 1996).

A useful functional parameter for assessing hydration of lichens is the water-holding capacity per unit area (WHC; reviewed by Gauslaa 2014), which translates to millimetres of rain needed for saturation. Cyanolichens have higher WHC than cephalo-/chlorolichens (Gauslaa & Coxson 2011), partly compensating for the cyanolichen dependency on infrequent rain/dew events (Lange *et al.* 1986) versus the frequent activation in humid air by green-algal lichens (Lange 2003). Water content drives the duration of photosynthetic periods in lichens (Gauslaa & Solhaug 1998); no carbon gain occurs in dry thalli.

The WHC not only depends on photobiont type but also on parameters such as growth form, surface area to volume ratio, thickness of cortex, hydrophobicity of thallus surface and presence/absence of a tomentum

(Larson 1987; Gauslaa & Solhaug 1998; Lakatos 2011; Esseen *et al.* 2015). Thin growth forms activate photosynthesis faster during water uptake and lose water more rapidly than thicker ones (Kershaw 1985; Hartard *et al.* 2009). Specific thallus mass (STM = dry mass (DM) per hydrated thallus area (A_{wet}), a proxy of thallus thickness, is a main driver for internal water holding capacity, $\text{WHC}_{\text{internal}}$ (Gauslaa & Coxson 2011; Gauslaa 2014; Merinero *et al.* 2014). The strong positive correlation between $\text{WHC}_{\text{internal}}$ and STM across growth forms (Esseen *et al.* 2015) indicates the need for increased DM investments per unit thallus area in order to enhance the water storage. In addition to species-specific differences, STM and thus $\text{WHC}_{\text{internal}}$ can acclimate to increasing light and evaporative force (Merinero *et al.* 2015). However, little is known about external water holding capacity ($\text{WHC}_{\text{external}}$) in lichens.

Here, we study three foliose cephalolichens in *Lobaria* (s. lat.): *L. pulmonaria* (L.) Hoffm., *L. virens* (With.) J. R. Laundon and *L. amplissima* (Scop.) Forssell. The two latter species are also reported as *Ricasolia amplissima* (Scop.) De Not. (Moncada *et al.* 2013) and *R. virens* (With.) H. H. Blom & Tønsberg (Tønsberg *et al.* 2016), and are thus taxonomically more closely related to each other than to *L. pulmonaria*. They often co-occur with cyanolichens and form the old forest *Lobarion* community favoured by ecological continuity (Rose 1976). *Lobarion* is widely distributed globally, however, the community is declining (Nascimbene *et al.* 2016). The *Lobaria* species are red-listed in most European countries (e.g. Türk & Hafellner 1999; Scheidegger *et al.* 2002; Martínez *et al.* 2003; ArtDatabanken 2015) but not in Norway (Timdal 2015) where the local abundance of these species allows access to lichen material. *Lobaria pulmonaria* is among the most frequently studied lichens worldwide; it has a well-documented size-dependent $\text{WHC}_{\text{internal}}$ (Gauslaa & Coxson 2011; Merinero *et al.* 2014). However, little is known about hydration traits in *L. amplissima* (Lidén *et al.* 2010) and *L. virens* (Honegger & Peter 1994). An

understanding of hydration traits in these species is useful for the development of species-specific conservation strategies such as reintroduction programmes by transplantation (e.g. Gilbert 2002; Smith 2014). Since hydration traits are subjected to acclimation (Merinero *et al.* 2015) and depend on habitat conditions (Gauslaa & Coxson 2011), a search for species-specific traits should compare species in mixed populations. Therefore, in the present work we quantify the species-specific size-dependency of WHC_{internal} and WHC_{external} in sympatric populations of the three epiphytic cephalolichens and test the hypothesis that the closely related *L. amplissima* and *L. virens* share more hydration traits than they do with the more distantly related and more widespread *L. pulmonaria*. Finally, we aim to discuss the implications of possible species-specific hydration traits on the ecological niches of these species.

Material and Methods

Lichen material

The epiphytic cephalolichens *Lobaria amplissima*, *L. pulmonaria* and *L. virens* were sampled from three sites with broadleaved deciduous forests in south and south-eastern Norway: 1) Kristiansand, Vest-Agder (58.1932–58.1960°N, 8.0094–8.0145°E, 70–80 m a.s.l.) with *Quercus petraea*-dominated forests; 2) Larvik, Vestfold (59.0966–59.0992°N, 9.8337–9.428°E, 120–160 m a.s.l.) with mixed forests of *Q. robur*, *Acer platanoides*, *Fagus sylvatica*; 3) Porsgrunn, Telemark (59.112–59.113°N, 9.832–9.835°E, 130–160 m a.s.l.) with mixed forests of *Q. robur*, *Fraxinus excelsior*, *Tilia cordata*, *Ulmus glabra* and *A. platanoides*. In each site, we searched for trees with many thalli of all three lichen species in mixed populations on the trunk. Sampled trees should be spaced >100 m apart to ensure a variation in the local habitat. The only tree species fulfilling these requirements were *Q. petraea* in the southernmost site (Kristiansand), and *Q. robur* and *A. platanoides* in the two other sites. All trees found were in open old forests with canopy gaps due to rocks, yet partly shaded from direct sun. We collected <50% of all thalli of each species present on each trunk at 1–3 m height in October 2015, with an emphasis on collecting a variety of thallus sizes. Debris, tree bark and bryophytes were removed. Then, the lichens were air-dried at room temperature and stored in a freezer at –18 °C until the start of the experiment in February 2016. In total, we collected 478 thalli: 109 *L. amplissima*, 144 *L. pulmonaria* and 225 *L. virens*; 176 from site 1, 200 from site 2 and 103 from site 3.

Quantification of functional traits

Before measurement, thalli were repeatedly sprayed on the upper surface with deionized water until full hydration, meaning that additional sprayings did not lead to any gain in wet mass. We measured wet mass (WM) in three steps: each fully water-saturated thallus was first weighed (WM_{max}), then gently shaken until no more drops were falling before weighing the wet mass (WM_{shaking}), followed by blotting twice with dry filter paper to quantify WM_{blotting} . The hydrated thallus area (A_{wet}) was measured with a Licor Leaf Area Meter (LI 3100). Afterwards, lichens were dried at 20 °C to a constant mass before recording their air-dry mass. On each weighing day, three thalli of each species were sacrificed in order to calculate a correction factor to estimate the oven-dry mass (DM). The sacrificed thalli were dried at 70 °C for 24 h before measuring DM. The ratio between DM and air-dry mass for these thalli was used as a correction factor to estimate the DM of all thalli.

The specific thallus mass (STM) was calculated as DM/A_{wet} . To calculate the water-holding capacity before (WHC_{max}), after shaking (WHC_{shaking}), as well as after blotting (WHC_{blotting}), we used WM_{max} , WM_{shaking} and WM_{blotting} , respectively, as WM in the formula $WHC = (WM - DM)/A_{\text{wet}}$. We considered the water left after blotting as internal water ($WHC_{\text{internal}} = WHC_{\text{blotting}}$), whereas the external water was computed as $WHC_{\text{external}} = WHC_{\text{shaking}} - WHC_{\text{blotting}}$. Percent water content, $WC = (WM - DM)/DM$, was calculated both after shaking and blotting.

Statistical analyses

Means, standard errors and medians were given for all traits. For each species, linear regressions with 95% confidence intervals were calculated to evaluate species-specific differences in the size-dependency of STM and WHC-parameters, and to investigate various relationships between traits. Even though log transformation was applied to improve data distributions, a nonparametric test (Kruskal-Wallis one-way analysis of variance on ranks with all pairwise multiple comparison procedures, Dunn's method) was used to assess differences between species. These analyses were run in SigmaPlot (Systat Software, San Jose, CA, USA). Finally, we ran a GLM in Minitab 16 (Minitab Inc., State College, PA, USA) on log-transformed WHC_{internal} with study site and lichen species as factors and thallus area as a covariate.

Results

The influence of collection site and tree species on response variables was assessed. Measured parameters did not differ between the tree species. The variation in hydration traits between sites was weak and inconsistent between species. For example, the site-specific mean WHC_{internal} ranged between

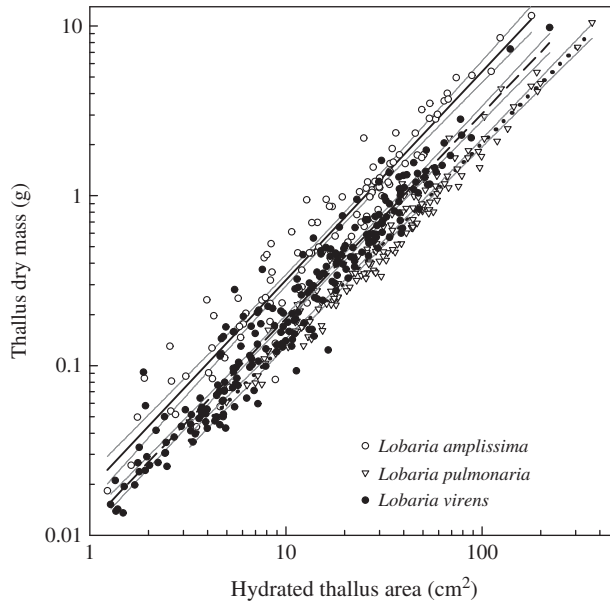


FIG. 1. Relationship between thallus dry mass and hydrated thallus area (A_{wet}) in three cephalolichen species (note log scales). Regression lines (black) for each species with corresponding 95% confidence intervals (grey lines) are given. For regression equations, r^2_{adj} and P -values, see Table 1. Solid line = *Lobaria amplissima*; dashed line = *L. virens*; dotted line = *L. pulmonaria*.

66.3 (site 3) and 67.4 mg $\text{H}_2\text{O cm}^{-2}$ (site 1) for *L. amplissima*, 21.4 (site 1) and 30.4 mg $\text{H}_2\text{O cm}^{-2}$ (site 2) for *L. pulmonaria* and 31.9 (site 2) and 40.6 mg $\text{H}_2\text{O cm}^{-2}$ (site 3) for *L. virens*. In a general linear model on log-transformed $\text{WHC}_{\text{internal}}$, with site and lichen species as fixed factors and thallus area (A_{wet}) as a covariate ($r^2_{\text{adj}} = 0.548$), species and area were highly significant ($P < 0.001$), but not the site ($P = 0.058$). Thus, further analyses focused only on effects of thallus size and lichen species.

In all species, lichen DM tightly followed A_{wet} in the log-log plot ($r^2_{\text{adj}} = 0.922\text{--}0.964$; Fig. 1). For parallel lines in a log-log plot, the uppermost line has a steeper slope in a linear plot than a line located beneath. Thus, along linear DM (g) and A_{wet} (cm^2) scales, the rise in DM with A_{wet} was fastest in *L. amplissima*

(slope = 0.061), more slowly in *L. virens* (slope = 0.038), and slowest in *L. pulmonaria* (slope = 0.026).

In log-log plots, STM (Fig. 2C) and $\text{WHC}_{\text{internal}}$ (Fig. 2B) significantly increased with hydrated thallus area (A_{wet}) in all three species ($P < 0.001$) (Table 1). Along linear scales (data not shown), $\text{WHC}_{\text{internal}}$ increased rapidly with size in *L. amplissima* (slope = 0.56), more slowly in *L. virens* (slope = 0.31) and slowest in *L. pulmonaria* (slope = 0.08); the slope was highly significant for all species. $\text{WHC}_{\text{internal}}$ was 2.1 (*L. pulmonaria*) – 3.6 (*L. virens*) times higher than $\text{WHC}_{\text{external}}$ (Table 2). Unlike $\text{WHC}_{\text{internal}}$, $\text{WHC}_{\text{external}}$ hardly depended on size (Fig. 2A; Table 1). Due to different size responses of $\text{WHC}_{\text{external}}$ (Fig. 2A) and $\text{WHC}_{\text{internal}}$ (Fig. 2B), the $\text{WHC}_{\text{external}}/\text{WHC}_{\text{internal}}$ ratio declined with

FIG. 2. Relationship between hydrated thallus area (A_{wet}) and (A) external ($\text{WHC}_{\text{external}}$), (B) internal water-holding capacity ($\text{WHC}_{\text{internal}}$) and (C) specific thallus mass (STM) in three cephalolichen species (note log scales). Regression lines (black) for each species with corresponding 95% confidence intervals (grey lines) are given. For regression equations, r^2_{adj} and P -values, see Table 1. Solid line = *Lobaria amplissima*; dashed line = *L. virens*; dotted line = *L. pulmonaria*.

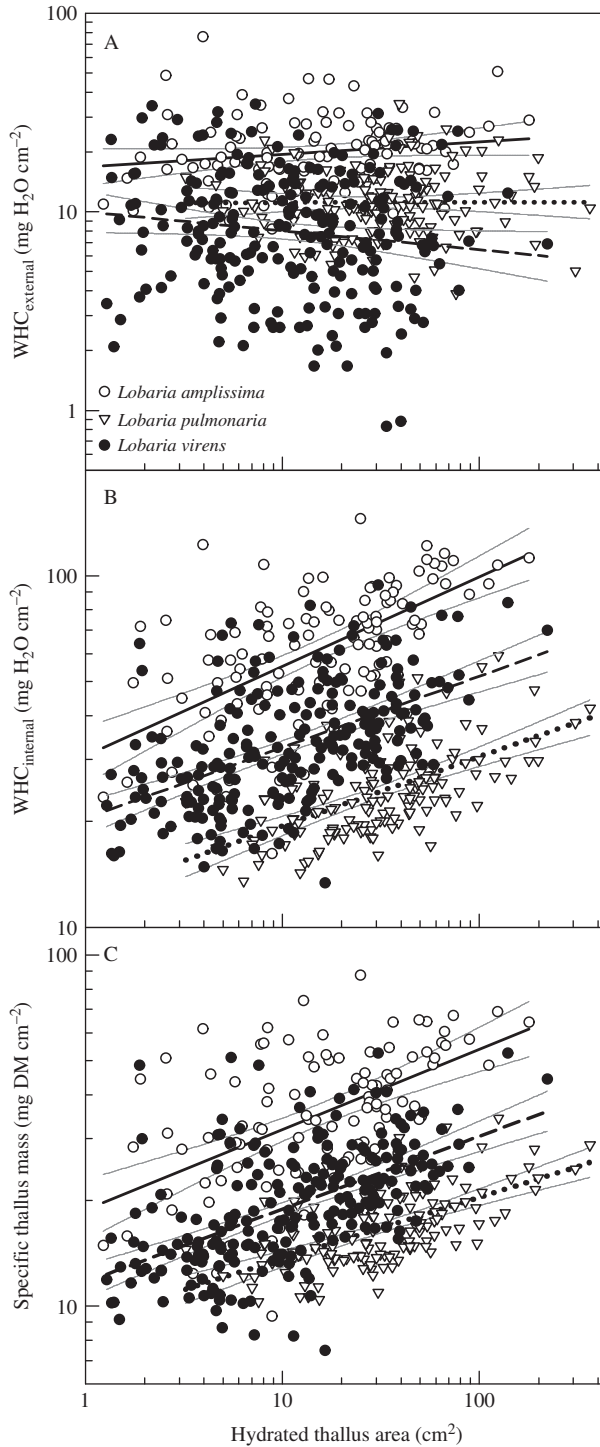


TABLE 1. Regression equations, r^2_{adj} , and P-values for the relationships shown in Figs 1–4 for *Lobaria amplissima* (n = 109), *L. pulmonaria* (n = 144), and *L. virens* (n = 225).

Fig.	Species	Parameter	Regression equation	r^2_{adj}	P-value
1	<i>L. amplissima</i>	$\log_{10}\text{DM}$	$-1.726 + 1.229 \times \log_{10}A_{\text{wet}}$	0.922	<0.001
	<i>L. pulmonaria</i>	$\log_{10}\text{DM}$	$-2.041 + 1.176 \times \log_{10}A_{\text{wet}}$	0.964	<0.001
	<i>L. virens</i>	$\log_{10}\text{DM}$	$-1.934 + 1.206 \times \log_{10}A_{\text{wet}}$	0.925	<0.001
2A	<i>L. amplissima</i>	$\log_{10}\text{WHC}_{\text{external}}$	–	–	ns
	<i>L. pulmonaria</i>	$\log_{10}\text{WHC}_{\text{external}}$	–	–	ns
	<i>L. virens</i>	$\log_{10}\text{WHC}_{\text{external}}$	$0.998 - 0.097 \times \log_{10}A_{\text{wet}}$	0.015	0.039
2B	<i>L. amplissima</i>	$\log_{10}\text{WHC}_{\text{internal}}$	$1.487 + 0.255 \times \log_{10}A_{\text{wet}}$	0.364	<0.001
	<i>L. pulmonaria</i>	$\log_{10}\text{WHC}_{\text{internal}}$	$1.090 + 0.198 \times \log_{10}A_{\text{wet}}$	0.346	<0.001
	<i>L. virens</i>	$\log_{10}\text{WHC}_{\text{internal}}$	$1.307 + 0.201 \times \log_{10}A_{\text{wet}}$	0.246	<0.001
2C	<i>L. amplissima</i>	$\log_{10}\text{STM}$	$1.274 + 0.229 \times \log_{10}A_{\text{wet}}$	0.287	<0.001
	<i>L. pulmonaria</i>	$\log_{10}\text{STM}$	$0.959 + 0.176 \times \log_{10}A_{\text{wet}}$	0.370	<0.001
	<i>L. virens</i>	$\log_{10}\text{STM}$	$1.066 + 0.206 \times \log_{10}A_{\text{wet}}$	0.262	<0.001
3A	<i>L. amplissima</i>	$\text{WHC}_{\text{external}}/\text{WHC}_{\text{internal}}$	$0.536 - 0.151 \times \log_{10}A_{\text{wet}}$	0.206	<0.001
	<i>L. pulmonaria</i>	$\text{WHC}_{\text{external}}/\text{WHC}_{\text{internal}}$	$0.790 - 0.205 \times \log_{10}A_{\text{wet}}$	0.238	<0.001
	<i>L. virens</i>	$\text{WHC}_{\text{external}}/\text{WHC}_{\text{internal}}$	$0.508 - 0.199 \times \log_{10}A_{\text{wet}}$	0.216	<0.001
4A	<i>L. amplissima</i>	$\log_{10}\text{WHC}_{\text{external}}$	$0.707 + 0.384 \times \log_{10}\text{STM}$	0.164	<0.001
	<i>L. pulmonaria</i>	$\log_{10}\text{WHC}_{\text{external}}$	$0.160 + 0.726 \times \log_{10}\text{STM}$	0.210	<0.001
	<i>L. virens</i>	$\log_{10}\text{WHC}_{\text{external}}$	$0.586 + 0.242 \times \log_{10}\text{STM}$	0.015	0.039
4B	<i>L. amplissima</i>	$\log_{10}\text{WHC}_{\text{internal}}$	$0.657 + 0.818 \times \log_{10}\text{STM}$	0.867	<0.001
	<i>L. pulmonaria</i>	$\log_{10}\text{WHC}_{\text{internal}}$	$0.050 + 1.093 \times \log_{10}\text{STM}$	0.882	<0.001
	<i>L. virens</i>	$\log_{10}\text{WHC}_{\text{internal}}$	$0.348 + 0.912 \times \log_{10}\text{STM}$	0.821	<0.001

A_{wet} = hydrated thallus area; STM = specific thallus mass; $\text{WHC}_{\text{external}}$ (external water-holding capacity) = $\text{WHC}_{\text{shaking}} - \text{WHC}_{\text{blotting}}$; ns = not significant, $P \geq 0.05$.

size in *L. pulmonaria* and *L. virens* from 0.79 and 0.51 in small thalli (1 cm²) to 0.28 and 0.02 in large thalli (300 cm²), respectively (Fig. 3; Table 1). Thus, the proportion of external to internal water was higher in smaller thalli. Shaking removed minor amounts of water, ranging from 1.4 (*L. virens*; 3.0 % of WHC_{max}) to 6.4 mg H₂O cm⁻² (*L. amplissima*; 14.6 % of WHC_{max}). Most water was stored inside the thallus in these species, evinced by their low $\text{WHC}_{\text{external}}$ (Table 2).

STM was the main driver for the internal water ($\text{WHC}_{\text{internal}}$) in all species (Fig. 4B); linear regression of log-transformed values showed that STM accounted for >88% of the variation in $\text{WHC}_{\text{internal}}$ (Table 1). There was substantial overlap between *L. amplissima* and *L. virens*, whereas the smaller thalli of *L. pulmonaria* in particular had lower $\text{WHC}_{\text{internal}}$ (Fig. 4B). $\text{WHC}_{\text{external}}$ increased with STM in all species (Fig. 4A). However, STM accounted for just 21% or less of the variation in $\text{WHC}_{\text{external}}$ for *L. amplissima* and *L. pulmonaria* ($P < 0.001$; Table 1), whereas the regression was just marginally

significant for the thin *L. virens* (Fig. 4A; Table 1).

All hydration parameters studied differed significantly between species (Table 2), also evidenced by the mostly non-overlapping 95% confidence interval lines (Figs 2–4). *Lobaria amplissima* had the highest STM (38.3 ± 1.5 mg DM cm⁻²), 1.8 times higher than in *L. virens* (20.9 ± 0.6 mg DM cm⁻²; Table 2) and 2.2 times higher than in *L. pulmonaria* (17.2 ± 0.4 mg DM cm⁻²). Likewise, *L. amplissima* had a WHC_{max} , $\text{WHC}_{\text{shaking}}$ and $\text{WHC}_{\text{internal}}$ more than twice that of *L. pulmonaria* (Table 2), despite *L. pulmonaria* thalli having a significantly larger thallus area than the other species (Table 2). By contrast, *L. pulmonaria* had the highest $\text{WHC}_{\text{external}}/\text{WHC}_{\text{internal}}$ -ratio (Table 2). *Lobaria amplissima* had most external water (21.8 ± 1.0 mg H₂O cm⁻²), and *L. pulmonaria* (12.0 ± 0.4 mg H₂O cm⁻²) had slightly more external water than *L. virens* (10.1 ± 0.5 mg H₂O cm⁻²; Fig. 4A, Table 2).

The dependency of $\text{WC}_{\text{internal}}$ and $\text{WC}_{\text{shaking}}$ on thallus area (A_{wet}), as well as

TABLE 2. *Thallus area (A_{wet}), dry mass (DM), specific thallus mass (STM), water-holding capacity (WHC) and water content (WC) for the three Lobaria species used in this study.*

Parameter	<i>Lobaria amplissima</i> (n = 109)	<i>Lobaria virens</i> (n = 225)	<i>Lobaria pulmonaria</i> (n = 144)
<i>A_{wet}</i> (cm ²)			
Mean ± 1SE	24.9 ± 2.6	18.8 ± 1.5	45.9 ± 4.2
Median	16.9 ^b	11.3 ^a	31.4 ^c
Min–Max	1.2–178.9	1.3–221.0	3.2–364.2
DM (mg)			
Mean ± 1SE	1160 ± 161	487 ± 61	918 ± 112
Median	613 ^b	209 ^a	518 ^b
Min–Max	18–11509	136–9804	51–10477
STM (mg DM cm ⁻²)			
Mean ± 1SE	38.3 ± 1.5	20.9 ± 0.6	17.2 ± 0.4
Median	36.3 ^c	19.0 ^b	16.2 ^a
Min–Max	9.4–87.6	7.5–61.8	10.3–34.2
WHC _{max} (mg H ₂ O cm ⁻²)			
Mean ± 1SE	92.0 ± 3.0	47.5 ± 1.3	43.8 ± 1.1
Median	89.4 ^b	43.2 ^a	41.2 ^a
Min–Max	24.9–203.9	5.8–126.8	25.7–97.8
WHC _{shaking} (mg H ₂ O cm ⁻²)			
Mean ± 1SE	88.9 ± 3.0	46.1 ± 1.3	37.4 ± 1.0
Median	87.0 ^c	42.0 ^b	34.9 ^a
Min–Max	24.3–198.9	5.7–125.4	21.2–84.7
WHC _{internal} (mg H ₂ O cm ⁻²)			
Mean ± 1SE	67.1 ± 2.5	36.0 ± 1.0	25.4 ± 0.7
Median	67.3 ^c	32.3 ^b	23.2 ^a
Min–Max	16.2–145.7	4.1–94.3	13.5–59.4
WHC _{external} (mg H ₂ O cm ⁻²)			
Mean ± 1SE	21.8 ± 1.0	10.1 ± 0.5	12.0 ± 0.4
Median	20.1 ^c	8.0 ^a	10.8 ^b
Min–Max	8.2–76.2	0.8–34.9	3.9–35.0
WHC _{external} /WHC _{internal} ratio			
Mean ± 1SE	0.36 ± 0.01	0.30 ± 0.01	0.49 ± 0.01
Median	0.35 ^b	0.26 ^a	0.47 ^c
Min–Max	0.09–0.80	0.01–1.03	0.13–1.10
WHC _{internal} /STM ratio			
Mean ± 1SE	1.77 ± 0.02	1.75 ± 0.02	1.47 ± 0.01
Median	1.75 ^b	1.77 ^b	1.45 ^a
Min–Max	1.22–2.43	0.90–2.42	1.11–1.95
WC _{max} (%)			
Mean ± 1SE	248 ± 4	237 ± 4	258 ± 4
Median	250 ^{ab}	234 ^a	255 ^b
Min–Max	149–426	94–410	158–377
WC _{shaking} (%)			
Mean ± 1SE	240 ± 4	228 ± 4	217 ± 3
Median	238 ^b	226 ^a	215 ^a
Min–Max	145–340	93–403	151–300
WC _{internal} (%)			
Mean ± 1SE	177 ± 2	174 ± 2	147 ± 1
Median	175 ^b	178 ^b	145 ^a
Min–Max	122–243	90–242	112–195
WC _{external} (%)			
Mean ± 1SE	63 ± 2	53 ± 2	71 ± 2
Median	61 ^b	70 ^b	46 ^a
Min–Max	15–135	2–193	21–157

WHC_{max} = Water Holding Capacity in wet thalli before shaking; WHC_{shaking} = WHC after shaking; WHC_{internal} = WHC after blotting; WHC_{external} = WHC_{shaking} - WHC_{blotting}; WC_{shaking} and WHC_{blotting} = percentage water content after shaking and blotting, respectively. *P*-values according to a Kruskal-Wallis one-way ANOVA, all parameters significantly differed among species (*P* < 0.001). Within a parameter, species sharing the same superscript letter do not differ significantly from each other (Dunn's pairwise method).

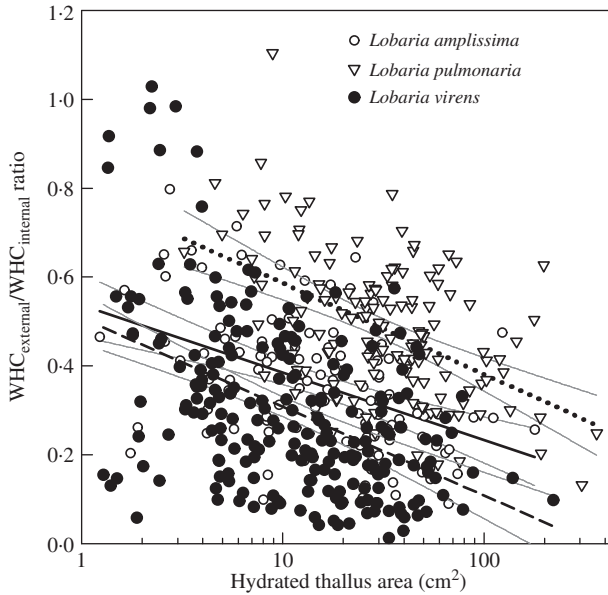


FIG. 3. Relationship between hydrated thallus area (A_{wet}) and the $WHC_{external}/WHC_{internal}$ ratio in three cephalolichen species. Regression lines (black) for each species with corresponding 95% confidence intervals (grey lines) are given. For regression equations, r^2_{adj} and P -values, see Table 1. Solid line = *Lobaria amplissima*; dashed line = *L. virens*; dotted line = *L. pulmonaria*.

their relationships with STM, were less clear (data not shown). Even when a relationship was significant, the regression model accounted only marginally for the variation in WC ($r^2_{adj} \leq 0.071$). There was a stronger negative relationship between $WC_{shaking}$ and STM in *L. amplissima* ($r^2_{adj} = 0.240$, $P < 0.001$) and *L. virens* ($r^2_{adj} = 0.108$, $P < 0.001$), but it was not significant for *L. pulmonaria*. *Lobaria amplissima* and *L. virens* had higher $WC_{internal}$ than *L. pulmonaria* (Table 2).

Discussion

This study demonstrates strong links between STM and $WHC_{internal}$ in cephalolichen members of *Lobaria*. The STM- $WHC_{internal}$ regression lines for these *Lobaria* species (Fig. 4B) fall between those of cyanolichens (Gauslaa & Coxson 2011) and a wide range of chlorolichens including foliose, fruticose and alectorioid growth forms (Gauslaa 2014; Esseen *et al.* 2015). *Lobaria pulmonaria* followed the 1:1.5 ratio

between STM and $WHC_{internal}$ consistent with earlier studies of this species (Gauslaa & Coxson 2011; Merinero *et al.* 2014). However, *L. amplissima* and *L. virens* had a 1:1.8 ratio, closer to the 1:2 ratio in cyanolichens such as *L. scrobiculata*, *L. hallii* and *L. retigera* (Gauslaa & Coxson 2011) than to the 1:1 ratio characterizing a wide range of chlorolichens (Gauslaa 2014; Esseen *et al.* 2015). The high STM in *L. amplissima* compared to the two other species is the result of its thicker thallus which has been reported as 475–645 μm (Degelius 1940) and 295–610 μm (Hale 1957). By contrast, the low STM in *L. pulmonaria* is consistent with a thinner thallus; 135–275 μm for pits versus 260–400 μm for veins (Jordan 1973). However, STM in *L. pulmonaria* has been shown to vary substantially in the literature (Fig. 5). STM was significantly higher in *L. pulmonaria* thalli on trunks in deciduous forests than those from branches of evergreen, more shaded spruce canopies. The two uppermost regression lines in Fig. 5,

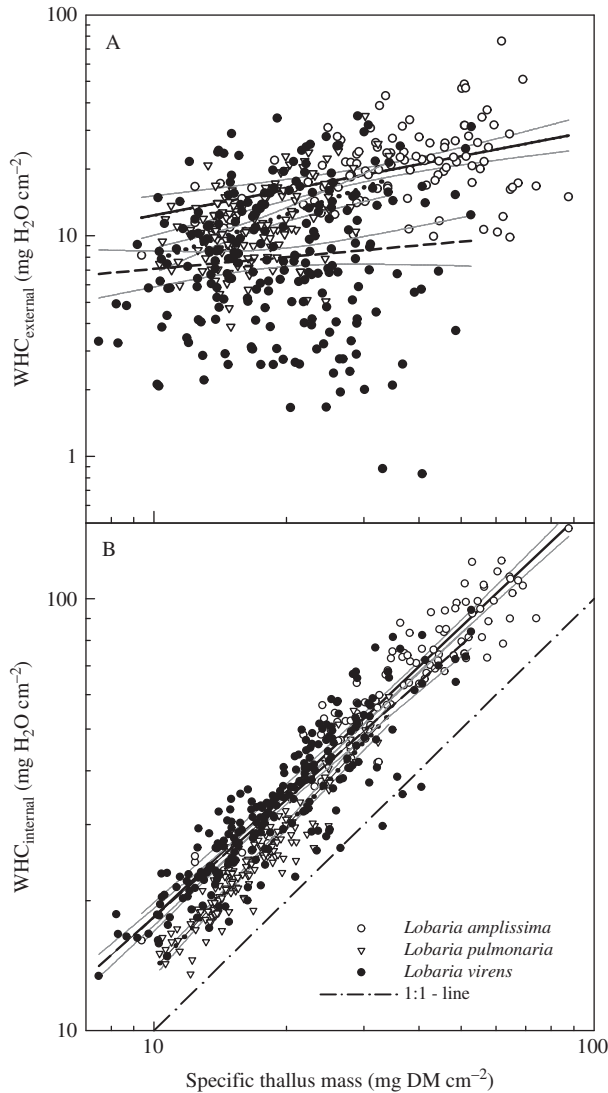


FIG. 4. Relationship between specific thallus mass (STM) and (A) external (WHC_{external}) and (B) internal water-holding capacity (WHC_{internal}). Regression lines (black) for each species with corresponding 95% confidence intervals (grey lines) are given. For regression equations, r^2_{adj} and P -values, see Table 1. Solid line = *Lobaria amplissima*; dashed line = *L. virens*; dotted line = *L. pulmonaria*.

comprising populations with the thickest thalli and overlapping STM values, were from open deciduous forests where *L. pulmonaria* grew together with *L. amplissima* and *L. virens* which had high STM and WHC (Table 2). *Lobaria pulmonaria* from drier Spanish oak trunks, where humid air is probably an important hydration source (Merinero *et al.*

2015), had lower STM than populations on trunks in Norway. Additionally, significantly lower STM occurred in less attached thalli on thin spruce branches in boreal rainforests, whereas the lowest mean STM so far measured in *L. pulmonaria* was from similarly thin spruce branches in inland forests in British Columbia (Fig. 5) where night-time humid

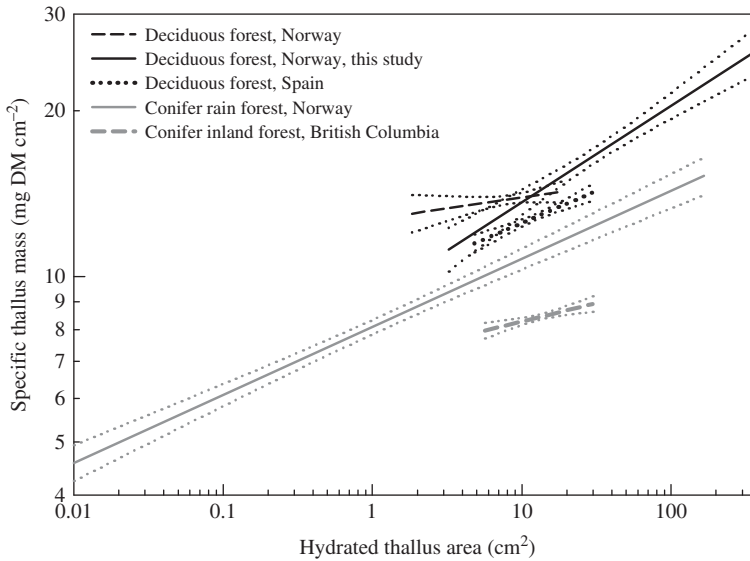


FIG. 5. Relationship between specific thallus mass (STM) and hydrated thallus area (A_{wet}) in *Lobaria pulmonaria* from various forest types and climates. Black regression lines represent populations sampled on trunks in broadleaved deciduous forests, grey lines represent populations sampled from conifer branches. Solid lines show allometric studies; the upper black line comprising data from this study, the lower grey line, thalli from spruce branches in boreal Norwegian rainforest (Merinero *et al.* 2014). Dashed and dotted lines represent populations sampled for transplantation experiments, consequently neither large nor small thalli were included. The dashed black line represents data from Norwegian forests with populations mixed with *L. amplissima* and *L. virens* (Gauslaa *et al.* 2006). The bold dotted black line represents data from oak forests in central Spain (Merinero *et al.* 2015). The dashed grey line represents data from spruce branches in inland forests of southern British Columbia (Gauslaa & Goward 2012; Bidussi *et al.* 2013). Dotted lines represent 95% confidence intervals.

air is the important hydration source (Bidussi & Gauslaa 2015). This large phenotypic plasticity in STM in *L. pulmonaria* (Fig. 5) may represent acclimation to site-specific dominant hydration sources.

A strong size dependency of both STM and $WHC_{internal}$ was demonstrated in the species studied, although regressions (Fig. 2; Table 1) were weaker than those found for foliose lichens on thin spruce branches (Merinero *et al.* 2014) and for fruticose lichens on oak branches (Gauslaa 2014). In general, lichens on branches are smaller and younger (foliose lichens; see Fig. 5) or fruticose. The $WHC_{internal}$ -STM relationships in these studies were probably stronger because specimens of such lichens were easier to define than were specimens on old tree trunks. Long-lived and old thalli often fragment and lose large portions. Additionally, small specimens on trunks also often

merge and form one larger thallus. Such processes are likely reasons for the weaker size-dependent regressions in our study. A size-dependency complicates comparison of species. However, non-overlapping 95% confidence intervals (Figs 2–4) are consistent with species-specific hydration traits. Furthermore, despite sampling fewer small thalli and more large ones for *L. pulmonaria*, it had the lowest STM and $WHC_{internal}$.

Values of $WHC_{external}$ in lichens are not well known. There are few data on $WHC_{shaking}$, and only for a small number of lichens (Green *et al.* 1985; Gauslaa 2014). The $WHC_{external}/WHC_{internal}$ ratios in the cephalolichens studied (0.26–0.47; Table 2) are substantially lower than the ratios reported by Gauslaa (2014) in the chlorolichens *Xanthoria aureola* (1.3) and *Hypogymnia occidentalis* (1.1), as well as in the cyanolichen *Pseudocyphellaria dissimilis* (0.9; Green *et al.*

1985) and in the hair lichen genus *Bryoria* in particular (4–5; Essen *et al.* 2017). Therefore, external water is less important in cephalolichens than in the other lichens measured so far. The lack of response of $\text{WHC}_{\text{external}}$ to increased thallus size (Fig. 2A), but weakly positive responses to increasing STM (Fig. 4A), suggest more irregular upper surfaces in thicker thalli that can hold more external water than thinner ones. For example, the higher $\text{WHC}_{\text{external}}/\text{WHC}_{\text{internal}}$ ratio in *L. pulmonaria* than in the other two species is likely due to its reticulate pattern facilitating water retention in the many depressions on the upper surface.

Excess hydration often causes depression of photosynthesis in lichens (Lange & Green 1996). A low $\text{WHC}_{\text{external}}$ may reduce the risk of prolonged suprasaturation in cephalolichens studied, and might explain not only why such lichens were much less damaged than a range of chlorolichens during a prolonged, very wet period (Gauslaa 2002) but also why these cephalolichens often characterize rainforests (Ellis 2016).

The low variation in hydration traits between sites is probably because the shared ecological niche for all species is narrower than the niche for individual species: mixed populations of three species inhabit a more specific habitat than populations of single species. Yet in sympatric populations with all species sampled from the same trunks, the species-specific contrasts in hydration traits were strong. This is consistent with a genetic basis for measured contrasts. Despite its high intraspecific flexibility (Fig. 5), *L. pulmonaria* differs from the two other species (Table 2), not only in its lower STM and $\text{WHC}_{\text{internal}}$, but also in its looser and less attached pendulous, spoon-shaped lobe ends exposed to ambient air. The other two lichens, *L. amplissima* and *L. virens*, have higher STM and $\text{WHC}_{\text{internal}}$ and grow closely attached to the tree bark. We believe that there are functional links between growth form and hydration traits such as $\text{WHC}_{\text{internal}}$. A lower STM and a less attached growth form in *L. pulmonaria* secure faster photosynthetic activation from humid air and/or dew (Larson & Kershaw 1976; Larson 1981) in

the absence of rain or stem flow. By contrast, the two other lichens, *L. amplissima* in particular, with its thick and more prostrate lobes, depend more on rain flowing down the trunk. Their average $\text{WHC}_{\text{internal}}$ ($67.1 \text{ mg H}_2\text{O cm}^{-2}$) largely exceeds the threshold level that humid air or dew can fill during one night; dew is $\leq 0.2 \text{ mm}$ water (Jacobs *et al.* 2002, 2006; Richards 2002; Xiao *et al.* 2013), equivalent to $\leq 20 \text{ mg H}_2\text{O cm}^{-2}$, as reviewed by Gauslaa (2014). Thus, there is a trade-off between low STM and the associated flexible use of various hydration sources versus high STM and a more conservative hydration strategy depending on rain and/or stem flow. The latter strategy as typified by *L. amplissima* and *L. virens*, requires greater water storage in order to prolong the rarer hydration periods than the *L. pulmonaria* strategy. Such a trade-off might explain why *L. pulmonaria* often grows abundantly on thin branches in humid forests (e.g. Larsson & Gauslaa 2011; MacDonald & Coxson 2013) whereas the other two cephalolichens are more restricted to trunks, with stem flow feeding these prostrate lichens with water. The more oceanic distribution of *L. amplissima* and *L. virens*, for example in Britain (Ellis 2016) and Norway (see maps generated in Timdal (2017)), is consistent with a stronger dependency of these species on rain.

Lobaria virens is a rarer and more oceanic species than the other two. With respect to hydration traits, it is neither as flexible as the common and widespread *L. pulmonaria*, nor as efficient in storing water as *L. amplissima*. Furthermore, *L. virens* is particularly susceptible to high light, especially when desiccated, and high light-induced damage is not easily reversible (Gauslaa & Solhaug 1996). Relative to the other two species, *L. virens* grows on lower portions of trunks and in more shielded positions (Asplund *et al.* 2010). A combination of less specialized hydration traits and low tolerance to high light likely jeopardize its survival outside rainforests. Finally, pure cyanomorphs have been shown to act as early juvenile stages of *L. virens* (Tønsberg *et al.* 2016). This might also explain the highly oceanic distribution of

this species, although it is not yet known if all early *L. virens* juveniles are cyanomorphs.

In conclusion, the three cephalolichens *L. amplissima*, *L. pulmonaria* and *L. virens* differ in all measured hydration traits, even when collected from mixed populations on trunks where all species occurred together. The most widespread species, *L. pulmonaria*, benefits from a flexible strategy due to its low STM, likely allowing rapid activation in humid air, whereas the two rarer species depend more on rain, particularly *L. amplissima* with the highest STM and associated high WHC_{internal}.

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