Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens

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Abstract: This review is a first attempt to combine and compare spatial distribution of the three main water sources, rain, dew and humid air, with water-related traits of mainly epiphytic macrolichens in a conceptual and functional model. By comparing climatic and lichenological knowledge, various effects of dewfall, rainfall and humid air on epiphytic lichen morphology and function are analyzed to search for traits and patterns. Although dew, rain and humid air cause lichen hydration and activate photosynthesis, these atmospheric hydration sources influence and shape lichens differently. In order to visualize hydration patterns, dew, rain and humid air are shown as corners in a triangle exhibiting the various combinations of these hydration sources. The sources of hydration vary on temporal scales, and on the spatial scales: regional, landscape, stand and tree. Lichen growth form, photobiont type, water-holding capacity (WHC) and suprasaturation depression show clear patterns within the hydration triangle. For most lichen species, one average pre-dawn dewfall approximately fills their average internal WHC. This suggests that lichens are optimally designed to utilize dew rather than rain, consistent with literature emphasizing dew as a driver for annual C-assimilation in chlorolichens. However, rain is needed to fill their external WHC and to fully hydrate most cyanolichens. Including the sources of hydration and internal lichen variables, such as water-holding capacity, will improve modelling of local and global future scenarios on lichen distribution and biomass production.

Key words: alectorioid lichens, functional groups, humidity, hydration, lichen morphology, review, water-holding capacity

Introduction

Lichens are used as indicators of environmental factors such as toxic pollutants (Cislaghi & Nimis 1997; Brunialti & Frati 2007), acid rain (Gauslaa 1995; Purvis *et al.* 2008), nitrogen deposition (van Herk *et al.* 2003; Frati *et al.* 2008; Hauck 2010; Johansson *et al.* 2010), ecological continuity in forest ecosystems (Rose 1976; McCune *et al.* 2000; Bolliger *et al.* 2007; Fritz *et al.* 2008), forest edge microclimate (Renhorn *et al.* 1997; Esseen & Renhorn 1998; Coxson & Stevenson 2007*b*) and climate change (Cornelissen *et al.* 2001; Walker *et al.* 2006; Lang *et al.* 2009). With their poikilohydric way of life, lichens also tell stories about spatial and temporal variation in hydration sources. Because many epiphytic lichens, macrolichens in particular, are exposed to ambient air with large area/biomass-ratios, they likely rank among the more responsive organisms to humidity. For example, two similar spruce canopies in one single valley with relatively low rainfall can host totally different epiphytic communities; the one exposed to atmospheric hydration sources only is heavily loaded with pendulous hair lichens (Fig. 1A), and the other, additionally influenced by liquid water from the spray zone of a waterfall, is loaded with foliose lichens (Fig. 1B). Many lichen species with broad distribution ranges seem to respond more strongly to humidity factors than to temperature. For example, Jørgensen (1996) showed that *c.* 50 oceanic lichen species occurring in Norway have their main

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FIG. 1. The lower parts of two spruce (*Picea engelmannii x glauca*) canopies located in the Clearwater valley, southern inland British Columbia. A, a tree in the upper-elevation forests (altitude 1800 m) of the Trophy Mountains with dense cover of *Alectoria sarmentosa* and various *Bryoria* spp., but without cephalo- or cyanolichens; B, a tree along the Murtle River within the outer spray zone of Dawson Falls (altitude 800 m), influenced by liquid water from the spray zone. This locality has a strong dominance of the cephalolichen *Lobaria pulmonaria*, with minor occurrences of cyanolichens such as *L. hallii, L. scrobiculata, Pseudocyphellaria anomala, Leptogium* spp. and *Collema* spp. Photographs: Y. Gauslaa. In colour online.

distribution area in tropical/subtropical rain-forests, this notwithstanding that some of them extend northwards to boreal rainforests at the arctic circle.

Recent efforts to model lichen distributions (Ellis *et al.* 2007*a*, *b*; Braidwood & Ellis 2012), as well as lichen growth (Eaton & Ellis 2012), by means of climatic variables have shown that climate matters, although such models consider rainfall as the only humidity parameter. Internal lichen parameters such as photobiont type (Lange & Kilian 1985), water-holding capacity (Green & Lange 1991; Gauslaa & Solhaug 1998), growth form (Kershaw 1985), hydrophobicity of lichen surfaces (Lakatos *et al.* 2006) and presence/

absence of cortex (Pardow *et al.* 2010) also greatly influence moisture relations in lichens. For example, gel lichens such as the cyano-bacterial *Collema* spp. accumulate considerable quanbities of water that keep the thallus hydrated for long periods (Galun 1963; Lange *et al.* 1998; Lange 2000). It is well known that the lichen water-holding capacity, which depends on morphological adaptation as well as on acclimation (Kershaw 1985; Gauslaa & Coxson 2011), determines the duration of hydration periods (e.g. Gauslaa & Solhaug 1998). Furthermore, species-specific internal factors influence lichen responses after hydration events (Jonsson *et al.* 2008). While several reviews pertaining to water relations

in lichens have been published over the years (e.g. Blum 1973; Kappen 1973; Kershaw 1985; Green *et al.* 2011), an overview linking the various sources of hydration to lichen morphology, function and distribution is lacking. This study attempts to combine and compare spatial distribution of the three main water sources of rain, dew and humid air with water-related traits of epiphytic macrolichens in a conceptual and functional model that may be useful for future modelling of lichens in climate change scenarios.

Main sources of hydration in lichens and their interaction with light

In order to visualize hydration patterns, the three main atmospheric hydration sources for lichens, rain, water vapour condensation (dew) and humid air, are placed as corners in a triangle (Fig. 2). Each location inside the triangle represents a certain combination of hydration sources. Hydration sources are partly coupled: rain and dew necessarily imply high air humidity, but humid air can

occur without the presence of liquid water. Liquid water can also come as fog/mist, but because fog provides droplets of water, fog is included under rain.

Light availability during hydration periods drives lichen photosynthesis and growth (Palmqvist 2000), although hydration during nights may also stimulate growth (Bidussi *et al.* 2013*a*). Even so, light availability (as shown in Fig. 2) is partly confounded with hydration sources (Stoutjesdijk & Barkman 1987) because solar radiation is also a driver of surface temperatures and thus strongly influences water loss and air humidity. At physical scales relevant to lichen physiology, the air during daylight hours is often more humid in the shade of forests than in open, well-lit places, but this relationship becomes inverted at night when cooling is strongest outside a shielding canopy (Geiger 1950). This implies that dew is particularly frequent in forest gaps [open shade habitats *sensu* Stoutjesdijk (1974)] which receive much diffuse sky light but little direct sun. Indirect light stimulates lichen growth (Gauslaa *et al.* 2006, 2007). In marked contrast, direct exposure to sunlight causes rapid drying (Lange *et al.* 2004) and adversely impacts epiphytic lichen growth (Gauslaa & Goward 2012; Bidussi *et al.* 2013*b*), although short-time sunflecks can have positive effects (Lakatos *et al.* 2006; Coxson & Stevenson 2007*a*). Light experienced during prolonged dry periods causes much more damage than desiccation *per se*, and substantially retards photosynthetic activation during subsequent hydration (Lidén *et al.* 2010; Gauslaa *et al.* 2012), particularly in epiphytic cephalolichens and shade-adapted chlorolichens (Gauslaa & Solhaug 1996; Jonsson Cabrajic *et al.* 2010).
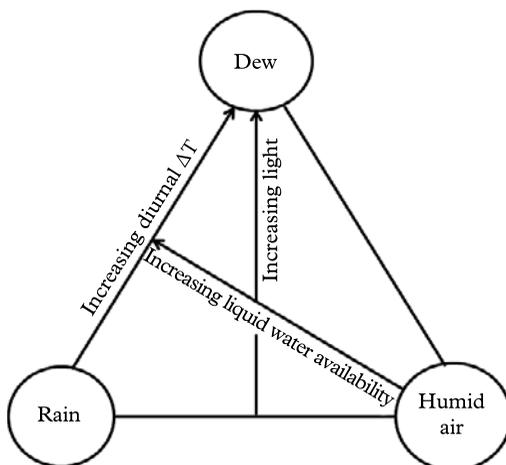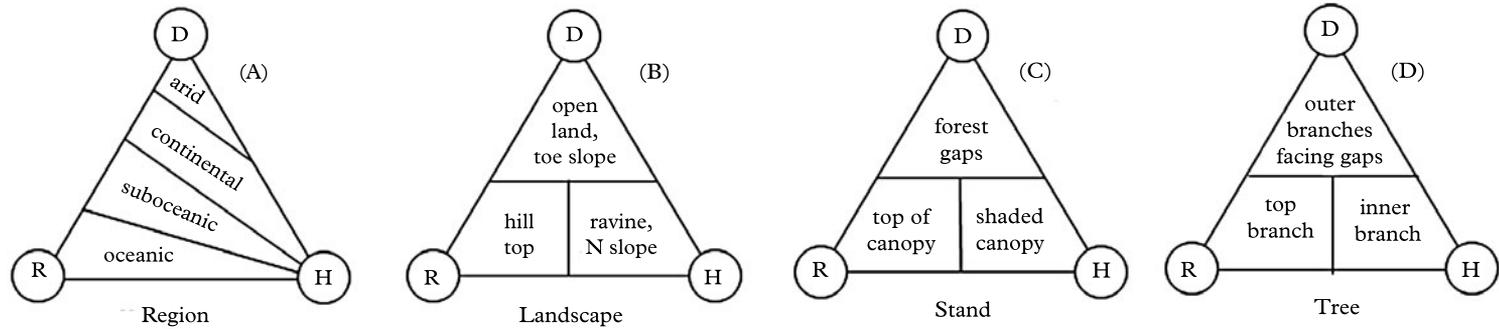

FIG. 2. Hydration source model for lichens, visualizing relationships between the three main sources of lichen hydration (rain, dew, humid air) and some important abiotic factors (temperature, light and liquid water availability). Each location inside the triangle represents a certain combination of hydration sources. $\triangle$T refers to the diurnal temperature amplitude.

Spatial variation in hydration sources

Regional scales

At regional scales (Fig. 3A), vegetation generally becomes more open and/or well spaced with increasing aridity (e.g. Walter & Breckle 1984). Under otherwise similar conditions, nocturnal cooling is much stronger
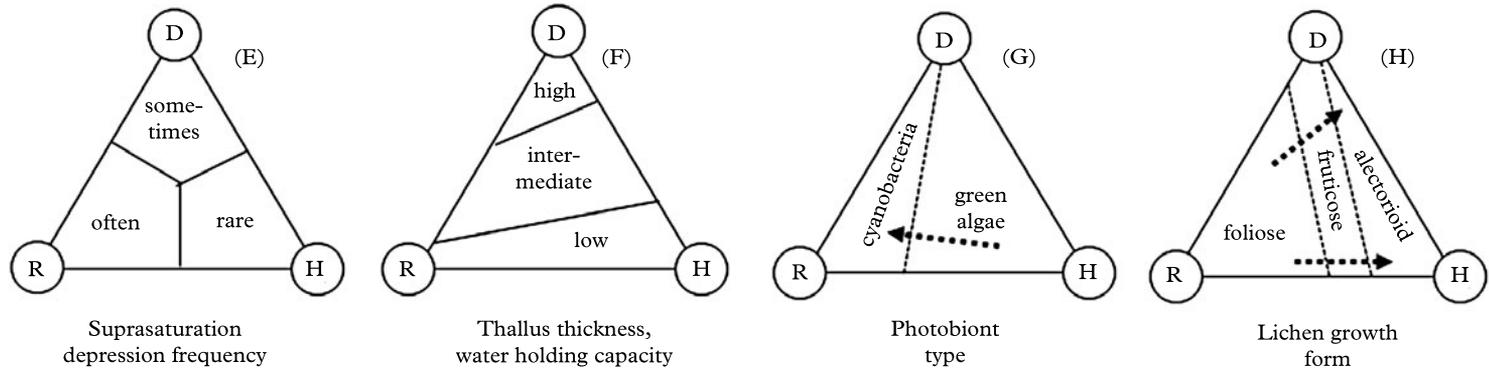
Spatial scales:

Lichen responses:

Fig. 3. Basic ideas and hypotheses regarding the hydration source model (Fig. 2) for lichen responses. A–D shows patterns on spatial scales; E–H, responses of forest lichens to hydration sources.

in open spaces than inside forests (Stoutjes-dijk & Barkman 1987). Pre-dawn dewfall in open habitats (Fig. 3B–D) increases with decreasing cloud cover (Xiao *et al.* 2013), increasing nocturnal cooling and thus increasing air humidity (e.g. Geiger 1950). A critical wind speed is needed to maximize dewfall rates; if wind is faster, which is often the case in coastal sites, condensation is offset by turbulent warming; if too slow, water for condensation cannot be replenished from humid air above (Oke 1987; Xiao *et al.* 2013). Strong dew formation is thus more common in inland climates (Fig. 3A). Dew and humid air in particular, are inaccessible to most vascular plants, but useful to lichens. Dry valleys of south-eastern Norway, located in rain shadows behind snow-capped mountains, have merely 300 mm rainfall (Fig. 4) and are surrounded by fairly dry areas (<700 mm according to Moen 1999; see Fig. 4). Surprisingly, these low rainfall areas support some oceanic lichens (Tønsberg *et al.* 1996). One example is *Menegazzia terebrata* (Fig. 4), which mainly grows on tree trunks in rainforests receiving ≥2000 mm rain along the western coast (enclosed by the solid line in Fig. 4; Moen 1999). Because canopies reduce the nocturnal cooling required for reaching the dew point, oceanic epiphytes cannot grow on their normal substratum of bark in the dry inland. Yet, they thrive on boulders and rocks in open, low-rainfall inland valleys. Their location in valleys with cold-air ponding ensures some, but little, wind replenishing moisture at ground level and causes heavy nocturnal dewfall (Oke 1987). Lichens in places with frequent dew experience less nutrient loss to leaching than their counterparts in rainy climates. This may contribute to higher diversity and abundance of members of the generally nutrient-demanding taxonomic groups *Physciaceae* and *Teloschistales* in dry valleys, compared to leached coastal and montane rainforests where such species are strongly associated with eutrophic habitats.

Dewfall can also be frequent in some deserts, as for example the Negev Desert which receives dew on an average of 198 nights per year (Lange *et al.* 1970, 1990). In the Namib Desert, dew alone resulted in photosynthetic activation providing 58–63% of total carbon gain in three epiphytic lichens (Lange *et al.* 2007). In the arid coastal parts of northern Chile, condensation is so strong that fog oases develop, associated with fairly hydrophytic lichen communities on spines of cacti (Lange & Redon 1983; Redon & Lange 1983). Dew events can be rare and/or seasonal in some arid habitats, but nocturnal cooling may still substantially raise the humidity and thus activate lichen photosynthesis (Lange *et al.* 1970).

Rain is most frequent on mountainous coasts along large oceans subjected to convective energy and moisture from the sea (Fig. 3A). Winds and cloud cover reduce nocturnal cooling. Hence there is often a trade-off between rainfall and dewfall. For example, the mean diurnal temperature amplitude increases from the rainy Pacific coastal forests of north-western North America to the inland rainforests further east (Table 1-1 in DellaSala *et al.* 2011*b*) with much less rain (Stevenson *et al.* 2011; 788–1240 mm per year). The occurrence of similar epiphytic vegetation in these two areas (Goward & Spribille 2005; Radies *et al.* 2009; DellaSala *et al.* 2011*a*), supporting many liquid water-demanding cyanolichens (Goward & Arsenault 2000), is probably caused by heavy dewfall compensating for less rain inland. In fact, cephalo- and cyanolichens became fully hydrated every morning by pre-dawn dew over two dry August weeks in the inland of British Columbia (Y. Gauslaa, pers. obs.). Because dew measured in mm of water is not enough to compensate for the large reduction in rainfall from the coast to the inland, the frequency of hydration rather than the total amount of rainfall matters for the rainforest lichen community.

Landscape scales

Stepping from regions down to a landscape scale, rainfall increases in intensity and frequency with altitude (orographic rain; e.g. Roe 2005) and thus causes longer periods of hydration on hill tops and rough terrain (Fig. 3B). Dewfall (Fig. 3B) is strong in lower
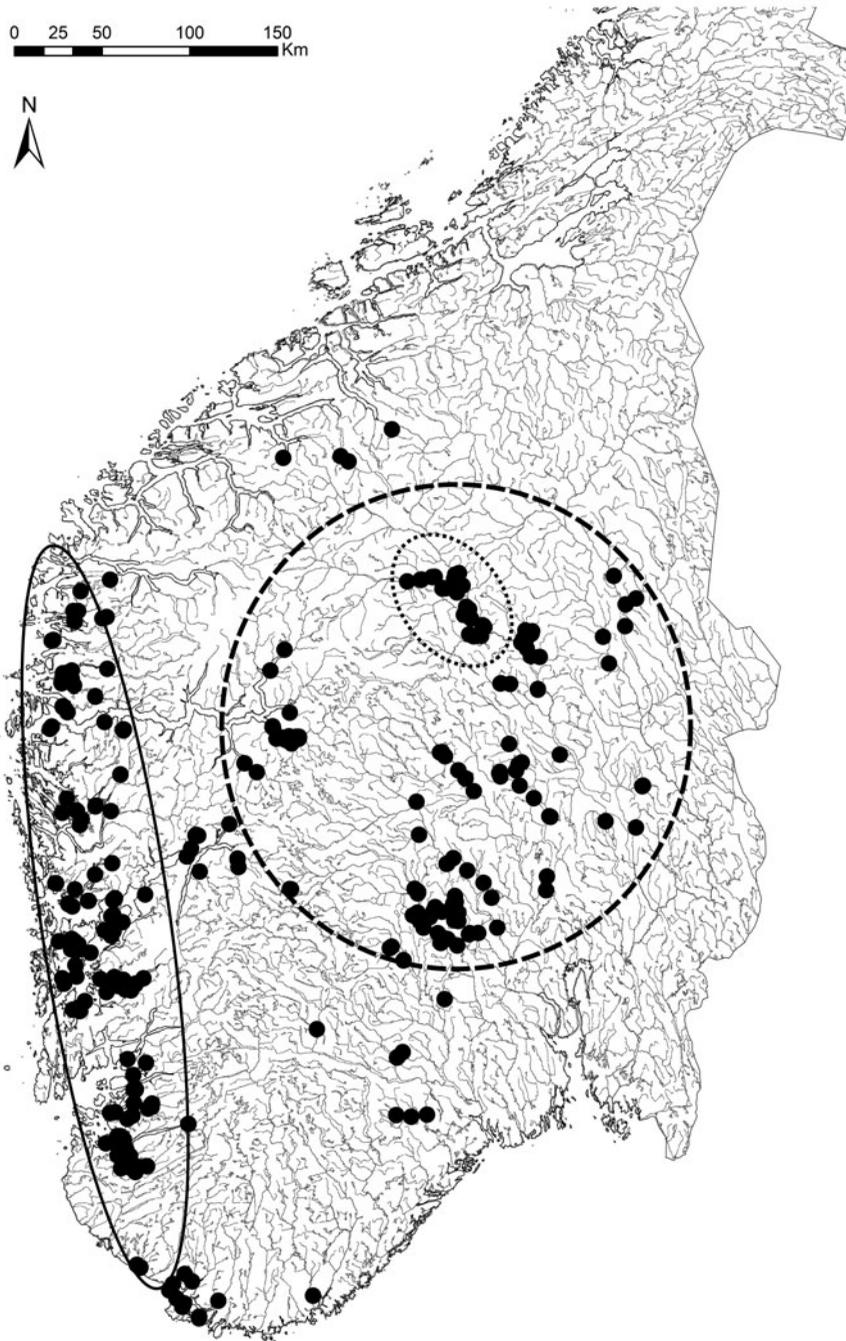
Fɪɢ. 4. Distribution map of *Menegazzia terebrata* in southern Norway, generated 24 October 2013 from the Norwegian Lichen Database (http://nhm2.uio.no/lav/web/index.html), The Lichen Herbarium, Natural History Museum, University of Oslo. Solid line oval: rainforest region (≥2000 mm rain) of western Norway with mainly epiphytic occurrences. Dotted line oval: rain shadow sites in dry inner valleys (300 mm rain). Short dashed circle: relatively dry areas (≤700 mm rainfall). In the dry areas the species grows on rocks and boulders in open landscapes.

parts of U-shaped valleys influenced by cold-air ponding (Oke 1987). Thereby a trade-off between increasing orographic rain and decreasing pre-dawn dew may occur with altitude above the valley bottom. As orographic rain is common during daytime, whereas pre-dawn dew consistently occurs at the diurnal minimum temperature, the growth rates of lichens in U-shaped valleys are not necessarily affected by elevation (Bidussi *et al.* 2013*b*). Dew is also frequent on northern slopes in the Northern Hemisphere (Kappen *et al.* 1980), where photosynthetic periods for lichens are substantially prolonged compared to eastern slopes (Lange *et al.* 1970).

Humid air habitats are forested ravines, shaded mountainsides and the surroundings of water bodies and mire complexes.

Stand scales

At a stand level (Fig. 3C), clear-cuts and forest gaps of certain sizes (Geiger 1950) are associated with frequent dew, particularly at northern exposures. Dew is probably an important reason why transplanted old forest lichens sometimes grow better in sheltered clear-cuts than inside intact old forests (Gauslaa *et al.* 2006; Larsson *et al.* 2012). Epiphytic lichens are not necessarily absent in clear-cuts just because of low water availability, but because stable substrata are scarce or absent. However, intact forests retain humidity after, for example, rain for longer periods than open sites during daylight, allowing accumulation of high lichen biomass (Esseen *et al.* 1996; see also Fig. 1 showing high biomass loadings).

Tree scales

Moving to the spatial scale of a tree (Fig. 3D), rain drains away from the stem and from the inner parts of the canopy (Beier *et al.* 1993), especially in the centrifugal type of crowns with hanging branches like most conifers (as reviewed by Barkman 1958). Rainfall is thus heaviest in the upper crown and in outer portions of branches. At the same time, dewfall is heaviest in the outer portions of branches at the north-facing

edges of large gaps (Stoutjesdijk 1974; Stoutjesdijk & Barkman 1987), where light is optimal for lichen growth. Dew can also be substantial in the upper, exposed canopy (Lüdi & Zoller 1953). Generally speaking, the lower forest canopy tends to be humid during the day (Geiger 1950), but lower canopy lichens often experience insufficient light for rapid growth. Slower drying inside shaded canopies compared to more light-exposed sites may partly compensate for the low photosynthetic rates associated with shade, although sunflecks have been shown to be important for the diurnal C-gain (Lakatos *et al.* 2006). Tree trunks and other habitats shielded from rain and run-off water may support ombrophobous lichen communities (see Barkman 1958), in which humidity is the only or main source of hydration. Recently, midday dew was found to be a significant source of humidity for crustose lichens on trunks in tropical rainforests (Lakatos *et al.* 2012) because of strongly delayed diurnal temperature minima in trunks acting as a heat reservoir. In principle, this should imply that the larger the trunk, the more delayed the dew event will be, leading to substantial benefits for tightly attached lichens because dew will then form during the daylight period. The highly interesting study of Lakatos *et al.* (2012) may explain why the lower portions of large trunks also in boreal and temperate environments often host rare lichens, and why ombrophobous lichen communities in old forests can host a high lichen diversity (Holien 1996). Such a mechanism depends on close thermal contact with the trunk. It thus works mainly for crustose lichens.

Links between lichen functioning and water-holding capacity

Water-holding capacity, WHC = [saturated wet mass (WM) – dry mass (DM)] / thallus area (A), gives the amount of water at saturation. This parameter is based on the thallus area that takes up and transpires water, harvests light and fixes carbon. From an ecological perspective, WHC (Fig. 5A) is thus a more functional measure than percent water
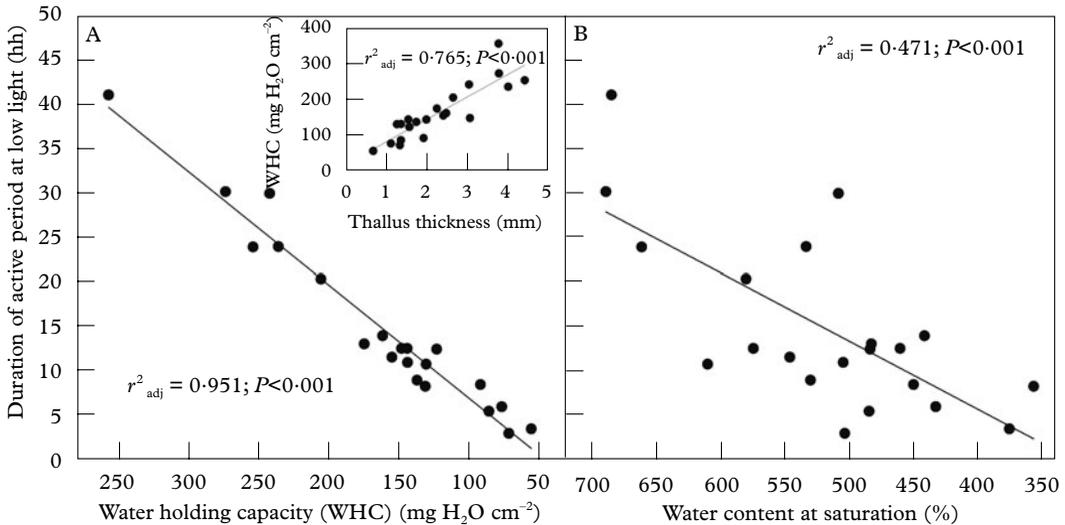
Fig. 5. The relationship between the duration of active metabolism in the cyanolichen *Degelia plumbea* at low light and A, the water-holding capacity (WHC) at saturation after shaking and B, the percent water content at the same conditions. The insert shows the relationship between WHC and the total thickness of the thalli studied with a size range of $1 \cdot 1 - 36 \cdot 4$ cm^2. The data are from Gauslaa & Solhaug (1998); A is redrawn from this paper; B and the insert are unpublished plots from the same data set.

at saturation (Fig. 5B), which is equivalent to the parameter $WHC_{DM} = (WM-DM)/DM$. WHC_{DM} is commonly used in fields such as soil science, but is less useful in lichen ecology. However, WHC as used in this paper ($=WHC_A$) directly translates to rain or dewfall (10 mg H$_2$O cm^{-2} equates to $0 \cdot 1$ mm dew or rain), and determines the duration of the physiologically active period across species and/or specimens subsequent to a hydration event (Fig. 5A).

Both WHC and percentage of water at saturation normally refer to water content after the fully hydrated thallus has been shaken or blotted with the proviso that water content is: 1) substantially higher after shaking than after blotting, and 2) higher when measured in the field than in the laboratory (i.e. owing to the presence of external water droplets; Lange *et al.* 1993*a*). $WHC_{blotting}$ mainly represents the internal WHC of a lichen thallus, whereas $WHC_{shaking}$-$WHC_{blotting}$ refers to external surface water removed by blotting (Green *et al.* 1985). Apparently, common rates of dewfall (Xiao *et al.* 2013) are often just enough to fill the $WHC_{blotting}$ of an aver-

age chlorolichen (Gauslaa & Coxson 2011). The average $WHC_{blotting}$ across lichens studied is 20 mg H$_2$O cm^{-2} (Gauslaa & Coxson 2011) and can fully utilize an average good dewfall of $0 \cdot 2$ mm (Jacobs *et al.* 2002, 2006; Richards 2002; Hao *et al.* 2012; Xiao *et al.* 2013). Such a link suggests that many lichens have evolved to function optimally with dew rather than rain. This hypothesis is consistent with the findings of Lange (Lange 2003) showing the importance of days with dew, but no rain, for the annual lichen carbon gain. By contrast, $WHC_{shaking}$ can mainly be filled with rain, as maximal dewfall rates seem to be just $0 \cdot 04$ mm h^{-1} (Xiao *et al.* 2013). Thus both these WHC measures are ecologically relevant. Measurement of $WHC_{blotting}$ is simpler to reproduce and compare, evidenced by the substantially lower standard errors (Table 1). For the lichens studied (Table 1), the average $WHC_{shaking}$/$WHC_{blotting}$ ratio was $1 \cdot 4$–$2 \cdot 1$. Therefore blotting removes substantial amounts of water. There is a need for $WHC_{shaking}$ data from more species and/or habitats. Unless specifically stated, WHC in this paper refers to $WHC_{blotting}$.

TABLE 1. *Comparison of water-holding capacity (mean ± standard error; in mg H$_2$O cm^{-2}) after shaking (WHC$_{shaking}$) and after blotting (WHC$_{blotting}$) in four lichen species.*

Species	Photobiont	n	WHC$_{blotting}$	WHC$_{shaking}$	sh/bl ratio
*Xanthoria aureola**[*]	Chloro	15	40·5 ± 1·6	91·2 ± 8·5	2·3
Hypogymnia occidentalis[†]	Chloro	200	19·1 ± 0·4	39·7 ± 0·7	2·1
Lobaria pulmonaria[†]	Cephalo	200	12·4 ± 0·1	17·1 ± 0·2	1·4
Pseudocyphellaria dissimilis[‡]	Cyano	3	13·3 ± 1·9	25·7 ± 4·1	1·9

[*] Gauslaa & Ustvedt (2003); [†] Gauslaa & Goward (2012) WHC$_{shaking}$ unpublished data; [‡] Computed from data in Green *et al.* (1985).

Gauslaa & Coxson (2011) showed that specific thallus mass, STM = DM/A, is the important driver for WHC in foliose lichens (Fig. 3F). STM is the inverse equivalent of the frequently used parameter specific leaf area (SLA = A/DM) in plant sciences (e.g. Poorter & Remkes 1990), intimately connected to the resource use economy of plants (Reich *et al.* 1998; Wright *et al.* 2004). This parameter was emphasized by Kershaw (1985) as an important lichen parameter for water loss and water uptake. STM is a rough measure of thallus thickness, and is higher in sun-adapted than in shade-adapted thalli. With increasing solar radiation exposure in nature from shaded forests to open sea cliffs, STM in studied chlorolichens increased from *c.* 7 (shade-adapted *Platismatia glauca*) to 70 mg DM cm^{-2} (*Anaptychia runcinata* thalli from open seashore), with a concurring increase in WHC from 7 to 70 mg H$_2$O cm^{-2} (Gauslaa & Coxson 2011). The 1:1 relationship found between WHC and STM in many foliose chlorolichens (Gauslaa & Coxson 2011) was also shown to hold fairly well for fruticose epiphytic chlorolichens in an oceanic oak forest in south-western Norway (Fig. 6; original data). Also for fruticose lichens, intra- and interspecific differences in WHC occur (Fig. 6). The strong 1:1 WHC-STM relationship for chlorolichens implies that WHC ≈ STM. Because lichen wet mass at saturation per thallus area (WM) = STM + WHC, a rough estimate of WHC in a chlorolichen approximates WM/2. The 1:1 WHC-STM relationship in Fig. 6 shows that enhanced internal water storage requires additional investment in carbon per thallus area, which in turn may imply a change in the balance between water use efficiency versus light use efficiency. The contrasts in thallus thickness between species suggest that STM is at least partly genetically determined.

The intraspecific variation in STM and WHC for the fruticose lichens (see Fig. 6) is mainly an effect of thallus size (data not shown). A range of sizes from small to large was measured for all species, and STM and WHC positively correlated with size. Also, for foliose canopy lichens WHC strongly increases with thallus size, from tiny juveniles to old reproducing stages (Merinero *et al.* 2014). As common intensities of dew and low rainfall match the WHC of specific size classes of lichens, the local hydration regime probably influences the maximal size of a lichen species in a given habitat.

Acclimation of STM has been noted after lichens were transplanted to new environments (e.g. Gauslaa *et al.* 2006, 2009). From a seasonal perspective, STM significantly increases when the lichen is exposed to high light and dry conditions, and again decreases during long darker and wetter periods (Larsson *et al.* 2012). Intraspecific STM responses triggered by increasing evaporative demands have also been noted in natural populations (Snelgar & Green 1981; Gauslaa & Coxson 2011; Merinero *et al.* 2014). To generalize, changes in STM effectively improve the storage of water in sites and during times when hydration is suboptimal. Prolonged exposure to full hydration has a stronger positive impact on thallus area growth than on biomass gain (Bidussi *et al.* 2013*a*), presumably because prolonged high turgor pressure stimulates fungal expansion, as discussed by Larsson *et al.* (2012) and Bidussi
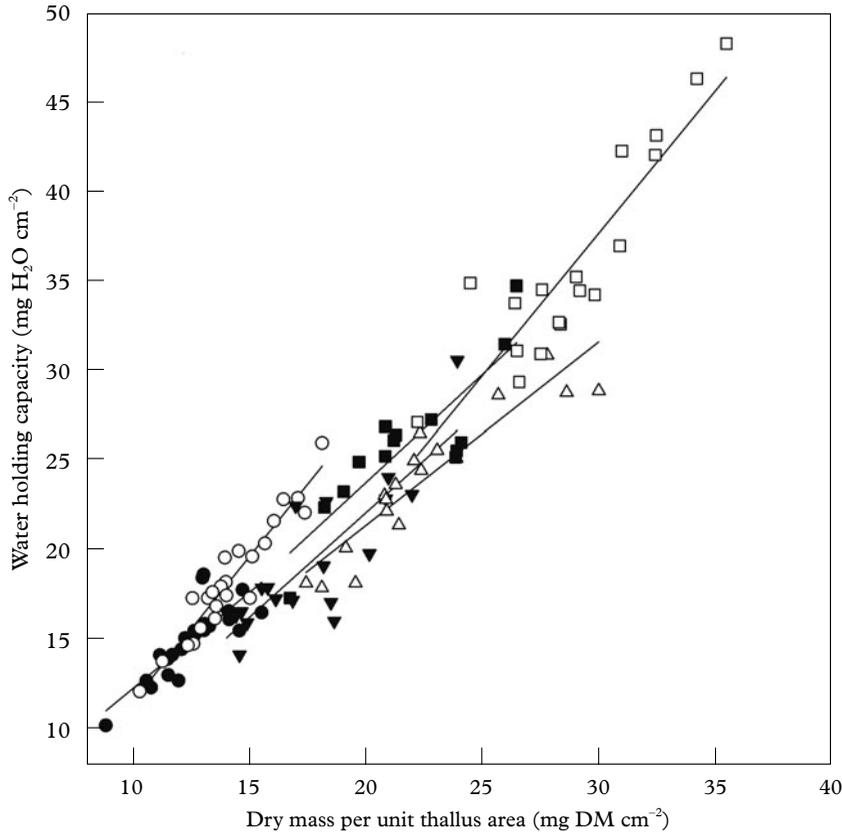
FIG. 6. Specific thallus mass (mg dry matter cm^{-2}) and water-holding capacity (mg H_2O cm^{-2}) in fully hydrated thalli after removing surface water by blotting. All fruticose epiphytic lichen species found in an Atlantic oak forest in Spindanger, Farsund, south-western Norway were included. ●, *Evernia prunastri*; ○, *Pseudevernia furfuracea*, ▼, *Ramalina farinacea*; △, *Usnea cornuta*; ■, *Usnea subfloridana*; □, *Sphaerophorus globosus*; species specific regression lines are shown. Thallus area in *E. prunastri*, *P. furfuracea*, *R. farinacea* and *S. globosus* was measured with a LI3100 Licor Area Meter (Lincoln, Nebraska, USA); areas in the two *Usnea* spp. were computed by imaging tools (ImageJ 1.46f version). In all species, a range of thallus sizes as measured (original data)

et al. (2013*a*). Such responses probably tune the WHC to seasonal and spatial evaporative demands.

Lichen responses to hydration sources

Many green algal lichens (chloro- and cephalolichens) can initiate photosynthetic activity in the absence of liquid moisture, although activation in humid air often occurs at slow rates (Jonsson Cabrajic *et al.* 2010). The relative humidity needs to exceed 75–80%, corresponding to a water potential ≈-38 MPa (Nash III *et al.* 1990) or lower (Green *et al.* 2011). Therefore, the term 'humid air' in Fig. 2 (right corner) refers to humidity levels above $\approx80\%$. Cyanolichens by contrast require liquid water as rain or dew to initiate normal photosynthesis (Lange *et al.* 1986, 1988, 1989, 1993*b*); their photosynthetic water compensation point is much higher than in chlorolichens, as reviewed by Green *et al.* (2011). Accordingly, cyanolichens are restricted to the left portion of the triangle, indicating a requirement for dew and rain (see e.g. Marini *et al.* 2011), whereas chloro- and cephalolichens utilize all

available hydration sources and are hence, as a group, more widespread (Fig. 3G). The fact, however, that cyanolichens often have substantially higher WHC than chloro- and cephalolichens (Gauslaa & Coxson 2011), may partly compensate for their more stringent hydration requirements for photosynthetic activation. At the same time, the cyanolichen *Lobaria scrobiculata* requires 2·5 times greater hydration for activation than the cephalolichen *L. pulmonaria* (MacKenzie & Campbell 2001), which complicates the story and emphasizes the need for further studies on lichen water use efficiency, as proposed by Máguas *et al.* (1997).

The bottom panel of triangles (Fig. 3E–H) summarizes various lichen responses to hydration. Excess hydration by liquid water often suppresses lichen photosynthesis, a phenomenon referred to as suprasaturation depression (Lange & Matthes 1981; Lange *et al.* 1993a, 2001). Suprasaturation depression does not occur during water uptake in humid air, but can instantaneously take place after additional spraying with water (Lange & Kilian 1985), unless the lichen surface is water-repellent (Lakatos *et al.* 2006; Hauck *et al.* 2008; Pardow *et al.* 2010). In a continuous year-long gas exchange measurement of the chlorolichen *Lecanora muralis* in an open habitat in Germany, 74 days of heavy rain resulted in only 2·4% of the annual carbon gain, whereas 105 days with dew accounted for 40% (Lange 2003). Depression of lichen photosynthesis by excess water is thus common in rainy events, rare with dew, and absent in humid air (Fig. 3E). As bryophytes in general are much better than lichens in handling excess water (Green *et al.* 2011), there is a higher bryophyte/lichen biomass ratio in rainy regions where bryophytes rather than lichens tend to dominate tree canopies.

Finely dissected and/or thin lichens (Fig. 1A) take up humidity rapidly, whereas thick and/or compact growth forms need a long time to become hydrated in humid air (Larson & Kershaw 1976; Larson 1981; Lange & Kilian 1985; Lange *et al.* 1986). Chlorolichens across studied macrolichen growth forms and taxonomic groups follow the 1:1 line in WHC-STM plots, equivalent to ≈100% water at saturation [Fig. 5 shows this for fruticose lichens; Gauslaa & Coxson (2011) shows foliose lichens]. Epiphytic cyanolichens tend to follow the 2:1 line equivalent to ≈200% water (Gauslaa & Coxson 2011). Such relationships suggest that chlorolichens have an opportunistic water economy, as the lower mass per thallus area allows more rapid use of humidity from the air. Cyanolichens have a more conservative water economy. They need higher water content in order to maximize the duration of hydration to compensate for the rarer hydration events by liquid water.

Alectorioid lichens (Figs 1A & 3H) are among the lichens with the largest surface area to biomass ratio. Among the alectorioid lichens, *Bryoria* species and *Ramalina thrausta* are the thinnest. As chlorolichens, they rapidly activate photosynthesis in equilibrium with high ambient air humidity (Lange *et al.* 1986). *Bryoria* biomass is much higher in inland regions with less rain than in coastal forests subjected to heavy rain (as shown for Scandinavia by Ahlner 1948; Bruteig 1993). Furthermore, excess rain or melting water from snow has been shown to damage *Bryoria* in western North America (Goward 1998), as well as being associated with temporary *Bryoria* dieback in Norwegian spruce canopies during unusually wet autumns (Y. Gauslaa, pers. obs.). Similar die-off events have been observed in foliose chlorolichens during an exceptional wet late autumn when no damage occurred in cephalo- and cyanolichens (Gauslaa 2002). The alectorioid genus *Usnea* is more flexible with respect to water sources than *Bryoria*, *Alectoria* and *Ramalina thrausta*. The genus as such has a highly variable morphology and anatomy (Motyka 1947), and occurs in well-lit portions of rainforests in most regions of the world (Halonen *et al.* 1998; Kantvilas & Jarman 1999; Antoine & McCune 2004), as well as in drier forests with abundant *Bryoria* biomass. *Usnea* is often represented with more species in the more oceanic areas than in dry areas (Bjerke *et al.* 2006), and growth rates in species such as *Usnea longissima* increase with increasing rainfall (Gauslaa *et al.* 2007). The *Usnea* species

shown in Fig. 6 have fairly high WHC, but they came from a coastal site where rain and wind are frequent and dew rarely appears, and where no specimens of *Bryoria* occurred. In contrast to other alectorioid lichens *(Alectoria, Bryoria, Ramalina thrausta)*, thick coastal *Usnea* species may depend on rain and may thus have optimized their water storage.

Individual lichen species may occupy narrow or wide species-specific areas within the triangle in Fig. 2. To give a few examples, the delicate, pendulous, capillary branches of *Ramalina thrausta* are apparently optimized for rapid, highly efficient activation in humid air, an inference supported by this species' remarkable ability to inhabit sites partially sheltered from rain and dew. By contrast, the foliose genera *Sticta* and *Pseudocyphellaria*, including cephalo- as well as cyanolichen members, inhabit rainy climates (Green & Lange 1991). Apparently, the presence of cyphellae and pseudocyphellae in *Sticta* and *Pseudocyphellaria*, respectively, permits CO_2 exchange through the lower cortex which allows more of the remaining thallus to store water without too severe suprasaturation depression (Green *et al.* 1981, 1985). Suprasaturation depression under rainforest conditions was less, or even absent, in *Sticta* at 500% water content having cyphellae than in *Lobaria* in which these structures are lacking (Lange *et al.* 2004). Another rain-dependent species is the cyanolichen *Degelia plumbea*, with such a high WHC (Gauslaa & Solhaug 1998) that it can never be fully activated by dew alone.

Conclusion

Various groups and species of epiphytic lichens have specialized morphology, anatomy and symbiotic relationships in order to function optimally under specific hydration regimes. In this respect, growth forms and photobiont type are important lichen traits. There is a need to quantify STM and WHC in more lichen species and growth forms. So far, WHC data are lacking for the many green-algal pendulous and fruticose lichens, as well as for cyanobacterial gel lichens. Another promising investigation would be to study the links between STM and activation time of photosynthetic acitivity in chloro- and cephalolichens in humid air. Such data are needed to establish quantitative links between availability of hydration sources and lichen traits in the model (Fig. 3E–H). Specifying the sources of hydration and including internal lichen variables such as water-holding capacity will probably improve modelling local and global future scenarios on lichen distribution and biomass production.

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