


Standard Paper

Growth-dependent acclimation constrains climatic response for the lichen epiphyte *Lobaria pulmonaria*

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Abstract

Species can respond to climate change by migrating to track their suitable climate space, and/or through adaptation (across generations) or acclimation (by individuals) to a changed *in situ* environment. Lichens provide an excellent model for studying acclimation; being poikilohydric, there is strong evidence that their phenotype presents an adaptation to different moisture regimes, and that key aspects of the phenotype, notably specific thallus mass (STM), have plasticity towards effective acclimation that maximizes water storage in drier environments. In this study we quantified acclimation of STM for *Lobaria pulmonaria* across a regional climatic gradient, and within sites for different microclimates, using a one-year common garden growth experiment. We found that STM tended to increase with thallus growth; however, when accounting for growth, STM shifted to be lower than average in wetter environments, higher than average in intermediate environments, and failed to respond in the driest environment where growth was compromised. The possibility of phenotypic acclimation in *Lobaria pulmonaria* appears to be functionally linked to the propensity for growth, and we present a scheme coupling growth with STM to define the limits of the species realized niche.

Keywords: climate change; common garden experiment; dry matter growth; phenotypic plasticity; specific thallus mass

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Introduction

Climate change is a major threat to biodiversity (Bellard *et al.* 2012) and understanding the species response to, and threat posed by, climate change is a central theme in conservation biology (Scheffers *et al.* 2016; Pecl *et al.* 2017). Species climate change response is generally considered as combining three processes: 1) individuals of a species may migrate to track the changing distribution of their suitable climate space (Parmesan & Yohe 2003; Chen *et al.* 2011), constrained by habitat fragmentation (Travis 2003; Hodgson *et al.* 2012); 2) individuals of a population may evolve and adapt *in situ*, effective across generations, to tolerate climate change (Hoffman & Sgrò 2011; Kelly 2019); 3) individuals may acclimate *in situ* through plasticity in morphology or physiology that allows persistence under climate change (Seebacher *et al.* 2015; Rohr *et al.* 2018). In the latter case, different species appear to have different modes of plasticity, with some species being more limited in their ability to acclimate than others.

Lichens have become established as an excellent study system for understanding acclimation to different environments through phenotypic plasticity. Lichens are poikilohydric, responding to the ambient environment by desiccating when the environment is dry (Kranter *et al.* 2008), and rehydrating only with ambient moisture (Jonsson *et al.* 2008) to become physiologically active

(Lange *et al.* 1986, 1993; Phinney *et al.* 2018). Lacking homeostatic control over their hydration status, and therefore physiological outcome, the lichen phenotype is thought to provide regulatory control of thallus water relations and for lichen epiphytes the phenotype varies among species in a way that reflects adaptation to different forest moisture regimes (Gauslaa 2014). A key parameter in this regard, analogous to specific leaf area (SLA), is specific thallus mass (STM), the mass per unit area of the lichen thallus. Different lichen species have different values for STM (cf. fig. 6 in Gauslaa (2014), and also Gauslaa & Coxson (2011); Wan & Ellis 2020; Trobajo *et al.* 2022), which combines with a species-specific water content (WC), the volume of water absorbed per unit mass, to determine the volume of water that can be absorbed internally per unit area, as the water-holding capacity (WHC_{internal}). The species-specific value of WHC_{internal} appears to be the point at which the photosynthetic rate is maximized (Solhaug *et al.* 2021). Accordingly, species with low STM have been referred to as having an ‘opportunistic’ moisture strategy (*sensu* Gauslaa 2014), tending to saturate their internal capacity (and maximize their photosynthetic rate) with lower volumes of water available as vapour or light dewfall. These species will also dry quickly and may be at particular risk of supersaturation under high moisture conditions, since relatively low volumes of water can meet the requirement of WHC_{internal} with subsequent moisture accumulation onto their outer surface limiting gas exchange across the thallus (Lange *et al.* 1996, 2000, 2004). In contrast, species with high STM have been referred to as having a ‘conservative’ water strategy (*sensu* Gauslaa 2014), requiring higher water volumes as heavy dewfall or rain to saturate their

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internal capacity (and maximize their photosynthetic rate), though drying more slowly (cf. Gauslaa *et al.* 2017; Phinney *et al.* 2018; Hovind *et al.* 2020).

Species with a more conservative strategy (relatively high STM) may be at particular risk of prolonged desiccation and extended physiological dormancy, since relatively low volumes of water may be insufficient to optimize thallus hydration at WHC_{internal} . It has been suggested that a key acclimation of such species, in response to lower water availability, may actually be to increase thallus STM. This pattern of acclimation in STM has previously been observed at multiple scales comparing wetter and drier sites regionally (Gauslaa *et al.* 2009), for wetter and drier microhabitats (Gauslaa & Coxson 2011; MacDonald & Coxson 2013; Merinero *et al.* 2014), and for wetter and drier periods seasonally (Larsson *et al.* 2012). It has been suggested that acclimation towards higher STM allows for the absorption of more water per unit thallus area when it is available, and with slower drying to prolong photosynthesis. If this is the case, then lichen thallus STM appears to be a viable metric with which to explore the lichen phenotypic response to climate variability at multiple scales, including climate change.

To aid our understanding of lichen epiphyte climatic response, including potential acclimation to climate change, we asked three questions: 1) to what degree might it be possible for individual lichen thalli (of a given species) to acclimate their STM in response to a changed climate; 2) what is the relative importance of regional larger-scale climate compared to buffering microclimatic conditions on this response; 3) can we identify the limits to this phenotypic response, marking the point at which acclimation is no longer possible? To answer these questions, we used a spatial design, growing the model lichen species, *Lobaria pulmonaria*, in different experimental microhabitats, corresponding to microclimates, nested within different regional larger-scale climates. We then quantified the relative dry matter growth as mass gain/loss, and the change in STM over the period of one year.

Methods

One-hundred and twenty juvenile thalli of *Lobaria pulmonaria* (L.) Hoffm. were collected from a donor site in the oceanic 'temperate rainforest' zone of western Scotland (Fig. 1; Barnluasgan Oakwood, 56.0619°N, 5.5488°W). They were transported to the Royal Botanic Garden Edinburgh (RBGE), cleaned of extraneous debris, fully hydrated by repeat spraying with distilled water, shaken and gently blotted to remove excess surface water, and then photographed when lightly pressed under a glass sheet (with millimetre scale), before being air-dried and weighed. Air-drying was in a climate-controlled laboratory at 21 °C with average relative humidity at 40%. The maximum time elapsed from field collection to deployment in the experiment was 10 days, with air-dried thalli stored in the dark when not undergoing measurement or experimental preparation. Individual thalli were gently bound, with cotton thread and a single length of plastic-coated wire, to mesh stretched onto frames that were angled at 45° at c. 1.5 m above ground height (Fig. 2). The mesh was horticultural shade-netting, with a major weave of 2 mm and a minor (intermediate) weave of 1 mm. The frames were distributed across five climatically contrasting study sites (Fig. 1) based on previous calculations of a regional hygrothermy index (Ellis 2016), which is a proxy for the transition from an oceanic to continental biogeography. Within each site the frames were orientated to face towards north-west and south-east aspects, with the thalli facing south-

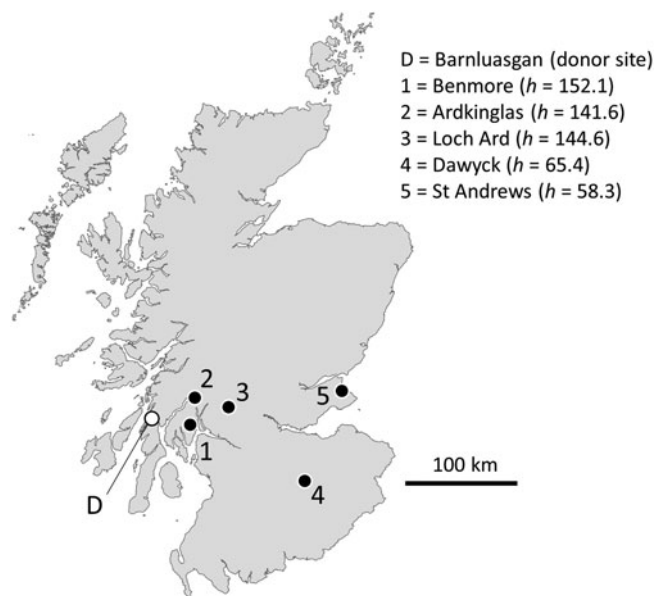


Figure 1. Location of the *Lobaria pulmonaria* donor site for the experimental lichen thalli (D), and the five experimental sites for lichen growth in Scotland; h = hygrothermy index according to Ellis (2016) which is a proxy for the transition from an oceanic to continental biogeography.

east either bound alone onto the mesh or placed above an underlying mat of the moss *Isoetecium myosuroides*, which is often closely associated in an epiphyte community with *Lobaria pulmonaria* (Ellis *et al.* 2015). There were eight thalli per microhabitat treatment, for different aspects, and with or without moss for south-east aspects, at each site.

Frames were positioned into different ecological settings that reflected the local character of each study site. At Benmore and Dawyck Botanic Gardens, frames were positioned in open areas adjacent to meteorological stations. At Ardkinglas and Loch Ard sites, frames were positioned beneath woodland canopies, and at St Andrews Botanic Garden, frames were in a gladed parkland setting. To account for these local differences, which might otherwise confound the contrasting hygrothermy among sites, the frames were accompanied by iButton hygrochron dataloggers (Analog Devices, Wilmington, USA) recording temperature and humidity at 2-h intervals over the course of the year and used to calculate a vapour pressure deficit. Vapour pressure deficit (VPD) was calculated as follows:

$$VPD = (1 - (RH/100)) \times SVP \quad (\text{Eq. 1})$$

where RH is the relative humidity and SVP is the saturated vapour pressure for the given air temperature. The VPD values recorded at 2-h intervals were summed into cumulative monthly values, which were then plotted as an annual time-series and as box plots for each site, with an annual mean also calculated.

Lichen thalli were grown for 12 months, from March 2017 to March 2018, and collected for return to RBGE, cleaned of extraneous debris, fully hydrated by repeat spraying with distilled water, shaken and gently blotted to remove excess surface water, and then photographed when lightly pressed under a glass sheet (with millimetre scale), before being air-dried and weighed. First, having compared the start weights of lichens across the different sites, and microhabitat treatments (combination of aspect

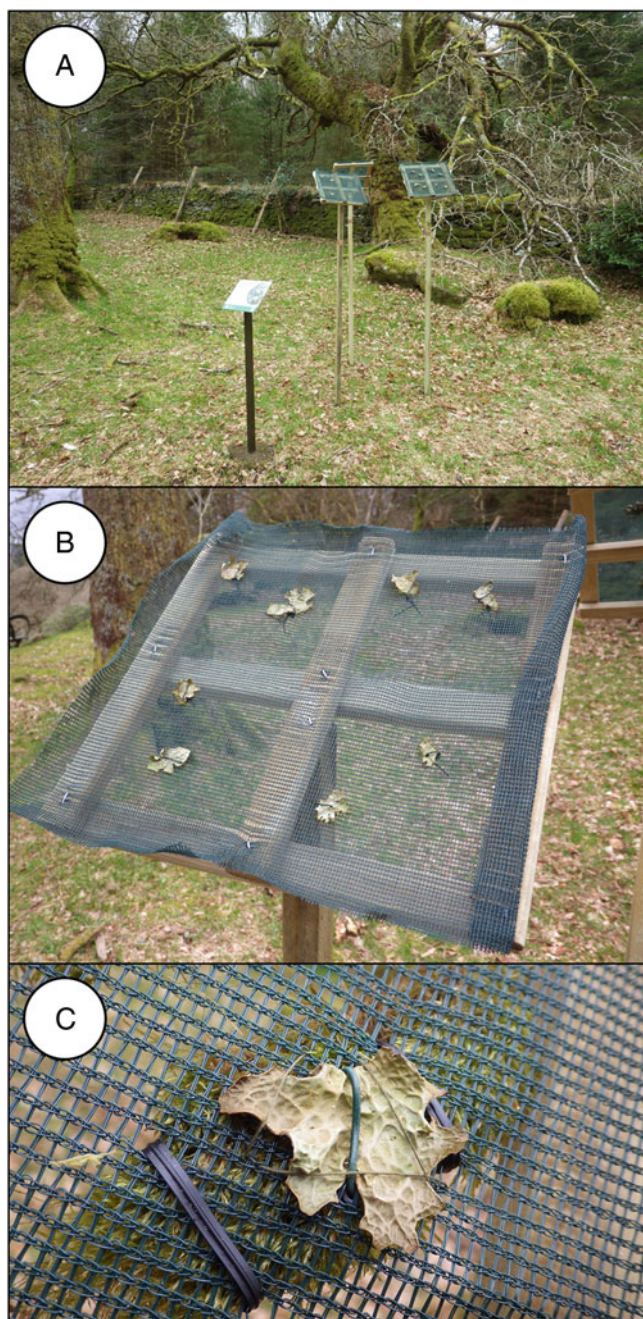


Figure 2. Examples of the experimental design for lichen growth using the epiphyte *Lobaria pulmonaria*, with thalli positioned onto angled mesh surfaces with or without an associated moss mat, located at sites across Scotland (see Fig. 1). In colour online.

and presence of moss), using a nested analysis of variance, we calculated the relative dry matter growth (DM_{growth}) of the lichen thalli, as follows:

$$DM_{\text{growth}}(\text{mg mg}^{-1}\text{yr}^{-1}) = (DM_{\text{final}} - DM_{\text{start}}) / DM_{\text{start}} \quad (\text{Eq. 2})$$

Second, having compared the start STM of lichens across the different sites, and microhabitat treatments, using a nested analysis of variance, we compared the DM_{growth} of the lichen thalli with the percent change in specific thallus mass (ΔSTM) over the course of the experiment, using ordinary linear regression;

STM was calculated as follows:

$$\text{STM} = \text{DM} / A \quad (\text{Eq. 3})$$

The photosynthetic surface area (A) of the lichen thalli was measured from their original photographs using ImageJ v.1.53 (National Institute of Health, USA).

Third, we calculated residuals from the regression between DM_{growth} and STM, plotted these as box plots, and calculated the variance explained by site, and microhabitat treatments, using a linear mixed effects model to accommodate thallus losses over the duration of the experiment and which resulted in an unbalanced design (Zuur *et al.* 2009; Crawley 2013).

Results

Calculated values of VPD, as a cumulative total per month, showed a pattern of seasonal change that was broadly coherent across the five study sites (Fig. 3), though being different in magnitude so that the microclimates experienced by lichen thalli were contrasting. Ardkinglas and Loch Ard were oceanic sites (hygrothermy = 142 and 145, respectively), with frames positioned in a sheltered woodland that explained low VPD. Benmore was also an oceanic site (hygrothermy = 152), but with frames positioned in a more open setting with intermediate VPD, while Dawyck was a drier site (hygrothermy = 65) with higher VPD, and St Andrews the driest and most continental site (hygrothermy = 58) with the highest VPD.

The mean start weight of individual lichen thalli was 42.75 ± 1.57 mg (\pm 1SE), with no significant difference among sites ($F = 0.508$, $P = 0.73$ with $df_{4,104}$) or among microhabitat treatments within site ($F = 0.834$, $P = 0.597$ with $df_{10,104}$). However, thallus growth was different among the sites (Fig. 4). Using GLMM for hierarchical partitioning, site explained *c.* 60.2% of the variance in growth, and its effect was broadly consistent with the different climates. Thallus growth was higher in wetter climates with lower VPD (Ardkinglas, Loch Ard) as well as for the intermediate Benmore site, becoming lower for progressively drier climates with higher VPD (Dawyck and St Andrews). Microhabitat treatment explained < 1% of the variance in growth (residual variance = 39.8%).

The mean start STM of individual lichen thalli was 9.2 ± 0.13 mg cm^2 (\pm 1SE), with no significant difference among sites ($F = 0.676$, $P = 0.61$ with $df_{4,104}$) but with a difference in STM among some of the microhabitat treatments within site ($F = 3.123$, $P = 0.0016$ with $df_{10,104}$). Thallus growth significantly explained the percent change in STM (ΔSTM) over the course of the experiment (adjusted $R^2 = 0.199$, $P < 0.0001$ with 109 df). Allowing for the positive relationship between growth and ΔSTM (Fig. 4), and using GLMM for hierarchical partitioning, site explained *c.* 46.5% of the residual ΔSTM and microhabitat treatment explained *c.* 6% (residual variance = 47.5%). Accordingly, ΔSTM tended to be lower than expected (Fig. 5) for the two wettest sites (Ardkinglas and Loch Ard), increasing for the intermediate Benmore site, with a smaller increase for the drier Dawyck site, and with little overall change (\pm normally distributed residuals) for the driest site (St Andrews).

Discussion

Phenotypic acclimation is an important biological response to environmental change, including climate change (Matesanz

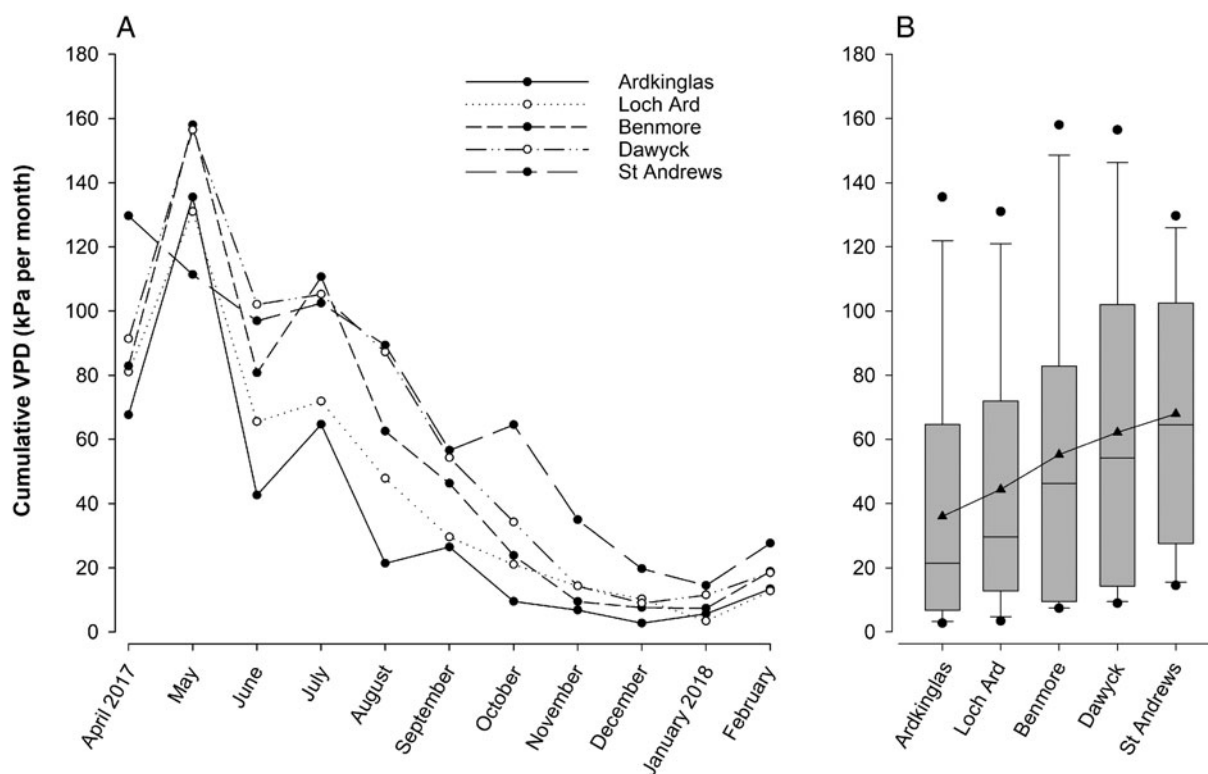


Figure 3. Microclimatic data at experimental sites for *Lobaria pulmonaria* growth across a regional climatic gradient in Scotland. A, time-series of monthly cumulative vapour pressure deficit (VPD) over the period of the growth experiment (line graph), for different experimental sites. B, the annual median and variability in monthly cumulative VPD within and among the sites (boxplots; showing inter-quartile range, 90th and 10th percentiles as whiskers, and 95th and 5th percentiles as dots), with the means (triangles).

et al. 2010; Nicotra *et al.* 2010). Acclimation under environmental change can therefore determine individual fitness, population viability, and moderates the risk to species. Considering the importance of moisture and thallus hydration in lichen photosynthesis and respiration (Green *et al.* 2010; Palmqvist *et al.* 2010), phenotypic change that modifies thallus water relations is thought to be a key route to lichen acclimation (Gauslaa *et al.* 2009; Larsson *et al.* 2012; Merinero *et al.* 2014), including in response to climate change. In this study we were interested in the limits to this process of acclimation, and how any such limits might shape the lichen realized niche.

First, we demonstrated for *Lobaria pulmonaria* that growth was higher in wetter compared to drier climates. Although a widespread species in old-growth forest stands, this matches with a more general skew towards oceanic climates in terms of the species frequency of occurrence and abundance (James *et al.* 1977; Ellis 2016), being consistent with bioclimatic trends observed in previous experimental growth studies (Eaton & Ellis 2012; see also Gauslaa *et al.* 2007; Ellis *et al.* 2017). However, there is evidence, both experimental (Gauslaa *et al.* 2016, 2017) and from field observations (Ellis 2020), that in the very wettest habitats *L. pulmonaria* growth might be constrained by suprasaturation. In establishing these patterns, VPD seems a useful compound metric for determining the moisture conditions relevant to *L. pulmonaria* growth (see e.g. Gaio-Oliveira *et al.* 2004), being consistent with the ability of the species to rehydrate under high humidity conditions. It is also related to dew formation as an additional source of moisture and reflects the ambient drying effect of the air (Barry & Blanken 2016), all of which will

determine the extent to which the lichen thallus remains hydrated. VPD has been used previously to explain the growth and distribution of lichen epiphytes (Rambo 2010b; Ellis 2020), including their responses to environmental change at different scales (Rambo & North 2012; Song *et al.* 2014), and more broadly to explain general patterns of epiphyte biomass and community structure (Rambo 2010a; Gotsch *et al.* 2017).

Second, we show a relationship between thallus growth and percent change in STM (Δ STM), since thalli that had grown more also tended to accumulate greater mass per unit area. This is consistent with previous growth studies for *L. pulmonaria* under field and laboratory conditions (Gauslaa *et al.* 2009; Bidussi *et al.* 2013) and may explain the widely reported allometric pattern in which larger thalli of a given species tend to have higher STM (Gauslaa & Solhaug 1998; Merinero *et al.* 2014; Longinotti *et al.* 2017). It is important to take account of this allometry when attempting to characterize acclimation, and we did this by considering whether residual values of Δ STM appeared to have a climate signature. Accordingly, we found that, despite relatively high growth for the two wettest locations, residuals were negative, indicating that the gain in thallus area was higher than might be expected relative to the increase in dry mass. Previous studies (e.g. Gaio-Oliveira *et al.* 2004; Gauslaa *et al.* 2009; Larsson *et al.* 2012) have suggested that this could occur in wetter environments, specifically conditions under which thallus hydration is sufficient to maintain turgor pressure required for the consistent expansion of fungal hyphae (Money 2007, 2008; Lew 2011). In contrast, at an intermediate location, residuals were positive, indicating that the increase in

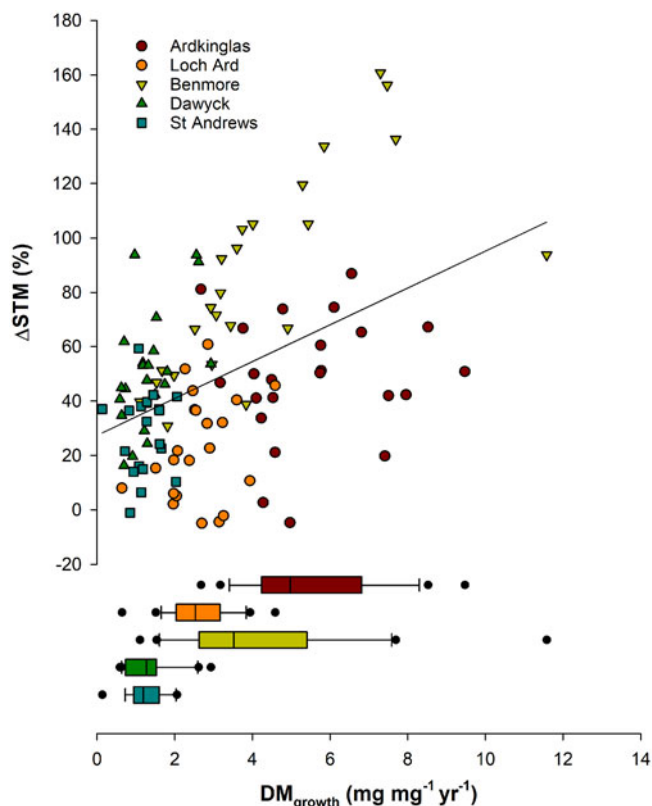


Figure 4. The change in specific thallus mass (STM) compared to growth (scatter plot; coded by experimental site) of *Lobaria pulmonaria*, and the median and variability in growth within and among the experimental sites (boxplots; showing interquartile range, 90th and 10th percentiles as whiskers, and 95th and 5th percentiles as dots). In colour online.

thallus dry mass was higher than might be expected relative to the gain in area. Again, previous studies (e.g. Gaio-Oliveira *et al.* 2004; Gauslaa *et al.* 2009; Larsson *et al.* 2012) have suggested that this could occur in environments where thallus water content tends to be below a threshold invoking two conditions: (i) photosynthesis still remains active, for example estimated at a minimum of *c.* 15–25% thallus water content (Gauslaa *et al.* 2017; Phinney *et al.* 2018), thus allowing an increase in dry mass, despite (ii) turgor pressure being lost, which is estimated at *c.* 40–60% thallus water content (Beckett 1995, 1996), and therefore preventing the expansion of fungal hyphae. However, the increase in residuals remains coupled to positive growth since the thalli become acclimated to maximize water storage, achieving longer periods of hydration. At the two driest locations, growth was highly limited or did not occur, and the consequence of this seems to have been an inability to sufficiently adjust STM. This would presumably be the case if both photosynthesis and turgor pressure remain low. Especially at the driest location, residual values were normally distributed and did not decline as might have been the case when acclimating to a drier environment. Incidentally, the driest site also suffered the highest rate of thallus mortality, at *c.* 21%.

There are several important limitations to our study. For example, our growth experiment lasted over the period of a year, and we assume that Δ STM reflects the annual pathway of climatic contrasts between sites. However, previous work has demonstrated that STM may acclimate over shorter seasonal timescales (Larsson *et al.* 2012), and it is possible that our final values

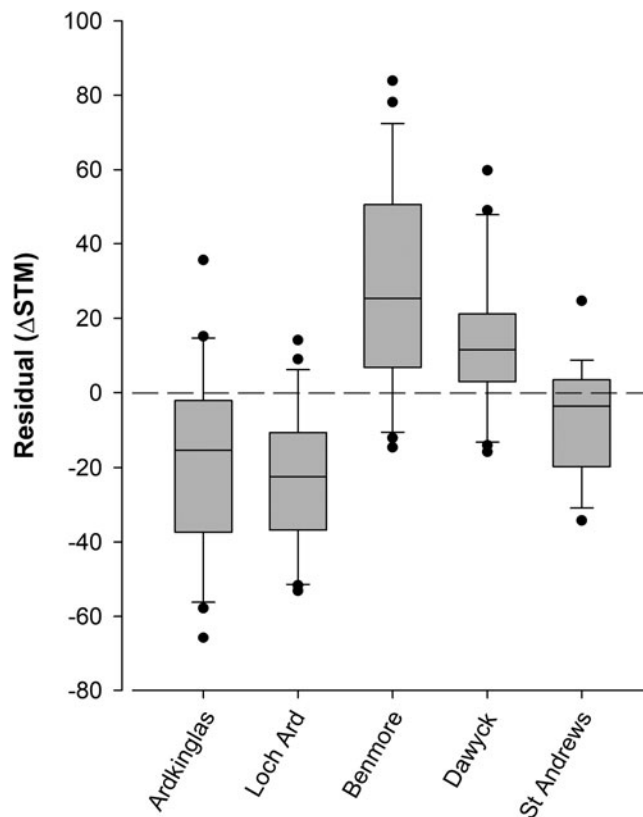


Figure 5. Residual values of the change in specific thallus mass (STM) of *Lobaria pulmonaria* when accounting for the effect of growth (cf. Fig. 4) at sites across a climatic gradient in Scotland.

of Δ STM reflect the climate over a shorter preceding period, such as the winter season prior to the samples being measured. Nevertheless, this shorter period sufficiently retains the climatic contrasts, with VPD for the winter season being strongly correlated with annual VPD among the sites (Pearson's product moment correlation for mean VPD: $r=0.9$, $P=0.036$ with 4 df). Considering the potential for extreme events under climate change (O'Gorman 2015; Horton *et al.* 2016), it is important to establish the shortest timescale over which the lichen thallus may acclimate to changed environmental conditions, referred to as the 'rate of reversible phenotypic plasticity' (Horton *et al.* 2016). Our results suggest that phenotypic changes relevant to hydration are limited by thallus growth, and extreme events that exceed or limit a growth rate response will weaken this aspect of acclimation. However, there may be more rapid constitutive responses to a changed environment, as demonstrated by effective acclimation of *L. pulmonaria* photosynthesis over monthly (MacKenzie *et al.* 2001; Schofield *et al.* 2003) to weekly timescales (MacKenzie *et al.* 2004), and a rapid regulatory response to temperature observed through gene expression (Kraft *et al.* 2022). Additionally, it was surprising that we found a minimal effect of microhabitat on growth and Δ STM, with respect to aspect and an accompanying moss layer, both of which can affect microclimatic conditions (see Veneklaas *et al.* 1990; Colesie *et al.* 2012; Larsson *et al.* 2012). It is possible that the climatic contrasts among sites was, owing to the experimental design, far greater than that realized by the microhabitat treatments within each site, while also having a higher statistical sample size ($n=24$), so that the sample size available to test microhabitat treatment

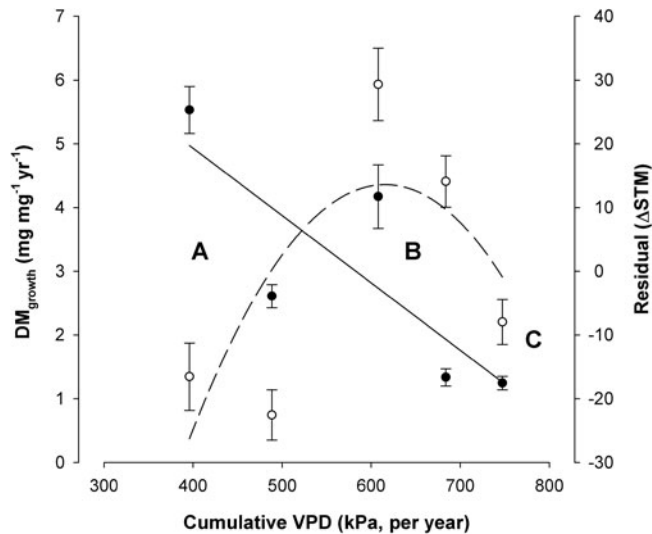


Figure 6. Summary acclimation response of *Lobaria pulmonaria*; closed symbols (\pm 1 SE) and the solid line show the growth (linear response), open symbols (\pm 1 SE) and the dotted line show the residual values of the change in specific thallus mass (Δ STM) (unimodal response, as a polynomial). In Zone A (wetter), growth is high and STM declines as the thallus becomes relatively thinner; in Zone B (intermediate), growth is lower but sufficient to increase STM prolonging thallus hydration; in Zone C (dry), growth is lowest and poses a limit to phenotypic acclimation.

($n = 8$) was just too small to detect an effect. Furthermore, a tendency for aerial extension of *Lobaria pulmonaria* lobes during growth, extending away from the substratum, may have weakened the effect of the moss layer.

Despite these limitations, we cautiously propose a simple three staged acclimation response for *L. pulmonaria* (Fig. 6), this being relevant within the context of the species' overall phenotypic adaptation to moisture regime. First, in a sufficiently wet environment both growth and turgor pressure are high, and consequently the relative STM decreases in favour of area gain. This thallus thinning increases the risk of suprasaturation, though with this risk being offset through aerial extension of lobes away from the substratum, facilitating airflow and evaporative drying (Zone A in Fig. 6). Second, in an intermediate environment, growth declines but remains positive, while turgor pressure is compromised, and consequently the relative STM increases in favour of thallus thickness, facilitating prolonged hydration during periods of water availability (Zone B in Fig. 6). Third, in a dry environment growth is very low or stops, preventing acclimation and representing the boundary of the species realized niche (Zone C in Fig. 6). On this basis, measures of thallus growth (as dry mass gain or loss) remain a useful functional metric for climate change response (see e.g. Ellis *et al.* 2017; Smith *et al.* 2018; Ellis 2019; Meyer *et al.* 2023) since they incorporate the ability to acclimate to environmental change. If climate change crosses a threshold beyond which growth is no longer possible, then phenotypic acclimation would no longer be effective for *L. pulmonaria*, and the species would be considered at risk.

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References

- Barry RG and Blanken PD (2016) *Microclimate and Local Climate*. Cambridge: Cambridge University Press.
- Beckett RP (1995) Some aspect of the water relations of lichens from habitats of contrasting water status studied using thermocouple psychrometry. *Annals of Botany* **76**, 211–217.
- Beckett RP (1996) Some aspects of the water relations of the lichen *Parmotrema tinctorum* measured using thermocouple psychrometry. *Lichenologist* **28**, 257–266.
- Bellard C, Bertelsmeier C, Leadley P, Thuiller W and Courchamp F (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters* **15**, 365–377.
- Bidussi M, Gauslaa Y and Solhaug KA (2013) Prolonging hydration and active metabolism from light periods into nights substantially enhances lichen growth. *Planta* **237**, 1359–1366.
- Chen I-C, Hill JK, Ohlemüller R, Roy DB and Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026.
- Colesie C, Scheu S, Green TGA, Weber B, Wirth R and Büdel B (2012) The advantage of growing on moss: facilitative effects on photosynthetic performance and growth in the cyanobacterial lichen *Peltigera rufescens*. *Oecologia* **169**, 599–607.
- Crawley MJ (2013) *The R Book*. Chichester: John Wiley and Sons.
- Eaton S and Ellis CJ (2012) Local experimental growth rates respond to macroclimate for the lichen epiphyte *Lobaria pulmonaria*. *Plant Ecology and Diversity* **5**, 365–372.
- Ellis CJ (2016) Oceanic and temperate rainforest climates and their epiphyte indicators in Britain. *Ecological Indicators* **70**, 125–133.
- Ellis CJ (2019) Interactions of climate and solar irradiance can reverse the bioclimatic response of poikilohydric species: an experimental test for *Flavoparmelia caperata*. *Bryologist* **122**, 98–110.
- Ellis CJ (2020) Microclimatic refugia in riparian woodland: a climate change adaptation strategy. *Forest Ecology and Management* **462**, 118006.
- Ellis CJ, Eaton S, Theodoropoulos M and Elliott K (2015) *Epiphyte Communities and Indicator Species. An Ecological Guide for Scotland's Woodlands*. Edinburgh: Royal Botanic Garden Edinburgh.
- Ellis CJ, Geddes H, McCheyne N and Stansfield A (2017) Lichen epiphyte response to non-analogue monthly climates: a critique of bioclimatic models. *Perspectives in Plant Ecology, Evolution and Systematics* **25**, 45–58.
- Gaio-Oliveira G, Dahlman L, Máguas C and Palmqvist K (2004) Growth in relation to microclimatic conditions and physiological characteristics of four *Lobaria pulmonaria* populations in two contrasting habitats. *Ecography* **27**, 13–28.
- Gauslaa Y (2014) Rain, dew, and humid air as drivers of morphology, function and spatial distribution in epiphytic lichens. *Lichenologist* **46**, 1–16.
- Gauslaa Y and Coxson D (2011) Interspecific and intraspecific variations in water storage in epiphytic old forest foliose lichens. *Botany* **89**, 787–798.
- Gauslaa Y and Solhaug KA (1998) The significance of thallus size for the water economy of the cyanobacterial old-forest lichen *Degelia plumbea*. *Oecologia* **116**, 76–84.
- Gauslaa Y, Palmqvist K, Solhaug KA, Holien H, Hilmo O, Nybakken L, Myhre LC and Ohlson M (2007) Growth of epiphytic old forest lichens across climatic and successional gradients. *Canadian Journal of Forest Research* **37**, 1832–1845.
- Gauslaa Y, Palmqvist K, Solhaug KA, Holien H, Nybakken L and Ohlson M (2009) Size-dependent growth of two old-growth associated macrolichen species. *New Phytologist* **181**, 683–692.
- Gauslaa Y, Alam MA and Solhaug KA (2016) How to optimize lichen relative growth rates in growth cabinets. *Lichenologist* **48**, 305–310.
- Gauslaa Y, Solhaug KA and Longinotti S (2017) Functional traits prolonging photosynthetically active periods in epiphytic lichens during desiccation. *Environmental and Experimental Botany* **141**, 83–91.
- Gotsch SG, Davidson K, Murray JG, Duarte VJ and Draguljić (2017) Vapor pressure deficit predicts epiphyte abundance across an elevational gradient in a tropical montane region. *American Journal of Botany* **104**, 1790–1801.

- Green TGA, Nash TH, III and Lange OL (2010) Physiological ecology of carbon dioxide exchange. In Nash TH, III (ed.), *Lichen Biology*. Cambridge: Cambridge University Press, pp. 154–183.
- Hodgson JA, Thomas CD, Dytham C, Travis JM and Cornell SJ (2012) The speed of range shifts in fragmented landscapes. *PLoS ONE* 7, e47141.
- Hoffman AA and Sgrò CM (2011) Climate change and evolutionary adaptation. *Nature* 470, 479–485.
- Horton RM, Mankin JS, Lesk C, Coffel E and Raymond C (2016) A review of recent advances in research on extreme heat events. *Current Climate Change Reports* 2, 242–259.
- Hovind ABÅ, Phinney NH and Gauslaa Y (2020) Functional trade-off hydration strategies in old forest epiphytic cephalolichens. *Fungal Biology* 124, 903–913.
- James PW, Hawksworth DH and Rose F (1977) Lichen communities in the British Isles: a preliminary conspectus. In Seaward MRD (ed.), *Lichen Ecology*. London: Academic Press, pp. 295–413.
- Jonsson AV, Moen J and Palmqvist K (2008) Predicting lichen hydration using biophysical models. *Oecologia* 156, 259–273.
- Kelly M (2019) Adaptation to climate change through genetic accommodation and assimilation of plastic phenotypes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 374, 20180176.
- Kraft M, Scheidegger C and Werth S (2022) Stressed out: the effects of heat stress and parasitism on gene expression of the lichen-forming fungus *Lobaria pulmonaria*. *Lichenologist* 54, 71–83.
- Kranner I, Beckett R, Hochman A and Nash TH, III (2008) Desiccation tolerance in lichens: a review. *Bryologist* 111, 576–593.
- Lange OL, Kilian E and Ziegler H (1986) Water vapor uptake and photosynthesis of lichens: performance differences in species with green and blue-green algae as phycobionts. *Oecologia* 71, 104–110.
- Lange OL, Büdel B, Meyer A and Kilian E (1993) Further evidence that activation of net photosynthesis by dry cyanobacterial lichens requires liquid water. *Lichenologist* 25, 175–189.
- Lange OL, Green TGA, Reichenberger H and Meyer A (1996) Photosynthetic depression at high thallus water contents in lichens: concurrent use of gas exchange and fluorescence techniques with a cyanobacterial and a green algal *Peltigera* species. *Botanica Acta* 109, 43–50.
- Lange OL, Büdel B, Meyer A, Zellner H and Zotz G (2000) Lichen carbon gain under tropical conditions: water relations and CO₂ exchange of three *Leptogium* species of a lower montane rainforest in Panama. *Flora* 195, 172–190.
- Lange OL, Büdel B, Meyer A, Zellner H and Zotz G (2004) Lichen carbon gain under tropical conditions: water relations and CO₂ exchange of *Lobariaceae* species of a lower montane rainforest in Panama. *Lichenologist* 36, 329–343.
- Larsson P, Solhaug KA and Gauslaa Y (2012) Seasonal partitioning of growth into biomass and area expansion in a cephalolichen and a cyanolichen of the old forest genus *Lobaria*. *New Phytologist* 194, 991–1000.
- Lew RR (2011) How does a hypha grow? The biophysics of pressurized growth in fungi. *Nature Reviews Microbiology* 9, 509–518.
- Longinotti S, Solhaug KA and Gauslaa Y (2017) Hydration traits in cephalolichen members of the epiphytic old forest genus *Lobaria* (s. lat). *Lichenologist* 49, 493–506.
- MacDonald A and Coxson D (2013) A comparison of *Lobaria pulmonaria* population structure between subalpine fir (*Abies lasiocarpa*) and mountain alder (*Alnus incana*) host-tree species in British Columbia's inland temperate rainforest. *Botany* 91, 535–544.
- MacKenzie TDB, MacDonald TM, Dubois LA and Campbell DA (2001) Seasonal changes in temperature and light drive acclimation of photosynthetic physiology and macromolecular content in *Lobaria pulmonaria*. *Planta* 214, 57–66.
- MacKenzie TDB, Johnson J and Campbell DA (2004) Environmental change provokes rapid macromolecular reallocations within the photosynthetic system in a static population of photobionts in the lichen *Lobaria pulmonaria*. *Lichenologist* 36, 425–433.
- Matesanz S, Gianoli E and Valladares F (2010) Global change and the evolution of phenotypic plasticity in plants. *Annals of the New York Academy of Sciences* 1206, 35–55.
- Merinero S, Hilmo O and Gauslaa Y (2014) Size is a main driver for hydration traits in cyano- and cephalolichens of boreal rainforest canopies. *Fungal Ecology* 7, 59–66.
- Meyer AR, Valentin M, Liulevicius L, McDonald TR, Nelson MP, Pengra J, Smith RJ and Stanton D (2023) Climate warming causes photobiont degradation and C starvation in a boreal climate sentinel lichen. *American Journal of Botany* 110, e16114.
- Money NP (2007) Biomechanics of invasive hyphal growth. In Howard RJ and Gow NAR (eds), *Biology of the Fungal Cell*. Berlin: Springer-Verlag, pp. 237–249.
- Money NP (2008) Insights on the mechanics of hyphal growth. *Fungal Biology Reviews* 22, 71–76.
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, et al. (2010) Plant phenotypic plasticity in a changing climate. *Trends in Ecology and Evolution* 15, 684–692.
- O'Gorman PA (2015) Precipitation extremes under climate change. *Current Climate Change Reports* 1, 49–59.
- Palmqvist K, Dahlman L, Jonsson A and Nash TH, III (2010) The carbon economy of lichens. In Nash TH, III (ed.), *Lichen Biology*. Cambridge: Cambridge University Press, pp. 184–217.
- Parmesan C and Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Pecl GT, Araújo MB, Bell JD, Blamchard J, Bonebrake TC, Chen I-C, Clark TD, Colwell RK, Danielsen F, Evengård B, et al. (2017) Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* 355, eaai9214.
- Phinney NH, Solhaug KA and Gauslaa Y (2018) Rapid resurrection of chlorolichens in humid air: specific thallus mass drives rehydration and reactivation kinetics. *Environmental and Experimental Botany* 148, 184–191.
- Rambo TR (2010a) Structure and composition of corticolous epiphyte communities in a Sierra Nevada old-growth mixed-conifer forest. *Bryologist* 113, 55–71.
- Rambo TR (2010b) Habitat preferences of an arboreal forage lichen in a Sierra Nevada old-growth mixed-conifer forest. *Canadian Journal of Forest Research* 40, 1034–1041.
- Rambo TR and North MP (2012) Influence of fuel-reduction forest thinning on growth of an arboreal forage lichen. *Forest Ecology and Management* 263, 208–215.
- Rohr JR, Civitello DJ, Cohen JM, Roznik EA, Sinervo B and Dell AI (2018) The complex drivers of thermal acclimation and breadth in ectotherms. *Ecology Letters* 21, 1425–1439.
- Scheffers BR, De Meester L, Bridge TCL, Hoffmann AA, Pandolfi JM, Corlett RT, Butchart SHM, Pearce-Kelly P, Kovacs KM, Dudgeon D, et al. (2016) The broad footprint of climate change from genes to biomes to people. *Science* 354, aaf7671.
- Schofield SC, Campbell DA, Funk C and MacKenzie TDB (2003) Changes in macromolecular allocation in nondividing algal symbionts allow for photosynthetic acclimation in the lichen *Lobaria pulmonaria*. *New Phytologist* 159, 709–718.
- Seebacher F, White CR and Franklin CE (2015) Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* 5, 61–66.
- Smith RJ, Nelson PR, Jovan S, Hanson PJ and McCune B (2018) Novel climates reverse carbon uptake of atmospherically dependent epiphytes: climatic constraints on the iconic boreal forest lichen *Evernia mesomorpha*. *American Journal of Botany* 105, 1–9.
- Solhaug KA, Asplund J and Gauslaa Y (2021) Apparent electron transport rate – a non-invasive proxy of photosynthetic CO₂ uptake in lichens. *Planta* 253, 14.
- Song L, Liu W, Zhang Y, Tan Z, Li S, Qi J and Yao Y (2014) Assessing the potential impacts of elevated temperature and CO₂ on growth and health of nine non-vascular epiphytes: a manipulation experiment. *American Journal of Plant Sciences* 5, 1587–1598.
- Travis JM (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London Series B* 270, 467–473.
- Trobajo S, Fernández-Salegui A, Hurtado P, Terrón A and Martínez I (2022) Interspecific and intraspecific variability of water use traits in

- macrolichen species in a fragmented landscape along a climatic ecotone area. *Fungal Biology* **126**, 438–448.
- Veneklaas EJ, Zagt RJ, Van Leerdam A, Van Ek R, Broekhoven AJ and Van Genderen M** (1990) Hydrological properties of the epiphyte mass of a montane tropical forest, Colombia. *Vegetatio* **89**, 183–192.
- Wan S and Ellis CJ** (2020) Are lichen growth form categories supported by continuous functional traits: water-holding capacity and specific thallus mass? *Edinburgh Journal of Botany* **77**, 65–76.
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA and Smith GM** (2009) *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer.