Macroclimate drives growth of hair lichens in boreal forest canopies

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Abstract

1. Epiphytic lichens are important biodiversity components of forest canopies worldwide, significantly contributing to ecosystem function. The RGR, a measure of fitness, drives population dynamics and shapes lichens’ large-scale distributions. In a climate change scenario, we need to know how external (macro- and microclimate, and nitrogen deposition) and internal factors (cortical pigments, chlorophyll and specimen size) affect RGR in these ecologically important canopy organisms.

2. We used dominant pendulous hair lichens widely distributed across the boreal biome to test the hypothesis that precipitation drives RGR of pale (Alectoria sarmentosa, Usnea dasopoga) and dark species Bryoria fuscescens differently across a large-scale gradient from continental to oceanic climates (precipitation: 450–2,600 mm) in Scandinavia (60–64°N, 5–19°E). After transplanting lichens to lower branches of Picea abies in nine boreal forest sites for 1 year, we used linear mixed effects models to analyse how total precipitation, rainfall, number of days with rain, temperature sum, nitrogen deposition, light, chlorophyll a (an indicator of photosynthetic capacity) and size influenced their RGR.

3. RGR was highest in the pale species (Alectoria and Usnea) and increased with amount and frequency of precipitation, with >3 times higher RGR in the wettest compared to the driest site. The number of days with rain was a better predictor of RGR than total precipitation or rain. By contrast, RGR of the dark Bryoria weakly increased with precipitation. RGR in all species increased with light and decreased with size. Chlorophyll a concentration, boosted by moderate nitrogen deposition, increased RGR of all species.

4. In conclusion, rainfall likely drives the distribution of the pale species due to their higher RGR and abundance in wet climates but cannot explain why Bryoria dominates drier inland forests. Our results highlight that the functional links between rainfall and RGR depends on both colour of the lichens (pale vs. dark pigments) and water storage traits.

5. Synthesis. Our findings may explain the global, regional and local distribution patterns of hair lichens and help us to predict how environmental hazards such as climate change and forestry influence these important boreal canopy components.

Keywords
chlorophyll, climate change, epiphytic lichens, lichen colour, nitrogen deposition, plant–climate interactions, rainfall, RGR

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1 | INTRODUCTION

Epiphytic lichens are important components of forest canopies world-wide and contribute substantially to ecosystem function (Asplund & Wardle, 2017; Porada et al., 2018). They act as microclimate buffers by modifying temperature and evaporation from their host plants (Pypker et al., 2017; Stanton et al., 2014), offer fodder and habitat for animals (Seaward, 1988) and are indicators of forest ecosystem integrity (Nimis et al., 2002). Hair (Alectoria, Bryoria) and beard lichens (Usnea, hereafter also referred to as hair lichens) form conspicuous epiphytic communities in boreal forests (Ahti, 1977; Boudreault et al., 2015; Hauck, 2011). They constitute an important diet of reindeer, caribou and other mammals (Hauck, 2011) and provide shelter for invertebrates, including high-quality prey for passerine birds (Pettersson et al., 1995). These lichens die or suffer from air pollutants (Bruteig, 1993; Johansson et al., 2010) and from other global change factors (Esseen et al., 2016; Nascimbene et al., 2019). Their abundance peaks in old forests (Bartels & Chen, 2015; Esseen et al., 1996; Price & Hochachka, 2001) and declines with short logging cycles (Boudreault et al., 2015; Dettki & Esseen, 1998, 2003; Lesica et al., 1991) threatening some of them (e.g. Rolstad et al., 2013; Sérusiaux, 1989). To secure such complex fungal-algal symbioses and their ecosystem functions in future forests, we apply experimental approaches to quantify and understand how environmental factors regulate their growth, distribution and abundance.

With a poikilohydric lifestyle, lichens’ hydration and concurring metabolism fluctuate with ambient air humidity (Proctor & Tuba, 2002). This lifestyle shortens their growth periods compared to homoiohydric plants that acquire soil water and regulate loss of water via stomata. First, macromelate, notably precipitation and temperature, interacts with forest canopy structure and creates microclimates (Stoutjesdijk & Barkman, 1987) that affect lichen growth rates and contribute to large-scale lichen distribution patterns (Esseen et al., 2016; Gauslaa, 2014; Gauslaa et al., 2007; Marini et al., 2011). Second, at microclimatic scales, irradiance received by hydrated lichens drives photosynthesis and growth (Dahlman & Palmqvist, 2003; Palmqvist & Sundberg, 2000). In forests, low light often limits lichen growth rates (Gauslaa et al., 2007), but high light does not always boost photosynthesis, as light-induced heating enhances evaporation (Stoutjesdijk & Barkman, 1987) that down-regulates photosynthesis. Light during long dry periods even damages lichens (Färber et al., 2014; Gauslaa et al., 2006, 2012). Third, lichens need nitrogen (N) to make new fungal and algal (photobiont) cells, often with strong, positive correlation between N availability and photobiont pools within and among species (Johansson et al., 2010; Palmqvist et al., 2002). Thus, internal factors like chlorophyll (Chl) concentration (a proxy of photosynthetic capacity and photobiont concentration) and specimen size also shape lichen growth rates (Dahlman & Palmqvist, 2003; Lange, 2002, 2003; Palmqvist et al., 2017).

The success of hair lichens is partly linked to their flexible use of water. At high relative humidity, they almost instantaneously activate photosynthetic processes (Phinney et al., 2018). However, rain is often necessary to fill their water storage pools (Eriksson et al., 2018; Esseen et al., 2015, 2017), which extend hydration and prolong metabolic activity (Gauslaa & Solhaug, 1998; Gauslaa et al., 2017). At the same time, excess rain can greatly impede the uptake of CO₂ (Lange et al., 1993). While macroclimatic gradients apparently drive regional distributions of epiphytic lichens (Coyle & Hurlbert, 2016), including hair lichens (Esseen et al., 2016), few have explored how macroclimate shapes lichen growth (Boucher & Nash III, 1990; Gauslaa et al., 2007), an important measure of lichen fitness.

Here, we investigate RGRs of three widespread species: Alectoria sarmentosa (Ach.) Ach. and Usnea dasopoga (Ach.) Nyl., which have the pale yellowish pigment usnic acid, and the dark melanic Bryoria fuscescens (Gyelnik) Brodo & D. Hawksw., all henceforth referred to by genus names. They have partly overlapping distributions, yet different habitat requirements (Ahlner, 1948; Esseen et al., 2016). We aim to examine how a broad-scale macroclimate gradient in combination with light and internal lichen traits (photosynthetic pigments, lichen colour and size) regulate the RGR of these dominant lichens in boreal forests and elucidate how such factors drive niche differentiation among the species. By transplanting lichens along a precipitation gradient (450–2,600 mm) from dry continental to wet oceanic climates in Scandinavia (Fick & Hijmans, 2017), we will test the following hypotheses: (a) Growth of pale species increases with precipitation and/or the annual number of days with rain. Lichens with pale cortices transmit more light to their photobionts than dark, melanic ones (Färber et al., 2014; Gauslaa et al., 2020), leading to higher carbon gain during dark and cloudy rainy weather in the former species. (b) Growth of the dark Bryoria decreases with precipitation and/or the annual number of days with rain. Its melanic solar screen (Färber et al., 2014) excessively reduces the light and thus photosynthesis in dark, rainy weather. Furthermore, Bryoria is intolerant to prolonged hydration (Coxson & Coyle, 2003; Goward, 1998) but activates quickly in humid air (Phinney et al., 2018). (c) The internal factor Chl a concentration, a proxy of photobiont population size (Palmqvist et al., 2002), increases with airborne N deposition in all species across the broad-scale gradient. (d) After controlling for precipitation, RGR increases with Chl a concentration at N depositions below critical levels. High N deposition may result in excessively high investments in photobiont cells and compromise symbiosis integrity (Dahlman & Palmqvist, 2003; Johansson et al., 2010; Palmqvist et al., 2002, 2017).

2 | MATERIALS AND METHODS

2.1 | Study species

Alectoria, with an incomplete circumpolar distribution and an oceanic tendency (Ahlner, 1948), peaks in old, humid boreal forests in Fennoscandia (Esseen et al., 2016). Bryoria and Usnea are circumpolar species that grow on a wide range of tree species (Thell & Moberg, 2011). Bryoria has the highest abundance in drier and
open boreal conifer forests, particularly in northern regions (Esseen et al., 2016). Usnea is most frequent in humid forests in southern-middle boreal zones.

2.2 | Study sites

We transplanted lichens to nine sites in Norway and Sweden (Figure 1). The study sites were selected such that: (a) a wide range in precipitation was represented; (b) a weather station was situated nearby; (c) there was a lack of sizable air pollution sources (major roads, large population centres, large-scale animal husbandry farms and factories) in the surroundings; (d) the forest was dominated by mature to old Picea abies (L.) H. Karst. with a moderately open canopy. The selected sites covered a large-scale gradient in total precipitation (452–2,572 mm, 56.3%–91.6% rain and the rest snow) and in annual number of days with rain (48–171), ranging from slightly continental to highly oceanic climate (Table 1).

Daily precipitation and temperature during the transplantation period were downloaded from the most representative meteorological stations with respect to distance and elevation (Norwegian Meteorological Institute, www.eklima.no; Swedish Meteorological and Hydrological Institute, www.smhi.se/data). A rain index comprised the total precipitation in days warmer than 0°C. The number of days with precipitation (≥1 mm) and rainfall were counted. We calculated mean annual temperature and the range for daily means as well as the effective temperature sum (growing degree days), here defined as the sum of daily means above 5°C. Temperature sum has been widely used in studies of growth and abundance of plants (e.g. Villen-Perez et al., 2020). The studied lichens have optimum photosynthesis at intermediate precipitation (site 2–6) and less so in the wettest position and abundance. They were most abundant in sites with many N-fixing cyanolichens intolerant of eutrophication.

Hair lichens occurred at all sites, but with varying species composition and abundance. They were most abundant in sites with intermediate precipitation (site 2–6) and less so in the wettest sites (8–9). Species typical for continental areas occurred in dry sites (e.g. Bryoria furcellata (Fr.) Brodo & D. Hawksw. and Usnea hirta (L.) F. H. Wigg.), while the wet sites hosted many rainforest lichens (Table S1), which strongly indicates that N deposition was below damaging levels. Even the three wettest sites with high N deposition had many N-fixing cyanolichens intolerant of eutrophication.

Dry and wet inorganic N deposition was estimated in Norwegian (Aas et al., 2017) and Swedish sites (www.smhi.se/klimatdata/miljo/atmosfarskemi), ranging from 1.3 to 8.5 kg N ha⁻¹ year⁻¹ (Table 1) with strong linear relationship between total N deposition and precipitation (\( R^2 = 0.966, p < 0.001 \)) for seven of the nine sites. Two sites had higher N deposition than predicted from precipitation: the driest site (1, 4.5 kg N ha⁻¹ year⁻¹) had scattered small-scale animal husbandry farms in the surroundings, and site 6 (6.5 kg N ha⁻¹ year⁻¹) was located 8 km away from wide agricultural landscapes. No site harboured nitrophytic lichens (e.g. members of the Physciaceae or the Teloschistales, Table S1), which strongly indicates that N deposition was below damaging levels. Even the three wettest sites with high N deposition had many N-fixing cyanolichens intolerant of eutrophication.

The forest structure at each site was described by measuring basal area by tree species with a relascope. We measured the height of the two tallest trees with a Suunto hypsometer and the DBH of all transplant trees varied from 19.7 cm (site 1) to 30.9 cm (site 5).

![Map of the nine study sites in Norway and Sweden and their precipitation (monthly totals, blue bars) and temperature (red lines, smoothed daily values) data for the transplantation period. Sites are ordered after increasing precipitation.](image-url)
| Site | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|------|---|---|---|---|---|---|---|---|---|
| **Location** |   |   |   |   |   |   |   |   |   |
| Latitude, longitude, DMS | 61°49′12″N 9°15′42″E | 64°27′59″N 18°35′15″E | 64°50′56″N 17°35′15″E | 64°14′3″N 19°48′56″E | 63°4′21″N 18°6′42″E | 60°12′1″N 10°32′40″E | 63°47′24″N 10°10′28″E | 64°1′55″N 10°26′10″E | 61°36′36″N 5°36′36″E |
| Elevation, m | 441 | 265 | 565 | 199 | 335 | 602 | 63 | 115 | 65 |
| **Climate classification** | SC | OC | OC | OC | O1 | O1 | O2 | O2 | O3 |
| **Weather** |   |   |   |   |   |   |   |   |   |
| Precipitation, mm | 452 | 485 | 506 | 628 | 964 | 1,045 | 1,140 | 1,520 | 2,572 |
| Rain, mm | 372 | 274 | 285 | 372 | 555 | 714 | 1,044 | 1,385 | 2,270 |
| Precipitation max daily, mm | 53 | 23 | 20 | 23 | 63 | 51 | 37 | 65 | 74 |
| No. days ≥ 1 mm precipitation | 74 | 99 | 102 | 114 | 115 | 126 | 146 | 157 | 205 |
| No. days rain ≥ 1 mm | 51 | 48 | 53 | 56 | 63 | 76 | 129 | 135 | 171 |
| Temperature mean, °C | 3.8 | 2.0 | 1.4 | 3.3 | 3.8 | 5.3 | 6.4 | 5.9 | 8.5 |
| Temperature range, °C | −24−24 | −27−24 | −27−24 | −19−24 | −20−23 | −15−24 | −10−26 | −13−26 | −7−27 |
| Temperature sum, degree days | 1,534 | 1,141 | 1,105 | 1,119 | 1,247 | 1,468 | 1,423 | 1,324 | 1,731 |
| **N deposition, kg N ha⁻¹ year⁻¹** | 4.5 | 1.9 | 1.3 | 2.9 | 3.5 | 6.5 | 4.5 | 5.5 | 8.5 |
| Basal area, m²/ha | 25.0 | 27.7 | 19.0 | 22.2 | 37.0 | 18.0 | 18.0 | 26.0 | 24.0 |
| Light transmittance, % | 15.5 ± 0.8 | 15.5 ± 0.8 | 16.9 ± 0.8 | 15.6 ± 0.7 | 13.0 ± 0.7 | 13.8 ± 1.2 | 20.9 ± 0.9 | 14.3 ± 1.0 | 11.6 ± 0.8 |

Note: Climate classifications (Ahti et al., 1968): SC = slightly continental, OC = indifferent, O1 = slightly oceanic, O2 = oceanic, O3 = highly oceanic. Rain = total precipitation when temperature ≥ 0°C. Temperature range is based on daily means.
2.3 | Transplant experiment

Lichens were collected between 2 August and 4 August 2017 from mixed populations in the lower canopy (2–4 m) of an old, mesic-moist *Picea abies* forest in Rödälden, north-eastern Sweden (64°37’13”N, 19°52’45”E, 160 m a.s.l.), 13 km south of site 4. The 16–20 m tall stand with a basal area of 25 m²/ha (88% *Picea*, 3% *Pinus*, 9% deciduous) hosted a high biomass of hair lichens. Collected lichens were dried at room temperature and stored 2–3 weeks in darkness until transplantation.

From this collection, 225 healthy thalli of each species were randomly chosen, cleaned of debris and weighed air-dry. Ten additional thalli from each species were also weighed air-dry and oven-dry (24 hr at 70°C); the percentage difference between these values was used as a correction factor to compute oven-dry mass (DM) of all air-dried transplant before the transplantation (DM_start). The basal part of one randomly selected thallus of each species (12–18 cm in length) was individually secured onto a PVC mesh netting (8 cm × 22 cm; mesh size 12 mm × 14 mm) using a fishing line (FireLine 0.2 mm), such that most of each thallus was free hanging (Figure S1). One thallus of each species was randomly distributed among the three positions on each net (left, middle and right).

The nets were set out between 17 August and 28 August 2017. At each site, we selected 25 live *P. abies*, 16–23 m tall, spaced >10 m apart, growing at moderately open positions and having branches below 2.1 m with lichens. One net was attached to each tree using cable ties onto SW−SE-facing, horizontal or moderately sloping live or dead branches, 1.7–3.2 m above the ground and 0.3–2.1 m from the trunk (Table S2). The amount of light was measured as PAR transmittance (Messier & Puttonen, 1995) using simultaneous PAR readings with two light metres (ULM-500, Walz). One light sensor was held horizontally directly above each spruce branch with the net, while the reference sensor was in a nearby open area with an unobstructed view of the sky. Measurements were done on overcast days, or with a clear sky with direct sunlight blocked by a small shield (20 cm in diameter, placed at 80 cm distance). Light transmittance was calculated as percentage of the open reference (Liefers et al., 1999; Messier & Puttonen, 1995). Light transmittance varied among individual nets (4.9%–30.5%) and sites (11.6%–20.9%, Table 1). The relationship between mean light transmittance and basal area was not significant (R² adj = 0.146, p = 0.168, N = 9), but light transmittance decreased slightly with DBH of transplant trees across sites (R² adj = 0.022, p < 0.014, N = 225).

The nets with lichens were collected between 20 August and 2 September 2018 and dried in the laboratory for 2 days. To account for visible damage (fragmented by wind, grazing, necrosis) or otherwise significantly matted or decayed thalli, each lichen was photographed. Missing or damaged thalli (>25% mass loss) were excluded from all analyses (Table S3) as such losses were caused by stochastic processes and not growth responses. Each thallus was removed from the net and weighed to determine dry mass, corrected to oven-dry mass (DM_end) as described above. Following weighing, the lichens were stored at -18°C. Growth was computed as RGR (Evans, 1972) and as percent increase in DM (% DM):

\[
\text{RGR} = \frac{\ln(\text{DM_end}/\text{DM_start}) \times 1000}{\text{no. of days}}
\]

\[
\% \text{DM growth} = \frac{\text{DM_end} - \text{DM_start}}{\text{DM_start}} \times 100
\]

2.4 | Chlorophyll

Chl *a* was quantified in 20 thalli per species at the start, and in all transplants at the end of the experiment. Each thallus was frozen in liquid N₂ in an 18 ml Poly-Q-Vial (Beckman) for 10–15 s together with two steel balls, pulverized in a ball mill, aliquoted for extraction in MgCO₃-saturated dimethylsulphoxide (DMSO) and heated at 60°C for 40 min. We used 10–30 mg lichen powder and 1.2 ml solvent for *Alectoria* and *Bryoria*, and 30–100 mg and 4 ml solvent for *Usnea*; larger samples were needed for *Usnea* that was difficult to pulverize to homogeneous samples due to their rigid central axis. Absorbances at 649.1, 665.1 and 750 nm were measured with a spectrophotometer (Jasco V-650, Jasco International) with 0.1 nm band width. Chl *a* was calculated by the following equation (Wellburn, 1994), using the absorbance at 750 nm for baseline (zero) correction:

\[
\text{Chl} a = 12.47A_{665.1} - 3.62A_{649.1}.
\]

For *Bryoria*, it was necessary to correct for the presence of melanin since this pigment absorbs light increasingly and nonlinearly with decreasing wavelength and obstructed the chlorophyll determination. Briefly, different concentrations of synthetic melanin (SIGMA-Aldrich CAS-number 8049-97-6) were used to derive standard curves for subtraction of the melanin absorbance of each sample (K. Palmqvist, unpublished data).

2.5 | Statistical analyses

Means and standard errors (SE) were calculated for RGR, % DM growth and Chl *a* for the three species and nine sites after the transplantation, and for a representative start sample of thalli for Chl *a* from the collection site. We used an ANOVA and a Tukey’s HSD post hoc test to compare species-specific Chl *a* concentrations (log-transformed) at start. The growth responses were analysed for all intact thalli (N = 615, see above and Table S3); the growth models were based on RGR as response variable.

We fitted linear mixed effects models (Harrison et al., 2018) to test our four hypotheses. Such models can handle the hierarchical structure of the data, with nine sites, 25 transplant trees per site and one net with three lichens per tree. The analysed data included 219 trees and were slightly unbalanced due to losses (see above). The fitting of mixed models was done with the lmer function in the R package lme4 (Bates et al., 2015). The random effects were site, and transplant tree nested under site. To test hypothesis 1, we first fitted a mixed model with RGR as the response variable.
and the variables total precipitation, species, light transmittance, DM<sub>start</sub> as well as all two-way interactions among these factors as fixed effects. For comparison, we replaced precipitation in this model with total rainfall, number of days with rain and temperature sum respectively. All precipitation variables were ln-transformed to obtain approximately linear relationships with RGR, whereas temperature sum, light and DM<sub>start</sub> were rescaled so that all variables were of the same magnitude. From these four models, we selected the macroclimate variable with highest explanatory power and included it in a ‘final’ model to test hypothesis 1. This model also included temperature sum, species, light, DM<sub>start</sub> and all two-way interactions as fixed factors. To test hypothesis 2, comparing RGR of dark (Bryoria) and pale species, we ran the above final model by pooling Alectoria and Usnea. To test hypothesis 3, we fitted a model for Chl<sub>a</sub> with N deposition, species, light, DM<sub>start</sub> as well as all two-way interactions as fixed effects. Finally, to test hypothesis 4, we fitted a model for RGR using Chl<sub>a</sub> as well as with the same precipitation variable as in the ‘final’ RGR model (see above) as fixed effects.

The models were simplified by successively removing non-significant interactions. Model selection was based on the second-order Akaike information criterion (AIC<sub>c</sub>), selecting the most parsimonious model with ΔAIC<sub>c</sub> < 2, compared to the model with minimum AIC<sub>c</sub> (Burnham & Anderson, 2002). The finally selected models were run with restricted maximum likelihood and checked with residual plots to identify heteroscedasticity and non-normality. Denominator degrees of freedom and p-values for the fixed effects were calculated with the Kenward–Roger method (Harrison et al., 2018) for the slightly unbalanced data. Following recommendations of Bates et al. (2015), the significance of model parameters was evaluated after calculating 95% confidence intervals (CI) by parametric bootstrapping with 1,000 iterations. Model performance was evaluated by calculating the marginal R<sup>2</sup> (R<sup>2</sup><sub>Cond</sub>), representing the variance explained by only the fixed effects, and the conditional R<sup>2</sup> (R<sup>2</sup><sub>Cond</sub>), representing the variance of the whole model (i.e. both fixed and random effects, Johnson, 2014; Nakagawa & Schielzeth, 2013). The analyses were run with R version 4.0.2 (R Core Team, 2020) using the libraries car, lmertest, matrix, MuMIn, nle, sjmisc and sjstats.

3 | RESULTS

3.1 | Growth rates

Most thalli gained mass: 97.1% of the Alectoria specimens, 96.8% of Usnea but only 77.2% of Bryoria. RGR in Alectoria was 1.3 times higher (0.484 mg g<sup>−1</sup> day<sup>−1</sup> = 20.2% DM growth) than that in Usnea (0.364 = 14.9%) and 3.7 times higher than that in Bryoria (0.158 = 6.5%; Table 2). Growth of the pale Alectoria and Usnea increased from the driest to the wettest sites, with the highest mean RGR in the three wettest sites (7–9), whereas the dark Bryoria showed a weakly increasing trend (Figure 2).

The mixed effects models for the weather variables were similar and showed that RGR increased significantly and nonlinearly with all three precipitation variables (Figure S2a–c; Table S4a–c). RGR was also influenced by species, light and DM<sub>start</sub>. The variance for the whole model (fixed plus random effects) was approximately the same among the models (R<sup>2</sup><sub>Cond</sub> = 0.588–0.604), whereas the fixed effects explained most variation in the model with number of days with rain (raindays, R<sup>2</sup><sub>Marg</sub> = 0.533), followed by the one with total rainfall (R<sup>2</sup><sub>Marg</sub> = 0.497) and lowest for total precipitation (R<sup>2</sup><sub>Marg</sub> = 0.466). Light had a positive effect on RGR in these models, with a significant light x species interaction, whereas DM<sub>start</sub> had a weak negative effect in all species. The model for the temperature sum resembled those for the precipitation variables, but had lower explanatory power (R<sup>2</sup><sub>Marg</sub> = 0.324; Figure S2d; Table S4d). Temperature sum was only significant in interaction with species. The relationship between RGR and temperature sum differed between Alectoria and Bryoria.

The final model showed that RGR increased with number of days with rain also after controlling for the temperature sum (Figure 3, R<sup>2</sup><sub>Marg</sub> = 0.531). The raindays x species and the light x species interaction were both significant with rain and temperature sum (Figure 3, R<sup>2</sup><sub>Marg</sub> = 0.466).

| TABLE 2 | Mean RGR and mean percent increase in dry mass (±1 SE) in studied species after 1 year of transplantation to nine sites. N = 16–25 per site (Alectoria, 20–25 (Usnea) and 14–25 (Bryoria)) |
|----------|---------------------------------------------------------------|
| Sites    | RGR, mg g<sup>−1</sup> day<sup>−1</sup> | Increase in DM, % |
|          | Alectoria     | Usnea     | Bryoria   | Alectoria | Usnea | Bryoria |
| 1        | 0.242 ± 0.034 | 0.213 ± 0.017 | 0.119 ± 0.032 | 9.5 ± 1.2 | 8.2 ± 0.7 | 4.7 ± 1.2 |
| 2        | 0.256 ± 0.033 | 0.167 ± 0.013 | 0.192 ± 0.022 | 10.1 ± 1.3 | 6.4 ± 0.5 | 7.4 ± 0.9 |
| 3        | 0.433 ± 0.033 | 0.185 ± 0.025 | 0.096 ± 0.057 | 17.5 ± 1.4 | 7.1 ± 1.0 | 4.0 ± 2.1 |
| 4        | 0.354 ± 0.024 | 0.267 ± 0.028 | 0.121 ± 0.041 | 14.0 ± 1.0 | 10.5 ± 1.1 | 4.8 ± 1.6 |
| 5        | 0.419 ± 0.042 | 0.206 ± 0.038 | −0.145 ± 0.058 | 170 ± 1.7 | 8.1 ± 1.4 | −4.7 ± 2.0 |
| 6        | 0.516 ± 0.027 | 0.316 ± 0.040 | 0.285 ± 0.034 | 20.9 ± 1.2 | 12.6 ± 1.5 | 11.2 ± 1.4 |
| 7        | 0.864 ± 0.062 | 0.636 ± 0.030 | 0.263 ± 0.082 | 38.3 ± 3.0 | 26.8 ± 1.4 | 10.9 ± 3.4 |
| 8        | 0.684 ± 0.057 | 0.568 ± 0.040 | 0.304 ± 0.088 | 29.5 ± 2.6 | 23.7 ± 1.8 | 13.0 ± 3.5 |
| 9        | 0.746 ± 0.059 | 0.693 ± 0.029 | 0.219 ± 0.056 | 32.6 ± 2.6 | 29.5 ± 1.4 | 9.0 ± 2.2 |
| 1–9      | 0.484 ± 0.020 | 0.364 ± 0.017 | 0.158 ± 0.019 | 20.2 ± 0.9 | 14.9 ± 0.7 | 6.5 ± 0.8 |
interactions were also significant (Table S5). The relationship for Alectoria was significantly steeper than in Bryoria, whereas the slope coefficient overlapped for the two pale species (Figure 4). By running the same model with pooling the pale species and using Bryoria as the reference, we found that the slope coefficient for Bryoria differed from zero (data not shown).

3.2 | Chlorophyll

Mean initial Chl \(\alpha\) concentration slightly differed among the species (ANOVA, \(p = 0.002; df = 2, 57\)). Bryoria (0.81 mg/g) had 11% higher Chl \(\alpha\) than Alectoria and 35% higher than Usnea (Table 3), but only Bryoria and Usnea differed significantly (Tukey’s HSD). During the transplant period, the mean Chl \(\alpha\) concentration increased in all species and in most sites (up to 85%), with the strongest increase in Alectoria and Usnea. The increase was strongest in the driest and the two wettest sites.

The fixed effects in the mixed model accounted for 41% of the variance in Chl \(\alpha\) (Figure 5; Table S6). Chl \(\alpha\) was significantly affected by N deposition, light and DM_{start}, as well as by the N...
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year
model that also included DM start deposition based on a mixed effects model that also included number of days with rain and species as fixed factors, and site as well as transplant tree (nested under site) as random factors. Lines show estimated RGR while holding light and species actions. We found no main effect of species, but Alectoria and Usnea had significantly steeper slopes than Bryoria. Light weakly affected Chl a, but only in combination with N deposition, whereas DM start had a negative effect in all species. RGR increased significantly with Chl a in all species after controlling for number of days with rainfall, but with steeper relationship in Bryoria (Figure 6; Table S7).

4 | DISCUSSION

4.1 | Macroclimate

This is the first study comparing growth of hair lichens across a broad-scale gradient from continental to oceanic climates. Precipitation drives the growth of the pale species (Alectoria and Usnea), consistent with our first hypothesis emphasizing the boosting role of hydration. The number of days with rain was a better predictor of lichen growth than total rain, showing that frequent hydration is more beneficial than high-intensity rainfall events. Lichens take up rain faster than vascular plants and activate rapidly (Proctor & Tuba, 2002). Temperature sum as a main effect did not affect growth, but these lichens are photosynthetically active over broad temperature ranges (Coxson & Coyle, 2003). The markedly lower RGR of deposition × species, N deposition × light and species × light interactions. We found no main effect of species, but Alectoria and Usnea had significantly steeper slopes than Bryoria. Light weakly affected Chl a, but only in combination with N deposition, whereas DM start

Note: Superscripts with different letters denote species with significantly different Chl a at start (p < 0.05, Tukey’s HSD post hoc).

FIGURE 5 Predicted relationship between Chl a concentration in Alectoria sarmentosa, Usnea dasopoga and Bryoria fuscescens after 1-year transplantation based on a mixed effects model that also included number of days with rain and species as fixed factors, and site as well as transplant tree (nested under site) as random factors. Lines show estimated RGR while holding number of days with rain constant (85.9 days per year). Symbols are observed RGR for the transplants (N = 615)

FIGURE 6 Predicted relationship between RGR and Chl a concentration in Alectoria sarmentosa, Usnea dasopoga and Bryoria fuscescens after 1-year transplantation based on a mixed effects model that also included number of days with rain and species as fixed factors, and site as well as transplant tree (nested under site) as random factors. Lines show estimated RGR while holding number of days with rain constant (85.9 days per year). Symbols are observed RGR for the transplants (N = 615)

TABLE 3 Mean percent chlorophyll a concentration (±1 SE) in studied lichens at start and after 1 year of transplantation to nine sites. N = 20 per species at start and N = 16–25 per site (Alectoria), 20–25 (Usnea) and 14–25 (Bryoria)

| Site | Chlorophyll a, mg/g DM |
|------|-----------------------|
|      | Alectoria | Usnea   | Bryoria |
| Start| 0.73 ± 0.05<sup>b</sup> | 0.60 ± 0.04<sup>b</sup> | 0.81 ± 0.04<sup>b</sup> |
| 1    | 1.15 ± 0.05   | 1.15 ± 0.06 | 1.26 ± 0.05   |
| 2    | 0.71 ± 0.03   | 0.54 ± 0.02 | 0.91 ± 0.03   |
| 3    | 0.69 ± 0.03   | 0.47 ± 0.05 | 0.72 ± 0.03   |
| 4    | 0.76 ± 0.02   | 0.74 ± 0.04 | 0.82 ± 0.02   |
| 5    | 0.84 ± 0.03   | 0.69 ± 0.03 | 0.70 ± 0.04   |
| 6    | 0.91 ± 0.04   | 0.84 ± 0.04 | 0.92 ± 0.02   |
| 7    | 0.87 ± 0.04   | 0.73 ± 0.03 | 0.93 ± 0.05   |
| 8    | 0.96 ± 0.05   | 0.83 ± 0.06 | 1.00 ± 0.04   |
| 9    | 1.31 ± 0.04   | 1.11 ± 0.06 | 1.22 ± 0.04   |
| 1–9  | 0.92 ± 0.02   | 0.79 ± 0.02 | 0.95 ± 0.02   |

Mean percent chlorophyll a concentration (±SE) in studied lichens at start and after 1 year of transplantation to nine sites. N = 20 per species at start and N = 16–25 per site (Alectoria), 20–25 (Usnea) and 14–25 (Bryoria).
the dark *Bryoria* than of the pale species is consistent with previous studies (Renhorn & Esseen, 1995; Stevenson & Coxson, 2003). After water, light is the second most important factor for lichen growth (Palmqvist, 2000). Although cortical pigments modified the light received by the photobiont, light canopy transmittance increased RGR. As the trade-off between melanic pigmentation and growth in hair lichens (this study) also occurs in foliose lichens (Gauslaa & Goward, 2020), lichen colour is a universal and important internal factor for lichen functioning.

The slightly lower RGR of *Usnea* than of *Alectoria* may be explained as follows: (a) *Usnea* allocates much carbon to dense central axes and symbiotic diaspores. A trade-off between growth and reproduction (Gauslaa, 2006) likely drains resources from photobionts, consistent with lower Chl a in *Usnea* than in *Alectoria* (Table 3). (b) Furthermore, *Alectoria* stores more internal water than *Usnea* (Eriksson et al., 2018; Esseen et al., 2015), prolonging hydration and thus growth.

Our second hypothesis predicting adverse effects of rain on *Bryoria* was not well-supported. Its weak response to rainfall (Figure 3) likely results from excess cortical light screening and high external water storage (Esseen et al., 2017) causing suprasaturation depression of photosynthesis. Prolonged excess hydration in sheltered canopy positions can cause dieback in *Bryoria* (Goward, 1998, 2003a), whereas wind and openness mitigate suprasaturation damage (Campbell & Coxson, 2001; Goward, 1998). Finally, the thin branches in *Bryoria* fragment more easily than in the other species (Esseen, 1985), contributing to its slow growth. Growth experiments over two or more years are needed to better understand how climate drives RGR (Ellis et al., 2017).

### 4.2 | Chlorophyll and nitrogen

The N deposition proportionally increased with rainfall. Thus, the N concentration in the precipitation was rather similar across the large-scale gradient, apart from sites 1 and 6 with elevated N deposition. The otherwise constant N concentration likely explains the absence of nitrophytic lichens across the gradient and lacking adverse effects in the N-rich wet sites. Increased N deposition significantly boosted the Chl a synthesis in all species (Figure 5), supporting our third hypothesis. Consistent with data from other lichens (Dahlan & Palmqvist, 2003; Palmqvist et al., 2017), photobiont growth is also strongly linked to external N addition in hair lichens. Even at high growth rates, the Chl a concentration increased in all three lichens (Table 3), not diluted by the formation of new fungal tissue. This indicates an ample external supply of N and a rapid response of photobiont growth to this supply. In the driest site, all three lichens displayed a high Chl a concentration, but low growth. Local N depositions from nearby (<100 m) farmland and roads likely boosted Chl a synthesis, but growth was instead limited by low rainfall.

Consistent with our fourth hypothesis, RGR increased with Chl a concentration and thus photosynthetic capacity in all three species after controlling for number of days with rain (Figure 6). The steeper slope for the dark *Bryoria* shows that this species must synthesize more Chl a to grow as fast as the pale species.

### 4.3 | Distribution patterns

Growth responses may explain why pale species, sharing some functional traits (Esseen et al., 2015; Färber et al., 2014), are more associated with high rainfall regions than dark ones. The pale species dominate old, humid forests, often with frequent fog (Nimis et al., 2018), decreasing towards open and dry forests (Ahlner, 1948; Esseen et al., 2016). Like *Usnea*, *Alectoria* grows well in oceanic sites and is abundant in wet forests of the Pacific coast of North America (Benson & Coxson, 2002). Its lower frequency in western Scandinavia is likely due to dispersal limitations in the previously heavily deforested coastal region. The large *Alectoria* fragments (Dettki, 1998; Renhorn & Esseen, 1995) poorly disperse over long distances (Goward, 2003b). Therefore, *Alectoria* is hardly limited by slow growth in oceanic forests. Although high rainfall was not very beneficial for *Bryoria*, growth responses to rainfall cannot explain this dark species’ strong dominance in drier continental forests.

### 4.4 | Local niche differentiation

The studied species dominate different sections of vertical and horizontal canopy gradients (Esseen, 2019; Gauslaa et al., 2008). *Bryoria* dominates upper canopies and open, low rainfall forests, whereas the pale species thrive in lower canopy and sheltered sites (Benson & Coxson, 2002; Campbell & Coxson, 2001). In wet forests, high loadings of *Alectoria* (Benson & Coxson, 2002) and *Usnea* (Antoine & McCune, 2004) extend high up in the canopies, implying wider ecological niches in rainforests. Thereby, pale species have a competitive advantage over *Bryoria* in wet climates. *Bryoria* would likely have grown faster if transplanted in upper canopies (Coxson & Coyle, 2003; Esseen et al., 2017).

### 4.5 | Environmental hazards

The results have implications for the lichens’ responses to global change, to which they are susceptible (Colesie et al., 2018; Ellis et al., 2007; Nascimbene et al., 2019). Esseen et al. (2016) proposed hypotheses predicting major shifts in the distribution of these lichens with changing climate, N deposition and forest structure. Our findings largely support their hypotheses but suggest that growth responses to macroclimate interacts with microclimates, particularly with the light regime in the lower canopy. For example, *Usnea* will likely grow better and expand northwards in predicted warmer and wetter climates (Hanssen-Bauer et al., 2017; Sjökvist et al., 2015) if enough light can pass through the canopy. *Alectoria*, with inefficient long-distance dispersal,
will likely decline in fragmented future landscapes and younger forests. *Bryoria*, adapted to cooler and drier climates, is expected to decrease (Esseen et al., 2016), adversely impacted by warmer and wetter winters, and by depressed growth in dense forests. Because these lichens are most abundant in old forests (Dettki et al., 2000; Esseen et al., 1996; Lesica et al., 1991), forest management must create a range of suitable microclimates to secure the abundance and ecosystem function of these species in future climate scenarios (cf. Greiser et al., 2020).

5 | CONCLUSIONS

Our findings explain how macroclimate drives RGR of hair lichens in boreal forest canopies. This knowledge is needed to develop a comprehensive theory on mechanisms regulating these lichens’ growth, distribution and abundance. The number of days with rain was a better predictor of growth than either total precipitation or rain. Growth of the pale *Alectoria* and *Usnea* strongly increased with amount and frequency of precipitation, while rain marginally increased growth of the dark *Bryoria*. Overall, the pale species grew faster than the dark one. Airborne N deposition at levels proportional to the total rainfall increased the Chl a concentration, boosting growth of all species. Our results highlight that growth responses of hair lichens to increasing rainfall depends on both colour of cortical pigments and water storage traits. These findings help to explain global, regional and local distribution patterns of the species and how environmental hazards such as climate change and forestry influence important components in forest canopies. Future studies should focus on examining how growth of hair lichens is linked to other functional traits than those studied here, and on using RGR as a tool for monitoring effects of climate change on epiphytes.

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AUTHORS’ CONTRIBUTIONS

P.-A.E., Y.G., K.P. and N.H.P. conceived the ideas and designed methodology; N.H.P. and P.-A.E. collected the growth data, and K.P. made the chlorophyll analyses; N.H.P., P.-A.E. and Y.G. analysed the data; N.H.P. and P.-A.E. led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.k0p2ngf65 (Phinney et al., 2020).

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