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Sunscreening fungal pigments influence the vertical gradient of pendulous lichens in boreal forest canopies

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Abstract. Pendulous lichens dominate canopies of boreal forests, with dark Bryoria species in the upper canopy vs. light Alectoria and Usnea species in lower canopy. These genera offer important ecosystem services such as winter forage for reindeer and caribou. The mechanism behind this niche separation is poorly understood. We tested the hypothesis that species-specific sunscreening fungal pigments protect underlying symbiotic algae differently against high light, and thus shape the vertical canopy gradient of epiphytes. Three pale species with the reflecting pigment usnic acid (Alectoria sarmentosa, Usnea dasypoga, U. longissima) and three with dark, absorbing melanins (Bryoria capillaris, B. fremontii, B. fuscescens) were compared. We subjected the lichens to desiccation stress with and without light, and assessed their performance with chlorophyll fluorescence. Desiccation alone only affected U. longissima. By contrast, light in combination with desiccation caused photoinhibitory damage in all species. Usnic lichens were significantly more susceptible to light during desiccation than melanin ones. Thus, melanin is a more efficient light-screening pigment than usnic acid. Thereby, the vertical gradient of pendulous lichens in forest canopies is consistent with a shift in type and functioning of sunscreening pigments, from high-light-tolerant Bryoria in the upper to susceptible Alectoria and Usnea in the lower canopy.

Key words: Alectoria sarmentosa; boreal forest; Bryoria spp.; desiccation tolerance; epiphytes; melanin; photoinhibition; sunscreening pigments; Totenåsen, Norway; Usnea spp.; usnic acid; Vindeln, Sweden.

INTRODUCTION

Pendulous lichens often envelop canopies in boreal forests (Esseen et al. 1996). Such epiphytic communities are dominated by the genera Alectoria, Bryoria, and Usnea, which play important functional roles. They provide winter forage for reindeer and caribou (Kinley et al. 2006, Kivinen et al. 2010) and habitat for canopy-living invertebrates constituting critical fodder for overwintering passerine birds (Pettersson et al. 1995). The biomass of pendulous lichens peaks in old forests (Esseen et al. 1996, Price and Hochachka 2001), and conversion of old forests to managed stands with short rotations (<100 years) has dramatically decreased this epiphytic component (Dettki and Esseen 1998, 2003). Several species, such as Usnea longissima, are of concern for conservation (Rolstad et al. 2013), as well as for ecosystem and wildlife management (Peck and McCune 1997).

Epiphyte communities often show vertical stratification (McCune 1993). Pendulous lichens in boreal forests form a vertical gradient, with Bryoria in the upper canopy (Fig. 1a) and Alectoria (Fig. 1b) and/or Usnea on lower, often defoliated branches (Campbell and Coxson 2001, Benson and Coxson 2002, Coxson and Coyle 2003). In Norwegian boreal forests, the biomass of Bryoria increased by a factor of 1.6 from 2–3 m to 5–6 m above the ground, with a concurrent decline (to 61%) in Alectoria and Usnea (Gauslaa et al. 2008); their sites are in the same bioclimatic region as our Norwegian site. The mechanism behind this niche partitioning is poorly understood, but various factors are apparently involved. Goward (1998, 2003) hypothesized that lack of Bryoria in the lower canopy is due to their susceptibility to prolonged wetting and preference for well-ventilated upper canopy. Coxson and Coyle (2003) supported this hypothesis and predicted higher photosynthetic rates for Alectoria sarmentosa in the lower canopy where it occurs, but concluded that growth responses alone did not explain the niche partitioning in pendulous lichens. Recently, phosphorus availability (McCune and Caldwell 2009) and exogenous carbohydrates (Campbell et al. 2013) have been introduced as factors influencing the realized niches for foliose canopy lichens.

Field evidence suggests that the bright pigment usnic acid (Alectoria and Usnea) vs. dark melanins (Bryoria) shape the vertical gradient. Alectoria and Bryoria
containing contrasting pigments are taxonomically more related to each other than to the genera (*Alectoria* and *Usnea*) containing usnic acid (Thell and Moberg 2011). Both melanins (e.g., Gauslaa and Solhaug 2001) and usnic acid (McEvoy et al. 2007) screen light, and thus protect underlying photobionts. However, these pigments function differently: melanins absorb light, whereas usnic acid reflects excess light (Solhaug and Gauslaa 2012). We do not know which screening mechanism is most efficient. Light-screening has not yet been directly measured in pendulous lichens. If these pigments play a functional role for vertical epiphyte distribution, we hypothesize that melanin is the most efficient screening compound. This needs to be tested, because lichen compounds may have multiple functions (Molnár and Farkas 2010).

The upper canopy experiences stronger solar radiation and desiccation than low branches (Parker 1997, Coxson and Coyle 2003). Because light is strongest in clear and dry weather, high light stress is confounded with desiccation stress. Both high light (Gauslaa and Solhaug 1996) and desiccation (Green et al. 1991) can adversely affect forest lichens. Here, we experimentally separated the effects of desiccation from those caused by high light by exposing six pendulous lichens to four drying regimes with and without light, using chlorophyll fluorescence to quantify damage and the recovery of the photosynthetic apparatus. We tested the following hypotheses: (1) lichens with melanins (*Bryoria*) are more tolerant to high light than *Alectoria* and *Usnea* with usnic acid; and (2) *Bryoria* species are more tolerant of desiccation than *Alectoria* and *Usnea*.

**MATERIAL AND METHODS**

*Lichen material and study area*

Among our species (Fig. 1c), *Alectoria sarmentosa* (Ach.) Ach., *Usnea dasypoga* (Ach.) Nyl., and *U. longissima* Ach. contained usnic acid, whereas *Bryoria capillaris* (Ach.) Brodo and D. Hawksw., *B. fuscescens* (Gyeln.) Brodo and D. Hawksw., and *B. fremontii* (Tuck.) Brodo and D. Hawksw. contained melanins. Lichens were collected August–October 2012 in old forests from *Picea abies* branches in the boreal sites Vindeln (northern Sweden) and Totenåsen (southeastern Norway). Sampling was done 2–4 m above ground because we wanted to study species-specific rather than environmental effects, and the lower canopy is the only vertical zone where all species may co-occur.

Vindeln had 600 mm annual precipitation (~65% as rain; snow from November–April); mean annual temperature was 2°C, −11°C in January and 14°C in July (Raab and Vedin 1995). Collections were done at 175–200 m above sea level; *B. fuscescens*, *B. fremontii* (64°13′47″ N, 19°46′57″ E), and *A. sarmentosa* (64°14′23″ N, 19°47′46″ E) were from mesic, semi-open stands with *Picea abies* and *Pinus sylvestris*. *Bryoria capillaris* was collected in a mesic, open *P. sylvestris* and *P. abies* stand (64°13′58″ N, 19°49′37″ E), whereas *U. dasypoga* (64°14′13″ N, 19°47′29″ E) was from a moist-wet, closed-canopy *P. abies* stand near a small stream.

In Totenåsen (60°35′15″ N, 11°02′04″ E; 720 m a.s.l.), all lichens were collected from the same branches. The open, old *P. abies* forest was moist (1000 mm annual precipitation; 180–190 d/yr had >0.1 mm, and snow lasting 175–199 d; Moen 1999), located in upper parts of a steep, northeast-facing slope. Mean annual temperature was 0–2°C, ranging from −8°C in January to 14°C in July.

Lichens were stored air-dry at −20°C (recommended by Honegger 2003). Six months later, two samples were taken from each specimen, resulting in n = 48 samples per species and site; n = 432 samples in total. Each sample was selected species-wise for a given desiccation/light treatment according to random numbers. Separate thalli were randomly taken for chlorophyll measurements (Appendix A).

**Preconditioning of lichens and measurement of chlorophyll fluorescence parameters**

Lichens were sprayed with deionized water and kept moist at 14°C in low light (20 μmol·m²·s⁻¹) for 24 h to reduce occasional photoinhibition from the field. Then they were kept 15 min in darkness before maximal quantum yield (Fm/Fv) of photosystem II (PSII),
maximal (Fm), and minimal fluorescence (F0), where variable fluorescence Fv, is the difference between Fm and F0 (Maxwell and Johnson 2000), were measured by a portable fluorometer (PAM-2000; Heinz Walz GmbH, Effeltrich, Germany), with the fiber optics 1 cm away from the sample using the 60° distance clip (Model 2010A; Heinz Walz GmbH). Each sample was arranged to fully cover the measuring area and the measuring light was set at intensity ~0.05 μmol·m⁻²·s⁻¹; the saturation pulse had the maximal intensity, and duration of 0.6 s. The lichens were then air-dried at 22°C.

**Light and desiccation treatment**

The experiment, modified after Gauslaa et al. (2012), was repeated three times. Two samples of each species × site combination were included in each replication (n = 6 samples per treatment). During treatment, air-dry lichens lay on a net, 5 mm below the lid of a clear, sealed plastic box (10 × 8 × 4 cm). Each box had 25 mL of saturated salt solutions or silica gel to obtain 75%, 55%, and 33% relative humidity using NaCl, Mn(NO₃)₉, and MgCl₂, respectively (Greenspan 1977), and 0% (silica gel).

Eight boxes, two for each humidity, were placed for 7 d at 14°C under a high-intensity (400 μmol·m⁻²·s⁻¹) LED light-diodes panel (SL3500; Photon Systems Instruments, Brno, Czech Republic). Boxes were rotated daily to ensure similar light doses for all treatments. Temperatures of lichens, salt solutions, and air inside boxes were measured with a thermocouple data logger (model TC-08; Pico Technology, St Neots, Cambridgeshire, UK). Lichens reached 22°C, salt solutions reached 19°C, and air temperature inside the boxes was 22°C. Another set of eight boxes (as previously described) were kept in darkness for 7 d at 22°C to eliminate temperature differences between light and dark treatments. Thereafter, lichens were hydrated with deionized water and were kept moist for 24 h. We measured Fv/Fm, Fm, and F0 as described for the preconditioning, but the kinetics during recovery were recorded after 15 minutes of dark adaptation at 30 min, 2 h, 6 h, and 24 h in low light.

**Statistical analyses**

We analyzed data from the two sites separately. General linear models (GLM with Tukey’s HSD post hoc test) were used to test if initial Fv/Fm, Fm, and F0 varied by species. Fm and F0 were square-root-transformed. We analyzed species performance after the experiment by expressing Fv/Fm as percentage of initial Fv/Fm values to remove the initial between-species variability. We ran a full GLM model with humidity, light treatment, and species as fixed factors. The temporal response during the recovery was analyzed in separate GLMs for 0.5 h and 24 h, because variances decreased over time following the increase in Fv/Fm. Heteroscedasticity and non-normality were checked by examining residuals. No transformation was needed for Fv/Fm. Analyses were done in IBM SPSS version 21 (IBM 2012).

**Results**

**Initial fluorescence parameters**

Initial fluorescence parameters showed similar patterns in Sweden and Norway (Table 1). In Sweden, Fv/Fm differed by species. The highest Fv/Fm (0.728) occurred in the darkly melanic B. fremontii and B. fuscens. The lowest values (≤0.694) were observed in the pale B. capillaris (Sweden) and the usnic lichens U. dasypoga and U. longissima (Norway). Maximal (Fm) and minimal fluorescence (F0) were strongly coupled across (r²_adj = 0.970; n = 432) and within (r²_adj = 0.854–0.966; P < 0.001; n = 48) all species × locality combinations. The species-specific differences were much stronger for Fm and F0 than for Fv/Fm (Table 1). At both sites, Fm was four times higher in A. sarmentosa
and U. dasypoga than in the melanic B. fremontii and B. fuscescens, with U. longissima and B. capillaris in between.

**Desiccation and light experiment**

As a percentage of initial values, $F_v/F_m$ differed strongly between light and dark treatments and between species (Fig. 2, Table 2). Desiccation in the absence of light (7 d), even at 0% relative humidity, had minor effects on $F_v/F_m$ (Appendix B). In some Bryoria species, mean $F_v/F_m$ at the end of the dark treatment exceeded initial values after 24 h of recovery at low light (Appendix C). However, in U. longissima the dark treatment caused substantially delayed recovery of $F_v/F_m$ (Fig. 2b). After 24 h of hydration, full recovery still had not taken place (94.1% ± 1.2%; mean ± 1 SE). Unlike the other species, U. longissima was thus susceptible to desiccation.

Light during desiccation caused significant and lasting $F_v/F_m$ depression (Fig. 2, Table 2). The light × humidity interaction was highly significant for the Swedish samples, implying that the hardest desiccation aggravated the decline of $F_v/F_m$ in light-treated specimens. Lichens exposed to light recovered more slowly than those kept dark (Fig. 2). Melanic and usnic species differed in post hoc tests after 30 minutes of recovery; confidence intervals did not overlap up to 6 h in any site. The melanic species were less photoinhibited than those with usnic acid. Usnea longissima was more light susceptible than the other species (Appendix C), with much delayed and incomplete recovery subsequent to hydration, followed by A. sarmentosa and U. dasypoga. Among usnic lichens, U. dasypoga was fairly similar to the most susceptible weakly melanic species, B. capillaris. The pale B. capillaris showed an initially deeper depression than the two dark Bryoria spp. (Fig. 2c), although the mean after 24 h of recovery did not differ much (Appendix C).

The intra- and interspecific variation in fluorescence parameters is shown in Fig. 3, where $F_v/F_m$ after 30 minutes of recovery was plotted against initial $F_0$ for samples subjected to light (Fig. 3a) and dark treatment (Fig. 3b). The light treatment during drying increased the variation in $F_v/F_m$ in all species apart from U. longissima, which exhibited strong variation also after desiccation in darkness. For lichens treated with light, there was a stronger decrease of $F_v/F_m$ with increasing $F_0$ than for those in darkness (Fig. 3). This discrepancy was stronger in a similar plot (not shown) with $F_v/F_m$ and $F_m$: for light, $r^2_{adj} = 0.211, P < 0.001$; for darkness, $r^2_{adj} = 0.015, P = 0.039 (n = 216)$.

**Discussion**

Although earlier studies on vertical niche partitioning in pendulous lichens have focused on growth and macroclimatic limitations (Goward 1998, 2003, Campbell and Coxson 2001, Coxson and Coyle 2003), this study emphasizes the role of cortical pigments. By screening excessive light for underlying photobionts, fungal pigments improve lichen functioning in well-lit habitats (Solhaug and Gauslaa 2012). Foliose usnic lichens are abundant in sun-exposed habitats at all latitudes (e.g., Elix 1994, Hauck et al. 2007), whereas melanic lichens grow in sunny habitats at high latitudes or altitudes (e.g., Brodo and Hawksworth 1977, Esslinger 1977, Hauck et al. 2007). Thus, both usnic acid and melanins may form efficient sunscreens. However, dark Bryoria species were more tolerant to light in the desiccated state than were similar life-forms with usnic acid (Fig. 2), consistent with higher screening by melanins. Recorded photoinhibition in usnic lichens, evidenced as depressed $F_v/F_m$, may explain why they are replaced by melanic species with increasing branch height. In a northern Sweden site, biomass of dark Bryoria had a higher canopy openness threshold than that of A. sarmentosa (P.-A. Esseen, unpublished data), showing that similar replacement processes along gradients from sun to shade occur on vertical as well as on horizontal forest scales. Shifts between melanic and pale lichens in coniferous canopies are probably driven by height- and/or canopy-openness-dependent variation in solar radiation, consistent with reported physical and physiological limitations of pendulous lichens (Coxson and Coyle 2003).
FIG. 2. Recovery of photosynthetic performance (measured as percentage of initial values of maximal quantum yield, \(F_v/F_m\)) in lichens with melanins (solid symbols) and usnic acid (open symbols) as sunscreening pigments after seven days’ treatment (a, b) in darkness and (c, d) in high light (400 \(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\)) in Sweden and Norway. Data were pooled over four humidity levels (0%, 35%, 55%, and 75%; \(n = 24\) replicates for each species \(\times\) light treatment \(\times\) site combination). Values are means with 95% confidence intervals; different letters in the keys indicate species that are significantly different (\(P < 0.05\)) after 0.5 h and 24 h.

TABLE 2. Summary of GLMs for maximal quantum yield (\(F_v/F_m\), percentage of initial values) for pendulous lichen species from two sites (Sweden and Norway), two light treatments, and four humidity treatments measured after 0.5 h and 24 h during recovery.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Sweden</th>
<th></th>
<th>Norway</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.5 h ((r^2_{adj} = 0.808))</td>
<td>24 h ((r^2_{adj} = 0.281))</td>
<td>0.5 h ((r^2_{adj} = 0.751))</td>
<td>24 h ((r^2_{adj} = 0.417))</td>
</tr>
<tr>
<td>Species, S</td>
<td>4</td>
<td>F</td>
<td>P</td>
<td>3</td>
</tr>
<tr>
<td>Light, L</td>
<td>1</td>
<td>82.48</td>
<td>&lt;0.001</td>
<td>63.2</td>
</tr>
<tr>
<td>Humidity, H</td>
<td>3</td>
<td>2.2</td>
<td>0.093</td>
<td>2.9</td>
</tr>
<tr>
<td>S × L</td>
<td>4</td>
<td>8.0</td>
<td>&lt;0.001</td>
<td>1.8</td>
</tr>
<tr>
<td>S × H</td>
<td>12</td>
<td>1.5</td>
<td>0.118</td>
<td>0.8</td>
</tr>
<tr>
<td>L × H</td>
<td>3</td>
<td>6.3</td>
<td>&lt;0.001</td>
<td>5.2</td>
</tr>
<tr>
<td>S × L × H</td>
<td>12</td>
<td>0.9</td>
<td>0.593</td>
<td>1.1</td>
</tr>
<tr>
<td>Total</td>
<td>240</td>
<td></td>
<td></td>
<td>240</td>
</tr>
</tbody>
</table>

Notes: The light treatments were 0 vs. 400 \(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\); the humidity treatments were 0%, 35%, 55%, and 75% relative humidity. Recovery was at 20 \(\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}\) in the hydrated state. Boldface indicates significance at \(P < 0.05\).
Initial $F_0$ and $F_m$ in usnic species were much higher than in melanic ones (Table 1). Because we used the same measuring light for recording fluorescence, differences in $F_0$ and $F_m$ should reflect differences in screening efficiency and/or chlorophylls. However, $F_0$ and $F_m$ cannot be explained by chlorophylls because the concentrations were as high or higher in melanic than in usnic species (Appendix A). The low $F_0$ and $F_m$ in the dark Bryoria species are thus consistent with high screening. The pale B. capillaris (Fig. 1c), with intermediate $F_0$ and $F_m$, has higher cortical transmission than the dark Bryoria, whereas A. sarmentosa and U. dasypoga have the weakest cortical screening (Table 1). Low screening in A. sarmentosa is consistent with higher modeled C fixation (Coxson and Coyle 2003) and higher growth rates of usnic compared to melanic species in the shaded lower canopy (Renhorn and Esseen 1995) in our Swedish collection site. Lack of height effects on growth in transplanted adult A. sarmentosa and B. fuscescens (Stevenson and Coxson 2003) suggests that impacts of photoinhibition on fitness may be a long-term effect or may operate more on juvenile stages.

The significant negative relationship between $F_o/F_m$ after light treatment and initial $F_0$ (Fig. 3a) supports the use of $F_0$ values as indicators of cortical screening efficiency for pendulous lichens. Removing the outlying species U. longissima strengthens the relationship, particularly in light (from $r_{adj}^2 = 0.160; n = 216$ to $r_{adj}^2 = 0.271; n = 192$), probably because it is susceptible to desiccation (Fig. 2b). We believe that its high susceptibility to desiccation as well as to light may contribute to its rareness and decline throughout Europe (Rolstad et al. 2013) and its restriction to humid coastal forests in North America. Otherwise, our data do not support the hypothesis that desiccation tolerance plays a role for the vertical stratification between usnic and melanic lichens.

Melanins and usnic acid are induced and regulated by UV-B (Solhaug et al. 2003, McEvoy et al. 2006), meaning that these pigments in general occur in higher contents in lichens of sun-exposed places as a result of acclimation to high light (Gauslaa and Solhaug 2001, McEvoy et al. 2007). At the same time, there is also a genetic control of the melanin synthesis, because some Bryoria species are pale, whereas others are dark (Brodo and Hawksworth 1977). Strong contrasts in color occur between B. capillaris and B. fuscescens, even when they grow on the same branch.

Despite their similar induction mechanism, melanins and usnic acid screen light differently. Pigments influence temperature, as shown in two hair-like mat-forming terricolous lichens with contrasting color. The reflecting A. ochroleuca (usnic acid) was much less heated than neighboring melanic Bryozaculum divergens (Gauslaa 1984). Darkly melanin lichens absorb visible and near-infrared light efficiently, whereas usnic lichens reflect much of the energy in both wavelength ranges (Gauslaa 1984). Thus, dark Bryoria species are heated and can melt the snow in tree canopies during winter and thus cause hydration and activation of photosynthesis (Coxson and Coyle 2003). Some melanic lichens are susceptible to heating by excess light (Gauslaa and Solhaug 1999). This may explain why some large melanic lichen genera such as Bryoria (Brodo and Hawksworth 1977) and Melanelia (Esslinger 1977) are restricted to cool-cold climates.

We treated lichens with light during desiccation, when repair mechanisms are inactive. Because long-lasting high light occurs in clear weather, our conclusions may not hold in rain forests. At a Scandinavian scale, there is a gradient from continental eastern parts to western oceanic sites (Gauslaa 2014), along which Usnea moves upward in the canopy (Y. Gauslaa, personal observations). Even U. longissima enters upper canopies of oaks in western rain forests (see photo in Gauslaa et al. 1992). In wet coastal sites, Bryoria species do not always occur (Bruteig 1993), presumably because of their susceptibil-

![Fig. 3. Relationship between maximal quantum yield ($F_o/F_m$, expressed as percentage of initial values) after 30 minutes of recovery subsequent to hydration, vs. initial $F_o$ values in all measured specimens of the three pendulous lichens with usnic acid (open symbols) and the three with melanins (solid symbols) that had been exposed to 7 days of (a) light and (b) darkness in recovery subsequent to hydration, vs. initial $F_o$ values in all measured specimens of the three pendulous lichens with usnic acid (open symbols) and the three with melanins (solid symbols) that had been exposed to 7 days of (a) light and (b) darkness in the desiccated state. Linear regression was much stronger after treatment in light ($r_{adj}^2 = 0.160, P < 0.001, n = 216$) than after dark treatment ($r_{adj}^2 = 0.053, P > 0.001, n = 216$).]
ity to excess wetting (Goward 1998). Consistent with Scandinavian patterns, *Alectoria* (Benson and Coxson 2002) and *Usnea* (Antoine and McCune 2004) occurred high up in the canopies of the wet forests of northern British Columbia and Washington, respectively.

In conclusion, melanin in *Bryoria* is a more efficient sunscreen than usnic acid in *Alectoria* and *Usnea*. Our experimental evidence provides a new functional mechanism for the vertical gradient of pendulous lichens in boreal forests, and may explain at least parts of the clear change from melanin *Bryoria* dominating the upper canopy to light-colored *Alectoria/Usnea* with usnic acid in the lower canopy (Fig. 1). The results suggest that the low tolerance to high light of *Alectoria* and *Usnea* contributes to their absence in the upper canopy.

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**Literature Cited**


IBM. 2012. IBM SPSS version 21. IBM Software Group, Chicago, Illinois, USA.


**SUPPLEMENTAL MATERIAL**

**Appendix A**

Chlorophyll contents in pendulous lichens, including chlorophyll methods (*Ecological Archives* E095-129-A1).

**Appendix B**

Recovery of maximal quantum yield, $F_v/F_m$, percentage of initial values, after desiccation treatments (*Ecological Archives* E095-129-A2).

**Appendix C**

Chlorophyll fluorescence parameters ($F_v/F_m$, $F_0$, and $F_m$) for all species and treatments (*Ecological Archives* E095-129-A3).