



Photoprotective strategies in pale versus melanic boreal hair lichens: non-photochemical quenching compensates for less protective fungal pigments

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Abstract

Main conclusion Hair lichen photoprotection involves algal and fungal strategies while hydrated, with pale lichens compensating weak fungal cortical pigments through high, rapidly induced non-photochemical quenching by the photobiont.

Abstract Hair lichens play vital roles in boreal forests by influencing nutrient cycles, microclimates, and providing habitats for invertebrates and forage for animals. This study examines two widespread and dominant species, *Bryoria fuscescens* and *Alectoria sarmentosa*, which possess different fungal pigments—dark light-absorbing melanin in *Bryoria*, and pale reflecting usnic acid in *Alectoria*. These cortical pigments affect species distribution, with *Bryoria* favoring sun-exposed forest canopies due to its efficient light-protective melanin, while *Alectoria* thrives in partly shaded, moist environments. By investigating sympatric populations, we explored whether non-photochemical quenching (NPQ) compensates for *Alectoria*'s less-effective sun-screening pigment. Our results reveal that *Alectoria* exhibits higher and more rapidly induced NPQ compared to *Bryoria*, along with faster recovery from photoinhibition. The flexibility and rapid response of *Alectoria*'s NPQ help mitigate high-light stress, optimizing growth in fluctuating light environments. These compensatory mechanisms suggest that, despite weaker cortical pigmentation, hydrated *Alectoria* can sustain photosynthesis and recover from light-induced damage more efficiently. However, because NPQ does not function in the desiccated state—where efficient sun-screening by cortical pigments is essential—*Alectoria* is confined to humid and sheltered forest canopies in drier macroclimates but not in rainforest climates. This study underscores the adaptive strategies of both photobionts and mycobionts in hydrated hair lichens to manage varying light conditions in boreal forests, highlighting NPQ as a compensating mechanism in lichen photoprotection. It advances our understanding by illustrating how the transition from dry to wet conditions amplifies the algal partner's contribution to overall photoprotection.

Keywords *Alectoria* · *Bryoria* · Boreal forest · Light stress adaptation · Melanin · Usnic acid · Non-photochemical quenching

Abbreviations

ETR	Electron transport rate
ETR _{App}	Apparent ETR
NPQ	Non-photochemical quenching
PAR	Photosynthetic active light

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Introduction

Thin hair lichens are often dominant in boreal forest canopies (Ahti 1977), forming a crucial component of these ecosystems (Edwards et al. 1960; Campbell and Coxson 2001; Stevenson 2001). They substantially increase in biomass with stand age (Esseen et al. 1996; Price and Hochachka 2001; Boudreault et al. 2015), trapping nutrients and water, and influencing canopy microclimate (Knops et al. 1996; Pypker et al. 2017). Additionally, hair lichens provide essential habitat for invertebrates, which serve as prey for various birds (Pettersson et al. 1995), and are a vital winter forage for animals such as reindeer (Heggberget et al. 2002;

Horstkotte et al. 2011) and the threatened mountain caribou (Rominger and Oldemeyer 1990; Rominger et al. 1996; Goward et al. 2024).

The two most important hair lichen genera in boreal forest are *Alectoria* and *Bryoria*. Despite their close taxonomic relation and morphological similarities, these genera are easily distinguished by their cortical fungal pigments: the pale yellowish usnic acid in *Alectoria* and the brown melanin in *Bryoria* (Brodo and Hawksworth 1977). This study focusses on the two common and widespread species, *Alectoria sarmentosa* (Ach.) Ach. and *Bryoria fuscescens* (Gyelnik) Brodo & D. Hawksw., hereafter referred to by their genus names. Although they have similar global distributions (<https://www.gbif.org/species>; accessed 11 April 2025), they often occupy different niches, resulting in distinct small-scale distribution patterns (Gauslaa and Goward 2023). *Bryoria* tends to dominate exposed upper canopies and open stands near hilltops (Goward et al. 2022), whereas *Alectoria* prefers lower, shaded canopies (Benson and Coxson 2002; Coxson and Coyle 2003).

The success of melanin hair lichens in sun-exposed sites has been attributed to the efficient high light protection provided by melanin, which reduces photoinhibitory damage (Färber et al. 2014; Gauslaa and Goward 2023). Effective solar screening for susceptible photobionts is particularly crucial during sunny and dry weather, as these conditions inactivates protective physiological processes and prevents the repair of high-light damage accumulating over time (Färber et al. 2014). Thus, the photoprotective role of melanin is well established. However, it remains unclear how usnic hair lichens cope with high light and how hydration status influences photoprotection in such thin lichens.

In hydrated lichens, fungal pigments influence various functions. For instance, dark pigmentation increases the compensation point for net photosynthesis in *Bryoria* (Coxson and Coyle 2003), which may explain its lower growth rate compared to *Alectoria* in shaded canopies (Esseen and Coxson 2024). Hydrated lichens have more tools to deal with high light stress than desiccated ones. Like other photosynthetic active organisms (Jung and Niyogi 2006), hydrated photobionts can dissipate excess absorbed light safely via mechanisms such as non-photochemical quenching (NPQ; Goss and Lepetit 2015), or detoxify reactive oxygen species to avoid damage (Beckett et al. 2021). These algal photoprotective mechanisms respond much faster to changing light than the slow fungal synthesis of light-screening pigments (as discussed by Solhaug et al. 2024). Additionally, *Bryoria* retains an unusually large amount of external water (Esseen et al. 2017) compared to usnic hair lichens (Eriksson et al. 2018), likely due to the high water-binding capacity of melanin (Beilinson et al. 2022). Excess external water significantly hinders CO₂ uptake by blocking diffusion pathways (e.g., Lange et al. 2001), which may contribute to

the low growth rates of *Bryoria* in wet climates (Phinney et al. 2021). This characteristic helps explain why melanin hair lichens prefer open forest and well-ventilated canopies, where moisture levels are lower and CO₂ diffusion is less impeded (Goward 1998; Goward et al. 2022).

Recent findings suggest that high and flexible NPQ can compensate for weak cortical pigmentation in thick mat-forming lichens that dominate alpine vegetation (Solhaug et al. 2024). Since NPQ is induced within minutes in hydrated lichens, it efficiently dissipates excess fluctuating light, optimizing lichen growth and photosynthesis during moist periods in tree canopies. Lower canopies experience temporal sunflecks (Coxson and Stevenson 2007; Way and Percy 2012; Demmig-Adams et al. 2014), where rapidly induced photoprotection would be particularly beneficial (Mkhize et al. 2022).

This study aims to quantify the NPQ in sympatric populations of two ecologically important and dominant hair lichens: the usnic *Alectoria* and the melanin *Bryoria*. Due to the difficulty of directly quantifying cortical light transmittance in such thin and brittle lichens, we will employ various photobiological approaches to seek indirect evidence of screening efficiency in the studied populations. The collected data will then be used to test our main hypothesis that high NPQ in hydrated hair lichens can compensate for less-efficient sun-screening pigments. Furthermore, we will provide reflectance spectra of both wet and dry hair lichens and use information from literature on high light tolerance of desiccated thalli of usnic and melanin hair lichens to establish a better understanding of why reported small-scale distribution patterns of *Alectoria* and *Bryoria* (Benson and Coxson 2002; Antoine and McCune 2004) differ between dry and humid forests.

Materials and methods

Lichen material

Alectoria sarmentosa and *B. fuscescens* were collected on May 24, 2023, from mixed populations on multiple trees in an open and low *Picea abies* forest (Fig. 1) situated on a northeast-facing slope in Sandvika, Verdal, Trøndelag (63.6509 N, 12.2506E, 441 m a.s.l.) in a humid, suboceanic climate with > 1000 mm precipitation a year (Moen 1999). However, the collection happened to take place at the end of an unusually dry period. The last 20 days before collection saw only minimal rain on two occasions, and April had only 45% of normal rainfall.

The lichens were dried at room temperature in the lab and then stored in a freezer (− 20 °C) until measurements were taken in October 2023, following the recommended storage protocol for later physiological studies



Fig. 1 One of the *Picea abies* canopies used for sampling of hair lichen thalli in Sandvika, Verdal, Trøndelag (63.6509 N, 12.2506E, 441 m a.s.l.; annual precipitation: > 1000 mm precipitation). Note that the usnic hair lichen *Alectoria sarmentosa* dominate this rather exposed canopy, but scattered melanic *Bryoria fuscescens* thalli can be seen in between the usnic hair lichen

(Honegger 2003). For each measurement specified below, new thalli were randomly selected from the freezer. They were then sprayed to saturation with deionized water and pretreated in the hydrated state for 20–24 h on moist filter paper under low light ($10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) in a temperature-controlled room at 15°C . This pre-treatment efficiently reduces the previous levels of photoinhibition (Solhaug 2018).

Spectral reflectance

The reflectance spectra of six thalli of each species were measured on (1) air-dry and (2) fully hydrated thalli using an integrating sphere (RT Sphere, Spectral Evolution, Haverhill, MA, USA) connected to a spectrophotometer (Model RS-3500, Spectral Evolution). Each thallus was arranged to fully cover the entire measurement area of approximately 3 cm^2 for each measurement.

Electron transport rate (ETR)

The ETR is calculated as $\Phi_{\text{PSII}} \times \text{PAR} \times 0.5 \times \text{Abs}$ (Baker 2008). Φ_{PSII} is the effective quantum yield of photosystem II (PSII); 0.5 assumes equal absorption of photons in PSII and PSI, and Abs is the fraction of incident light absorbed in PSII and PSI. Φ_{PSII} was measured from 0 to $803 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, using a red-light imaging-PAM M-series fluorometer (Heinz Walz GmbH, Effeltrich, Germany). The Abs parameter is typically assumed to be 0.85 in green leaves, but is lower in lichens due to screening by cortical pigments (Solhaug et al. 2010). We assessed apparent ETR (ETR_{App}) in 12 thalli of each species by setting $\text{Abs} = 1$. Because ETR_{App} does not include the unknown Abs parameter, it is higher than the real ETR. A higher ETR_{App} in one species normally implies higher cortical screening.

Photoinhibition

Twelve hydrated thalli from each species were kept continuously hydrated during a 20-h pre-treatment at low light ($10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). Afterward, all thalli were randomly placed under a LED lamp (Model SL3500, Photon System Instruments, Brno, Czech Republic) producing $750 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ with equal amounts of red, green, and blue light. The lichens (checked for uniform light) were repeatedly sprayed to keep them moist during the 4 h light exposure. The pre-treatment and subsequent high-light treatment were conducted in a temperature-controlled room at 15°C . After exposure to low light ($8 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) for 5 min, 30 min, 1 h, 2 h, 4 h, and 24 h (each followed by 5 min of darkness), the maximum quantum yield of PSII (F_v/F_m) was measured using a red LED Imaging-PAM M-series chlorophyll fluorometer and ImagingWin v2.46i software (Heinz Walz) to document the recovery kinetics after the high-light treatment.

Non-photochemical quenching (NPQ)

New thalli, pretreated for 24 h at $10 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, were used for NPQ measurements at 233 and $613 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ($n = 12$ per each species at each light level). The highest light level was chosen, because it was needed for light saturation of ETR in both species and is thus ecologically relevant. The lichens were then dark adapted for 10 min and placed in the Imaging-PAM for NPQ analyses. F_m was measured with a strong light flash and no actinic light, giving the fluorescence of a closed PSII. The actinic light was then turned on, and the program initiated saturating light pulses ($3000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) nine times at regular intervals for 23 min. At each point, the fluorescence was measured. This was followed by nine measurements of fluorescence in the dark for 10 min. Non-photochemical

quenching was calculated as $NPQ = (F_M - F_M')/F_M'$ where F_M is F_M' from the first measurement at PAR = 0 (Schreiber et al. 1986).

Chlorophyll content

Chlorophyll (Chl) content was measured in the thalli used for the reflectance measurements. Approximately 15–20 mg dry, intact lichen material was weighed and placed in Eppendorf tubes. Each tube was then filled by 1.5 ml DMSO to extract the Chl over a period of 20 h in darkness at room temperature. After centrifugation, 1 ml of each solution was analyzed using a UV-2101PC spectrometer (Shimadzu Scientific Instruments, Kyoto, Japan).

The *Bryoria* extracts contained substantial amounts of melanic compounds that absorb at the wavelengths used for Chl quantification. Therefore, it was essential to separate and remove melanin using a C18 solid-phase extraction column (Agilent Bond Elut C18; Agilent Technologies Inc, Santa Clara, CA, USA). First, the raw spectrum of the DMSO extract was measured. Then, the melanin spectrum from the C18 was subtracted from the raw spectrum before computing Chl using the formulae provided by Welburn (1994). Details

on the C18 solid-phase are given by Solhaug and Gauslaa (2025). No such treatment was needed for *Alectoria*.

Statistical methods

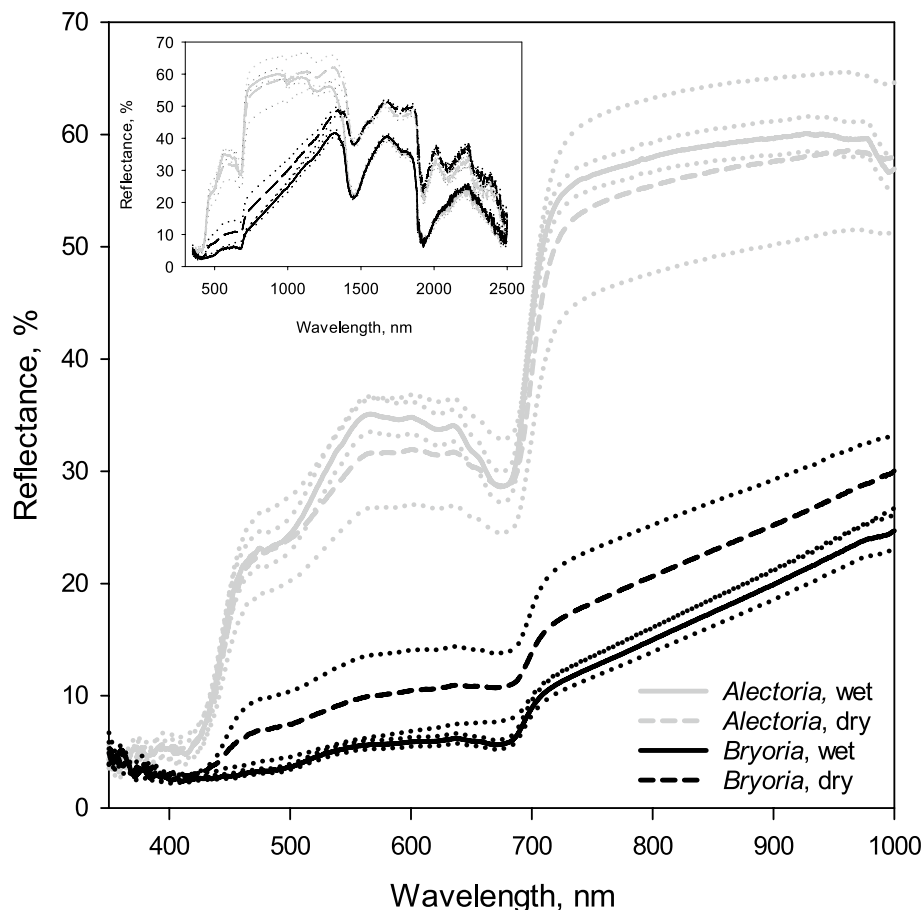
Means and standard errors were calculated and presented in tables and figures and expressed as mean \pm standard error (SE) in the text. Regression equations, along with associated 95% confidence intervals, R^2_{adj} , and P values were generated using SigmaPlot version 14.0. A Student's t test was conducted to examine species-wise differences in Chl concentration and the Chl a/b -ratio.

Results

Cortical pigments shape hair lichen reflectance spectra

While hydrated, the reflectance of photosynthetic active light (PAR) in *Bryoria* was consistently low, never exceeding 6%. In contrast, *Alectoria* exhibited substantially higher PAR reflectance, peaking at 36% in the green part of spectrum (563–570 nm; Fig. 2). *Bryoria* displayed a subtle peak in the

Fig. 2 Mean reflectance spectra (350–1000 nm) from densely packed thalli of the pale usnic *Alectoria sarmentosa* and the darkly melanic *Bryoria fuscescens*. Reflectance spectra are shown for both air-dry (hatched lines) and fully hydrated thalli (solid lines) of both species. The dotted lines on both sides of solid and hatched lines (mean values) show \pm SE ($n = 6$). The inset shows the entire reflectance spectra of the same species from 350 to 2500 nm)



PAR-range at red light (632–644 nm). Both species showed a minimum in reflectance at 670–680 nm, with *Alectoria* having a much sharper minimum. From this red minimum, both species experienced a sudden rise in reflectance in the near infrared range. The rise was much stronger in *Alectoria*, which had significantly higher reflectance in the 700–1400 nm range compared to *Bryoria* (Fig. 2).

Desiccation did not significantly alter the shape of the reflectance spectra, but the difference between the two species diminished after drying (Fig. 2). Drying increased the reflectance between 420 and 1400 nm in the melanic lichen and decreased it in the usnic species. The PAR reflectance of *Bryoria* was significantly higher in dry thalli compared to wet thalli, as evidenced by non-overlapping 95% confidence intervals. In contrast, the visible reflectance between dry and wet in *Alectoria* did not significantly differ (Fig. 2). Although the green peak was reduced after drying, it remained distinct in dry *Alectoria*, but was barely visible in the dry *Bryoria* (Fig. 2).

At approximately 1400 nm, the reflectance spectra of both species abruptly declined and converged, showing no more significant differences between the species up to the highest measured wavelengths at 2500 nm (Fig. 2; insert). However, hydration reduced the reflectance in both species between 1400 and 2500 nm.

Light response curves of ETR_{App}

Bryoria exhibited significantly higher ETR_{App} compared to *Alectoria*, with the gap widening as light intensity rose (Fig. 3). Despite this difference, the light response curves for both species had a similar shape, showing light saturation at 500–600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. The relative difference between the species remained fairly constant with increasing light intensity.

Fast recovery after high-light exposures of hydrated thalli

The maximum quantum yield of PSII (F_V/F_M) after 24 h of low-light pre-treatment was low in both *Alectoria* (0.444 ± 0.011 ; mean \pm SE) and *Bryoria* (0.535 ± 0.012 ; Fig. 5, inset). A 4-h high-light exposure at 750 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ reduced F_V/F_M to one-third of initial values in both species. However, photoinhibition recovered within 24 h under low light (Fig. 4). Recovery kinetics showed a rather linear increase along the log-transformed time scale, with highly significant linear regression lines ($P < 0.001$) for both *Bryoria* ($R^2_{adj} = 0.752$) and *Alectoria* ($R^2_{adj} = 0.840$). Notably, *Alectoria* recovered much faster than *Bryoria*, reaching initial values within 10 h of recovery (Fig. 4). This was evidenced by non-overlapping 95% confidence intervals after 30 min of recovery (Fig. 4). Consequently, the difference in

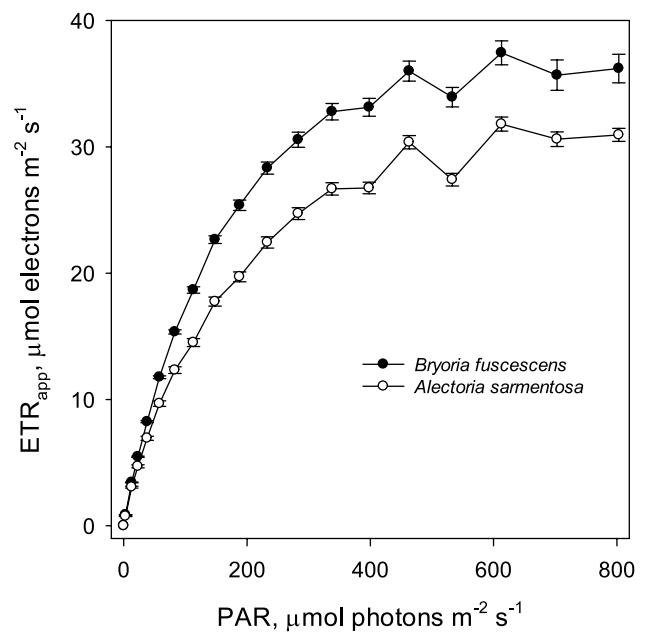


Fig. 3 Light saturation curves of mean apparent electron transport rate (ETR_{App}) in spring for the usnic *Alectoria sarmentosa* (open symbols) and the darkly melanic *Bryoria fuscescens* (black symbols) measured with red actinic light. Error bars show standard error ($n = 12$)

F_V/F_M between the species diminished significantly after 24 h recovery (*Alectoria*: 0.505 ± 0.015 ; *Bryoria*: 0.471 ± 0.009 ; mean \pm SE).

Non-photochemical quenching

NPQ increased with light intensity but responded more strongly and quickly to sudden light exposure in *Alectoria* compared to *Bryoria* (Fig. 5). After an initial linear increase in NPQ lasting approximately 2.5 min, NPQ accelerated for the next 2 min in both hair lichens. The increase then slowed, peaking after 15 min in *Alectoria* while NPQ continued to rise at a slower rate in *Bryoria*, peaking at 19 min under 233 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ light exposure (Fig. 5A), or continuing to increase until end of the 23-min exposure at 613 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ light exposure (Fig. 5B).

When the light was switched off, NPQ rapidly relaxed, with the fastest rate observed after the highest light exposure. Relaxation was slightly faster in *Alectoria* than in *Bryoria* (Fig. 5), but both species reached the same NPQ-level at the end of the 10-min dark exposure.

Chlorophylls

Despite their similar morphology, the darkly pigmented *Bryoria* had a 1.8 times higher total Chl concentration

Fig. 4 The mean kinetics of recovery from photoinhibition after a 4-h exposure of $750 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ for hydrated thalli of the usnic *Alectoria sarmentosa* (open symbols; $R^2_{\text{adj}} = 0.840$; $P < 0.001$) and the darkly melanic *Bryoria fuscescens* (black symbols; $R^2_{\text{adj}} = 0.752$; $P < 0.001$). F_V/F_M is expressed as percent of the pre-start values of dark-adapted specimens. The inset shows the mean F_V/F_M of both species at start. Error bars show standard error ($n = 12$). The regression line with corresponding 95% confidence interval (dotted lines) is given for each species

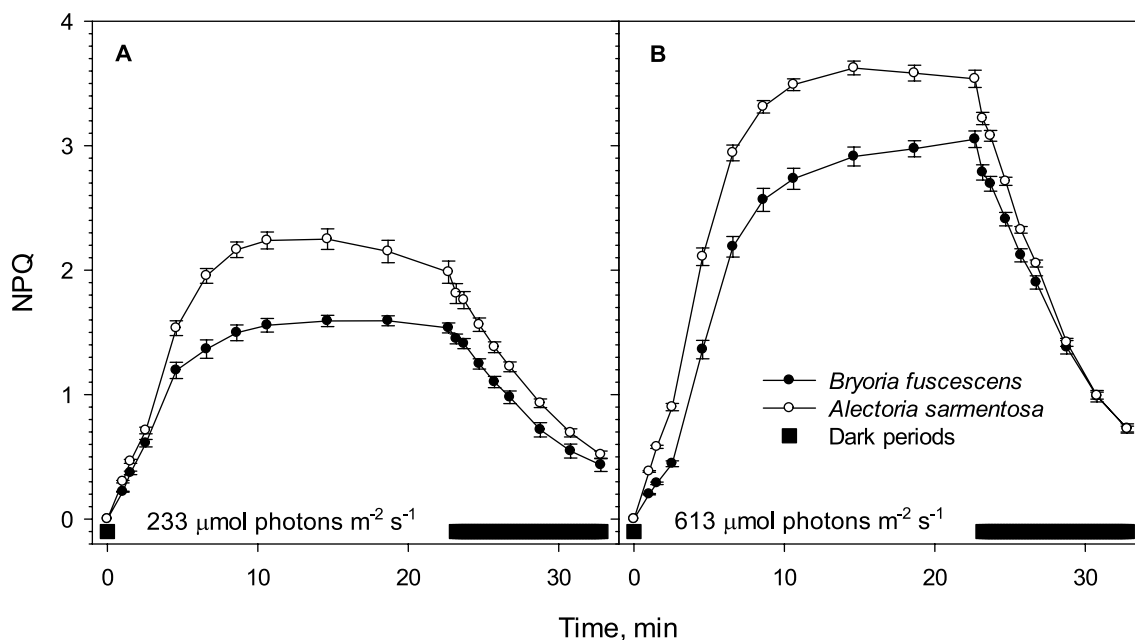
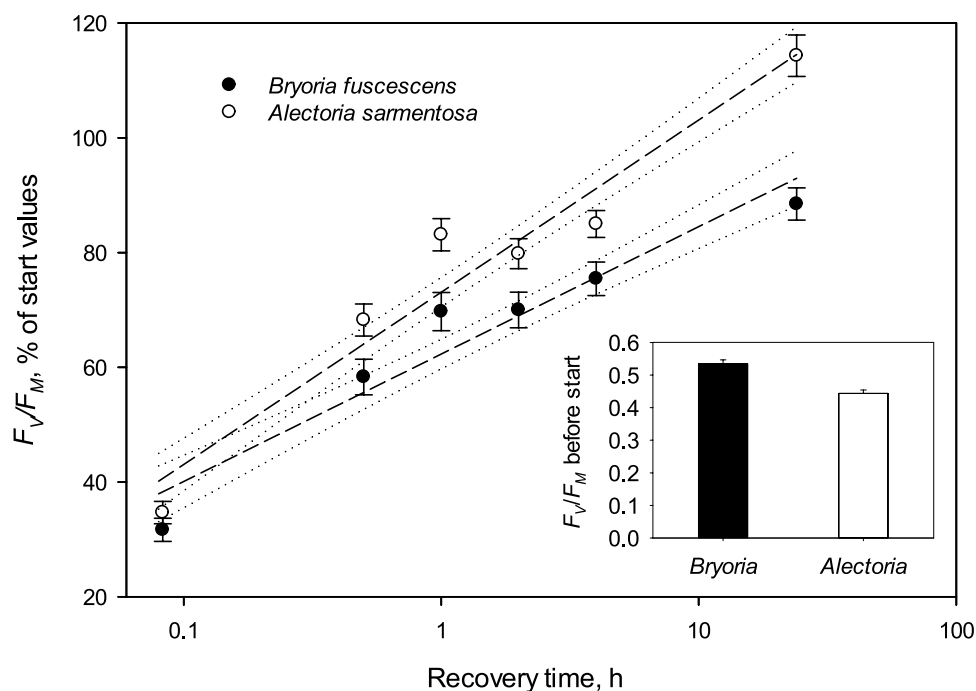


Fig. 5 The mean kinetics of non-photochemical quenching (NPQ) in dark-adapted intact thalli of the usnic *Alectoria sarmentosa* (open symbols) and the darkly melanic *Bryoria fuscescens* (black symbols). Thalli were exposed to 233 (A) and 613 (B) $\mu\text{mol photons m}^{-2} \text{s}^{-1}$,

respectively, for 23 min followed by a 10 min dark period (shown by the thick horizontal black bar). Error bars show mean \pm SE when larger than symbol size ($n = 12$)

($0.698 \pm 0.075 \text{ mg g}^{-1}$; mean \pm SE) than the sympatric, but pale *Alectoria* ($P = 0.009$). Additionally, *Bryoria* had 1.5 times higher Chl *a/b*-ratio (4.87 ± 0.26) than *Alectoria* ($P = 0.002$; Table 1).

Discussion

Lichens are remarkable successful photosynthetic organisms, thriving in some of the most sun-exposed and

Table 1 Total chlorophyll concentration and chlorophyll *a/b*-ratio in the hair lichens *Alectoria sarmentosa* and *Bryoria fuscescens*

	<i>Alectoria sarmentosa</i>	<i>Bryoria fuscescens</i>	<i>t</i> value	<i>P</i> value
Total Chl (mg g ⁻¹)	0.397 ± 0.028	0.698 ± 0.075	− 3.78	0.009
Chl <i>a/b</i> -ratio	3.31 ± 0.05	4.87 ± 0.26	− 5.75	0.002

Mean values ± standard error (*n* = 6) are given.

extreme habitats on Earth (Kappen 1973). They can survive extended exposure to outer space (Sancho et al. 2007; Onofri et al. 2012) and photosynthesize under simulated Martian conditions (de Vera et al. 2010; de Vera 2012), indicating their possession of highly effective photoprotective mechanisms. Lichens utilize a variety of sun-screening fungal pigments, such as parietin (Solhaug and Gauslaa 1996), atranorin (Solhaug et al. 2010), usnic acid (McEvoy et al. 2006; 2007), vulpinic acid (Phinney et al. 2019), and melanin (Gauslaa and Solhaug 2001). Comparing the efficiency of screening mechanisms is complex due to the different ways in which reflecting pigments like usnic acid and absorbing pigments like melanin handle solar radiation (Gauslaa and Goward 2023). However, our study provides valuable insight into the efficiency of these cortical pigments through the photobiological responses of sympatric usnic and melanic hair lichens.

The usnic *Alectoria* displayed a significantly stronger green reflectance peak than *Bryoria*, indicating greater exposure of its Chl to ambient light outside the screening lichen cortices in *Alectoria*. This occurs despite *Bryoria* having a higher total Chl concentration than *Alectoria*. However, when Chl concentrations were adjusted to Chl content per thallus area, using specific thallus mass data provided by Esseen et al. (2015) for hair lichens, the contrast between species was markedly reduced. In the melanic species, Chl was less visible through a hydrated cortex, as evidenced by its considerably weaker green reflectance. Upon desiccation, *Bryoria*'s red reflectance increased more than its green reflectance, causing the faint green tinge to disappear, whereas the green reflectance peak remained distinct in *Alectoria*. This pattern is also observed in other pairs of melanic and usnic hair lichen species (Gauslaa 1984). The higher visibility of Chl in the usnic species suggests greater cortical transmittance, which likely contributes to the increased susceptibility to high light in desiccated usnic hair lichens compared to melanic ones (Färber et al. 2014).

During high-light exposures while hydrated, *Alectoria* exhibited significantly higher and more rapidly induced NPQ, as well as faster relaxation in darkness, compared to its melanic counterpart. This aligns with the recent findings showing more flexible NPQ responses to high light exposures in usnic versus melanic species of sympatric mat-forming alpine lichens (Solhaug et al. 2024). Both usnic and melanic populations of these thick mat-forming lichens, as

well as the thin hair lichens in this study, had acclimated to similar external light conditions by forming species-specific cortical pigments. We assume that hydrated lichen species exposed to the same external light condition require a similar ability to handle ambient light, but that their set of tools to manage excess excitation energy differs. Given NPQ's flexibility and rapid response, our data suggest that insufficient fungal screening could be compensated by the measured enhanced NPQ observed in *Alectoria* photobionts.

NPQ in hair lichens exposed to light tended to decrease over time, especially in the usnic species and at lower light level. This decline may occur, because some time is needed for full activation of photosynthesis, which, once activated, can handle more light, reducing the need for NPQ to mitigate oxidative stress. The stronger decline in NPQ in mat-forming lichens (Solhaug et al. 2024) compared to hair lichens suggests that thin hair lichens need shorter time for full photosynthetic activation.

Alectoria recovered more quickly than *Bryoria* from photoinhibition experienced after a 4-h high-light treatment in the hydrated state (Fig. 4), a response opposite to that observed in desiccated thalli (Färber et al. 2014). The fast recovery of *Alectoria* at low light after photoinhibition is not entirely understood. Its initial F_v/F_M was lower than that of *Bryoria*, likely due to the exceptionally sunny and dry weather before sampling, which may have affected *Alectoria* more. Thus, the post-stress 24-h relaxation at low light could also have allowed some recovery from residual photoinhibition experienced in the field before the artificial high-light treatment. In seasonal climates, normal acclimation involves a significant reduction in F_v/F_M during periods when photosynthesis is constrained by factors such as low temperature or drought, which limit the ability to manage excess light (e.g., Vrábliková et al. 2006; Veres et al. 2022). Vernal photoinhibition observed in indigenous lichens from pristine, unpolluted forest hardly indicates impaired viability.

The two sympatric hair lichens exhibited light saturation at relatively high light levels, aligning with the open and sun-exposed canopies from which they were sampled (Fig. 1). A higher ETR_{App} in one species suggests a greater degree of cortical screening, assuming that the relative increase is similar across various irradiance levels. Conversely, a higher ETR_{App} observed only at high irradiance indicates enhanced photosynthetic capacity. The combination of higher ETR_{App} in *Bryoria* and a similar relative rise in

ETR_{App} with increasing light for both species suggests more effective fungal screening in *Bryoria* compared to *Alectoria*. This is corroborated by the strong green reflectance peak in *Alectoria* (Fig. 2), suggesting that more light penetrates through the cortex and reaches the photobiont layer beneath the usnic cortex compared to the melanic cortex. Finally, the more pronounced drying-induced relative reduction of the green reflectance in *Bryoria* than in *Alectoria* (Fig. 2) aligns with the reported strong high-light tolerance in desiccated thalli of melanic hair lichens (Färber et al. 2014).

In conclusion, melanin serves as a more efficient sun-screen than usnic acid in thin hair lichens. The robust screening by dry melanic cortices enables *Bryoria* to thrive in the upper tree canopies of drier climates during extended dry and sunny periods when NPQ cannot operate. In contrast, the usnic lichen *Alectoria*, with less-effective solar radiation screening, exhibits the highest and most rapidly induced NPQ when hydrated. This supports the hypothesis that the fungal pigment usnic acid alone is inadequate for preventing photoinhibitory damage in sun-exposed hair lichens. *Alectoria*'s preference for lower humid canopy layers exposed to intermittent sunflecks is likely facilitated by its adaptable NPQ, optimizing photosynthesis during hydration periods under fluctuating light conditions. *Alectoria*'s success in well-lit upper canopies of rainforest (Benson and Coxson 2002; Antoine and McCune 2004) hinges on frequent hydration, which not only enables NPQ but also repairs photoinhibitory damage that would otherwise accumulate in drier climates. While the mycobiont offers primary photoprotection in dry lichens, the NPQ of the photobiont complements the photoprotective role of fungal pigments in hydrated lichens.

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Data availability Original excel files for the data shown in Figures and Tables are available on request.

Declarations

Conflict of interest The authors have no financial or proprietary interests in any material discussed in this article.

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