The Lichenologist (2021), **53**, 409–414
doi:10.1017/S0024282921000323

CAMBRIDGE UNIVERSITY PRESS

Standard Paper

Shade lichens are characterized by rapid relaxation of non-photochemical quenching on transition to darkness

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Abstract

Non-photochemical quenching (NPQ) plays an important role in protecting photosynthetic organisms from photoinhibition by dissipating excess light energy as heat. However, excess NPQ can greatly reduce the quantum yield of photosynthesis at lower light levels. Recently, there has been considerable interest in understanding how plants balance NPQ to ensure optimal productivity in environments in which light levels are rapidly changing. In the present study, chlorophyll fluorescence was used to study the induction and relaxation of non-photochemical quenching (NPQ) in the dark and the induction of photosynthesis in ten species of lichens, five sampled from exposed and five sampled from shaded habitats. Here we show that the main difference between sun and shade lichens is the rate at which NPQ relaxes in the dark, rather than the speed that photosynthesis starts upon illumination. During the first two minutes in the dark, NPQ values in the five sun species declined only by an average of 2%, while by contrast, in shade species the average decline was 40%. For lichens growing in microhabitats where light levels are rapidly changing, rapid relaxation of NPQ may enable their photobionts to use the available light most efficiently.

Key words: chlorophyll fluorescence, photoprotection, photosynthesis, sunfleck, xanthophyll cycle

(Accepted 14 July 2021)

Introduction

Many lichens possess a variety of tolerance mechanisms that enable them to grow in habitats where they are exposed to levels of light that are far greater than lichen photobionts can use in carbon fixation (Beckett *et al.* 2021). However, some species grow in more shaded microhabitats. Long-term adaptations of lichens growing in shade include having lower light saturation and compensation points than those from sun-exposed habitats (Green *et al.* 1997), and also less cortical pigments (Dietz *et al.* 2000). Many lichens from shaded habitats experience short-term (s-min) changes in light levels. For example, for lichens growing on the trunks of trees, gaps in the canopy expose the lichens to rapidly changing light levels in ways that depend on the diurnal variations in the angle of sunlight, tree architecture and movements of the tree branches. Lichens in such habitats experience rapidly changing levels of irradiance; the relatively brief periods that lichens are exposed to high light levels are known as 'sunflecks'. In higher plants, it is known that the ability of photosynthesis to adapt to these fluctuations is under genetic control (Cruz *et al.* 2016) and that the speed of these responses can be improved by exploiting natural genetic variation (Morales & Kaiser 2020).

Lichen photobionts need to optimally use the light that becomes available to them in a sunfleck. A few minutes of illumination at least are needed for Calvin cycle intermediates to reach critical levels, and this 'induction requirement' of photosynthesis determines how fast a lichen photobiont can respond to an increase in photon irradiance. Previous workers emphasized the need for a rapid increase in photosynthesis following illumination in both lichens (Lakatos *et al.* 2006) and bryophytes (Kubasek *et al.* 2014) growing in shaded environments. However, it appears that no comprehensive survey of the speed of induction of photosynthesis in 'sun' and 'shade' lichens has been carried out. In general, induction of photosynthesis occurs more quickly in lichens and bryophytes than in higher plants, probably at least in part because the former do not possess stomata that need to be opened (Lakatos *et al.* 2006).

In addition to the need for rapid induction of photosynthesis, lichens must protect themselves from damage that could result from a sudden increase in light. Excess light energy can result in elevated levels of reactive oxygen species (ROS) produced by chlorophyll ($^1O_2$) and electron transport chains (O_2^- and H_2O_2), which can cause photo-oxidative damage (Roach & Krieger-Liszkay 2019). Photobionts use several processes to regulate the efficiency with which light energy is used, collectively referred to as non-photochemical quenching (NPQ). Lichens possessing green (chlorophycean) photobionts have light harvesting

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Cite this article: Beckett RP, Minibayeva FV and Mkhize KWG (2021) Shade lichens are characterized by rapid relaxation of non-photochemical quenching on transition to darkness. *Lichenologist* **53**, 409–414. https://doi.org/10.1017/S0024282921000323

complex (LHC) antenna proteins and, as a result, dissipate excess energy using strategies similar to those found in bryophytes and higher plants (Beckett *et al.* 2021). In the enzyme-catalyzed xanthophyll cycle, the carotenoid violaxanthin is converted to zeaxanthin in a pH-regulated process that occurs during increases in light intensity. However, NPQ plays both positive and negative roles in ensuring optimal plant productivity in environments in which light levels are rapidly changing (Murchie & Ruban 2020). Positively, NPQ delays the onset of photoinhibition by reducing ROS production. However, negatively, while not affecting photosynthesis in high light, NPQ can greatly reduce the quantum yield of photosynthesis at lower light levels. In other words, under low light a lichen 'expressing' high NPQ will require a higher irradiance to achieve the same photosynthetic rate as one without it. Recently, NPQ induction and relaxation in higher plants was accelerated by over-expressing violaxanthin de-epoxidase and zeaxanthin epoxidase. When grown in the field, these plants possessed higher biomass and yield, and in particular CO_2 assimilation rates were enhanced during the transition to low light (Kromdijk *et al.* 2016). The implication for lichens could be that shade species growing in habitats subjected to rapidly changing light levels will benefit from more rapid relaxation of NPQ on transition to low light, enabling lichens to efficiently utilize the lower light levels available after a sunfleck has passed.

Perhaps surprisingly, the relaxation of NPQ on transition from light to dark has not been systematically studied in lichens. We therefore used chlorophyll fluorescence to measure both the induction of photosynthesis on exposure to light and the rates of NPQ relaxation in the dark in lichens. We compared species growing in exposed habitats with those growing in generally shaded habitats, but ones in which lichens experience rapidly changing light levels. Results showed that the main differences between lichens that grow in full sun and those in more shaded habitats are not in the speed of activation of photosynthesis, but rather that sunfleck species show much faster relaxation of NPQ, particularly during the few minutes of transition to the dark.

Materials and Methods

Lichen material

The list of species used and their microhabitats are described in Table 1. Lichens were collected from a small patch of Afromontane forest in Fort Nottingham, KwaZulu Natal, South Africa and some surrounding drier savannah. Lichens were cleaned and stored refrigerated for up to 2 weeks. For uniformity, before the start of each experiment all material was initially hydrated by spraying with distilled water followed by moist storage for *c.* 24 h in dim light (20 µmol photons m^{-2} s^{-1}) at 12 °C.

Chlorophyll fluorescence measurements

Chlorophyll fluorescence was measured using a PAM 2500 fluorimeter (Walz, Effeltrich, Germany) using the red LED. After a dark adaptation period of at least 10 min, the maximal efficiency of photosystem II (PSII; F_v/F_m) was measured, where F_m = maximum fluorescence and F_v = variable fluorescence or ($F_m - F_0$), with F_0 = minimal fluorescence yield of the dark-adapted state. Thalli with anomalous values of F_v/F_m were discarded. Rapid light response curves of electron transport rates (ETR) were measured by increasing the actinic light in 11 small steps of 10 to 20 s each from 0 to 475 µmol photons m^{-2} s^{-1} (at 12, 33, 56, 81, 106, 141, 185, 238, 301, 383 and 475 µmol photons m^{-2} s^{-1}) with saturating flashes at the end of exposure to each light level. The relative ETR was calculated as:

$$\text{rETR} = 0.5 \times \varphi\text{PSII} \times \text{PAR}$$

where PAR = photosynthetically active radiation and ΦPSII is the effective quantum yield of PSII photochemistry calculated as $(F_{m'} - F_t)/F_{m'}$ (where $F_{m'}$ = maximal fluorescence yield of the light-adapted state and F_t = stable fluorescence signal in the light).

The equation derived by Eilers & Peeters (1988) was used to calculate the following parameters:

$rETR_{MAX}$: the maximal relative ETR reached during light curve recording, reflecting the light saturated capacity of the sample (units: µmol electrons m^{-2} s^{-1}).

lk: the light intensity at which PAR saturation sets in. This is estimated by constructing a linear regression of the initial part of the light response curve and extrapolating it until it hits an ETR value corresponding to the estimate of $rETR_{MAX}$. The light intensity where the two lines intersect is lk (units: µmol photons m^{-2} s^{-1}).

To determine the induction of rETR, and the induction and relaxation of NPQ, thalli were dark-adapted for 10 min and F_v/F_m measured; thalli with anomalous values were discarded. An actinic light of 100 µmol photons m^{-2} s^{-1} was then turned on, and saturating flashes applied at increasing intervals for 11 min. The actinic light was then turned off and relaxation measured for 8 min, with saturating flashes given at increasing intervals. NPQ was calculated using the formula of Bilger *et al.* (1995):

$$\text{NPQ} = (F_m - F_{m'})/F_{m'}$$

In initial experiments we tested the induction of NPQ using a variety of light intensities, but in a laboratory setting values much above 100 µmol photons m^{-2} s^{-1} tended to cause some photoinhibition. To avoid progressive development of any slow relaxing photoinhibitory quenching (qI), we therefore elected to standardize at 100 µmol photons m^{-2} s^{-1}.

Results

Table 2 presents a summary of the data derived from the rapid light curves. Comparing the sun and shade lichens, both $rETR_{MAX}$ and the PAR where saturation sets in (lk) were more than double in the sun compared with the shade species. Figures 1 and 2 compare the induction and relaxation of NPQ and the induction of rETR in shade and sun species respectively. Induction of rETR by 100 µmol m^{-2} s^{-1} was rapid, and similar in sun and shade species. The proportion of $rETR_{MAX}$ induced after 30 s was almost the same in sun and shade species (Table 2). NPQ tended to be induced more slowly in shade than sun species, and was not complete even after 11 min in *Lepraria* and *Roccella*. However, the final values of NPQ (after 11 min) induced in shade species were on average almost double that of sun species (Table 2). Shade and sun lichens differed mainly in their rate of relaxation of NPQ, particularly in the first 2 min of darkness. While in the five sun species NPQ declined only by an average of 2%, in shade species the average decline was 40%, with two species (*Lobaria* and *Roccella*) declining by more than 50%. Correlation analysis showed that the PAR where saturation sets in was very strongly correlated with $rETR_{MAX}$ (Fig. 3A) and

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Table 1. Collection sites, habitats and photobiont types of the lichen species used in this study.

Species	Collection site	Probable photobiont	Microhabitat
Shade species			
Cetrelia cetrarioides	Afromontane forest, Fort Nottingham, KwaZulu Natal	*Trebouxia*	Tree trunk, deep shade
Crocodia aurata	Afromontane forest, Fort Nottingham, KwaZulu Natal	*Symbiochloris*	Tree trunk, deep shade
Lepraria incana	Afromontane forest, Fort Nottingham, KwaZulu Natal	*Asterochloris*	Tree trunk, deep shade
Lobaria quercizans	Afromontane forest, Fort Nottingham, KwaZulu Natal	*Symbiochloris*	Tree trunk, deep shade
Roccella montagnei	Afromontane forest, Umgeni Nature Reserve, Howick, KwaZulu Natal	*Trentepohlia*	Base of tree-shaded cliffs
Sun species			
Cladonia coniocraea	Savannah, Cumberland Nature Reserve, KwaZulu Natal	*Asterochloris*	Exposed rocky outcrops
Parmelia saxatilis	Savannah, Cumberland Nature Reserve, KwaZulu Natal	*Trebouxia*	Exposed rocky outcrops
Ramalina celastri	Afromontane forest, Fort Nottingham, KwaZulu Natal	*Trebouxia*	Periphery of canopy
Usnea undulata	Afromontane forest, Fort Nottingham, KwaZulu Natal	*Trebouxia*	Periphery of canopy
Xanthoparmelia conspersa	Savannah, Cumberland Nature Reserve, KwaZulu Natal	*Trebouxia*	Exposed rocky outcrops

Table 2. Summary of photosynthetic parameters of sun and shade lichen species. The start of light saturation (Ik) and maximal relative electron transport rate ($rETR_{MAX}$) were derived from rapid light curves, while other values were derived by illuminating dark-adapted lichens to light at 100 μmol m^{-2} s^{-1} and measuring the time course of the induction of ETR and non-photochemical quenching (NPQ) for 11 min, and the relaxation of NPQ for 8 min after switching off the light. Figures are given as ± SE, n = 10–15.

Species	$rETR_{MAX}$	Ik (μmol m^{-2} s^{-1})	% $rETR_{MAX}$ after 30 s	NPQ after 11 min	% NPQ relaxed after 2 min*
Shade species					
Cetrelia cetrarioides	15.0 ± 2.0	43 ± 7	71	0.67 ± 0.08	15 ± 1
Crocodia aurata	13.1 ± 0.8	50 ± 3	70	0.95 ± 0.08	46 ± 2
Lepraria incana	8.6 ± 0.6	31 ± 3	65	0.49 ± 0.10	31 ± 3
Lobaria quercizans	12.9 ± 1.1	39 ± 4	66	1.44 ± 0.07	54 ± 1
Roccella montagnei	6.9 ± 2.1	29 ± 11	71	0.66 ± 0.11	54 ± 4
Mean for shade species	11.3	38	69	0.84	40
Sun species					
Cladonia coniocraea	21.1 ± 1.1	73 ± 4	84	0.58 ± 0.09	−1 ± 4
Parmelia saxatilis	25.2 ± 1.7	93 ± 7	66	0.51 ± 0.04	7 ± 2
Ramalina celastri	30.8 ± 2.4	105 ± 10	57	0.39 ± 0.05	−5 ± 4
Usnea undulata	32.6 ± 2.9	128 ± 14	67	0.43 ± 0.03	4 ± 3
Xanthoparmelia conspersa	28.9 ± 2.2	97 ± 7	67	0.54 ± 0.06	−2 ± 3
Mean for sun species	27.7	99	67	0.49	2

* negative values indicate stimulation of NPQ

was significantly negatively correlated with the proportion of NPQ relaxed after 2 min (Fig. 3B).

Discussion

Lichens growing in shaded habitats often experience short-term (s-min) changes in light levels. The duration of periods of relatively bright and dim light varies greatly between habitats, but the average duration of sunflecks in subtropical Afromontane forests is probably *c.* 2 min (Pallardy 2008). While lichens need to optimize the use of brief periods of high light, at the same time they must also protect themselves from damage that could result from ROS formation. One of the most powerful ways photobionts can reduce ROS formation is by inducing NPQ. However, while strong quenching will delay the onset of photoinhibition during a sunfleck, it will simultaneously greatly reduce the quantum yield of photosynthesis when light returns to lower levels. Results presented here show that sun and shade lichens differ mainly in the rate of relaxation of NPQ during the first few minutes that light levels fall. Rapid relaxation of NPQ probably has little selective advantage for lichens growing in exposed sites, where during the day the only major changes in light levels result from changes in cloud cover and occur over periods of hours rather than minutes. By contrast, the rapid relaxation of NPQ

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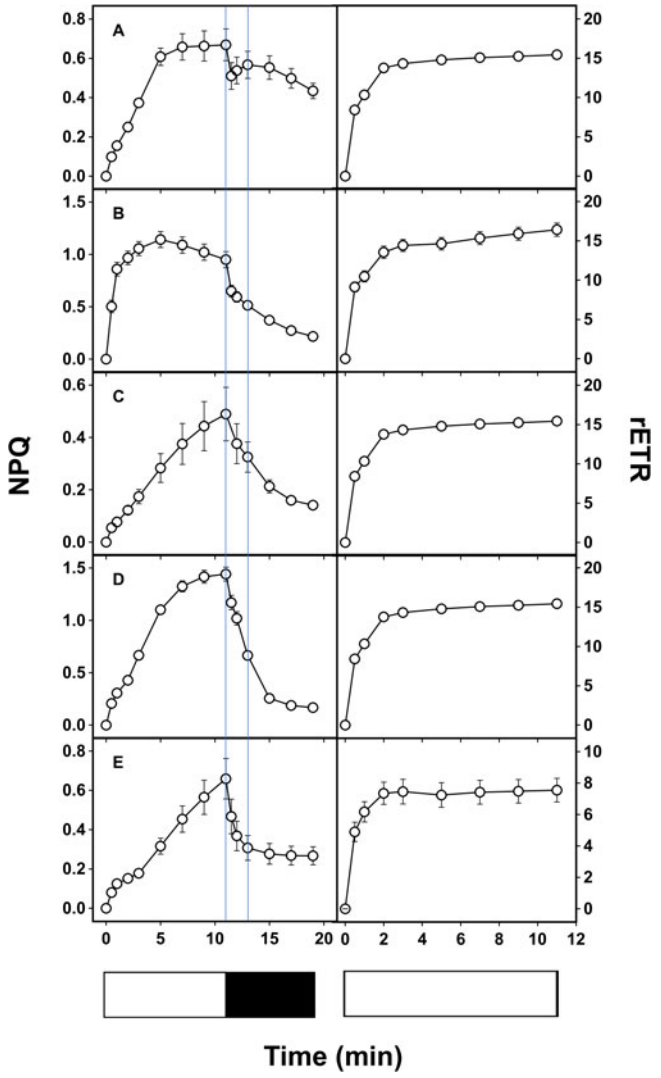

Fig. 1. Induction and relaxation of non-photochemical quenching (NPQ), and induction of relative electron transport rate (rETR) in shade species of lichens in response to light at 100 µmol m^{-2} s^{-1}. A, *Cetrelia cetrarioides*. B, *Crocodia aurata*. C, *Lepraria incana*. D, *Lobaria quercizans*. E, *Roccella montagnei*. Error bars denote the standard error, $n = 10–15$. Vertical lines on the plots delimit NPQ during the first 2 min of darkness. White and black sections in the boxes at the base of the plots indicate the time periods when samples were exposed to light or darkness respectively. In colour online.

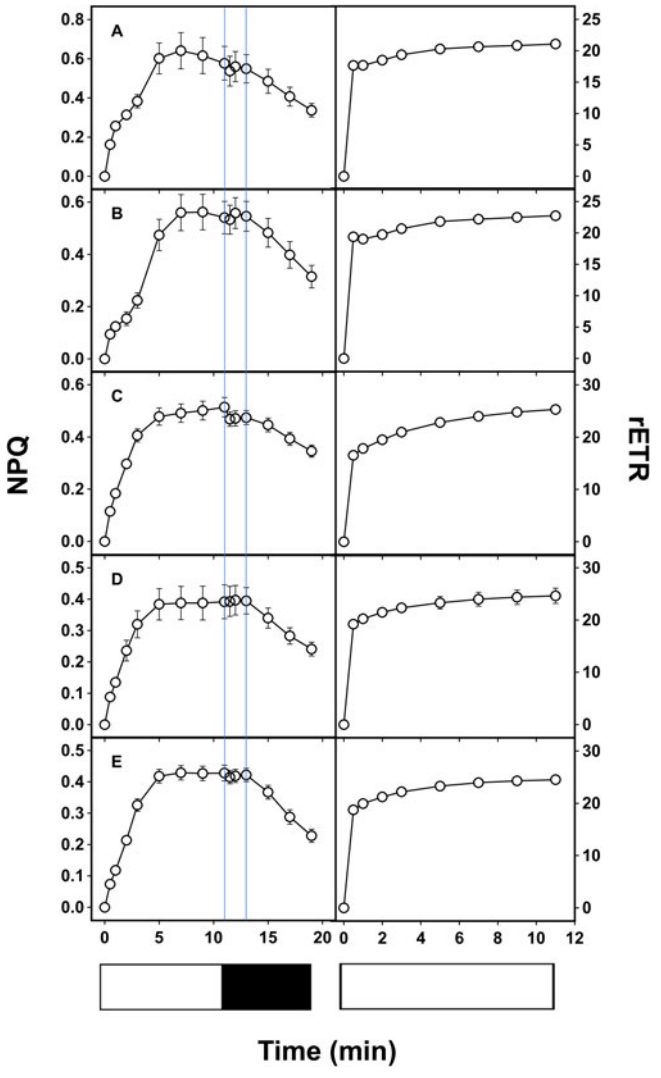

Fig. 2. Induction and relaxation of non-photochemical quenching (NPQ), and induction of relative electron transport rate (rETR) in sun species of lichens in response to light at 100 µmol m^{-2} s^{-1}. A, *Cladonia coniocraea*. B, *Xanthoparmelia conspersa*. C, *Parmelia saxatilis*. D, *Ramalina celastri.* E, *Usnea undulata*. Error bars denote the standard error, $n = 10–15$. Vertical lines on the plots delimit NPQ during the first 2 min of darkness. White and black sections in the boxes at the base of the plots indicate the time periods when samples were exposed to light or darkness respectively. In colour online.

observed in lichens that grow in microhabitats where light levels are rapidly changing will enable their photobionts to efficiently utilize the lower light levels that occur once a sunfleck has passed.

Rapid light curves

Parameters derived from the rapid light curves indicate that the light intensity where saturation of photosynthesis sets in (lk) is much lower in the shade species than in the sun species (33 compared with 99 µmol m^{-2} s^{-1}; Table 2). Furthermore, the average $rETR_{MAX}$, the maximal relative electron transport rate reached during light curve recording (reflecting the light saturated rate of photosynthesis), is much lower in shade than sun species (11.3 compared with 27.7). It is well known that higher plants growing in bright habitats have a greater capacity for photosynthetic electron transport (greater abundance of transport components such as Cyt b559, Cyt b563, Cyt f and plastoquinone) and a greater capacity for ATP synthesis per unit of chlorophyll compared with shade plants (Greer 2021). This results in higher rates of photosynthesis in sun plants, and photosynthesis that saturates at higher light levels, as found in the present study for lichen photobionts. Although there are few comparable studies with lichens, Piccotto & Tretiach (2010) surveyed a range of lichens from contrasting habitats and found that the 'potential solar irradiation' of each site was significantly correlated to lk and maximum rates of photosynthesis. In the present study, $rETR_{MAX}$ and lk were highly significantly correlated (Fig. 3A). While no actual measurements of field light intensities were taken in the present study, visual inspection suggests that lk, or the PAR where saturation starts, appears to be a good quantitative measure of the light regimes of the habitats that the lichens were collected from.

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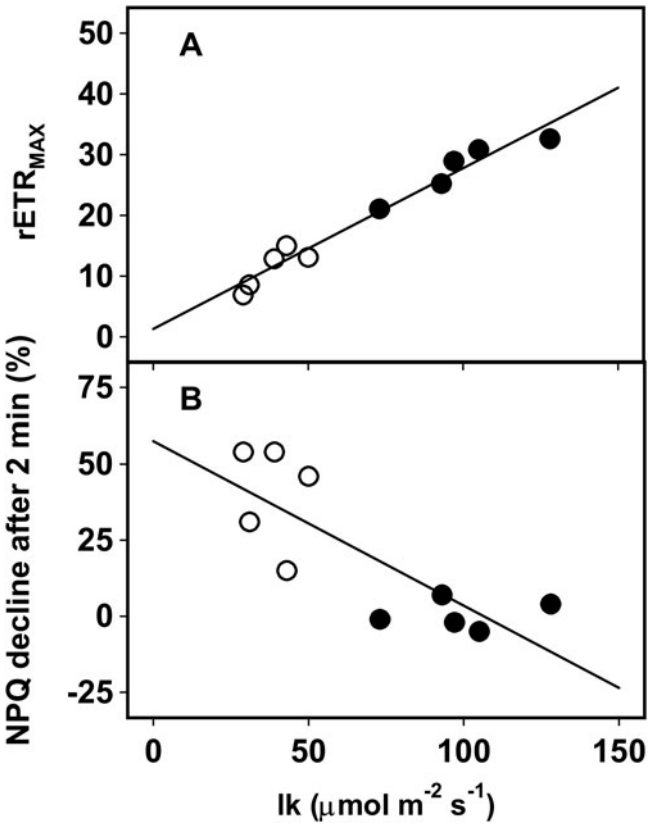

Fig. 3. A, correlation between Ik (the photosynthetically active radiation (PAR) where light saturation sets in) and maximal relative electron transport rate (rETR$_{MAX}$) ($P <$ 0.001). B, correlation between Ik and the percentage drop in maximum values of non-photochemical quenching (NPQ) (after illumination for 11 min) during the first 2 min of darkness ($P < 0.01$). Each point is the average of at least 10 values.

Dark relaxation of NPQ

The main differences between the sun and shade species of lichens studied here was in the rate of dark relaxation of NPQ. During the first two minutes of darkness NPQ declined only by on average 2% in the sun species (and in some species NPQ marginally increased), whereas in the shade species NPQ declined by an average of 40% (Table 2). The decline in NPQ during the first two minutes of darkness was significantly negatively correlated with Ik (Fig. 3B). Work with higher plants suggests that there are several possible mechanisms that could promote fast relaxation during the transition from high to low light. First, shade species may possess higher activities of xanthophyll epoxidases (Kaiser *et al.* 2019). Second, the speed of NPQ relaxation is strongly modulated by the K^+ antiporter KEA3 (Armbruster *et al.* 2014, 2016; Correa Galvis *et al.* 2020). KEA3 transfers K^+ into the lumen and H^+ out to the chloroplast stroma, decreasing pH and accelerating NPQ relaxation, leading to a fast recovery of CO_2 assimilation (Armbruster *et al.* 2014). Further work is needed to investigate these possibilities in lichen photobionts, and also to study any metabolic costs associated with rapid relaxation. Interestingly, while the induction (rather than the relaxation) of NPQ in some shade species (e.g. *Lepraria* and *Roccella*; Fig. 1C & E) was slower than in sun species and was not complete even after 11 min, average values of NPQ after 11 min were higher in shade than sun species (Table 2). High values of NPQ in shade species might appear surprising, but in higher plants fluctuating light has been reported to increase the protective capacity of NPQ (Alter *et al.* 2012; Caliandro *et al.* 2013). Presumably, in shaded habitats light levels can increase very suddenly, potentially causing oxidative stress, and therefore effective defence mechanisms must be constitutively in place. Theoretically, faster relaxation in shade species could be simply because they contain lower pool sizes of xanthophyll cycle pigments. However, this appears unlikely because in general NPQ is positively correlated with absolute levels of xanthophyll cycle pigments (Demmig-Adams *et al.* 2020), and the higher values of NPQ in shade species suggests that they contain larger, not smaller xanthophyll pool sizes.

It is perhaps surprising that there have been no previous attempts to compare the rates of NPQ relaxation in sun and shade lichens. In the comparable survey of bryophytes by Proctor & Smirnoff (2015), results showed that NPQ on transition to darkness tends to display relatively simple exponential decay curves, unlike the rather complex kinetics of induction and relaxation reported here for lichens. Although relaxation rates in bryophytes appear to be faster than those in lichens, Proctor & Smirnoff (2015) also found that NPQ generally relaxes faster in shade than in sun bryophytes. Limited comparable data is available for microalgae. Environments characterized by particularly large light fluctuations include shallow waters. Here, microalgae employ rapidly reversible NPQ, presumably to cope with more variable light fields, whereas motile benthic algae display sustained NPQ (Fisher *et al.* 2020). For example, Derks & Bruce (2018) compared the induction and relaxation of NPQ in two diatoms from contrasting habitats. *Navicula* grows in a stable high irradiance light environment, while *Nitzschia* grows in churning water with a high particulate content and is exposed to rapid (s-min) changes in light levels. Both species were exposed to 500 μmol m^{-2} s^{-1} for 10 min, followed by 15 min of darkness. NPQ was induced rapidly in both species and was higher in *Nitzschia* than in *Navicula*. Interestingly, however, similar to the results presented here, the main difference between the species was in the rate of relaxation of NPQ, which was much faster in *Nitzschia* than in *Navicula*.

Finally, it is worth noting that differences in rates of relaxation of NPQ are not simply correlated to photobiont type (Table 1). The photobionts of the shade species sampled here are more diverse than those of the sun species, and include *Trentepohlia* and *Symbiochloris*. Nevertheless, two shade species, *Cetrelia* and *Lepraria*, contain *Trebouxia* or the closely related *Asterochloris*, possessed by all the sun species sampled here. Interestingly, Nelsen *et al.* (2021) suggested that early *Trebouxia* lineages were largely forest specialists or habitat generalists, and were found in moderate climates. *Trebouxia* then diversified in non-forested and more stressful habitats (Nelsen *et al.* 2021). It seems likely that as *Trebouxia*-containing lichens emerged from shaded habitats, the pattern of NPQ relaxation changed from rapid to more gradual relaxation. Today, both patterns of relaxation are found in trebouxioid lichens.

Conclusions

Some authors have emphasized the need for lichens growing in habitats with rapidly changing light levels to rapidly induce photosynthesis on illumination (Lakatos *et al.* 2006). However, results from the present study show that rETR induces at very similar rates in shade and sun lichens (Table 2). A more fundamental difference between sun and shade lichens appears to be

https://doi.org/10.1017/S0024282921000323 Published online by Cambridge University Press

the rate at which NPQ relaxes. Future work needs to investigate at a biochemical level the mechanisms that enable shade lichens to relax NPQ faster than sun species, for example by studying the expression of the xanthophyll epoxidases and the KEA ion transporter. Recently, there has been great interest in understanding how relaxation of NPQ is controlled, with a view to increase yield in crop plants (Kromdijk *et al.* 2016). Comparative studies of sun and shade lichens may facilitate the bioengineering of other organisms to display accelerated responses to natural shading events.

Acknowledgements. RB thanks the Russian Government Program of Competitive Growth of Kazan Federal University for partial financial support. FM thanks the Russian Science Foundation (grant no. 18-14-00198, rapid light curves) and the Russian government assignment of FRC Kazan Scientific Center of RAS for financial support. KM thanks the DAAD In-Country award (South Africa) for a bursary.

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https://doi.org/10.1017/S0024282921000323 Published online by Cambridge University Press