

Curling during desiccation protects the foliose lichen *Lobaria pulmonaria* against photoinhibition

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Abstract This study aims to assess the photoprotective potential of desiccation-induced curling in the light-susceptible old forest lichen *Lobaria pulmonaria* by using chlorophyll fluorescence imaging. Naturally curled thalli showed less photoinhibition-induced limitations in primary processes of photosynthesis than artificially flattened specimens during exposures to $450 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the laboratory after both 12- (medium dose treatment) and 62-h duration (high dose treatment). Thallus areas shaded by curled lobes during light exposure showed unchanged values of measured chlorophyll fluorescence parameters (F_V/F_M , $\Phi_{\text{PS II}}$), whereas non-shaded parts of curled thalli, as well as the mean for the entire flattened thalli, showed photoinhibitory limitation after light treatments. Furthermore, the chlorophyll fluorescence imaging showed that the typical small-scale reticulated ridges on the upper side of *L. pulmonaria* caused a spatial, small-scale reduction in damage due to minor shading. Severe dry-state photoinhibition readily occurred in flattened and light-treated *L. pulmonaria*, although the mechanisms for such damage in a desiccated and inactive stage are not well known. Natural curling is one strategy to reduce the chance for serious

photoinhibition in desiccated *L. pulmonaria* thalli during high light exposures.

Keywords Chlorophyll fluorescence imaging · *Lobaria pulmonaria* · Photoprotection · Poikilohydric organisms

Abbreviations

Chl	Chlorophyll
HD	High light dose
MD	Medium light dose
PS II	Photosystem II
$\Phi_{\text{PS II}}$	Quantum yield of photochemical reactions in photosystem II

Introduction

Light is a vital ecological factor for a lichen-forming fungus being dependent on a close symbiotic association with its autotrophic photobiont partner. The amount of light received by the photobiont during periods of thallus hydration may determine lichen growth (Dahlman and Palmqvist 2003), and thereby also the success of the lichen in forest ecosystems. At the same time, light represents a significant stress factor, not only because direct solar radiation promotes rapid desiccation in poikilohydric organisms, but also because excess light may cause severe and long-lasting photoinhibition in lichens (Gauslaa and Solhaug 1996, 2000). In this paper, we define photoinhibition to be a sustained depression of maximal photochemical quantum yield of PS II. Desiccated lichens are assumed to be resistant to high light, because desiccation reduces the transmittance of solar radiation through a protecting

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upper cortex (Ertl 1951; Gauslaa and Solhaug 2001), and stabilizes the photosynthetic apparatus by causing a functional disconnection of its components (Sigfridsson 1980; Bilger et al. 1989). However, in nature, lichens experience considerably longer periods of high solar radiation in the desiccated compared to the hydrated state (Lange et al. 1999), since they dry rapidly in the sun. Furthermore, repair mechanisms are switched off during desiccation. Extended excess light has been shown to cause more damage in the air-dry compared to the hydrated state in some old forest lichens (Gauslaa and Solhaug 1999, 2004), although the site of the damage is not well known. In such a perspective, various processes taking place during desiccation should be carefully examined to search for co-acting photoprotective strategies.

Lichen communities appear more dominant and impressive to a human eye when hydrated, because loss of water during clear weather decreases thallus area by shrinking and/or curling. Such a simple visual observation shows that most lichens undergo hygroscopic movements. These movements are particularly distinct in foliose vagrant desert lichens that roll up in a ball and expose their lower surface during desiccation (Rogers 1971; Lumbsch and Kothe 1988), which assumingly protects the algal layer against excessive light (Rogers 1977). However, sessile foliose lichens also shrink and curl (Ertl 1951), although their movements are less spectacular and rarely mentioned in literature. Lobe tips and margins often roll up or bend to a more vertical position during drying, enhancing the topography of the lichen surface. Such movements have the potential to shade the photobiont layer, but also to place the young photobiont layer more parallel to sunrays when the sun is high. Curling during desiccation reduces light-induced damage in poikilohydric vascular plants (Muslin and Homann 1992; Lebkuecher and Eickmeier 1992; Farrant et al. 2003; Lebkuecher and Eickmeier 1993), and was recently reviewed as one of various photoprotective mechanisms in desiccation tolerant plants (Alpert and Oliver 2002).

An increasing number of physiological studies in lichens have been devoted to photoprotection by pigments of xanthophyll cycle pool, photoprotective pigments, and antioxidative substances (e.g., Demmig-Adams et al. 1990a; Solhaug and Gauslaa 1996; Barták et al. 2004; Vráblíková et al. 2006). However, not much is known about the photoprotective potential of lichen curling. In this study, *Lobaria pulmonaria* (L.) Hoffm., a high-light susceptible foliose old forest lichen (Gauslaa and Solhaug 1999), was exposed to high light in the dry state in a naturally curled position and in a flattened position. We aim to quantify possible photoprotective

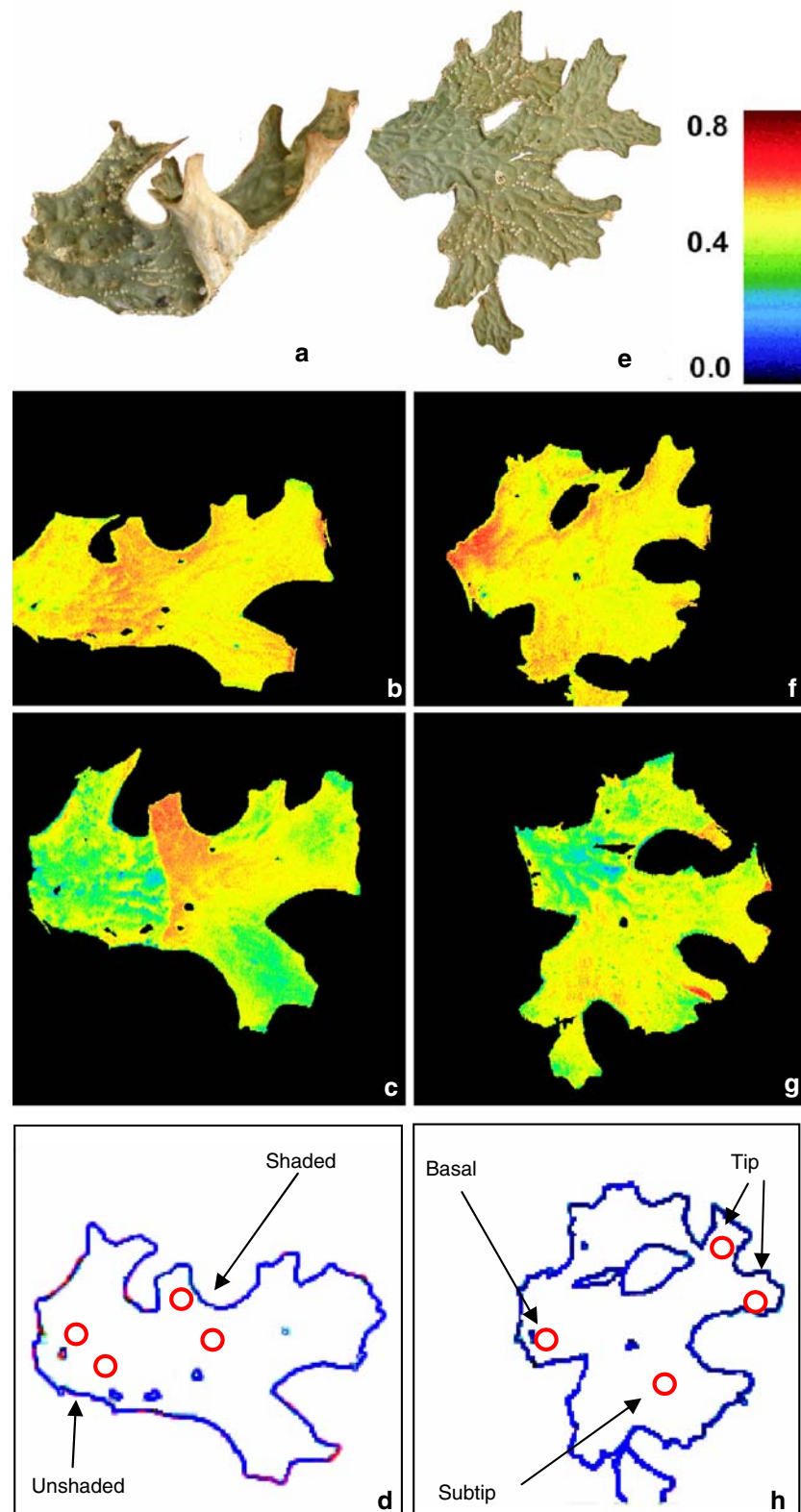
effects of curling by studying the spatial variation of photoinhibition with chlorophyll fluorescence imaging. Since little is known about the nature of photoinhibition in desiccated lichens, we also aim at using the results to discuss mechanisms for photoinhibition in dry lichens.

Materials and methods

Ten branched thalli were collected in October 2003 from a rich *L. pulmonaria* population on stems of *Salix caprea* in old, open and mixed boreal forests with *Picea abies* in Østmarka (59°50'N 10°59'E), SE Norway. Collected lichens were air dried at room temperature at low light and stored at 4°C for 1 week before experiments started. Each thallus was then cut in two pieces at a major branching point, resulting in two similar lobes; mean dry weight, 100 mg; area, 9.7 cm² (Fig. 1). The ten pairs were randomly divided to two sets, five pairs in each. All lobes were slowly sprayed with deionized water and left on moist filter papers in darkness at room temperature for 24 h before pre-measurements of chlorophyll fluorescence parameters. Afterwards, the lobes desiccated at room temperature in darkness. The curled lobes desiccated without any hindrance, flattened samples desiccated between sheets of filter papers with a light pressure on top preventing curling.

Both sets were exposed to light (450 μmol m⁻² s⁻¹) in a ventilated growth cabinet at 13°C. This light is approximately 25% of maximal natural levels encountered in open habitats during clear summer days (Gauslaa and Solhaug 2000). Light was supplied by one mercury metal halide lamp (Osram Powerstar HQI-BT 400 W daylight; Osram, Norway). This lamp does not produce UV-B or UV-C (unpublished data). An aluminium foil with a hole was placed between the lamp and the samples, screening a substantial part of the diffuse, reflected light. This set up produced a fairly unidirectional and uniform light level at an area sufficiently large for mounting the lichens. Desiccated curled and flattened lichens were fastened by double-sided Scotch tape to a white styrofoam plate. A fan installed at 1 m distance avoided excessive heating by convectional cooling. The wind did not cause movements in the thalli. During the exposure, thallus temperature was recorded by six thermocouples placed in three curled and three flattened lobes. The exposure experiment was run twice, one set was exposed for 62 h of continuous exposure (high dose, HD), one for 12 h only (medium dose, MD). During the light exposures, the thallus temperature was 26.5°C. There were no significant temperature differences between the curled

Fig. 1 False colour images of chlorophyll fluorescence image data of curled (**a–d**) and flattened (**e–h**) *L. pulmonaria* thalli. **a, e** Photos of thalli; **b, f** F_V/F_M before light treatment; **c, g** F_V/F_M immediately after light treatment; **d, h** contour of thalli with marked places of analysis for Tables 1 and 2



and flattened lobes, or between the two dose experiments (two-way ANOVA; data not shown), meaning that the level of desiccation could not differ between the curled and flattened pair. No dark controls were

used because previous experiments have shown that *L. pulmonaria* can be kept desiccated for longer periods in the dark without adverse effects on F_V/F_M values (Gauslaa and Solhaug 1999).

After exposure, photos were taken of all lobe pairs to document the location and degree of curling. Then, lobes were hydrated with sprayings of deionized water, and chlorophyll fluorescence parameters were measured after 3, 5, 24, 48 and 72 h in the hydrated state in darkness at room temperature for those receiving the HD, and after 3, 5 and 24 h for those exposed to the MD.

Chlorophyll (Chl) fluorescence was measured with a portable kinetic chlorophyll fluorescence camera FluorCam HFC 010 (Photon System Instruments, Czech Republic) equipped with an imaging system (software FluorCam v. 5.0). The light source consisted of four panels, each with 42 super-bright orange light-emitting diodes (LEDs, $\lambda=620$ nm). The LEDs generated measuring light, actinic light and saturation pulses in order to induce background Chl fluorescence (F_0), variable Chl fluorescence on light-adapted sample (F_V) and maximum Chl fluorescence on dark- (F_M) and light-adapted sample ($F_{M'}$). Temporal variations in Chl fluorescence signals were detected by a CCD camera with F1/1.4 objective, and recorded as 512×512 pixel false colour images with maximum recording rate of 20 ms. The images showed the actual level of light-induced Chl fluorescence for each pixel, respectively. Measurements started with F_0 determination in dark-adapted thalli followed by F_M determination after the application of a pulse of high light ($1,100 \mu\text{mol m}^{-2} \text{s}^{-1}$). Then, after 10 s in darkness, $65 \mu\text{mol m}^{-2} \text{s}^{-1}$ was applied for 60 s to induce the Chl fluorescence to reach a steady-state (F_S). Finally, another pulse of saturating light was applied to reach the maximum Chl fluorescence in light-adapted lichen samples ($F_{M'}$). Quantum yield of photochemical reactions in photosystem II (PS II) was calculated using the equation: $\Phi_{\text{PS II}}=(F_{M'}-F_S)/F_{M'}$ (Genty et al. 1989). The kinetics of Chl fluorescence parameters during measurements were monitored by a fluorometric CCD camera at 50-ms intervals, and F_V/F_M and $\Phi_{\text{PS II}}$ were computed for each pixel. To analyse protective effects of curling, two approaches were used: The first exploited mean values of Chl fluorescence parameters for the whole lobe before photoinhibitory treatment and at specified occasions during dark recovery after the treatment (see above). The second approach assessed Chl fluorescence parameters for randomly selected subareas (10 mm in diameter) within each lobe (Fig. 1d, h). In naturally curled lobes, four subareas were taken within a single lobe. Two of them were located close to the tip where curling took place (denoted as 'shaded' in the following text), and the remaining two as not shaded and thus unprotected parts of the lobe (denoted as 'unshaded'). In flattened lobes prevented from curling (denoted as 'flattened'),

three sample areas were chosen for a single lobe. One area was located close to the tip where curling would occur under unrestricted drying, the other two areas in subtip and basal part, respectively. This second approach assessed the effect of shading on photochemical processes of photosynthesis at a lobe level by calculating means of chlorophyll fluorescence parameters for five replicates (lobes). For all approaches (Fig. 2, Tables 1, 2), measured variables did not differ between selected groups of thalli/areas and light treatments (HD/MD) prior to experiment ($P>0.05$; two-way ANOVA; data not shown), meaning that the dataset is well suited to detect differences due to treatment.

Finally, hydrated lobe area was measured with a leaf area meter (LI 3100 Licor, Lincoln, Neb., USA). Saturation weight was measured (± 1 mg) after blotting excess water from the samples with filter paper. Hydration led to flattening of lobes. The dry weight (± 0.1 mg) was measured after storing air-dry thalli in a desiccator at 20°C for 2 days. Studied lobes had a specific thallus weight of 110 g DM m^{-2} , and a water holding capacity of $152 \text{ g H}_2\text{O m}^{-2}$. There were no significant differences in these two parameters between curled and flattened lobes as well as between lobes selected for the two experiments (ANOVA, data not shown).

Results

Lobe ends and margins of *L. pulmonaria* thalli curled upwards during natural desiccation (Fig. 1a), shading the curled and adjacent parts during light exposure. Every time one specific lobe desiccated, it curled in a similar way, causing the same portions to be shaded. Young and apparently actively growing lobe tips were those that exhibited the strongest hygroscopic movements, old and mature lobe tips curled less, or did not curl (Fig. 1a). High light led to a strong inhibition of photochemical processes of photosynthesis (F_V/F_M) in flattened dry thalli (see Fig. 1g). In naturally curled thalli, areas shaded by curled lobes exhibited no reduction in F_V/F_M (Fig. 1c), whereas remaining not shaded parts showed a strong reduction in F_V/F_M . A reduction of F_V/F_M was also apparent in the curled tips, the lower cortex of which was oriented upwards during the exposition to light (Fig. 1a, c). Although curling produced distinct patterns of F_V/F_M in all studied thalli after light exposures, as in the illustrated lobe (Fig. 1c), there was some additional small-scale spatial heterogeneity in F_V/F_M related to the small-scale reticulated pattern with tiny ridges typical for *L. pulmonaria* (Fig. 1b, c, f, g).

Fig. 2 Time recovery of chlorophyll fluorescence parameters of curled (filled symbols) and flattened (open symbols) *L. pulmonaria* thalli averaged for whole lobe after exposure to 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 62 h (left) and for 12 h (right). Data are means \pm SE ($n=5$)

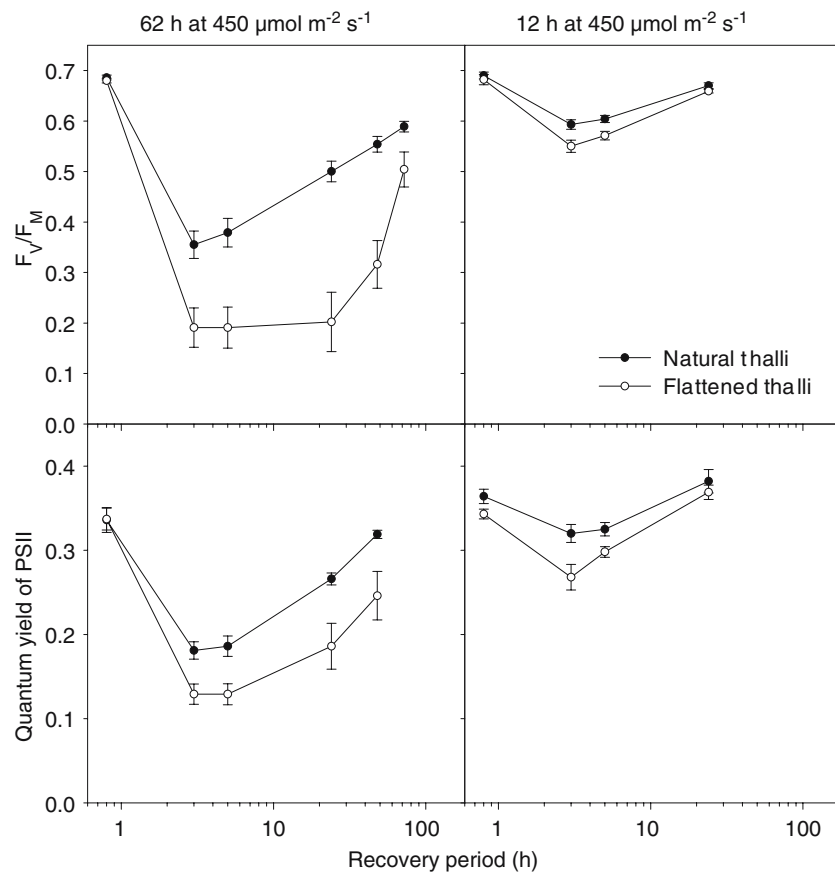


Table 1 Chlorophyll fluorescence parameters (means \pm SE; $n=5$) for curled *L. pulmonaria* thalli measured at shaded and unshaded thalli parts of *L. pulmonaria* thalli before and immediately after the HD and MD treatment

	High light dose treatment (HD) 62 h at 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$				Medium light dose treatment (MD) 12 h at 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$			
	Shaded parts		Unshaded parts		Shaded parts		Unshaded parts	
	Before HD	After HD	Before HD	After HD	Before MD	After MD	Before MD	After MD
F_v/F_M	0.681 \pm 0.005	0.621 \pm 0.003	0.689 \pm 0.002	0.149 \pm 0.008	0.693 \pm 0.008	0.672 \pm 0.008	0.688 \pm 0.010	0.531 \pm 0.014
Φ_{PSII}	0.353 \pm 0.020	0.299 \pm 0.020	0.339 \pm 0.021	0.115 \pm 0.002	0.382 \pm 0.015	0.377 \pm 0.015	0.349 \pm 0.017	0.285 \pm 0.018

There were highly significant effects of the HD treatment (before/after; $P < 0.0001$) and shade ($P < 0.0001$) on both variables (two-way ANOVA). Similar level of significance was also found in the MD treatment for F_v/F_M , but for Φ_{PSII} the effects were less significant ($P = 0.048$ for the before/after contrast; $P = 0.0014$ for the shade/unshade contrast; two-way ANOVA)

Natural curling significantly also reduced the photoinhibition in desiccated *L. pulmonaria* thalli when mean chlorophyll fluorescence parameters were averaged over the entire lobe (Fig. 2). Both curled and flattened thalli exposed to the MD recovered from photoinhibition within 24 h (Fig. 2). However, the photoinhibition after 3 and 5 h was significantly stronger in the flattened replicates. After the HD exposure, the curling-induced photoprotection was substantial (Fig. 2) with deeply depressed F_v/F_M values in flattened thalli (28% of initial, pre-treatment values) compared to the curled thalli (52%). F_v/F_M values of flattened thalli remained low for the first 24 h, but

some recovery occurred during the following days. After 72 h, the F_v/F_M values reached 74% of initial values. The curled thalli showed an earlier and faster recovery, reaching 85% after 72 h.

Shade provided by curling led to spatial variations in photoprotection within a thallus (Table 1). In curled parts of a HD-treated *L. pulmonaria* thallus, curling-induced shading caused only minor levels of photoinhibition (91.2 and 84.7% of initial F_v/F_M and Φ_{PSII} levels, respectively). In flat exposed parts of the same thalli, the HD treatment led to a dramatic decrease in F_v/F_M and Φ_{PSII} (21.6 and 33.9% of initial level, respectively). The MD treatment led to much less, but still highly

Table 2 Chlorophyll fluorescence parameters (means \pm SE; $n=5$) for flattened *L. pulmonaria* thalli measured at lobe tips, subtips and basal parts before and immediately after HD and MD treatment

	High light treatment (HD) 62 h at 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$		Low light treatment (MD) 12 h at 450 $\mu\text{mol m}^{-2} \text{s}^{-1}$	
	Before HD	After HD	Before MD	After MD
F_V/F_M				
Tip	0.679 \pm 0.006	0.131 \pm 0.027	0.655 \pm 0.006	0.525 \pm 0.010
Subtip	0.685 \pm 0.009	0.200 \pm 0.046	0.669 \pm 0.007	0.562 \pm 0.017
Basis	0.680 \pm 0.010	0.181 \pm 0.030	0.683 \pm 0.008	0.544 \pm 0.029
$\Phi_{PS II}$				
Tip	0.334 \pm 0.026	0.108 \pm 0.009	0.370 \pm 0.005	0.294 \pm 0.005
Subtip	0.341 \pm 0.018	0.133 \pm 0.014	0.342 \pm 0.011	0.288 \pm 0.014
Basis	0.320 \pm 0.016	0.126 \pm 0.009	0.322 \pm 0.007	0.277 \pm 0.016

Within each of the two light treatments, all variables differed before and after treatment ($P<0.0001$), whereas no significant effect of location was found ($P>0.05$; two-way ANOVA)

significant, decrease in F_V/F_M and $\Phi_{PS II}$ in unshaded areas (77.2 and 81.7% of initial level). Portions of MD thalli protected by curling exhibited insignificant photoinhibition measured as negligible reductions in F_V/F_M and $\Phi_{PS II}$.

Thalli artificially flattened prior to light exposure did not show any statistically significant ($P<0.05$) intrathalline heterogeneity in measured variables, neither prior to, nor after, the light treatment (Table 2; ANOVA, data not shown). The HD treatment reduced F_V/F_M and $\Phi_{PS II}$ to 25 and 37% of initial level, respectively, the MD treatment had also highly significant effect, but smaller depression of F_V/F_M .

Discussion

Chlorophyll fluorescence imaging shows that the desiccation-induced curling of *L. pulmonaria* prevents dry-state photoinhibition in areas adjacent to curled margins (Fig. 1). A photoprotective role of curling was indirectly inferred under field conditions in photos of *L. pulmonaria* transplanted to a sunny site, showing less visible bleaching in curled lobe tips than in flat, central parts (Gauslaa and Solhaug 2000). We believe that curling may contribute substantially to the photoprotection of some lichens, and may alter the overall photosynthetic activity, as shown by Lange et al. (1990) for some vagrant lichens curled under different modes of hydration. Since the photoprotection due to curling presumably increases with increasing light exposure (Fig. 2), its ecological significance should increase with increasing solar exposure in nature. At the same time, curling of foliose lichen species may have additional roles, like aiding the dispersal of soredia (Jahns et al. 1976), and enhancing the competitive power relative to neighbours (Hestmark 1997). We also believe that the small-scale reticulated ridges on the upper surface of

L. pulmonaria produce tiny, local patches of shade, evidenced by photos of patchy chlorophyll degradation in the field (Gauslaa and Solhaug 2000). Both curling and the reticulated pattern (Fig. 1) may function to increase the area of surviving patches during severe high light stress after logging, allowing regeneration lobules to be formed after later acclimation (Gauslaa et al. 2006) and subsequent growth of trees. Additionally, thalli in nature are shaded by neighbouring, partly overlapping thalli.

Several laboratory- and field-based studies of lichen photosynthesis show that photoinhibition can occur in wet or partly hydrated lichens (Demmig-Adams et al. 1990b; Valladares et al. 1995; Barták et al. 2003). The photoinhibition in dry lichen tissue (Figs. 1, 2) suggests that the photoprotection in dry lichen tissue is not merely a result of dehydration-induced inactivation of physiological processes of photobiont (Bilger et al. 1989) and increased reflectance from the cortex (Solheim et al. 2000). Our experimental design and the strictly controlled climatic conditions during the experiment eliminated or minimized effects of spatial variations in thallus temperature causing a uniform desiccation level. The photoinhibitory limitation of primary photosynthetic processes (Fig. 2, Table 1) actually also takes place in desiccated thalli. A high susceptibility to photoinhibition clearly sustains even in fully desiccated *L. pulmonaria* exposed to high light. Demmig-Adams et al. (1990b) showed that hydrated foliose green algal lichens stressed by high light had slower recovery than desiccated replicates. The difference was attributed to less adverse effects to a dry photosynthetic apparatus. Gauslaa and Solhaug (1996) reported permanent and severe reductions in F_V/F_M in some old forest lichens subjected to light stress in the air-dry state, and Gauslaa and Solhaug (2004) suggested that lichens differ with respect to the hydration state in which they are most susceptible.

The HD treatment of dried *L. pulmonaria* led to a significantly deeper decrease in F_v/F_M and $\Phi_{PS II}$ than the MD treatment. However, even the MD induced detectable decreases in F_v/F_M and $\Phi_{PS II}$ of dry and flattened *L. pulmonaria* thalli, opposing current views assuming a high stability of the photosynthetic apparatus in desiccated green algal lichens. Apparently, our results suggest that the structure (and function after rehydration) of pigment–protein complexes of thylakoid membrane can be adversely affected by light in the desiccated and inactive state of a lichen photobiont. However, the molecular mechanisms are unknown. The capacity to quench excitation energy in the PS II of hydrated lichens is presumably high. In drying lichens, however, several mechanisms might cause a gradual loss of photosynthetic activity and increased photoprotection. The excitation of PS II by light in dry lichens does not lead to any destruction of PS II (Heber et al. 2001). These authors suggest that substantially increased energy dissipation takes place in drying and/or dry poikilohydric organisms due to a strong quenching of chlorophyll fluorescence. Strong quenchers in plants, like oxidized carotene and reduced chlorophyll in PS II, are not main mechanisms for quenching excitation energy in PS II of drying lichens (Shuvalov and Heber 2003). This paper suggests auxiliary roles of these mechanisms in photoprotection of drying poikilohydric organisms. The energy dissipation in PS II of drying lichen thalli is not related to protonation and zeaxanthin availability, but rather to the oxidized core of photosystem I (PS I), which seems to be a strong quencher of chlorophyll fluorescence (Heber et al. 2000). Bukhov et al. (2004) pointed out permanent irreversible oxidation of PS I in dry lichen thalli exposed to continuous irradiation. The capacity of this mechanism is considered to be sufficient for an effective photoprotection in dry poikilohydric organisms. However, our results indicate photoinhibition of primary photosynthetic processes in PS II in desiccated *L. pulmonaria* exposed to light. Therefore, the capacity of oxidized PS I is not necessarily sufficient.

F_0/F_M was significantly higher after light exposure (data not shown), indicative of PS II inactivation. However, curling reduced the increase in F_0/F_M . An increase in F_0/F_M is attributed to high light-induced changes in light harvesting complexes and PS II centres. F_0 remained constant after light treatments (data not shown). Therefore, the increase in F_0/F_M was caused by F_M decrease. This suggests that inhibition of photochemical processes in high light exposed dry *L. pulmonaria* is induced rather in PS II centres than in light harvesting complexes. This corresponds to previ-

ous observations of species-specific responses of F_0 to high light (Barták et al. 2000).

In conclusion, photoinhibitory damage can take place in desiccated tissues of some lichens during high light exposures. Natural curling is one strategy to reduce the chance for serious photoinhibition in desiccated *L. pulmonaria* thalli.

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