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The significance of thallus size for the water economy of the cyanobacterial old-forest lichen *Degelia plumbea*

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Abstract Rosette-formed, circular thalli of *Degelia plumbea* were studied in the laboratory. Regardless of thallus size, the optimal quantum yield of photosystem II (F_V/F_M) remained at a high, constant level during a drying cycle starting with fully hydrated thalli until the thallus water content reached about 200%. Net photosynthesis reached a maximum level at this hydration level. Thereafter, both F_V/F_M and net photosynthesis fell rapidly to zero at a water content of somewhat less than 100%. There was a highly significant, positive relationship between thallus size and the water-holding capacity, as well as a strong, negative correlation between size and water loss per thallus area. Consequently, an increase in thallus size from 1 to 36 cm² lead to a tenfold prolongation of the photosynthetically active period during a drying cycle at a low radiation regime. The improved water-holding capacity in larger thalli is mainly a result of a thicker hypothallus. The fast desiccation of small thalli suggests that the regeneration of *D. plumbea* could be severely hampered by nearby logging that raises the evaporative demand by increasing radiation loads and wind exposure at remaining lichen sites.

Key words Epiphytic lichens · Hypothallus · Photosynthesis · Water loss · Water-holding capacity

Introduction

The importance of size within a single species is a frequently neglected parameter in physiological and ecological studies, although its significance has clearly been recognised for the water economy of vascular plants (Donovan and Ehleringer 1992; de Soyza et al. 1996),

photosynthetic capacity (Zotz 1997) and for the partitioning of resources to reproduction (Shiple and Dion 1992; Totland and Birks 1996; Worley and Harder 1996). Very few studies have focused on size-dependent physiological processes in lichens (Larson 1979, 1984; Hestmark et al. 1997). Small thalli have a low boundary layer resistance which may cause a high water loss rate (Hoffman and Gates 1970; Green et al. 1985); small thalli may also have a low water-holding capacity (Degelius 1935). Unlike most vascular plants with deep roots and mycorrhizal symbionts, lichens are unable to utilise a vast soil water reservoir. Their growth is therefore dependent on highly temporal incidents with humid air and/or rain. Consequently, the growth rate, especially of small thalli, may be reduced by changed environmental factors reducing the frequency and duration of hydration events.

Logging influences dramatically epiphytic lichen communities of old-growth forests in various ways (James et al. 1977; McCune 1993). Logging which normally forms larger openings than natural gap dynamic processes increases the radiation load abruptly along edges, and reduces the boundary layer by increasing wind exposure, causing an elevated evaporative demand of remaining moist surfaces. Small specimens of lichen species with size-dependent moisture reserves and/or rates of water loss may be more adversely affected by various types of logging than large and well-established thalli of the same species.

Degelia plumbea (Light.) P.M. Jørg. & P. James, a cyanobacterial foliose member of the Pannariaceae with *Nostoc* as the photobiont (Jørgensen and James 1990), is considered to be an old-forest lichen (Rose 1976, 1992) reported to be sensitive to various forestry operations (Degelius 1935; Sérusiaux 1989; Aronsson et al. 1995; Hultengren and Nordén 1996). It is a predominantly European lichen with its largest intact populations in north-west Britain and west Norway (Degelius 1935; Jørgensen 1978; Jørgensen and James 1990) characterised by an oceanic climate. Large thalli seem to have higher survival after logging than small thalli, especially

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when growing on naked bark without a continuous cover of bryophytes (Y. Gauslaa, personal observation). *D. plumbea* (Demmig-Adams et al. 1990) and other commonly co-occurring lichens within the old-growth-forest lichen-dominated epiphytic community *Lobarion* (see Barkman 1958; Rose 1988) have already been documented to be intolerant to high light. Even dry thalli of such lichens can be highly susceptible to high light (Gauslaa and Solhaug 1996), and thalli impaired by reduced frequency and duration of hydration incidents for recovery might be especially vulnerable. On the other hand, the distribution of *D. plumbea* may additionally or alternatively be limited by other factors such as dispersal or availability of appropriate substrates.

Some lichens have a thick and conspicuous hypothallus, in *D. plumbea* consisting of a very dense and thick felt of rhizines protruding along the margins. The ecological significance of a hypothallus is not well studied. Assumed roles are to improve the water economy by acting as a sponge accumulating water during rainy periods (Goebel 1926; Hannemann 1973), and to slowly supply photosynthetically active parts of the thallus with water during a subsequent drying cycle (Degelius 1935). Organising a thallus in a way that separates the water reservoir from the photosynthetically active sites could potentially be a strategy to overcome the photosynthetic depression at suprasaturation water contents that has frequently been reported in lichens (e.g. Lange et al. 1993, 1995, 1996; Lange and Green 1996).

A main objective is to study and quantify the size dependency of water-holding capacity and water loss rates in *D. plumbea*. For a poikilohydric lichen, these two factors have a dominant influence upon the duration of the photosynthetically active period. The size-dependent duration of this period will be assessed, emphasis will be put on a physical interpretation of underlying causes, and implications for survival will be discussed. A second objective is to measure the CO₂ exchange rate in relation to thallus water content, since we have not seen such data, neither for *D. plumbea* nor for other species with such a thick, dense and protruding hypothallus.

Material and methods

Plant material, storage and preconditioning

Whole *D. plumbea* thalli were collected from various deciduous trees in Åfjord, Sør-Trøndelag, central Norway, NR 6075 (UTM grid) on 3 June 1996. The thalli were air-dried at room temperature and stored in a fridge (6–7°C) for 1 week before measuring chlorophyll fluorescence. CO₂ exchange was measured in thalli stored for 12 months in a freezer (–20°C), a storage that did not affect chlorophyll fluorescence. Before all measurements, thalli were slowly moistened by repeated sprayings with distilled water for about 10 min, and kept hydrated for 3 days at 16–17°C by regular sprayings with distilled water, a preconditioning eliminating most of the remaining photoinhibition from the field (Gauslaa and Solhaug 1996). Thalli used for chlorophyll fluorescence measure-

ments were preconditioned at 20 µmol photons m⁻² s⁻¹, thalli used for CO₂ exchange rate measurements were preconditioned at either 100 or 430 µmol photons m⁻² s⁻¹. The 21 thalli selected for studying size-dependent responses were the most intact and most circular rosette-formed specimens. Thalli larger than the largest selected were frequent, but these were excluded because of eroded or missing portions in the centre or along the periphery.

Chlorophyll *a* fluorescence

Chlorophyll *a* induction curves were recorded with a portable fluorimeter (Plant Efficiency Analyser, Hansatech) during a drying cycle starting with fully hydrated thalli. Fluorescence induction curves of 5 s duration were recorded on each thallus during exposure to a photon flux density of about 1500 µmol photons m⁻² s⁻¹. Twenty-one whole, more or less circular thalli ranging in size from 1 to 36 cm² were simultaneously measured while drying at 17°C, 50% relative humidity, and 2 µmol photons m⁻² s⁻¹. Each thallus was weighed (±1 mg), and F_V/F_M was subsequently measured at two randomly selected positions (see below) of the thallus surface without dark adaptation, and the mean value was treated as one observation. The number of replicate measurements was a compromise between the need for many data points to cover the surface representatively, and the need to measure 21 thalli simultaneously with short time intervals. Two measurements of 21 samples took approximately 20 min. Measurements continued until F_V/F_M could no longer be measured (i.e. $F_V/F_M < 0.02$) in two subsequent recording intervals. After F_V/F_M had started to decline, one of the two measurements was always made in the most moist part of the thallus. However, F_V/F_M declined more homogeneously across the thallus than was demonstrated in the crustose *Buellia frigida* (Schroeter et al. 1992). Apart from the short periods of handling, thalli were lying in a horizontal position on the table.

Weight and size parameters

Area was measured in the hydrated state with a Licor Leaf Area Meter (LI 3100). The saturation weight was measured to the nearest milligram by spraying preconditioned hydrated thalli with distilled water until they became dripping wet, excess water being removed by gentle shaking. The oven-dry (80°C) weight was measured (±0.1 mg) after the end of the experiment. The specific thallus weight represents mg oven-dried weight cm⁻². The water-holding capacity in mg H₂O cm⁻² comprises the difference between the water-saturated weight cm⁻² and specific thallus weight.

Thallus and hypothallus thickness were measured by moistening the oven-dried lichens. A 2 to 3-mm-broad cross-section through the thallus passing the centre was cut and examined at ×20 under a dissecting microscope. The thickness was measured to the nearest 0.025 mm at a minimum of seven positions regularly located along the whole section, and the mean value was treated as one observation.

CO₂ exchange

Photosynthesis was measured during a drying cycle with a Ciras 1 portable photosynthesis system (PP Systems) at 350 ppm CO₂, 40% relative humidity, 21°C, and a photon flux density of 430 µmol photons m⁻² s⁻¹ (halogen lamp) which was near the saturation level. All six measured thalli had an intermediate size of 8.4–14 cm². Before measurements, thalli were stored at 100 µmol photons m⁻² s⁻¹, then put within the cuvette that was enclosed in aluminium foil in order to measure dark respiration. Immediately afterwards, the aluminium foil was removed for measuring photosynthesis; thereafter, the lichen was removed from the cuvette and transferred to 100 µmol photons m⁻² s⁻¹ to slow down the water loss rate. Photosynthesis was additionally

measured in four similar-sized thalli that were stored at $430 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ before and between measurements while drying.

Results

Net photosynthesis was clearly depressed at suprasaturation water contents; it was always positive, but close to zero at water saturation (700%). During a drying cycle at $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, photosynthesis increased until a maximum was reached at a thallus water content of around 200% (Fig. 1). Further desiccation resulted in a rapid decline in CO_2 uptake which ceased completely at a thallus water content of approximately 100%. Dark

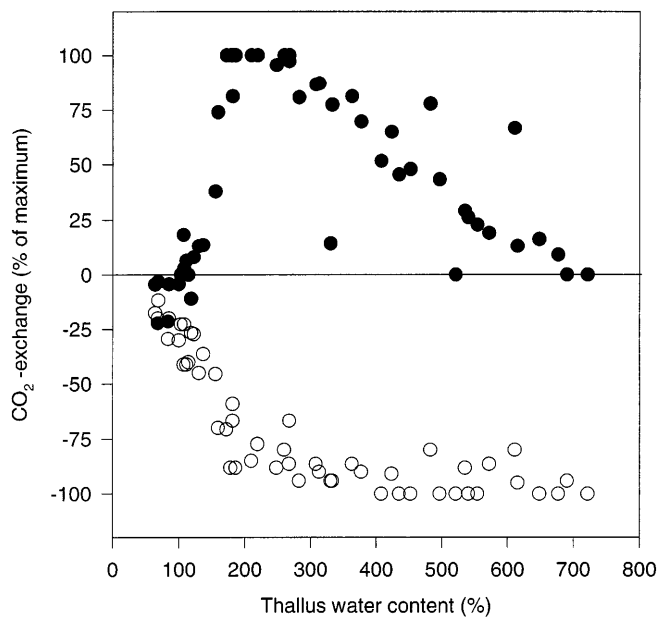


Fig. 1 Net photosynthesis and dark respiration as percent of maximum values in six medium-sized *Degelia plumbea* thalli as a function of thallus water content. Measurements were made during desiccation cycles starting with fully hydrated thalli, at $430 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 21°C and a relative humidity of 40% (see Table 1 for thallus size and weight). Mean maximum net photosynthesis: $2.27 \pm 0.42 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$, mean maximum respiration: $1.80 \pm 0.09 \mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$

Table 1 Water loss rate, length of the photosynthetically active period, and maximum net photosynthesis (*NP*) (mean \pm standard errors of means) during drying cycles made under three contrasting light regimes. Environmental conditions were: $2 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, relative humidity 50%, air temperature 17°C ; 100 and $430 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, relative humidity 40%, air temperature 21°C . Photosynthesis was measured at $430 \mu\text{mol pho}$

Light treatment ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	2	100	430
Number of thalli	10	6	4
Thallus area (cm^2)	11.4 ± 1.0	10.9 ± 0.9	12.6 ± 0.9
Dry weight (g)	0.369 ± 0.054	0.439 ± 0.086	0.567 ± 0.049
Water loss ($\text{g m}^{-2} \text{s}^{-1}$) when $\text{NP} > 0$	0.028 ± 0.001	0.082 ± 0.005	0.157 ± 0.019
Length of photosynthetically active period (h)	15.3 ± 1.7	7.4 ± 0.8	2.6 ± 0.2
Maximum NP ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{s}^{-1}$)	–	2.27 ± 0.42	2.08 ± 0.45

respiration remained at a fairly constant and high level during a drying cycle until it started declining near the peak in net photosynthesis (Fig. 1). Thalli dried faster at 430 compared to $100 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, causing a reduction of the photosynthetically active period in medium-sized thalli from 7.4 to 2.6 h. However, neither the maximum net photosynthesis (Table 1), nor the shape of the water content response curve (data not shown) were changed.

The optimal quantum yield of photosystem II (F_V/F_M) did not show any depression at suprasaturation water contents (Fig. 2). However, like net photosynthesis, F_V/F_M declined rapidly at a water content below 200%. Since measurements of F_V/F_M are much faster and simpler than of photosynthesis, the chlorophyll

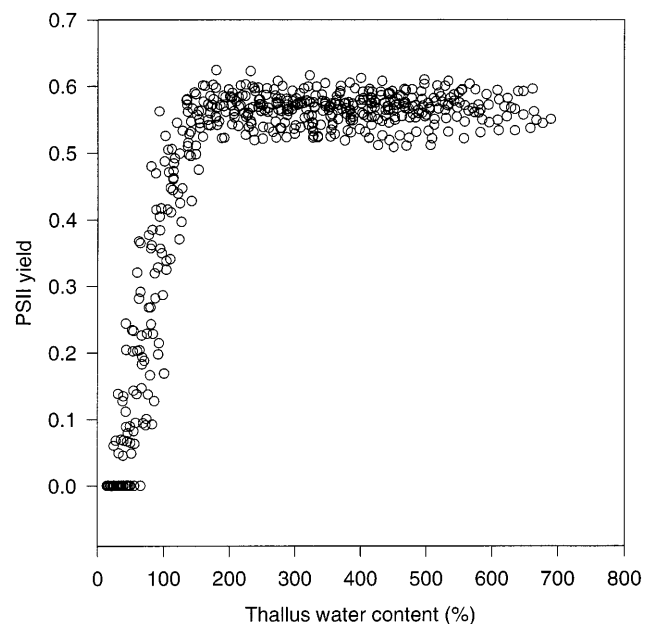


Fig. 2 The relationship between the optimal quantum yield of photosystem II (F_V/F_M) and the thallus water content during a drying cycle starting with fully hydrated thalli of *D. plumbea*. Measurements were made at $2 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, 17°C and a relative humidity of about 50%. Values for all measured thalli ($n = 21$) ranging in size from 1 to 36 cm^2 (Table 2) were included

$\text{tons m}^{-2} \text{s}^{-1}$ in the two highest light treatments, but thalli were preconditioned and stored between each measurement at 100 and $430 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively. In the low light treatment the data of medium-sized thalli in the main experiment measuring F_V/F_M were used, conforming to the size of thalli used for measurements of photosynthesis

Table 2 Thallus characteristics of the 21 studied *Degelia plumbea* thalli. *Specific thallus weight* represents oven-dry weight (80°C) per thallus area, *water-holding capacity* represents amounts of water per thallus area in soaking wet thalli after gentle shaking. *Water loss* per thallus area refers to the linear water loss phase under the experimental conditions. The duration of the photosystem II (*PSII*) *active period* refers to the period with measurable values of F_V/F_M . *Water content* refers to (1) saturation after gentle shaking and (2) the stage when F_V/F_M is no longer measurable. **Asterisked values* are extrapolated data (linear regression) due to missing data

Thallus no.	Thallus area (cm ²)	Thickness		Specific thallus weight (g dry mass m ⁻²)	Water-holding capacity (g H ₂ O m ⁻²)	F_V/F_M maximum value	Water loss *10 ⁻² (g m ⁻² s ⁻¹)	PSII active period $F_V/F_M > 0$ (h)	Thallus water content	
		Thallus (mm)	Hypothallus (mm)						Saturation (%)	$F_V/F_M = 0$ (%)
1	36.4	0.20	3.58	522	3574	0.598	2.18	41.1	685	45
2	21.6	0.20	2.85	476	2423	0.597	2.18	30.0*	509	35*
3	20.0	0.20	3.59	397	2738	0.596	2.38	30.2*	689	53*
4	16.4	0.20	3.82	442	2360	0.623	2.47	24.0	534	50
5	16.0	0.20	2.45	354	2056	0.624	2.53	20.4	581	55
6	14.4	0.17	1.40	254	1229	0.520	2.52	12.5	484	33
7	11.7	0.17	4.26	384	2541	0.616	2.72	24.0	662	49
8	10.2	0.17	2.08	361	1746	0.585	3.20	13.1	483	65
9	9.6	0.20	1.34	312	1439	0.592	2.83	12.6	461	33
10	9.6	0.15	2.92	257	1479	0.605	3.02	12.6	575	43
11	8.8	0.15	1.77	203	916	0.543	2.83	8.5	451	23
12	8.5	0.22	1.04	214	1304	0.536	3.17	10.8	610	25
13	8.3	0.20	2.28	365	1615	0.580	3.03	14.0	442	35
14	6.7	0.17	2.24	283	1549	0.575	3.35	11.6	547	36
15	5.6	0.20	1.54	258	1369	0.581	3.92	9.0	531	39
16	5.5	0.20	1.79	284	1437	0.569	3.47	11.0	505	23
17	3.9	0.20	0.91	176	763	0.536	3.55	6.0	433	15
18	3.5	0.17	1.19	366	1310	0.553	4.05	8.3	357	21
19	3.3	0.15	1.21	176	854	0.560	4.08	5.5	485	26
20	1.9	0.25	0.42	147	552	0.543	4.62	3.5	376	25
21	1.1	0.17	1.16	141	712	0.533	6.28	3.0	504	23
Mean		0.19	2.09	304	1617	0.575	3.26	14.8	519	36

fluorescence technique was applied for studying size-dependent responses during drying cycles.

The maximum F_V/F_M value varied between individual thalli from 0.520 to 0.624, (mean 0.575, Table 2), which represents a typical range for healthy cyanobacterial lichens (Demmig-Adams et al. 1990; Sundberg et al. 1997). A positive correlation ($r = 0.763$, $P < 0.001$) was found between F_V/F_M and the thickness of the hypothallus (Table 3). Nevertheless, all thalli showed a similar response of F_V/F_M against water content (Fig. 2), regardless of size or hypothallus thickness.

The thallus remained thin (0.19 mm) and of fairly constant thickness throughout the studied size range (Table 2), with no significant correlation to any of the measured variables (Table 3). The thickness of the hypothallus (mean 2.09 mm) increased considerably, the thickest hypothallus (4.26 mm) being ten times thicker than the thinnest (Table 2). Large thalli often incorporated more than one dead and decaying layer of overgrown thallus within the hypothallus. The lower parts of the hypothallus had also engulfed tree bark fragments, and deeply penetrated bark crevices and decaying layers of the tree-bark, especially under large thalli. However, in order to measure water-holding capacity and specific thallus weight, the hypothallus was cut at the lower continuous section, and deeper layers with fragmented hypothallus in bark fissures were removed. The measured part of the hypothallus averaged 91% of the total measured thallus thickness (total range: 40–96%).

Area-related water-holding capacity (Table 2) was closely correlated to hypothallus thickness, and was therefore also strongly size dependent ($r = 0.896$, $P < 0.001$, Table 3). Accordingly, measured thalli showed highly contrasting time courses of photosystem II activity during drying cycles (Fig. 3). F_V/F_M of small thalli decreased more suddenly than of larger thalli. The thallus with the smallest water-holding capacity remained photosynthetically active for only 3 h, while the one with the largest capacity was active for 41 h under the experimental conditions (Table 2, Fig. 4). Increasing the photon flux density from 2 to 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ reduced the length of the photosynthetically active period from 15.3 to 7.4 h in medium-sized specimens (Table 1). Small thalli dried more evenly over the whole surface than large thalli maintaining moist patches at a stage when margins became visually partly desiccated, visualised by the jagged curves in late desiccation stages for some specimens in Fig. 3. Photosynthesis terminated completely at about the stage when the thallus colour changed markedly from dark brown to light grey. F_V/F_M started to decline before any changes in thallus colour could be seen.

Both thallus size and hypothallus thickness gave significant contributions ($P > 0.001$) as predicting variables for the water-holding capacity in a multiple regression analysis ($r = 0.961$). Thallus area, weight, thickness of the hypothallus, water-holding capacity and the duration of the photosynthetically active period were highly intercorrelated, while no significant correlations

Table 3 Pearson correlation matrix with correlation coefficient (lower part) and level of significance (upper part) ($n = 21$, original data in Table 2)

	DW	SW	Area	Thickness		WHC	Time	% H ₂ O	$F_V/F_M = 0$		WLR
				Thallus	Hypothallus				Saturation	F_V/F_M	
Dry weight (DW)	1										
Saturation weight (SW)	0.992	1									
Thallus area	0.977	0.965	1								
Thallus thickness	0.167	0.167	0.124	1							
Hypothallus thickness	0.682	0.673	0.698	-0.150	1						
% dry matter (DM)	-0.549	-0.584	-0.610	0.061	-0.705	1					
Specific thallus weight (STW)	0.826	0.783	0.803	0.093	0.778	-0.402	1				
Water-holding capacity (WHC)	0.902	0.896	0.896	0.102	0.875	-0.691	0.920	1			
Time to reach $F_V/F_M = 0$	0.947	0.934	0.949	0.150	0.836	-0.660	0.891	0.977	1		
% water at saturation	0.593	0.639	0.643	-0.014	0.724	-0.984	0.441	0.737	0.705	1	
% water at $F_V/F_M = 0$	0.496	0.481	0.546	-0.052	0.713	-0.577	0.625	0.686	0.607	0.570	1
Maximum F_V/F_M	0.513	0.491	0.525	0.073	0.763	-0.526	0.650	0.693	0.639	0.744	0.744
Water loss rate (WLR)	-0.628	-0.589	-0.740	-0.044	-0.629	0.503	-0.678	-0.698	-0.727	-0.564	-0.564

*** $P < 0.01$; **** $P < 0.001$; ns not significant

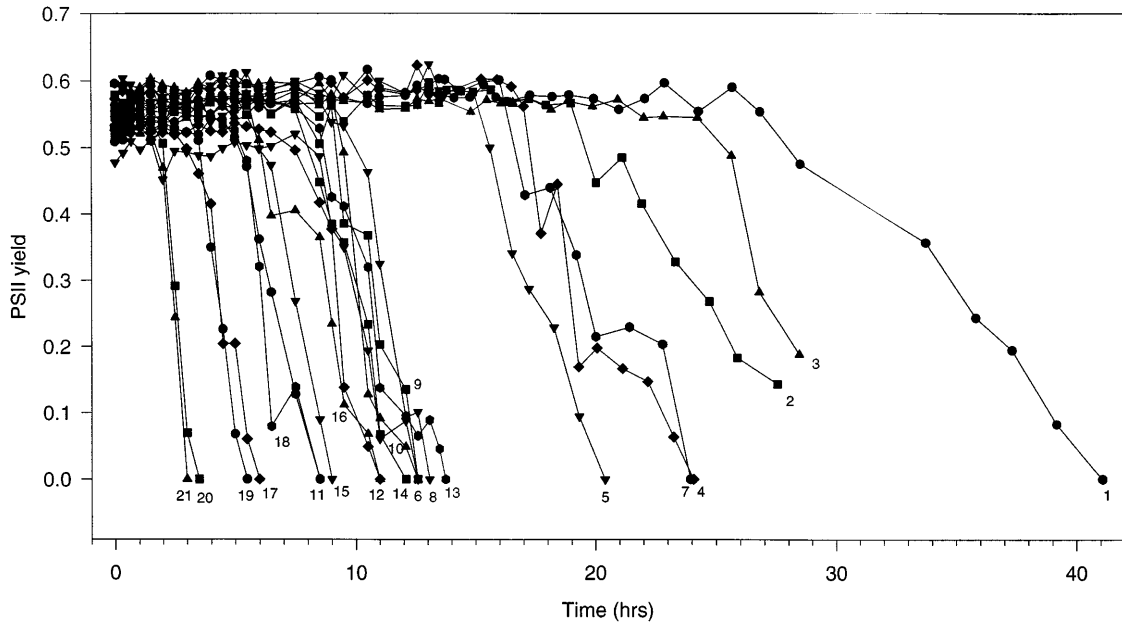


Fig. 3 Time course of the optimal quantum yield of photosystem II (F_V/F_M) during drying cycles in *D. plumbea*, based on the same dataset shown in Fig. 2. Symbols connected by one line represent one individual specimen, and specimens are ranked in order of increasing size. Numbers refer to thallus number in Table 2 where size and other relevant variables are specified

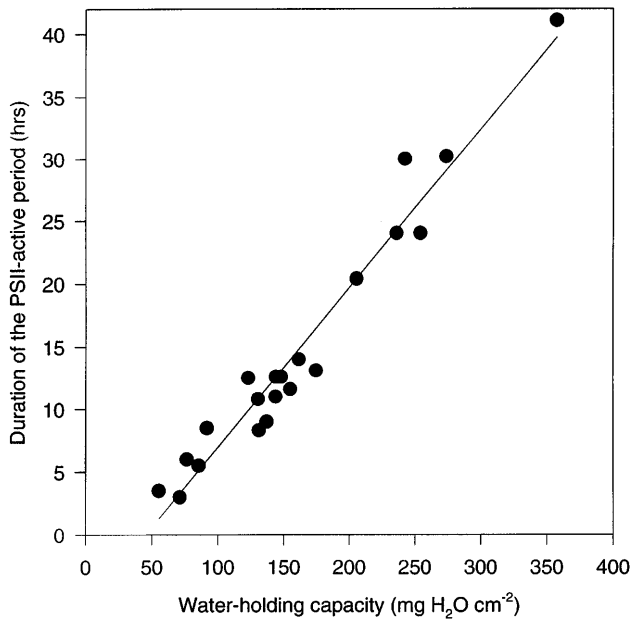


Fig. 4 The relationship between water-holding capacity and the length of the PSII-active period in *D. plumbea*. The line represents the linear regression, $r = 0.977$. All thalli were measured simultaneously under the environmental conditions specified in Fig. 2

were found between thallus size and thickness of the thallus and the threshold level of water content for photosystem II activity (Table 3).

Regardless of size, each thallus maintained its own specific water loss rate that was fairly constant over time

throughout the photosynthetically active range of the drying cycle (data not shown). Therefore, the water loss rate at the hydration level when F_V/F_M reached zero was still substantial. The water loss per thallus area was calculated in this linear phase for each thallus separately (Table 2), and a very close negative relationship was found between thallus size and water loss per thallus area in a log-log plot ($r = -0.971$; Fig. 5). Consequently, a high water loss rate per area in a low-radiation regime is associated with a small thallus size, and therefore also with a low water-holding capacity (Table 3).

Discussion

The length of the photosynthetically active period during a drying cycle increases considerably with increasing thallus size in *D. plumbea*. A similar size dependency of drying events has previously been demonstrated for some umbilicate lichens (Larson 1984; Hestmark et al. 1997) and for a globose crustose lichen (Pérez 1997), but by no means represents a universal pattern among the lichens (Larson 1984). The short photosynthetically active period in a small and young *D. plumbea* thallus is not only a result of a low available water reservoir per area, but also of a distinctly higher water loss per area compared to larger thalli. In *D. plumbea*, as well as in the cyanobacterial *Lobaria scrobiculata* (Y. Gauslaa, unpublished data), the photosynthetically active period corresponds to the duration of hydration levels causing a black-brown colour of the thallus. Hardly any photosystem II activity is left at the desiccation stage coincident with a sudden and distinct lightening of the upper surface. This seems to be in contrast with the situation in studied *Umbilicaria* species where the lightening in thallus colour has been observed to fall within the

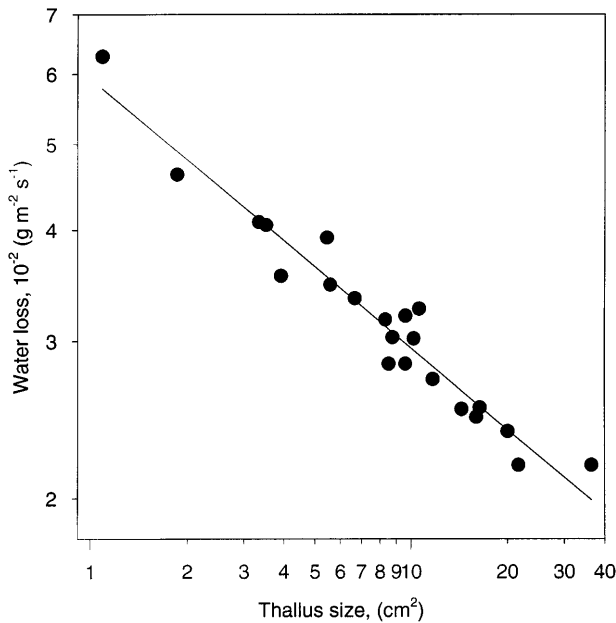


Fig. 5 Relationship between thallus size of *D. plumbea* and water loss rate per thallus area (log-log plot) during the linear water loss phase that comprised the whole photosynthetically active period during the drying cycle. The line represents the linear regression, $r = -0.971$. All thalli were measured simultaneously under the environmental conditions specified in Fig. 2

optimum water content for photosynthesis, i.e. 100–150% (Sancho and Kappen 1989; Sancho et al. 1994).

Some lichens show a very low resistance to evaporative water loss at water contents equal to or higher than those for optimal photosynthesis (Harris 1976; Green and Snelgar 1982). A very low thallus resistance implies that the thickness of the boundary layer plays an important regulatory role for the water loss rate (Gates 1980). The boundary layer resistance increases with size (Gates 1980). Therefore, the high water loss rates in small *D. plumbea* thalli are probably mainly a result of small boundary layer resistance. One could argue that the boundary layer resistance of a foliose lichen thallus attached to a larger surface of bark or rock is less important than that of the bark surface itself. A prostrate lichen thallus could be considered to be a physically integrated part of its substratum. This might be the case when a thallus grows on top of a closed canopy of bryophytes and other lichens with similar water-holding capacities. However, *D. plumbea* has a higher water-holding capacity than associated species (Degelius 1935), and is reported to be frequent directly on naked bark or rock (Degelius 1935; Jørgensen 1978) which dries much faster.

A considerable portion of the thallus water in fully hydrated *D. plumbea* seems to be surface water or capillary-held liquid water within the thick hypothallus felt, visible in a dissecting microscope as a thick, free water film around the hypothallus. In general, extracellular water does not seem to exist in the intercellular spaces of a water-saturated lichen thallus (Honegger et al. 1996;

Scheidegger et al. 1997). The hypothallus of *D. plumbea* forms an exception, like the spongy hypothallus of *Anzia* (Scheidegger et al. 1997). The strong correlation between water-holding capacity and hypothallus thickness (Table 3), as well as the contrasting scales in which thallus and hypothallus thickness were measured (Table 2), are further indications that the hypothallus felt is the most important thallus structure for the water retention capacity in *D. plumbea*, not a prosoplectenchymatic medullae as in some *Umbilicaria* species (Sancho and Kappen 1989). A high water loss rate, and therefore a low thallus resistance, prevails throughout the photosynthetically active thallus water range in *D. plumbea*. Highly contrasting water loss kinetics have been documented in *Parmelia saxatilis* (Jahns 1984). A high water loss rate even during later stages of a drying cycle (50% water content) could hardly be possible without an efficient translocation of water within the hypothallus felt. This results in smaller spatial variations in water content across a thallus, and hence of F_V/F_M , than has been reported during drying cycles in the crustose lichen *Buellia frigida* (Schroeter et al. 1992).

Although increased radiation increases the water loss rate (Table 1), the duration of a drying cycle for *D. plumbea* in the field under a clear sky has been reported to be long-lasting, considerably longer compared to those of other co-occurring species (Degelius 1935). Drying cycles might operate on another time-scale in lichen species with a smaller water-holding capacity. Nevertheless, the more rapid growth reported in large compared to small thalli of other foliose old-growth forest lichens (Rhoades 1977; Scheidegger et al. 1995) could possibly be influenced by similar size-dependent drying events.

Forestry manipulations suddenly raising the radiation, and thereby increasing the evaporative demands of remaining thalli (Degelius 1935, pp. 245–251), might shorten the hydration events and the duration of productive periods. Reported size-dependent water relations suggest that the duration of transient hydration events in *D. plumbea* are progressively reduced with decreasing thallus size. Logging might therefore be more detrimental to small specimens, and size-dependent drying characteristics could be one reason why a higher survival of large thalli is observed under certain circumstances. Adult stages of some commonly co-occurring old-forest lichens could be successfully transplanted in sites where juvenile thalli disappeared very quickly (Scheidegger et al. 1995). Further, for the high-light-susceptible *D. plumbea* (Demmig-Adams et al. 1990), the photoinhibition caused by partial canopy removal can possibly be more severe for smooth, thin and small thalli compared to large and thick thalli with more irregular upper surfaces. Degelius (1935, p. 294) observed that all sun-exposed specimens of *D. plumbea* died after logging in a previously rich locality. Mechanisms to repair high-light damage are only activated during periods of hydration, while both hydrated and desiccated old-forest lichens

can be damaged (Gauslaa and Solhaug 1996). Therefore, partial canopy clearings in a locality with optimal light conditions for *D. plumbea* probably result in hydration events that are too short to allow satisfactory growth and to restore high-light damage, especially in small thalli. Regeneration of new thalli could, therefore, be further hampered.

D. plumbea, like other cyanobacterial lichens, needs to be moistened with liquid water to restore normal photosynthesis (Lange et al. 1986). Unlike green-algal lichens, moist air alone could do nothing but reduce the water loss rate for *D. plumbea* and, hence, lengthen the photosynthetically active period subsequent to rainfall. A strong dependency of liquid water for restoring normal photosynthesis presumably implies a strong evolutionary selection for some adaptations to reduce this dependency. The hypothallus of *D. plumbea* exerts a dominant influence on the water-holding capacity, and hence the duration of physiologically active periods. Acting like a substantial water reservoir, a hypothallus possibly reduces the dependency on frequent wetting incidences, especially when growing in open-shade habitats sensu Stoutjesdijk (1974) with low evaporative demands. The importance of the hypothallus in the field is probably larger than indicated by the measured water-holding capacity, as there are additional hyphae penetrating decaying layers of the tree bark. Therefore, a larger water reservoir than that maintained by the studied detached specimen is available. *D. plumbea* thalli are often observed to be moist in situ even several days after the last rainfall (Y. Gauslaa, personal observation), and the species seems to be able to inhabit drier sites than other *Degelia* species (Jørgensen and James 1990). The hypothallus of other members of the Pannariaceae and the dense tomental hairs in many cyanobacterial lichens probably have a similar function. The thicker tomentum and rhizine felt of sun populations compared to shade populations of *Pseudocyphellaria dissimilis* has been shown to store larger amounts of water (Snelgar and Green 1981).

The spatial segregation of a photobiont-free water-holding hypothallus and a photosynthetically active thallus in *D. plumbea* is not an efficient arrangement for removing photosynthetic depression at suprasaturation water contents, at least not under the experimental conditions with water being sprayed from above. *D. plumbea* has a pored epicortex (Lumbsch and Kothe 1992) which could probably be blocked by rain water. The species has a fairly similar photosynthetic response to thallus water content as the C-type response demonstrated in some rainforest species (Lange et al. 1993) as well as in some steppe lichens (Lange et al. 1995). A suprasaturation depression represents a real fall in photosynthetic rate due to blockage of diffusive pathways for CO₂ (e.g. Lange et al. 1996). Such depressions are common even among rain forest lichens in situ (Lange et al. 1993), and could be one reason why *D. plumbea* is excluded by bryophytes in very humid microsites. A partial removal of the canopy under such

humid circumstances could possibly change the competition to the advantage of *D. plumbea*.

The hypothallus of *D. plumbea* absorbs liquid water instantaneously; faster than measured associated lichens (Degelius 1935), it gains capillary-held liquid water and conducts the first flushing water from tiny rain tracks farther into the thallus (Y. Gauslaa, personal observation). Lobarion species, to which *D. plumbea* belongs, have been shown to be associated with mineral-rich microhabitats (Gauslaa 1995). Both leaking of ions during sudden resaturation in cyanobacterial lichens (Buck and Brown 1979) as well as a photosynthetic depression, could possibly be reduced on a vertical trunk in situ by a buffering water-absorbing hypothallus.

In conclusion, the strong increase in hypothallus thickness with increasing thallus size seems to cause a highly size-dependent water-holding capacity in *D. plumbea* thalli. The strong size dependency of independent and ecologically important variables in this study confirms earlier findings (Larson 1979, 1984; Hestmark et al. 1997) that size will have to be considered as an essential parameter in future ecological and physiological studies.

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