PHOTOSYNTHETICA 37 (3): 393-404, 1999

Osmotic and atmospheric dehydration effects in the lichens *Hypogymnia physodes, Lobaria pulmonaria,* and *Peltigera aphthosa*: an *in vivo* study of the chlorophyll fluorescence induction

M. JENSEN, Samira CHAKIR, and G.B. FEIGE

Universität-GH Essen, FB 9 Botanik, Universitätsstr. 5, D-45117 Essen, Germany

Abstract

Inactivation of photosynthesis during atmospheric and osmotic (highly concentrated NaCl or sucrose solutions) dehydration was monitored by measurement of chlorophyll fluorescence induction (OIP-phase, Kautsky-curves) in three lichen species. The induction curves were changed in a very similar way by all three treatments. All dehydration effects were rapidly reversible after rehydration. At relatively mild water stress, the rise time to the transient peak F_p was prolonged, and the variable part of fluorescence was diminished. In addition, at severe water stress, a considerable decline of the F_0 value was observed. For NaCl treatment this effect started at water potentials <-8.5 MPa in *P. aphthosa*, <-12 MPa in *H. physodes,* and <-21 MPa in *L. pulmonaria*. Above these water potentials, our observations are in agreement with values from desiccation-tolerant algae, higher plants, and lichens, where an inactivation on the photosystem 2 (PS2) donor side has been postulated. At very low water potentials, the decrease in F_0 probably monitors changes in the organization of the antenna apparatus of PS2.

Additional key words: green algae; NaCl; sucrose; water potential; water stress.

Introduction

Desiccation stress of lichens produced by an exposure to dry air or to an osmotic medium shows features similar to reversible photoinhibition (Jensen and Feige 1991,

Received 29 March 1999, *accepted* 30 December 1999.
e-mail: manfred.jensen@uni-essen.de, homepage: http://www.uni-essen.de/botanik
Presented at the 2nd Regional Photosynthesis Workshop "Chlorophyll Fluorescence: Emotions & Reason", Lipno/Šumava, Czech Republic, January 31-February 3, 1999.
Acknowledgments: We are grateful to G.H. Krause for helpful discussions, to K.A. Santarius for his help with the freezing point depression data of sucrose, and to M. Neugebauer for technical assistance. We thank Scott LaGreca for the revision of the English text. This work was supported by the DAAD.

Mohanty and Yamamoto 1996, Chakir and Jensen 1999). Water loss from lichen thalli is accompanied by a total inactivation of photosynthetic gas exchange and loss of variable chlorophyll (Chl) fluorescence (Lange *et al.* 1970, Lange and Tenhunen 1982, Kappen and Breuer 1991, Schroeter *et al.* 1991), but rewetting with liquid water normally restores photosynthetic activity within minutes (Feige and Jensen 1987, Coxson 1988, Lange *et al.* 1989). Upon drying, low temperature (77 K) and room temperature Chl fluorescence both indicate changes in the antenna apparatus and its coupling to PS2 (Sigfridsson 1980, Sigfridsson and Öquist 1980, Jensen and Feige 1987, 1991, Bilger *et al.* 1989, Lange *et al.* 1989). This effect is considered to lower the photosynthetic activity. Room temperature Chl fluorescence induction studies with some desiccation-tolerant algae and higher plants, on the other hand, negate the participation of antennae in the inactivation process during drying (Mohanty *et al.* 1974, Wiltens *et al.* 1978, Govindjee *et al.* 1981, Chen and Hsu 1995). Instead, a decreased electron donation rate to PS2 is the favoured interpretation. The main differences between these studies and those with lichens are: (*1*) the water potentials reached in lichens are much lower; (*2*) in lichens, there are optical transparency changes in the mycobiontal cortex on top of the algal layer (Büdel and Lange 1994, Sancho *et al.* 1994, Scheidegger and Schroeter 1995) which may interfere with the determination of fluorescence yields. In order to circumvent the difficulties with transparency changes, and to judge whether the inactivation process in lichens can be explained on an osmotic basis (Nash *et al.* 1990), we exposed lichens to concentrated salt and sugar solutions reaching very low water potentials (similar to drying experiments) and analysed the corresponding Chl fluorescence induction curves (OIP-phase, Kautsky-curves, cf. Govindjee 1995).

Materials and methods

Lichen collection: *Peltigera aphthosa* (L.) Willd. was collected on the Inner Bergli, Mathon, Paznauntal (Austria) at 0 °C. The thalli were kept wet and cold (<10 °C) for 3 d, dried for 4 h in the laboratory, and then stored at -25 °C. *Hypogymnia physodes* (L.) Nyl. was collected from the bark of oak trees in the Eifel mountains near Gemünd (Germany), dried, and frozen down to -25 °C one day after collection. Dry material of *Lobaria pulmonaria* (L.) Hoffm. growing on *Pinus canariensis* and *Erica arborea* was collected in La Palma (Canary Islands, Spain) at the Cumbre nueva. This material was frozen at -25 °C one week after collection.

Pretreatments: After 1-2 years, frozen lichen thalli were thawed and artificially rewetted. The samples were stored for at least 15 h in a refrigerator at about 7 °C in darkness, and then for 2 h at room temperature at about 6 μmol(photon) m^{-2} s^{-1}. This procedure normally leads to a high physiological activity and low zeaxanthin content of the samples (Jensen *et al.* 1993). The physiological viability of the lichen material was routinely tested by the measurement of Chl fluorescence with the *PAM* system (*Walz*, Effeltrich, Germany) and light-dependent oxygen exchange within a *LD2* cuvette (*Hansatech*, King's Lynn, Norfolk, England) at 100 μmol(photon) m^{-2} s^{-1},

22 °C, and high CO_2-concentrations (3 drops of 0.5 M $NaHCO_3$ on a layer of black velvet). Samples with F_v/F_m-values <0.64 or negative net photosynthetic rates were not used.

Dehydration treatment and Chl fluorescence induction: Measurements of Chl fluorescence induction curves (OIP-phase) were performed with discs of 2 cm diameter in the *LD2* chamber (Merschhemke and Jensen 1993). Excess water from wet samples was removed with filter paper, and after two control measurements the samples were dehydrated in a stepwise manner every 30 min. Dehydration took place in darkness either in the laboratory air (at *ca.* 35 % rel. humidity) or by immersing and stirring the thallus pieces in NaCl or sucrose solutions for 15 min. Excess solution on the thallus surface was removed. After retransferring into the *LD2* cuvette the samples could equilibrate in the cuvette atmosphere for about 12 min before fluorescence measurements were started. As a control, the back-scattered + reflected portion (B+R) of the measuring radiation was monitored through the side window of the *LD2* cuvette with a *UDT500D* photodiode. This was done in order to assess B+R changes which occur in the mycobiontal cortex layer on top of the photobiont cells during atmospheric drying. The water content of desiccated samples was determined after each fluorescence measurement. For this purpose the samples were removed from the cuvette and immediately weighed. The actual water content was calculated later according to: 100 (actual mass – dry mass)/dry mass [%] (Lange *et al.* 1970). After the dehydration steps (down to -27 MPa) were completed, the samples were rewetted by spraying with or stirring in pure water for 15 min and fluorescence was recorded again in order to check the reversibility of dehydration effects. The dry mass of the samples was determined after 48 h of drying over silicagel.

Chl fluorescence parameters F_0 and F_v/F_m: In an independent series of experiments, F_0, F_v/F_m, and B+R measuring radiation were determined with a *MINI-PAM* apparatus (*Walz*) and a *UDT500D* photodiode equipped with an additional light guide. Lichen discs were fixed with nylon threads in a small cuvette with two attached silicon tubes. Through the inlet tube either water, NaCl, or sucrose solution was pumped. The lichen surface was continuously rinsed by these solutions. With this experimental design it was possible to expose lichen samples to solutions of stepwise decreasing water potentials without any change of the geometric arrangement. F_0 and B+R were recorded on a chart recorder in almost complete darkness (except the weak red measuring beam). Every 20 min the pumping was stopped, a saturing flash (1.2 s) was fired by the *MINI-PAM* apparatus for the determination of the F_v/F_m value, and the solution was changed (decreasing water potentials). At the end of the series, the lichen disc was rinsed with pure water again (reversibility test).

Determination of the water potential of dehydrated samples: Calibration values of water content *versus* water potential (Fig. 1) were obtained by placing thalli for at least 1 d over NaCl solutions adjusted to stepwise decreasing water potential (from wet to dry samples). The fitting curves were calculated by the computer program *TableCurve* (*Jandel Scientific*). The water potentials in and over the NaCl solutions

were calculated according to Slavík (1974). The water potentials of sucrose solutions up to 2.56 M were calculated from the freezing point depression data of Levitt (1956) and Santarius (1992) and extrapolated up to 2.8 M by the polynom function: $y = bx + cx^2 + dx^3 + ex^4$ with constants b = -1.3307, c = -1.9781, d = 0.9711, e = -0.393 (for 20 °C; software: *SigmaPlot, Jandel Scientific*). Chemicals were purchased from *Serva* (NaCl, sucrose) or *Promochem* [DCMU = 3-(3,4-dichlorophenyl)-1,1-dimethyl urea]. DBMIB (2,5-dibromo-3-methyl-6-isopropyl-*p*-benzoquinone) was a gift from W. Oettmeier (Bochum, Germany).

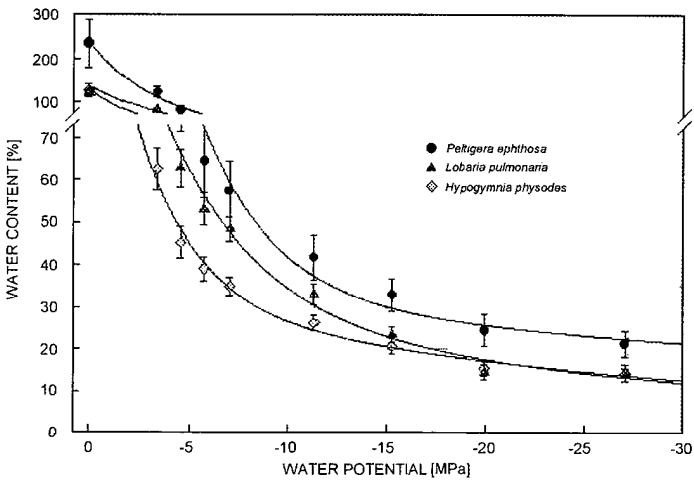

Fig. 1. Water content of lichens after equilibration with air humidity at 20 °C over NaCl solutions of the indicated water potential. The direction of measurements was from wet to dry conditions. Each point represents the average value of 5 thalli, the bars indicate the corresponding standard deviation. The fitting lines are exponentials with 2 components (see text).

Results

To compare the effects of atmospheric *versus* osmotic dehydration on water potential, we first prepared calibration curves for the atmospheric dehydration treatments. For this purpose, we placed lichen thalli for at least 24 h in exsiccators over salt solutions of known water potential, allowed them to equilibrate with the corresponding air humidity, and determined their water content. The obtained mean values (Fig. 1) could be fitted with two component exponential curves according to the equation: $y = a \exp(-x/b) + c \exp(-x/d)$ with $r^2 > 0.99$ (*P. aphthosa, H. physodes)* and $r^2 = 0.984$ (*L. pulmonaria)*. From the fitting the following constants were obtained: *P. aphthosa* a = 33.78, b = -65.15, c = 203.04, d = -3.61; *L. pulmonaria* a = 29.65, b = -32.58, c = 108.34, d = -4.63; *H. physodes* a = 31.94, b = -31.92, c = 98.11, d = -2.91. In the covered range, the water content sequence was *P. aphthosa* > *L. pulmonaria* > *H. physodes.*

The fitting curves were then used to estimate the water potentials of the drying samples from their water contents. The advantage of this indirect method is the short time range (*ca.* 6 h) in which the following desiccation experiments could be performed. This was identical to the time range of the osmotic treatment experiments.

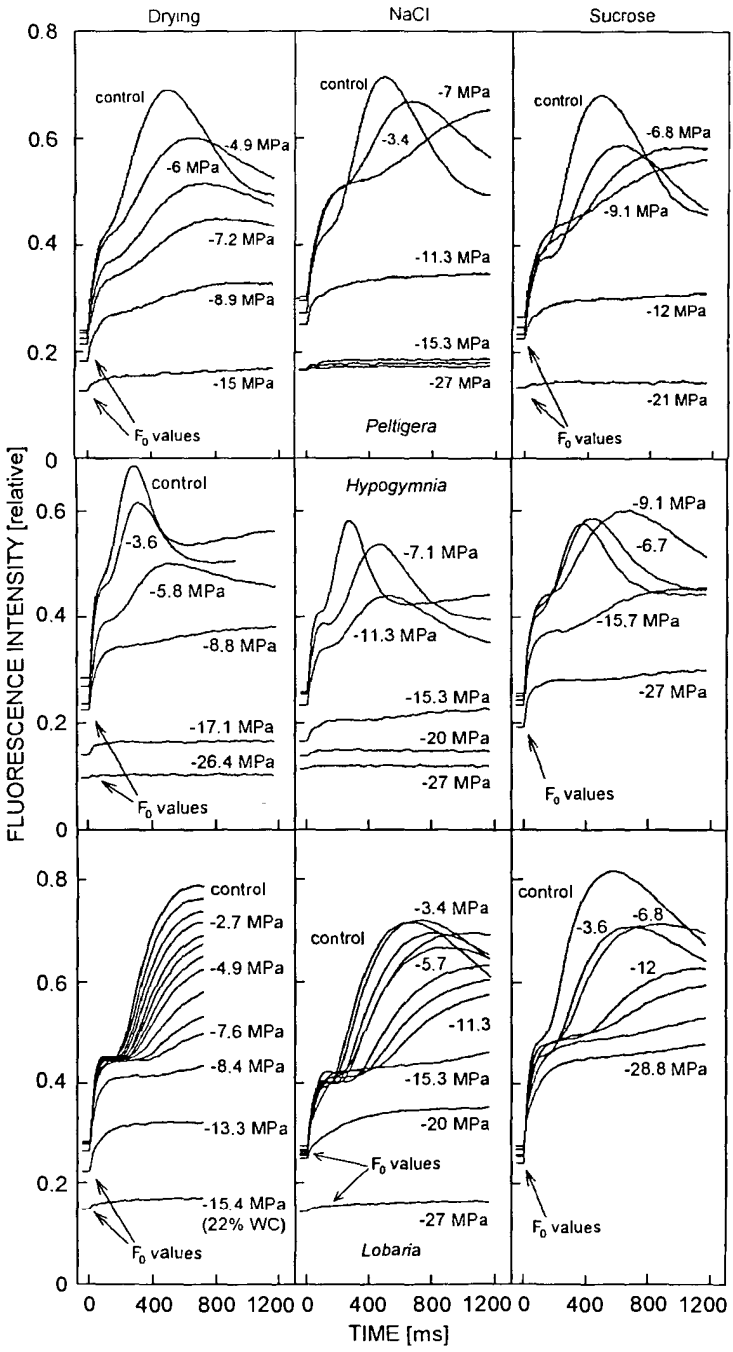

Fig. 2. Dependence of Kautsky-curves of individual lichen thalli (*P. aphthosa*, *H. physodes*, *L. pulmonaria*) on the water potential. Treatments NaCl and sucrose denote temporary (15 min) immersing of the thalli in solutions of the indicated water potential.

Table 1. Dependence of F_0 [relative] and F_{VP}/F_P on osmotic dehydration in the presence of 10 μmol DCMU or DBMIB for *P. aphthosa*.

DCMU + sucrose			DCMU + NaCl			DBMIB + sucrose		
Water potential	F_0	F_{VP}/F_P	Water potential	F_0	F_{VP}/F_P	Water potential	F_0	F_{VP}/F_P
0.0	0.284	0.644	0.0	0.251	0.639	0.0	0.257	0.621
-3.6	0.272	0.603	-3.3	0.216	0.585	-3.6	0.236	0.622
-6.8	0.273	0.554	-4.5	0.253	0.553	-5.0	0.245	0.588
-9.1	0.262	0.473	-7.0	0.289	0.482	-6.8	0.224	0.564
-12.0	0.236	0.316	-8.3	0.264	0.412	-9.1	0.204	0.340
			-13.7	0.248	0.210	-12.0	0.129	0.227

In the fluorescence induction curves of the 3 investigated species in a wide range of dehydration states (Fig. 2), the same actinic irradiance of 100 μmol(photon) m^{-2} s^{-1} was applied. The shapes of the control curves at zero water potential are somewhat different for the 3 species. This is due to the fact that they contain 3 different photobiont species. *Parmelia sulcata* and *H. physodes*, containing the same unicellular green photobiont (*Trebouxia*), showed similar induction curves. Material of *L. pulmonaria* collected in the Alps did not differ from the La Palma material. Beyond the differences between species, a general response to decreasing water potentials could be observed. This can be divided into 3 phases: during the first phase the time needed to reach the transitory peak (F_p-level) increases; in the second phase the peak level F_p is diminished; and in the third phase the ground level F_0 declines substantially. Of course, there was some overlapping of the phases. During the first phase and a large part of the second phase, the S-shape of the curves was maintained (even in the presence of DBMIB), but not during the third phase. At lower irradiances [<30 μmol(photon) m^{-2} s^{-1}], this was not observed well (not shown). In the presence of the electron transport inhibitors DCMU or DBMIB (Table 1), on the other hand, where the F_p levels (almost) reached the maximal possible value, the distinct F_p decline was very clearly pronounced. In Table 1, the parameter $F_{VP}/F_P = (F_P - F_0)/F_P$ is shown instead of F_P, because this parameter—in the presence of DCMU—is close to F_v/F_m. The decline of this parameter without a concomitant decline of F_0 demonstrates fluorescence quenching within the PS2 reaction centre (Butler and Kitajima 1975, Butler 1978, Krause and Weis 1991).

All dehydration effects were largely reversible within minutes, when the samples were rehydrated in pure water (not shown). Usually, rehydration could restore the Kautsky-curves within 10-20 min.

Differences between species (Fig. 3) were found in the parameters F_0, F_v/F_m, and (B+R). *P. aphthosa* turned out to be the most sensitive species, as the curves were changed at the highest water potentials. During treatment with NaCl or sucrose, the F_0 decline became obvious at about -8.5 (±1.1 SD, $n = 4$) or -7.3 (±1.5, $n = 3$) MPa for *P. aphthosa*, at about -12.3 (± 1.5, $n = 3$) or -14.4 (±1.3, $n = 5$) MPa for *H. physodes*, and beyond -20 MPa for *L. pulmonaria*. For the last species, the F_0 decline

was usually only small.

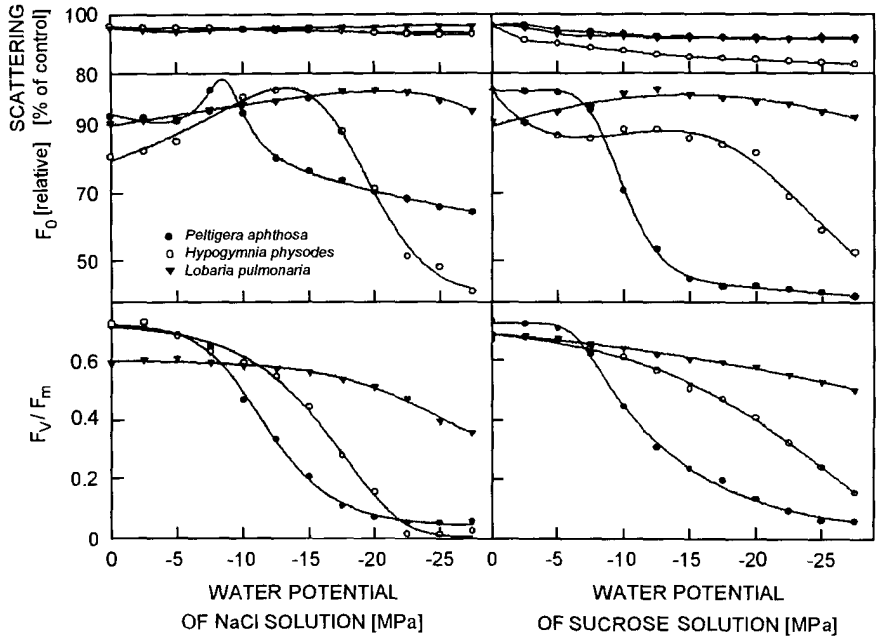

Fig. 3. Comparison of NaCl and sucrose effects for the three lichen species *P. aphthosa*, *H. physodes*, and *L. pulmonaria*. Typical curves of the dependence of backscattered+reflected light (scattering, *upper diagrams*), F_0 (*central diagrams*), and F_v/F_m (*lower diagrams*) on the water potential are shown. Unlike Fig. 2, the thalli were continously exposed to the NaCl or sucrose solutions and were not removed from the cuvette during the experiments.

During atmospheric drying, the F_0 decline always started at a relatively high water potential as compared to osmotic treatment (see Fig. 2). This should be a consequence of gas bubbles in the cortex (colour change to grey-milky, Scheidegger and Schroeter 1995) which appear only during atmospheric but not osmotic dehydration. It is accompanied by a 30 % increase in B + R and surely influences F_0 determinations.

In principle, however, the effects of drying, NaCl, and sucrose treatment on *P. aphthosa* and *H. physodes* were comparable, with drying > NaCl ≈ sucrose. There was some variation between different thalli, especially in *L. pulmonaria*. In the experimental setup in which the samples were continuously exposed to liquid (Fig. 3) we did not always observe a large F_0 decline. However, if the thalli were removed from the osmotic solution and temporarily exposed to air as in Fig. 2, the F_0 value maximally decreased to 50 % in the NaCl experiments.

Discussion

Desiccation-dependent photosynthetic inactivation of lichen photobionts and algae has been generally attributed to an impairment of electron transport or—more specifically—to a down regulation of PS2 efficiency (Wiltens *et al.* 1978, Sigfridsson and Öquist 1980, Jensen and Feige 1991, Sass *et al.* 1996). The mechanism was ascribed either to the PS2 donor side or preferentially to the PS2 antenna apparatus. The present results do not offer a decision for one or the other of these discrepant ideas. However, the analysis of Chl fluorescence induction during progressive water stress can help to assess which process is important at mild, intermediate, and severe water stress.

At severe water stress, we mostly observed a substantial F_0 decrease during dehydration. It was very striking in *H. physodes* [down to a 6-fold decrease; cf. *Ramalina maciformis* (Lange *et al.* 1989)], began at the highest water potential in *P. aphthosa* (2-fold decrease), and was less clear in *L. pulmonaria* (down to a 2-fold decrease, cf. Scheidegger *et al.* 1997). According to the theory of Butler (1978), this would imply that Chl fluorescence quenching produced by desiccation is antenna-type. A more recent theory called 'rapid equilibrium model' (Schatz *et al.* 1988), however, does not admit such a conclusion, *i.e.*, thermal deactivation in the antennae cannot be discriminated from that occurring in the reaction centres by means of induction curve and F_0 analysis (Giersch and Krause 1991). On the other hand, Chl fluorescence measurements at 77 K (spectra and kinetics) indicate changes in the antenna domains during dehydration of lichens (Sigfridsson 1980, Sigfridsson and Öquist 1980, Jensen and Feige 1987, Bilger *et al.* 1989). In a recent photoinhibition model (Mohanty and Yamamoto 1996), antenna-type quenching is accompanied by a F_0 decrease and the reaction centre-type quenching is not. From this point of view, the phase of large F_0 decrease most probably represents antenna-type quenching. The F_0 decline occurred only at relatively low water potentials.

Our present results for *H. physodes* differ somewhat from previous results where an early F_0 decline during desiccation was shown (Jensen and Feige 1991). These previous results we now partly interpret as an artifact that may be the result of 2 processes:

(*1*) Desiccation leads to transmission changes in the cortex (up to 50 %, W. Bilger, Oslo, personal communication), linked to a 30 % increase in (B+R) due to the formation of gas bubbles. This mimics a F_0 decrease.

(*2*) The earlier measurements were not performed in a cuvette but in laboratory air. This leads to an uneven desiccation within thallus pieces. Thinner border regions desiccate earlier than the central part, a fact that can very easily be observed for the cortex colour change in *L. pulmonaria*. If thallus pieces are repeatedly allowed to equilibrate with wet air as in our present investigations, desiccation is clearly more uniform, and the start of F_0 decline can be assessed more correctly. The early start of F_0 decrease in former investigations therefore partly derives from advanced border desiccation. The still well-watered central part reflects a high water content that is not valid for the whole thallus.

We tried to separate dehydration from irradiation effects by keeping the thalli in darkness during the dehydration process. If the lichens are strongly irradiated during dehydration, additional fluorescence quenching due to the formation of zeaxanthin can be observed (Demmig-Adams *et al.* 1990a,b). This effect can be largely ruled out for the present results (Jensen *et al.* 1993).

As the unicellular green algae within the lichens shrink during advanced atmospheric dehydration (Scheidegger and Schroeter 1995, Honegger *et al.* 1996), one may argue that the observed F_0 changes are not directly linked to the photosynthetic apparatus, but to a decrease in excitation rates caused by changes in scattering, reflectance, absorption other than by photosynthetic pigments, or a lower macroscopic cross-section of the antennas. This certainly plays a role during *atmospheric* dehydration as pointed out above. During *osmotic* dehydration and during treatment with high concentrations of DMSO, however, we could not find large changes in the B+R. DMSO, which rapidly permeates through biomembranes, does not cause cell shrinkage (Chakir and Santarius 1995) and should not have macroscopic cross-section effects, but nevertheless it leads to a F_0 decline (not shown). For these reasons we attach only a low significance to a possible decrease in excitation rates. Rather, a lower fluorescence quantum yield of PS2 as a consequence of redistribution of excitation radiation in favour of photosystem 1 (Chakir and Jensen 1999) and/or increased fluorescence reabsorption by antenna complex aggregation (Ottander *et al.* 1995, Horton *et al.* 1996) may explain the observed F_0 decline.

During the first and intermediate stages of dehydration, when F_0 changes are absent or low (Figs. 2 and 3), such antenna type effects are less important. Instead, reaction centre effects have to be considered. There is additional information from the kinetic behaviour of the fluorescence induction curves (see Fig. 2). The effects of atmospheric and osmotic dehydration are very similar and should therefore be interpreted in the same way. In principle, the fast fluorescence transients (Kautsky-curves) are similar to those obtained for desiccating marine algae (Wiltens *et al.* 1978), some higher plants (Govindjee *et al.* 1981), and for the desiccation-tolerant leaves of *Craterostigma plantagineum* (Schwab *et al.* 1989), where only small F_0-decreases were found. As in *C. plantagineum*, the first states of dehydration can be characterized by a preferential decrease in the I-P rise and a concomitant shift of F_p to a later time. In all 3 mentioned reports, this has been interpreted as a result of reduced electron donation to PS2. It has also been argued that during advanced dehydration the donor side reaction $Z \rightarrow P^+$ is so heavily inactivated that it cannot compete anymore with the rate of the back reaction $P^+ + Q_A^- \rightarrow P + Q_A$. By such a mechanism, all variable fluorescence would finally vanish (Wiltens *et al.* 1978). The complete suppression of F_v during dehydration of lichens could be measured during dehydration in the presence of DCMU, when Q_A^- oxidation by the secondary acceptor plastoquinone is hindered, and in the presence of DBMIB, when plastochinol reoxidation is inhibited (Table 1). The Kautsky curves (cf. Fig. 2) in the presence of DBMIB were sigmoid as long as there was a measurable F_v (not shown). This indicates a functional plastoquinone reduction. Therefore, substantial PS2

acceptor-side modifications should not be the main reason for osmotic inactivation. Rather, donor-side inactivation of PS2 should take place. At present, the most striking evidence for this interpretation comes from thermoluminescence studies with *Cladonia convoluta* (Sass *et al.* 1996). In this lichen atmospheric dehydration leads to a special arresting of the S-states of PS2 that can be released by rehydration. The donor-side effect appears to inhibit the photosynthetic light reactions with the possibility of rapid reactivation. In other words, this is the essential on/off switch triggered by the water potential. During the main inactivation phase, *i.e.*, at intermediate water potentials, antenna effects (except possible zexanthin formation in strong irradiance) appear to be less important. From the ecological point of view, additional effects such as changes in the antenna system and transparency changes of the cortex are beneficial for survival of lichen photobionts during longer periods of dehydration by keeping the absorbed, harmful radiation away from the vulnerable PS2 reaction centres.

References

Bilger, W., Rimke, S., Schreiber, U., Lange, O.L.: Inhibition of energy-transfer to photosystem II in lichens by dehydration: Different properties of reversibility with green and blue-green phycobionts. - J. Plant Physiol. **134**: 261-268, 1989.

Büdel, B., Lange, O.L.: The role of cortical and epinecral layers in the lichen genus *Peltula*. - Crypt. Bot. **4**: 262-269, 1994.

Butler, W.L.: Energy distribution in the photochemical apparatus of photosynthesis. - Annu. Rev. Plant Physiol. **29**: 345-378, 1978.

Butler, W.L., Kitajima, M.: Fluorescence quenching in photosystem II of chloroplasts. - Biochim. biophys. Acta **376**: 116-125, 1975.

Chakir, S., Jensen, M.: How does *Lobaria pulmonaria* regulate photosystem II during progressive desiccation and osmotic water stress? A chlorophyll fluorescence study at room temperature and at 77 K. - Physiol. Plant. **105**: 257-265, 1999.

Chakir, S., Santarius, K.A.: Freezing of isolated thylakoid membranes in complex media. IX. The effect of rapidly penetrating and nonpenetrating cryoagents. - Cryo-Lett. **16**: 114-121, 1995.

Chen, Y.H., Hsu, B.D.: Effects of dehydration on the electron transport of *Chlorella* - an *in vivo* fluorescence study. - Photosynth. Res. **46**: 295-299, 1995.

Coxson, D.S.: Recovery of net photosynthesis and dark respiration on rehydration of the lichen, *Cladina mitis*, and the influence of prior exposure to sulphur dioxide while desiccated. - New Phytol. **108**: 483-487, 1988.

Demmig-Adams, B., Adams, W.W., III, Czygan, F.-C., Schreiber, U., Lange, O.L.: Differences in the capacity for radiationless energy dissipation in the photochemical apparatus of green and blue-green algal lichens associated with differences in carotenoid composition. - Planta **180**: 582-589, 1990a.

Demmig-Adams, B., Adams, W.W., III, Green, T.G.A., Czygan, F.C., Lange, O.L.: Differences in the susceptibility to light stress in two lichens forming a phycosymbiodeme, one partner possessing and one lacking the xanthophyll cycle. - Oecologia **84**: 451-456, 1990b.

Feige, G.B., Jensen, M.: Photosynthetic properties of lichens stored at -25 C for several years. - Bibl. Lichenol. **25**: 319-323, 1987.

Giersch, C., Krause, G.H.: A simple model relating photoinhibitory fluorescence quenching in chloroplasts to a population of altered Photosystem II reaction centers. - Photosynth. Res. **30**: 115-121, 1991.

Govindjee: Sixty-three years since Kautsky: Chlorophyll *a* fluorescence. - Aust. J. Plant Physiol. **22**: 131-160, 1995.

Govindjee, Downton, W.J.S., Fork, D.C., Armond, P.A.: Chlorophyll *a* fluorescence transient as an indicator of water potential of leaves. - Plant Sci. Lett. **20**: 191-194, 1981.

Honegger, R., Peter, M., Scherrer, S.: Drought-induced structural alterations at the mycobiont photobiont interface in a range of foliose macrolichens. - Protoplasma **190**: 221-232, 1996.

Horton, P., Ruban, A.V., Walters, R.G.: Regulation of light harvesting in green plants. - Annu. Rev. Plant Physiol. Plant mol. Biol. **47**: 655-684, 1996.

Jensen, M., Feige, G.B.: The effect of desiccation and light on the 77 K chlorophyll fluorescence properties of the lichen *Peltigera aphthosa*. - Bibl. Lichenol. **25**: 325-330, 1987.

Jensen, M., Feige, G.B.: Quantum efficiency and chlorophyll fluorescence in the lichens *Hypogymnia physodes* and *Parmelia sulcata*. - Symbiosis **11**: 179-191, 1991.

Jensen, M., Roosen, B., Kuffer, M.: Quantification of the xanthophyll cycle-carotenoids in lichens by HPLC. - Bibl. Lichenol. **53**: 109-114, 1993.

Kappen, L., Breuer, M.: Ecological and physiological investigations in continental Antarctic cryptogams. II. Moisture relations and photosynthesis of lichens near Casey Station, Wilkes Land. - Antarctic Sci. **3**: 273-278, 1991.

Krause, G.H., Weis, E.: Chlorophyll fluorescence and photosynthesis: The basics. - Annu. Rev. Plant Physiol. Plant mol. Biol. **42**: 313-349, 1991.

Lange, O.L., Bilger, W., Rimke, S., Schreiber, U.: Chlorophyll fluorescence of lichens containing green and blue-green algae during hydration by water vapor uptake and by addition of liquid water. - Bot. Acta **102**: 306-313, 1989.

Lange, O.L., Schulze, E.-D., Koch, W.: Experimentell-ökologische Untersuchungen an Flechten der Negev-Wüste. II. CO_2-Gaswechsel und Wasserhaushalt von *Ramalina maciformis* (DEL.) Bory am natürlichen Standort während der sommerlichen Trockenperiode. - Flora **159**: 38-62, 1970.

Lange, O.L., Tenhunen, J.D.: Water relations and photosynthesis of desert lichens. - J. Hattori bot. Lab. **53**: 309-313, 1982.

Levitt, J.: The Hardiness of Plants. - Academic Press, New York 1956.

Merschhemke, C., Jensen, M.: Das FluOx-Algentestsystem. Ein automatisches Algentestgerät zur kontinuierlichen Gewässerüberwachung. - Limnologica **23**: 323-333, 1993.

Mohanty, N., Yamamoto, H.Y.: Induction of two types of non-photochemical chlorophyll fluorescence quenching in carbon-assimilating intact spinach chloroplasts - the effects of ascorbate, de-epoxidation, and dibucaine. - Plant Sci. **115**: 267-275, 1996.

Mohanty, P., Govindjee, Wydrzynski, T.: Salt-induced alterations of the fluorescence yield and of emission spectra in *Chlorella pyrenoidosa*. - Plant Cell Physiol. **15**: 213-224, 1974.

Nash, T.H., III, Reiner, A., Demmig-Adams, B., Kilian, E., Kaiser, W.M., Lange, O.L.: The effect of atmospheric desiccation and osmotic water stress on photosynthesis and dark respiration of lichens. - New Phytol. **116**: 269-276, 1990.

Ottander, C., Campbell, D., Öquist, G.: Seasonal changes in photosystem II organisation and pigment composition in *Pinus sylvestris*. - Planta **197**: 176-183, 1995.

Sancho, L.G., Valladares, F., Ascaso, C.: Effect of hydration on colour and temperature in thalli of Umbilicariaceae. - Crypt. Bot. **4**: 227-232, 1994.

Santarius, K.A.: Freezing of isolated thylakoid membranes in complex media. VIII. Differential cryoprotection by sucrose, proline and glycerol. - Physiol. Plant. **84**: 87-93, 1992.

Sass, L., Csintalan, Z., Tuba, Z., Vass, I.: Thermoluminescence studies on the function of photosystem II in the desiccation tolerant lichen *Cladonia convoluta*. - Photosynth. Res. **48**: 205-212, 1996.

Schatz, G.H., Brock, H., Holzwarth, A.R.: Kinetic and energetic model for the primary processes in photosystem II. – Biophys. J. **54**: 397-405, 1988.

Scheidegger, C., Frey, B., Schroeter, B.: Cellular water uptake, translocation and PSII activation during rehydration of desiccated *Lobaria pulmonaria* and *Nephroma bellum*. – Bibl. Lichenol. **67**: 105-117, 1997.

Scheidegger, C., Schroeter, B.: Effects of ozone fumigation on epiphytic macrolichens: ultrastructure, CO_2 gas exchange and chlorophyll fluorescence. - Environ. Pollut. **88**: 345-354, 1995.

Schroeter, B., Kappen, L., Moldaenke, C.: Continuous *in situ* recording of the photosynthetic activity of Antarctic lichens - Established methods and a new approach. - Lichenologist **23**: 253-265, 1991.

Schwab, K.B., Schreiber, U., Heber, U.: Response of photosynthesis and respiration of resurrection plants to desiccation and rehydration. - Planta **177**: 217-227, 1989.

Sigfridsson, B.: Some effects of humidity on the light reaction of photosynthesis in the lichens *Cladonia impexa* and *Collema flaccidium*. - Physiol. Plant. **49**: 320-326, 1980.

Sigfridsson, B., Öquist, G.: Preferential distribution of excitation energy into photosystem I of desiccated samples of the lichen *Cladonia impexa* and the isolated lichen-alga *Trebouxia pyriformis*. - Physiol. Plant. **49**: 329-335, 1980.

Slavík, B.: Methods of Studying Plant Water Relations. - Springer-Verlag, Berlin 1974.

Wiltens, J., Schreiber, U., Vidaver, W.: Chlorophyll fluorescence induction: an indicator of photosynthetic activity in marine algae undergoing desiccation. - Can. J. Bot. **56**: 2787-2794, 1978.