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Quantum Efficiency and Chlorophyll Fluorescence in the Lichens *Hypogymnia psysodes* and *Parmelia sulcata*

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Abstract

Chlorophyll fluorescence (modulated measuring system) and photosynthetic O_2-production were measured with thalli of *Hypogymnia physodes* and *Parmelia sulcata* as a function of water content and light intensity. During continuous drying in darkness, the fluorescence parameters F_0 (base fluorescence yield), F_M (maximum fluorescence yield determined during short flashes of strong light) and F_V (= F_M *minus* F_0) all strongly decline. This process is dominated by a quench of F_0 in both species. The ratio F_V/F_M (indicative of energy transfer probabilities) is little affected for large ranges of water loss. The possible role of a massive increase in radiationless energy dissipation within the antennae apparatus and state shifts in favour of photosystem I is discussed. Simultaneous measurements of oxygen evolution and chlorophyll fluorescence revealed a proportional decrease of F_M/F_0 ratios and gross photosynthetic rates during drying of both species. A linear relationship between F_M/F_0 and quantum yields could also be confirmed, when different thalli were investigated at high water contents. Therefore, F_M/F_0 appears to be an ideal indicator of photobiont vitality in field work. In this respect, the determination of the fluorescence quenching parameters q_Q and q_E is less valuable, because no clear correlation to quantum yields could be found and because upon variation of light intensity the relationship between photochemical yields (= quantum yield/q_Q) and q_E was not linear for most thalli.

Keywords: lichens, *Hypogymnia physodes*, *Parmelia sulcata*, chlorophyll fluorescence, dehydration, energy transfer, photosynthesis, lichen vitality, field measurements

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1. Introduction

Measurements of chlorophyll fluorescence are a convenient tool for estimation of photosynthetic activity and vitality of plant tissue (Krause and Weis, 1984; Renger and Schreiber, 1986). Chlorophyll *a* fluorescence has been frequently used to assess effects of environmental stress on plants like heat stress (Weis, 1985; Schreiber and Bilger, 1987), drought stress (Cornic et al., 1989), light stress and photoinhibition (Björkman, 1987; Demmig and Björkman, 1987; Krause, 1988), cold acclimation and freezing stress (Krause and Somersalo, 1989), and the midday depression of photosynthesis in higher plants (Demmig-Adams et al., 1989). For field work, the main advantages as compared to direct gas exchange measurements are: (1) the plant material is not destroyed, (2) it can be left in its natural habitat, (3) some parameters (F_0, F_M/F_0, F_V/F_M) can be determined very quickly after dark adaptation of the samples, and (4) detailed information on the stage of the pigment apparatus can be obtained.

In order to get an impression on the potential of fluorescence measurements in sensing photosynthetic key reactions in lichens, we measured photosynthetic O_2-evolution and fluorescence parameters under various conditions of light intensity and water content. One aim of this investigation was to get more insight in those processes which reversibly switch photosynthesis off and on during dehydration/hydration cycles. Another aim was the determination of those fluorescence parameters which are highly correlated with gas exchange data and are therefore of most practical value for field measurements.

2. Materials and Methods

Thalli of *Hypogymnia physodes* (L.) Nyl., *Parmelia sulcata* Th. Tayl. and *Cladonia rangiformis* Hoffm. were collected near Mechernich, West-Germany; *Peltigera aphthosa* (L.) Willd. was collected near Kühtai, Austria; *Lobaria meridionalis* Vain. and *Sticta canariensis* Bory ex Del. were collected near Erjos, Tenerife, Canary Islands. The lichen material was partly air-dried and stored at −25°C until use, partly it was stored at 2°C and measurement were then performed within 4 days. O_2 evolution was measured in a Hansatech LD2 cuvette (approximately 6 ml gas room) at 20°C. High CO_2 concentrations within the cuvette were maintained by 3 drops of 0.5 M $KHCO_3$. The cuvette was equipped with a special cover to take up the branched light guide for chlorophyll fluorescence measurements. For determination of fluorescence parameters a pulse amplitude modulation fluorometer (PAM 101, WALZ, West-Germany) working with a weak modulated measuring beam was

used. 0.8 s flashes of 5000 $\mu E/(m^2 \cdot s)$ (PAM 103) forced transient closure of all PS II reaction centers and allowed measurement of maximal fluorescence yield F_M. Determination of quenching parameters q_Q and q_E was performed according to Schreiber et al., 1986. Prior to the experiments, the thalli were sprayed with liquid water and illuminated with light from fluorescent lamps at 150 $\mu E/(m^2 \cdot s)$ for 1 hr in order to activate photosynthesis. For the drying experiment, some samples were placed on a weigher in darkness, and F_0-level was registered continuously. In this case, every 20 min a PAM 103 flash was fired and the weight of the sample was registered. Other thalli were placed in a LD2 cuvette for measurement of O_2-evolution and fluorescence yield. The dehydration occurred discontinuously by transient removing of the thalli from the cuvette. Outside the cuvette, the samples were weighed and allowed to dry out for 20 min in the dark. Then they were place back into the cuvette. Afterwards, they were left in darkness for 10 min to reach constant water content, before the actinic light (150 $\mu E/(m^2 \cdot s)$), SCHOTT KL1500 lamp + red RG 610 filter) was switched on. This light source was also used for measurement of light dependencies. It was connected to a DC power supply (type EA 3016, max. 20V 10A) in order to stabilize light intensities. Light intensities were controlled by LI-COR 185B quantum sensor. Water content is expressed as % of dry weight (over silica gel). Drying occurred at room temperature at about 35% relative humidity.

3. Results

In Fig. 1, the typical course of chlorophyll fluorescence parameters F_V/F_M, F_M/F_0 and F_0 is shown when thalli of H. physodes or P. sulcata dry out. In this experiment, the time course of F_0 was measured continuously in the dark, while the determination of F_V/F_M and F_M/F_0 was made possible by short, high intensity flashes every 20 min. The thalli were placed on a weigher and were not moved during the experiments. In addition, backscattering of the weak measuring beam was monitored by a photodiode in order to get unbiased F_0 levels. Especially for thalli of P. sulcata, there was some increase in backscattering (up to 30%) indicating decreasing absorption, when dehydration proceeded. However, *relative* absorption decrease was small and correction of original measured F_0 levels was not necessary. Because of these precautions, it is clear from the curves of Fig. 1, that the decline of fluorescence parameters during drying is actually dominated by a F_0 quench. This parameter already decreases at medium water contents, when F_M/F_0 is less affected and F_V/F_M is almost unaffected. For thalli of P. sulcata, the decrease in F_0 started always at about 70% water content, while the start point of F_0 decline was more variable

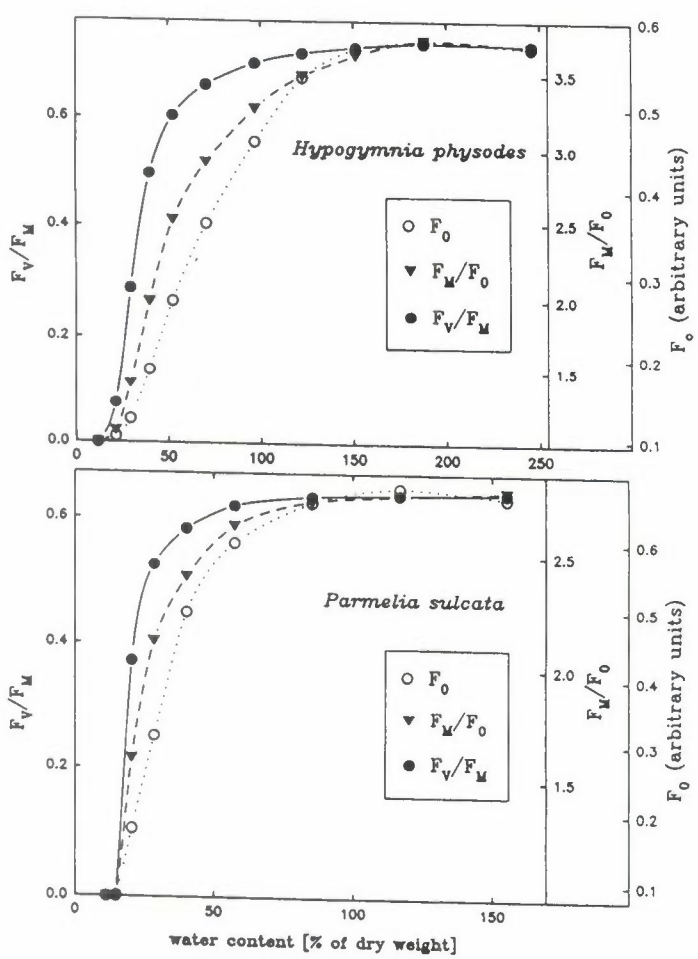

Figure 1. Dependence of chlorophyll fluorescence parameters F_0, F_M/F_0, and F_V/F_M on the water content of *Hypogymnia physodes* (a) and *Parmelia sulcata* (b) during a drying experiment.

for thalli of H. physodes according to varying thallus morphologies or varying portions of cavities within the thalli, i.e. varying capacity of water absorption. For Fig. 1 a thallus with especially high capacity of water absorption was chosen and therefore, the decline in F_0 already started at a water content higher than 120%. In other thalli of H. physodes, F_0 decline started between 120 and 70% water content. A final constant value of F_0 was reached at about 15–20% water content. The main drop of F_V/F_M was always restricted to a relatively small range above this point, at which no more variable fluorescence could be detected.

Figure 2 shows, how besides the decline of chlorophyll fluorescence parameters photosynthetic oxygen evolution at a limiting photon flux density is simultaneously hindered during drying of lichen thalli. In these experiments, chlorophyll fluorescence parameters and O_2 concentration changes were measured within a closed cuvette, and stepwise dehydration occurred outside the cuvette (see methods). The best correlation between gross photosynthetic rates and chlorophyll fluorescence parameters was obtained for the fluorescence parameter F_M/F_0 (see Fig. 2) in thalli of H. physodes as well as of P. sulcata. For F_M/F_0 and O_2 data, a linear relationship could be established, although there was some variation in the extrapolated y-axis value (compare insets of Fig. 2) between different thalli. Quench analysis, i.e. determination of 'energy'-dependent chlorophyll fluorescence quench parameter q_E and quench parameter q_Q, which indicates the redox state of photosystem II (PS II) primary acceptor Q, did not reveal a clear correlation to O_2 data. Both parameters declined slightly during drying, but increased during the last steps of dehydration (data not shown). At the moment, an interpretation of this behavior seems to be difficult. In the experiments of the following sections, no controlled variation of water status of the thalli was performed, but only thalli with water contents greater than 70% were selected. In Fig. 3, the F_M/F_0 value of several thalli was plotted versus the quantum yield of photosynthesis at 150 $\mu E/(m^2 \cdot s)$ red light. At this photon flux density (PFD), the light response curves of the investigated lichens were still almost linear. Besides thalli of H. physodes and P. sulcata, thalli of *C. rangiformis, P. aphthosa, L. meridionalis* and *S. canariensis* were integrated in this figure. If *C. rangiformis* is omitted, a linear relationship between F_M/F_0 and O_2 values turns out, although some thalli lie slightly beyond the 95% confidence lines of the regression line. Moreover, the regression line should cross the y-axis at F_M/F_0 values greater than 1. Apparently, differences between the thalli produced to much variation to get an ideal line. It should be pointed out, however, that F_M/F_0 values were highly reproducible for individual thalli. Interestingly, a linear relationship between photon yields and F_M/F_0 were observed up to PFD's as high as 1000 $\mu E/(m^2 \cdot s)$. The relatively low photon yield of *C. rangiformis* podetia at a high F_M/F_0 value was not surprising because of its completely different morphology and because the illumination could reach only less than half of the photobiont layers.

We also investigated quantum yield and quenching parameters q_E and q_Q at different light intensities in order to check the role of non-photochemical, radiationless energy dissipation of PS II. According to Weis and Berry (1987), the dependence of photochemical yield (= quantum yield/ qQ, taking into account only open PS II centers) on qE is linear or slightly curved with hanging ends for higher plants. The results of such an analysis for lichen thalli are

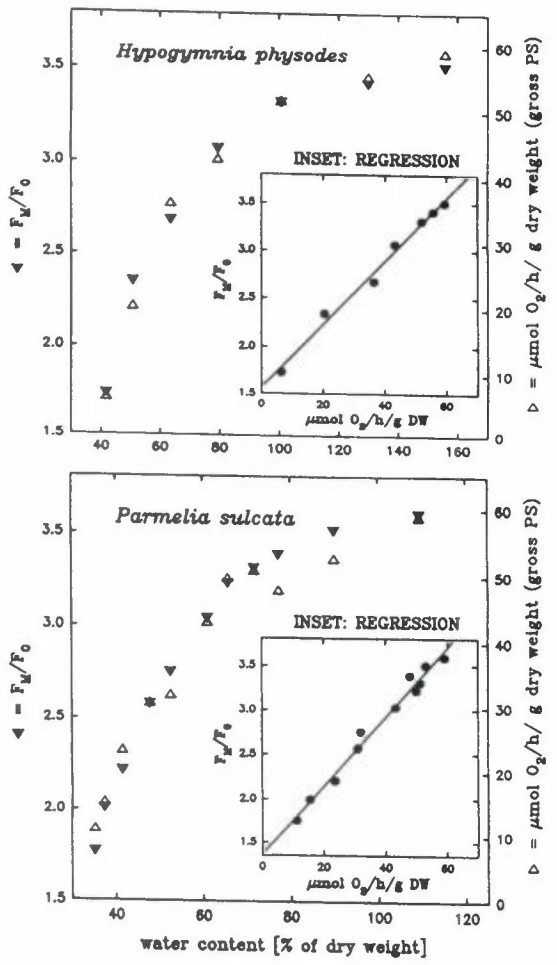

Figure 2. Dependence of chlorophyll fluorescence parameter F_M/F_0 and of gross photosynthetic activity (net photosynthetic O_2 evolution + dark respiration) at 150 $\mu E/(m^2 \cdot s)$ on the water content of *Hypogymnia physodes* (a) and *Parmelia sulcata* (b) (drying experiment). Insets: Regression of F_M/F_0 versus gross photosynthetic rate.

shown in Fig. 4. Only for one thallus of H. physodes with a low quantum yield a straight line could be found. The other curves strongly differed from those published for higher plants, as their characteristics were particularly high photochemical yields at low light intensities (low q_E values). This analysis showed, that in lichens, it is not possible to predict quantum yields from q_E and q_Q values.

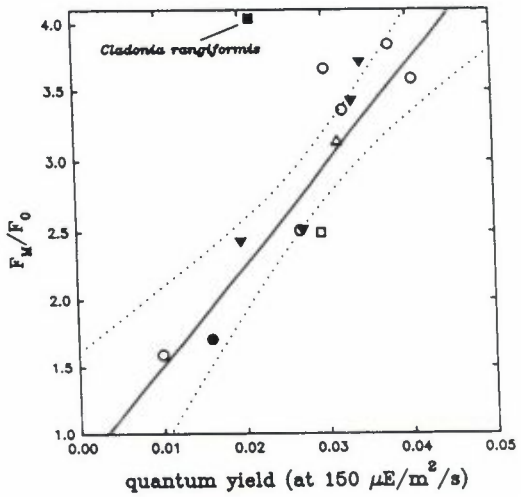

Figure 3. Plot of F_M/F_0 versus quantum yield of photosynthesis at 150 $\mu E/(m^2 \cdot s)$ red light for thalli of *Hypogymnia physodes* (○), *Parmelia sulcata* (▼), *Peltigera aphthosa* (△), *Sticta canariensis* (●), *Lobaria meridionalis* (□), and *Cladonia rangiformis* (■). The water contents of the thalli were greater than 70%. Quantum yield calculations were based on gross photosynthetic rates and on incident light intensity. A regression line with 95% confidence lines (dotted) was calculated from all thalli except *Cladonia rangiformis*.

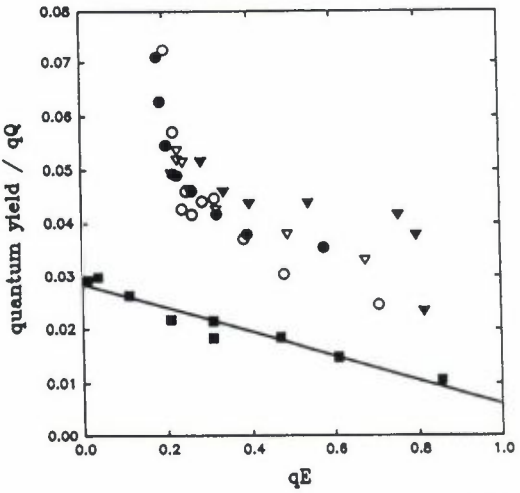

Figure 4. Plot of photochemical yield (= quantum yield/q_Q) versus quenching parameter q_E as obtained by variation of light intensity (between 20 and 1070 $\mu E/(m^2 \cdot s)$ red light). A linear regression was possible only for one thallus of *Hypogymnia physodes* (■) with a low F_M/F_0 ratio (1.6), but not for thalli of *Hypogymnia physodes* (▽, ▼) and *Parmelia sulcata* (○, ●) with F_M/F_0 values greater than 3.4.

4. Discussion

For the reversible depression of photosynthesis during desiccation of lichens, two mechanisms of regulation on the level of the pigment apparatus have been discussed up to now. For *Peltigera aphthosa* and *Cladonia impexa*, a state shift characterized by an increase in the proportion of energy distributed to photosystem I (PS I) has been reported (Jensen and Feige, 1987; Sigfridsson and Öquist, 1980). State shifts are also known for *Nephroma laevigatum* containing cyanobacteria (Canaani, 1988). However, in lichens with blue-green photobionts like *Peltigera rufescens*, the functional detachment of the major light harvesting pigment complex of PS II (phycobilin pigments) was found to be responsible for the depression of photosynthesis in the desiccated state (Bilger et al., 1989). In *Ramalina maciformis*, containing the green alga *Trebouxia*, an impairment of the functional connection between PS II and the chlorophyll *b* containing light harvesting complex could be observed by means of fluorescence excitation spectra at 77 K (Bilger et al., 1989). Our data on H. physodes and P. sulcata, as presented in Fig. 1, cannot directly confirm one of the mentioned processes. However, it is clearly shown, that F_0-quench precedes the decline of F_V/F_M and the situation therefore differs from the so-called 'midday depression' of photosynthesis of *Arbutus unedo* (Demmig-Adams et al., 1989) or from photionhibition of spinach at 4°C (Krause and Somersalo, 1989). In *R. maciformis* a marked increase in F_0 during rehydration from the desiccated state has been reported (Lange et al., 1989). Therefore, similar processes might occur in this lichen and in the lichens investigated here.

The following section discusses the characteristics of fluorescence decline and of photosynthesis depression for H. physodes and P. sulcata. Although many types of quenching of F_V/F_M and F_0 have been described, some of them can be ruled out because of the observed behaviour of fluorescence decline.

All quenching processes acting primarily at the reaction center site would influence only F_V/F_M, but not F_0 (cf. Neubauer and Schreiber, 1987; Schreiber and Neubauer, 1987). Therefore, they are unlikely to occur during drying of H. physodes and P. sulcata. At most, they are important during the last steps of dehydration. These considerations are supported by the finding, that the quench parameters q_E and q_Q particularly rise in this phase (experiment of Fig. 2, see results).

In the original models of Butler (1978), the parameter F_V/F_M, often referred to as photochemical efficiency of PS II, represents the energy transfer probabilities between antennae and reaction centers, and a decline of this parameter could — alternatively to a reaction center quench — secondly indicate impaired energy transfer to PS II. A simple detachment of light harvesting

chlorophyll protein (LHCP) from PS II core protein, however, would result in a concomitant increase in F_0. Apparently, such a process does not play a major role during drying of H. physodes and P. sulcata. In *R. maciformis*, on the other hand, the 686 nm fluorescence emission at 77 K, attributed to LHCP (Krause and Weis, 1984), relatively increased during rehydration and this would indicate a decoupling/coupling of LHCP to PS II during dehydration/rehydration cycles (Bilger et al., 1989).

Another possibility would be an increase in radiationless energy consumption within the antennae (e.g. thermal energy dissipation, k_D-process), which according to Butler (1978) would lead to a decrease of F_M, F_0 and, to a lesser extent of F_V/F_M. In an experimental approach with low concentrations of quinones, which increase thermal energy dissipation within the pigment bed, a decrease of F_0 and F_M without a proportional decrease of F_V/F_M was found (Kitajima and Butler, 1975). Only at higher concentrations and substantial decrease of F_0 and F_M the ratio F_V/F_M was diminished, too. This behavior of fluorescence parameters is very similar to those in our experiments upon drying. Therefore, an increase in K_D may indeed occur during some phases of water loss of H. physodes and P. sulcata. Recently, Demmig-Adams et al. (1990a) reported on an increase in k_D in several chlorophyceen lichens after exposure to high quantities of light. It has also been shown, that this is accompanied by zeaxanthin production (Demmig-Adams et al., 1990b), which is thought to be the natural quenching agent. The role of k_D increase during drying of lichens will therefore be elucidated by the determination of zeaxanthin levels in future investigations.

A possible further explanation for the decline of fluorescence parameters would be a state shift in favour of PS I (see above). A state shift would predominantly result in a F_0-quench and would leave F_V/F_M unaffected. Whether large state shifts really take place in H. physodes and P. sulcata during dehydration, must still be shown directly by 77 K fluorescence methods. Possibly, a combination of state shift and k_D-process occurs first and quenching at the reaction center dominates afterwards during dehydration of the investigated lichens.

Interestingly, the photon yields during drying are less closely related to the F_V/F_M – or the F_0-quench than to the fluorescence parameter F_M/F_0, which can also be written as $(F_V + F_0)/F_0$. If F_V/F_M indicates the effectivity of energy transfer ϵ_T (cf. Butler, 1978), the parameter F_M/F_0 indicates $1/(1-\epsilon_T)$ (simple recalculation). It is easy to see, that in the case of a decrease in ϵ_T the parameter F_M/F_0 also decreases, but in a hyperbolic manner. Therefore, this could mean that photon yield depends on ϵ_T in a hyperbolic manner. The linear relationship between F_M/F_0 and photon yield may also yield information about

the mechanism of photosynthetic depression, as photon yield decline produced by state shifts should not influence F_M/F_0. In contrast, a *massive* increase in k_D does diminish photon yield *and* F_M/F_0. The depression of photosynthesis during dehydration may therefore be mainly governed by a k_D process, i.e. an increase in radiationless energy dissipation within the antennae apparatus.

F_M/F_0 covariates with photon yield not only for individual lichen thalli with varying water content, but also with different vitality of the photobionts of different lichen thalli at a high water content (see Fig. 3). Together with the results of Fig. 2, this offers a convenient method of estimating lichen vitality in the field: by spraying with liquid water, a high water content can be achieved and subsequently, after a period of dark adaptation, the parameter F_M/F_0 can be determined within 0.8 s. The lichens could be left *in situ* and F_M/F_0 regarded as an estimator of photosynthetic potential of the thallus. Furthermore, a great advantage of F_M/F_0 for the field worker arises from its low temperature sensitivity. Therefore, it is more an indicator of photosynthetic potential of lichens than a precise indicator of actual photon yield. Of course, one should be aware, that neither the photosynthetic capacity at high light intensity nor the state of the dark reaction enzymes are reflected by F_M/F_0. Moreover, it does not account for different activities in the center and in the rim ranges of a thallus. In any case, however, the determination of F_M/F_0 is a more sensitive indicator of lichen health than observation by eye. Whether the determination of F_M/F_0 is valuable for crustose lichens, too, remains to be demonstrated. For lichens with cyanophyceen photobionts, this method unfortunately cannot be applied, since F_M does not reach its maximum value after periods of darkness (data now shown, cf. also Canaani, 1988).

On the other hand, the relatively time consuming determination of the quench parameters q_E and q_Q is only useful for the field worker, if special types of inhibition of photosynthesis, e.g. by heat stress (Bilger et al., 1987) or freezing stress (Krause and Somersalo, 1989), are to be investigated. They are not generally correlated to photon yields of lichens and the dependence of photochemical yield on q_E is not linear. A linear relationship, which does not even hold for all higher plants (Genty et al., 1989), would be needed for the prediction of photon yields on the basis of q_Q and q_E values (Weis and Berry, 1987). Our data show, however, that the dependence of lichen photon yield on light intensity cannot simply be explained by the regulation of radiationless energy dissipation at the PS II reaction centers.

Acknowledgements

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REFERENCES

Bilger, W., Schreiber, U., and Lange, O.L. 1987. Chlorophyll fluorescence as an indicator of heat induced limitation of photosynthesis in *Arbutus unedo*. In: *Plant Response to Stress*. J.D. Tenhunen, F.M. Catarino, O.L. Lange and W.C. Oechel, eds. Springer-Verlag, Berlin, pp. 391–399.

Bilger, W., Rimke, S., Schreiber, U., and Lange, O.L. 1989. 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.

Björkman, O. 1987. Low temperature chlorophyll fluorescence in leaves and its relationship to photon yield of photosynthesis in photoinhibition. In: *Topics in Photosynthesis, Vol. 9: Photoinhibition*. D.J. Kyle, C.B. Osmond and C.J. Arntzen, eds. Elsever, Amsterdam, pp. 123–144.

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

Canaani, O. 1988. Light regulation of electron transport in N_2-fixing cyanobacteria in lichens. *Symbiosis* **6:** 1–16.

Cornic, G., Le Gouallec, J.-L., Briantais, J.M., and Hodges, M. 1989. Effect of dehydration and high light on photosynthesis of two C_3 plants (*Phaseolus vulgaris* L. and *Elatostema repens* (Lour.) Hall f.). *Planta* **177:** 84–90.

Demmig, B. and Björkman, O. 1987. Comparison of the effect of excessive light on chlorophyll fluorescence (77 K) and photon yield of O_2 evolution in leaves of higher plants. *Planta* **171:** 171–184.

Demmig-Adams, B., Adams III, W.W., Winter, K., Meyer, A., Schreiber, U., Pereira, J.S., Krüger, A., Czygan, F.-C., and Lange, O.L. 1989. Photochemical efficiency of photosystem II, photon yield of O_2 evolution, photosynthetic capacity, and carotenoid composition during the midday depression of net CO_2 uptake in *Arbutus unedo* growing in Portugal. *Planta* **177:** 377–387.

Demmig-Adams, B., Máguas, C., Adams III, W.W., Meyer, A., Kilian, E., and Lange, O.L. 1990. Effect of high light on the efficiency of photochemical energy conversion in a variety of lichen species with green and blue-green phycobionts. *Planta* **180:** 400–409.

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

Genty, B., Briantais, J.-M., and Baker, N.R. 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochim. Biophys. Acta* **990:** 87–92.

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

Kitajima, M. and Butler, W.L. 1975. Quenching of chlorophyll fluorescence and primary photochemistry in chloroplasts by dibromothymoquinone. *Biochim. Biophys. Acta* **376:** 105–115.

Krause, G.H. and Weis, E. 1984. Chlorophyll fluorescence as a tool in plant physiology. II. Interpretation of fluorescence signals. *Photosynth. Res.* **5:** 139–157.

Krause, G.H. 1988. Photionhibition of photosynthesis. An evaluation of damaging and protective mechanisms. *Physiol. Plant.* **74:** 566–574.

Krause, G.H. and Somersalo, S. 1989. Fluorescence as a tool in photosynthesis research: application in studies of photionhibition, cold acclimation and freezing stress. *Phil. Trans. R. Soc. Lond. B* **323:** 281–293.

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

Neubauer, C. and Schreiber, U. 1987. The polyphasic rise of chlorophyll fluorescence upon onset of strong continuous illumination: I. Saturation characteristics and partial control by the photosystem II acceptor side. *Z. Naturforsch.* **42c:** 1246–1254.

Renger, G. and Schreiber, U. 1986. Practical applications of fluorescence methods to algae and higher plant research. In: *Light Emission by Plants and Bacteria.* Govindjee, J. Amesz and D.H. Fork, eds. Academic Press, New York, pp. 587–619.

Schreiber, U., Schliwa, U., and Bilger, W. 1986. Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. *Photosynth. Res.* **10:** 51–62.

Schreiber, U. and Bilger, W. 1987. Rapid assessment of stress effects on plant leaves by chlorophyll fluorescence measurements. In: *Plant Response to Stress.* J.D. Tenhunen, F.M. Catarino, O.L. Lange and W.C. Oechel, eds. Springer-Verlag, Berlin, pp. 27–53.

Schreiber, U. and Neubauer, C. 1987. The polyphasic rise of chlorophyll fluorescence upon onset of strong continuous illumination: II. Partial control by the photosystem II donor side and possible ways of interpretation. *Z. Naturforsch.* **42c:** 1255–1264.

Sigfridsson, B. and Öquist, G. 1980. 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.

Weis, E. 1985. Light- and temperature-induced changes in the distribution of excitation energy between photosystem I and photosystem II in spinach leaves. *Biophys. Acta* **807:** 118–126.

Weis, E. and Berry, J. 1987. Quantum efficiency of photosystem II in relation to energy-dependent quenching of chlorophyll fluorescence. *Biochim. Biophys. Acta* **849:** 198–208.