V. Photosynthetic activity of the lichen *Xanthoria elegans* in relation to the daily course of temperature and humidity, a field study in the Piora valley, Ticino, Switzerland.

***Donald Shuka*[1]*, Anxhela Rredhi*[2]*, Besimi Gurra*[1]*, Reinhard Bachofen*[3]

[1] Department of Biology, Faculty of Natural Science, University of Tirana, Tirana, Albania
[2] Matthias Schleiden Institute of Genetics, Bioinformatics and Molecular Botany, Friedrich Schiller University Jena, Jena, Germany
[3] Department for Plant- and Microbiology, University of Zürich, Zürich, Switzerland

Abstract

At high altitudes in the absence of vegetation of woody and scrubby plants lichens are dominant primary producers on boulders and rocks. To live there, lichens are forced to be well adapted to alpine environmental stress factors including extreme temperature changes and high solar radiation, including UV. This often results in high rock surface temperatures, low air humidity and drought. To study the dependence of the cellular activity of lichen on temperature and humidity, the initial fast chlorophyll fluorescence rise, indicating photosystem II (PS II) activity, was measured on site with dry and hydrated samples of *Xanthoria elegans*. *Xanthoria elegans* is frequently found on calcareous-dolomitic and siliceous rock surfaces, typically also on stony walls and roofs of old agricultural buildings in the Piora Valley, Ticino, Switzerland. Although a complete desiccation of the lichen leads to a full loss of the photosynthetic activity (Brock 1975, Lange & Matthes 1981, Lange et al. 1994, Lange 2003, Ding et al. 2013, Phinney et al. 2019), the lichen *Xanthoria elegans* fully recovered within few minutes upon rehydration. As measure for photosynthetic activity, the optimal yield of photosystem II, F_v/F_m, was determined. *Xanthoria elegans* reached maximum values of up to 0.63-0.67 in the hydrated state. The photosynthetic activity decreased during water loss and dropped more rapidly at temperatures higher than 20°C. Water saturation was followed by the electrical conductivity at the thallus surface. Drought is the main environmental stress regulating photosynthesis and growth in lichens in alpine regions.

Keywords: Lichens, fluorescence, Alps, dehydration/rehydration*, Xanthoria elegans*

Riassunto

In alta quota in assenza di vegetazione di piante legnose e arbustive i licheni sono produttori primari dominanti su massi e rocce. Per vivere a queste altitudini, i licheni

sono costretti ad adattarsi bene ai fattori di stress ambientale alpino: gli sbalzi di temperatura estremi e l'elevata radiazione solare, compresi i raggi UV. Questo si traduce spesso in alte temperature della superficie della roccia, bassa umidità dell'aria e siccità. Per studiare la dipendenza dell'attività cellulare del lichene dalla temperatura e dall'umidità, il rapido aumento iniziale della fluorescenza della clorofilla, indicante l'attività del fotosistema II (PS II), è stato misurato in loco con campioni secchi e idratati di *Xanthoria elegans*. Questo lichene si trova frequentemente su superfici di roccia calcare-dolomitica e silicea, tipicamente anche su muri di pietra e tetti di vecchi edifici agricoli nella Valle di Piora, Ticino, Svizzera. Sebbene un completo essiccamento del lichene porti a una totale perdita dell'attività fotosintetica (Brock 1975, Lange & Matthes 1981, Lange et al. 1994, Lange 2003, Ding et al. 2013, Phinney et al. 2019), il lichene *Xanthoria elegans* si è completamente ripreso in pochi minuti dopo la reidratazione. Come misura per l'attività fotosintetica, è stata determinata la resa ottimale del fotosistema II, F_v / F_m. *Xanthoria elegans* ha raggiunto valori massimi fino a 0,63-0,67 allo stato idratato. L'attività fotosintetica è diminuita durante la perdita d'acqua e si è ridotta più rapidamente a temperature superiori a 20°C. La saturazione dell'acqua è stata seguita dalla conduttività elettrica sulla superficie del tallo. La siccità è il principale stress ambientale che regola la fotosintesi e la crescita dei licheni nelle regioni alpine.

Parole chiave: Licheni, fluorescenza, Alpi, disidratazione/reidratazione, *Xanthoria elegans*

Introduction

Lichens cover about 8% of the terrestrial part of the world. They are found in a wide variety of habitats on earth, from the Arctic to the Antarctic, at sites of extreme environmental conditions lacking higher vegetation and over a wide range of altitudes (Galloway 1996). Taxonomically they belong to fungi, however, they are grouped separately because of the symbiosis with algae (*Chlorophyta*) or bacteria (*Cyanobacteria*) (Honegger 1991; Nash 1996, Barták 2014). Lichens are considered as stable self-supporting associations of a fungus (mycobiont) and a photosynthesizing partner (photobiont), where the mycobiont is the exhabitant, which forms the external structure that enclose the photobiont (Friedl & Büdel 1996). This structure forms the lichen body or the thallus. The fungus stores water and inorganic nutrients and provides these to the photobiont, which, by photosynthesis, feeds the fungus with carbohydrates and other organic compounds (Hawksworth 1988; Honegger 1991). Interestingly, the symbiosis between fungi and algae can occasionally include more than two bionts, (Tuovinen 2019).

Living in such different and stressing habitat types, lichens need high adaptability to survive. At higher altitudes, above the tree line with minimal vegetation, they are exposed to high UV radiation, frost, drought and other extreme environmental stress. Furthermore, in polar regions despite extreme environmental conditions, lichens are considered to be among the first organisms that occupy the surface of rocks (Galloway 1996, De Vera et al. 2008, Feuerer & Hawkworth 2007, Colesie et al. 2016).

Overall, above ground net primary production is linearly correlated to precipitation (Knapp & Smith 2001), this holds also for lichen. During the daily and the seasonal cycle lichens on rock surfaces undergo permanently drying and wetting processes, following air humidity (Kranner et al. 2008). Below minimal water content, photosynthesis stops and the photobiont reaches a state of dormancy (Kranner et al. 2008). Lichens as poikilohydric organisms are lacking the ability to maintain water homeostasis. For this a broad range of physiological adaptation mechanisms help the lichen to overcome inhospitable conditions, such as drought or excess light (Heber et al. 2000, Heber & Lüttge 2011).

Pioneering work by Lange and Matthes (1981) showed the lichens gas exchange, CO_2 assimilation and respiration, to be highly dependent on lichen moisture. Several reports described later that chlorophyll fluorescence in different species of lichens is as well influenced by environmental factors, especially by thallus humidity and temperature (Lange et al. 2001, Heber & Lüttge 2011, Wu et al. 2013a; Wu et al. 2013b). Desiccation acts as quencher of chlorophyll fluorescence (Maksimov et al. 2014), yet lichen can survive for long drought periods, even at higher temperatures on the surface of rocks (Chakir & Jensen 1999; Gauslaa & Solhaug 2004), but recover rapidly after water uptake.

In our study we have investigated the photosynthetic performance using the fast chlorophyll fluorescence rise in relation to the hydration state and the temperature in situ with the foliose lichen *Xanthoria elegans* (Link) Th. Fr. with *Trentepohlia* sp. as photobiont (Beck et al. 1998), which is widely found on the surface of calcareous-dolomitic and granitic rocks and the stony walls and roof of a building of the Alpine Center Cadagno in the Piora valley in the Swiss Alps at 1900 m a.s.l.

Fast chlorophyll-*a* fluorescence techniques have been established to measure the fitness of or the stress upon plants caused by environmental factors such as temperature, water availability or nutrients. This non-invasive and rapid technique is ideal for field measurements (Kalaji et al. 2016). A strong light flash initiates chlorophyll-*a* fluorescence to rise from a minimal value at time 10 µs ($O = F_o$ = initial fluorescence) to a maximum at 0.3 to 1s ($P = F_m$ = maximal fluorescence). When plotted in a logarithmic scale, this transient shows polyphasic kinetics, with steps at 2 ms (J-step) and 30 ms (I-step). This sequence has been named the OJIP-test (Strasser & Strasser 199, Strasser *et al.* 2004). The F_v/F_m value is frequently used in the literature, designating the maximum quantum yield of the photosystem II, F_v being the variable fluorescence (F_m - F_o). For a detailed discussion on the theory behind the OJIP-test see Strasser et al. (2004) and Stirbet et al. (2018).

Materials and Methods

Xanthoria elegans is well known for its wide distribution range from the sea level up to high altitudes in alpine regions. It is common on silicate rock surfaces, schist and gneiss. We found the lichen dominating on the granitic walls of many old the buildings including the ones of the Alpine Biology Center originating from the 16th century in the Piora valley (Canton Ticino) in the Swiss Alps. The center is located at 46.546487, 8.715996, at an

altitude of 1960 m. The size of *X. elegans* thalli between 3 and 8 cm suggested a live age of around 50 to 100 years, however, some rocks are completely overgrown with *Xanthoria* (Fig. 1 and Spinelli & Vust 2012).

Fig. 1: Rocks on the wall on the eastern side of the building of the Alpine Center Cadagno.

The photosynthetic activity of the lichen was studied at two different expositions, on the western and the eastern side on the walls of the building, by fast chlorophyll fluorescence using the portable fluorometer Pocket PEA (Hansatech, King's Lynn, England). Excitation intensity of 3500 µmol photons m^{-2} s^{-1} with red light of 650 nm for 3 sec was used. The fluorescence signal with high temporal resolution from 10 µsec to 3 sec shows a polyphasic kinetic when plotted in a log time scale. The instrument determines the initial (F_o) and maximum (F_m) fluorescence and calculates the variable fluorescence (F_v) over the induction phase and provides further specific parameters such as the potential quantum yield of PS II (F_v / F_m), the relative fluorescence at specific time points during the fluorescence rise, or the performance index (PI_{ABS}) (Jensen & Kricke 2002). The thalli were measured fixed on the rocks at their site of growth and actually prevailing environmental conditions. Therefore commercial leaf clips could not be used, instead a foam rubber ring glued on the fixing part of a leaf clip ensured a tight contact to the lichen and prevented interferences by daylight when the instrument was pressed on the thalli during the measurement. Each measurement was repeated 10 times within 2 min. After the first sampling, the lichens were sprayed with tap water and their rehydration followed by fluorescence measurements in time intervals of about 1 hour. In parallel the following environmental parameters were recorded: Air humidity and temperature were measured using a PCE 555 thermo-hygrometer, thallus moisture was estimated with two methods: the electric resitance of the thallus surface with a Brennenstuhl MD moisture detector (www.brennenstuhl.com) modified with 5 cm long flat electrodes and the dielectric moisture detector Trotec BM31 (www.trotec.com). These instruments are calibrated for measuring bound water in wood or concrete, for this reason the numbers obtained had to be calibrated for lichen thalli. As *Xanthoria elegans* could not be removed from the rock substratum without distroying the thallus, the lichen *Xanthoria parietina* grown on a smooth concrete wall was used. Air-dried thalli were separated from the concrete surface, then soaked for 30 min. in tap water and the attached water removed with soft paper. The thalli were kept at room temperature until the air-dried state was reached. In regular intervals the electric conductivity, the dielectric signal and the weight was measured.

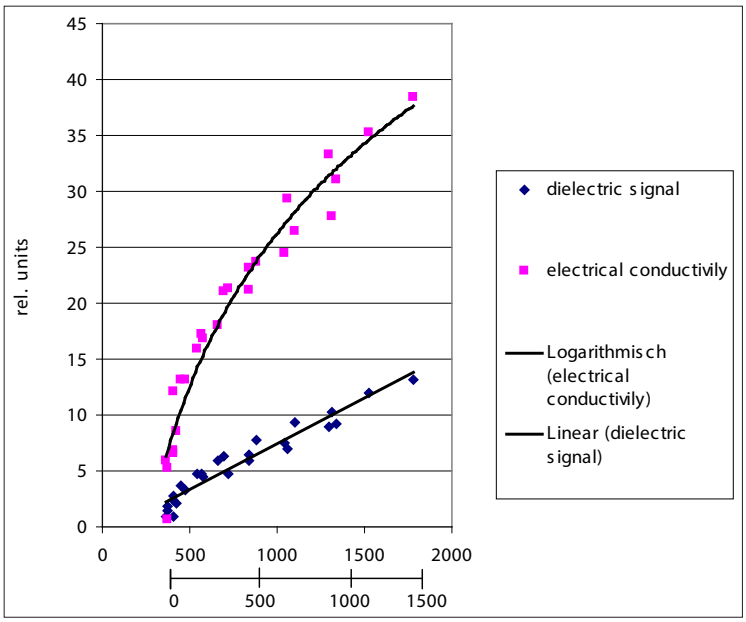

Fig. 2: Calibration curve for the electric conductivity and the dielectric signal. The dry weight of the Xanthoria parietina thallus was 366 mg. Each point was obtained after multiple 20 min soaking in water followed by a drying process at room temperature with humidity measurements in 60 min intervals. The added x axis indicates the weight of the water absorbed by the lichen.

Thallus temperature was obtained with a Voltcraft IR-352 thermometer.
All instrumental datas were analysed using Microsoft Excel.

Results and discussion

The instrument calibration (Fig. 2) clearly showed the relation between weight and the signal from the two different moisture detectors. The calibration curves resulted in a slightly logarithmic relation between thallus weight and electric conductivity and a linear dependence with the dielectric measurement (Fig. 2). These arbitrary units were then converted in % saturation. The fast water saturation allowed the lichen to store for longer times large amounts of water within the thallus, mandatory for the photosynthetic process.
In the field at ambient conditions and in air-dried state *Xanthoria elegans* showed no fluorescence rise, the signal remained below 50 arbitrary units and was very noisy (Fig. 3a). Following the hydration of the lichens by spraying with tap water, the fluorescence induction signals rapidly recovered and reached values up to 20'000 units. Due to the local environmental conditions the fluorescence activity differed between the samples from the western and eastern side of the building. Ten single fluorescence scans in short intervals between 10 and 15 seconds from different positions of the same lichen thallus resulted in large differences in photosynthetic activity (Figs. 3a -3d). Note the different scaling of the Y-axis.

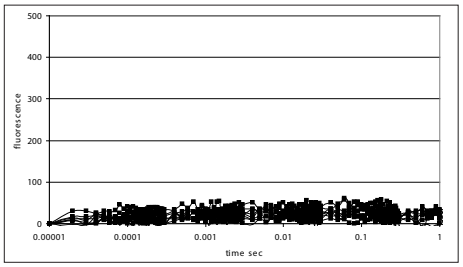

Fig. 3a: Fluorescence induction by Xanthoria on the eastern side of the building in dry state before wetting (2.8.2017, 08.45).

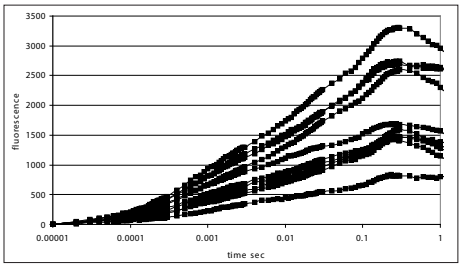

Fig.3b: Fluorescence induction by Xanthoria on the eastern side of the building one hour after wetting (2.8.2017, 09.05).

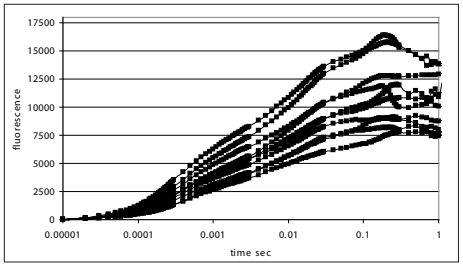

Fig. 3c: Fluorescence induction by Xanthoria on the western side of the building in slightly wet state after nightly rain before wetting (2.8.2017, 08.50)

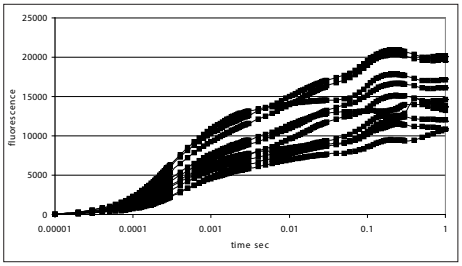

Fig. 3d: Fluorescence induction by Xanthoria on the western side of the building one hour after wetting (2.8.2017, 10.15).

This demonstrates that thallus patches of the lichen of about 3 to 6 cm in size were quite heterogeneous concerning the actual local photosynthetic activity, as described earlier by Baruffo et al. (2008). Between the lowest and the largest fluorescence signal differences by a factor of 2 (Fig. 3d) to 5 were observed (Fig. 3b). This may be due to different factors, such as a heterogenic distribution of the photobiont within the lichen tissue, varying chlorophyll content in the algal cells, or a heterogenic relative humidity in the lichen thalli due to an uneven uptake of water at different sites of the lichen. Furthermore, *Xanthoria* contains variable amounts of Parietin, an anthraquinone like secondary compound shielding excess illumination (Solhaug & Gauslaa 2012) which may not be equally distributed in the thallus.

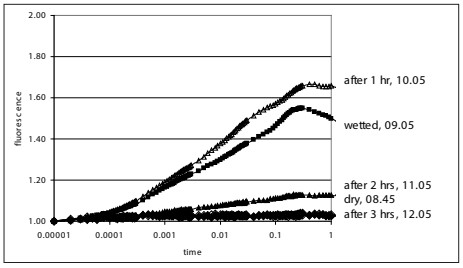

Fig. 4a: Time course of F_t/F_o induction curves at a site on the eastern side of the building. Mean of 10 measurements.

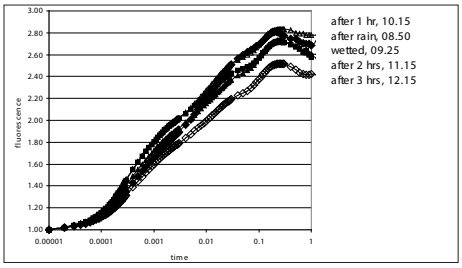

Fig. 4b: Time course of F_t/F_o induction curves at a site on the western side of the building, Mean of 10 measurements

In Fig. 4a and 4b the rapid rise of the fluorescence is depicted as F_t / F_o, showing the kinetics of the rise of the fluorescence (F_t) in relation to the minimum fluorescence F_o at time zero. The sun exposed eastern side showed hardly a fluorescence signal before wetting (Fig. 3a and 4a). Fluorescence raised rapidly after wetting, however, somewhat higher values were finally reached only one hour later. Although the recovery starts within minutes, it takes up to one hour until the whole thallus is hydrated and the photobiont active. After 2 hours most of the activity was lost and after 3 hours in the sun the activity was similar to the one at the start of the experiment.
In contrast the data on the western side of the building demonstrated in the morning only a minor effect of the artificial wetting, as in the night before some precipitation had wetted the western front of the building. A minor drop in activity was observed only after 3 hours at a sunny day where the western side remained in the shadow. A large activity difference between and within the two sites must be noted, indicating the importance of micro niches in field experiments.
The often-used relative presentation of the fluorescence data with $F_o = 0$ and $F_m = 1$ was not possible for partially or fully dried lichen, due to the high noise level of the signal (Fig. 5a). The structure of the Chl *a* fluorescence induction transients of the lichen *X. elegans* is less pronounced compared to the ones of higher plants (Strasser & Strasser 1995, Strasser et al. 2004).

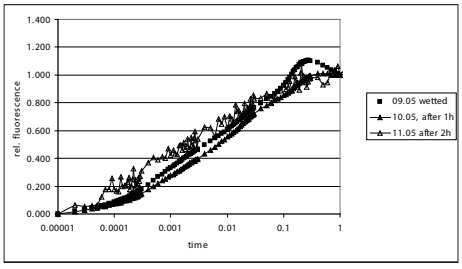

Fig. 5a: Time course of relative fluorescence induction at a site on the eastern side. Mean of 10 measurements

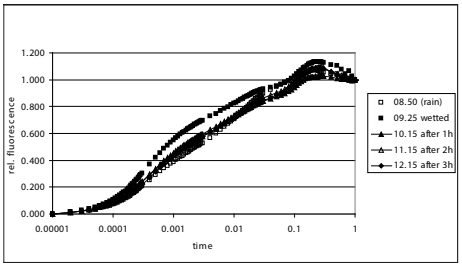

Fig. 5b: Time course of relative fluorescence induction at a site on the western side. Mean of 10 measurements

While in Fig. 5a (eastern side) the J and I steps are hardly seen, they are better visible in Fig. 5b with the less stressed thalli on the western side of the building. Typically the value of F_o is lower in non-stressed organisms (Feng et al. 2010), $F_{20\mu s}$ stays between 0.010 and 0.014, while on the eastern side in dry state (08.45, 11.05, 12.05) it increased up to 10-fold.

The ratio F_v/F_m is frequently used as measure of the photosynthetic activity, although compared with other markers extracted from fast fluorescence kinetics, the F_v / F_m is less sensitive to environmental influences. F_v / F_m indicates the efficiency of the electron transport from photosystem II to the primary acceptor quinone. In higher plants it reaches a maximum around 0.85. In lichen the F_v / F_m varies depending on the water content from near 0 in dried state up to 0.7 for fully water saturated state. At humidity controlled conditions the photosynthetic activity of a wide range of lichen species started between 75% and 90% relative humidity (Phinney et al. 2019), depending on the photobiont. Species with *Trentepohlia* sp. reached higher F_v / F_m ratios compared to other photobionts

and became active at lower relative humidity. This fits well to the observed seasonal variations of some basic fluorescence rise parameters (Baruffo & Tretiach 2007).

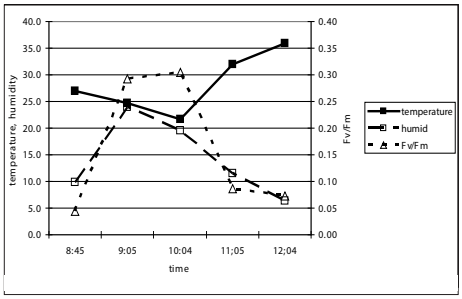

Fig. 6a: Time course of temperature, humidity of the lichen thallus and F_v/F_m on the eastern side, 1.8.2017. (lichen humidity as electrical conductivity in arbitrary units)

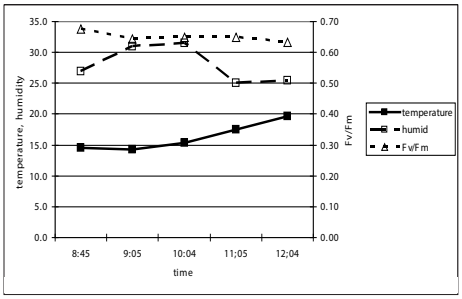

Fig. 6b: Time course of temperature, humidity of the lichen thallus and F_v/F_m on the western side, 1.8.2017. (lichen humidity as electrical conductivity in arbitrary units)

The time course of F_v/F_m during the day in *Xanthoria elegans* clearly follows the values of the electrical conductivity of the lichen thallus (Figs. 6a and 6b). In contrast, the thallus temperature gives a mirror image to the relative humidity: when its temperature increases, the humidity and the F_v/F_m drop and vice versa. The lichen thallus seems to be in a rapid equilibrium with the relative air humidity determined by the actual environmental conditions (Phinney et al. 2018, Phinney et al. 2019). While the mycobiont acts as buffer for the water content, the photobiont determines the threshold for the photosynthetic activity. The F_v/F_m value on the western side of the building stayed the full morning between 0.63 and 0.68, a number which seems typical for active lichen (Phinney et al. 2020); so far no higher values have been published. This long during active state is the result of some rain in the night before, wetting the wall. In contrast the sun exposed but rain sheltered eastern side is air-dried in the morning, leading to minimal photosynthetic activity. Artificial wetting brings the F_v/F_m to around 0.3, but 2 hours later, while warmed up by the sun, the signal decreased drastically and the F_v/F_m dropped to 0.09. Such results cannot be used for further calculations.
When the F_v/F_m is depicted as a function of lichen humidity or temperature, a clear correlation on lichen humidity and temperature is evident (Fig. 7a and 7b).

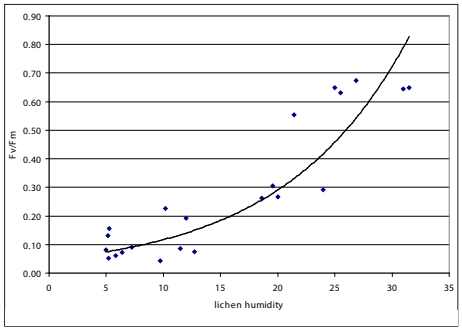

Fig. 7a: Relation between F_v/F_m and humidity, with exponential trendline.

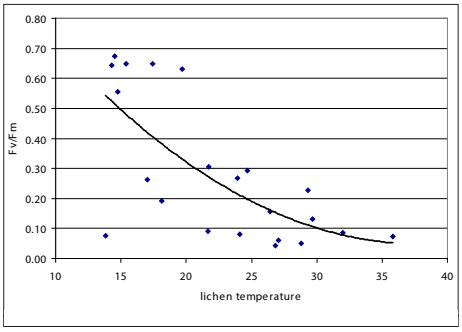

Fig. 7b: Relation between F_v/F_m and temperature, with polynomic trendline.

Conclusion

The fact that the fast Chlorophyll fluorescence rise provides a sum of information on the photosynthetic activity of plants makes it a valuable tool for ecophysiological studies to evaluate environmental effects on plant metabolism. Under natural conditions, F_v/F_m, an accepted indicator of the photosynthetic activity, remains at a relative stable high level and decreases when the photosynthetic part of the lichen turned into stress conditions. The experiments show that the thallus of *Xanthoria elegans* is quite heterogeneous concerning the photosynthetic activity, due to various internal and external factors. In addition we confirmed that in lichens fast fluorescence rise is strongly related to the water content of the lichen tissue and is indirectly determined by the air temperature and solar insulation. This allows in alpine regions only for short periods of activity resulting in a yearly growth of very few mm of thallus size.

Acknowledgement

We thank Reto Strasser for the use of the PEA fluorometer and many fruitful discussions, Alberto Spinelli for the introduction in lichen biology, and the Alpine Biological Center Piora (http://www.cadagno.ch) for the nice hospitality. The work was generously supported by the Hydrobiologie-Limnologie Stiftung für Gewässerforschung, Zürich, the Stiftung Dreiklang für ökologische Forschung und Bildung, Basel, the Zürcher Universitätsverein, ZUNIV, Zürich, the Department of Plant and Microbial Biology of the University of Zürich and the Stiftung Centro di Biologia Alpina Piora, Bellinzona.

References

Bartak M. (2014): Lichen Photosynthesis. Scaling from the cellular to the organism level, in: Advances in Photosynthesis and Respiration 39: 379-400.

Baruffo L. & Tretiach M. (2007): Seaonal variations of Fo, Fm and Fv/Fm in an epiphytic population of the lichen *Punctelia subudecta* (Nyl.) Krog. The Lichenologist 39: 555-565.

Baruffo L., Piccotto M. & Tretiach M. (2008): Intrathalline variation of chlorophyll a fluorescence emission in the epiphytic lichen *Flavoparmelia caperate*. Ecologist 111: 455-462.

Beck A., Friedl T. & Rambold G. (1998): Selectivity of photobiont choice in a defined lichen community: inferences from cultural and molecular studies. New Phytologist 129: 709-720.

Brock T. D. (1975): The effect of water potential in photosynthesis in whole lichens and in their algal components. Planta 124: 13-23.

Chakir S. & Jensen M. (1999): 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. Plantarum 105: 257-265.

Colesie C., Gree T. G. A., Raggio J. & Büdel B. (2016): Summer activity patterns of Antarctic and high alpine lichen-dominated biological soil crusts – similar but different? Arctic Antarctic and Alpine Research 48: 449-460.

De Vera J.-P., Rettberg P. & Ott S. (2008): Life at the limits: Capacities of isolated and cultured lichen symbionts to resist extreme. Origin of Life Evolution Biosphere 38: 457-468.

Ding L., Zhou Q. & Wei J. (2013): Estimation of *Endocarpon pusillum* Hedwig carbon budget in the Tengger Desert based on its photosynthetic rate. Science China, Life Sciences 56: 848-855.

Feuerer T. & Hawkworth D. L. (2007): Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's floristic regions. Biodiversity and Conservation 16: 85-98.

Friedl T. & Büdel B. (2008): Photobionts. In: Nash, T.H., Lichen Biology, Cambridge University Press, Cambridge p. 9-26,

Galloway D. J. (1996): Lichen biogeography. In: Nash, T. H., Lichen biology. Cambridge University Press, p: 199-216.

Gauslaa Y. & Solhaug K. A. (2004): Photoinhibition in lichens depends on cortical characteristics and hydration. The Lichenologist 36: 133-143.

Hansatech Operations Manual (2006).

Hawksworth D. L. (1988): The variety of fungal algal symbioses, their evolutionary significance, and the nature of lichens. Botanical J. Linnean Society 96: 3-20.

Heber U., Bilger W., Bligny R. & Lang, O. L. (2000): Phototolerance of lichens, mosses and higher plants in an alpine environment: analysis of photoreactions. Planta 211: 770-780.

Heber U. & Lüttge U. (2011): Lichens and bryophytes: light stress and photoinhibition in desiccation/rehydration cycles – mechanisms of photoprotection. In: Plant desiccation tolerance, Ecol. Studies 215: 121-137.

Honegger R. (1991): Functional aspects of the lichen symbiosis. Annual Reviews Plant Physiology Plant Molecular Biology 42: 553-578.

Honegger R. (1996): Mycobionts. In: Nash, T. H., Lichen biology. Cambridge University Press, Cambridge, p. 24-36.

Jensen M. & Kricke R. (2002): Chlorophyll fluorescence measurements in the field: assessment of the vitality of large numbers of lichen. In: Nimis, P. L., Scheidegger, C. and Wolseley, P. A. (eds.), Monitoring with lichens – monitoring lichens, p. 327-332.

Kalaji H. M., Jajoo A., Oukarroum A., Brestic M., Zivcak M., Samborska I. A., et al. (2016): Chlorophyll a fluorescence as a tool to monitor physiological status of plants under stress conditions. Acta Physiol. Plant. 38, 102. DOI: 10.1007/s11738-016-2113-y

Knapp A.K. & Smith M.D. (2001): Variation among biomass in temporal dynamics of aboveground primary production. Science 291: 481-484.

Kranner I., Beckett R., Hochman A. & Nash T. H. (2008): Desiccation-tolerance in lichens: a review. Bryologist 111: 576-593.

Lange O. L. & Matthe, U. (1981): Moisture-dependant CO_2 exchange of lichens. Photosynthetica 15: 555-574.

Lange O.L., Meyer A., Zellner H. & Heber U. (1994): Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namid Desert. Funct. Ecol. 8: 253-264.

Lange O. L., Green T. G. A. & Heber U. (2001): Hydration-dependent photosynthetic production of lichens: what do laboratory studies tell us about field performance. J. Experim. Botany 52: 2033-2042.

Lange O.L., (2003): Photosynthetic productivity of the epilithic lichen *Lecanora muralis*: long-term field monitoring of CO_2 exchange and its physiological interpretation III. Diel, seasonal, and annual carbon budgets. Flora 198: 277-292.

Maksimov E. G., Schmitt F. J., Tsoraev G. V., Ryabova A. V. & Friedrici T. (2014): Fluorescence quenching in the lichen *Peltigera aphthosa* due to desiccation. Plant Physiology and Biochemistry 81: 67-73.

Nash T. H. (1996): Lichen Biology. Cambridge University Press, Cambridge.

Oukarroum A., El Gharous M. & Strasser R. J. (2017): Does *Parmelia tiliacea* lichen photosystem II survive at liquid nitrogen temperatures? Cryobiology 74: 160-162.

Oukarroum A., Strasser R. J. & Schansker G. (2012): Heat stress and the photosynthetic electron transport chain of the lichen *Parmelia tiliacea* (Hoffm.) in the dry and the wet state: differences and similarities with the heat stress response of higher plants. Photosynthesis Research 111: 303-314.

Phinney N. H., Solhaug K. A. & Gauslaa Y. (2018): Rapid resurrection of chlorolichens in humid air: specific thallus mass drives rehydration and reactivation kinetics. Environm. Experiment. Botany 148: 184-191

Phinney N. H., Solhaug K. A. & Gauslaa Y. (2019): Photobiont-dependent humidity threshold for chlorolichen photosystem II activation. Planta 250: 2023-2031.

Solhaug K. A. & Gauslaa Y. (2012): Secondary lichen compounds as protection against excess solar radiation and herbivores. In: Progress in Botany 73 (Lüttge, U. et al., editors), 283-304.

Spinelli A. & Vust, V. (2012): Licheni della Val Piora (Cantone Ticino, Svizzera). In: Biodiversità della Val Piora (F. Rampazzi, M. Tonolla and R. Peduzzi, eds.), Società ticinese di scienze naturali Lugano, 11: 147-155.

Stirbet A., Lazar D., Kromdijk J. & Govindjee (2018): Chlorophyll a fluorescence induction: Can just a one-second measurement be used to quantify abiotic stress responses. Photosynthetica 56: 86-104. DOI: 10.1007/s11099-018-0770-3

Strasser B. J., & Strasser R. J. (1995): Measuring fast fluorescence transients to address environmental questions: the JIP-test. In: Photosynthesis: From light to biosphere. Proceedings of the 10th International Photosynthesis Congress. Montpellier, Mathis, P. (ed.), pp. 977-980. Dordrecht, Netherland, Kluwer Academic Publishers.

Strasser R. J., Srivastava A., & Tsimili-Michael M. (2004): Analysis of the chlorophyll a fluorescence transient. In: Chlorophyll a fluorescence. A signature of photosynthesis. Papageorgiu G. C., Govindjee (eds.), Advances in Photosynthesis and Respiration 19, pp. 321-362. Dordrecht, Netherland, Springer.

Tuovinen V., Ekman S., Thor G., Vanderpool D., Spribille T. & Johannesson H. (2019): Two basidiomycete funghi in the Cortex of Wolf Lichens. Current Biology 29: 476–483.

Wu L., Lan S., Zhang D. & Hu C. (2013a): Functional reactivation of photosystem II in lichen soil crusts after long term desiccation. Plant Soil 369: 177-186.

Wu L., Lan S., Zhang D. & Hu C. (2013b): Recovery of chlorophyll fluorescence and CO_2 exchange in lichen soil crusts after rehydration. Europ. J. Soil Biology 55: 77-82.

Yemets O., Gauslaa Y., & Solhaug K.A. (2015): Monitoring with lichens - Conductivity methods assess salt and heavy metal damage more efficiently than chlorophyll fluorescence.