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In situ Comparison of Daily Photosynthetic Activity Patterns of Saxicolous Lichens and Mosses in Sierra de Guadarrama, Central Spain

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Abstract. *Diurnal time courses of* in situ *photosynthetic activity of lichens and mosses growing on a granitic boulder in Sierra de Guadarrama, central Spain, were measured during five days in October, 1993. A portable chlorophyll fluorometer was used for assessing photosynthetic activity of four lichen and two bryophyte species together with photosynthetic photon flux density (PPFD) incident at the thallus surface and thallus temperature. The quantum efficiency of photosystem II (PSII; $\Delta F/Fm'$), and the apparent electron transport rate through PSII ($\Delta F/Fm' \times$ PPFD) were calculated. The weather changed from wet to dry conditions during the period of measurements. Exposure- and species-related differences in the photosynthetic performance were observed. Both moss species,* Hedwigia ciliata *and* Grimmia pulvinata, *showed no sign of thallus drying and the photochemical efficiency of both species was mainly controlled by the diel patterns of PPFD. In contrast, water loss was the major limiting factor for metabolic activity in the lichen species. Exposure- and species-related changes in thallus color indicating water loss occurred as early as on 18 October in* Umbilicaria spodochroa *and with a 24-hr-delay in* Lasallia hispanica *and* Umbilicaria grisea *(19 October). In* Lasallia pustulata *thallus color changes were visible only on 20 October when dry weather induced severe dehydration in all lichen species. Within the same species, different microhabitat resulted in a different physiological performance depending on water balances as well as on PPFD conditions. The data demonstrate the potential of field measurements of chlorophyll a fluorescence as a non-intrusive tool for the analysis of the* in situ *photosynthetic performance of poikilohydric organisms without altering rates of water loss and uptake, which are always crucial in the photosynthetic performance of poikilohydric organisms under natural conditions.*

In contrast to attached leaves of higher plants, which are easily accessible (Schulze et al. 1982), the 3-dimensional thallus structure of lichens and bryophytes and their often close attachment to their substrate cause serious technical problems for *in situ* measurements of photosynthetic activity of these poikilohydric organisms. The development of the CO_2-porometer (Lange et al. 1984, 1985), which minimizes the time periods of the exposure of the sample in the measuring cuvette, resulted in a substantial increase of knowledge about the diurnal photosynthetic activity patterns of cryptogams under "natural" or semi-natural conditions (Bruns-Strenge & Lange 1991; Hahn et al. 1989, 1993; Kappen & Breuer 1991; Kappen et al. 1996; Lange et al. 1991, 1996; Sancho et al. 1997*a,b*; Schroeter et al. 1991*a,b*). The crucial problem, however, remained unresolved: the lichen or moss sample still had to be removed from its habitat at regular intervals even if only for short periods to measure the gas exchange. Modifications to the technique allowed the *in situ* measurement of CO_2 gas exchange of crustose lichens without removing them from their substratum (Kappen et al. 1990), but the system was very laborious and was little used. Recently, Lange and coworkers (Lange & Green 1996; Lange et al. 1997) developed a fixed version of the CO_2-porometer which by automatic enclosure of an epilithic lichen thallus allows unattended, intermittent measurements of the CO_2 gas exchange under natural conditions. However, even this system has limitations, in particular, the occasional enclosure of the sample in a cuvette will still lead to changes in water exchange because of unavoidable alterations to the radiation environment and through deflection of rain and fog and the sample is still required to be removed from its original location with consequent disruption from water supply from the substrate.

Progress in the measurement of chlorophyll *a*

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fluorescence has now made available a different technique for the assessment of photosynthetic activity. Primarily used as a tool for the quantification of stress effects on photosynthesis (Krause & Weis 1991), highly sensitive chlorophyll fluorometers, e.g., PAM-technique (*P*ulse-*A*mplitude-*M*odulation), now allow rapid, non-destructive measurements of the quantum efficiency of photosystem II (PS II) under ambient light conditions without special pre-adaptation of the sample (Bolhàr-Nordenkampf et al. 1989; Schreiber et al. 1986, 1994). Portable PAM-systems are now available that allow measurements of *in situ* photosynthetic performance making them especially suitable for studies on samples, such as lichens and mosses, which are difficult to handle in gas exchange measurements (Schroeter et al. 1997*b*), and for automatic measurements over long periods even in extreme environments like the Antarctic (Leisner et al. 1996; Schroeter 1991; Schroeter et al. 1991*b*, 1997*a*). Although PS II activity measured by fluorescence may allow calculation, with certain assumptions, of CO_2 fixation for higher plants (Edwards & Baker 1993; Genty et al. 1989) this is far from certain for lichens and mosses and, in these groups, it can really only be used as an indicator of activity rather than as an absolute indicator of carbon gain (Green et al. 1998; Schroeter et al. 1995; Sundberg et al. 1997). In the study presented here we have used the chlorophyll *a* fluorescence yield as a tool to assess the photosynthetic performance of different cryptogams, mosses and lichens, growing together on one large boulder in the Sierra de Guadarrama in central Spain. The primary objective was to use the non-intrusive methodology to demonstrate the complex interactions between, position, microclimate, and plant form that may not be revealed when the samples are removed for measurement.

SITE DESCRIPTION, VEGETATION, PLANT MATERIAL, AND METHODS

Research site.—The field study was carried out on a large granitic rock, about 0.5 km from the Estación Biogeológica del Ventorllo (CSIC), Sierra de Guadarrama, Madrid, at 1550 m a.s.l. (see also Sancho et al. 1997*b*). The boulder was surrounded by a pine forest (*Pinus sylvestris* L.) mountain community Junipero-Cytisetum oromediterranii pinetosum sylvestris Rivas Martínez (Rivas-Martínez 1988). The granitic boulder, 4–6 m high and 4–5 m wide, was almost totally covered by cryptogams. The northerly and westerly exposed surfaces had a rich lichen and moss vegetation with typical saxicolous species of the mediterranean mountains, such as *Lasallia hispanica* (Frey) Sancho & Crespo, *L. pustulata* (L.) Mérat, *Parmelia pulla* Ach., *Umbilicaria freyi* Codogno, Poelt & Puntillo, and *U. grisea* Hoffm., growing together with several epiphytic lichens such as *Hypogymnia farinacea* Zopf, *Parmelia sulcata* Taylor, *P. tiliacea* (Hoffm.) Ach., *Platismatia glauca* (L.) W. Culb. & C. Culb., and *Pseudevernia furfuracea* (L.) Zopf (Table 1). The eastern and southern surfaces of the boulder were also densely covered by lichens, but with fewer mosses. Although cryptogamic saxicolous communities were dominated by macrolichens (Table 1), crustose lichens were also frequent, mainly on eastern and southern exposures. Among them *Aspicilia* gr. *cinerea*, *Lecanora bolcana* (Pollin.) Poelt, *Lecidea atrobrunnea* (Lam. & DC.) Schaer., and *Protoparmelia badia* (Hoffm.) Hafellner were the most common crustose species. A list of the macrolichens and mosses growing on the different surfaces of the boulder is given in Table 1, together with an index of the relative abundance of each species (Braun-Blanquet 1964).

Species studied.—Four different species of macrolichens and two moss species were investigated. The species were selected to represent different exposure, water uptake strategies, and growth form. *Lasallia hispanica* (Frey) Sancho & Crespo is characterized as an aerohygrophytic and photophilic species, while *L. pustulata* (L.) Mérat is a substrate-hygrophytic lichen that prefers less inclined slopes with trickling water (Sancho & Crespo 1989; Sancho & Kappen 1989). Both species grow sympatrically in the supra- and oromediterranean belts. *Umbilicaria spodochroa* (Ach.) DC. is a typically substrate-hygrophytic species that occasionally occurs associated with *Lasallia* species if enough surface water is available. In contrast, *Umbilicaria grisea* Hoffm is an aerohygrophytic thermophytic lichen that grows in the supra- and mesomediterranean belts on strongly inclined or overhanging rock faces, more or less protected from rainfall (Sancho & Kappen 1989; Sancho et al. 1997*b*). The moss, *Hedwigia ciliata* (Hedw.) P. Beauv., shows a nearly cosmopolitan distribution and is common on dry granitic boulders and rock ledges in the open or in forests. *Hedwigia ciliata* is known to grow preferably on inclined to vertical north-facing rock walls, which have low potential rates of evaporation and comparatively high water availability (Alpert & Oechel 1984, 1987). *Grimmia pulvinata* (Hedw.) Sm. is the most common *Grimmia* species in Europe. It grows in small cushions that are able to preserve water for extended periods of time even in dry habitats (Probst 1986).

Chlorophyll a fluorescence measurements.—The effective quantum yield of photosystem II ($\Delta F/Fm'$) of the selected lichen and moss samples was measured in regular intervals using a PAM-2000 portable fluorometer (Walz Gmbh, FRG) as described in Schroeter et al. (1992). The fluorometer was equipped with a special microquantum and temperature sensor (FL-2030, Walz Gmbh, FRG) and the photosynthetic photon flux density (PPFD, $\mu mol\ m^{-2}\ s^{-1}$) incident at the thallus surface as well as the thallus temperature were determined simultaneously with the fluorescence measurement. Pulses of measuring and saturating light were applied through a fibreoptics (ca 0.5 cm ⌀) pointing at an angle of 60° to the sample taking care to minimize shading effects of the fluorescence probe. The apparent electron transport rate through PSII (ETR) was calculated as $ETR = \Delta F/Fm' \times PPFD$ (see Bilger et al. 1995; Genty et al. 1989). Incident PPFD was used and not the value at the photobiont which is certainly lower. The values calculated for ETR in lichens are, therefore, most probably overestimated, nevertheless, these values give a reasonable relative measure of the metabolic activity of the photobionts of the lichen if not the absolute rates.

Sampling procedure.—Thalli of the selected species were marked at selected points on the rock. After initial trials it was realized that sample heterogeneity, particularly differential drying times across a single thallus, varied exposure and slope differences together with time con-

TABLE 1. Relevées taken in different expositions on the boulder at Sierra de Guadarrama, Madrid. Macrolichens and mosses are listed in decreased order of abundance. Indices express the relative abundance of each species in the relevée (+ = just present; 1 = very sparse; 2 = scattered; 3 = frequent; 4 = very frequent; 5 = dominant).

N° of relevée	1	2	3	4	5	6	7	8	9	10	11	12
Exposure	NW	N	ESE	N	ESE	SE	SE	SE	S	SW	W	NW
Slope	90°	80°	−10°	−10°	60°	0°	45°	−20°	70/90°	−10°	−10°	0°
Number of species	14	12	2	4	8	10	16	3	11	8	6	11
Parmelia saxatilis	2	1	—	+	2	3	+	—	3	2	2	2
Parmelia pulla	1	—	—	—	—	2	2	1	2	1	1	3
Lasallia hispanica	3	+	—	—	3	+	1	—	2	—	—	3
Parmelia loxodes	—	—	—	2	—	1	1	1	1	3	3	—
Umbilicaria spodochroa	3	—	—	—	—	2	1	—	2	4	3	—
Parmelia omphalodes	3	3	—	—	1	2	2	—	—	—	—	2
Umbilicaria polyphylla	+	—	4	4	2	1	1	—	—	—	—	—
Lasallia pustulata	—	—	—	—	2	3	2	—	3	—	—	3
Parmelia tiliacea	—	—	—	—	—	—	1		2	1	1	2
Umbilicaria crustulosa	—	—	1	2	2	—	+	—	+	—	—	—
Platismatia glauca	2	3	—	—	—	—	—	—	+	1	—	—
Hypogymnia farinacea	1	1	—	—	—	—	—	—	—	1	—	—
Pseudevernia furfuracea	1	1	—	—	—	—	—	—	—	—	1	—
Umbilicaria grisea	—	—	—	—	—	—	+	4	—	—	—	—
Parmelia conspersa	—	—	—	—	—	—	2	—	—	—	—	+
Cladonia coccifera	—	+	—	—	—	—	2	—	—	—	—	—
Ramalina capitata	—	—	—	—	—	—	—	—	—	—	—	2
Parmelia sulcata	1	—	—	—	—	—	—	—	—	—	—	—
Bryoria fuscescens	—	+	—	—	—	—	—	—	—	—	—	—
Umbilicaria polyrrhiza	+	—	—	—	—	—	—	—	—	—	—	—
Grimmia pulvinata	2	3	—	—	1	1	2	—	1	—	—	2
Orthotrichum rupestre	—	+	—	—	—	1	1	—	2	2	—	1
Hedwigia ciliata	2	3	—	—	1	—	1	—	—	—	—	2
Hypnum cupressiforme	—	2	—	—	—	—	—	—	—	—	—	—
Antitrichia curtipendula	1	—	—	—	—	—	—	—	—	—	—	—

straints would limit sample numbers. It was therefore decided to use single thalli of each species on different exposures and slopes, but to make multiple measurements on the thallus at each measurement interval. Fluorescence determinations, therefore, were made at eight to ten random points on each thallus at each sampling (except for single measurements in darkness), and the mean value and standard deviation were calculated. In some cases more than one sample was measured for a species, but only one is reported since there were few differences between the samples. Records were also made of temperature, PPFD for each single chlorophyll fluorescence measurement, and the mean value and standard deviation were calculated. The color of lichen thalli was also recorded and the change of thallus color due to change in the thallus water content was noted (see Sancho et al. 1994). Descriptions of the sites are given in Table 1.

RESULTS

Diurnal courses, for the selected samples, of the effective quantum yield of PSII (ΔF/Fm′) and the apparent relative electron transport rate through PSII (ΔF/Fm′ × PPFD) together with the thallus temperatures and PPFD incident at the thallus surface as measured with the PAM-2000 are shown in Figures 1–5. Measurements were made over a six day period, 15 to 20 October, 1993.

Weather.—The weather was variable as is typical during autumn in the Mediterranean region. Prior to the research period the weather, initially wet and cold, was then warm and dry for more than two weeks. Several days of intermittent rainfall then followed so that all samples were fully hydrated at the beginning of the measurement period. The highly hydrated status of the lichens was easily seen by their dark-brown thallus color and adhering surface water droplets. On 15 October, rain fell early in the morning but the remainder of the day was dry although overcast. The next day was very wet and several hours of heavy rainfall and a storm prevented any measurements. The sky continued overcast on 17 October and rain fell during most of the day. On 18 October, the weather became drier and only light rain showers occurred occasionally. On the last two days the weather was dry with a cloudless sky and temperatures that were much warmer than the earlier, wet days when temperatures as low as 0°C occurred in the morning and temperatures at noon were only mild.

Photosynthetic activity N and NW aspects.—Figure 1 illustrates the microclimate and photochemical efficiency of *Lasallia hispanica* growing on a northwestern exposure (relevé 1, Table 1). Over the whole period, PPFD was low, maxima around 100 μmol m^{-2} s^{-1}, despite the clear skies on the last two days. Thallus temperatures also only started to rise from around a low 5°C during the last two

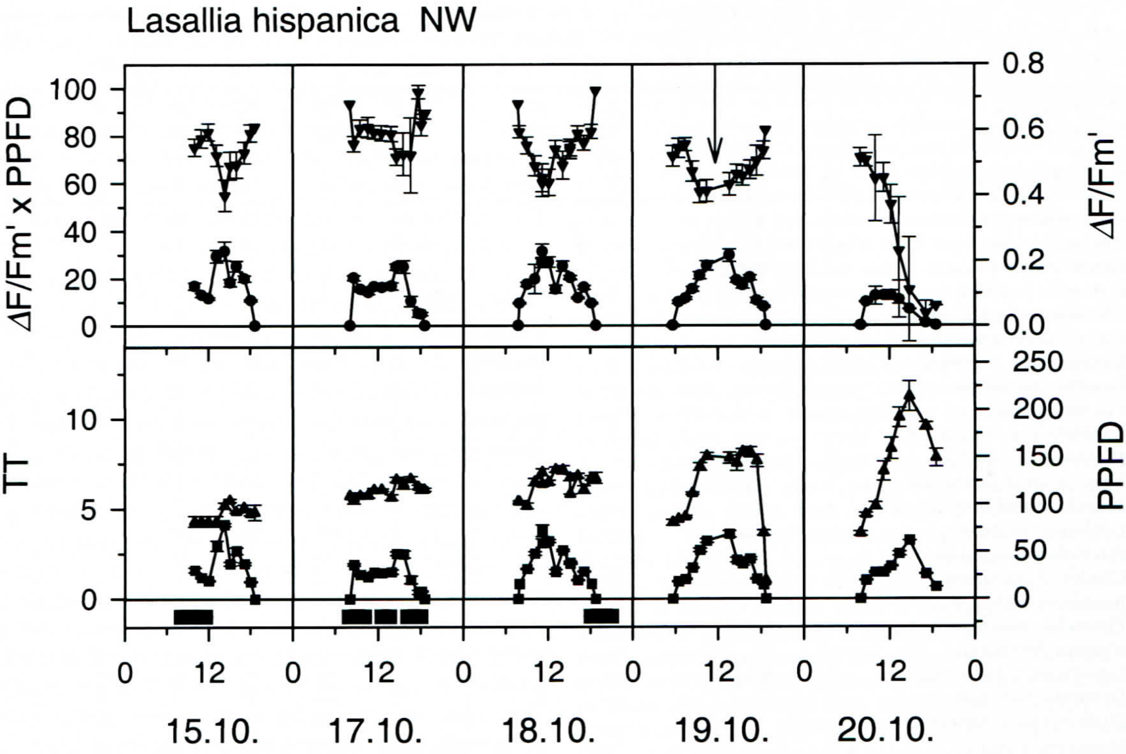

FIGURE 1. Diurnal courses of thallus temperature (▲, TT, °C), photosynthetic photon flux density (■, PPFD, μmol m^{-2} s^{-1}), effective quantum yield of PSII (▼, ΔF/Fm′), and relative rate of electron transport through PSII (●, ΔF/Fm′ × PPFD) in *Lasallia hispanica* growing in northwestern exposure during five days in October. All datapoints are means of 8–10 single measurements except for single measurements in darkness. Vertical bars indicate the standard deviation of the mean. Black bars indicate rainfall. The vertical arrow indicates thallus color change from dark-brown to whitish-gray.

days. The effective quantum yield of PSII clearly revealed the changing microclimatic conditions of the thallus. The high effective quantum yield of PSII (ΔF/Fm′), showing only a slight decline, over the first four days indicating that the thallus was hydrated. On 19 October at 13.30 hr, the thallus color changed from olive-green to whitish-gray indicating dehydration of the thallus surface and upper cortex. With dehydration the thallus became more and more rigid. But it was not until the final day, 20 October, that the desiccation was severe enough to cause a rapid decline in ΔF/Fm′ and ETR. There was little evidence that the thalli could rehydrate overnight since ΔF/Fm′ were normally identical on the evening and following morning.

In contrast, the photosynthetic performance of the mosses *Grimmia pulvinata* and *Hedwigia ciliata* growing with a similar northern exposure (relevé 2, Table 1) remained more or less unaffected by the changing weather conditions over the entire period (Fig. 2). Although PPFD hardly exceeded 100 μmol m^{-2} s^{-1} it controlled the photosynthetic performance of both mosses because of the almost constant ΔF/Fm′. The mosses remained wet and active also under the dry weather conditions on 20 October and *Grimmia pulvinata* could take advantage of the direct sunlight that reached the thallus at ca 15.00 hr and resulted in the highest ETR during the period of measurements. Two other replicates behaved similarly (data not shown).

P-SE and SE aspects.—Over the first four days the PPFD conditions were similar for all samples and, because of the cloudy weather, also to that on the northern side (Figs. 3–5). All lichen species also showed a similar slight decrease of the quantum efficiency of PSII occurring over these days, indicating a slow dehydration. Over the last two days, all lichens showed various degrees of desiccation depending substantially on ambient PPFD. Although the samples were only a few cm apart they received different PPFD conditions: maximum PPFD was 130 μmol m^{-2} s^{-1} for *Lasallia pustulata* (15 October, 11.50 hr), while *L. hispanica* received $>$ 400 μmol m^{-2} s^{-1} on 19 October (12.10 hr) and again on 20 October (12.20 hr; Fig. 3, see relevé 5, Table 1). The greater PPFD values for *Lasallia hispanica* resulted in higher thallus temperatures and substantially higher ETR. Higher dehydration

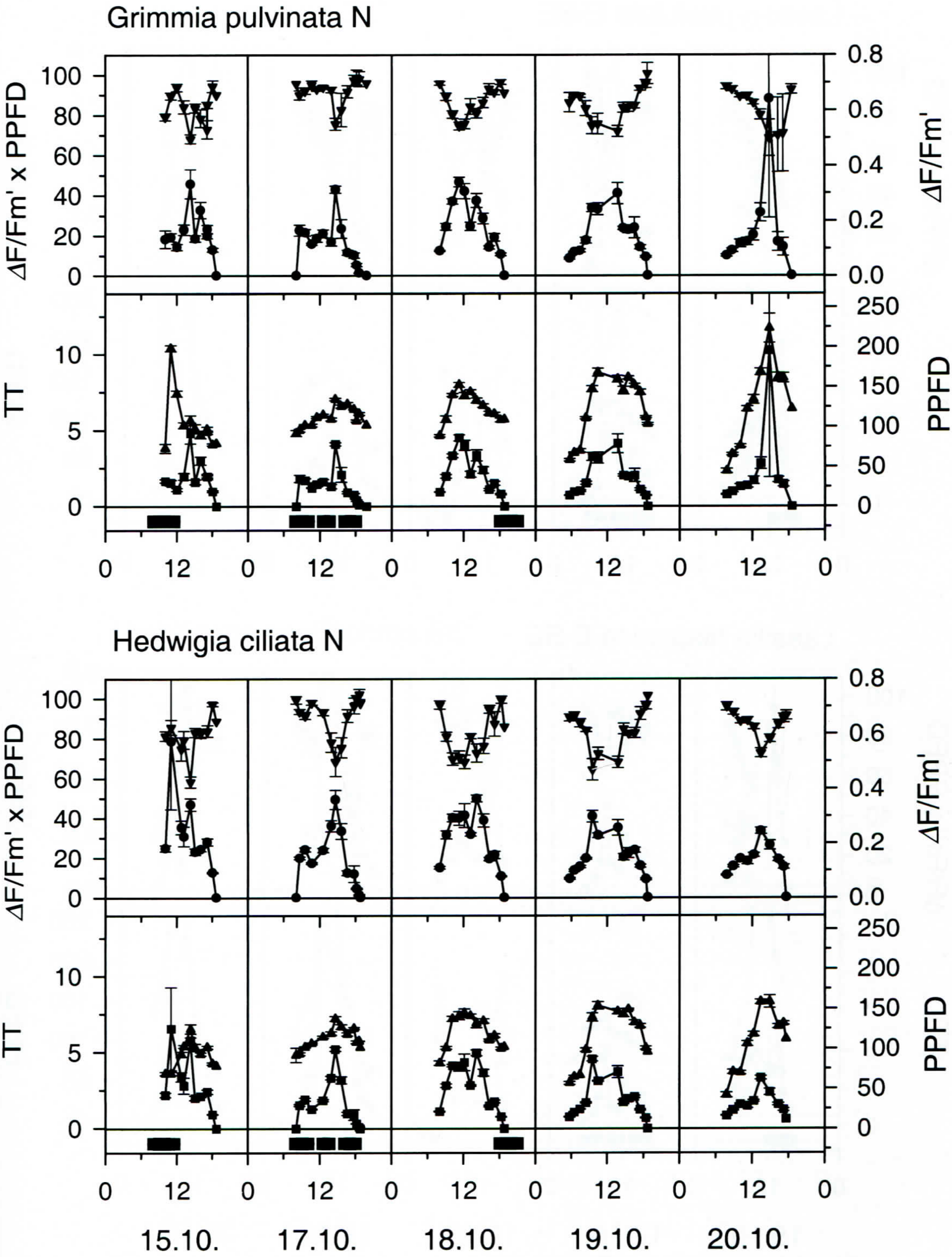

FIGURE 2. Diurnal courses of thallus temperature (▲, TT, °C), PPFD (■, μmol m^{-2} s^{-1}), effective quantum yield of PSII (▼, ΔF/Fm′) and relative rate of electron transport through PSII (●, ΔF/Fm′ × PPFD) in *Grimmia pulvinata* and *Hedwigia ciliata,* both growing in northern exposure during five days in October. All datapoints are means of 8–10 single measurements except for single measurements in darkness. Vertical bars indicate the standard deviation of the mean. Black bars indicate rainfall.

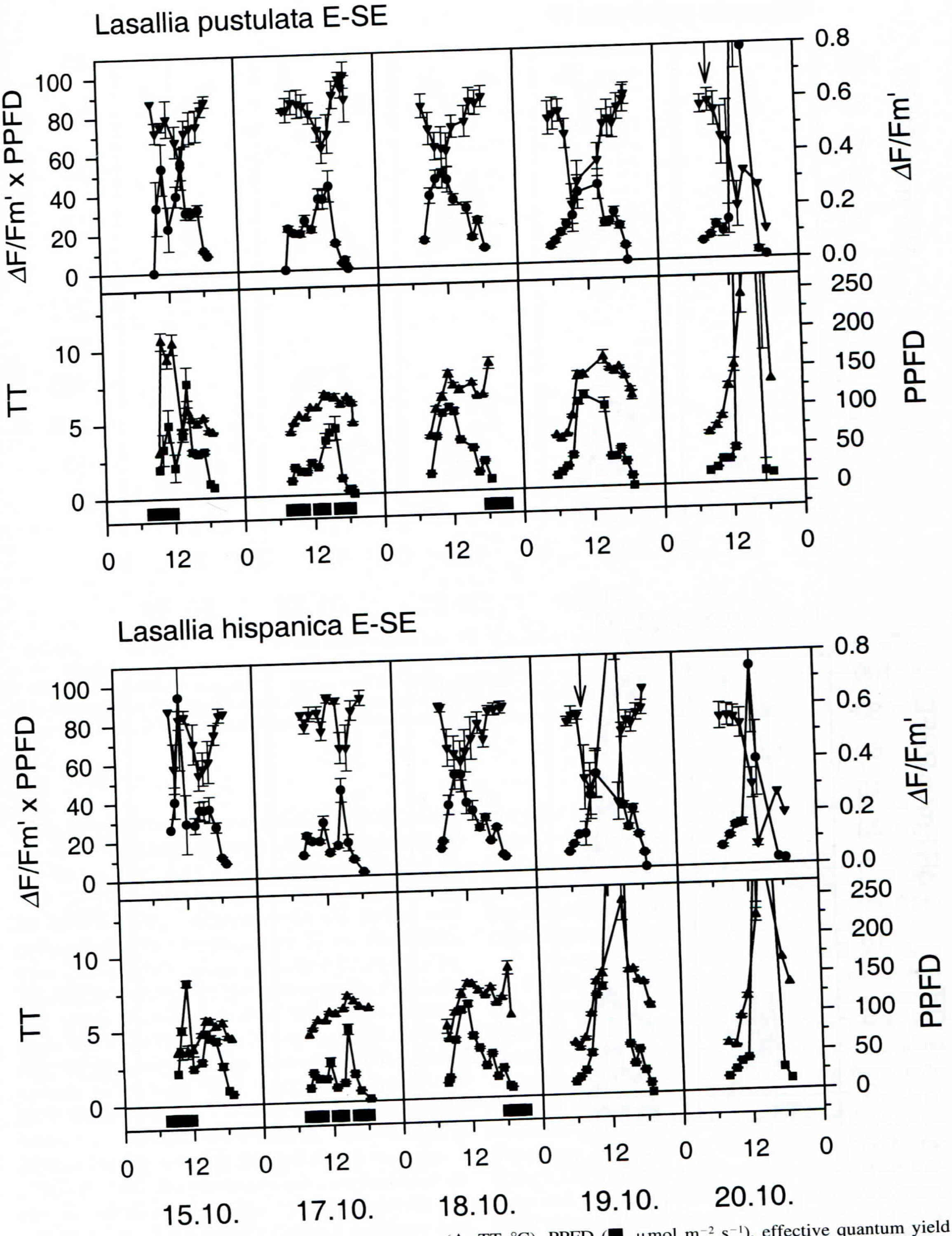

FIGURE 3. Diurnal courses of thallus temperature (▲, TT, °C), PPFD (■, μmol m^{-2} s^{-1}), effective quantum yield of PSII (▼, ΔF/Fm′) and relative rate of electron transport through PSII (●, ΔF/Fm′ × PPFD) in *Lasallia pustulata* and *Lasallia hispanica* growing in east and southeastern exposure during five days in October. All datapoints are means of 8–10 single measurements except for single measurements in darkness. Vertical bars indicate the standard deviation of the mean. Black bars indicate rainfall. The vertical arrows indicate thallus color change from dark-brown to whitish-gray.

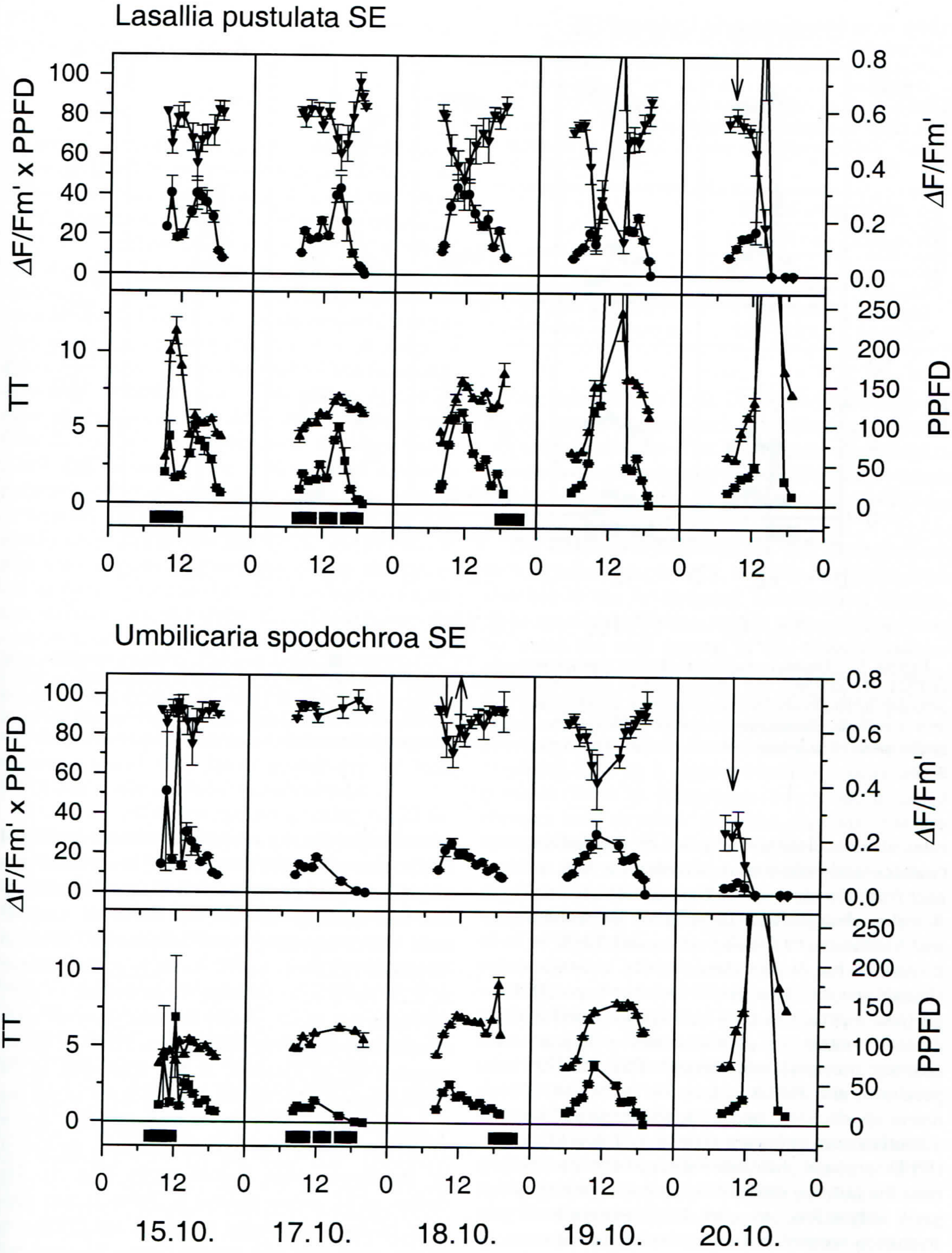

FIGURE 4. Diurnal courses of thallus temperature (▲, TT, °C), PPFD (■, μmol m^{-2} s^{-1}), effective quantum yield of PSII (▼, ΔF/Fm′) and relative rate of electron transport through PSII (●, ΔF/Fm′ × PPFD) in *Lasallia pustulata* and *Umbilicaria spodochroa* growing in southeastern exposure during five days in October. All datapoints are means of 8–10 single measurements except for single measurements in darkness. Vertical bars indicate the standard deviation of the mean. Black bars indicate rainfall. The vertical arrows top-down indicate thallus color change from dark-brown to whitish-gray, the vertical bottom-up arrow indicates a reverse color change.

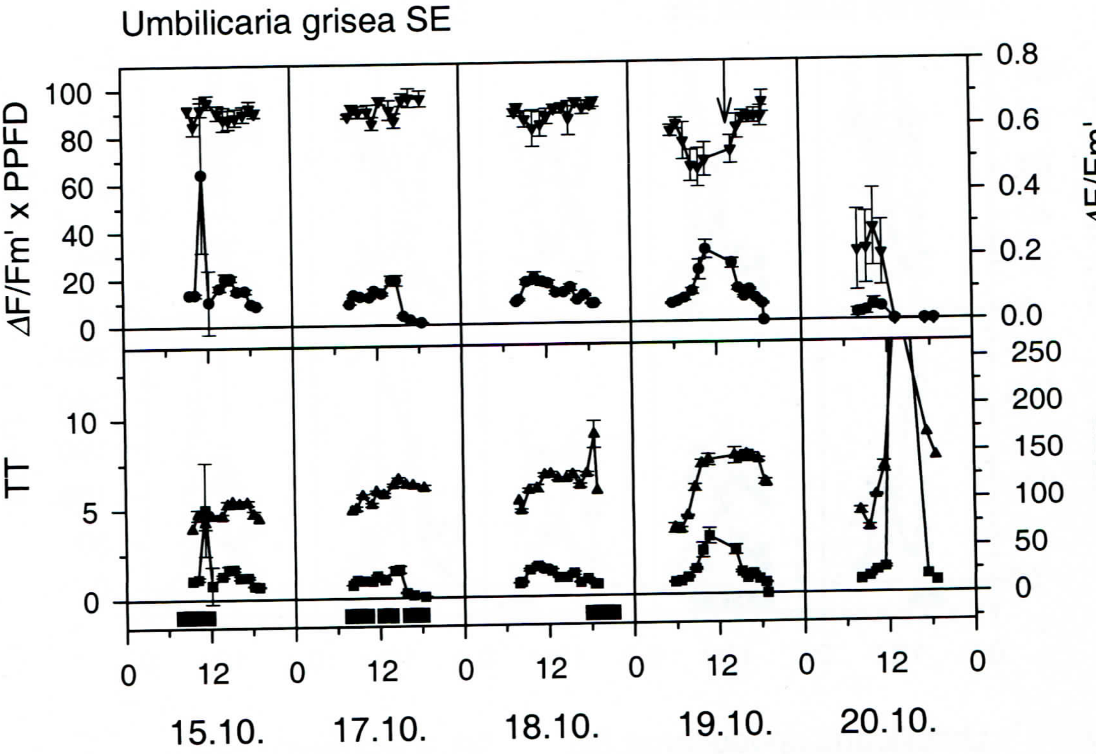

FIGURE 5. Diurnal courses of thallus temperature (▲, TT, °C), PPFD (■, μmol m^{-2} s^{-1}), effective quantum yield of PSII (▼, ΔF/Fm′) and relative rate of electron transport through PSII (●, ΔF/Fm′ × PPFD) in *Umbilicaria grisea* growing in southeastern exposure at an overhanging rock wall during five days in October. All datapoints are means of 8–10 single measurements except for single measurements in darkness. Vertical bars indicate the standard deviation of the mean. Black bars indicate rainfall. The vertical arrow indicates thallus color change from dark-brown to whitish-gray.

rates also occurred as indicated by the thallus color changes and substantial dehydration was evident also from the state of the thallus that became rigid. A color change from olive-green to whitish-gray was visible on 19 October at around 10.30 hr in *L. hispanica,* but *L. pustulata* showed a similar color change one day later on 20 October from 10.00 hr on over a period of ca 4 hr. Figures 4 and 5 show diurnal courses of photochemical efficiency and electron transport rate through PSII, thallus temperatures, and PPFD in *Lasallia pustulata, Umbilicaria spodochroa,* and *U. spodochroa* growing on a southeastern exposure (relevé 7, Table 1). Again, PPFD climate differed substantially particularly over the last two days, between both samples which grew only a few cm apart, but photosynthetic performance seemed to be more related to species. A major difference between *Lasallia pustulata* and *Umbilicaria spodochroa* in the water relations was obvious. Although a change in thallus surface color on 20 October from 10.10 hr to 15.05 hr indicated thallus dehydration in *L. pustulata,* the photochemical efficiency remained almost unaffected by water loss. The highest relative rates of ETR were observed under the dry climatic conditions on 19 and 20 October when PPFD was high. In contrast, photosynthetic performance of *Umbilicaria spodochroa* was strongly affected by increased temperatures and a resulting rapid dehydration, although incident PPFD was lower. As early as 18 October, at 9.20 hr, a color change (from brown to gray) started in the thallus center but was reversed when rainfall rehydrated the thallus at ca 13.00 hr. On the morning of 20 October, at the beginning of the measurements, the thallus was strongly rolled due to severe water loss and was completely dry at 11.40 hr, indicated by visible measures as well as by the fluorescence measurements (Fig. 4). The thallus of *U. grisea* (relevé 8, Table 1) was sheltered by the overhanging rock wall and PPFD conditions were low and mainly below 50 μmol m^{-2} s^{-1} except for short period on 15 and 20 October (Fig. 5). The PPFD conditions limited the photosynthetic performance and a small increase in PPFD always resulted in a substantial increase in ETR, for instance compare the rates on 17/18 October with those on 19 October. Despite the low

PPFD, severe drying terminated the photosynthetic activity of *U. grisea* on 20 October.

DISCUSSION

One of the main objectives of this work was to investigate the chlorophyll *a* fluorescence technique as a simple but effective way to reveal the effects of different microclimates on the photosynthetic activity of the lichens and mosses. The major advantage would be the elimination of the need to place the samples in a cuvette with its consequent alteration of microclimate. The results certainly seem to support the use of this technique. A wide range of activity patterns were found with differences often occurring within a few centimetres, depending more on the species and slope than the site aspect. Overall, the two mosses behaved similarly, but in a different manner to the lichens. Both *Grimmia pulvinata* and *Hedwigia ciliata* showed no signs of desiccation limitation over the week. ETR was mainly small and determined by the low PPFD, but high values occurred transiently during short periods of direct sunshine (Fig. 2). The lack of limitation through drying is not unexpected since the cushion form is highly effective for water storage and some species, especially *Grimmia pulvinata,* are known to effectively reduce the rate of water loss by hair points (Proctor 1982). The north-facing rock surfaces should also have had lower potential evaporation and also lower probability of high PPFD that might produce photoinhibition.

In contrast, all lichen species growing on all aspects studied showed the effects of drying over the period of study. Measurements of the water status of thalli of *Umbilicaria grisea* and *U. freyi* at the same spot and time period revealed that substantial desiccation occurred during the measurement period (see Sancho et al. 1997*b* figs. 5–6). However, because of the destructive experimental procedure with regular weighings the photosynthetic activity in those samples ceased much earlier than in the non-disturbed samples in the present study.

Only a slow decline in maximal $\Delta F/Fm'$ occurred over the period, which is indicative of slight, but increasing, desiccation stress and many samples had depressed ETR on the final day. However, many of the responses did not fit expectations. From laboratory response curves of photosynthesis to temperature for the investigated lichen species (Kappen et al. 1996; Sancho & Kappen 1989; Sancho et al. 1997*b*) it is obvious that all species approached their temperature optimum for photosynthesis when temperature increased on the final days. On the final days *Lassallia hispanica* showed greater desiccation stress, including falling ETR despite high PPFD, at the north rather than the south, sun-facing aspect (Figs. 1, 4). *Umbilicaria spodochroa,* on the southeastern aspect, was almost completely desiccated with low ETR on the final day while *L. pustulata* thalli, only a few cm distant, showed no effects despite having had much higher PPFD on the penultimate day (Fig. 4).

TABLE 2. Relationship between the change of thallus color from dark brown-green to opaque whitish-gray during dehydration and thallus water content (in percentage of dry weight, %d.wt.) and the rate of net photosynthesis (NP, as CO_2 gas exchange) for four species of Umbilicariaceae. Data from unpublished measurements and from Kappen et al. (1996); Sancho & Kappen (1989); Sancho et al. (1994, 1997*b*).

	Thallus color change at	
	WC (%d.wt.)	Rate of NP
Lasallia hispanica	120–140%	Maximal
Lasallia pustulata	120–140%	Maximal
Umbilicaria grisea	95–120%	Maximal
Umbilicaria spodochroa	100–125%	Maximal

The different drying rates are well illustrated not only by a decrease in ETR, but also by thallus color changes in the investigated *Lasallia* and *Umbilicaria* species. Hydration related changes in the thallus color are well known in the Umbilicariaceae (Ertl 1951; Sancho & Kappen 1989) and are due to water loss from the upper cortex of the thallus (Sancho et al. 1994). These changes of thallus color have proved to be a reliable indicator of water loss occurring only in a narrow band of thallus water contents (Table 2). It has been shown that the color changes tend to occur at water contents that are optimal for gas exchange, and just above water contents that will start to cause a depression as drying proceeds (Table 2). In our experiments, there were substantial differences between species in the time at which the color changes occurred. Most sensitive was *Umbilicaria spodochroa* with a southeastern exposure which, due to its substrate-hygrophytic nature, dried as soon as the trickling water supply on the rock face stopped on 18 October (Fig. 4). Color changed for *Lasallia hispanica* on 19 October at the northwestern (Fig. 1), east, and southeastern (Fig. 4) aspects.

Umbilicaria grisea, with a southeastern exposure (Fig. 5), changed on the same day, but in contrast, thallus color changes in *Lasallia pustulata* could only be observed 24 hr later on 20 October. Irrespective of exposure or growth form, all lichen thalli from vertical or overhanging rock walls dehydrated faster than those growing on less inclined walls as was indicated by the changes in thallus color and thallus rigidity. It seems, at least during our period of measurements in autumn, that the slope of the microhabitat played a greater role in determining thallus hydration than site aspect.

Monitoring of color changes offers substantial possibilities for the monitoring of lichen water relations, but better methods for measurement are still needed.

The data presented here demonstrate the heterogeneity in the exploitation of moisture by cryptogams co-occurring in the very same rock. The photosynthetic activity of the investigated poikilohydric organisms, indicated by chlorophyll *a* fluorescence and color changes for the lichens, was controlled by a complex interaction of thallus growth form, inclination, and exposure of the microhabitat resulting in different kinetics of water uptake and loss under transient microclimatic conditions. The differences were fully preserved by the non-contact assessment methodologies and not altered by experimental procedures such as inclusion in a cuvette. The samples remained fully attached to the substrate without any interference. Detachment of the thallus for weighing and gas exchange measurements in regular intervals caused a significantly higher dessiccation rate in *Umbilicaria grisea* as was measured at the same spot during the same measurement period by the authors (see Sancho et al. 1997*b*, fig. 5). Non-intrusive measurements of chlorophyll *a* fluorescence have a great potential in the study of lichen and bryophyte ecophysiology. Measurements take only a few seconds and, as was demonstrated here, many different samples (only eight out of 11 samples measured in parallel are shown here) could be measured by the same experimenter. Chlorophyll *a* fluorescence measurements are also well suited for unattended long-term measurements of photosynthetic performance in poikilohydric organisms (Schroeter & Schulz 1995; Schroeter et al. 1991*b*, 1997*a,b*). As well as its use as an indicator of stress effects on photosynthesis, chlorophyll *a* fluorescence measurements are well suited to 1) measure the influence of microhabitat changes within the same community or population of lichens and mosses (Hestmark et al. 1997); 2) measure the cryptogams *in situ* especially if the samples could not be removed from their substratum without damage, as is the case in many lithobiontic mosses as well as in crustose and soil-crust lichen species; 3) detect differences in the photosynthetic performance among species of different growth form or samples of the same species growing in different microhabitats, as investigated here; and 4) analyze small scale differences in hydration-related variations within one thallus (Hestmark et al. 1997; Schroeter 1994; Schroeter et al. 1992, 1997*b*).

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