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Photosynthetic and cytological recovery on remoistening *Syntrichia caninervis* Mitt., a desiccation-tolerant moss from Northwestern China

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Abstract

Syntrichia caninervis Mitt. is the dominant species in the moss crusts of the Gurbantunggut Desert, Northwestern China. We experimented with this species under controlled environmental conditions. Modulated chlorophyll (Chl) fluorescence was used to test the speed of recovery as evidenced by the time course of photosynthetic activity following remoistening. Transmission electron microscopy was used to explore the cytological characteristics of the leaf cells. Minimum and maximum fluorescence (F_0 and F_M) and photosynthetic yield (F_V/F_M) of photosystem II (PSII) recovered quickly when shoots were remoistened in the dark. This was especially the case of F_V/F_M; within the first minute of remoistening this reached 90% or more of the value attained after 30 min. These physiological changes were closely paralleled by cytological changes that indicated no damage to membranes or organelles. Correlation analysis showed that Chl fluorescence decreased both above and below a narrow moisture optimum. Our results underline the capability of *S. caninervis* to photosynthesize after remoistening. Utilizing precipitation events such as dew, fog, rain, and melting snow allows *S. caninervis* to survive and grow in a harsh desert environment.

Additional key words: Chl fluorescence; moisture content; moss crusts; remoistening; *Syntrichia caninervis*; ultrastructure.

Introduction

Biological soil crusts occur worldwide in desert areas and may constitute as much as 70% of the living ground cover of some plant communities (West 1990). In the Gurbantunggut Desert, biological soil crusts occur in dense patches that are heavily dominated by lichens but there are also occasional patches of mosses (Zhang *et al.* 2007). *Syntrichia caninervis* Mitt. (syn. *Tortula caninervis*) is the dominant species in moss crusts in the Gurbantunggut desert (Fig. 1). Mosses in soil crust communities experience physiological stress due to extreme environmental conditions, including high temperature, high radiation and frequent cycles of hydration and dehydration (Harel *et al.* 2004, Barker *et al.* 2005).

Unlike vascular plants, in which vegetative desiccation tolerance is rare, the majority of moss species can survive desiccation during their vegetative growth period (Proctor and Tuba 2002, Proctor *et al.* 2007b, Wood 2007). Studies of bryophyte desiccation tolerance underline their physiological ability to recover rapidly during rehydration (Tuba *et al.* 1996, Tuba *et al.* 1998, Marschall and Proctor 1999, Proctor and Smirnoff 2000, Proctor 2002, Proctor *et al.* 2007a, Hájek and Beckett 2008, Lüttge *et al.* 2008, Pressel *et al.* 2009). Other studies discuss the effects of desiccation and rehydration on cells (Bartoškova *et al.* 1999, Pressel *et al.* 2006, Proctor *et al.* 2007a, Pressel *et al.* 2009) and on membrane permeability and integrity (Platt *et al.* 1994).

Mosses are poikilohydric and cannot maintain constant internal water content by regulating water loss (Proctor *et al.* 2007a). Chl fluorescence experiments show that half-recovery times for F_V/F_M may be as short as 20–40 s (Proctor and Smirnoff 2000, Proctor 2001) and F_V/F_M can reach approximately 80% of its predesiccation value within approximately 10 min after

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Abbreviations: Chl – chlorophyll; F_0 and F_M – minimum and maximum fluorescence in dark-adapted state; F_V/F_M – maximum quantum yield of PSII; PSII – photosystem II.
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rewetting (Proctor *et al.* 2007a). Rapid recovery of net CO_2 uptake has been recorded within 10 min (Graham *et al.* 2006) and net carbon balance restored after approximately 0.3–1 h (Proctor *et al.* 2007a).

The ability of many bryophytes to withstand drying out and recover normal metabolism on rewetting is commonly observed and remarked upon. Early studies of bryophyte desiccation tolerance focused on the ability of cells to undergo plasmolysis as an indicator of survival (Schnepf *et al.* 1986, Cook *et al.* 1997). Modulated Chl fluorescence measurements are now widely used to investigate photosynthetic electron transport and associated physiological processes, particularly as a means of providing insights into desiccation tolerance (Tuba *et al.* 1997, Proctor 2003, Juneau *et al.* 2005, Hájek and Beckett 2008, Pressel *et al.* 2009).

Our objectives are (*1*) to evaluate the recovery capacity of photosynthetic function following remoistening, (*2*) to investigate the relationship between the physiological and cytological processes following remoistening, and (*3*) to analyze the ability of *S. caninervis* to respond following severe water deficit.

Materials and methods

Study site: The moss crusts used in our experiments were collected from the Gurbantunggut desert (44°11′–46°20′N, 84°31′–90°00′ E), situated in the center of the Junggar Basin, Xinjiang Uygur autonomous region of China. This is the second largest desert in China covering 4.88×10^4 km^2. The Himalayan range to the south creates a "blocking effect"; consequently, moist air currents from the Indian Ocean fail to reach the area, resulting in a vast expanse of arid terrain. Mean annual precipitation is approximately 79.5 mm, most of which falls in spring. The mean annual pan evaporation is 2,606.6 mm. The mean annual temperature is 7.26°C, while the maximum temperature is over 40°C. Wind speeds are greatest during late spring, with an average of 11.17 m s^{-1}, and are predominantly from the WNW, NW and N directions. The natural vegetation is dominated by *Haloxylon ammodendron* and *H. persicum* (Amaranthaceae subfamily Chenopodioideae), with vegetation cover of less than 30%. The area is covered by massive, dense semifixed sand dunes with stable moisture content. Biological soil crusts are abundant in the desert. Vegetative activity occurs during cool, wet periods (fall and early spring) when moisture from dew, fog, or ephemeral rainfall events can be utilized by soil crust species (Kidron *et al.* 2002, Zhang *et al.* 2007).

Sample collection: Samples of moss crusts were collected from the Gurbantunggut desert, using micro-lysimeters with a diameter of 6 cm and a height of 3.5 cm. The micro-lysimeters were pushed into the ground to collect soil columns covered by representative moss crusts. The edges of the micro-lysimeters were close to the surface of the ground and their bases were covered. Moss samples were transported to the laboratory within 24 h of collection. Samples were placed on filter paper moistened with distilled water in 15 cm-diameter Petri dishes. These were then left for three days under the experimental conditions (25°C and 150 μmol m^{-2} s^{-1}). The moss samples appeared to be green and healthy (Fig. 1). During the experimental time, green shoots were blotted and allowed to dry out on filter paper freely exposed to the laboratory atmosphere.

Chl fluorescence was measured with a pulse-modulated fluorometer (*MINI-PAM, Heinz*, Walz, Germany). The optic fiber was pointed at each sample from a distance of 2–4 mm and at an angle of 60°. To minimize scattering of data, the initial position of the optic fiber was not changed during the experiment.

The samples were dark-adapted for 30 min, then the measuring radiation (< 1 μmol m^{-2} s^{-1}) was switched on to determine the dark-adapted minimum fluorescence (F_0), following a 0.8-s saturating pulse (8,000 μmol m^{-2} s^{-1}) applied to obtain the dark-adapted maximal fluorescence (F_M). The maximum quantum yield of PS II (F_V/F_M) was calculated as $(F_M - F_0)/F_M$.

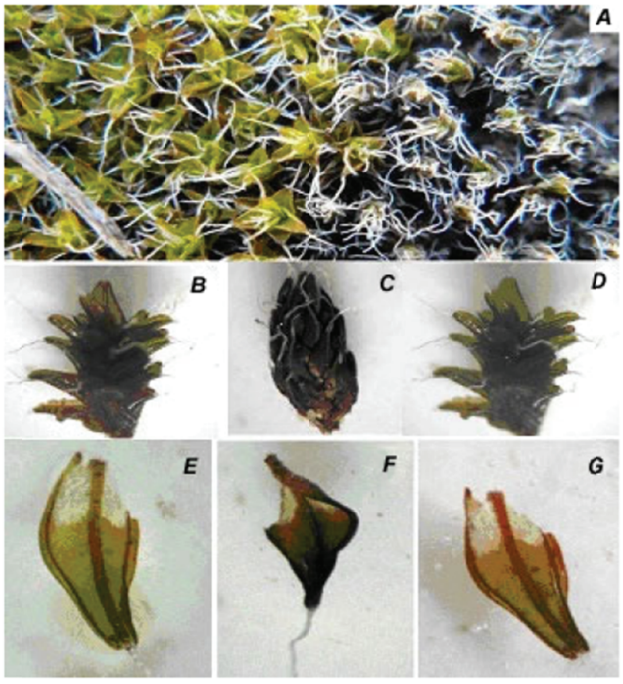

Fig 1. Photographs of *S. caninervis*. *A*: wet and dry patches; shoots (*B*: fully hydrated; *C*: dehydrated; *D*: rehydrated; same shoots in each), and detached leaf of *S. caninervis* Mitt. (*E*: fully hydrated; *F*: dehydrated; *G*: rehydrated; the same leaf in each).

Cytological protocols: Proctor *et al*. (2007a), experimented with leaves from fully desiccated and hydrated mosses, and mosses 6 h after remoistening. The leaves were cut into 2-mm lengths and fixed at room temperature for 3 h at pH 7 in 3% (v/v) glutaraldehyde, 1% formaldehyde and 0.75% tannic acid in 0.05 M Na-phosphate buffer. Leaf samples from dry shoots were fixed in 0.1 M Na-phosphate buffer. Subsequently, the samples were rinsed, post-fixed overnight with 1% osmium tetroxide in 0.1 M buffer, pH 6.8, and then dehydrated and embedded in Spurr's resin *via* propylene oxide, as described by Ligrone and Duckett (1994). Semithin sections, cut with a diamond knife, were sequentially stained with methanolic uranyl acetate and basic lead citrate and examined with a *Hitachi 600* transmission electron microscope. The samples were photographed with an optical microscope (*Olympus, Cover-018*, Japan).

Moisture measurements: Moss cores were sprayed with distilled water until they were fully turgid. Each replicate was blotted to remove superficial water, weighed, and then placed in a 3.5-cm plastic Petri dish to dry in the dark. Samples were weighed after each fluorescence measurement. At the end of the experiment, the samples were placed in a drying oven at 80°C for 24 h. Moisture content was quantified by measuring current mass and expressing it as percentage of dry mass.

Dew amount measurements: Dewfall was measured using micro-lysimeters (Boast and Robertson 1982). This method allows a soil core to be taken while leaving the surface intact, thus observations can be repeated on the same sample. Moss crust samples were not collected near shrub canopies and thus microclimatic effects of shrubs were avoided.

The soil samples were weighed using a balance to a precision of ± 0.01 g. The dewfall for each day was determined by calculating the difference between the mass in the morning and that at sunset the previous day. In order to obtain a better insight into the time-course of dew deposition, intensive measurements were carried out for several days on different samples. The weighing interval was 2 h. The quantity of dew deposition (in mm) was calculated from these weights.

Soil temperature measurements: The soil temperature was measured by a temperature sensor buried 5 cm below the soil surface with or without soil crusts covering. The soil temperature was recorded at 1-h intervals using a data logger.

Statistical analyses: Data were analyzed by one-way analysis of variance (*ANOVA*) to test for differences in parameters, using the *SPSS* statistical package (*SPSS*, Chicago, USA). Data is presented as means with standard errors.

Results

Chl fluorescence changes: F_V/F_M recovered quickly while shoots were remoistened in the dark; within the first minute reaching 90% or more of the value attained after 30 min (Fig. 2*B*). It was noteworthy that the fluorescence level of the dry moss was comparable to that after rewetting and that there was measurable variable fluorescence, giving a mean F_V/F_M of just under 0.03. Dry levels of F_0 and F_M were 81.6 and 100, respectively, as shown by the point (with error bars) at zero time on the graph (Fig. 2*A*). These increased very rapidly on rewetting. Generally, the fast initial rises of F_0 and F_V/F_M were completed within 30 min. Later changes were slow and not as obvious.

In order to understand the changes in Chl fluorescence parameters following remoistening, much longer time courses of variation in F_0, F_M, and F_V/F_M were investigated. The initial recovery of F_0 and F_V/F_M was very rapid within the first 0.5 h, reaching approximately 80% and 90% of their maximal values respectively (Fig. 2*C*,*D*). The recovery rate of F_M was slower than those of F_0 and F_V/F_M, reaching about 65% of its maximal values within the first 0.5 h (Fig. 2*C*). During the second stage of recovery, F_0 and F_V/F_M recovered more slowly, remaining constant for around 8 h following remoistening. In contrast, F_M showed a steady increase and reached its maximal value at 6 h after remoistening. Subsequently, all parameters declined dramatically. Nevertheless, the decline in F_0 and F_M was not simultaneous. Eight hours after remoistening, F_0 decreased by 18% from its maximum and F_M decreased by 26%. Following this, F_0, F_M, and F_V/F_M showed a steep decline, returning to their initial value (Fig. 2*C*,*D*).

Cytological changes: After 3 days of air-drying, the grana in the thylakoid system were small and underdeveloped (Fig. 3*A*), the osmiophilic globuli were small and distributed randomly throughout the chloroplasts (Fig. 3*A*). The membranes of the chloroplasts remained intact during the process of desiccation (Fig. 3*B*).

In fully hydrated condition, the bilayer membrane and the integrity of membrane system can be seen clearly on the outside of the chloroplast (Fig. 3*C*). The main body of each chloroplast was packed with well organized grana. The thylakoids with rich lamellae were interconnected by numerous parallel intergranal thylakoids (Fig. 3*D*). A few, small osmiophilic globuli were scattered through the chloroplasts (Fig. 3*C*).

Six hours after remoistening, the chloroplast was fully developed (Fig. 3*E*). The bilayer membrane and the integrity of membrane system were clear and visible

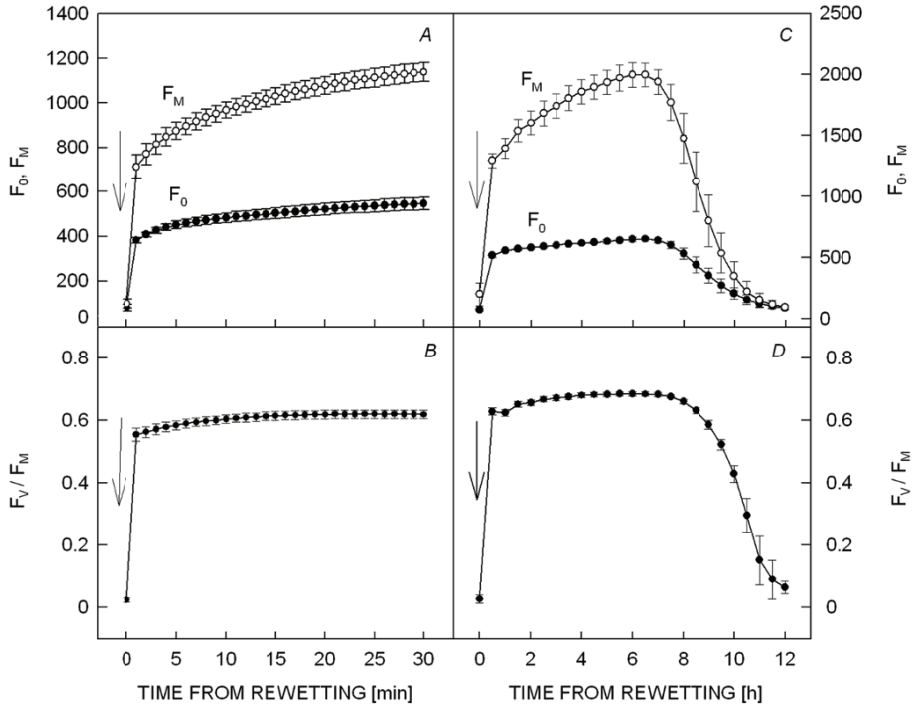

Fig. 2. Rapid recovery (*A*,*B*) and time course (*C*,*D*) of the changes of chlorophyll fluorescence parameters of *S. caninervis* on remoistening (*arrowed*) after 3 days of air-drying. (*A*,*C*) Absolute values of minimal (F_0) and maximal (F_M) fluorescence. (*B*,*D*) F_V/F_M – maximal quantum efficiency of photosystem II. Each point is the mean ± SE of five replicates.

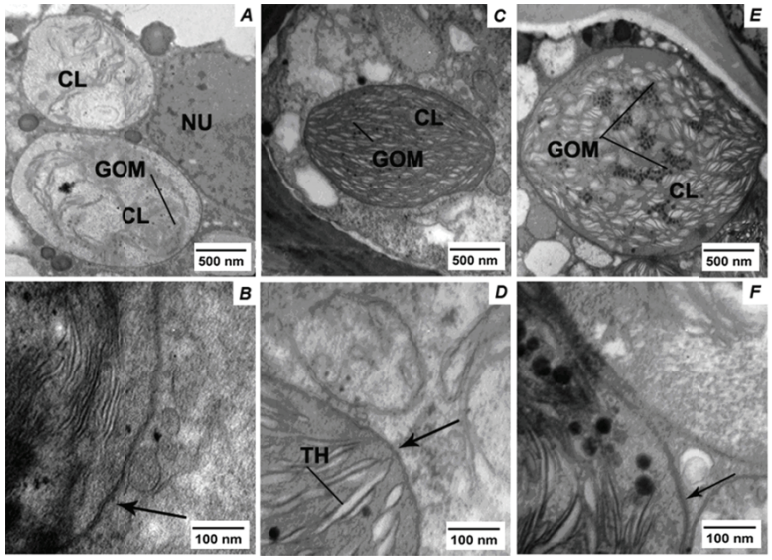

Fig. 3. Transmission electron microscopy of leaf cells of *S. caninervis* under different hydrated conditions. *A*, *B*: fully desiccated leaf cells; *C*, *D*: fully hydrated leaf cells; *E*, *F*: leaf cells of 6 h after remoistening. CL – chloroplast; GOM – osmiophilic globule; TH – thylakoid; NU – nucleolus. *Arrows* point at chloroplast membrane. *Scale bars*: *A*, *C*, *E* = 500 nm; *B*, *D*, *F* = 100 nm.

outside the chloroplast (Fig. 3*E*). The lamella of the thylakoids was richer than that of the fully hydrated leaf-lamella cells (Fig. 3*F*). There was a dramatic increase in the number and the volume of the osmiophilic globuli in the chloroplasts (Fig. 3*E*). The distribution of the osmiophilic globuli was rather different from that in the hydrated leaf-lamella cells, in which they were no longer scattered but rather densely clustered together (Fig. 3*E*).

Effects of desiccation on Chl fluorescence: The minimal fluorescence (F_0) of *S. caninervis* was lower at high moisture content and reached its peak at a moisture content of 30% (Fig. 4*A*). Below 30% moisture content there was a steep decline of F_0 to zero. Fully saturated samples of *S. caninervis* initially had low values of F_M that gradually increased as water loss progressed. The optimum moisture content for F_M varied from 20 to 50% (Fig. 4*A*). When the moisture content declined below the optimum for photosynthetic activity, F_M decreased sharply (Fig. 4*A*). The fluorescence parameter (F_V/F_M) remained approximately constant after remoistening until the moisture content reached 20% (Fig. 4*B*). Below this moisture content, F_V/F_M declined dramatically.

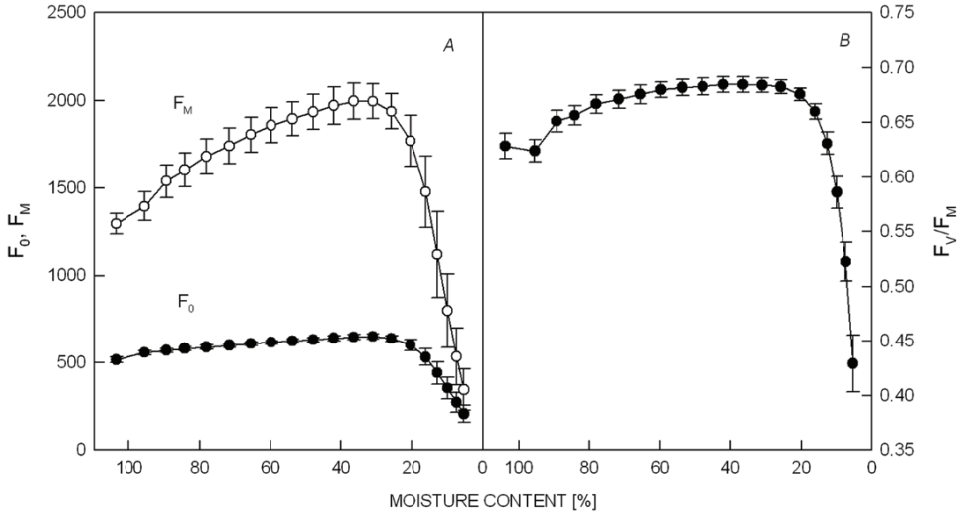

Fig. 4. Relationship between crust moisture content and minimal fluorescence (F_0); maximal fluorescence (F_M); and maximal quantum efficiency of photosystem II (F_V/F_M) in *S. caninervis*. Each point is the mean of three replicates; *bars* indicate ± SE of the mean.

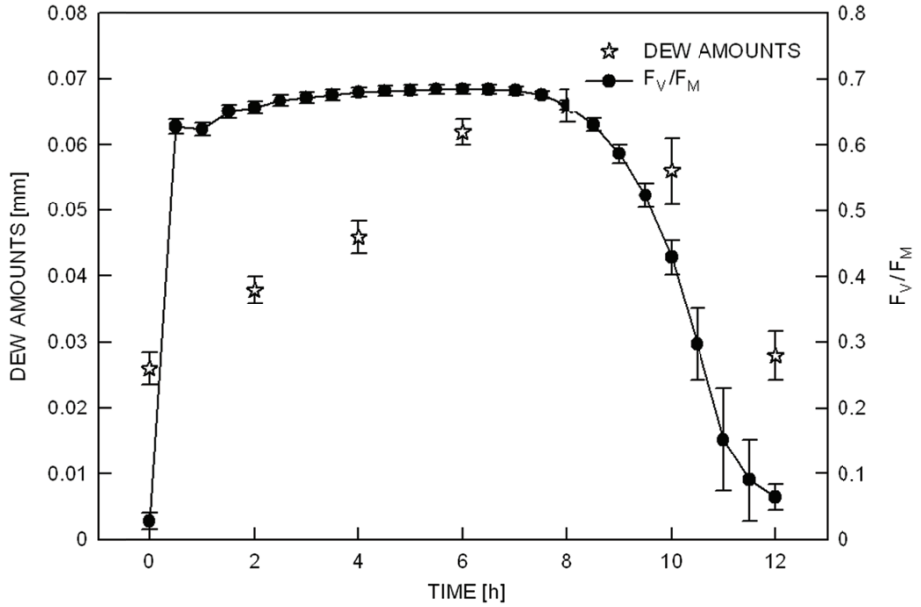

Fig. 5. Relationship between maximal quantum efficiency of photosystem II (F_V/F_M), and dew amounts. *Bars* represent one standard error. For dew amounts, $n = 5$; for F_V/F_M, $n = 3$.

Relationships between Chl fluorescence and environmental factors: To obtain a better insight into the relationships between Chl fluorescence and environmental factors, we further analyzed the above results. A similar trend was noted in the time course of the fluorescence parameter F_V/F_M and dew amounts (Fig. 5). Dewfall increased gradually until 8 h and while F_V/F_M was more sensitive than dewfall, the initial rise of F_V/F_M was very fast and kept constant for about 8 h. Following this both declined steeply.

Soil temperature variation presented the opposite pattern. As daytime temperature rose, amount of dew declined, paralleled by F_V/F_M (Fig. 6).

Discussion

Rapid recovery: The response of fully desiccated *S. caninervis* to remoistening involved a dramatic increase in F_0 and F_V/F_M within the first minute (Fig. 2*A*,*B*). This was followed by a more gradual increase in F_0 and F_V/F_M for 6 to 8 h after remoistening (Fig. 2*C*,*D*). The half-recovery time for the initial rapid exponential rise of F_V/F_M in *Weymouthia mollis* after 20 h drought was 36 s (Proctor 2004). In *Polytrichum formosum*, F_V/F_M reached approximately 80% of its predesiccation value within approximately 10 min of rewetting (Proctor *et al.* 2007a).

Dark-adapted F_V/F_M provides an estimate of the maximal quantum efficiency of PSII; in healthy, unstressed material this is generally around 0.76–0.83 (Proctor 2003). In our study, F_V/F_M of *S. caninervis* rose rapidly on remoistening to 0.6 and then remained relatively steady at around 0.7 for 8 h.

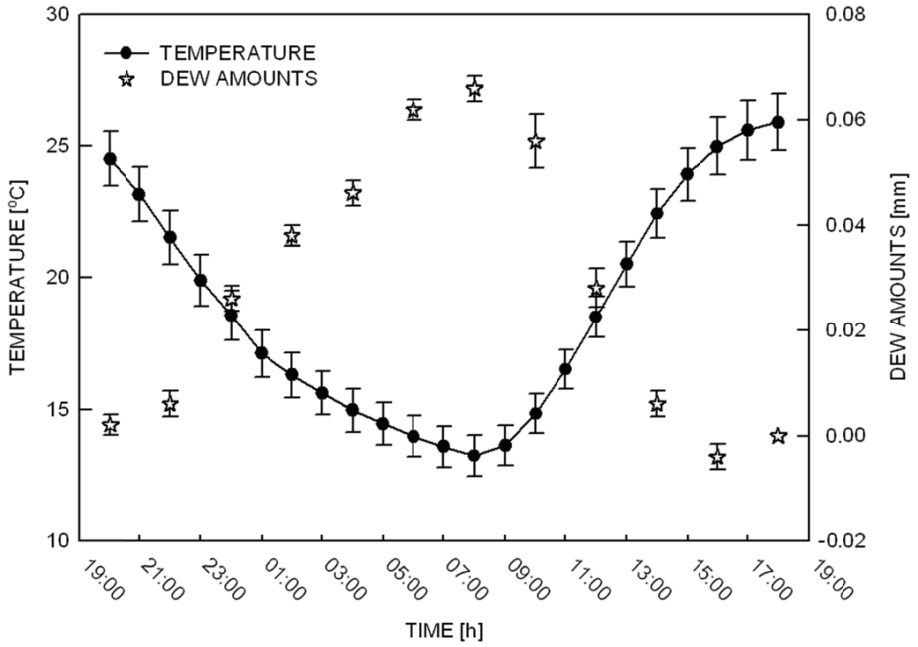

Fig. 6. Relationship between dew amounts and soil temperature (5 cm below) of the moss crusts observed in the interdune areas of the Gurbantunggut desert. *Bars* represent SE. For dew amounts, n = 5; for soil temperature, n = 24.

Cytological evidence: Our findings indicate no damage to membranes or organelles during desiccation or recovery, but suggest that there are remarkable morphological changes in the chlorophyllose cells. This is in accordance with previous findings (Platt *et al.* 1994, Proctor 2000, Proctor and Smirnoff 2000, Pressel *et al.* 2006, Proctor *et al.* 2007a).

In particular, 6 h after remoistening there was a dramatic increase in the number and volume of the osmiophilic globuli (Fig. 3*E*). We also noted that the distribution of the osmiophilic globuli was rather different from that in the hydrated leaf cells, they were no longer scattered but clustered closely together. The increase in number of osmiophilic globuli may be causally related to the disappearance of the lamellar membrane observed by Lichtenthaler (1968). He found that if lamellar synthesis was prevented or the lamellae broke down, the number and volume of globuli increased.

Changes in thylakoids were also observed in this study. Six hours after remoistening, the lamellae of the thylakoids were richer than those of the hydrated leaf-lamella cells (Fig. 3*F*). This led to an increase in the surface area of the lamellar extensions, resulting in the enhanced exchange of metabolites between the chloroplasts and cytoplasm (Proctor *et al.* 2007a). In contrast, the grana in the thylakoid system of leaf cells air-dried for 3 days were small and underdeveloped.

Responses to moisture content: *S. caninervis* is a typical desiccation-tolerant moss and can alter the position of its leaves in response to moisture. The leaves are widely outspread when they are fully turgid, and tightly wound round the stem when they are dry (Fig. 1). The very low, initial fluorescence values from desiccated plants may largely reflect the photoprotection afforded by leaf curling. When leaves twist tightly around the stem, the area of chlorophyllose cells exposed to incoming radiation is significantly reduced. This is considered to be one means by which this plant is able to survive extreme desiccation (Proctor 2001).

The moisture content of biological soil crusts is considered to be one of the chief factors involved in regulating photosynthetic activity (Shields and Durrell 1964). In the Gurbantunggut desert, *S. caninervis* can utilize a range of different periodic water supplies including sudden rain showers, dew, fog, and melting snow, to activate their photosynthetic activity. It is interesting to compare our time lines for F_V/F_M with those of dew accumulation and temperature over a twenty-four-hour period from an earlier field study (Zhang *et al.* 2009). Given overnight dew deposition, moss crusts are ideally positioned to gain maximum benefit from the first light. The fluorescence parameter F_V/F_M is close to the maximum for photosynthetic activity (Fig. 5). As daytime temperatures rises, the moisture content declines, paralleled by F_V/F_M levels (Fig. 6). In previous studies of the relationship between the spectral indices and photosynthetic capacities of different kinds of biological soil crusts in the Gurbantunggut desert, no photosynthetic activity was detected for dry crusts, but F_V/F_M values of hydrated crusts were significantly higher than those of dry crusts (Yamano *et al.* 2006). In addition, due to nocturnal hydration (nightly rain, fog, and/or dew condensation), soil-crust lichens activated dark respiration, and this was followed after sunrise by a short period of positive net photosynthesis that continued until metabolic inactivation occurred from desiccation (Lange *et al.* 1994, 1999).

Conclusions: Within the first minute of remoistening desiccated leaves of *S. caninervis* we observed a dramatic increase in F_0, F_M, and F_V/F_M. All parameters reached their peak values at about 6 h after remoistening, and eventually returned to a point close to their original levels. Cytological changes paralleled the physiological changes. There were remarkable morphological changes in the photosynthetic structures although there was no indication of damage to membranes or organelles during or following recovery. Our results also revealed that the responses of the photosynthetic physiology and the chloroplast structure to remoistening occurred simultaneously. These rapid physiological and cytological responses allow optimum utilization of small and infrequent precipitation events, enabling *S. caninervis* to survive and grow in an otherwise hostile desert environment, where it plays a crucial role in soil stabilization. Our results contribute to a better understanding of the remarkable ability of *S. caninervis* to grow in severe environments, and provide fundamental ecological information with implications for productivity in this challenging and changing environment.

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