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HEAT TOLERANCE CHANGES OF AN INTACT SEMI-DESERT CRYPTOBIOTIC CRUST DURING DESICCATION DOMINATED BY *DIDYMODON* SPECIES

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Abstract: The thermal stability of photosysthetic apparatus was examined under different (light and desiccation) treatments in the mosses (*Didymodon luridus* Hornsch*, Didymodon nicholsonii* Culm) dominated intact semi-desert cryptobiotic crusts. The relatively low temperature tolerance measured in default state (non-energised thylakoids at full turgor) in the samples was inadequate to survive the thermal conditions of the original habitat. This was also manifested in the temperature sensitivity of optimal quantum yield (F_v/F_m) measured in dark-adapted state. The temperature dependence of the steady-state level of fluorescence, measured in light adapted state, indicated a moderate decrease in heat sensitivity of PS II which was further enhanced by moderate water deficit. Moreover, a considerable water loss extremely increased the thermal stability of PS II in both dark and light-adapted states. Temperature dependence of the different quenching parameters suggests that in light-adapted state, the secondary effects of low lumen pH may protect against both temperature stress and water loss: i.e., it is likely that protection against the effects of light, temperature, and water deficit can be partly based on common bases. At very high temperatures the thermal damage of the oxygen-evolving complex is unlikely to be avoided, however, under continuous actinic light, the variable fluorescence (F_m'–F_s=ΔF) was partially recovered even above the critical temperature values of the F_s-T curves. This indicates the partial restoration of the electron donation of the PS II reaction centres by alternative electron donors. These changes in heat tolerance play a significant role to tolerate the effects of daily changing of the ecological factors in the habitat and it has a pronounced ecological significance and partly explains the survival of the examined crusts even under extreme semi-desert conditions.

Keywords: critical temperature, heat stress, multiple stresses, photosynthesis, thermal tolerance, cryptobiotic crust, *Didymodon*

Abbreviations used: AL, actinic light; F_m, maximal fluorescence; F_m', maximal fluorescence of illuminated samples; F_0, initial level of fluorescence; F_s, steady-state fluorescence; F_v, variable fluorescence; F_v/F_m, maximum (optimal) quantum yield of PS II; $\Delta F/F_{m'}$, Y(II), effective quantum yield of PS II; NPQ, non-photochemical quenching; OEC, oxygen-evolving complex; PSI, photosystem I; PSII, photosystem II; Y, yield; Y(NO), quantum yield of non-regulated energy dissipation; Y(NPQ), quantum yield of regulated energy dissipation.

INTRODUCTION

The heat sensitivity of plants is closely connected to the thermal stability of PSII. Above the optimum temperature, the structure and the operation of photosynthetic apparatus could be reversibly or irreversibly damaged (Dulai *et al*. 1998; Wang *et al*. 2018; Szopkó and Dulai 2018). The measure of the damage is significantly affected by the growth temperature, the acclimatization and genetic properties. During heat stress, a decline of linear electron transport and photophosphorylation happens (Björkman *et al*. 1978). The inhibited photophosphorylation is partly attributed to the increase in the permeability of photosynthetic membranes reducing the proton motive force (Havaux *et al*. 1996). Heat decreases of the strength of hydrophilic interactions and thereby the link the light harvesting complex (LHCII) to PSII core complex (CCII) and as a result, it causes the lateral reorganization of the thylakoid membranes, which includes several *sub*-phenomena (Gounaris *et al*. 1984). In addition, thermal stability of PSII is also closely related to the heat sensitivity of the oxygen-evolving complex (OEC) (Yamane *et al.* 1998; Wang *et al.* 2010). The inhibition of OEC is mainly due to the detachment of the manganese-stabilizing extrinsic protein from PSII and the release of manganese ions (Nash *et al*. 1985; Enami *et al*. 1994). Apart from changes affecting the donor side, the acceptor side of PSII may also be limited due to a disruption of the electron transfer between the primary (Q_A) and the secondary (Q_B) acceptor of PSII resulting in the accumulation of reduced Q_A (Kouril *et al.* 2004).

The heat tolerance of PSII can be characterized by the breakpoints (T_c, critical temperature; T_p, peak temperature) of initial (F_0) and steady-state fluorescence (F_s) *vs*. temperature (T) curves (*Figure 3*, Schreiber and Berry 1977; Dulai *et al*. 1998; Molnár *et al*. 1998; Hill *et al.* 2009). Moreover, the temperature dependence of F_0 is directly influenced by membrane fluidity and lipid-protein interactions therefore T_c can be used as an indicator of the thermotolerance of the photosynthetic apparatus in connection with the integrity of thylakoid lamellaes (Hill *et al.* 2009).

For the desiccation tolerant cryptobiotic crusts perhaps the most common combined stress is the water loss together with high temperature, which frequently occurs in hot semi-desert climate area with daily periodicity. The abiotic ecological factors (temperature, light, water conditions) typical here vary in interdependence with each other. These simultaneous stress factors may elicit a response different from that given to a single factor (Osmond *et al.* 1986). A good example for this is that the photosynthetic apparatus is probably more heat-stable in light than in dark (Molnár *et al.* 1998) and water deficit also enhances the thermal stability of PSII (Dulai *et al.* 2006). The study of these problems is further justified by the fact that under natural conditions high light intensity, heat stress, and water deficit occur in combination with each other. Under semi-desert conditions parallel with the increase of irradiation and fast water loss the leaf temperature increases rapidly in poikilohydric crusts. Thus, to achieve an acceptable dry matter production and growth rate, an efficient photosynthetic functioning is necessary even under such unfavorable conditions: the effect of the three stress factors needs to be tolerated here, which is impossible without high thermal stability of photosynthetic functions. All these confirm that the rapid acclimation/acclimatization processes which protect against the simultaneous effects of environmental factors have a pronounced ecological significance for the survival of the examined crusts even under extreme semi-desert conditions. According to the above mentioned facts, this paper reports on the thermal stability changes of photosysthetic apparatus under different (light and desiccation) treatments in the *Didymodon luridus* and *Didymodon nicholsonii* dominated intact semi-desert cryptobiotic crusts.

MATERIALS AND METHODS

Plant materials

Crusts were collected from a lime-sandstone rock with semi-desert vegetation 17 km of Tataouine, between old and new Chenini, Tunisia (*Table 1, Figures 1* and *2*). Chenini in southern Tunisia lies at the border of semi-desert and desert zones. The average annual precipitation in Chenini is 148 mm, with maximum in December (19 mm) and minimum in July (1 mm). The mean daily maximum temperature in January 16, in July and August 37°C. The mean daily minimum temperature in January 5 while in July and August 19°C. The samples were then stored in an air-dry state at dark chambers with room temperature in the herbarium of Eszterházy Károly Catholic University (EGR) in Eger, Hungary. All treatments were performed on original crusts together with their bases of *Didymodon luridus* and *Didymodon nicholsonii* dominated samples within one year of the collection. Before the measurements the samples were rehydrated and transferred to a growth chamber for two days at 25°C where mosses were stored under fluorescent illumination with a 12–h photoperiod of white light at a photosynthetic photon flux density of 200 μmol m^{-2} s^{-1} and at 100% relative air humidity. The color temperature of the fluorescent lamps was 6000 Kelvin, which approximately corresponds to the daytime spectral composition of solar radiation. Desiccation treatments were carried out by desiccators at relative air humidities at 100%, 75%, 54% and 32% for 24 hours.

Heat-induced chlorophyll fluorescence

The responses of the *in vivo* chlorophyll *a* fluorescence to heat were measured in dark-adapted green segments with a pulse amplitude modulation fluorometer (Imaging PAM M-series, Walz, Effeltrich, Germany) as described by Dulai *et al.* (1998). The initial level of fluorescence (F_0) was detected after 15–min dark adaptation and excited by a weak 650–nm modulated beam. The maximal fluorescence level of the dark-adapted (F_m) and light-adapted (F_m’) leaves was induced by saturating flashes of 0.8 s duration. Photosynthesis was induced for 15 min by continuous actinic light of 216 µmol m^{-2} s^{-1}. To determine the breakpoints (T_c) of the F_0 *vs.* T

or the steady-state fluorescence (F_s) *vs.* T curves the heat induction of fluorescence method was applied as described by Schreiber and Berry (1977). The minimum chlorophyll fluorescence (F_0) was monitored in intact green segments of crusts exposed to elevated temperature from 25°C to 60°C at a rate of 1°C min^{-1}. F_s *vs.* T curves were started when the photosynthesis was steady at 216 µmol m^{-2} s^{-1} actinic light intensity.

Table 1. Collection data andshort habitat description of 13160 D sample.

Location, habitat	Taxa
EL KSOUR: 17 km W of Tatouine, between old and new CHENINI. N 35°32', E 09°30'. Hab.: Calcareous sandstone boulders with semidesert vegetation N 32°55.003', E 10°16.365', at 360 m alt. Coll.: S. & T. PÓCS, S. DULAI, M. MARSCHALL; Date: 20 September 2013 Det. T. PÓCS	*Didymodon luridus,* *Didymodon nicholsonii*

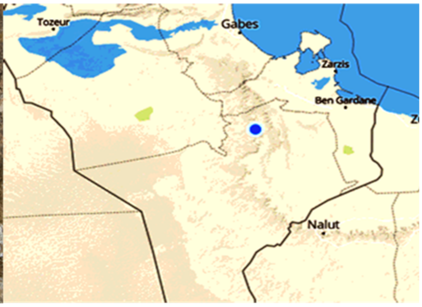

Figure 1. Microhabitat of the 13160 D sample; **Figure 2.** Location of the 13160 D sample.

The saturation light pulse was applied at 25, 30, 35, 38, 41, 43 and then at any further 2°C temperature rise to detect F_m'. T_c was determined as the interception of regression lines fitted to F_0 and F_s data. The fluorescence parameters were calculated as described by Klughammer and Schreiber (2008) on the basis of the following equations: maximal quantum yield of PSII, $F_v/F_m=(F_m-F_0)/F_m$; effective quantum yield of PSII, $Y(II)=(F_m'-F_s)/F_m'$; quantum yield of regulated energy dissipation, $Y(NPQ)=(F_s/F_m')-(F_s/F_m)$; quantum yield of nonregulated energy dissipation, $Y(NO)=F_s/F_m$.

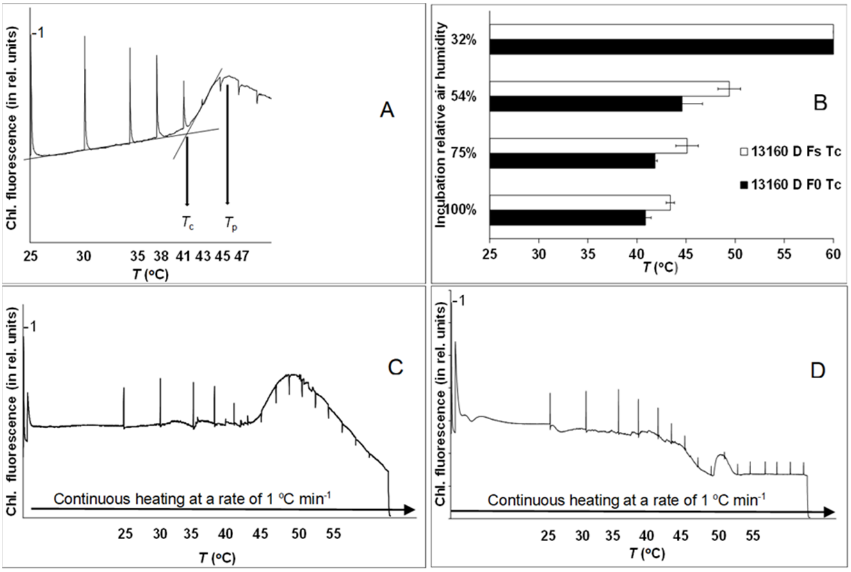

Figure 3A, Original recording of the temperature dependence of initial fluorescence (F_0–T curve) of 13160 D sample; **B**, Breakpoints of F_0–T and F_s–T curves at desiccation treatments of 100%, 75% 54% and 32% relative air humidities for 24 hours for 13160 D sample; **C**, Original recording of an F_s–T curve at full turgor of 13160 D sample; **D**, Original recording of an F_s–T curve after 24 hours desiccation treatments at 54% relative humidity of 13160 D sample. The saturation light pulse was applied at 25, 30, 35, 38, 41, 43 and then at any further 2°C temperature rise to detect F_m'. The results are the means ± LSD$_{5\%}$ of the data of five plants per treatment in the case of B *sub* diagram.

RESULTS AND DISCUSSION

The two *Didymodon* (*Barbula*) species belong to *Pottiaceae* family. Members of this family are mostly drought tolerant species, occurring on exposed rocks, steppe soil or even on rocks and soil of the deserts and semi-deserts, dominating the plant cover on the surface. In the original semi-desert habitat of the examined sample the ground level temperature often rises above 50°C, which is always coupled with high irradiation (≥1500 µmol m^{-2} s^{-1}) and very low relative air humidity (RH ≥ 20%). Although it is well known that light enhances the thermal stability of PSII (Molnár *et al*. 1998, Dulai *et al*. 2002) the original recording of the F_0 and F_s *vs*. T curves (*Figures 3A, C*) and the data in *Figure 3B* show that heat stability of

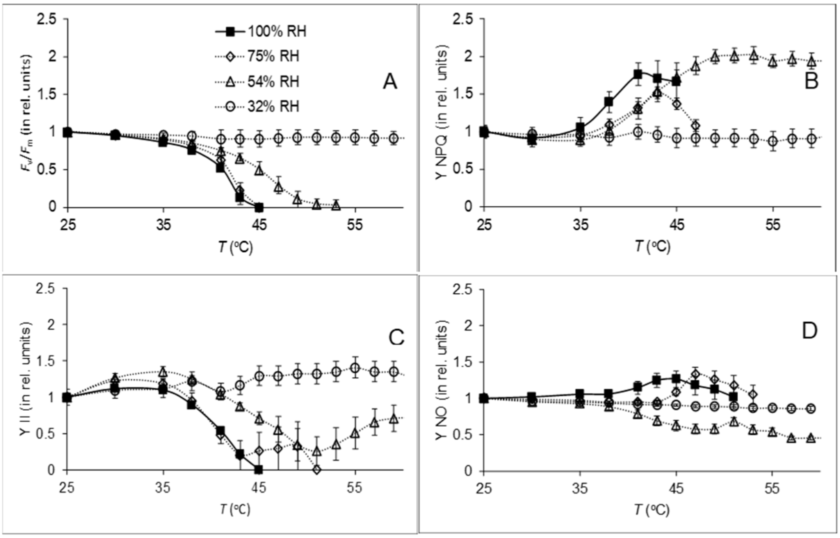

Figure 4. Effects of different desiccation treatments (incubation at 100%, 75% 54% and 32% relative air humidities for 24 hours in desiccators) for the temperature dependence of the chlorophyll *a* fluorescence induction parameters A, F_v/F_m; B, Y(NPQ); C, Y(II); D, Y(NO) measured at 216 µmol m^{-1} s^{-1} AL intensity in 13160 D sample. The results are the means ± LSD$_{5\%}$ of the data of five plants per treatment.

PSII is not sufficient for the toleration of such high temperatures at full turgor neither in dark nor in light adapted state. According to the T_c points of the F_0–T curves, the thermal stability of PSII was not improved by moderate water loss (≤25%) in the absence of light since no significant shift in T_c points was detected (*Figure 3B*). The temperature dependence of F_v/F_m (*Figure 4A*) also confirmed that there was no heat tolerance increase at a weak water deficit. In the presence of light (216 µmol m^{-2}s^{-1}), a moderately decreased heat sensitivity was observed already in the case of control plants (*Figure 3B*) by comparison with dark-adapted samples and it was further enhanced by a moderate desiccation treatment as reported by Dulai *et al.* (2002). This was also reflected by the temperature dependence of the effective quantum yield of PSII and quantum yield of non-regulated energy dissipation (Y/NO/): at ≈ 75% water content the $\Delta F/F_m'$ was measurable even around 45°C (*Figure 4B*) and Y(NO) also started to rise only at higher temperatures than in the case of control (*Figure 4D*). In connection with this it demonstrated by several studies that water deficit before heating could increase the thermal stability of PSII, which may be reflected in the lower heat sensitivity of effective quantum yield of PSII (Dulai *et al*. 2002, 2006; Ribeiro *et al*. 2008). With stronger desiccation treatment (≈ 54%), the T_c values shifted significantly higher both in the dark and in the light-adapted state, but under continuous illumination, this thermal stability increase was much higher: T_c values reached 49°C (*Figure 3B*). In case of even stronger pretreatment (≈ 32%), the T_c values were not even detectable up to 60°C. This large, unusual increase in thermal tolerance caused a decrease in the temperature sensitivity of both the optimal and the effective quantum yield of PSII.

During dehydration, it may become increasingly common for plants to tolerate the combined effects of the abiotic stress factors (Szopkó and Dulai 2018). Consequently, the productivity of desiccation tolerant plants depends on by their ability to coordinate mechanisms protecting against multiple stresses (Dulai *et al*. 2002). Thus the synchronization of regulating/protecting processes largely influences the flexibility of plants' tolerance to the effects of the combined factors and it may be essential for the adequate photosynthesis and growth (Szopkó and Dulai 2018). The non-radiative dissipation of excitation energy depends on both the intrathylakoid *p*H gradient and the activity of the xanthophyll cycle (Demming-Adams 1990). It is also well known that heat-induced and rapid conformational change in the pigment-protein complexes of PSII favours the development of NPQ. At a low lumen *p*H the activity of the xanthophyll cycle, besides its role in the photoprotection, may increases the heat tolerance of PS II (Havaux and Tardy 1996; Molnár *et al*. 1998), since the zeaxanthin accumulation, not only promotes the induction of non-photochemical quenching (Kiss *et al.* 2008) but also it maintains the stability of the thylakoid membranes (Havaux *et al.* 1996; Dulai *et al*. 2002; Lavaud and Kroth 2006). The values of the quantum yield of regulated energy dissipation (Y/NPQ/) in the treated plants significantly surpassed the control already at normal temperatures (not shown by data) and maximal Y(NPQ) values were closed to the T_c points of F_s–T curves at the applied light intensity (*Figure 4C*). Based on the temperature dependence of the Y(NPQ), it can be seen that the secondary effects of low lumen pH (Müller *et al.* 2001) may also play an important role in the protection against both the heat and the dehydration. All this is also confirmed by the fact that significant shifts in T_c values could be generated by presence of light already in non-stressed plants in comparison with the T_c values measured in the dark. Furthermore, the desiccation treatments applied in parallel with light have already resulted in more significant differences between the treatments (*Figure 3*).

The oxygen-evolving complex (OEC) of the photosynthetic apparatus is also extremely sensitive to high temperature stress, and as a result of its damage, the reaction center of PSII can also be inactivated. The loss of OEC activity is mainly due to the detachment of the manganese-stabilizing extrinsic protein from PSII (Enami *et al*. 1994) and the release of manganese ions (Nash *et al*. 1985). Thus the thermal tolerance of photosynthesis is closely related to the heat sensitivity of OEC (Yamane *et al.* 1998; Wang *et al.* 2010). The thermal damage of the OEC occurs immediately before the T_p values of the F_s–T curves. It can be seen in *Figures 3C, D* and *Figure 4B* that the variable fluorescence detected under continuous actinic light (F_m'–F_s=ΔF) was disappeared just before reaching the T_p value, indicating thermal damage to the OEC. Inhibition of electron donation to the reaction center increases the probability of accumulation of Tyr_Z^+ $P680^+$ (donor side photoinhibition). However, under stronger desiccation (≈ 54%), ΔF was partially detectable again beyond T_p (*Figures 3D* and *4B*), despite the continuously increasing temperature, which could be related to the partial recovery of the primary charge separation. This might be partially explained by the cyclic electron transport around PSII, but it is even more likely that, in case of damage to the OEC, other alternative electron donors deliver electrons to the photosynthetic electron transport chain instead of water molecules through the Tyr_Z and the reaction center (Tóth *et al*. 2007). These results are consistent with the observations that after heat inactivation of OEC, ascorbate can act as an alternative electron donor and thereby partially restore photosynthetic electron transport. This is also supported by the fact that the electrons from ascorbate are present in the intersystem chain and PSI (Tóth *et al*. 2009) in several cryptogams and vascular plants.

In conclusion, the strong decrease in water content increases the temperature stability of the photosynthetic apparatus in both dark and light-adapted conditions in this cryptobiotic crust.

In light-adapted state, even a slight loss of water causes an increase in heat tolerance. This change in heat tolerance plays a significant role in preventing the effects of daily changing ecological factors in the original habitat. The secondary effects of low lumen pH may also play a role in protection against the effects of temperature stress and water loss: i.e. it is likely that the protection against the effects of light, temperature and water deficit reveals common characteristics, in this crust, at least. The thermal damage of the OEC is probably unavoidable at high temperature, but the electron donation of the reaction centre can be partially restored. Thus, in addition to secondary effects of thylakoid energization, other alternative processes may also play a role in the development of extreme heat tolerance during dehydration. All these facts confirm that the rapid acclimation/acclimatization processes which protect against the simultaneous effects of environmental factors have a pronounced ecological significance and partly explain the survival of the examined crusts even under extreme semi-desert conditions.

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