

UV-B effects on filamentous alga *Zygnema* strain (EEL201) from Antarctica

Marina Prieto-Amador*

University of Salamanca, Faculty of Biology, Campus Miguel de Unamuno, 370 07 Salamanca, Spain

Abstract

Filamentous alga *Zygnema* sp. is frequently found in extreme polar environments with freshwater availability for at least part of summer season. In such habitats, *Zygnema* might be exposed to several stress factors, like freeze, desiccation and high irradiation levels. This study investigated the effect of UV-B on primary photosynthetic processes in *Zygnema* sp. (EEL201 strain) from Antarctica. Samples were cultivated in liquid medium and exposed to supplemental UV-B (1.4 W m^{-2}) for 6 h. During the UV-B treatment and following recovery, the changes in chlorophyll fluorescence parameters caused UV-B were measured. Negative effects on F_v/F_m and Φ_{PSII} were found after 6 h treatment with only limited recovery in dark. The only parameter that recovered was photochemical quenching (qP) indicating a potential to restore photosynthesis in the reaction centres that were not damaged by UV-B treatment. However, the share on damaged RC PS II was much higher compared to those showing the recovery. Thus, the effect of short-term supplemental 1.4 W m^{-2} UV-B light was considered heavy causing substantial damages to PS II. These results provide insights on the effects of UV-B light on *Zygnema* sp. that can help in the interpretation of response mechanisms of Arctic algae to radiation.

Key words: James Ross Island, chlorophyll fluorescence parameters, photosystem II, photoinhibition, absorption spectrum

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Introduction

Zygnema is a filamentous alga which never branches and which can be easily recognized by having two stellate chloroplasts which are located in the central part of each cell. *Zygnema* cells are cylindrical with a flat cell wall. Between the chloroplasts we can find the core. *Zygnema* filaments are thin threads of green silk, a little

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*Corresponding author: Marina Prieto-Amador <marina95septiembre@hotmail.com>

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sticky to the touch, like his close relative *Spirogyra*. Ultraviolet (UV) radiation is an important stress factor in polar regions. Solar radiation, despite being an essential factor for photosynthesis, can also be stressful, this occurs mainly in midsummer when the daily energy income reaching the Earth's surface at the poles is higher than that on the equator. UV radiation affects to the vegetative Arctic freshwater alga *Zygnema*, which is used in this experiment. Microalgae isolated from an extreme environment like the Arctic region are a good model organisms for studying adaptive strategies, the organism living in extreme areas need to possess adaptations that allow them to survive in such a hard conditions. *Zygnema* sp. is one of the most common algae in the Arctic and Antarctica, usually forming extensive mats, living at the transition between aquatic and aeroterrestrial environments. Recently, *Zygnema* from alpine and polar regions is studied in details, its resistance to stress factors in particular (reviewed by Pichrtová 2014). In the studies, several anatomical, morphological and physiological aspects are related to particular environmental factors, such as *e.g.* osmotic stress (Pichrtová et al. 2013), desiccation (Kaplan et al. 2013, Holzinger et al. 2009), and nitrogen limitation (Pichrtová et al. 2014a). Some short-wavelength radiation induced changes in physiological processes are studied as well (Choi et al. 2014). Recently, production of secondary metabolites in *Zygnema* is studied (Pichrtová et al. 2014b).

Light has numerous effects on plant growth and metabolism due to the fact that the majority of plants are directly light-dependent organisms. Apart from visible light that is important in photosynthesis, UV light reach the earth's surface and its increased input becomes a serious problem owing to depletion of stratospheric ozone. The harmful effects of UV-B on plants include damage of molecular targets, causing problems to photosynthetic processes and consequently changing the community

structure and productivity of aquatic ecosystems. The harmful effects of UV-B on autotrophs include damage of molecular targets, causing problems to photosynthetic processes and consequently changing the community structure and productivity of aquatic ecosystems (Häder et al. 2003, 2007) as well as algal cultures cultivated under laboratory conditions (Estevez et al. 2001).

White et Jahnke (2002) overviewed a wavelength dependency of UV radiation, effects of UV-A and UV-B on photosynthesis in algae in particular. The authors reported direct negative effects on F_v/F_M caused by UV-A but not UV-B. Similarly, Stamenkovic et Hannelt (2014) showed a higher extent of photosynthesis reduction in UV-A than UV-B treated *Cosmarium* sp. However, only limited number of researchers studied UV-A effect in algae (*e.g.* Dring et al. 1996) because UV-A radiation incident to the Earth surface is not affected by ozone layer depletion. Incident UV-B radiation, contrastingly, increases with attenuation of ozone layer. Therefore, UV-B effects in green alga have been studied much more within last few decades addressing a wide variety of responses including growth and development, biomass, sensitivity, photosynthetic pigments, UV-B absorbing compounds, photosynthesis, activation of antioxidative systems (Tian et Yu 2009), protein and DNA damage, enzyme activity, nitrogen fixation and assimilation of nitrogen, and activation of protective mechanisms (for review *see* Xue et al. 2005).

UV radiation effects have been studied in snow algae as well. However, most of the studies have been conducted in ubiquitous flagellate green algae which have a capability to migrate within the snow pack column. The studies have been done mainly on *Chlamydomonas* sp., *Chloromonas* sp. (*see e.g.* Leya et al. 2009). Recently, also non-motile green algae thriving in snow are studied (Rivas et al. 2016). Algae in freshwater ecosystems demonstrate a

wide range of sensitivity to UV-B. Karentz et al. (1991) and Xiong et al. (1997) suggested that susceptibility to UV-B may be related to algal cell size and shape. The smaller cells (*i.e.* high surface area to volume ratio) are considered to be more sen-

sitive thanks to potentially lower photoprotection. In this concept, a larger cell has more UVB-absorbing content (protein and amino acids) in the cytoplasm, which shields the UVB-sensitive nuclear DNA.

Material and Methods

Zygnema collection and handling

A *Zygnema* strain EEL201 (Collection of Extreme Environment Life Laboratory, Masaryk University, Brno, Czech Republic) was used for this experiment (Fig. 1). The samples were taken from temporary streams running through a long term research plot LTRP near to Mendel station, at James Ross Island in January 2015 (for details *see* Barták et al. 2015a,b). The samples were distributed in 30 ml plastic tubes, after that it were stored in a refrigerator at

5°C. Then the samples were transported to a laboratory maintaining it at 7°C thanks to freeze packs inserted into a portable refrigerator box. In the laboratory, *Zygnema* sp. was inoculated to a BBM (Bold's Basal Medium) agar and cultivated during several weeks in Petri dishes at 22°C. Then, the alga was placed in a liquid medium and cultivated in 100 ml glass flasks during 14 days.



Fig. 1. *Zygnema* sp. (strain EEL201) during cultivation on agars (left) and liquid medium (right). Photo by K. Skácelová.

High-light exposition

Zygnema sp. (EEL 201) was exposed to UV-B irradiance (1.4 W m^{-2}) for 6 hours to see the responses of photosynthetic apparatus, chlorophyll fluorescence parameters, and photoprotective mechanisms activated during UV-B treatment. After the UV-B treatment, the samples were allowed 120 min. recovery in dark to see whether or not a fast phase of recovery of chlorophyll fluorescence parameters appears. During the

exposition, the samples with *Zygnema* sp. (1 ml in a microbiological plates, hole size 5 ml) were placed on a surface of aluminium block surrounded by ice to maintain a constant low temperature. Light was provided by a source of white bright LED. In these treatments, the extent of treatment-induced photoinhibition was evaluated as a change in chlorophyll fluorescence parameters.

Chlorophyll fluorescence measurements

Effects of UV-B light treatment on photosynthetic processes of *Zygnema* sp. EEL201 was evaluated by several chlorophyll fluorescence parameters. For chlorophyll fluorescence measurements it was used a FluorCam (HFC-010, Photon Systems Instruments, Czech Republic) and the method of slow Kautsky kinetics of chlorophyll fluorescence supplemented by the analysis of quenching mechanisms (for method description *see e.g.* Conti et al. 2014). The method determines the basic fluorescence (F_0) and maximum fluorescence (F_M) in dark adapted state. Then, a set of light-adapted chlorophyll fluores-

cence parameters is measured. For this study, we selected the following parameters (*see e.g.* Maxwell et Johnson 2000 for definitions): F_V/F_M , Φ_{PSII} , qP , and NPQ_{PIN} ($NPQ_{PIN} = (F_{Mcontrol} - F_M') / F_M'$, where $F_{Mcontrol}$ is maximum fluorescence in control dark-adapted sample, and F_M' is maximum fluorescence in light-adapted sample). Chlorophyll fluorescence measurements were taken before photoinhibitory treatment, then after 2, 4, and 6 h of UV-B treatment. The parameters were measured during consequent recovery (in dark) in 30 min. interval for 2 h.

Pigments and UV-B screening compounds

Absorbance within the wavelength range of 190–700 nm was measured in *Zygnema* cultivated in a liquid medium. UV-VIS spectrophotometer (Specord 205, Analytik Jena, Germany) was used to measure absorbance in control samples and those exposed to UV-B irradiance

(1.4 W m^{-2}) for 2, 4, and 6 h, respectively. To evaluate an effect of short-term UV-B treatment, the change in specific absorbance (684 nm for chlorophyll content - Rodrigues et al. 2011) was evaluated and expressed in relation to untreated control.

Results and Discussion

Exposure of *Zygnema* sp. to UV radiation led to a photoinhibition which is observable as a decrease in F_V/F_M (Fig. 2). As expected, F_V/F_M dropped to the value

of around 0.46 after 2 hours of exposure. Low values (around 0.2) measured after UV exposure are an indicator that the photosystems were almost inactivated.

With following exposition, F_V/F_M showed further but relatively small decrease in F_V/F_M . Following dark recovery did lead a slight increase in F_V/F_M but full recovery was far from being completed (only 50 % of initial value). Similar response was found for Φ_{PSII} , *i.e.* fall from initial value (0.465) to 0.18 followed by the values oscillating around the latter one during following UV-B exposition and recovery. Therefore, no dark recovery of Φ_{PSII} was apparent. Strong UV-B induced photoinhibition contrasts to data presented by Herburger et al. (2015) who reported no photoinhibition by photosynthetically-active radiation (PAR) up to $2000 \mu\text{mol m}^{-2} \text{s}^{-1}$. This was, however, true only for young cultures, the old ones (older than 9 months) showed PAR-induced photoinhibition at light doses above $800 \mu\text{mol m}^{-2} \text{s}^{-1}$. The likely reason is that in the study of Herburger et al. (2015), samples were exposed to particular PAR doses only for 30 s, while UV-B exposure in *Zygnema* sp. EEL201 lasted 6 h. Therefore, more pronounced PAR photoinhibition might be expected when PAR exposition would last longer (in terms of hours) in the study of Herburger et al. (2015). For future photoinhibitory studies in *Zygnema*, a combination of PAR and UV-B in several doses and exposition duration seems to be a promising set up to learn more about sensitivity of the alga to photoinhibition. Such approach involving two factors might be beneficial and would result in new findings since Germ et al. (2009) report for *Zygnema* either no UV-B photoinhibition in a single-factor design (low UV-B) or remarkable photoinhibition in 1) chlorophyll fluorescence parameters in high UV-B and 2) two-factor design (UV-B plus selenium). Moreover, long-term exposition to UV-B (in terms of hours and days) may lead to acclimation of photosynthetic processes in photosystem II of green algae since Tilbrook et al. (2016) reported mechanisms preserving proteins D1 and D2 in

Chlamydomonas reinhardtii under UV-B stress.

NPQ_{PIN} increased to its maximum after 2 h of UV-B treatment (0.747), then decreased to 0.673 at the end of UV-B treatment and, similarly to Φ_{PSII} showed no recovery in dark for next 20 h. Photochemical quenching (qP), however, exhibited exponential decrease with the time of UV-B treatment followed by a full recovery to prephotoinhibitory values. Moreover, fast phase of qP recovery was apparent within the first 120 min. in dark (*see* Fig. 2). This might be explained by full restoration of openness of those PS II reaction centres that were not damaged by UV-B treatment. However, proportion of those functioning PS II centres had to be very small to those that were destructed since F_V/F_M and Φ_{PSII} did not show any recovery in dark. Therefore, majority of PS II had to be heavily damaged or destructed by the UV-B treatment used in this study. Another explanation is that capacity of resynthetic processes was very small in *Zygnema* sp. (strain EEL201) and thus insufficient to restore PS II during 120 min. recovery. Therefore, it might be concluded that the exposure to UV lead to strong inhibition of primary photosynthetic processes in *Zygnema* and likely partial destruction of pigment protein complexes in PS II and LHCs since no fast phase of recovery in F_V/F_M and Φ_{PSII} was apparent.

As regards UV-B effect on green algae, Rivas et al. (2016) reported inhibition of F_V/F_M in *Chlorella* caused by UV treatment. The authors analysed wavelength effects on F_V/F_M decrease. They concluded that a high UV tolerance exist in *Chlorella*, at least within the first 12 h of exposition to the light with a high UV-B to UV-A ratio. Similarly, Wong et al. (2007) reported a higher tolerance of *Chlorella* (strain UMACC 237) to UV-B from Antarctics than temperate and tropical regions. Rivas et al. (2016) reported an effect of

UV-A+B treatment on photosynthetic electron transport rate (ETR) calculated from chlorophyll fluorescence data, effective quantum yield of PS II in particular. The study focused on temperature interaction with UV-A+B. Light-response curves of ETR indicated lower photosynthesis in samples incubated to 5°C compared to higher temperatures.

UV-B effects in green algae from terrestrial habitats in polar regions are dose- and time-dependent. In this study, 1.4 W m⁻² (UV-B) was used which typical-

ly induce negative effects in photosynthetic apparatus after 10 to 48 h of exposition (Monteiro Estêvão 2015, Medina et Avalos-Chacon 2015). *Zygnema* strain EEL201, however responded much faster, even after several minutes and showed a substantial decrease in F_V/F_M and Φ_{PSII} . The difference might be attributed to an effective screening of incident UV-B radiation by Antarctic *Nostoc commune* (Monteiro Estêvão 2015) and lichens (Medina et Avalos-Chacon 2015).

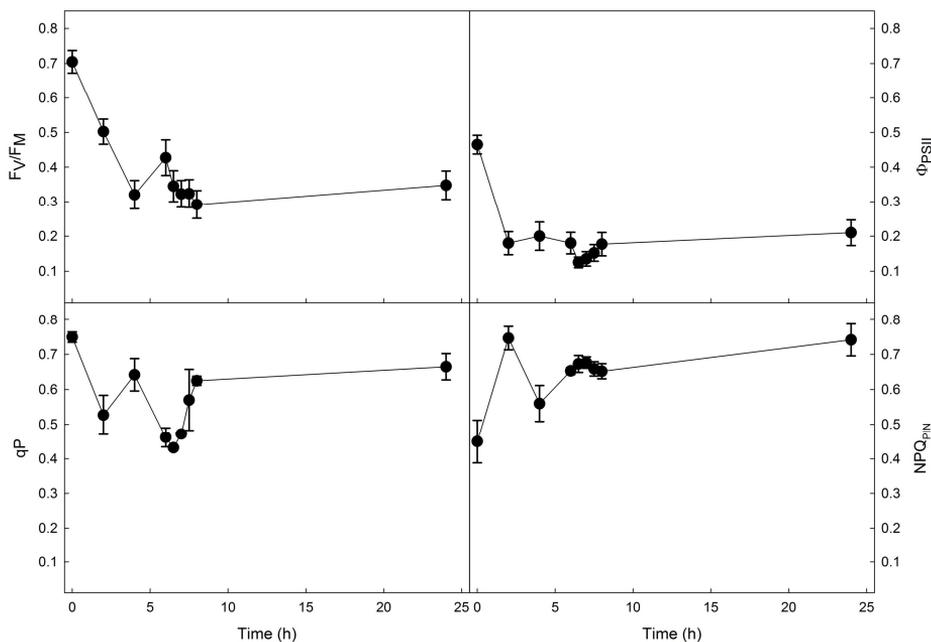


Fig. 2. Time course of potential (F_V/F_M), effective quantum yield (Φ_{PSII}), photochemical (qP) and non-photochemical quenching (NPQ_{PIN}) recorded before, during (1-6 h), and after (6-24 h) photoinhibitory UV-B treatment (recovery).

In *Zygnema*, constitutive pool of UV-screening components might be lower and perhaps less effective than in Antarctic chlorolichens and microbial mats. Conclusion of a heavy negative effects of UV-B on PS II might be supported by Fig. 2 which shows uncompleted recovery of F_V/F_M (60% of pretreated value) after 24h

in dark. However, UV-B protective mechanisms are reported for *Zygnema* (Holzinger et al. 2009). Their pools and involvement into a short-term response to UV-B are the matter of recent investigations. UV-B treatment of *Zygnema*, however, led to an involvement of non-photochemical quenching of light energy absorbed in

PS II. In *Zygnema*, evaluation of non-photochemical quenching (NPQ) meets some problems, since the UV-B induced changes in ChlF transients (Fig. 4), Thanks to the fact that F_M in control is substantially higher than F_M in UV-B treated sample, NPQ calculated from actual F_M may rise numerically with UV-B stress. Thus we used F_M of control for the calculation of NPQ_{PIN} in UV-B-treated *Zygnema* sp. In this concept, NPQ_{PIN} rises with the time of exposition to UV-B stress (see Fig. 2). This conclusion is consistent with evidence from a wide variety studies reporting both a short-term (Berteotti et al. 2016) and a long-term NPQ increase in algae treated by high UV-B/PAR doses (Stamenkovic et al. 2014). With time of exposition to high PAR and/or UV-B doses, however, share of components forming non-photochemical quenching (qE, qT, and qE) may change as

reported by Erickson et al. (2015) for *Chlamydomonas reinhardtii*. In the field, *Zygnema* populations grow typically in water column, a depth of which is 0-50 cm. Therefore, absorption of UV-B in water column might be an important factor attenuating UV-B dose. Biomass / Density of *Zygnema* population is another interacting factor causing a reduction of UV-B along the pathway of UV-B radiation passing through the population. Thus, *Zygnema* filaments from lower part of a water column may benefit from a reduction of UV-B happening in the upper parts of the water column. Therefore, UV-B induced PS II inhibition might be much less pronounced in lower compared to upper layers of water column. More field-based research is, however, needed to prove such conclusion.

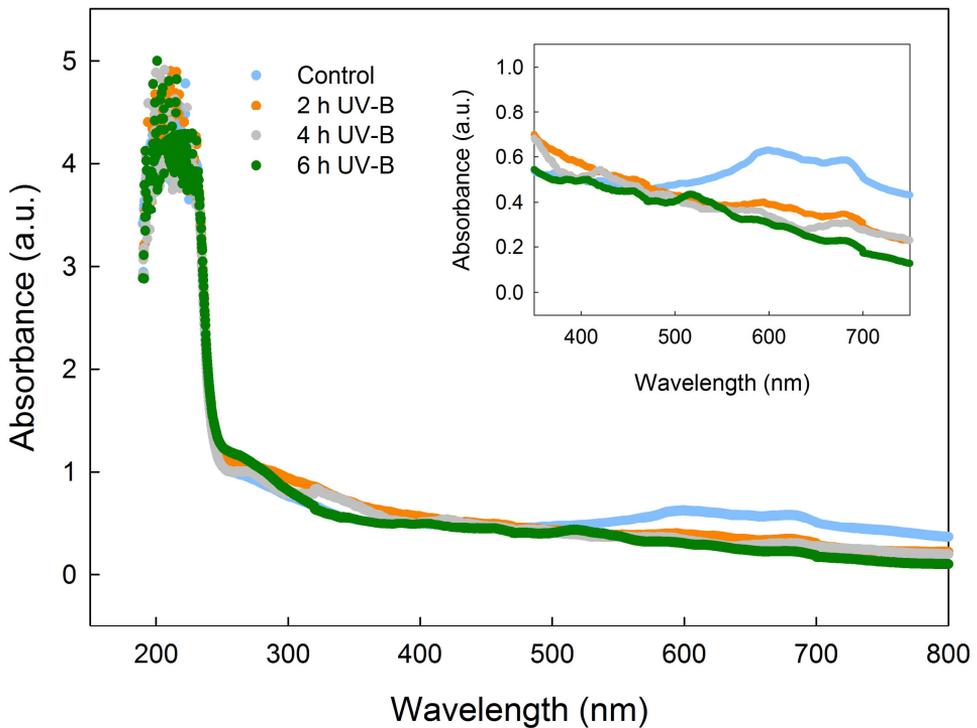


Fig. 3. Absorbance of *Zygnema* sp. (EEL201 strain) recorded in control (blue), and UV-B-treated samples (2 h – orange, 4 h – grey, 6 h – green).

Spectral absorbance changes caused by UV-B treatment are presented in Fig. 3. They comprised decrease of absorbances in the wavelength of 600 and 685nm. The latter one might be attributed to UV-B induced degradation in chlorophyll contents, which decrease to 58.5, 51.9, and 38.4% of untreated control after 2, 4 and 6 h, respectively. The most apparent reduction was achieved after 2 h, then further decrease in

absorbance was less pronounced with the exposition time. Absorbance in the wavelength range corresponding to carotenoids did not change with UV-B treatment, therefore the likely UV-B induced *de-novo* synthesis and utilization of carotenoids will be addressed in further study. Absorbance in the range of 190-250 nm changed only slightly.

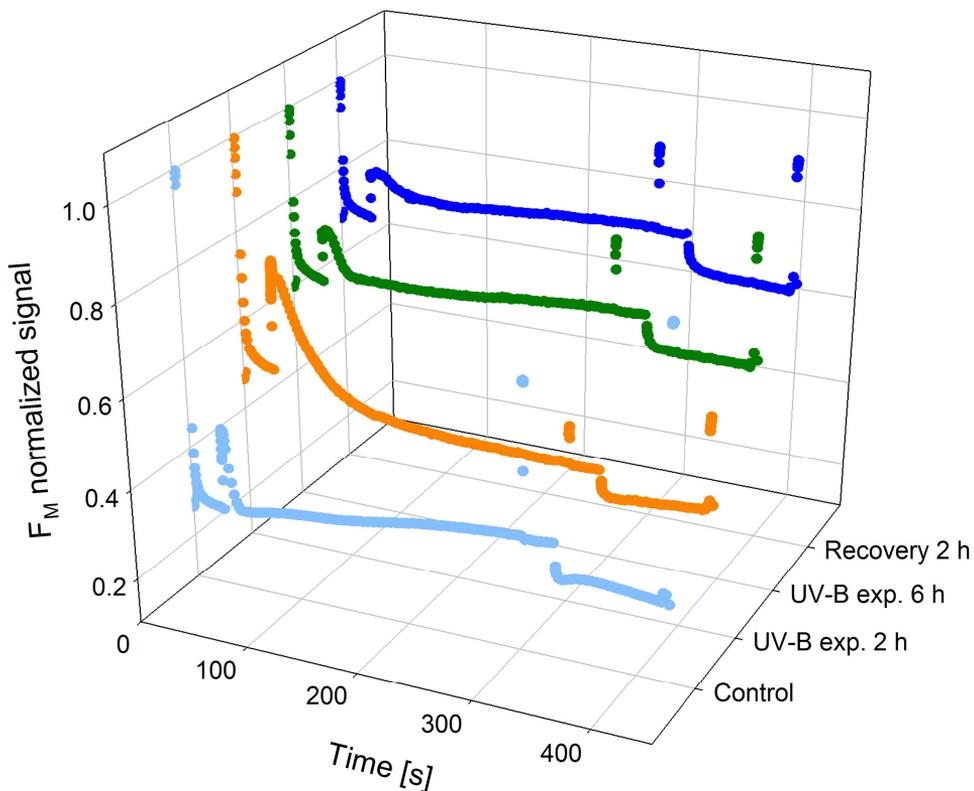


Fig. 4. F_M -normalized transients of chlorophyll fluorescence recorded before (control) and after 2, and 6 h of exposition to UV-B, respectively. Last transient (deep blue) shows post exposition chlorophyll fluorescence recorded after 2 h dark recovery.

Concluding remarks

This study has brought an information of medium to severe photoinhibition caused by UV-B with only limited recovery in *Zygnema* EEL201 strain. Since majority of

previous studies reported a high degree of resistance to PAR- (Thangaraj 2015) and UV-B-induced (Holzinger et al. 2009) photoinhibition, a further study is needed to ad-

dress the likely causes of such sensitivity to UV-B. In conclusion, data on F_v/F_m and Φ_{PSII} presented in this study indicated a strong stress induced by supplemental UV-B. Moreover, the UV-B dose used in this study was higher than that in the field during mid austral summer and causing negative effects in PS II (F_v/F_m , Φ_{PSII}) with only limited short-term recovery. Further study is needed to evaluate potential of *Zygnema* to cope with medium to high UV-B doses. The UV-B effects on primary photosynthetic processes should be studied as a change in chlorophyll fluorescence parameters but also as a changes in the shape of chlorophyll fluorescence transient (see Fig. 4) which may provide a deeper insight into the involvements of quenching mechanisms. In the follow studies, other interacting factors, such as e.g. water temperature and/or initial stages of *Zygnema* population dehydration will be addressed.

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