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Does ultraviolet radiation affect the xanthophyll cycle in marine phytoplankton?†

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This Perspective summarizes the state of knowledge of the impact of ultraviolet radiation on the photoprotective xanthophyll cycle in marine phytoplankton. Excess photosynthetically active radiation (PAR; 400–700 nm) and ultraviolet radiation (UVR; 280–400 nm) affect various cellular processes and can potentially lead to reduced growth or viability loss *in situ*. Algae deploy photoprotective mechanisms that limit the hazardous effects of excess light exposure. Xanthophyll cycle pigments play a crucial role in photoprotection *via* the development of non-photochemical fluorescence quenching (NPQ) during excess radiation exposure. Research on the interacting effects of excess PAR and UVR exposure on xanthophyll cycle pigment synthesis and xanthophyll cycle activity has produced contrasting views. The current contribution summarizes research on photoprotection *via* photoregulation (xanthophyll cycle activity) and photoacclimation (adjustment of the xanthophyll cycle pigment pool) for marine phytoplankton. Subsequently, UVR effects on the xanthophyll cycle and on xanthophyll cycle pigment pools are discussed and results of supporting experiments with the common diatom *Thalassiosira weissflogii* are presented. We show that UVR exposure may enhance xanthophyll cycle pigment synthesis. This suggests that UVR-induced reduction in de-epoxidation state does not necessarily imply reduced energy dissipating potential.

Excess irradiance responses of marine phytoplankton

Excess irradiance exposure in marine environments

The light that drives phytoplankton photosynthesis is highly dynamic in terms of quantity and spectral composition. Seasonal and diurnal cycles, stratospheric ozone and meteorological conditions (aerosols, passing clouds), optical properties of the water column (attenuation, focusing of light by waves), tidal cycles, and wind-driven transport (vertical mixing) contribute to these dynamics.[1–3] Although water column stratification moderates the dynamic conditions of wind-driven vertical mixing, all marine habitats are characterized by dynamic and unpredictable irradiance at some point in time. For phytoplankton, the perceived light can range from full sunlight to complete darkness and fluctuations can occur on a time scale that varies from seconds to hours. When residing in the upper part of the water column phytoplankton can be exposed to high photosynthetically active radiation (PAR; 400–700 nm), which can coincide with exposure to the short wavelength ultraviolet A radiation (UVAR; 315–400 nm) and ultraviolet B radiation (UVBR; 280–315 nm) of the solar spectrum. UVR is attenuated faster than PAR, causing a vertical gradient in spectral composition in the water column. Therefore, frequency and duration of high PAR and UVR exposure also depend on the turbulence in the aquatic environment.[4,5]

Lab and field investigations into the photosynthesis–irradiance relationship of marine phytoplankton have shown that algal photosynthesis typically saturates below 200 μmol photons m^{-2} s^{-1}, which comprises around 10% of maximal incoming radiation at the water surface.[6] This implies that phytoplankton residing near the water surface can experience irradiance far in excess of their photosynthetic capacity. Because excess light exposure, including UVR, is a natural stressor that can periodically decrease photosynthesis (reviewed by Villafañe *et al.*[7]), all marine phytoplankton require mechanisms for protection (photoprotection). In the present Perspective we will address primarily xanthophyll cycle activity and xanthophyll cycle pigment synthesis. We will distinguish between photoregulatory and photoacclimatory processes, with the former operating on a short time scale (milliseconds, minutes) and the latter on longer time scales (hours to days) since this process requires new synthesis of cellular components. Furthermore, the impact of UVR on xanthophyll cycle activity is discussed based on earlier work as well as new data, the latter derived from experiments with the temperate diatom *Thalassiosira weissflogii* exposed to natural solar radiation.

Potential effects of excess irradiance and photoprotection

Exposure to excess irradiance can cause the accumulation of inactive PSII reaction centers.[8] This phenomenon is called photoinhibition and becomes manifest as a reduced ability to perform linear photosynthesis. Apart from reduced carbon fixation, prolonged excess radiation exposure may cause viability loss.[9] The chain of events that leads to photoinhibition is disputed and may depend on the investigated species and environmental variables.[10] Exposure to excess light can over-reduce the photosynthetic electron transport chain. Over-reduction of the plastoquinone pool can promote the formation of triplet excited chlorophyll states that can generate formation of reactive oxygen species (ROS).[11] This

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can damage the D1 and D2 reaction centre core binding proteins of PSII.[12] Furthermore, radiation below ~360 nm does not drive photosynthetic electron transport, but due to the short wavelength it can damage organic molecules directly or indirectly. UVR effects show strong wavelength dependency.[13] Research on cultivated phytoplankton species have identified numerous targets that are influenced by UVR. RUBISCO activity can decrease after UVBR exposure.[14,15] This directly affects linear photosynthesis, and may simultaneously increase the proliferation of oxidative stress related symptoms such as PSII inactivation due to enhanced damage to the D1 reaction centre protein or membrane peroxidation. UVBR has been demonstrated to induce DNA damage (reviewed by Buma *et al.*[16]), although UVR-induced photoinhibition is believed to dominate under natural conditions.[17]

In order to maintain active PSII centers over a broad range of radiation conditions, algae deploy numerous mechanisms that prevent damage to PSII (photoprotection), or that repair PSII damage. The damaged D1 proteins are continuously replaced in a light-dependent repair cycle (the PSII repair cycle).[18] Repair of inactive PSII by synthesis and reassembly is a complex, metabolically expensive and time consuming process. The combination of excess PAR with other stressors such as suboptimal temperature and UVR exposure can enhance photoinhibition compared to excess PAR alone.[19] ROS can inhibit the PSII repair cycle.[20] Furthermore, UVBR can slow down the PSII repair cycle.[21,22] UVBR tolerance was shown to be related to a strong D1 turnover capacity for several algal species.[23,24] High irradiance acclimation also increases D1 turnover rates, which results in a faster PSII repair cycle.[12,25]

Apart from repair pathways, the excitation energy of PSII can be regulated at the pigment level. Xanthophyll cycle pigments are specialized carotenoid pigments in the light harvesting antenna that have a central role in photoprotection against excess irradiance. The effectiveness of photoprotection depends on their epoxidation state. Epoxidated xanthophylls assist light harvesting by transferring energy to chlorophylls. In contrast, de-epoxidated xanthophylls do not transfer energy but are involved in thermal dissipation of excess absorbed energy.[26,27] How de-epoxidated xanthophylls initiate heat dissipation in the light harvesting antenna remains to be elucidated. It has been hypothesized that de-epoxidated xanthophylls prevent the occurrence of chlorophyll triplet states by a conformational change in the light harvesting antenna, and by directly scavenging energy from chlorophylls.[28] Epoxidated and de-epoxidated xanthophylls can be inter-converted enzymatically in response to irradiance changes. The activity of de-epoxidation enzyme increases, whereas the activity of the epoxidation enzyme is inhibited by acidification of the thylakoid lumen. Although the importance of the photoprotective role of the xanthophyll cycle is not disputed, other processes can also regulate excitation energy on a short time scale. First, it has been shown that high light-acclimated plants have an enhanced ability to build up a proton gradient compared to low light-acclimated plants. Second, state transitions (redistribution of light energy between PSII and PSI) have been identified in green algae and prochlorophytes,[29,30] but no clear evidence has been found for the existence of state transitions in diatoms. In the latter group cyclic electron flow around PSII has been suggested to play a major photoprotective role during excess irradiance exposure.[31,32]

Photoregulation by xanthophyll cycle activity and NPQ

The process of photoregulation is utilized to optimize photosynthesis and photoprotection during irradiance dynamics that occur on a shorter time scale than pigment synthesis responses, the induction of PSII repair pathways, and adjustments in Calvin cycle activity. After (linear electron flow) photosynthesis saturates, cyclic electron flow between cytochrome bf_6 and PSI creates a proton gradient over the thylakoid membrane.[33] This activates processes that reduce excitation energy transfer to the reaction centers and are partly responsible for non-photochemical chlorophyll fluorescence quenching (NPQ). NPQ comprises a number of processes, which can be separated by their relaxation time.[34,35] The slowly relaxing (hours) NPQ component is due to repair of inactive PSII reaction centers, whereas fast relaxing NPQ (minutes up to 1–2 h) is believed to originate from epoxidation of de-epoxidated xanthophyll cycle pigments and state transitions. Fast NPQ *via* the xanthophyll cycle provides a mechanism to rapidly switch from a state of light harvesting to a state of thermal energy dissipation and therefore provides flexibility during sudden irradiance changes. This limits photoinhibition during excess irradiance exposure and the fast reversible NPQ ensures that photosynthesis can be resumed after a return to favorable conditions without high metabolic costs. Therefore, NPQ *via* the xanthophyll cycle is increasingly recognized as a key protective process in photosynthesis and a major adaptation for environments that are characterized by irregular light exposure. The effectiveness of NPQ and xanthophyll cycle activity during co-occurring UVR exposure has revealed conflicting views (see further below).

Photoacclimation by pigment pool adjustments

Photoacclimation can be defined as the responses that ensure optimal photosynthesis and photoprotection *via* the adjustment of intracellular pools. The intrinsic sensitivity of algae to excess radiation, including UVR, depends for a large part on the photoacclimation state, which expresses the balance between photosynthetic and photoprotective potential.[36] Generally, marine phytoplankton exhibit considerable plasticity in their changing environment, because they can adjust their photoprotective–photosynthetic pigment ratio. The ability to deploy NPQ is typically increased under high light conditions *via* an increased cellular abundance of xanthophyll cycle pigments, often coinciding with decreasing light-harvesting pigments.[37–40] Regulation of light-harvesting pigmentation occurs on a time scale of hours to days, whereas phytoplankton reportedly can adjust xanthophyll cycle pigment pools *via de novo* synthesis on time scales that range from one to several hours, as measured in Mediterranean, temperate and Antarctic phytoplankton, respectively[41,42] (this study, see below). Therefore, synthesis of xanthophyll cycle pigments should be taken into account when evaluating xanthophyll cycle activity over such time scales.[43]

Photoacclimation state and relative xanthophyll cycle pigment abundance is also modulated by other abiotic factors such as temperature, nutrient availability, and irradiance dynamics.[44,9,45] For the Antarctic diatom *Chaetoceros brevis* we compiled data on the ratio between xanthophyll cycle (diadinoxanthin and diatoxanthin) and light harvesting (chlorophyll *a*) pigments from

own experiments (Fig. 1). In this diatom, acclimation to increased irradiance caused a linear increase in xanthophyll cycle/chl *a* ratio up to a maximum of around 0.7. In addition, nutrient limitation further enhanced the xanthophyll cycle/chl *a* ratio, primarily due to decreased cellular photosynthetic pigment content.[9] However, cultivation under dynamic irradiance regimes caused cultures of *C. brevis* to express a lower irradiance-acclimated response, as compared with identical constant dose rates, resulting in a lower ratio between xanthophyll cycle pigments and chlorophyll *a* (Fig. 1).[46,45] Therefore, under natural conditions, ratios of xanthophyll cycle pigments relative to chlorophyll *a* above 0.4 are probably only observed during nutrient limitation in this species. Protection *via* the xanthophyll cycle is particularly favorable during nutrient depleted conditions because it lowers the metabolic repair costs after excess light exposure.

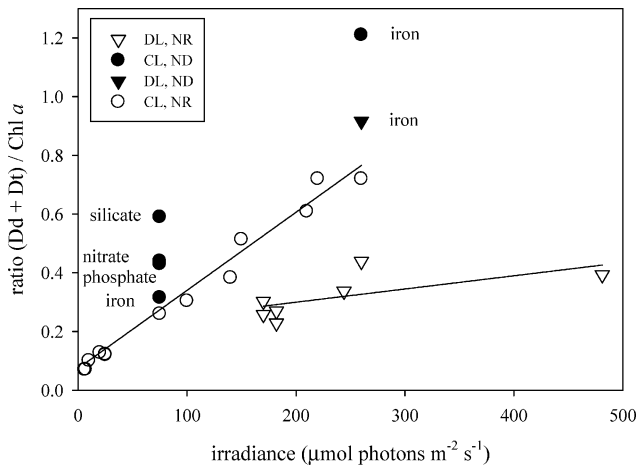

Fig. 1 Variability in ratio between the xanthophyll cycle pool (diadinoxanthin, Dd, and diatoxanthin, Dt) and chlorophyll *a* in the Antarctic diatom *C. brevis*, acclimated to a range of irradiance (constant light: CL, circles, and dynamic light: DL, triangles), both with a light–dark cycle) and nutrient (nutrient replete: NR, open symbols, and nutrient deplete: ND, closed symbols) conditions. Irradiance for the dynamic conditions are the average light received during the light period, the algae were exposed to fluctuations between 20 and 1000 µmol photons m^{-2} s^{-1} on a 2–4 h time scale. For nutrient deplete conditions, data for nitrate, phosphate, silicate, and iron limitation are shown. Data are taken from Van de Poll *et al.*,[9,45] Janknegt *et al.*,[69] and Boelen *et al.* (unpublished).

Enhanced xanthophyll cycle pigment levels due to photoacclimation limits photoinhibition and ensure survival during prolonged excess radiation exposure. Indeed, the variable xanthophyll cycle/chl *a* ratio induced by different environmental conditions (dynamic irradiance, nutrient deplete, Fig. 1) showed levels of viability loss during excess irradiance exposure in accordance with the photoacclimation state.[9,47,46] Recent experiments with high light-acclimated *C. brevis* and *Phaeocystis antarctica* showed a stronger capacity to develop fast NPQ in concert with increasing xanthophyll cycle pigment abundance during exposure to excess irradiance than low light-acclimated cultures of the same species (Van de Poll *et al.*, unpublished).

Species specific plasticity in photoregulation and photoacclimation

The two most common classes of xanthophyll cycle pigments that can be found in phytoplankton are the diadinoxanthin–diatoxanthin (Dd–Dt) cycle pigments and the violaxanthin–antheraxanthin–zeaxanthin (VAZ) cycle pigments. The latter are found in chlorophytes and prasinophytes and are similar to the xanthophyll cycle pigments in higher plants, whereas the former can be found in algae that have fucoxanthin as a major accessory pigment (Haptophyceae, Dinophyceae, Bacillariophyceae). In diatoms such as *Phaeodactylum tricornutum* both xanthophyll cycles can be observed in tandem, although the Dd–Dt cycle dominates. Apart from the involved pigments, distinct differences have been found between the two xanthophyll cycles. The VAZ cycle involves the chloroplast-encoded PsbS protein, which has not been identified in diatoms.[48] Furthermore, several differences have been noted with regard to the enzymatic de-epoxidation and epoxidation.[31] The de-epoxidation of diadinoxanthin in *P. tricornutum* is activated at a higher pH than that of violaxanthin in higher plants.[49,50] Furthermore, the proton gradient is a prerequisite for maintaining de-epoxidated xanthophyll cycle pigments of the VAZ cycle, whereas less coupling between these two was observed for the Dd–Dt cycle pigments.[43] Therefore, de-epoxidation of the VAZ cycle cannot be maintained in darkness. In contrast, epoxidation of diatoxanthin occurs only under weak light.[51] The existence of different diatoxanthin pools has been suggested for diatoms.[52] For *Cyclotella meneghiniana*, differences in quenching efficiency and de-epoxidation relaxation time were observed.[53] An active xanthophyll cycle is not found in Rhodophyceae, Cryptophyceae, Cyanophyta, and Prochlorophytes, although zeaxanthin and other de-epoxidized xanthophylls are present.[54]

Xanthophyll cycle pigment abundance and the capacity for fast NPQ has been linked to the light conditions under which algal species prevail, which implies (genetic) adaptation in NPQ capacity.[55] In this respect, an estuarine diatom (*P. tricornutum*) which frequently encounters light fluctuations in a shallow mixed layer, combined with strong light attenuation, possessed a higher capacity for NPQ than the oceanic diatom *Thalassiosira oceanica* that originated from the more stable, stratified open ocean.[32] Therefore, acclimation potential in the xanthophyll cycle pigment abundance and activity may be crucial in defining ecological niches of phytoplankton species.[56] Furthermore, differences in photoprotective responses have been linked to the dominance of the haptophyte *Phaeocystis antarctica* in deeply mixed parts of the Ross Sea, whereas diatoms often dominate the shallow areas.[57,58] In accordance with these observations, our own experiments showed pronounced differences in NPQ and xanthophyll cycle pigment abundance between *P. antarctica* and the small Antarctic diatom *C. brevis* acclimated to high and low PAR. In the latter species, xanthophyll cycle pigment abundance was consistently higher, and this species displayed a higher capacity for fast NPQ during exposure to excess irradiance than the haptophyte (Van de Poll *et al.*, unpublished). Furthermore, *C. brevis* retained the ability for fast recovery of NPQ after acclimation to low irradiance, in contrast to *P. antarctica*, which became highly susceptible to excess irradiance exposure. This suggests that differences in photoprotective adaptations between these taxa may have a role in defining their ecological success under the prevailing conditions.

The requirement for NPQ may be related with growth temperature. Algae that have a temperature optimum that allows growth at high temperatures (20–26 °C) may depend less on NPQ induced by xanthophyll de-epoxidation because elevated RUBISCO activity

can be a more efficient sink for electrons. Furthermore, the PSII repair cycle is more efficient at high temperatures. Therefore, a higher cultivation temperature may result in a lower ratio of xanthophyll cycle pigments relative to chlorophyll *a* because linear electron flow can continue up to higher irradiance. Furthermore, higher cultivation temperatures may favor responses *via* synthesis pathways (synthesis of xanthophyll cycle pigments, PSII repair cycle). For example, in the Mediterranean synthesis of xanthophyll cycle pigments occurred within one hour.[42] In contrast, in the cold Antarctic waters (below 3 °C) algae are continuously limited in linear electron transport due to low RUBISCO efficiency and also possess a slower metabolic repair activity.

Effectiveness of the xanthophyll cycle during UVR exposure

UVR effects on xanthophyll cycle activity

Effects of UVR on the xanthophyll de-epoxidation state have not been extensively studied and the reported experiments have produced contrasting results, ranging from a stimulation, inhibition or no effect at all. Enhanced xanthophyll de-epoxidation in response to UVR exposure were reported by Goss *et al.*[59] for *P. tricornutum*, by Sobrino *et al.*[60] for *Nanochloropsis gaditana*, and for *T. weissflogii* and *Dunaliella tertiolecta* by Buma *et al.*[61] UVR exposure can increase PSII inactivation and reduce RUBISCO activity.[14] This inhibits linear electron flow, which causes faster induction of NPQ by cyclic electron flow *via* PSI compared to PAR exposure alone. It should be noted that UVR-induced inhibition of photosynthesis was reported in concert with increased de-epoxidation.[60,61] Therefore, de-epoxidation failed to protect photosynthesis completely against the damaging effects of UVR. This agrees with the idea that inactivation of linear photosynthesis induces xanthophyll de-epoxidation activity. Reduced de-epoxidation of diatoxanthin into diadinoxanthin in *P. tricornutum* in response to strong UVBR was reported by Mewes and Richter.[62] They proposed that UVBR increased thylakoid membrane permeability, which reduced the proton gradient over this membrane. With a reduced proton gradient a smaller portion of de-epoxidated xanthophylls can be maintained. Oxidative stress related effects on the xanthophyll cycle were also proposed by Rijstenbil.[63] This reduces NPQ and therefore would reduce protection against excess light. Furthermore, reduced build up of zeaxanthin was observed during field experiments with the green macroalga *Ulva lactula*,[14] although experiments with another *Ulva* species produced opposite results under higher natural UVR.[64] Other investigations reported no UVR effect on xanthophyll de-epoxidation in *Gymnodinium breve* under natural solar irradiance.[65] and in *Thalassiosira antarctica* and *T. weissflogii*[47] under artificial light. For low and high light-acclimated *C. brevis* and *P. antarctica* we observed no UVR effect on xanthophyll de-epoxidation during 200 min artificial excess light exposure (PAR: 1100 µmol photons m^{-2} s^{-2}, UVAR: 43 W m^{-2}, UVBR: 3.3 W m^{-2}; Van de Poll, unpublished results). Due to the differences in applied (spectral) radiation conditions, investigated species, and pre-cultivation conditions (irradiance, temperature) the reported investigations are difficult to compare. The following section will discuss how these differences may have influenced the results.

Explanations for UVR-induced variability in xanthophyll cycle activity

Laboratory experiments are often characterized by unnatural radiation conditions with regard to UVR/PAR ratios, spectral composition, and duration of exposure. UVR effects in the aquatic environment are caused by a mixture of direct and indirectly affected processes that all show strong wavelength and dose dependency. Furthermore, processes that counteract UVR effects can be affected by un-balanced spectral radiation conditions. High UVBR exposure combined with low background PAR will not produce efficient xanthophyll de-epoxidation because this reaction is triggered by an excess PAR induced proton gradient. For example, exposure of *Cylindrotheca closterium* to 1.0 W m^{-2} UVBR with a 250 µmol m^{-2} s^{-1} photons PAR background induced a maximum of 22% de-epoxidation of diadinoxanthin into diatoxanthin.[63] Because these spectral combinations do not occur in nature, these experiments have little ecological relevance with regard to UVR effects on xanthophyll cycle activity. In general, unbalanced radiation conditions tend to exaggerate UVBR effects compared to those caused by excess PAR and UVAR.

Apart from the differences in applied radiation conditions, experiments that deal with UVR effects on the xanthophyll cycle were performed with a variety of organisms, obtained from contrasting environments. Species such as *C. brevis* and *P. antarctica* may rely more on heat dissipation *via* the xanthophyll cycle during excess radiation than species that grow in warmer regions. As a consequence, UVR that has been shown to affect RUBISCO activity and PSII, can have different effects on species that come from contrasting environments. Moreover, the ability to perform fast NPQ in response to excess radiation is not only dependent on cultivation conditions but showed strong variation between species, as discussed above.

Finally, UVR exposure has been reported to induce rapid xanthophyll cycle pigment synthesis in some algae, since acclimation to UVR increased the xanthophyll cycle pool relative to chlorophyll in *T. weissflogii*.[66] We recently performed experiments with the same species (*T. weissflogii*) under natural radiation. Here high PAR-acclimated cultures were exposed outdoors for 6 h on two days, during which induction of xanthophyll cycle pigments and xanthophyll cycle activity were investigated. These results suggested UVR-induced reduction of xanthophyll cycle activity on an experimental day with relatively low incident irradiance levels due to overcast weather (Fig. 2, right panels, November 27th). However, this reduction appeared to be related with the fast UVR mediated synthesis of the xanthophyll cycle pigment diadinoxanthin (Fig. 2D), showing a more rapid induction in PAR + UVR cultures as opposed to PAR exposed cultures. As a result, the decreased de-epoxidation state on this day would falsely imply that de-epoxidation was inhibited (Fig. 2F). In contrast, a similar experiment carried out a few days earlier showed no UVR mediated enhancement of xanthophyll cycle pigment synthesis, likely due to the higher radiation levels (Fig. 2, left panels, November 24th). In these cultures UVR exposure increased de-epoxidation over a 6 h exposure period compared to PAR. Similarly, experiments conducted in 2006 with the same species showed enhanced de-epoxidation by both UVAR and UVBR during outdoor exposure.[61] In this earlier study, wavelength dependent enhancement of de-epoxidation was found to be corre-

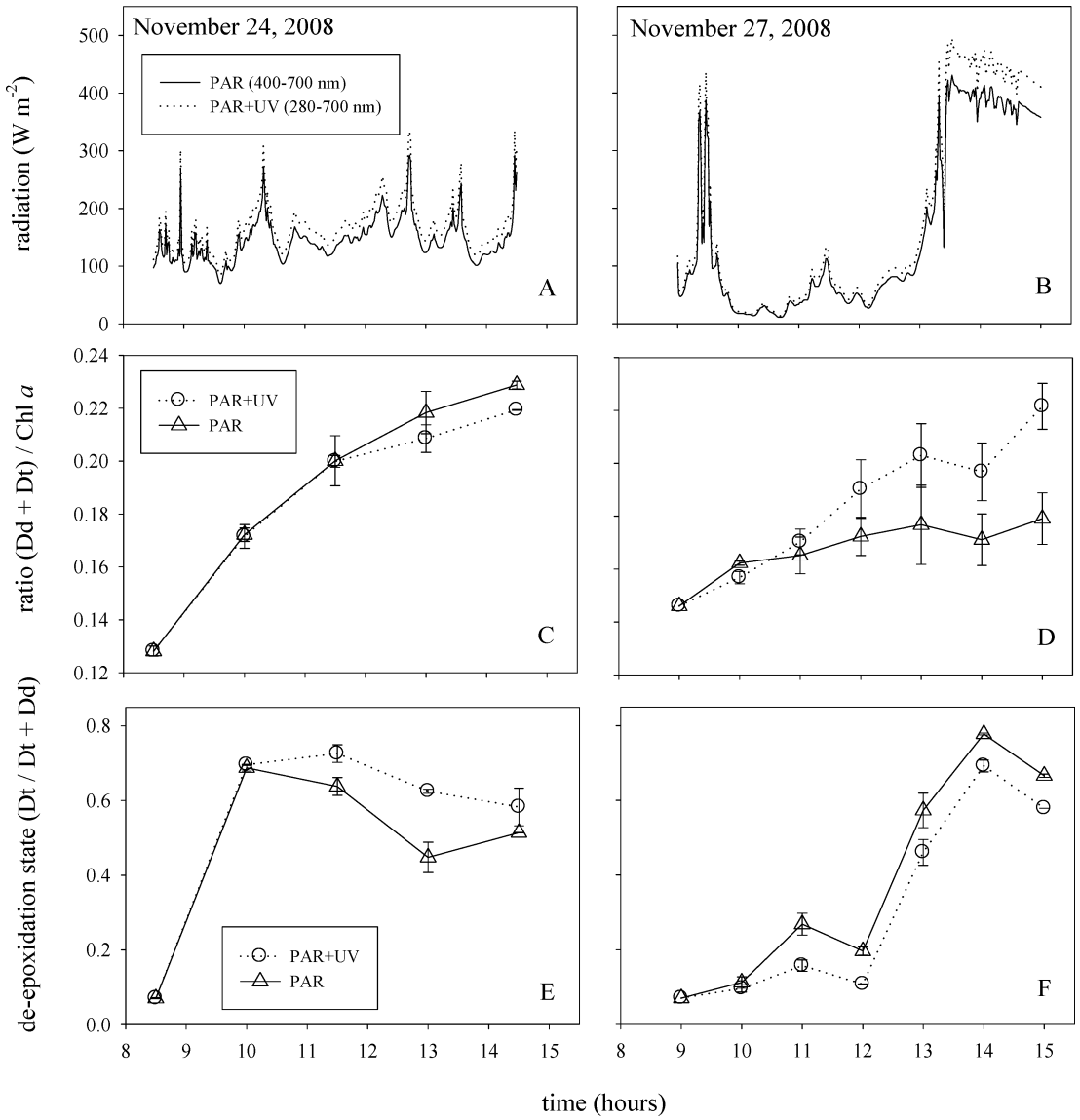

Fig. 2 Pigment responses of high irradiance-acclimated *T. weissflogii* during natural solar radiation (PAR, PAR + UVR) incubations (Playa Union, Argentina, 2008) on different days (November 24: A, C, E; November 27: B, D, F) with variable atmospheric conditions. Panel A, B: radiation conditions during experimental time interval; C, D: changes in the ratio between xanthophyll cycle pigments (Dd + Dt) and chlorophyll *a* over time for PAR and UVR exposed cultures; E, F: de-epoxidation state of the xanthophyll cycle pigments (Dt/Dt + Dd) of the PAR and UVR-exposed cultures during outdoor exposure.

lated with increased inhibition of ^{14}C assimilation and inhibition of effective quantum yield. It was concluded that enhanced de-epoxidation as observed here was not functional with respect to amelioration of UVR stress. In contrast, the strong similarity in biological weighting functions for effective quantum yield of PSII, xanthophyll de-epoxidation and carbon assimilation was thought to be related with damage to targets further downstream the photosynthetic process (such as RUBISCO). The 2006 experiments were performed in the middle of summer with clear skies. Therefore, hourly averaged UVAR and UVBR dose rates between 9.00 and 12.00 ranged between 44.0–57.0 and 1.12–1.79 W m^{-2}, respectively. The experiments conducted in November 2008 were performed in overcast conditions, and here hourly-averaged UVAR and UVBR dose rates were in the range of 17.8–21.9 and 0.44–0.67 W m^{-2}, respectively, on November 24th (Fig. 2A), whereas two days later UVAR and UVBR were even lower (11.8–16.3 W m^{-2} for UVAR; 0.34–0.37 W m^{-2} for UVBR). Obviously, the overall mild natural radiation levels during the November 2008 experiments promoted xanthophyll *de novo* pigment synthesis while the lowest UVBR dose rates on November 26th further enhanced xanthophyll synthesis as compared with PAR only cultures.

Given these recent experiments it can be hypothesized that short term high UVR exposure could induce enhanced de-epoxidation, due to the earlier described phenomenon of an inhibitory process further downstream the photosynthetic process. At lower UVR dose rates, rapid *de novo* synthesis of diadinoxanthin also occurred, leading to overall lower de-epoxidation state. Counterintuitively, an enhanced de-epoxidation state could imply adverse UVR responses, while depressed de-epoxidation might imply an active

photoprotective response to UVR exposure *via* enhanced diadinoxanthin synthesis.

Concluding remarks

Several studies demonstrated that acclimation to high radiation (without UVR exposure) reduced the effects of UVR exposure.[9,47] As discussed above, other processes than xanthophyll cycle activity, such as the PSII repair cycle, are also more active at high light conditions, which may compensate the effects of UV induced PSII inactivation. In some algae such as *P. antarctica* and *Chaetoceros dichaeta*, high PAR exposure may increase the cellular abundance of UV absorbing compounds,[39] which also increases UV tolerance.[67] In addition, acclimation to mild UVR exposure decreases UV effects on photosynthesis as has been observed for phytoplankton assemblages from the field and for cultivated species,[13,68] in accordance with our recent findings of xanthophyll cycle pigment synthesis under mild natural UVR exposure in *T. weissflogii* (Fig. 2). Although photoregulation (xanthophyll cycle activity) and photoacclimation (pigment synthesis) and repair (PSII repair cycle, RUBISCO activity) responses operate on different time scales, they also co-occur simultaneously during excess radiation exposure. Therefore, it is difficult to address the contributions of these pathways separately.

In conclusion, differences in the xanthophyll cycle de-epoxidation state as a result of UVR exposure may be caused by the synthesis of xanthophyll cycle pigments (photoacclimation) rather than by the differences in enzymatic conversion (photoregulation). Increased synthesis of xanthophyll cycle pigments under UVR compared to PAR exposure indicate a higher requirement for NPQ, but enhanced synthesis may only occur under mild UVR levels. At higher UVR levels, other targets may be affected that indirectly promote xanthophyll de-epoxidation, however without being fully effective in counteracting UVR stress. It is undisputed that UVR exposure causes an ecological significant reduction of phytoplankton primary production. However, it is unlikely that this is caused by UVR effects on the xanthophyll cycle. In contrast, this effect appears to be part of a response that contributes to the reduction of UVR effects.

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