**Photosynthesis, photosynthetic pigments and mycosporine-like amino acids after exposure of the marine red alga Chondrus crispus (Gigartinales, Rhodophyta) to different light qualities**

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Low light–adapted laboratory-grown thalli of Chondrus crispus were transferred into shallow water and exposed to the natural irradiance prevailing in May–June at Helgoland (German Bight). A set of cut-off filters was used to study the wavelength-dependent response of photosynthesis as well as pigment and mycosporine-like amino acid (MAA) formation. Due to the higher natural irradiance and in some cases additional ultraviolet (UV) radiation, a depression of maximal quantum yield coinciding with a decline in maximal electron transport rate could be observed during the first days of the experiment. Faster recovery of maximal quantum yield and maximal electron transport rate might be related to the increase in lutein and α- and β-carotene concentration. In addition, higher rates of electron transport might be supported by increased chlorophyll a concentration. In parallel, MAA concentration increased resulting in an effective UV sunscreen. Our data suggest that lutein and α- and β-carotene are involved in the recovery of the algae to long-wavelength UV-A and photosynthetically active radiation.

The results showed that accumulated MAA concentration differed in quality and quantity with respect to spectral distribution. Asterina-330, palythinol and palythine were mainly induced by UV-B radiation. In contrast, short-wavelength UV-A exhibited the highest quantum efficiency on shinorine and palythine synthesis, whereas UV-B radiation had a negative effect on their accumulation.

Because differences in maximal quantum yield of photosynthesis (Fv/Fm) between algae exposed under different cut-off filters were small, the reason for the pronounced negative effect to UV-B wavebands of shinorine and palythine accumulation remained unclear. It might be due to a UV-B–induced impairment of algal metabolism. Franklin et al. (1999) found a significant UV-B–induced growth inhibition of sublittoral C. crispus transferred to shallow water. On the other hand, it could also be due to some unknown wavelength-dependent characteristic of the mechanism triggering MAA formation. To get more information on the UV-B effect on MAA accumulation, we repeated the experiment in a similar set-up. In addition to MAA samples, photosynthesis vs irradiance curves (PI curves) and maximal quantum yield of photosynthesis were measured, and samples for pigment analysis were taken. These additional biological variables should provide a greater insight on the general effect of different light qualities (especially additional UV-B radiation) on the metabolism of C. crispus during acclimation to higher light intensities. This will allow the previously isolated discussion on wavelength-dependent MAA induction to be set in a more general context.

**INTRODUCTION**

Chondrus crispus Stackhouse is an abundant red alga of the North Atlantic, inhabiting the intertidal and upper sublittoral zone of rocky shorelines (Lüning 1990). Therefore, specimens have to cope either with extreme periodical variation in solar irradiance or with relatively constant low irradiances in deeper or turbid waters, depending on the vertical position on the shore, the state of the tide and seasonal and diurnal changes in solar elevation.

The occurrence of this species in a wide variety of habitats and the fact that pronounced differences in ultraviolet (UV) sensitivity have been observed between intertidal and subtidal macrophyte species and individuals (Bischof et al. 1998a, b; Karsten et al. 2001; van de Poll et al. 2001, 2002) have spurred an interest to investigate acclimation responses of C. crispus to various ecological parameters and UV effects (Kübler & Davison 1993, 1995; Sagert et al. 1997; Collén & Davison 1999; Franklin et al. 1999; Bischof et al. 2000b; Yakovleva & Titlyanov 2001).

One mechanism in the acclimation to changing light, especially UV conditions, is the accumulation of UV-absorbing mycosporine-like amino acids (MAAs) (for overview see Bandaranayake 1998; Shick et al. 2000; Shick & Dunlap 2002), although the degree of protection varies (Garcia-Pichel et al. 1993; Lesser 1996; Franklin et al. 1999). The synthesis of MAAs is dependent on both the quality and dose of radiation applied (Carreto et al. 1990; Riegger & Robinson 1997; Karsten et al. 1998).

Previously, we have studied the wavelength dependence of MAA synthesis of laboratory-grown algae transferred to shallow water under natural solar radiation (Kräbs et al. 2002).

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**MATERIAL AND METHODS**

**Algal material and experimental conditions**

Thalli of C. crispus, originally isolated on Helgoland (German Bight, North Sea; 54°11’N, 7°53’E) were cultivated in glass...
beakers in the laboratory [15°C, 16:8 hours light-dark, 30 \mu mol m^{-2} s^{-1} photosynthetically active radiation (PAR)]. In May 2001, approximately 2 cm long tips were transplanted into boxes (18 × 18 × 5 cm; one box per treatment) within an open flow through basin (150 × 50 × 10 cm) mounted on the roof of the laboratory (Biologische Anstalt Helgoland, Helgoland, Germany) and exposed to natural solar radiation. The spectral response to photosynthesis as well as pigment and MAA induction was studied by placing 120 samples into each box covered with different cut-off filters (WG305, WG320, WG335, WG360, GG400, GG420 and GG495; Schott, Mainz, Germany), thus generating different spectral radiation conditions. The number in the name of the used cut-off filters refers to the wavelength where 50% of irradiance is absorbed by the filter (for spectral irradiance see Kräbs et al. 2002). Additionally, one box was left uncovered (`unfiltered') to study the effect of the whole light spectrum.

Throughout the experiment, the whole set-up was additionally covered with two layers of black gauze (Haver & Boecker, Oelde, Germany) to reduce light intensity neutrally (transmission = 40%). The boxes were perforated at opposite sides to allow water exchange. The basin was continuously flushed with filtered North Sea water using two sequential pumps (1060; Eheim, Deizisau, Germany). Throughout the experiment, radiation conditions at Helgoland were monitored by a PUV-500 radiometer (Biophysical Instruments, San Diego, CA, USA), which was mounted on the roof of the institute. Unfiltered irradiance spectrum measurements were made at noon on a sunny day with a fast-scanning monochromator spectroradiometer (UV320D; Instruments Systems, Munich, Germany), equipped with a cosine sensor.

**Light measurements**

Throughout the experiment, radiation conditions at Helgoland were monitored by a PUV-500 radiometer (Biophysical Instruments, San Diego, CA, USA), which was mounted on the roof of the institute. Unfiltered irradiance spectrum measurements were made at noon on a sunny day with a fast-scanning monochromator spectroradiometer (UV320D; Instruments Systems, Munich, Germany), equipped with a cosine sensor.

**Biological variables**

During exposure, the maximal quantum yield of photosystem II electron transport of dark-adapted algae (4 min) was determined by the ratio of variable to maximal chlorophyll fluorescence (Fv/Fm) with a PAM 2000 chlorophyll fluorimeter (Walz, Effeltrich, Germany), following the protocol described in detail by Hanelt (1998). PI curves were recorded with the same fluorimeter as described by Bischof et al. (1999). Measurements of Fv/Fm and PI curves were conducted in triplicates from randomly collected and independent samples.

Changes in the pigment (chlorophyll a, lutein, α- + β-carotene, zeaxanthin) composition and content were analysed as described by Bischof et al. (2002a). Pigment data were obtained from independent triplicate samples. Changes in MAA composition and content were analysed as described by Kräbs et al. (2002) with the modification of the mobile phase to 5% aqueous methanol (v/v) plus 0.1% acetic acid (v/v) in water. MAA data were obtained from five independent samples.

**Polychromatic response spectra**

Polychromatic response spectra were based on the same spectral irradiances calculated for each cut-off filter as in the previous study (see Kräbs et al. 2002, fig. 1A).

The respective MAA concentration accumulated in *C. crispus* exposed under different filter treatments was used to calculate polychromatic response spectra. First, a second-order polynomial (for shinorine) and a linear equation for each of palynthone and asterina-330, respectively, was fitted through single measured data points for the respective MAA concentration accumulated in algae exposed under each filter. Using the obtained equation, a ‘theoretical’ concentration of the respective MAA was calculated for the third day of the experiment. A mean value was calculated and used for a group of filter treatments with no statistical difference in MAA concentration, whereas the calculated value was used directly if the pattern in MAA accumulation under the filter in question was significantly different from neighbour filter treatments. To calculate the polychromatic response spectrum for the total MAA concentration, the mean value for the steady state was calculated using the data from the third (1800 hours), fifth and ninth days. Statistically significant differences between different filter treatments were taken into consideration as described above.

Response spectra were calculated using this statistically adjusted data set. The difference in MAA concentration in algae grown under two sequentially numbered cut-off filters was divided by the difference in total irradiance between the two light fields under the filters (Rundel 1983). All calculations of polychromatic response spectra are based on the median wavelength of the difference in total irradiance obtained by subtraction of two sequential light fields, as described by Rieger & Robinson (1997).

**Data treatment**

Statistical significance of difference between Fv/Fm values and PI curves was calculated using the Mann–Whitney test ($P < 0.05$; Lozán & Kausch 1998). Using the pooled data of the measured PI curves, statistical significance ($P < 0.05$) of difference between PI curves measured on different days was tested by two-way analysis of variance followed by the least significant difference test.

Means and standard deviations ($\bar{x} \pm s$) were calculated from the respective replicates (but NB Fig. 5 gives standard errors $s$). Statistical significance ($P < 0.05$) of difference in MAA and pigment content accumulated under each cut-off filter and for different times and their combined effect was tested by two-way analysis of variance followed by least significant difference test. Calculations were done using the program Statistica Kernel-Version 5.5A (StatSoft, Tulsa, OK, USA).

**RESULTS**

**Environmental conditions**

Solar irradiation varied markedly in the course of the experiment due to prevailing weather conditions. Sunny and cloudy conditions often changed rapidly, sometimes interrupted by rainfall, as indicated by the course of PAR (Fig. 1). The re-
Table 1. Daily dose of solar radiation during the course of the experiment.

| Date        | Day | 305 nm | 320 nm | 340 nm | 380 nm | 400–700 nm |
|-------------|-----|--------|--------|--------|--------|------------|
| 23 May 2001 | 0   | 0.576  | 7.118  | 12.974 | 22.141 | 55.695     |
| 24 May 2001 | 1   | 0.408  | 5.748  | 10.722 | 18.126 | 43.556     |
| 25 May 2001 | 2   | 0.597  | 7.296  | 13.296 | 22.980 | 56.435     |
| 26 May 2001 | 3   | 0.423  | 5.786  | 10.533 | 17.529 | 42.106     |
| 27 May 2001 | 4   | 0.207  | 3.172  | 5.885  | 9.651  | 22.572     |
| 28 May 2001 | 5   | 0.181  | 2.134  | 3.687  | 5.797  | 12.214     |
| 29 May 2001 | 6   | 0.604  | 7.340  | 13.334 | 22.643 | 55.618     |
| 30 May 2001 | 7   | 0.550  | 7.175  | 13.133 | 22.192 | 54.415     |
| 31 May 2001 | 8   | 0.285  | 4.321  | 7.959  | 13.339 | 30.481     |
| 01 Jun. 2001| 9   | 0.431  | 5.728  | 10.333 | 17.177 | 39.970     |

Fig. 1. Changes in PAR irradiance at the study site over the course of the experiment.

Effects on photosynthesis

After the first day of the experiment, a pronounced inhibition of maximal quantum yield of photosynthesis (Fv/Fm) could be observed in the morning (Table 2). Even so, there was no clear trend; thalli exposed under cut-off filters to UV radiation of shorter wavelengths (WG305–WG360) were more inhibited than thalli exposed to PAR, whereas thalli exposed unfilted to the full solar radiation exhibited relatively high Fv/Fm values almost throughout the experiment. In the morning of the fifth and ninth day of the experiment, Fv/Fm values recovered to 65–86% of the start value (taken in the evening before inserting algae into the experimental set-up), with no significant variations between the different filter treatments.

PI curves recorded in the morning revealed no significant variation between algae exposed under different cut-off filters. Therefore, measured PI curves were pooled to test differences in the shape of the PI curves between different days of the experiment. These data showed a decline in maximal electron transport rate during the time of low Fv/Fm values (Fig. 2). Parallel to the recovery of Fv/Fm, the maximal electron transport rate increased over the values of the start measurements. For statistical significance of difference between the different days, see Table 3.

Changes in the pigment content

The internal concentration of chlorophyll a, lutein and α- and β-carotene increased significantly during the experiment, whereas the concentration of zeaxanthin remained constant (for example see GG495; Fig. 3). Significant variations in the pigment composition and content between the different filter treatments could not be observed.

MAA content and induction

Samples taken before the start of the exposure contained only traces of the MAA palythine. After thalli were transferred to the experimental treatments and a short lag phase, an induction of shinorine, palythine (Fig. 4) and asterina-330 (10–15% of total MAA concentration) could be observed. Shinorine was accumulated more rapidly than the other MAAs, reaching the maximal concentration between the third and fifth day of the experiment. After that, a decline of shinorine concentration could be observed. Palythine and asterina-330 were accumulated steadily throughout the experiment.

In general, the total MAA concentration exhibited in algae exposed under the filter WG305 was significantly higher than in algae exposed under the other radiation conditions, whereas in algae exposed to PAR excluding the major part of blue light (GG495), the lowest MAA concentration could be detected (Table 4; Fig. 5). Polychromatic response spectra calculated from shinorine and the total MAA concentration indicated that UV-B has the highest quantum efficiency for the accumulation of MAAs (Fig. 6; calculated for the cut-off filters WG305–GG495). However, the response spectra calculated for palythine and asterina-330 revealed a difference in the wavelength-dependent response between the steadily accumulated MAAs and shinorine. Thus, the response spectra for palythine and asterina-330 exhibit the highest quantum efficiency in the long waveband UV-A (λmax = 386 nm) and a second response peak in the blue light region of the spectrum (λmax = 466 nm).

DISCUSSION

Our results show that low light–adapted laboratory-grown thalli of C. crispus transferred to high natural sunlight can acclimate within certain limits to the radically changed irradiance conditions (see also Franklin et al. 1999). The recovery of Fv/Fm values to only 65–86% of the initial value might be due to the unusually high initial values (0.686 ± 0.008, x± s) of the C. crispus culture that was used. Reported Fv/Fm values of healthy C. crispus thalli in the field are between 0.6 (Sagert et al. 1997; Bischof et al. 2000b) and 0.65 (Franklin
Table 2. Maximal quantum yield of photosynthesis (Fv/Fm) of thalli exposed under different cut-off filters measured between 0500 and 0700 h. x ± s; n = 3; brackets: percent of the control value (0.686 ± 0.008) measured in the evening before inserting samples into the experimental set-up.

| Day | Unfiltered | WG305 | WG320 | WG335 | WG360 | GG400 | GG420 | GG495 |
|-----|------------|-------|-------|-------|-------|-------|-------|-------|
| 0   | 0.694 ± 0.001 (101%) | 0.689 ± 0.021 (99%) | 0.692 ± 0.020 (101%) | 0.693 ± 0.009 (101%) | 0.688 ± 0.007 (100%) | 0.677 ± 0.001 (95%) |
| 1   | 0.430 ± 0.065 (63%)    | 0.367 ± 0.155 (54%)    | 0.421 ± 0.154 (65%)    | 0.432 ± 0.050 (56%)    | 0.472 ± 0.042 (69%)    | 0.514 ± 0.069 (75%)    |
| 2   | 0.324 ± 0.106 (100%) | 0.092 ± 0.100 (100%) | 0.266 ± 0.067 (58%) | 0.382 ± 0.050 (56%) | 0.365 ± 0.064 (50%) | 0.346 ± 0.011 (50%) |
| 3   | 0.324 ± 0.106 (100%) | 0.092 ± 0.100 (100%) | 0.266 ± 0.067 (58%) | 0.382 ± 0.050 (56%) | 0.365 ± 0.064 (50%) | 0.346 ± 0.011 (50%) |
| 5   | 0.324 ± 0.106 (100%) | 0.092 ± 0.100 (100%) | 0.266 ± 0.067 (58%) | 0.382 ± 0.050 (56%) | 0.365 ± 0.064 (50%) | 0.346 ± 0.011 (50%) |
| 9   | 0.324 ± 0.106 (100%) | 0.092 ± 0.100 (100%) | 0.266 ± 0.067 (58%) | 0.382 ± 0.050 (56%) | 0.365 ± 0.064 (50%) | 0.346 ± 0.011 (50%) |

Fig. 2. PI curves showing relative electron transport rate (rel. ETR) of mean values calculated from all measured thalli irrespective of the filter treatment; ✓, day 0; △, day 1; ○, day 2; ■, day 3; □, day 5; ●, day 9; x ± s; n = 24.

Table 3. Statistical significance of difference between PI curves on different days measured in C. crispus. Statistically significant differences (P < 0.05) are marked with ✓.

| Day | Day 1 | Day 2 | Day 3 | Day 5 | Day 9 |
|-----|-------|-------|-------|-------|-------|
| Day 0 | ✓      |       | ✓     | ✓     | ✓     |
| Day 1 |       | x     |       | ✓     |       |
| Day 2 |       |       |       |       |       |
| Day 3 |       |       |       |       |       |
| Day 5 |       |       |       |       |       |

et al. 1999, 2001). The Fv/Fm values measured on the fifth and ninth day of the experiment are similar to these values. Due to higher irradiance and additional UV wavelengths, a depression of maximal quantum yield could be observed within the first days. There seems to be no explanation for the relatively constant and high Fv/Fm values of algae exposed to full unfiltered solar radiation. Because cut-off filters absorb approximately 10% of the prevailing PAR intensity, one explanation might be a different ratio of UV–PAR. In future work this issue might be clarified by using a UV-transparent filter (e.g. quartz, WG280, ...). In parallel to the depressed Fv/Fm values, the maximal electron transport rate declined. Similar results were found in several Arctic macrophytes after prolonged exposure to UV radiation (Bischof et al. 2000a). Even though photosynthetic capacity was impaired, a rapid induction of chlorophyll $a$, lutein and $\alpha$- and $\beta$-carotene formation could be observed, indicating that photosynthetic activity was sufficient to provide the necessary energy equivalents for pigment synthesis.

An increase in lutein and $\alpha$- and $\beta$-carotene concentration may be an important part of the acclimation to higher irradiance because both $\alpha$- and $\beta$-carotene–derived xanthophylls contribute to the nonphotochemical quenching of excess light energy (Niyogi et al. 1997; Pogson et al. 1998). For example, lutein prevents an increased formation of reactive oxygen species during photosynthetic activity and thus the photo-oxidation of the photosynthetic apparatus by dissipating excessively
absorbed light energy, similar to the de-epoxidation of violaxanthin (Asada & Takahashi 1987). This function may be essential because C. crispus lacks the xanthophyll cycle, which protects plants and macroalgae from photodamage caused by high PAR (Vershinin & Kamnev 1996; Hanelt et al. 1997; Schofield et al. 1998; Harker et al. 1999; Bischof et al. 2002a, b). Low and constant concentrations of zeaxanthin, which also contributes to nonphotochemical quenching (Niyogi et al. 1999; Kagawa et al. 1998; Wilson et al. 2003), further emphasize the importance of lutein and α- and β-carotene in C. crispus. Therefore, increased lutein and α- and β-carotene concentrations may be responsible for the recovery of maximal quantum yield and thus also for the recovery of maximal electron transport rate. Together with the recovery of optimal quantum yield, the initial shape of the PI curves typical for shade-adapted thalli (start of the experiment) was altered to a course characteristic for thalli exposed to high irradiance. This enhancement of maximal electron transport rate might be related to the change in chlorophyll a concentration.

Although slight – yet insignificant – differences in Fv/Fm values could be detected between different experimental treatments, this was not reflected in the PI curves. One reason for this might be the small number of replicates (three). Another might be that transferring algae from low to high light intensities causes greater stress than that caused by adding UV. One argument that confirms this idea might be the finding of Bischof et al. (2002b) that PAR alone inhibits maximal quantum yield of photosynthesis (Fv/Fm) more than PAR + UV-A and PAR + UV-A + UV-B in the green alga Ulva aff. rotundata. The recovery of photosynthesis occurs in a similar time frame to that reported for sublittoral C. crispus transferred to shallow water (Franklin et al. 1999).

Parallel to pigment synthesis, a steady accumulation of MAAs was observed, with a shift from shinorine to palythine as the major MAA during the course of MAA induction as previously described (Franklin et al. 1999; Kräbs et al. 2002). Whereas pigment content increases irrespective of the filter treatment, differences in MAA accumulation were observed at different wavelengths. Algae exposed to PAR without the major part of blue light exhibit the lowest MAA concentration, followed by specimens exposed to PAR. Additional UV radiation increases the concentration of MAAs markedly, whereas short-wavelength UV-B leads to markedly lower MAA concentration (unfiltered treatment). This results in two polychromatic response spectra (calculated for the cut-off filters WG305–GG495), one for shinorine accumulation and another one for palythine and asterina-330 accumulation. The polychromatic response spectrum for the total concentration of MAAs coincides with that of shinorine.

According to Coohill (1992, 1994), polychromatic response spectra tend to obscure the photoreceptor molecule and cannot conclusively show what the respective absorption spectrum would look like. This is the case for the present data. Because MAA accumulation occurs already in specimens exposed to PAR without the major part of blue light (GG495), the polychromatic response spectrum calculated for shinorine and the total MAA concentration cannot reflect the absorption spectrum of the photoreceptor triggering MAA formation. On the other hand, the broader the light spectrum under which algae were grown, the more MAAs were accumulated [except for short-wavelength UV-B (unfiltered treatment)]. Hence, a combination of both calculated polychromatic response spectra might be a better fit for the absorption characteristics of the photoreceptor responsible for MAA induction. The calculated polychromatic response spectra may therefore reflect differences in the biological response due to different UV–PAR ratios or an interconversion within MAAs (for detailed discussion see Kräbs et al. 2002 and references therein).

Until now, we have not considered MAA accumulation in specimens exposed to full unfiltered solar radiation. These specimens accumulated significantly lower MAA concentrations than those exposed under the filter WG305; this would result in a pronounced negative effect of short-wavelength UV-B and may be in line with our previous results. Specimens exposed in a similar experimental set-up, but higher light intensities, exhibited a significantly lower MAA concentration under the filter WG305 than those under the filter WG320 (Kräbs et al. 2002), indicating a negative UV-B effect dependent on light intensities. Thus, the UV-B effect is more pronounced and extending to longer wavelengths under ‘high’ irradiance than under ‘low’ irradiance. The negative effect of UV-B radiation on MAA formation may indicate an inhibitory effect of UV-B radiation on MAA formation alone because the synthesis of pigments was similar in all algae irrespective of the filter treatment.

Differences between these results and previous data (Kräbs et al. 1999; KraÈbs et al. 2002).
Fig. 4. Time course of accumulation of shinorine (○), palythine (■) and total concentration of MAAs (●) in *C. crispus* exposed to natural solar radiation under different cut-off filters; $x \pm s$; $n = 5$. 
et al. 2002) are mainly due to the lower irradiance during this experiment (1–3 days at c. 75% and 4–9 days at c. 40% of the previous levels). The depression of optimal quantum yield is due to higher irradiance during the first day (day 0) and the lack of a stepwise acclimation of cultural C. crispus to natural irradiance, as we have done during the previous experiment. Optimal quantum yield and maximal electron transport rate recover when the lutein and α- and β-carotene concentrations increased, indicating that they play an important role during acclimation to high irradiance (PAR). Higher electron transport rates may be due to increased chlorophyll a concentrations.

The generally lower MAA concentrations in the present data set reflect the lower irradiance during the experiment. Even though UV-B radiation had an effect on maximal quantum yield, we could demonstrate that this is not an unequivocal sign of an impaired metabolism. Pigment synthesis was unaffected by UV-B radiation, indicating a sufficient pool of energy equivalents and a functioning metabolism. The negative effect of UV-B radiation on MAA formation might therefore suggest a direct inhibition of enzymes involved in MAA synthesis or an indirect inhibition caused by an insufficient flow of energy equivalents and nutrients into MAA synthesis. Nevertheless, in all treatments internal MAA concentration was sufficient to protect specimens against UV radiation.

The accumulation of MAAs may be considered to be an additional but important acclimation mechanism, which has its advantage over long time scales. In C. crispus this additional protection can be established parallel to the acclimation of photosynthetic activity, whereas the diatom Thalassiosira weissflogii (Grunow) G. Fryxell & Hasle first accomplishes photoacclimation by an increase in xanthophyll cycle pigments and begins MAA synthesis only after the recovery of photosynthesis is complete (Zudaire & Roy 2001). As soon as the maximal MAA concentration is accumulated, the concentration of photoprotective xanthophyll cycle pigments declines in T. weissflogii, which emphasizes the importance of MAAs as photoprotective compounds. Yet these two examples clearly demonstrate the importance of investigating different acclimation mechanisms because every species may regulate energy and carbon flow to different metabolic mechanisms and within different timescales. This may result in a different sequence and importance of photoprotective compounds.

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