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# PHOTOSYNTHETIC INSENSITIVITY OF THE TERRESTRIAL CYANOBACTERIUM *NOSTOC FLAGELLIFORME* TO SOLAR UV RADIATION WHILE REHYDRATED OR DESICCATED[1]

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**Photosynthetic performance of the terrestrial cyanobacterium *Nostoc flagelliforme* (M. J. Berkeley et M. A. Curtis) Bornet et Flahault during rehydration and desiccation has been previously characterized, but little is known about the effects of solar UV radiation (280–400 nm) on this species. We investigated the photochemical activity during rehydration and subsequent desiccation while exposing the filamentous colonies to different solar radiation treatments. Photochemical activity could be reactivated by rehydration under full-spectrum solar radiation, the species being insensitive to both ultraviolet-A radiation (UVAR; 315–400 nm) and ultraviolet-B radiation (UVBR). When the rehydrated colonies were exposed for desiccation, the effective PSII photochemical yield was inhibited by visible radiation (PAR) at the initial stage of water loss, then increased with further decrease in water content, and reached its highest value at the water content of 10%–30%. However, no significant difference was observed among the radiation treatments except for the moment when they were desiccated to critical water content of about 2%–3%. At such a critical water content, significant reduction by UVBR of the effective quantum yield was observed in the colonies that were previously rehydrated under indoor light [without ultraviolet radiation (UVR)], but not in those reactivated under scattered or direct solar radiation (with UVR), indicating that preexposure to UVR during rehydration led to higher resistance to UVR during desiccation. The photosynthetic $CO_2$ uptake by the desiccated colonies was enhanced by elevation of $CO_2$ but was not affected by both UVAR and UVBR. It increased with enhanced desiccation to reach the maximal values at water content of 40%–50%. The UV-absorbing compounds and the colony sheath were suggested to play an important role in screening harmful UVR.**

***Key index words:*** **$CO_2$; cyanobacterium; desiccation; *Nostoc flagelliforme*; photosynthetic carbon fixation; PSII photochemical activity; solar UV radiation**

***Abbreviations:*** **P, photosynthetically active radiation (400–700 nm) treatment; PA, PAR+UVAR treatment; PAB, PAR+UVAR+UVBR treatment; UVAR, ultraviolet-A radiation (315–400 nm); UVBR, ultraviolet-B radiation (280–315 nm); UVR, ultraviolet radiation (280–400 nm); $\Delta F/F'_m$, effective photochemical quantum yield**

Nitrogen-fixing cyanobacteria are important contributors to overall primary productivity in ecosystems, especially in extreme environments, such as hypersaline pools, hot springs, deserts, alkali lakes, and polar areas (Whitton and Potts 2000). Cyanobacteria, like all photoautotrophs, depend on solar radiation as their primary source of energy. However, increasing solar ultraviolet-B radiation (UVBR, 280–315 nm) reaching the earth's surface because of anthropogenic depletion of the stratospheric ozone layer (Kerr and McElroy 1993) may become detrimental to photosynthetic organisms. Key metabolic activities in cyanobacteria, such as photosynthesis and N-fixation, are extremely sensitive to ultraviolet radiation (UVR; Sinha et al. 1997, Kumar et al. 2003). The UVR may also harm nutrient transport (Sinha et al. 1997), cell differentiation (Blakefield and Harris 1994), and gliding motility (Donkor et al. 1993) of cyanobacteria. Recently, it was determined that solar UVR broke the filaments and altered the spiral structure of the economic cyanobacterium *Arthrospora platensis* (Nordst.) Gomont (Wu et al. 2005).

Photosynthetic organisms exposed to visible and UV radiation in their natural habitats possess efficient defense mechanisms counteracting the harmful effects of UVR, such as behavioral avoidance (Bebout and Garcia-Pichel 1995), repair of UV-damaged DNA by photoreactivation and excision repair (Sinha and Häder 2002), and accumulation of carotenoids and detoxifying enzymes or radical quenchers that provide protection by

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scavenging harmful radicals or oxygen species (Wolfe-Simon et al. 2005). Accumulation of UV-absorbing compounds, such as mycosporine-like amino acids (MAAs) or scytonemin (Ehling-Schulz et al. 1997, Büdel et al. 1997), are supposed to play an important protective role for some cyanobacteria and algae.

The terrestrial cyanobacterium *Nostoc flagelliforme* is an economic species that has been used by the Chinese for hundreds of years. It is distributed in arid or semiarid districts of northern and west-northern China, and its habitats are characterized by intense solar radiation, extreme temperature differences, and high altitude (1000–2800 m above sea level; Gao 1998). High altitude, by decreasing the path length for atmospheric attenuation, results in high incident solar radiation at the earth's surface. The altitude gradients for UVR are much steeper than those for visible radiation (PAR), and thus the ratio of UVR to PAR increases with altitude (Castenholz and Garcia-Pichel 2000). However, little is known about the physiological performance of *N. flagelliforme* under solar radiation and its response to UVR.

Photosynthesis in dried colonies of *N. flagelliforme* is not active but can be reactivated by rehydration (Gao et al. 1998). The reactivated photosynthetic activity was light- and $K^+$-dependent (Qiu and Gao 1999). *Nostoc flagelliforme* uses bicarbonate to photosynthesize when submerged, and the bicarbonate uptake is associated with $Na^+/HCO_3^-$ symport (Gao and Zou 2001). Being a desiccation-tolerant cyanobacterium, *N. flagelliforme* maintains its superoxide dismutase for years while being stored dry (Qiu et al. 2003). Nevertheless, previous studies were carried out under indoor conditions with PAR as the light source. As the effects of solar UVR were not considered, the physiological performance of *N. flagelliforme* may be different under sun exposure.

The aim of this study was to investigate the photosynthetic responses of *N. flagelliforme* to solar UVR while rehydrated or desiccated so as to understand the influence of solar UVR on this terrestrial economic cyanobacterium.

## MATERIALS AND METHODS

Dry colonies of *N. flagelliforme*—filaments ~3–11 cm long and hair shaped—were collected in 2004 from Sunitezuoqi (43.85° N, 113.7° E) of Inner Mongolia and stored dry at room temperatures in darkness before use in the experiments.

*Reactivation of photosynthetic activity.* *Nostoc flagelliforme* colonies were rehydrated either under controlled indoor conditions at 80 μmol photons·$m^{-2}$·$s^{-1}$ and 25°C for 9–10 h (Gao et al. 1998) or outdoors under either direct or scattered (under shade) sunlight. The BG11 medium (Stanier et al. 1971) was used for the rehydration. For the outdoor rehydration, quartz chambers (15 × 15 × 5 cm) were used to allow both solar UVR and visible PAR to pass through, where the filaments were completely submersed for as long as the indoor treatment with the air flowing through above the soaking medium.

*Solar radiation measurements and treatments.* Incident solar radiation [UVBR: 280–315 nm; ultraviolet-A radiation (UVAR): 315–400 nm; and PAR: 400–700 nm] was continuously monitored by a broadband filter radiometer (ELDONET; Real Time Computer Inc., Erlangen, Germany) permanently installed on the roof of a building at Shantou University (23.3° N 116.6° E). This instrument, having been used worldwide and its reliability internationally accepted (Häder et al. 1999), measures direct and indirect radiation (Ulbrich integrating sphere) in three different wavebands—PAR, UVAR (315–400 nm), and UVBR (280–315 nm)—every second and records the averaged data at 1 min intervals.

Three different solar radiation treatments were implemented: (i) colonies receiving full solar radiation (PAB treatment, 280–700 nm), quartz chamber covered with no film; (ii) colonies receiving UVAR and PAR (PA treatment, 320–700 nm), quartz chamber (15 × 15 × 5 cm) covered with Folex 320 (Montagefolie, Nr. 10155099, Folex, Dreieich, Germany); (iii) colonies receiving only PAR (P treatment, 400–700 nm), quartz chamber covered with Ultraphan film 395 (UV Opak; Digefra, Munich, Germany). The transmission spectra of these filter films have been published by Figueroa et al. (1997). These foils reflect an additional 3%–6% PAR compared with the quartz tubes.

*Estimation of water loss.* When the rehydrated *N. flagelliforme* was exposed for desiccation, water loss [WL (%)] from the colonies was assessed continually as follows:

$$\text{WL}\ (\%) = (W_0 - W_t)/(W_0 - W_d) \times 100 \qquad (1)$$

where $W_0$ is the initial wet weight measured after removing water drops by lightly blotting with tissue paper; $W_t$, instantaneous weight of the samples measured at time intervals; and $W_d$, the dry weight (dwt) measured after the samples had been dried at 80°C for 20–24 h and cooled in a desiccator. Relative water content [RWC (%)] was estimated as (100 − WL).

*Measurement of photochemical efficiency.* During the rehydration and desiccation of *N. flagelliforme* colonies, effective quantum yield ($\Delta F/F_m'$) of PSII was determined with a portable pulse modulation fluorometer (PAM 2000; Waltz GmbH, Effeltrich, Germany) in a light-adapted state (Genty et al. 1989). Accordingly,

$$\Delta F/F_m' = (F_m' - F_s')/F_m' \qquad (2)$$

where $F_s'$ is the current steady-state fluorescence, which was measured with a modulated red light of 0.3 μmol photons·$m^{-2}$·$s^{-1}$, and $F_m'$ is the maximal fluorescence yield of the light-adapted sample, which was measured by an 0.8 s saturating pulse of approximately 6000 μmol photons·$m^{-2}$·$s^{-1}$. The colonial filaments were arrayed one by one on a transparent plastic sheet, which was then sandwiched and measured as a ''leaf'' during the period of January 20–25, 2005 (Gao et al. 1998).

*Measurement of photosynthetic $CO_2$ fixation.* During the desiccation of wet (physiologically reactivated) *N. flagelliforme* colonies, photosynthetic $CO_2$ uptake was measured using a portable photosynthesis analyzer (LCA-4 infrared analyzer; Analytical Development Company, Hoddesdon, Herts, England). The cover of the assimilation chamber was replaced with a quartz one to allow full-spectrum solar radiation to penetrate. About 0.06 g (dwt) samples (>100 rehydrated colonies) were spread on a plastic net (6 × 4 cm) before being sealed in the chamber. Solar radiation treatments (PAB, PA, P) were implemented as mentioned above, and independent experiments were performed during periods centered around noontime (10:00 a.m.–3:00 p.m.) on different days through the periods of December 21–29, 2004, and January 6–12, 2005. While the colonies were desiccated and their photosynthesis

monitored, the radiation treatments were switched either from P to PA then to PAB, or from PAB to PA and then to P by changing the cutoff filters to see if the exposing order of the radiation treatments would affect photosynthesis. Measurement under each radiation took about 5 min. The temperature within the chambers fluctuated from 19°C to 21°C during the measurements; no difference in temperature within the chamber was observed among the different radiation treatments because of the flow-through air. Such photosynthetic measurements were carried out at 180, 360, or 720 ppmv $CO_2$. Air bags (1 $m^3$) were used to maintain constant $CO_2$ concentrations. $CO_2$ in the ambient air was reduced by pumping it through a soda lime column to acquire the low $CO_2$ concentration of 180 ppmv. A concentration of 720 ppmv $CO_2$ was obtained by injecting pure $CO_2$ before pumping outdoor air into the air bag.

Photosynthetic carbon-fixation rate ($P_n$) [μmol $CO_2 \cdot$ mg (chl $a$)$^{-1} \cdot h^{-1}$] was calculated as follows:

$$P_n = \Delta C \times F \times 60 \times 273/[(273+T) \times 22.4 \times \text{chl } a] \quad (3)$$

where $\Delta C$ is the difference in $CO_2$ concentration (ppmv) between the inlet and outlet air; $F$, the gas flow rate ($L \cdot min^{-1}$); $T$, temperature (°C) inside the assimilation chamber; and chl $a$, the amount of chl $a$ in the samples.

Chlorophyll $a$ was determined, according to Vonshak (1997), after extracting the samples in 100% methanol (>12 h in darkness) and measuring the absorbance using a spectrophotometer (DU-530, DNA/protein analyzer; Beckman, Palo Alto, CA, USA).

*Data analysis.* The UVR-induced inhibition of photosynthetic $CO_2$ uptake was evaluated as follows:

$$\text{Inh}_{\text{UVR}}(\%) = (S_P - S_{PAB})/(S_P) \times 100 \quad (4)$$

where $S_P$ and $S_{PAB}$ represent the photosynthetic $CO_2$-uptake rate of samples exposed to PAR only and PAR+UVAR+UVBR, respectively. Data were analyzed by $t$-test or one-way analysis of variance (ANOVA); treatments effects were considered significant at $P < 0.05$.

## RESULTS

*Reactivation of photosynthetic activity.* *Nostoc flagelliforme* colonies are photosynthetically inactive when they are dry. We rehydrated and reactivated these colonies under indoor light (without UVR) or shaded (with scattered UVR) or direct solar irradiance and investigated their photochemical and $CO_2$-fixation performances during the rehydration and subsequent desiccation (dehydration) to see how solar PAR and UVR would affect them. When the dry, photosynthetically inactive *N. flagelliforme* colonies were rehydrated in shaded outdoor radiation, the effective quantum yield became detectable and then gradually increased with time during the rehydration to reach about 0.3 at the end of the day (Fig. 1a). Further rehydration overnight raised the value to about 0.6 in the early morning of the next day. Under direct solar irradiance, where the PAR level was ~2.5 times that in the shade, photochemical reactivation was also achieved (Fig. 1b). The effective quantum yield was reactivated similarly to about 0.3 after 7 h exposure to solar radiation. Further reactivation overnight brought the yield to only ~0.4 in the early morning of the next day, lower compared with that obtained in the shade and under UV-free indoor light conditions (value at the initial desiccation in Fig. 2). No significant difference ($P > 0.05$) in the effective quantum yield was found among the radiation treatments; that is, UVAR and UVBR did not affect the photochemical recovery during rehydration either in shade or under direct solar radiation. Higher levels of direct solar radiation resulted in faster initial reactivation but lower final values of the yield compared with shaded light ($P < 0.05$; Fig. 1)

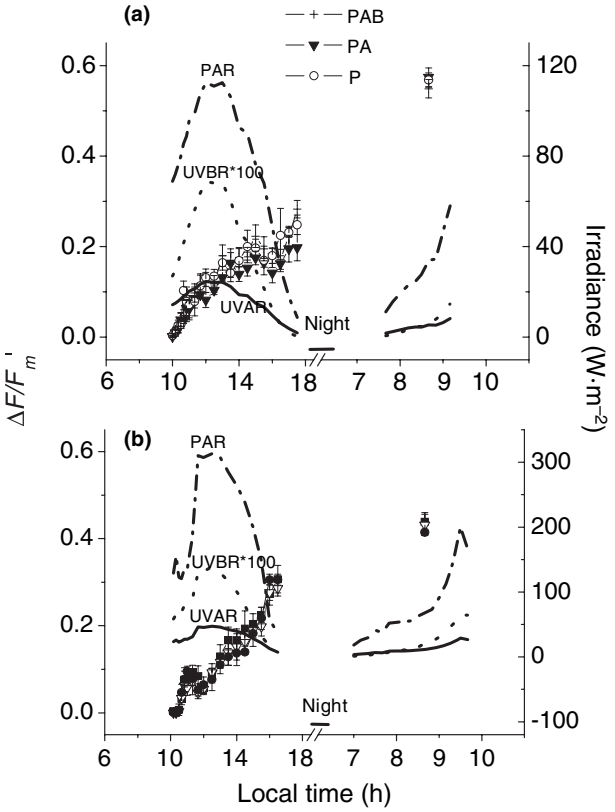


FIG. 1. Effective quantum yield ($\Delta F/F_m'$) of *Nostoc flagelliforme* colonies during rehydration in the shade (a) or under the sun (b) while exposed to different solar radiation treatments: PAB, full spectrum of solar radiation; PA, solar radiation without UVBR; P, solar radiation without UVAR and UVBR. Shade or direct solar irradiances were for January 21–22 (a) and January 24–25 (b), 2005, respectively. Vertical bars for the yield data represent SD for triplicate measurements of different samples.

*Changes in effective quantum yield during desiccation and subsequent rewetting.* When *N. flagelliforme* colonies that were previously photosynthetically reactivated under UV-free indoor conditions were exposed and desiccated under different solar radiation treatments, their effective PSII photochemical activities ($\Delta F/F_m'$) declined from a maximum at the fully hydrated initial phase until the water content reached about 60% (Fig. 2). Such photochemical reduction in this phase was associated with the highest solar irradiance at noon (Fig. 2b), when the highest levels of PAR, UVAR, and UVBR were 296,

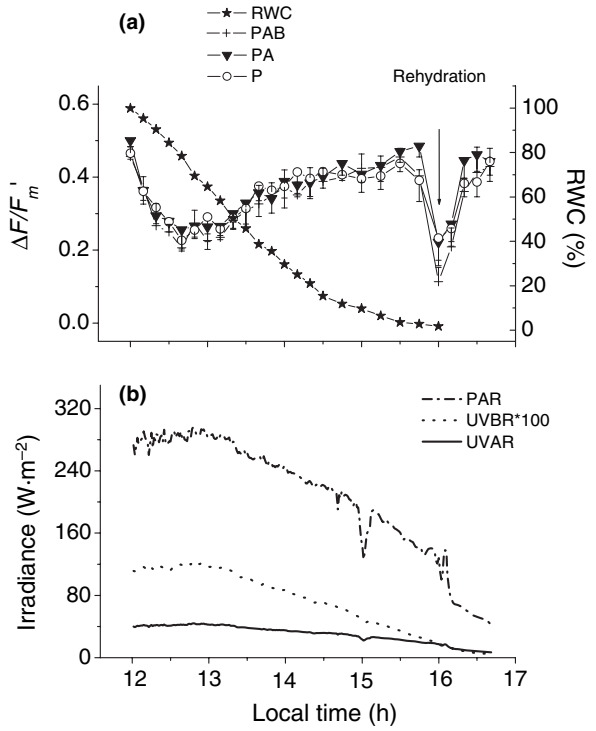


FIG. 2. (a) Effective quantum yield ($\Delta F/F_m'$) of fully indoor-reactivated (rehydrated) *Nostoc flagelliforme* colonies that were reactivated under UV-free indoor conditions while exposed to air under different solar radiation treatments (PAB, full spectrum of solar radiation; PA, solar radiation screened of UVBR; P, solar radiation without UVAR and UVBR). RWC indicates relative water content during the exposure. (b) Solar irradiance during the measuring period on January 20, 2005. Vertical bars for the yield data represent SD for triplicate measurements.

44, and 1.2 W·m$^{-2}$, respectively. Further desiccation of the colonies gave rise to a gradual increase in the effective quantum yield, reaching the initial values at the start of desiccation, when the colonies contained ~4% water. There was no significant difference ($P > 0.1$) in the effective quantum yield among the three solar radiation treatments, indicating that yield was reduced by PAR but not affected by UVAR and UVBR. The effective quantum yield declined sharply ($P < 0.01$) when the relative water content reached <2% (Fig. 2). At this critical point of water content, the values in P and PA treatments were significantly higher ($P < 0.01$) than those in the PAB treatment, indicating an effect of UVBR, though its irradiance was much reduced in the late afternoon. When the colonies at this stage were completely rehydrated, the effective quantum yield rose immediately ($P < 0.01$) under all radiation treatments, increasing by 50% in about 10 min under the PAB treatments. However, significant differences among the three solar radiation treatments were not observed in the recovered values after the second rewetting ($P > 0.5$). For the colonies whose photochemical reactivation (rehydration) was achieved under scattered (shade) sunlight (Fig. 3a), similar patterns of the change in the effective quantum yield were found: a decrease with enhanced desiccation under high levels of solar radiation, then an increase with further water loss, and a further decrease to the lowest values at a critical water content of ~3%. For the colonies that were rehydrated and photochemically reactivated under direct sunlight (Fig. 3c), the effective quantum yield

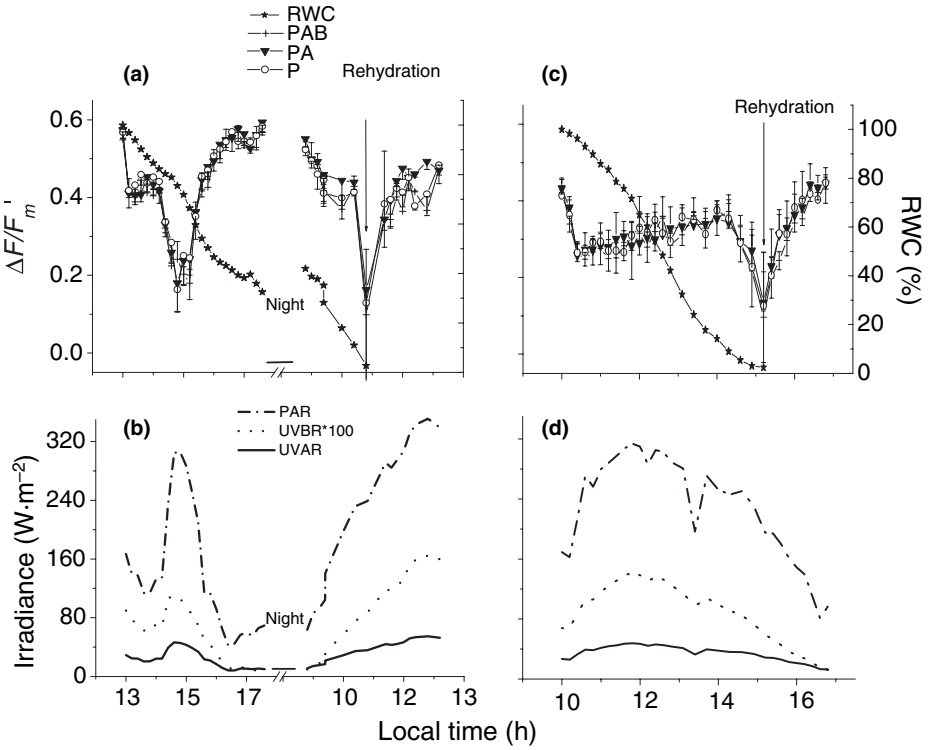


FIG. 3. Changes in the effective quantum yield ($\Delta F/F_m'$) during desiccation of *Nostoc flagelliforme* colonies that were previously photosynthetically reactivated (rehydrated) in the shade (a) or under the sun (c). Desiccation occurred under different solar radiation treatments (PAB, full spectrum of solar radiation; PA, solar radiation without UVBR; P, solar radiation without UVAR and UVBR). RWC indicates relative water content during the exposure. (b and d) Solar irradiance during the measuring period January 22–23 and January 25, 2005. Vertical bars for the yield data represent SD for triplicate measurements.

decreased to a lesser extent compared with those rehydrated indoors or in the shade. At the levels of critical water content, reduction of the effective quantum yield by UVBR was to the same extent of ~0.1 among the colonies previously rehydrated under either indoor light (without UVR) or shaded or direct solar radiation (Figs. 1 and 2). However, the instant solar radiation values at the moments of the critical water content were correspondingly 150, 280, and 230 $W \cdot m^{-2}$ (PAR), being 53%–87% higher for the samples previously rehydrated under shaded or direct sunlight than those indoor-reactivated. The yield reduction in PAR+UVAR+UVBR treatment was significantly different only in the colonies previously rehydrated under indoor light (without UVR; Fig. 3) compared with those in PAR+UVAR or PAR alone. It appeared that pre-exposure to solar UVR during rehydration led to reduced sensitivity to UVBR.

*Changes in photosynthetic $CO_2$ fixation during desiccation.* When the rehydrated colonies of *N. flagelliforme* were desiccated under solar radiation, their photosynthetic $CO_2$ uptake increased with water loss to reach a maximum and then decreased with further desiccation (Fig. 4). A similar pattern was seen under different radiation treatments at reduced or elevated $CO_2$ levels (Fig. 4). It was the desiccation that affected the rate of photosynthetic $CO_2$ uptake (Fig. 5). The sequence of radiation treatments, changing from PAB to P or from P to PAB, did not result in any difference in the photosynthetic performance (Fig. 5). The maximal rate of the photosynthetic $CO_2$ uptake was achieved at a water content of 40%–50% (Fig. 5) and increased with increased $CO_2$ concentrations in the air ($P < 0.01$; Fig. 6a). The rates at 720 ppmv $CO_2$ were 58% and 29% higher than those at 180 and 360 ppmv $CO_2$ concentrations, respectively. When UVR-induced inhibition of $CO_2$ uptake was analyzed at all levels of dehydration and plotted against $CO_2$ concentrations, it became obvious that the changing rate in photosynthetic $CO_2$ uptake at different levels of water loss or time was not affected by UVAR or UVBR, as seen in the absence of inhibition caused by UVBR or UVAR (Fig. 6b). Such an insensitivity of photosynthetic performance to UVR was identical even at elevated or reduced $CO_2$ concentrations.

## DISCUSSION

*Nostoc flagelliforme*, as a terrestrial cyanobacterium, experiences frequent rehydration due to dew or rain and subsequent desiccation under sunlight. The present study showed that the photosynthetic recovery process of dry colonies during rehydration

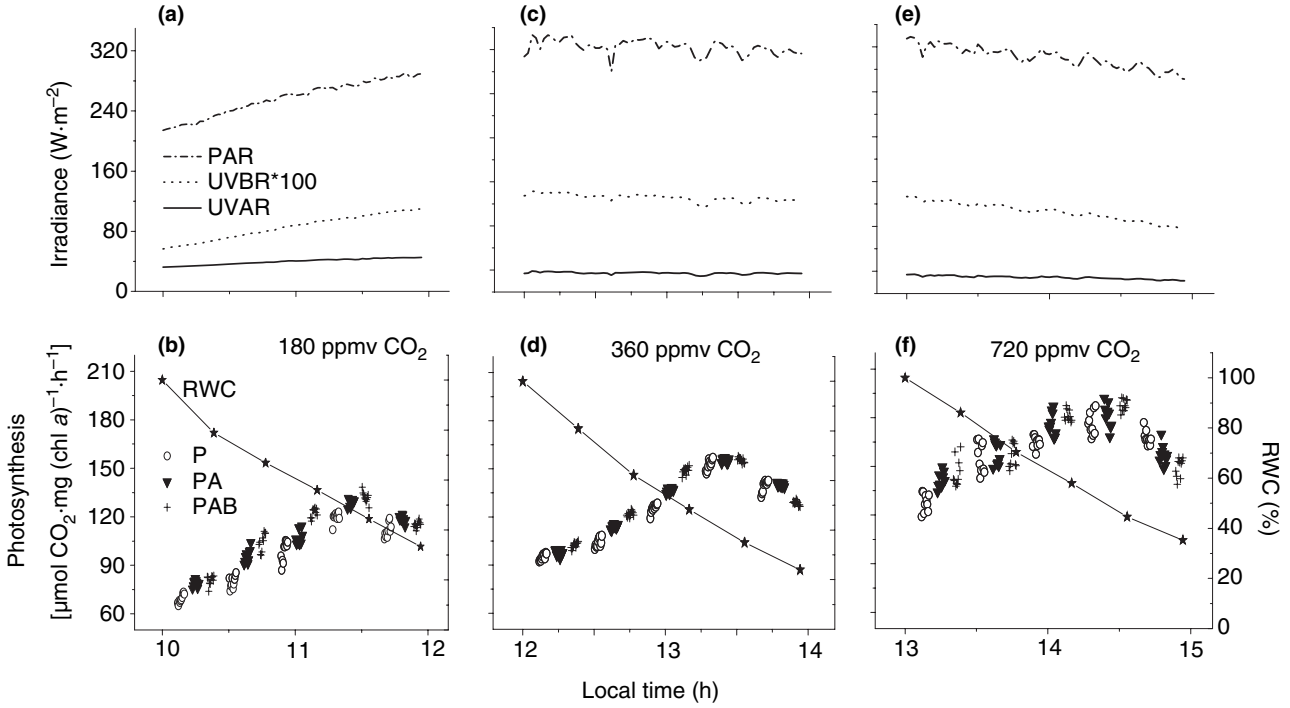


FIG. 4. Representative patterns of change in the photosynthetic $CO_2$-uptake rate of *Nostoc flagelliforme* colonies while desiccated at 180 (b), 360 (d), and 720 ppmv $CO_2$ (f) under different solar radiation treatments (PAB, full spectrum of solar radiation; PA, solar radiation screened of UVBR; P, solar radiation without UVAR and UVBR). (a), (c), and (e) represent solar irradiance during the measuring periods on December 29 and December 22, 2004, and January 6, 2005, respectively. RWC indicates relative water content during the exposure. Repeated measurements were carried out on January 6–7, 2005, at 180 ppmv $CO_2$; on December 21–23, 2004, at 360 ppmv $CO_2$; and on January 6, 9, 10–12, 2005, at 720 ppmv $CO_2$ as shown in Figure 5.

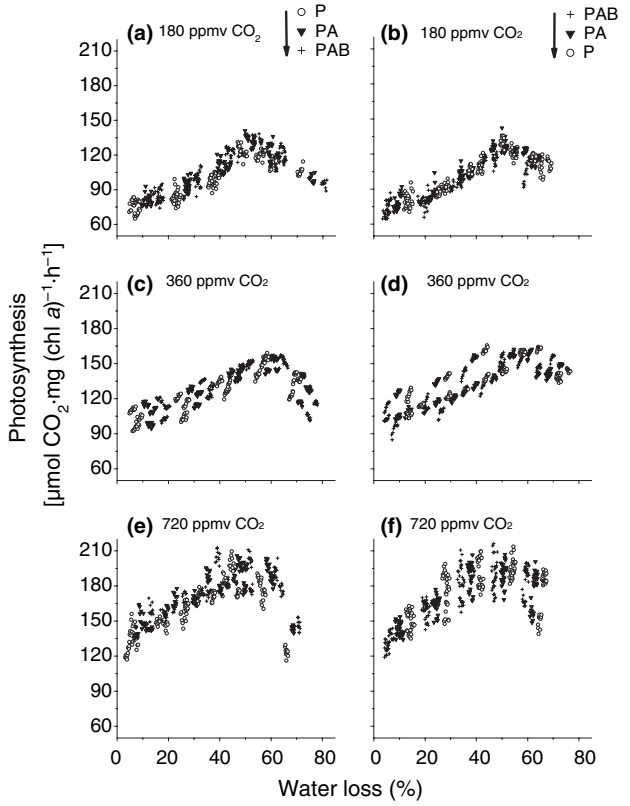


FIG. 5. Rate of photosynthetic $CO_2$ uptake as a function of water loss (%) of rehydrated and photosynthetically reactivated *Nostoc flagelliforme* colonies when exposed to different solar radiation treatments at 180 (a, b), 360 (c, d), and 720 (e, f) ppmv $CO_2$. Measured dates: December 21–29, 2004, and January 6–12, 2005. Sequences of solar radiation treatments were either P-PA-PAB (a, c, and e) or PAB-PA-P (b, d, and f). Each panel represents the data obtained with different samples (>100 filamentous colonies) during the periods centered around noon (1000–1500 hours) on at least three different days.

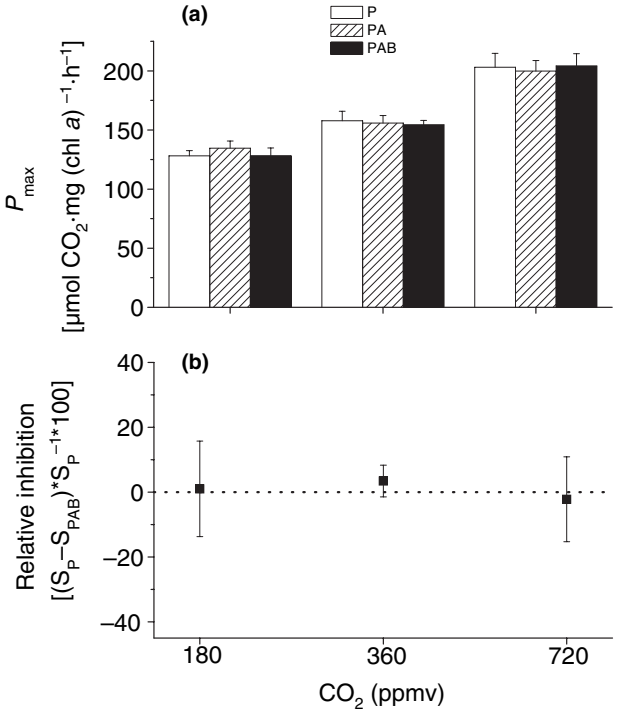


FIG. 6. Maximal rates of photosynthetic $CO_2$ uptake ($P_{max}$) (a) and UVR-induced inhibition (b) of *Nostoc flagelliforme* colonies during desiccation at different $CO_2$ levels while exposed to different solar radiation treatments measured at 180, 360, and 720 ppmv $CO_2$.

and $CO_2$-uptake rate during desiccation were insensitive to solar UVAR and UVBR. This insensitivity was constant when the colonies were exposed to lower (180 ppmv) or higher (720 ppmv) $CO_2$ levels, though enriched $CO_2$ enhanced the photosynthetic rate of the wet colonies while exposed for desiccation.

The PSII effective quantum yield of the rehydrated colonies of *N. flagelliforme* was inhibited by higher solar irradiance at the initial stage of desiccation. This decline was invoked by high levels of PAR, rather than UVR, as no difference was observed when UVR was filtered out. High levels of PAR led to enhanced thermal dissipation of excessive excitation energy and damage to PSII, resulting in decreased $\Delta F/F_m'$ (Franklin et al. 2003). The UVBR additionally reduced quantum yield compared to UVAR when the colonies reactivated (rehydrated) under indoor light (without UVR) contained ~2% water. However, such UVBR-induced damage was not significant for the colonies that were rehydrated in the presence of UVBR under shaded or direct solar radiation when compared among the different radiation treatments, in spite of the higher levels of solar radiation in late morning and early afternoon when the critical water content was reached. Preexposure to UVBR during rehydration could have aided in activating the UV-protective mechanisms in *N. flagelliforme*. Simultaneous illumination by visible light and UVBR impairs PSII activity to a lesser extent than independent damaging events (Sicora et al. 2003).

The photosynthetic $CO_2$-uptake rate of *N. flagelliforme* colonies (rehydrated) increased with increased dehydration during desiccation. Repeated exposures of 5 min intervals to each of the radiation treatments, either in a sequence of P, PA, and then PAB or vice versa, did not result in any difference in the photosynthetic response. Such insensitivity to both UVAR and UVBR was constantly observed within the range of ~35%–93% water content. This finding contrasts with the significant reduction in photosynthetic $O_2$ evolution in an outdoor-grown strain of the cyanobacterium *Arthrospira plantensis* exposed to solar radiation with UVR for less than 5 min (Wu et al. 2005).

The responses of photochemical activity and photosynthetic $CO_2$-uptake rate to desiccation showed a remarkable discrepancy in *N. flagelliforme* (Fig. 7). At the initial phase of desiccation, the effective

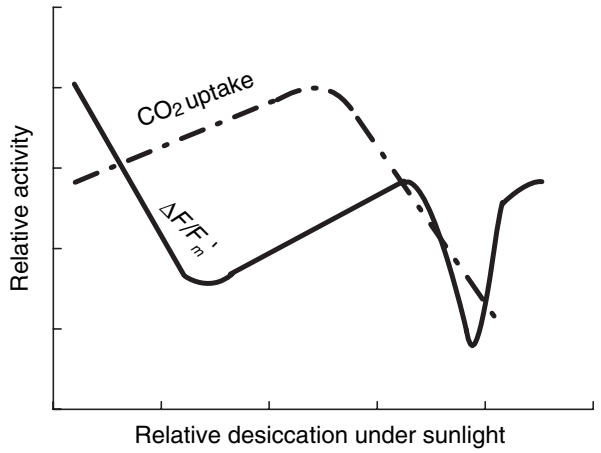


FIG. 7. Illustration of the discrepancy between the change patterns of the effective photochemical activity and photosynthetic $CO_2$-uptake rate in the *Nostoc flagelliforme* colonies during desiccation.

quantum yield decreased sharply because of high PAR, while the photosynthetic $CO_2$ uptake increased with water loss from the colonies. The initial loss of the yield caused by solar PAR around noontime could be a response to higher excitation pressure on electron transport, reflecting a photoprotective down-regulation to avoid photoinhibition by PAR (Franklin et al. 2003). The enhanced $CO_2$ fixation due to moderate desiccation, as reported previously (Qiu and Gao 2001), could be related to a reduced water layer around the colonies and, consequently, a decreased barrier for $CO_2$ diffusion, as $CO_2$ diffuses about 10,000 times slower in water than in air. Further progress of the desiccation resulted in a parallel rise in the photochemical yield and $CO_2$ fixation until the critical water content was reached. For PSII photochemical activities, the highest value appeared at relative water content of ~5%, while for the photosynthetic $CO_2$ uptake, the highest value was at 44%–55% water content. Photosynthetic $O_2$ evolution and maximal quantum yield of PSII of *N. flagelliforme* have been observed to increase with increased concentration of NaCl under aquatic conditions (Shi et al. 1992, Ye and Gao 2004). It is possible that both photosynthetic carboxylation and PSII photochemistry of this terrestrial cyanobacterium are highly sensitive to osmotic changes, to which $CO_2$ uptake and PSII activity might respond differentially in terms of the extent and time. Synthesis of key proteins for the photosynthetic carbon fixation could be stimulated by desiccation as the activity of total carbonic anhydrase in *N. flagelliforme* increased with desiccation (C. Ye, K. Gao, and M. Giodano, unpublished data). The ecological implication is that the distinctive patterns of photosynthetic $CO_2$ uptake and PSII activity observed in *N. flagelliforme* enable this species to protect itself under high solar radiation by reducing its quantum yield and at the same time sustain high efficiency of $CO_2$ fixation due to desiccation-facilitated $CO_2$ uptake, making it possible for this organism to survive in habitats where drought occurs.

Ultraviolet-absorbing pigments, water stress protein (Wsp), and extrapolysaccharides (EPS) were found in the cyanobacterial sheath of *Nostoc* sp. (Hill et al. 1994), and the cyanobacterial sheath has been suggested to associate with cellular resistance against environmental stresses. In *Nostoc commune* Vaucher ex Bornet et Flahault DRH1, UVA/B irradiation stimulated the UV-absorbing pigments as well as the extracellular glycan (Ehling-Schulz et al. 1997, Potts 2000). The EPS are known to provide a water repository for the cells (Potts 1999, Hill et al. 1997) and, together with the water they hold, may reduce the levels of attenuated UVR and PAR. The Wsp, constituting some 70% of total soluble protein of the colonies, could also contribute partially to reduce UVR through the sheath. The UV-absorbing pigments, MAAs, and scytonemin occur in many species of cyanobacteria (Cockell and Knowland 1999, Castenholz and Garcia-Pichel 2000) and are induced by exposure to UVR and periodic desiccation (Sinha et al. 2001, Dillon et al. 2002). Studies have shown that the incident UVAR entering the cells may be reduced by ~90% because of the presence of scytonemin in the cyanobacterial sheaths (Garcia-Pichel et al. 1992, Brenowitz and Castenholz 1997). *Nostoc flagelliforme* appeared to contain such UV-absorbing compounds, as indicated by the absorption peaks through the UV range (data not shown). The photosynthetic insensitivity of *N. flagelliforme* colonies to solar UVR must involve highly efficient protective mechanisms, which need to be studied further.

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