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Effects of solar UV radiation on photosynthetic performance of the diatom *Skeletonema costatum* grown under nitrate limited condition

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Availability of nutrients is known to influence marine primary production; and it is of general interest to see how nutrient limitation mediates phytoplankton responses to solar ultraviolet radiation (UVR, 280-400 nm). The red tide diatom *Skeletonema costatum* was cultured under nitrate (N)-limited and N-replete conditions and exposed to different solar irradiation treatments with or without UV-A (315-400 nm) and UV-B (280-315 nm) radiation. Its photochemical quantum yield decreased by 13.6% in N-limited cells as compared to that in N-replete ones under photosynthetically active radiation (PAR)-alone treatment, and the presence of UV-A or UV-B decreased the yield further by 2.8 and 3.1%, respectively. The non-photochemical quenching (NPQ), when the cells were exposed to stressful light condition, was higher in N-limited than in N-replete grown cells by 180% under PAR alone, by 204% under PAR + UV-A and by 76% under PAR + UV-A + UV-B treatments. Our results indicate that the N limitation exacerbates the UVR effects on the *S. costatum* photosynthetic performance and stimulate its NPQ.

Key Words: diatom; N limitation; N repletion; photosynthesis; *Skeletonema costatum*; UVR

INTRODUCTION

Solar ultraviolet radiation (UVR, 280-400 nm) is a crucial environmental factor to influence marine primary productivity and consequently the marine ecosystems (Häder 2011). UVR can decrease phytoplankton growth and photosynthesis as well as nutrients uptake (Sobrino et al. 2004, Gao et al. 2007*a*, Korbee et al. 2010), harm DNA or protein molecules (Roy 2000, Wei et al. 2004) and even lead to cell death (Agustí and Llabrés 2007), and therefore, can alter community structures (Marcoval et al. 2008, Beardall et al. 2009). On the other hand, longer UV-A wavebands (320-400 nm) are known to function in photorepairing the UV-B induced damages to DNA (Buma et al. 2003), trigger chlorophyll fluorescence (Halldal 1967) and energize the photosynthesis of coastal phytoplankton assemblages (Helbling et al. 2003, Mengelt and Prézelin 2005, Gao et al. 2007*b*, Li and Gao 2013).

Availability of nutrients is known to affect the photosynthetic responses of algae to UVR (Beardall et al. 2001, 2009). Nutrient limitation reduced the sensitivity of the diatom *Chaetoceros brevis* to photo-induced viability loss (van de Poll et al. 2005). A greater UV-A induced reduction on the dimethysulfide production of the diatom *Thalassiosira oceanica* was observed under nitrate-limited condition (Harada et al. 2009), as well as the reduced contents of saturated fatty acids in the diatoms *Phaeodactylum tricornutum* and *Chaetoceros muelleri* (Liang et al. 2006).

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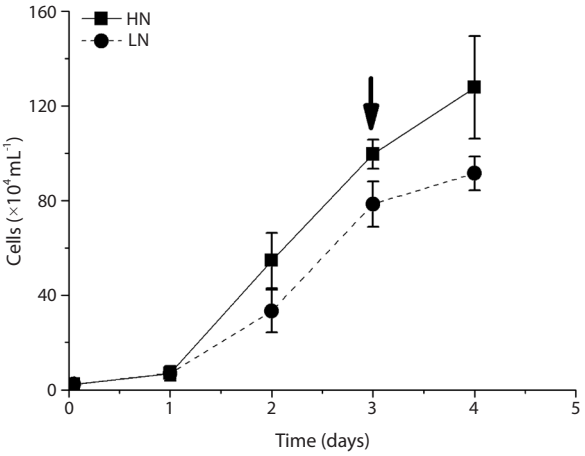

Fig. 1. Cell concentrations of *Skeletonema costatum* grown in N-replete (HN) or N-starved (LN) conditions during the cultured period. The arrow indicates that the culture was taken and diluted to 3-4 × 10^4 cell mL^{-1} in the evening before the outdoor experiments next morning. Vertical bars represent the standard deviations (n = 3).

The increased UVR sensitivity of the dinoflagellates *Gymnodinium sanguineum* and *Gymnodinium cf. instriatum* was also found under nitrate-limited conditions (Litchman et al. 2002), as well as the increased tolerance of the dinoflagellates *Heterocapsa* sp. to UVR stress under nitrate replete conditions (Korbee et al. 2010). However, the knowledge on the combined effects of UVR and nitrate limitation has been scarcely documented, especially on the photophysiology of diatoms.

The diatom *Skeletonema costatum* is distributed abundantly and cosmopolitanly in the word's oceans (Kooistra et al. 2008) and is well known as a typical species of harmful algal blooms (Wang et al. 2008). Long-term UV-B exposure increased its contents of carotenoids and UV-absorbing compounds (Wu et al. 2009); short-term UV-B exposure decreased its protein expression (Wei et al. 2004), but increased its competitive ability as compared to the dinoflagellate *Alexandrium tamarense* and thus broke their competition balance in growth (Zhang et al. 2007). Nevertheless, this diatom showed a rapid acclimation to solar UVR, even after having been maintained indoor for decades under low UVR-free light condition (Guan and Gao 2008). Since *S. costatum* is found in waters of varied nitrate concentrations of e.g., from 0 to 12.3 μmol L^{-1} in the South China Sea (Ning et al. 2004), and little is known about the combined effects of UVR and nitrate limitation on its photochemical performance. Therefore, the aim of this study was to examine the effects of solar UVR on the photosynthetic performance of the diatom *S. costatum* while growing under nitrate-limited and replete conditions.

MATERIALS AND METHODS

Organism and culture

The diatom *Skeletonema costatum* (Greville) Cleve (strain 2042) was obtained from the algal species conversation center of Xiamen University and was grown in sterilized artificial seawater at 20°C and 350 μmol photons m^{-2} s^{-1} (~75 W m^{-2}) photosynthetically active radiation (PAR) irradiance (12 : 12 LD cycle). Two levels of nitrate were set: 830 μmol L^{-1} nitrate of the standard f/2 medium (N-replete, HN) and 0.83 μmol L^{-1} (N-limited, LN) of nitrate, the same f/2 medium with the nitrate reduced to be equivalent to the surface level of the South China Sea (Li et al. 2012). The cells at mid-exponential phase (Fig. 1) were diluted to 30,000-40,000 cells mL^{-1} with fresh medium (LN or HN) in the evening before the outdoor experiments started next morning.

Irradiance treatments and measurements

In the early morning (7:00 am) of August 4 and 8 of 2010, both the diluted cultures (LN or HN) were dispensed into 500 mL UV-transparent quartz tubes that were incubated in a flow-through water tank to control temperature (20 ± 0.5°C) and exposed to 3 irradiation treatments (triplicate tubes for each nutrient level): a) uncovered quartz tubes, the cells received full sunlight (PAR + UV-A +UV-B [PAB], irradiances above 280 nm); b) quartz tubes wrapped in Folex 320 (Montagefolie, No. 10155099; Folex, Dreieich, Germany), the cells received PAR + UV-A (PA, irradiances above 320 nm); and c) quartz tubes covered with Ultraphan film 395 (UV Opak; Digefra, Munich, Germany), the cells received PAR alone (P, irradiances above 395 nm). The transmission spectra of the tubes and filters are available elsewhere (Sobrino et al. 2004). A radiometer (Eldonet XP; Real Time Computers Inc., Möhrendorf, Germany) was used to monitor the incident solar radiation; it measures every second of UV-B (280-315 nm), UV-A (315-400 nm), and PAR irradiance (400-700 nm) and records the minute-averaged values (Häder et al. 1999). This device has been regularly calibrated with a certified calibration lamp (DH 2000; Oceanic Optics Inc., Dunedin, FL, USA). The PAR irradiance was converted from W m^{-2} to photon flux (μmol photons m^{-2} s^{-1}) by multiplying by 4.60 according to Neale et al. (2001).

Photophysiological parameter measurements

During the incubations (7:00 am to 18:00 pm), 5 mL

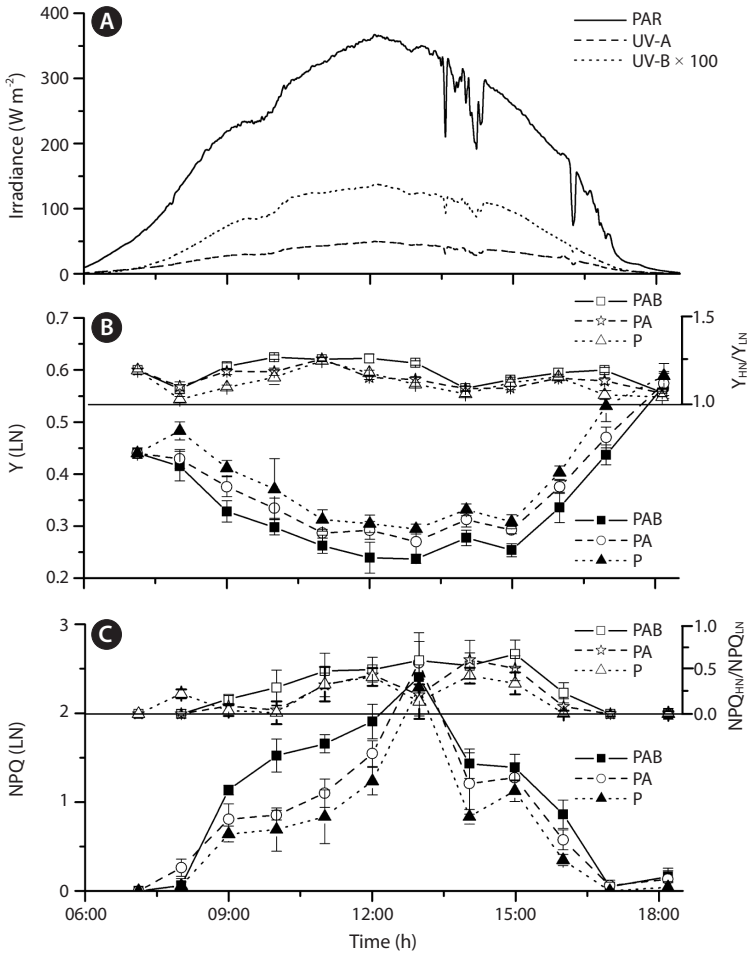

Fig. 2. (A) Representive incident solar photosynthetically active radiation (PAR, 400-700 nm), UV-A (315-400 nm), and UV-B (280-320 nm) irradiances in W m^{-2}. (B) Diurnal variations in effective quantum yield (Y). (C) Non-photochemical quenching (NPQ) of *Skeletonema costatum* cells grown under nitrate (N)-limited condition (LN) and exposed to PAR + UV-A + UV-B (PAB, 280-700 nm), PAR + UV-A (PA, 320-700 nm), and PAR (P, 400-700 nm), and their ratios to that of the cells grown under N-replete condition (HN). Vertical bars represent the standard deviations (n = 3).

samples were taken every hour from each tube to determine the photosynthetic performance of *S. costatum* with a pulse amplitude modulated fluorometer (Xe-PAM; Walz, Effeltrich, Germany). Effective photochemical quantum yield (Y) was determined by measuring the instant maximal fluorescence (F_m') and steady state fluorescence (F_t) of light-adapted cells, and calculated according to Genty et al. (1990) as: $Y = (F_m' - F_t) / F_m'$. The non-photochemical quenching (NPQ) was determined (van Kooten and Snel 1990) as $NPQ = (F_m - F_m') / F_m'$, where F_m was the maximal fluorescence of dark-acclimated (overnight) cells obtained prior to the outdoor exposure. The saturating pulse was set at 4,800 μmol photons m^{-2} s^{-1} for 600 ms and the actinic light at 350 μmol photons m^{-2} s^{-1} (~75 W m^{-2}) for the effective quantum yield measurement. We are aware the effects of solar UVR could be exaggerated by shifting the cells cultured indoor to the outdoor conditions, but it indeed happens in natural conditions such as after typhoon event (Li et al. 2009) or after heavy cloud covers (Gao et al. 2007*a*) and so provides very useful information to accomplish this study's objective.

Data analyses

UV-A or UV-B induced inhibition of Y was calculated as:

$$UV\text{-}B_{Inh} = (Y_{PA} - Y_{PAB}) / Y_P \times 100\%;$$
$$UV\text{-}A_{Inh} = (Y_P - Y_{PA}) / Y_P \times 100\%$$

, where $UV\text{-}B_{Inh}$ and $UV\text{-}A_{Inh}$ indicate UV-B and UV-A induced inhibition; Y_{PAB}, Y_{PA}, and Y_P indicate Y values of the cells under PAB, PA, and P treatments, respectively.

To determine the significant differences ($p < 0.05$) among three light treatments and between two nutrient

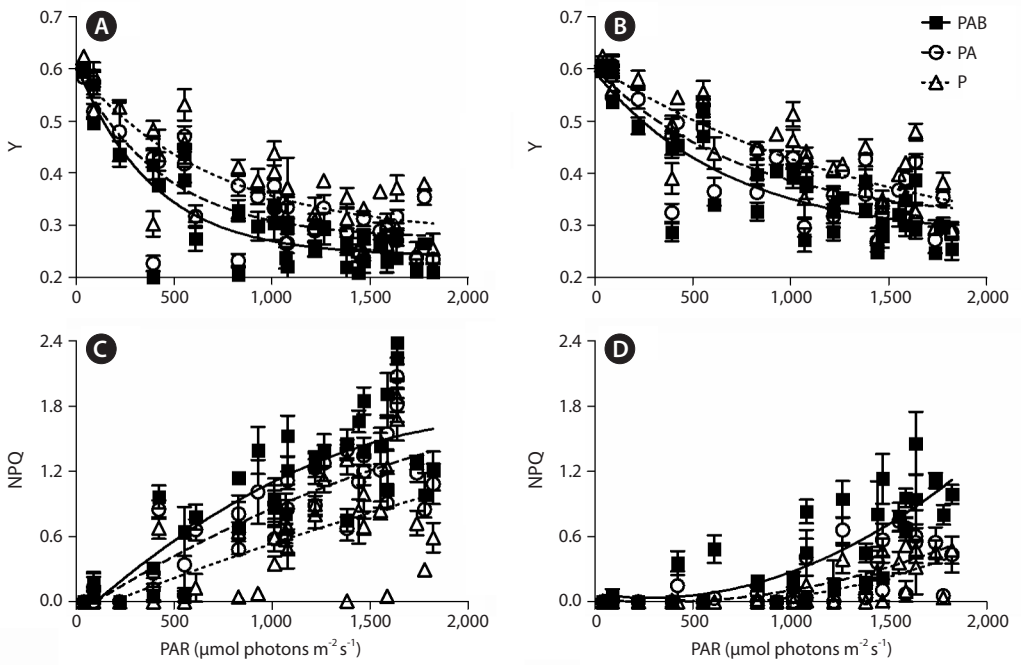

Fig. 3. Effective quantum yield (Y) (A & B) and non-photochemical quenching (NPQ) (C & D) of *Skeletonema costatum* cells grown under N-limited (A & C) or N-replete (B & D) conditions and exposed to photosynthetically active radiation (PAR) + UV-A + UV-B (PAB, 280-700 nm), PAR + UVA (PA, 320-700 nm), and PAR (P, 400-700 nm) of overall two days experiments, as a function of PAR. Vertical and horizontal bars represent the standard deviations (n = 3).

treatments, paired-t test was used for the whole day's comparisons and one way-ANOVA was used for the each time-point comparisons. Non-linear curve fit was used to obtain the relationships between Y (or NPQ) and PAR irradiance, whereas Kendall's τ test was used to establish the correlations of Y and UV inhibition between the HN and LN treatments.

RESULTS

During a diurnal cycle of solar radiation (Fig. 2A), the effective quantum yield (Y) decreased with increasing solar radiation regardless of the radiation treatments with or without UVR, to a minimum value at noon, and then increased with decreasing solar radiation (Fig. 2B). The cells grown under nitrate (N)-limited condition had a relatively lower Y value than those under N-repletion e.g., 0.44 in the early morning, that decreased to a minimum of 0.29 at noon and almost completely recovered in the late afternoon (Fig. 2B). The diurnal changes of NPQ displayed an opposite pattern to Y (Fig. 2C), with the higher values in the presence of UVR than that in PAR alone ($p < 0.01$). In view of the NPQ ratios of HN to LN grown cells, higher NPQ were found in the LN-grown cells (Fig. 1C), indicating a higher heat dissipation. UVR significantly increased the NPQ ($p < 0.05$), by approximately 57% in LN and 30% in HN-grown cells at noon (Fig. 2C).

When PAR intensity increased over 1,500 μmol photons m^{-2} s^{-1} (326 W m^{-2}), the Y values decreased by approximately 60% as compared to the initials in LN grown cells (Fig. 3A & B) with the presence of UV-A reducing the yield by 2.2-21% and addition of UV-B further decreasing it by 6.0-24%, the total inhibition caused by UVR being 12 to 30%. The NPQ value reached 0.89 in LN-grown cells as the PAR was over 1,500 μmol photons m^{-2} s^{-1} (326 W m^{-2}), being elevated by 46 and 31% respectively by solar UV-A and UV-B. The N limitation enhanced the NPQ by 180% under PAR alone, by 204% under PA and by 76% under PAB, compared to that in N repletion (Fig. 3C & D). Moreover, a clear threshold of NPQ of LN-grown cells (Fig. 3C & D) occurred when the PAR irradiance was ~230 μmol photons m^{-2} s^{-1} (50 W m^{-2}) – one fourth of that in HN-grown cells, providing evidence that the lower light energy is needed to spike the NPQ under N-limited conditions.

Fig. 4 showed the relationships of the Y values, UV-A and UV-B caused inhibition between LN- and HN-grown cells. The LN-grown cells showed about 13% lower Y values than that of HN-grown cells (Fig. 4A), and 24.4 and 21.4% higher inhibition caused by UV-A and UV-B,

respectively (Fig. 4B & C), indicating the N limitation exacerbated the UVR effects on the diatom photosynthetic performance.

DISCUSSION

Grown under nitrate limited condition, the diatom *S. costatum* exhibited lower effective quantum yields (Y) and higher NPQ, as well as higher sensitivity to UVR in contrast to that under N-replete condition. The PAR intensity that initiated the NPQ of N-limited grown cells was one fourth of that of N-replete grown ones. Light history would affect the photophysiological performances of phytoplankton when being shifted from the indoor- to outdoor-conditions, such as the *S. costatum* strain maintained in the laboratory for decades showed differential responses to UV compared to the strain isolated from coastal water (Guan and Gao 2008), and the *Thalassiosira pseudonana* showed differential photoinactivations of photosystem II after acclimating to different light levels (Li and Campbell 2013). In natural environments, the light acclimation from very low to very high levels with or without UVR also happens, such as that after typhoon event (Li et al. 2009) or after heavy cloud covers for days or during a diel cycle (Gao et al. 2007*a*), which would cause the exaggerated photoinhibition of *S. costatum* by solar PAR or UVR (Figs 2 & 3) although this diatom species could rapidly acclimate to the field light conditions (Guan and Gao 2008).

While *S. costatum* showed similar diurnal patterns of both the yield and NPQ under sunlight to other phytoplankton species or communities (e.g., van de Poll et al. 2005, Marcoval et al. 2008), nitrate limitation decreased its yield and increased its NPQ either in the presence or absence of solar UVR (Figs 3 & 4). Higher availability of nitrogen usually leads to less inhibition by stressful light (Litchman et al. 2002, Korbee et al. 2010, Loebl et al. 2010), since the repair of photodamage can be better achieved with more N-requiring enzymes and / or protein cofactors (Roy 2000, Beardall et al. 2001). Other enzymes such as peroxidase and catalase, that also need N, and can detoxify UVR-induced reactive oxygen species (Lesser 1996) and might also be responsible for the smaller UVR effects under N replete conditions.

The threshold of light intensity that triggers the NPQ in LN-grown cells was one-fourth of that of HN-grown cells (Fig. 3C & D). The NPQ, an important strategy for phytoplankton to rapidly (seconds to minutes) regulate photochemistry, is one of the first lines of defense that

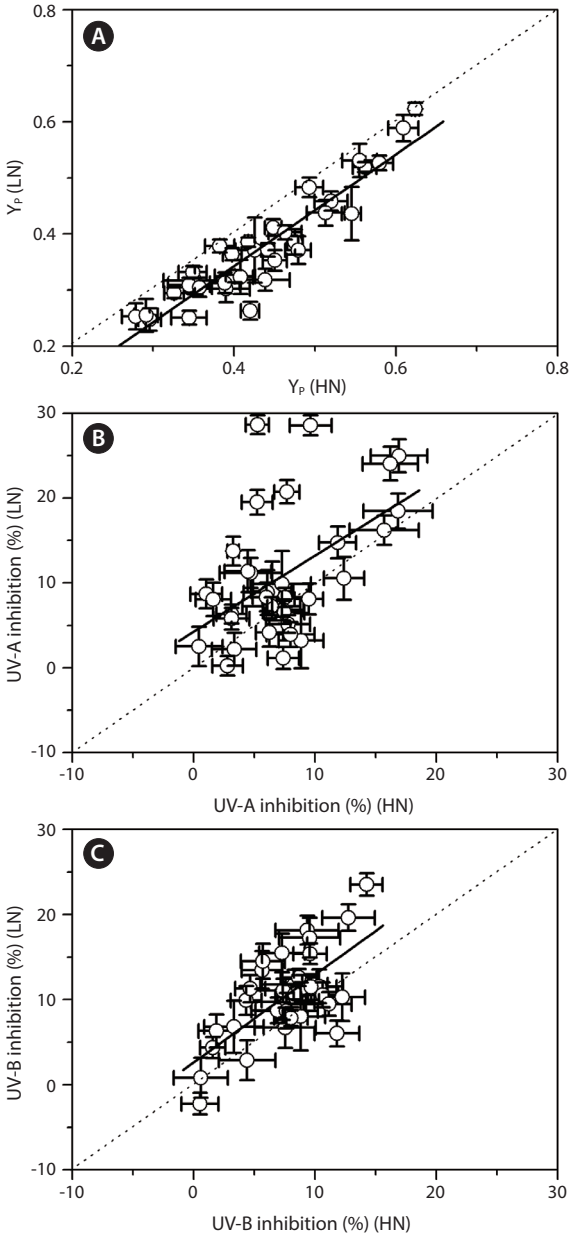

Fig. 4. Effective quantum yield (A), UV-A induced (B), and UV-B induced (C) inhibition on *Skeletonema costatum* cells grown under N-limited condition (LN) versus that of the cells grown under N-replete condition (HN). The bold lines show significant relationships, with r^2 of 0.93 for Y_P, 0.26 for UV-A and 0.47 for UV-B inhibition ($p < 0.01$), respectively. Vertical and horizontal bars represent the standard deviations ($n = 3$). $r_A = 0.92912$, $p < 0.0001$; $r_B = 0.5074$, $p = 0.00219$; $r_C = 0.68274$, $p < 0.0001$.

diatoms use to attenuate the photoinhibitory oxidative damage caused by light stress (Lavaud et al. 2007, Korbee et al. 2010). The LN-grown cells had significantly ($p < 0.01$) higher NPQ and lower light to trigger NPQ, comparable to the HN-grown ones (Fig. 3C & D); they could have

dissipated the excessive energy more effectively under stressful light condition, thus protecting the cells from photoinhibition and maintaining their photosynthetic activity. The field measurements of NPQ by Kashino et al. (2002) and Fujiki et al. (2003) also indicated that the NPQ process is of importance to maintain the photosynthetic activity of phytoplankton. On the other hand, the substances, that need N for their synthesis, e.g., UV-screening compounds like mycosporine-like amino acids were recorded to increase with increasing nitrogen levels (Litchman et al. 2002, Korbee et al. 2010, Barufi et al. 2011) and might also attribute to the higher UVR sensitivity in LN- than in HN-grown cells.

The diatom grown under N-limited condition exhibited higher sensitivity to UVR than that grown under N-replete condition, based on the changes in the photochemical quantum yield and NPQ, which indicates that the N limitation exacerbates the effects of UVR on its photosynthetic performance and stimulate its NPQ. Presently, the increased global temperature has directly and indirectly altered the natural conditions of aquatic bodies, e.g., increasing the stratification of surface ocean and making it more oligotrophic (Boyd et al. 2010). Taking into account the worldwide oligotrophic oceans wherein the growth of phytoplankton is limited and the limitation could be exacerbated by the decreased nutrient levels within the upper mixed layer; the negative effects caused by solar UVR would be exacerbated, making phytoplankton cells more sensitive to ambient UVR stress.

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