Inhibition of photosynthesis by UV-B exposure and its repair in the bloom-forming cyanobacterium *Microcystis aeruginosa*

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Abstract The photosynthetic performance of *Microcystis aeruginosa* FACHB 854 during the process of UV-B exposure and its subsequent recovery under photosynthetic active radiation (PAR) was investigated in the present study. Eight hours UV-B radiation (3.15 W m^{-2}) stimulated the increase of photosynthetic pigments content at the early stage of UV-B exposure followed by a significant decline. It suggested that UV-B damage was not an immediate process, and there existed a dynamic balance between damage and adaptation in the exposed cells. Short-term UV-B exposure severely inhibited the photosynthetic capability, but it could restore quickly after being transferred to PAR. Further investigations revealed that the PS II of *M. aeruginosa* FACHB 854 was more sensitive to UV-B exposure than PS I, and the oxygen-evolving complex of PS II was an important damage target of UV-B. The inhibition of photosynthetic performance caused by UV-B could be recovered to 90.9% of pretreated samples after 20 h exposure at low PAR, but it could not be recovered in the dark as well as under low PAR in the presence of Chloromycetin. It can be concluded that PAR and de novo protein synthesis were essential for the recovery of UV-B-damaged photosynthetic apparatus.

Keywords Bloom-forming cyanobacteria ·
Electron transport · *Microcystis aeruginosa* ·
Photosynthesis · Pigments · UV-B

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Introduction

Increases of UV-B radiation reaching the Earth's surface due to stratospheric ozone depletion have received much attention over the last few decades (Crutzen 1992; Madronich et al. 1998; McKenzie et al. 2007). The enhanced solar UV radiation is considered to be detrimental to almost all forms of life, especially photosynthetic organisms due to their requirement for light (Day and Neale 2002; Häder et al. 2003), although positive effects of UV radiation have also been reported. Gao et al. (2007) have found that solar UV radiation can act as an additional source of energy for photosynthesis and drive CO_2 fixation in tropical marine phytoplankton.

Cyanobacteria are important ubiquitous prokaryotes which populate terrestrial and aquatic habitats and are important contributors to global photosynthetic biomass production (Whitton and Potts 2000). It is found that enhanced UV-B can affect cyanobacterial growth, photosynthesis, pigments, and morphology, though different responses are observed in different species treated with different UV doses (Jiang and Qiu 2005; Wu et al. 2005; Rath and Adhikary 2007; Pattanaik et al. 2008). On the other hand, cyanobacteria are the oldest autotrophic inhabitants of the planet and have evolved efficient mechanisms to cope with the stress of UV exposure (Castenholz and Garcia-Pichel 2000). Despite extensive investigations, the influence of UV-B radiation on cyanobacteria and their repair mechanisms still need to be elucidated since these organisms show large differences in UV sensitivities and photorepair mechanisms.

The occurrence of cyanobacterial blooms in freshwater has increased apparently over the last few decades all over the world (Xu et al. 2000; Chen et al. 2003; McCarthy et al. 2007). These blooms degrade the recreational value of

water surfaces, impair water supply, cause deoxygenation of the water by decomposition, and lead to fish death (Oliver and Ganf 2000). Because these bloom-forming cyanobacteria usually accumulate at the surface of freshwater, they will be influenced by enhanced UV-B. The effects of UV-B on bloom-forming cyanobacteria have received more and more attention in recent years (Liu et al. 2004; Jiang and Qiu 2005; Sommaruga et al. 2009). *Microcystis aeruginosa* is the most notorious bloom-forming cyanobacterium in freshwater. Our previous works have found that UV-B influences the CO_2-concentrating mechanism of *M. aeruginosa*, and this cyanobacterium has many adaptive strategies to cope with the prolonged UV-B exposure (Jiang and Qiu 2005; Song and Qiu 2007). In the present study, *M. aeruginosa* was chosen for further investigation on the UV-B damage and the repair of photosynthetic apparatus.

Materials and methods

Organisms and growth conditions The bloom-forming cyanobacterium *Microcystis aeruginosa* FACHB 854 was obtained from the Freshwater Algae Culture Collection of Institute of Hydrobiology, Chinese Academy of Sciences. The samples were cultivated in BG_{11} medium (Stanier et al. 1971) at 25°C with continuous light irradiance of 40 μmol m^{-2} s^{-1}. Visible irradiance was measured with a quantum sensor (QRT1, Hansatech Instruments Ltd., UK). All experiments were conducted with exponential growing cells after 1 week of cultivation.

UV-B irradiation source Exponential growing cultures (150 mL) were placed in Petri dishes (diameter, 15 cm) and exposed to 3.15 W m^{-2} biological effective UV-B radiation provided by fluorescent UV-B lamps (TL 40 W/ 12RS, Philips, Germany). The emission spectra of UV-B fluorescent lamps were measured with a scanning spectroradiometer (SPR-920, Sanse Instrument Ltd., Zhejiang, People's Republic of China) as described in a previous paper (Jiang and Qiu 2005). The biological spectral weighting function of Flint and Caldwell (2003) was adopted, and weighted UV-C radiation was less than 0.263 W m^{-2} during the incubation of UV-B-treated samples.

Measurement of pigment contents Exponentially growing cells of *M. aeruginosa* FACHB 854 were exposed to 3.15 W m^{-2} UV-B and 20 μmol photons m^{-2} s^{-1} photosynthetic active radiation (PAR) at 25°C. At 0.5, 1, 2, 4, and 8 h, the samples were harvested for pigment measurement. Chlorophyll *a* (Chl *a*) content was determined spectrophotometrically in 80% acetone extracts (Inskeep and Bloom 1985). Pelleted cells were extracted with 90% acetone, and carotenoids (CAR) content was estimated from the optical density at 480 nm using an extinction coefficient of 2,500 mM^{-1} cm^{-1} (Davies 1976). The biliproteins were extracted with repeated freezing in liquid N_2 and thawing at 4°C in the presence of 0.05 mol L^{-1} phosphate buffer (pH 6.7). The homogenate solutions were centrifuged at 4,000×g for 15 min, and then the absorbency of supernatant was determined. The concentrations of phycocyanin (PC) and allophycocyanin (APC) were calculated according to Siegelman and Kycia (1978).

Measurement of net photosynthesis and dark respiration Exponential growing samples of *M. aeruginosa* FACHB 854 were exposed to 3.15 W m^{-2} UV-B and 20 μmol photons m^{-2} s^{-1} PAR for 80 min. At 0, 20, 40, and 80 min, the rates of net photosynthesis and dark respiration were determined with a Clark-type oxygen electrode (Chlorolab 2, Hansatech Instruments Ltd., UK) at 25°C. Samples were harvested by centrifugation and resuspended in fresh BG_{11} medium. The reaction medium was buffered with 25 mmol L^{-1} Bis-Tris propane (BTP) at pH 7.8. The oxygen electrode was calibrated with air-equilibrium distilled water for full scale and by adding some Na_2SO_3 powder for the zero point. Temperature was controlled with a polystat refrigerated bath (Cole-Parmer Instrument Co., USA). Illumination was at 600 μmol photons m^{-2} s^{-1} provided by a light housing and stabilized power supply, and light was passed through a fiber optic cable to the surface of the reaction cuvette.

Measurement of electron transport activity After 20 min exposure to UV-B (3.15 W m^{-2}) and 20 μmol photons m^{-2} s^{-1} PAR, samples were harvested and resuspended in fresh BG_{11} medium, and electron transport activities were assayed with Clark-type oxygen electrode at 600 μmol photons m^{-2} s^{-1} and 25°C. PS II activity was determined as oxygen evolution by using H_2O as the electron donor and *p*-benzoquinone (*p*-BQ) as the electron acceptor. Measurements were done in 2 mL fresh BG_{11} medium containing 25 mM BTP (pH 7.8) and 1 mM *p*-BQ. PS I activity was measured as the light-dependent oxygen uptake in the presence of 25 mM BTP (pH 7.8), 0.1 mM 2,6-dichlorophenol indophenol (DCPIP), 5 mM ascorbate (reducing DCPIP to $DCPIPH_2$), 0.1 mM methyl viologen (MV), 1 mM NaN_3 (inhibiting respiration), and 10 μM DCMU (inhibiting PS II activity). The whole electron transport activity was determined by monitoring the light-dependent oxygen uptake with H_2O as the electron donor and MV as the electron acceptor in 2 mL fresh BG_{11} medium containing 25 mM BTP (pH 7.8), 1 mM NaN_3, and 0.1 mM MV. The whole electron

transport activity in the absence of water-splitting complex was measured by incorporating diphenylcarbazide (DPC) as an electron donor in the assay mixture, which bypasses the oxygen-evolving complex and donates electrons to the PSII reaction center. DPC was prepared in acetone and added to the assay mixture at a final concentration of 0.5 mM.

Measurement of chlorophyll fluorescence during UV-B exposure and subsequent recovery Samples were cultured at 40 μmol photons m^{-2} s^{-1} PAR to the exponential phase, adjusting OD_{750} values to 0.1, and then were transferred to UV-B exposure (3.15 W m^{-2}) plus 40 μmol photons m^{-2} s^{-1} PAR. After 80 min exposure, UV-B lamps were turned off, and the cells were recovered under three different conditions: (a) 20 μmol photons m^{-2} s^{-1} PAR, (b) dark, and (c) 20 μmol photons m^{-2} s^{-1} PAR and 2.5 μM chloromycetin. During the UV-B exposure and recover periods, the chlorophyll fluorescence of samples was investigated with a Plant Efficiency Analyser (Hansatech Instruments Ltd., UK) as described previously (Jiang and Qiu 2005).

Statistical analyses All experiments were performed in more than three replicates. Data shown in this study were presented in means ± standard deviation (SD). Statistical calculations were performed using Statistica® 6.0 (StatSoft Inc., USA) and Origin® 6.1 (Originlab Corporation, USA). One-way analysis of variance was used to determine the effect of treatments, and Tukey's honestly significant difference (HSD) test was conducted to test the statistical significance of the differences between means of various treatments.

Results

Changes of pigment contents under UV-B exposure Changes of Chl *a*, CAR, PC, and APC contents in the exponential cells of *M. aeruginosa* are shown in Fig. 1. After 8 h UV-B (3.15 W m^{-2}) treatment, all pigment contents except for Chl *a* were reduced significantly (Tukey's HSD, $P<0.05$). However, it was very evident that all pigments increased at the beginning of UV-B exposure. Chl *a* concentration increased significantly during the first 4 h UV-B exposure (Tukey's HSD, $P<0.05$), then decreased, and its content after 8 h UV-B exposure showed no difference with the initial value (Tukey's HSD, $P>0.05$). CAR content increased during the first 2 h and then declined with subsequent UV-B exposure (Tukey's HSD, $P<0.05$). Eight hours UV-B exposure significantly reduced the CAR content of *M. aeruginosa* (Tukey's HSD, $P<0.05$). The
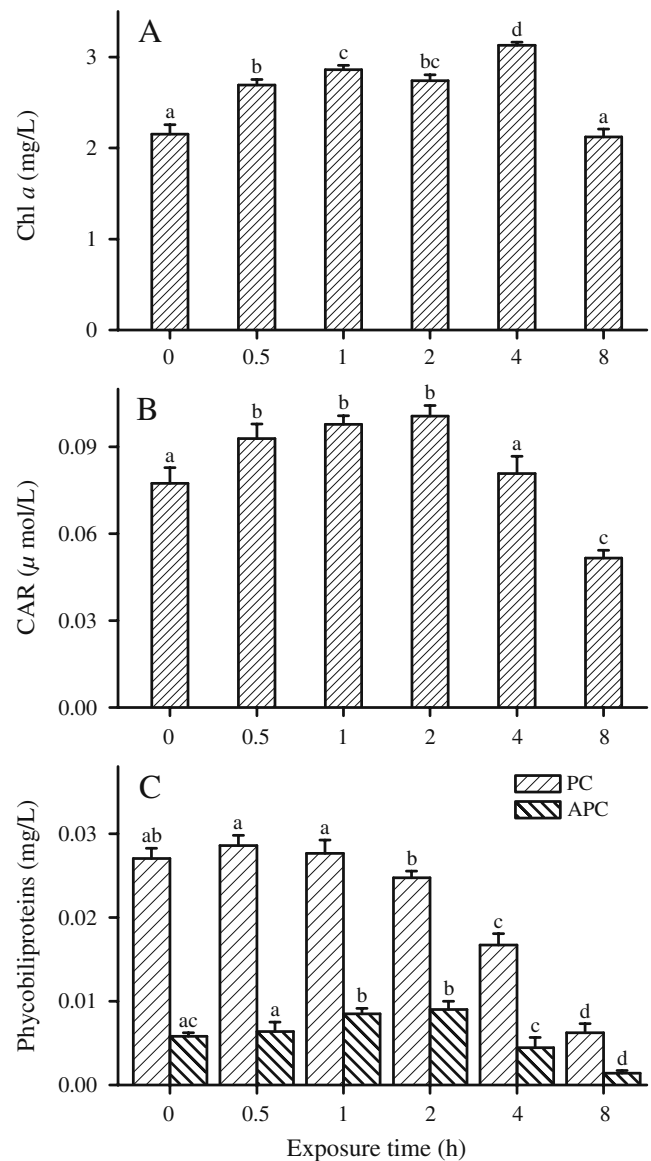

Fig. 1 Pigment changes of *Microcystis aeruginosa* FACHB 854 treated with 8 h 3.15 W m^{-2} UV-B exposure: (**a**) Chl *a*, (**b**) CAR, and (**c**) phycobiliproteins. Means with *different letters* (*a–d*) of the same type of *column* are significantly different (Tukey's HSD, $P<0.05$). Data are means ± SD ($n=3–4$)

APC and PC contents decreased significantly after 8 h UV-B exposure (Tukey's HSD, $P<0.05$), while APC content increased during the former 2 h.

Changes of net photosynthesis and dark respiration caused by UV-B After 80 min UV-B treatment (3.15 W m^{-2}), the net photosynthesis of *M. aeruginosa* was gradually reduced to 0.101 μmol O_2 mg^{-1} Chl *a* min^{-1}, which was only 2.2% of the unexposed cells (Tukey's HSD, $P<0.05$; Fig. 2). In contrast to net photosynthesis, dark respiration did not show significant inhibition by UV-B treatment (Tukey's HSD, $P>0.05$).
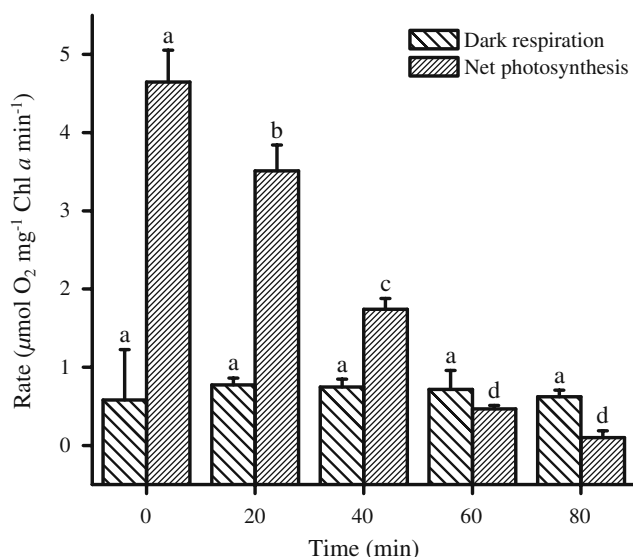
Fig. 2 Net photosynthesis and dark respiration of *Microcystis aeruginosa* FACHB 854 with 80 min 3.15 W m^{-2} UV-B treatment. Means with *different letters* (*a–d*) of the same type of *column* are significantly different (Tukey's HSD, $P<0.05$). Data are means ± SD ($n=3$)

suggested that UV-B might affect the oxygen-evolving complex of PS II.

Chlorophyll fluorescence of M. aeruginosa during UV-B exposure and subsequent recovery Chlorophyll fluorescence was investigated during the UV-B exposure and the subsequent recovery under three different conditions (Fig. 3). After 80 min UV-B exposure (3.15 W m^{-2}), the potential quantum yields of PS II (F_v/F_m) of *M. aeruginosa* reduced as much as 86.2% (Tukey's HSD, $P<0.05$). However, there were evident differences during the subsequent recovery process under three different recovery conditions. After being transferred to 20 μmol photons m^{-2} s^{-1} PAR for 24 h, F_v/F_m gradually recovered to 90.9% of the initial value. However, in the presence of 2.5 μM chloromycetin, F_v/F_m could not recover at 20 μmol photons m^{-2} s^{-1} and even decreased significantly (Tukey's HSD, $P<0.05$). In the dark, F_v/F_m did also not recover (Tukey's HSD, $P>0.05$).

Effects of UV-B on the electron transport activities Table 1 shows the photosynthetic electron transport activities of *M. aeruginosa* with or without UV-B treatment. PS II activity (H$_2$O → *p*-BQ) was significantly inhibited by 20 min UV-B treatment (3.15 W m^{-2}) and was decreased by 63.2% of the control (*t* test, $P<0.05$). The PS I activity (DCPIPH$_2$ → MV) was deceased by 29.8% of the control after 20 min UV-B treatment (*t* test, $P<0.05$), which indicated that PS I was less sensitive than PS II. The electron transport activities of whole chain were measured in the presence or absence of DPC. The activities determined both from H$_2$O to MV and from DPC to MV were significantly inhibited by 20 min UV-B treatment (3.15 W m^{-2}), 27.9% and 13.3% less than the control, respectively (*t* test, $P<0.05$). The difference between them indicated that the activity of H$_2$O → MV was more prone to be inhibited by UV-B exposure than the activity of DPC → MV. This

Discussion

Bloom-forming cyanobacteria usually accumulate at the surface of freshwater in a very huge amount; thus, they will be inevitably influenced by enhanced UV-B caused by stratospheric ozone depletion. Our previous studies have illuminated that long-term moderate UV-B exposure (1.05 W m^{-2}) inhibits the growth of *M. aeruginosa* FACHB 854 and reduces its photosynthetic capability, although the inhibition site of UV-B is still unclear (Jiang and Qiu 2005). In the present study, we have obtained a further conclusion that PS II of *M. aeruginosa* is more sensitive to UV-B irradiance than PS I, and the oxygen-evolving complex of PS II may be an important damage target of UV-B (Table 1). The D$_1$ protein of PS II reaction center is usually considered to be the most susceptible target to UV-B, and the degradation of D$_1$ protein may contribute greatly to PS II downregulation (Campbell et al. 1998; Bouchard et al. 2006). Except for D$_1$ protein, the PS II core antennae of

Table 1 Electron transport activities of *Microcystis aeruginosa* FACHB 854 with 20 min UV-B (3.15 W m^{-2}) or without UV-B exposure

Electron transport activity	Rate (μmol O$_2$ mg^{-1}Chl *a* min^{-1})			
	Control		20 min UV-B	
Whole chain (H$_2$O → MV)	1.834±0.102	100.0a	1.322±0.215	72.1b
Whole chain (DPC → MV)	1.981±0.133	100.0a	1.717±0.117	86.7b
PSI (DCPIPH$_2$ → MV)	13.564±0.570	100.0a	9.519±1.602	70.2b
PSII (H$_2$O → *p*-BQ)	4.504±0.240	100.0a	1.658±0.113	36.8b

Data are means ± SD ($n=3$–4)

Those with different lowercase letters in the same row are significantly different (*t* test, $P<0.05$)
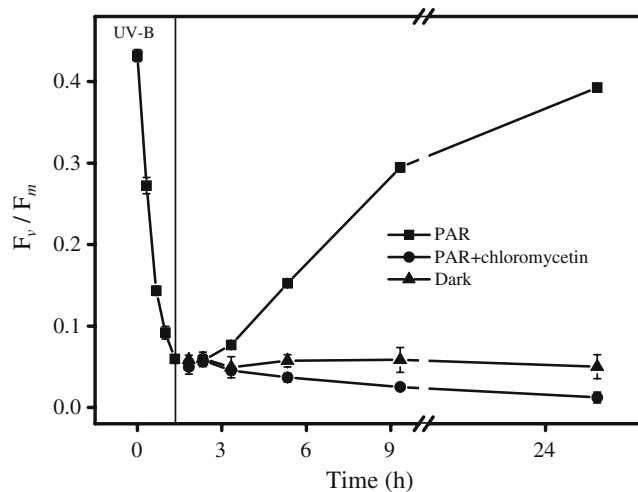
Fig. 3 PS II potential quantum yields (F_v/F_m) of *Microcystis aeruginosa* during UV-B exposure and subsequent recovery. The exponential samples were exposed to 3.15 W m^{-2} UV-B for 80 min, then recovered under 20 μmol photons m^{-2} s^{-1} PAR, 20 μmol photons m^{-2} s^{-1} PAR plus 2.5 μmol L^{-1} chloromycetin, or in the dark at 25°C for 24 h. Data are means ± SD ($n=3$)

chlorophyll proteins CP47 and CP43 in the cyanobacterium *Spirulina platensis* have been proven to be affected by UV-B exposure (Rajapopal et al. 2000). In the present study, the oxygen-evolving complex of PS II in *M. aeruginosa* was found to be another inhibition site of UV-B, which could be concluded from the difference between the whole electron transport activities: the activity from H$_2$O to MV was 27.9% inhibited by UV-B, while the activity from DPC to MV was 13.3% inhibited. The oxygen-evolving complex, also known as the water-splitting complex, is a water-oxidizing enzyme involved in the photooxidation of water during the light reaction of photosynthesis. A 33-kDa protein of water-splitting complex is sensitive to UV-B (Prabha and Kulandaivelu 2002); thus, its degradation contributes importantly to the decline of electron transport rate. By transient absorption measurements and vibrational spectroscopic techniques, Lukins et al. (2005) had shown that the predominant sites of UV-B damage in PS II were at the oxygen-evolving center (OEC) itself, as well as at specific locations near the OEC-binding sites. In higher plant such as spinach, UV-B sensitivity has been reported to be dependent on the oxidation state of the water-splitting complex of PS II (Szilárd et al. 2007). In conclusion, although the UV-B damage to photosystem is complicated, PS II in *M. aeruginosa* is proven to be more sensitive to UV-B than PS I from our present study. Moreover, except for the D$_1$ protein and core antennae of chlorophyll proteins, the oxygen-evolving complex probably contributes mostly to the UV-B sensitivity of PS II.

Cyanobacteria have many strategies to cope with UV-B since they have been exposed early in their evolution to

UV-B fluxes much higher than the relatively low present-day UV-B levels (Whitton and Potts 2000). For cyanobacteria, almost all of the solar energy is absorbed by their light-harvesting pigment–protein complexes called phycobilisomes and the chlorophyll–protein complexes. In the present study, it was interesting to find that the content of phycobiliproteins, Chl *a*, and CAR of *M. aeruginosa* FACHB 854 increased during the earlier UV-B exposure. Phycobilisomes strongly absorb in the UV region due to their protein nature. Increased phycobilisomes on the thylakoid membranes, which form several layers around the cell, make it possible for them to serve as a screen against further damage for the reaction centers but also for DNA (Lao and Glazer 1996). *Microcystis aeruginosa* has been shown to be able to regulate their phycobilisomes content according to light intensity and light quality when cells are exposed to high light stress (Raps et al. 1985). Aráoz and Häder (1997) have found that UV-B could induce both degradation and synthesis of phycobilisomes in *Nostoc* sp. with the balance of recovery and damage. CAR is regarded as protective pigments since they are effective quenchers of free radicals and active oxygen species (Götz et al. 1999). Our previous work had found that prolonged moderate UV-B resulted in the increase of CAR content in *M. aeruginosa* FACHB 854 (Jiang and Qiu 2005). In the present study, the higher UV-B dose stimulated the increase of pigments during the early stage of exposure. However, with prolonged exposition, higher dose UV-B would induce serious cells damage, such as reactive oxygen species and even DNA breakage (He and Häder 2002), which would result in the degradation of these pigments. Therefore, the UV-B damage is likely not to be an immediate process, but a dynamic balance between damage and adaptation.

The damage of photosynthetic apparatus due to UV-B could be recovered quickly when damaged cells were transferred to PAR. The restoration of photosynthesis, especially the synthesis of D$_1$ protein, has been proved to be light dependent, which is probably due to a light-regulated expression of the gene *psb*A at the transcriptional and translational level (Kettunen et al. 1997; Sicora et al. 2008). Except for PAR, de novo protein synthesis was required for the recovery process of UV-B damaged photosystem. Some major functional proteins such as D$_1$/D$_2$ proteins of PS II reaction center and some important enzymes such as Rubisco, which are known to be sensitive to UV-B (Rajapopal et al. 2000; Bouchard et al. 2006), must turn over rapidly and are replaced by newly synthesized polypeptides.

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