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博 士 学 位 论 文

硅藻对海洋酸化及 UV 辐射的生理学响应

Physiological Responses of Diatoms to Ocean Acidification and Ultraviolet Radiation

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摘要

大气 CO_2 浓度升高引起的海洋酸化，经大量研究表明，会减少海洋钙化植物与动物的钙化量；然而，非钙化浮游植物如何响应海洋酸化的问题，尚未见报道。海水 pCO_2 的升高尽管会增加浮游植物光合作用的底物浓度，但酸化引起的海水化学变化会对浮游植物产生胁迫。与此同时，阳光 UV 辐射也会对浮游植物产生胁迫。酸化与 UV 对浮游植物的影响，是叠加、拮抗还是无耦合效应？这是迄今尚未得到充分认识的科学问题。硅藻在海洋 CO_2 生物泵中起着重要的作用，其生理学过程如何响应酸化及 UV 的问题，亟需探讨。本文通过 CO_2 加富调控海水碳酸盐系统，模拟本世纪末海洋酸化状态（pCO_2: 800-1000 ppmv, pH: 7.80-7.90），对两种硅藻，三角褐指藻（*Phaeodactylum tricornutum*）和假微型海链藻（*Thalassiosira pseudonana*），进行了研究，并结合 UV 辐射及航次的实验结果，综合分析了硅藻及浮游植物群落对酸化及 UV 的生理学响应。主要结果如下：

三角褐指藻，适应酸化后（>20 代），生长和光合速率分别提高了 5.2 和 10.8%；同时，呼吸速率增加了 34.4%，且在强光下表现出较高的光抑制。尽管 pCO_2 的升高显著提高了该藻的光化学效率，降低了非光化学淬灭（NPQ），但酸化会导致 NPQ 升高，表明酸化对细胞造成胁迫。虽然 pCO_2 升高对假微型海链藻的光化学效率有一定的促进作用，然而适应酸化的细胞生长速率却下降。适应酸化的两种硅藻细胞，光合作用对 CO_2 的亲和力明显下降，HCO_3^- 或 CO_2 的主动运输能力降低，表明其无机碳浓缩机制（CCM）被明显下调。CCM 的下调节省了 CCM 运作的能耗，然而细胞并没有下调其天线色素的含量，而是减少了 PSII 光能捕捉复合体的有效截面积（σPSII）。

酸化虽然导致三角褐指藻更易受高光胁迫，却能够缓解 UV 辐射对其产生的负面效应。酸化条件下，UV 对 PSII 光化学效率的抑制作用较低。σPSII 在适应酸化的细胞中变小；而较小的 σPSII 会下调 PSII 接收 UV 辐射的量，从而减少了 UV 导致的损伤。进一步的实验发现，适应酸化的细胞修复损伤蛋白速率较快，且弱光下 PSII 关联蛋白的合成也较快。

硅藻类及其它浮游植物的 CCMs 和光合作用，依赖于无机碳的吸收及转化，为此依赖于胞内外的碳酸酐酶。室内与航次实验均显示，碳酸酐酶抑制剂（ethoxyzolamide）对浮游植物群落的光合固碳量有明显的抑制效应，在南海外海水

域抑制率达 23%，且与 UV-B 有着明显的协同效应，表明 CCMs 对缓和 UV 伤害方面起到了一定的作用，也暗示酸化会对南海表层浮游植物 CCMs 及固碳量产生影响。

总之，海洋酸化提高了两种硅藻的光合效率，但对两种硅藻的生长产生了不同的影响。同时，酸化促进了呼吸速率，下调了其 CCM，导致光抑制率升高。UV 与酸化的耦合效应与光强的关系决定 UV 的正面与负面效应。浮游植物不同功能类群如何响应海洋酸化，以及真光层内光合固碳量与酸化及其它环境因子的复合关系，还有待于进一步探讨。

缩略词：CCM, UV 辐射，光合固碳，硅藻，海洋酸化

Abstract

The CO_2-driven ocean acidification (OA) has been shown to reduce the calcification of marine calcifiers. However, little knowledge has been documented on non-calcifying organisms. Though elevated pCO_2 in seawater provides more substrate for photosynthetic carbon fixation, changes of the seawater carbonate system induced by OA could stress the cells. On the other hand, solar UV radiation would affect phytoplankton in different ways. If OA and UV would act synergistically, antagonistically or neutrally is an important question to be investigated. Diatoms play a fundamental role in marine biological CO_2 pump, thus their physiological responses to OA and UV need to be explored. In this study, we used pH/pCO_2 perturbation technique to cultivate two diatom species (*Phaeodactylum tricornutum* and *Thalassiosira pseudonana*) and natural phytoplankton assemblages under two different pCO_2 levels, representing the atmospheric pCO_2 of present and the year around 2100 (pCO_2: 800-1000 ppmv, pH: 7.80-7.90), and in combination with UV technique, to evaluate the physiological responses of the diatoms and phytoplankton assemblages to OA, and revealed the combined effects of OA and UV. The main results are as follows:

After acclimation to high CO_2/low pH (HC) for 20 generations or more, the growth rate and photosynthetic carbon fixation of *P. tricornutum* were respectively enhanced by 5.2 and 10.8%, meanwhile, the dark respiration was enhanced by 34.4%, and the HC grown cells were more sensitive to high light. Though short-term manipulation of carbonate system indicated that the elevated CO_2 increased effective quantum yield and decreased non-photochemical quenching (NPQ), the increased NPQ of HC grown cells reflected that increase in acidity is a stressor. The elevated CO_2 increased the effective quantum yield of *T. pseudonana*, but decreased its growth rate. Moreover, OA affects the inorganic carbon acquisition mechanisms of both diatoms, down-regulated their carbon concentrating mechanisms (CCMs) and the ability to actively take up HCO_3^- or CO_2. The down-regulation of CCM led to down-regulated functional absorption cross-section of PSII (σPSII), without altering its antenna pigment content.

Though OA increased the sensitive of *P. tricornutum* to high PAR, it alleviated the UV-induced inhibition on PSII. Meanwhile, the functional cross section of PSII (σPSII) of HC grown cells was smaller in HC grown cells,, which could be responsible for the lower UV-related inhibition since decreased σPSII leads to less UV exposures. Additional experiments showed that the UV-induced protein damages were repaired faster, and the synthesis of PSII proteins appeared faster in the HC-grown cells.

The photosynthetic carbon fixation and CCMs of diatoms and phytoplankton assemblages depend on the acquisition and conversion of inorganic carbon, thus depend on the activity of carbonic anhydrase. The membrane permeable inhibitor of carbonic anhydrase (ethoxyzolamide, EZ) inhibited photosynthetic carbon fixation significantly, up to 23% in the open ocean of South China Sea (SCS). Moreover, EZ synergistically increased UV-B inhibition on photosynthesis, indicating that CCMs could act in remediating UV-induced harms. The result implies that OA could affect the photosynthetic carbon fixation of phytoplankton assemblages and their response to UV in the SCS.

In conclusion, OA increased photosynthetic performance, but differentially affected the growth of the two diatoms. It down-regulated CCM and increased dark respiration rate and the sensitivity to high light. The interactive effects of OA and UV depend on the levels of PAR as well as UV. Responses of different phytoplankton functional groups to OA, and the combined effects of OA with other environmental factors on photosynthetic carbon fixation in the euphotic zone, need to be further investigated.

Keywords: CCM, diatom, ocean acidification, photosynthesis, UVR