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Biotransformation of mycosporine like amino acids (MAAs) in the toxic dinoflagellate *Alexandrium tamarense*

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Abstract

Changes in mycosporine-like amino acids (MAAs) induced by the increase of photosynthetically active radiation (PAR) were studied in the toxic dinoflagellate *Alexandrium tamarense*. Cultures of *A. tamarense* were maintained at exponential growth under low (25 μmol quanta $m^{-2}\ s^{-1}$) PAR irradiance. The cultures were nutrient enriched and one day later exposed to higher irradiance (150 μmol quanta $m^{-2}\ s^{-1}$). The content of MAAs was determined by means of high performance liquid chromatography (HPLC). Eleven MAAs, including some partially characterized compounds, were identified. The MAAs synthesis induction can be described as a two-stage process. The first one involves the net synthesis of the MAAs bi-substituted by amino acids. In the second stage these compounds were transformed into other secondary MAAs. The two most prominent changes were observed in the concentration of porphyra-334 and palythene. The cellular concentration of porphyra-334 increased during the first 2 h of exposure to higher irradiance and then decreased rapidly. In contrast, the cellular concentration of palythene showed a continuous accumulation since the beginning of the exposure. In *A. tamarense* the main route of MAAs transformation has porphyra-334 as a precursor of a sequential conversion resulting in the accumulation of palythene.

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1. Introduction

A marked decrease in the level of the stratospheric ozone, with the consequent increase in the ultraviolet radiation flow on the terrestrial surface, has been observed throughout the last years [1]. UV radiation has caused a broad spectrum of genetic and cytotoxic effects in aquatic organisms. However, these responses are partly offset by different protection strategies such as avoidance, screening, photochemical quenching and repair [2]. As a consequence, the synthesis and accumulation of UV-absorbing compounds in living organisms have been object of intensive research, especially the MAAs. These compounds, which are widely distributed among freshwater and marine organisms [3–6], are composed of a cyclohexenone or cyclohexenimine chromophore conjugated with a substituent nitrogen of an amino acid, amino alcohol, or amino group. The MAAs have a maximum of absorption between 310 and 360 nm (UVB and UVA), covering the spectral regions of major biological damage. About 20 MAAs have been characterized until the present, but this number seems to grow every year as a consequence of the increase in the number of studied organisms and the development of more efficient high-performance liquid chromatography (HPLC) separation techniques [7–10].

Only bacteria and algae can synthesize MAAs; other marine organisms acquire and metabolize these compounds by trophic transference and by symbiotic or bacterial association [3,5]. Many phytoplankton organisms from different regions and taxonomic groups have been found to contain UV-absorbing compounds [7]. For

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natural phytoplankton samples, the highest concentrations of UV-absorbing compounds were found associated with surface blooms of dinoflagellates [7,11,12].

In cultures of three species of dinoflagellates (*Alexandrium tamarense*, *Alexandrium catenella* and *Alexandrium minutum*) Carreto et al. [9] observed that palythene is the predominant MAAs in high light intensity conditions, followed by palythine, mycosporine glycine, porphyra-334 and palythenic acid, being palythinol and usujirene minor components. Nevertheless, several studies in culture have demonstrated that there are large variations among species and even between strains of the same species [7]. Also, in *A. tamarense* the MAAs abundance and composition depends on the intensity and spectral composition of the incident radiation [13]. Although, some organisms need of UVA-radiation and particularly of UV-B radiation for the synthesis of MAAs [14], other species like dinoflagellates have high levels of MAAs without being exposed to UV radiation [7,13].

According to Favre-Bonvin et al. [15], the synthesis of mycosporines would have its origin in the route of Shikimate. These authors showed that the precursor of the six-carbon ring common to all mycosporines in fungi was 3-dehydroquinato (3-DHQ). The synthesis of fungal mycosporines would presumably proceed from 3-DHQ through gadusol or deoxygadusol, being these last two compounds possibly the precursors of mycosporine glycine. The blockage of the MAAs synthesis in the coral *Stylophora pistillata* produced by the addition of a Shikimate route inhibitor (glyphosate = *N*-phosphonomethyl-glycine) provided the first direct evidence of the MAAs synthesis starting from this route in marine organisms [14]. Recently, Portwich and Garcia-Pichel [16] detected the specific incorporation of ^{14}C-glycine and ^{14}C-serine into the corresponding side chains of mycosporine glycine and shinorine using radiolabelled amino acids, demonstrating that these free amino acids are their direct precursors. In another experiment, these authors demonstrated that mycosporine glycine is the direct metabolic precursor of the MAA bisubstituted shinorine. However, some details of the biosynthesis and specially of the biotransformations of different MAAs in marine algae and phototropic symbiotic organisms are still unknown [5] and remain a topic of great discussion. Nevertheless, it has been assumed that the high diversity of MAAs present in marine organism is derived from the transformation of mycosporine glycine, porphyra-334, shinorine and other MAA bisubstituted by amino acids [9,10,17,18]. According to Shick's proposition [17], these compounds (mycosporine glycine, porphyra-334 and shinorine) will be referred to as primary MAAs, and the other MAAs, probably derived from these primary MAAs, will be referred to as secondary MAAs.

In cultures of *Alexandrium excavatum*, transferred from low to high intensity conditions, Carreto et al. [13] observed that the synthesis of MAAs is accompanied by a sequential change in the UV absorption spectrum, which is compatible with interconversions among different MAAs. The authors suggested that porphyra-334 could be the precursor of palythenic acid. In a second stage, this compound could get transformed to usujirene and palythene [13]. In a later work with *A. catenella* cultures exposed at photoinhibitory irradiation levels (PAR, UVA and UVR), Carreto et al. [9] observed that the increase in the amount of palythenic acid, usujirene and palythene is accompanied by a concomitant decrease of porphyra-334 abundance. As the photochemical stability of porphyra-334 is very high [19], Carreto et al. [9] speculated that the changes observed would be a consequence of metabolic changes induced by high light conditions.

These results and the capacity of *A. tamarense* to synthesize MAAs in a scale of hours indicate the feasibility of using this organism for the study of MAAs biotransformation. In order to increase our knowledge on biotransformation pathways of MAAs, this work examines the changes in MAAs composition induced by the increase of light (PAR) conditions on the toxic bloom forming dinoflagellate *A. tamarense.*

2. Materials and methods

2.1. Strain and growth conditions

A strain of *A. tamarense* (MDQ1096) isolated from the Mar del Plata coast (Argentina) was used for the experiment. A culture was maintained in a chamber with a constant temperature of 16 °C, using L1 medium without silicon addition [20]. Aged and filtered (Sartorius Type SM 50, 0.45 μm) seawater from a fixed station located to 38°28′S–57°47W was used as base medium. The culture was maintained 20 days in exponential growth in 5 l glass bottles under irradiance of 40 μmol quanta $m^{-2}\,s^{-1}$ PAR on a 14:10 light:dark cycle, provided by an Osram Power Star lamp (HQI-TS 150W/NDL) covered with a cut-off filter for UV radiation (<400 nm). The irradiance (PAR) was measured with a QSL-100 quantum sensor (Biospherical Instruments). Concluded this period, the culture was photo-acclimated during 5 days to 25 μmol quanta $m^{-2}\,s^{-1}$ PAR 14:10 Light:dark cycles. One day before the end of this adaptation period, 2 ml of the nutrient solution of the L1 medium were added [21]. On the following day, during the first 4 h of the light photoperiod, the culture was transferred to 150 μmol quanta $m^{-2}\,s^{-1}$ PAR. A sample for MAAs analysis was taken from the culture at the beginning and after each hour during the first 6 h of exposition to high light irradiance and then at 8 and 10 h during the experiment.

2.2. Cell count

Samples were taken for growth control and before the experiment. The number of cells were determined using an automatic particle counter, Coulter Coulter (model PCA I).

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