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Irradiance-mediated dimethylsulphoniopropionate (DMSP) responses of red coralline algae

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ABSTRACT

Red coralline algae produce significant quantities of dimethylsulphoniopropionate (DMSP), whose breakdown products include the important climate gas dimethylsulphide (DMS) but little is known about how environmental factors influence this DMS(P) production. The effect of photosynthetically active radiation (PAR) on intracellular DMS(P) concentrations in the red coralline algae *Lithothamnion glaciale* was investigated using short (30 min) and longer-term (up to 507 h) acclimatory responses and control and high-PAR light regimes. Longer-term acclimatory intracellular DMS(P) concentrations were significantly reduced following exposure to high-PAR (220–250 μmol m^{-2} s^{-1}). No short-term acclimatory effects were observed. We conclude that while DMS(P) content in *L. glaciale* does respond to changes in irradiance, the effect takes place over hours – days rather than minutes, suggesting a continued turnover of DMS(P) to combat oxidative stress induced by prolonged high-PAR exposure. Immediate short-term acclimatory responses do not appear to occur.

1. Introduction

Free-living, red coralline algae (Rhodophyta: Corallinales), commonly known as maerl or rhodoliths, are long-lived and extremely slow growing (0.1–2 mm yr^{-1}) (Blake and Maggs, 2003; Bosence and Wilson, 2003), factors that may improve their resistance to environmental perturbations. Red coralline algae form extensive, globally distributed beds in coastal waters composed of layers of living and dead thalli overlaying carbonate rich sediments (Steller and Foster, 1995; Foster, 2001; BIOMAERL et al., 2003). Red coralline algae are usually found subtidally in the photic zone, due to their intolerance to desiccation (Wilson et al., 2004), and are depth limited by the level of light penetration (Foster, 2001).

Dimethylsulphoniopropionate (DMSP) is a methionine-derived sulphonium compound that was first isolated from the red macroalga *Polysiphonia fastigiata* (Challenger and Simpson, 1948). DMSP may function as a compatible solute in osmotic regulation (Karsten et al., 1992), a cryoprotectant (Karsten et al., 1992), an overflow mechanism for dissipating excess energy and reduced compounds (Stefels, 2000), as an antioxidant (Sunda et al., 2002) and as an activated defence against herbivory (Van Alstyne et al., 2001; Wolfe et al., 2002). Phytoplankton are thought to be the dominant global producers of DMSP due to their large range and extensive blooms, but many species of macroalgae also contain intracellular DMSP + dimethylsulphide (DMS) (DMS(P)) concentrations in the μM – mM range (e.g. Karsten et al., 1994; Van Alstyne, 2009), including red coralline algae (Kamenos et al., 2008b). Tropical coral reefs (Broadbent et al., 2002), coral mucus and mucus ropes (Broadbent and Jones, 2004) are often considered to be the most important benthic producers of DMS(P). However, DMS(P) concentrations in red coralline algae are reported to be comparable to concentrations observed in Chlorophyta and coral reefs and may make red coralline algae one of the largest macroalgal DMS(P) producers (Kamenos et al., 2008b).

The intracellular DMS(P) content of marine algae is affected by a variety of environmental factors including salinity, temperature, nutrient availability, cell age and light intensity (Malin and Kirst, 1997; Stefels, 2000; Stefels et al., 2007; Van Alstyne and Puglisi, 2007). Increased irradiance has been shown to increase intracellular DMSP content in polar and temperate green macroalgae (Karsten et al., 1990, 1992; Lyons et al., 2010) and phytoplankton (e.g. *Phaeocystis* and *Emiliania huxleyi*, Matrai et al., 1995; Slezak and Herndl, 2003).

DMSP/DMS research has focussed on their roles in the biogeochemical sulphur cycle and potential impacts on climate. DMS flux from the ocean to the atmosphere accounts for one-quarter of

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global sulphur emissions (Liss et al., 1997). Atmospheric oxidation of DMS to sulphate aerosol particles may promote the formation of cloud condensation nuclei, influencing climate through increased cloud albedo (Andreae, 1990; Liss et al., 1997). An algal-aerosol-climate feedback loop has been proposed (Charlson et al., 1987), although this depends on a direct link between algal DMSP production and the formation between DMS-derived CCN. Oceanic DMS emissions depend on sea surface concentrations and the gas transfer velocity (Archer et al., 2009), while reactions with halogens and the presence of sea-salt particles and other aerosols in the atmosphere will affect the production of DMS-derived CCN (O'Dowd et al., 2002; Von Glasow and Crutzen, 2004; Leck and Bigg, 2005).

The aim of this investigation was to determine the effect of irradiance on intracellular DMS(P) content in the red coralline alga *Lithothamnion glaciale* in the context of short- and longer-term acclimatory responses to environmental variability. This took into account an immediate response to change in irradiance and a longer-term acclimatory response, which may be important given the slow growth rate of *L. glaciale* ($\sim$200 μm yr^{-1}, Kamenos et al., 2008a), and slow production of DMSP by algae (e.g. Karsten et al., 1992; Lyons et al., 2010).

2. Materials and methods

2.1. Sample collection and handling

Lithothamnion glaciale thalli were collected randomly from Loch Sween (56°02′N 05°36′W), Scotland, UK in November 2010. Thalli were collected at −6 m chart datum using SCUBA. Samples were transported to the University of Glasgow in seawater and held in 112 L recirculating seawater tanks (flow rate of 216 L h^{-1}) under ambient field conditions (10 ± 1 °C, 7:17 h light:dark regime, 70 μmol m^{-2} s^{-1} PAR, pH 8.1) for 4 weeks until the experiments were conducted.

2.2. Photosynthetically active radiation (PAR) measurements

Light intensity in experimental tanks and in the field was measured using an Apogee QSO-E underwater electric calibrated sensor and Gemini voltage data logger. Field PAR data was collected from Loch Sween over four days to determine the ambient range of PAR experienced by *Lithothamnion glaciale* at that time of year (62 ± 30 μmol m^{-2} s^{-1}, mean ± SD, n = 928, excludes night-time measurements). These data informed the experimental control level. Experimental PAR was regulated using 24 W T5 white fluorescent tubes, high intensity (14 000 K) 24 W T5 white fluorescent tubes and an Aquabeam 1000 HD LED light tile. The light produced by the Aquabeam tile decreased in intensity away from the center of the tank therefore thalli in this treatment were exposed to a light intensity range of 220–250 μmol m^{-2} s^{-1} within the experimental area (225 cm^2).

2.3. Short-term acclimatory responses to brief PAR exposure

Thalli were acclimated under control conditions for 48 h after transfer from the holding tank to the experimental tanks before the experiment was conducted. To determine the DMS(P)-manifested short-term acclimatory responses to PAR intensity, DMS(P) was quantified before and after 30 min exposure to four PAR treatments: 0, 70 (control intensity), 140 and 220–250 μmol m^{-2} s^{-1}. Each PAR treatment was replicated in each of the three experimental tanks (thalli n = 10 per tank, n = 30 per treatment).

2.4. Longer-term acclimatory responses to extended PAR exposure

A time-series experiment was conducted to investigate the effect of PAR on DMS(P)-manifested longer-term acclimation responses in *Lithothamnion glaciale* over 98 h. Thalli were acclimated under control conditions for 48 h after transfer from the holding tank to the experimental tanks before the experiment was conducted. Experiments were conducted at 70 μmol m^{-2} s^{-1} (control treatment) and 220–250 μmol m^{-2} s^{-1} (high-PAR treatment) in separate tanks (n = 2) with thalli (n = 10) positioned to ensure an even distribution of PAR (the short-term acclimatory response experiments had shown no tank-effect on DMS(P) concentrations). Thalli were sampled in the dark (0 h) and after 0.5, 1, 1.5, 6, 50 and 98 h of PAR exposure under a 7:17 h light:dark regime. All replicate thalli were sampled at each sampling event, thus time was considered as a repeated measure.

To examine the effect of increased PAR on DMS(P) concentration over an even longer period, additional thalli (n = 10) were exposed to PAR treatments of 70 and 220–250 μmol m^{-2} s^{-1} (7:17 h, light:dark regime) and sampled once after 3 weeks (507 h).

2.5. Effect of burial on DMS(P) content

To investigate the effect of burial on DMS(P) content, thalli (n = 10) were half buried in carbonate sand sediment and exposed to 70 μmol m^{-2} s^{-1} PAR. Thalli were acclimated under control conditions for 48 h after transfer from the holding tank to the experimental tanks before the experiment was run. A control treatment of unburied thalli was run simultaneously in a separate tank and exposed to 70 μmol m^{-2} s^{-1} PAR (the short-term acclimatory response experiments had shown no tank-effect on DMS(P) concentrations). Thalli were sampled for DMS(P) after 3 weeks.

2.6. DMS(P) quantification

For DMS(P) determination, $\sim$0.5 g of branch tips were sampled from each *Lithothamnion glaciale* thallus. Thalli tips were patted dry, cleaned to remove any attached sediment or debris and weighed. Thalli tips were quickly transferred to 14 ml vials containing 2000 μl of 10 M NaOH. NaOH hydrolysis results in a 1:1 conversion of algal DMSP to DMS, which diffuses into the vial headspace. Vials were immediately sealed using PharmaFix septa. Samples were incubated at room temperature in the dark for at least 48 h before analysis. This method does not differentiate between intracellular DMSP and DMS thus all measurements refer to intracellular DMS(P) concentration. DMS(P) was quantified using a Shimadzu 2014 gas chromatograph equipped with a flame photometric detector and capillary column (5% diphenyl-95% dimethyl polysiloxane; length 25 m; inner diameter 0.25 mm; film thickness 0.25 μm). The temperature of the injector, oven and detector were 45 °C, 45 °C, and 200 °C, respectively. DMS retention time was $\sim$ 1.5 min. Samples were analysed using direct injection of 100 μl from the vial headspace. Concentrations were calibrated against a DMSP standard (Research Plus Inc.) and normalised for algal biomass (5% of total mass for *L. glaciale*, as determined by Kamenos et al. (2008b)). The standard and sample detection limit was 960 ng of sulphur per headspace injection (sample peaks were $\sim$5× the magnitude of the detection limit) and precision was within 3%.

2.7. Statistical analysis

All statistical analyses were performed using R v.2.12.1. Data in all experiments were log transformed to homogenise variance and meet assumptions of parametric testing. General linear models (GLMs) were used to analyse data from short-term acclimatory and