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Seasonal and spatial variability of dimethylsulfoniopropionate (DMSP) in the Mediterranean seagrass *Posidonia oceanica*

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ABSTRACT

We investigated for the first time the occurrence of dimethylsulfoniopropionate (DMSP) in the leaves of *Posidonia oceanica* and we report its variability during 4 sampling periods covering the seasonal cycle (February, June, August and November) and along a gradient from 10 m to 30 m depth. The *P. oceanica* leaf DMSP content expressed per mass of dry weight (dw) ranged from 0.1 to 33.9 $\mu mol\ g_{dw}^{-1}$ and averaged 5.0 $\mu mol\ g_{dw}^{-1}$. It was higher than the DMSP content of roots and rhizomes that averaged ~0.5 $\mu mol\ g_{dw}^{-1}$. The leaf DMSP content showed seasonal variations, being highest in summer when primary production and biomass of *P. oceanica* were also highest. In August, the leaf DMSP content showed variations with depth, increasing from 30 m to 10 m depth. In summer, the leaf DMSP content was highest in the youngest sections of leaves (closest to base) than in the older ones (closest to apex). The seasonal and depth distribution suggest that the DMSP leaf content is positively related to irradiance, hence, we hypothesize that DMSP in *P. oceanica* plays a role as an antioxidant against reactive oxygen species, although we cannot unambiguously exclude other potential roles such as grazer deterrent. The average leaf DMSP content of *P. oceanica* is modest compared to high DMSP producing macroalgae and phytoplankton. Yet, the integrated DMSP stock associated to the meadows of *P. oceanica* is very large due to its enormous biomass, and at the community level it is 2 orders of magnitude higher than the potential integrated DMSP stock related to phytoplankton in the same area.

1. Introduction

Dimethylsulfoniopropionate (DMSP) is produced by a variety of marine organisms including phytoplankton (Keller et al., 1989; Stefels et al., 2007), macroalgae and invertebrates (Van Alstyne and Puglisi 2007). DMSP has also been reported in numerous higher plants (Paquet et al., 1995), but usually in low concentrations. Out of the 177 species of terrestrial angiosperms studied by Paquet et al. (1995), only seven had a DMSP content per mass of dry weight (dw) between 0.1 and 1 $\mu mol\ g_{dw}^{-1}$, all the others being characterized by undetectable DMSP levels. Only a few species of higher plants have a high DMSP content, either strictly terrestrial plants such as sugar cane (*Saccharum*) and *Wollastonia biflora* and intertidal plants such as some species of *Spartina* (Otte et al., 2004; Dacey et al., 1987). The only study so far that has investigated the occurrence of DMSP in seagrasses was carried out by Dacey et al. (1994) who attributed the occurrence of DMSP in samples from three species (*Halodule wrightii*, *Syringodium filiforme*, *Thalassia testudinum*) to epiphyte algae and not to the actual tissue of the seagrasses. Jean et al. (2006) hypothesized that the high dissolved DMSP (DMSPd) concentrations in coastal bays along the French Mediterranean coastline could be related to the presence of the marine phanerogam *Posidonia oceanica* meadows, although the DMSP content of *P. oceanica* tissues was not measured by these authors.

The content of DMSP in marine autotrophs is highly variable (Table 1). For phytoplankton, the DMSP content is highest in Dinoflagellates, Chrysophytes and Haptophytes (>100 $\mu mol\ g_{dw}^{-1}$), extremely low in Prochlorophytes and Cyanophytes (<0.1 $\mu mol\ g_{dw}^{-1}$), and intermediary in Prasinophytes and diatoms. In most red, brown and green algae, the DMSP content is low or below detection limit (d.l.), with the exception of two species of red algae, and the group of *Ulvales* (Table 1). The DMSP content of three *Spartina* species, a halophyte abundant in salt marshes, is high and falls within the range for different phytoplankton groups, although numerous other salt-marsh plants (including several other species of *Spartina*) have undetectable levels of DMSP.

Several physiological and ecological roles have been attributed to DMSP (Table 2). Some are common to phytoplankton, macroal-

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Table 1
Dimethylsulfoniopropionate (DMSP) content per dry wet (dw) ($\mu mol\ g_{dw}^{-1}$) in major phytoplanktonic groups based on Stefels et al. (2007), macroalgae based on Van Alstyne and Puglisi (2007), intertidal marsh plants based on Otte et al. (2004) and Dacey et al. (1987). The values for phytoplankton initially given in molS:molC were converted into dry weight using a carbon to total dry weight of 50% (Reynolds 2006). The values for *Spartina* given initially in wet weight were converted to dry weight using a water content of 73% (Otte et al., 2004). d.l. = Detection limit.

		DMSP ($\mu mol\ g_{dw}^{-1}$)
Phytoplankton		
Diatoms		14 ± 21
Chrysophytes		317 ± 250
Dinoflagellates		367 ± 533
Prasinophytes		83 ± 117
Haptophytes		183 ± 117
Prochlorophytes/Cyanophytes		0.03 ± 0.07
Macroalgae		
Red algae		
	Polysiphonia sp. and *Halopytis sp.*	*23 ± 122*
	Other red algae	<2
Brown algae		<3
Green algae		
	Ulvales	145 ± 150
	Caulerpales	<d.l.
	Dasycladales	<d.l.
	Siphonocladales	<d.l.
Higher plants		
Intertidal marsh plants		
	Spartina anglica	15-185
	Spartina alterniflora	*33-259*
	Spartina foliosa	*26-30*
	Spartina patents	*<d.l.*
	Spartina cynosuroides	<d.l.
	Distichlis spicata	<d.l.
	Juncus sp	*<d.l.*
	Salicornia europeae	<d.l.
	Phragmites communis	*<d.l.*
	Rhizophora mangle	*<d.l.*

Table 2
Functions of dimethylsulfoniopropionate (DMSP) reported in phytoplankton (based on Stefels et al., 2007), macroalgae (based on Van Alstyne and Puglisi 2007) and *Spartina* (based on Otte et al., 2004).
N/A = Not applicable.
N/T = Not tested.

	Phytoplankton	Macroalgae	*Spartina*
Osmolyte and osmoregulation	x	x	x
Herbivore deterrent	x	x	x
Cryoproctectant	x	x	x
Antioxidant function against reactive oxygen species (ROS)	x	x	X
Carbon (C) and nitrogen (N) overflow mechanism	x	*N/T*	X
Antibiotic (virus and bacteria)	x	*N/T*	*N/T*
Antifouling against epiphytes	*N/A*	*N/T*	X
Sulfide (H_2S) detoxification	*N/A*	*N/T*	X

x = Cited in literature.
N/A = Not applicable.
N/T = Not tested.

gae and *Spartina* such as osmolyte, osmoregulator, herbivore deterrent, cryoprotectant and antioxidant against reactive oxygen species (ROS). Other possible roles could be common to phytoplankton, macroalgae and *Spartina* but have not been hypothesized nor tested in all, such as overflow mechanism for carbon (C) or antibiotic against viruses or bacteria. Some are not applicable to phytoplankton such as antifouling against epiphytes and H_2S detoxification.

Here, we investigate, for the first time, the spatial and seasonal variability of DMSP in the marine phanerogam *P. oceanica*. This seagrass is endemic of the Mediterranean Sea, present from near-surface to ~40 m depth, characterized by high gross primary production (GPP) (e.g. Champenois and Borges 2012) and by below-ground and above-ground biomass that exceeds those of other seagrasses (Green and Short 2003). The aims of this study are to determine if DMSP occurs in *P. oceanica* tissues and if there are variations of DMSP content within the plant (among leaves and along the length of leaves), among individual shoots, with depth and with season. Based on these variations we discuss the possible physiological roles that DMSP could play in *P. oceanica*.

2. Material and methods

2.1. Sampling

Sampling was carried out in northern part of the Bay of Revellata in Corsica (8.725°E 42.580°N) close to the Stareso research station in a dense and healthy *P. oceanica* meadow. Due to the steep rocky shores, the meadow starts at about 8 m depth and extends to 38 m. Background information on the meadow in the Bay of Revellata is given by Gobert et al. (1995).

We carried out a first sampling in August 2012 aiming at determining the dimethylsulfide (DMS) and DMSPd distribution in the water column and related benthic fluxes with incubation chambers. Based on the obtained DMS and DMSPd results (hereafter) and on preliminary determination of DMSP leaf content of *P. oceanica* on a very limited number of samples (not shown), we setup a more detailed study of the DMSP content in tissues of *P. oceanica* to investigate variability among and within shoots as well as seasonally and along a depth gradient.

Between 2 and 3 shoots of *P. oceanica* were collected by self-contained underwater breathing apparatus (scuba) at 10, 15, 20, 25 and 30 m on 28/11/2012, 14/02/2013, 3/06/2013, and 13/08/2013. Shoots of *P. oceanica* have typically between 5 and 10 leaves (Gobert et al., 1995). The leaves were sorted into 3 classes: the two most external leaves on each side (called "external"), the following two leaves on each side (called "intermediary"), all of the following leaves (called "internal"). The leaves were scrapped with a razor blade to remove epiphytes (Dauby and Poulicek 1995), and cut into sections of 10 cm starting at the base of the leaf. They were dried at 60 °C for 48 h, wrapped in aluminum foil and stored dry until further analysis, as recommended for the analysis of the DMSP content in macrophytes (Karsten et al., 1994; Van Alstyne et al., 2003). The length of the leaf is given from the base (0 cm), increasing towards the apex. The leaf grows from the base, so the younger section of the leaf corresponds to the first section (0–10 cm) according to our convention. The sampling was carried out to collect only the shoots avoiding to remove the roots to minimize damage of the meadow. When roots and rhizomes were accidentally removed, they were collected and stored dried, resulting in a more limited amount of samples.

In August 2012, water samples were collected for the determination of DMS concentration in the water column above and within the canopy of the *P. oceanica* meadow at 10 m depth. The evolution of the DMS and DMSPd concentrations in an incubation chamber deployed on the sediment and enclosing a *P. oceanica* shoot was also determined during a 24 h cycle starting at dawn, using the same apparatus as for O_2 incubations described in details by Champenois and Borges (2012). Sampling was done three times during the 24 h (dawn, dusk and dawn the day after) by scuba diving and water samples collected in 60 mL plastic syringes. For the determination of DMS, aliquots of 10 mL were transferred within 30 min after sampling to 20 mL borosilicate vials, sealed with gas tight polytetrafluoroethylene coated silicone septa and stored in the dark at 4 °C until further analysis (within 12 h). For the determination of DMSPd, aliquots were filtered, within 30 min after