Production of dimethylsulfonionpropionate and dimethylsulfide in intertidal sediment ecosystems.
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Summary

Sulfur is an essential element of all living systems. The trace gas dimethylsulfide (DMS) is an important component of the global biogeochemical cycle of this element because it is a major atmospheric carrier of sulfur from the marine environment, where it is abundant, to the land surfaces. Moreover, DMS is proposed to play a role in a climatic feedback system: increases in temperature and irradiance at the Earth’s surface would stimulate the flux of DMS to the atmosphere where it is converted into aerosols which enhance the reflectance of clouds and thus decrease temperature and irradiance at the Earth’s surface. The flux of DMS from marine systems is the result of a complex set of production and consumption processes, starting from the production of dimethylsulfoniopropionate (DMSP) by algae.

The research presented in this thesis was carried out as part of a joint Dutch research project (Trace Gas Project) in the framework of the National Research Program (NOP) Global Change. The general aim of this project was to obtain insight in factors controlling fluxes of DMS from intertidal sediment ecosystems to the atmosphere, by integrating ecological, physiological and modeling studies. This thesis focused on the contribution of oxygenic phototrophic microorganisms to production processes of DMSP and DMS in intertidal sediments.

In chapter 2 it was shown that benthic diatoms were more important producers of DMSP than cyanobacteria. This conclusion was based on measurements in cultures of a large number of strains that were isolated from the sediment during this study or were obtained from culture collections. In most species of diatoms that were tested as well as in mixed natural populations of diatoms, the specific DMSP content increased with salinity. However, because the DMSP content of diatoms was observed to increase during growth in batch culture at constant salinity, it was concluded that salinity did not strictly regulate the production of DMSP. Although light intensity, temperature and nitrogen deficiency all affected growth and chlorophyll a content of the diatoms, an unequivocal effect of these factors on DMSP production was not observed. The regulation of DMSP production was not elucidated in this study and therefore this remains an important objective to be pursued in future research. Activity of DMSP-lyase, the enzyme that catalyzes the cleavage of DMSP to DMS, was not detected in crude extracts of a number of diatoms, implying that the contribution of diatoms to production processes of DMS is restricted to the production of its precursor DMSP.

Chapter 3 describes long-term and short-term effects of salinity on the DMSP content of the benthic diatom Cylindrotheca closterium. During growth in batch
culture at several salinities DMSP increased with increasing salinity, confirming the results presented in chapter 2. Salinity downshocks caused excretion of DMSP by *C. clösterium* with highest amounts of DMSP excreted upon severest downshocks. Salinity upshocks caused a very slow production of DMSP, but production was higher at relatively higher upshocks. Furthermore, *C. clösterium* was able to take up DMSP when supplied in the medium. It was concluded that DMSP production was an integral part of osmoacclimation in *C. clösterium*, but did not play an important role in short-term recovery of internal osmotic balance. An osmoprotective function of DMSP in *C. clösterium* was inferred from the observation that uptake of DMSP from the medium was higher after a salinity upshock from 11 to 33 PSU, than from 11 to 22 PSU. Uptake of DMSP by eukaryotic algae has not been described before.

In chapters 4 and 5 field data are presented. The data reported in chapter 4 were collected at low tide from an intertidal sediment site at the Westerschelde, which was covered by a fairly dense film of diatoms. This chapter shows the diel variations of chlorophyll *a* and of the total DMS(P) content and concentration of DMS(P) dissolved in the porewater. Both pools of DMS(P) (total and dissolved) were constant and did not respond to changing conditions of light and oxygen in the sediment. DMS(P)\textsubscript{total} was about 100 μM, which was three orders of magnitude higher than DMS(P)\textsubscript{porewater} (about 100 nM). Only after the onset of a heavy rainfall DMS(P)\textsubscript{porewater} suddenly increased up to several μM, which was explained by the excretion of DMSP by diatoms in response to the salinity downshock. Potential degradation rates of DMSP and DMS were determined in sediment slurries prepared from sediment collected at the sampling site. Degradation of both DMSP and DMS was fast and closely followed first order kinetics. This was in agreement with the degradation of DMSP and DMS as it was modelled in chapter 7.

In chapter 5 the seasonal variation of DMS(P)\textsubscript{total} and pigment content at a sandy sediment site at the Oosterschelde and a muddy sediment site at the Westerschelde were measured. The results of these measurements confirmed the findings obtained from culture studies of benthic diatoms and cyanobacteria (chapter 2), namely that diatoms account for the high DMSP content in intertidal sediments and that the contribution of cyanobacteria is insignificant. Variations in pigment-specific DMS(P)\textsubscript{total} content could not be explained by variations in temperature, salinity or dissolved inorganic nitrogen concentration. Therefore, it was concluded that biomass and species composition were the main factors determining the DMS(P)\textsubscript{total} content at these sampling sites.

Chapter 6 introduces a very special intertidal sediment. At the Marennes-Oléron Bay at the Atlantic coast of France, dense colonies of the marine flatworm *Convoluta roscoffensis* were observed in the surface layer of the sediment. These organisms seemed to emit a high amount of DMS, judging from the clear smell of DMS that was detected when walking along the green patches on the sediment. The results obtained in this study showed that the smell of DMS originated from DMSP that was present in *C. roscoffensis*. It was assumed that DMSP was produced by the endosymbiotic alga *Tetraselmis* sp., but that it may have accumulated in the host
tissue. Fixation of samples, containing *C. roscoffensis*, using glutaraldehyde, resulted in a very rapid cleavage of DMSP. The results suggested that this cleavage was mediated by DMSP-lyase, which may have been associated with the flatworm. It was concluded that salinity was not an important factor controlling DMSP turnover in sediments inhabited by *C. roscoffensis*.

Chapter 7 presents the mathematical model that was developed in cooperation with other participants in the Trace Gas Project. Since most of the research in this thesis was performed after the development of this model, the data presented in the previous chapters have not been incorporated into the model. The model describes the flux of DMS from an intertidal sediment ecosystem, resulting from the metabolic activities of the functional groups of microorganisms present in intertidal sediments, dictated by the daily varying conditions of light/dark and oxic/anoxic. The model predicts that increased DMSP loads, caused by osmotic stress, result in increased fluxes of DMS from the sediment. That excretion of DMSP in response to osmotic stress may indeed occur in these systems was confirmed experimentally, in cultures of *C. closterium* as well as in the field (Chapters 3 and 4).

In chapter 8, the average flux of DMS from an intertidal sediment ecosystem that was predicted by the model (chapter 7) was compared with flux measurements reported in the literature and differences between the model prediction and field measurements were discussed. Fluxes from intertidal sediments were also compared with fluxes from marine pelagic systems. It was concluded that intertidal sediments, despite their high productivity and high total concentrations of DMSP, do not emit high amounts of DMS to the atmosphere. This is explained by a relatively slow release of particulate DMSP present in diatoms, relatively high degradation rates of dissolved DMSP and DMS and a relatively low sediment-air exchange of DMS.