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Biogeochemistry of dissolved inorganic carbon and nutrients in seagrass (*Zostera noltei*) sediments at high and low biomass

Marie Lise Delgard*, Bruno Deflandre, Emeric Kochoni, Jonathan Avaro, Florian Cesbron, Sabrina Bichon, Dominique Poirier, Pierre Anschutz

University of Bordeaux, EPOC, UMR CNRS 5805, F33615 Pessac, France

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Nutrient recycling is highly controlled by benthic macrophytes in shallow coastal zones. In seagrass bed, this recycling mainly occurs in sediment porewater, which is considered to be the main source of nutrients for plant growth. This work investigated the effect of a *Zostera noltei* meadow on the biogeochemistry of inorganic nutrients and carbon in vegetated sediments of the Arcachon Bay. We characterized the vertical distributions of dissolved inorganic C (DIC), NH_4^+, dissolved inorganic P (DIP) and redox-sensitive particulate inorganic P in bare sediments and in sediments heavily or sparsely colonised by *Z. noltei*. The obtained concentration profiles were used to calculate benthic production rates or particulate stocks. The porewater nutrient concentrations measured in vegetated sediments were depleted by a factor of 10–100 compared to bare sediments. The concentrations of NH_4^+, DIP and DIC exhibited a strong vertical zonation reflecting successive layers of intense production or consumption within the root zone often considered and sampled as a homogeneous zone. The deeper root zone showed higher consumption rates of dissolved inorganic nutrients compared to the upper root zone as young roots growing deeper in the sediment played a major role in nutrient plant uptake. A consumption of DIC was consistently recorded in the root zone. We hypothesized that this could result from a transport of CO_2 from roots to leaves supporting photosynthetic activity as suggested for freshwater plants. We pointed out to what extent the influence of seagrasses changed between sparse and dense meadows. This work emphasizes the high spatial variability in biogeochemical processes occurring at small scale within the root zone or between dense and sparse seagrass patches. Such a variability should be considered when dealing with the role of seagrass in biogeochemical cycles, especially in the context of global decline of seagrass.

1. Introduction

Shallow coastal lagoons shelter very high biological production and play a key role for economy (Costanza et al., 1997; Barbier et al., 2011). Human activity has greatly increased nutrient fluxes to coastal areas leading to severe eutrophication problems such as proliferation of algal blooms and "dead zones" (Justić et al., 1995; Havens et al., 2001; Nixon et al., 2001; Diaz and Rosenberg, 2008). In these shallow environments where ample sunlight reaches the seafloor, benthic autotrophs are the main primary producers and control nutrient cycling (McGlathery et al., 2001, 2007). In coastal sediments, availability of porewater nutrients and resulting nutrient exchanges at the sediment–water interface are also influenced by intense early diagenetic processes (Jahnke et al., 2003; Sakamaki et al., 2006; Holmer and Nielsen, 1997).

Seagrasses grow in shallow marine waters and, contrary to macroalgae, have an extensive root-rhizome system. They can export high amounts of photosynthetates that fuel microbial benthic mineralisation (Kaldy et al., 2006; Papadimitriou et al., 2006), and enhance inorganic nutrient release in sediment porewaters of the root zone (Opsahl and Benner, 1993; Holmer and Olsen, 2002). On the other hand, to maintain growth, seagrasses require dissolved inorganic nitrogen (N) and phosphorus, (P) thus acting as potential efficient sinks for nutrients in both sediment

* Corresponding author. Present address: Department of Environmental Sciences, University of Virginia, 291 McCormick Road, Charlottesville, VA, USA.
E-mail addresses: marielise.delgard@gmail.com, mld4n@virginia.edu (M.L. Delgard).

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porewaters and water column (Pedersen and Borum, 1992; Hemminga et al., 1994; Nielsen et al., 2006; Deborde et al., 2008a). As nitrate (NO_3^-) assimilation is energetically costly (Lara et al., 1987; Turpin 1991), ammonium (NH_4^+) is often considered as the main source of N for seagrasses (e.g. Alexandre et al., 2011) whereas the main P source is PO_4^{3-} (Lee et al., 2007). Carbon constitutes from 30 to 40% of seagrass tissue dry weight (Duarte, 1990; Fourqurean et al., 1997; Lee and Dunton, 1999). Dissolved inorganic carbon (DIC) is also largely assimilated by plants for their photosynthetic needs. The CO_2 uptake occurs by passive diffusion, but seagrasses have also adapted strategies to utilize HCO_3^- for C fixation (Beer and Rehnberg, 1997; Invers et al., 2001).

Through the mechanisms described above, seagrasses can favour both the production and the consumption of dissolved inorganic nutrient in the root zone. The resulting net effect of seagrass on nutrients in sediment porewaters is then highly dynamic but needs to be well understood to assess the role of seagrass in controlling the nutrient cycling of coastal waters. This net effect has been investigated by several studies focusing on the biogeochemistry of NH_4^+ and/or DIP (e.g. Fourqurean et al., 1992; Lillebo et al., 2006, Hebert et al., 2007; Deborde et al., 2008a). However, the dynamic of DIC in vegetated sediments has still been poorly evaluated to date even though the presence of seagrass may affect its porewater concentrations by fuelling mineralisation or carbonate dissolution processes (Burdige and Zimmerman, 2002; Devereux et al., 2011).

In addition, the dynamic of the benthic biogeochemistry in seagrass beds is expected to be significantly related to plant biomass/density but our understanding of these relations are still tenuous. Holmer et al. (2003) showed that sulfate reduction (SR) was positively correlated with belowground biomass in a Zostera marina bed, whereas Smith et al. (2004) had previously found that SR in Santa Rosa Sound T. testudinum beds were negatively correlated with belowground biomass. The same discrepancy occurred with porewater DIC, which correlated to shoot density in a study performed by Burdige and Zimmerman, 2002 but not in the one performed by Devereux et al. (2011) even though both authors worked on the same species, i.e. *Thalassia testudinum*. In the present context of global seagrass decline (Orth et al., 2006; Waycott et al., 2009), threaten seagrass habitats with low biomass/density are more common. Consequently, further studies are clearly needed to better assess how benthic biogeochemical processes in seagrass beds may vary spatially in relation to plant biomass/density.

The present study aimed to improve our understanding of the biogeochemistry of nutrients and carbon in seagrass beds by investigating the spatial variability of benthic biogeochemical processes in a threatened heterogeneous *Zostera noltei* meadow of the Arcachon Bay. Particularly, we evaluated how the spatial changes of *Z. noltei* biomass affects the biogeochemistry of the inorganic dissolved phase of nutrients (N and P) and C in sediment porewaters, which is among the most dynamic pool of nutrient and carbon pool in the benthic compartment. Dissolved inorganic N

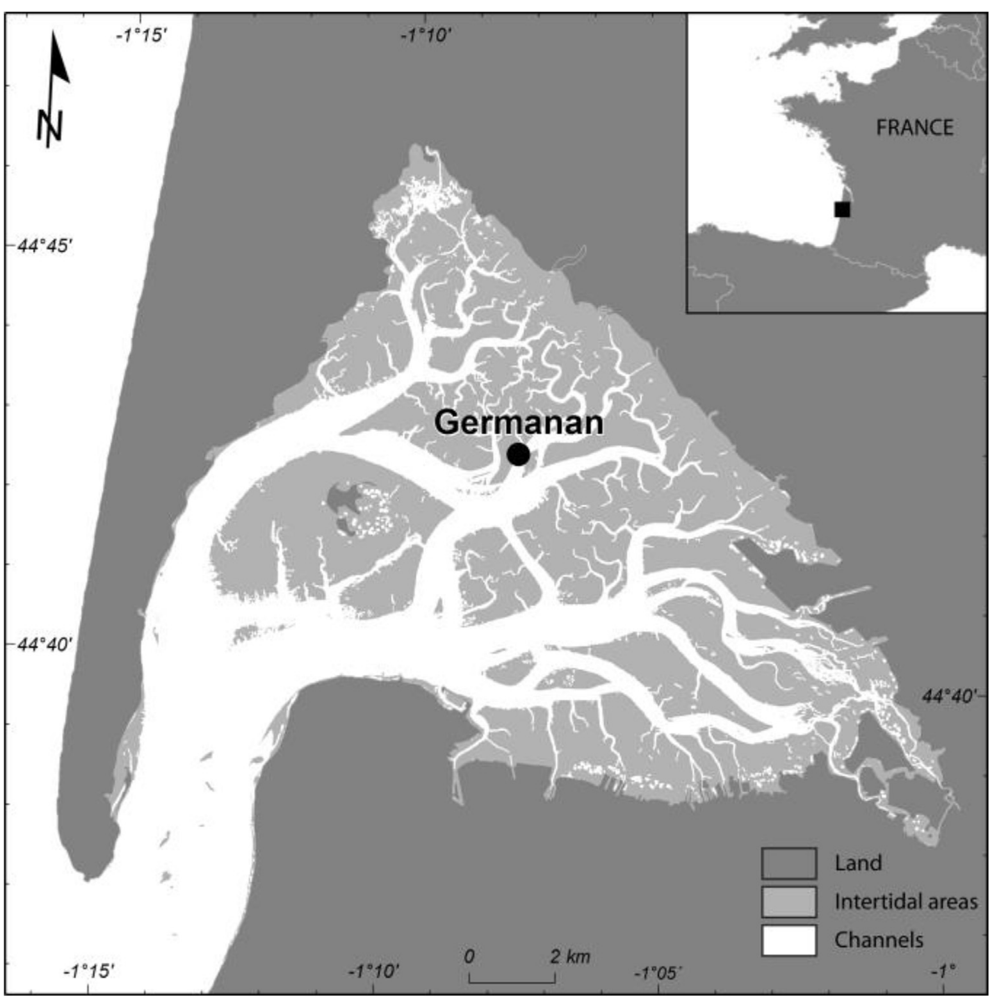

Fig. 1. Map of Arcachon Bay (France) showing the study site.