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The microbial role in carbon cycling within seagrass sediments

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Abstract

Seagrasses are an important feature of coastal systems worldwide, capable of fixing significant amounts of carbon dioxide from the atmosphere into cellular material, potentially helping to alleviate rising carbon dioxide levels. However, the capacity of seagrass beds to act as carbon sinks is largely dependent on the amount of organic matter accumulated within the sediments following transformations by the microbial community. The microbial role in carbon cycling within seagrass sediments has been poorly researched, most likely because the importance of marine microbes in ocean cycling processes was only recently recognized, due to key advancements in molecular biology. This review examines carbon sources within seagrass sediments, their utilization by the microbial community, and their ultimate fates, in order to elucidate current understanding of carbon cycling in seagrass sediments. Future research should incorporate molecular techniques to further establish the microbial role in carbon cycling within seagrass sediments, and ultimately ascertain the capacity of seagrass beds to act as sinks of organic matter.

Introduction

Seagrasses are a polyphyletic group of aquatic plants that inhabit shallow coastal sediments (Kaiser *et al.*, 2005), comprising of over 50 species (Touchette, 2007), all classified within the superorder Alismatiflorae (Larkum *et al.*, 2006). Seagrasses feature belowground roots and rhizomes, coupled via a functional vascular system to discrete photosynthetic shoots aboveground (Di Carlo and Kenworthy, 2008). Seagrasses are the only fully marine descendants of terrestrial angiosperms (Welsh, 2000), first appearing in the fossil record ca. 90 million years ago (Beer and Koch, 1996). This unique group of plants form extensive meadows termed “seagrass beds” (Nakaoka, 2005), which are present in all the world’s coastal seas except Antarctica (Kaiser *et al.*, 2005), covering approximately 0.1 - 0.2% of the global ocean (Duarte, 2002)

Seagrass beds have long been recognised as highly important in coastal systems due to the complex habitat they provide for macro-organisms (Jackson *et al.*, 2001; Kaiser *et al.*, 2005; Nakaoka, 2005), their role in shoreline protection (Duarte, 2002; Kaiser *et al.*, 2005), and their potential to mitigate problems of eutrophication due to the entrapment of nutrients as leaf litter for relatively long time periods (Kaiser *et al.*, 2005). In addition, seagrasses are important primary producers, rivaling the most productive autotrophic communities on the planet (Duarte and Chiscano, 1999), with net production estimated at $0.6 \times 10^{15} \text{ g C yr}^{-1}$ (Duarte, 2002). The significant amount of carbon dioxide fixed into cellular material by seagrass beds may help offset rising carbon dioxide levels, although the capacity of seagrass beds to act as carbon sinks depends ultimately on the amount of carbon accumulated in the sediment as organic matter (Larkum *et al.*, 2006). In order to assess the accumulation of organic matter within the sediment, and thus the ability of seagrass beds to act as carbon sinks, the cycling of carbon through the system must be investigated. Carbon cycling refers to the flux of carbon through interconnected reservoirs, such as the ocean, atmosphere and sediments (Munn, 2004), and is mediated by processes such as photosynthesis, respiration and decomposition.

Carbon cycling within seagrass sediments is poorly understood, probably because the microbial role in this process has previously been overlooked. The term microbe or microorganism includes the *Bacteria*, *Archaea*, *Fungi*, protists and viruses, and the development of culture-independent techniques has led to astounding discoveries of their abundance, diversity and roles in global ocean processes, including the carbon cycle (Munn, 2004). However, these approaches have generally yet to be applied to the study of microbes in seagrass sediments, and as a consequence the microbial role in carbon cycling within these environments is largely unknown. The purpose of this review is to establish present knowledge of carbon cycling within seagrass sediments to identify areas that require further research. This will be achieved by examining the sources of organic carbon within seagrass sediments, its utilization by the microbial community, and its ultimate fates. Gaps in current knowledge will be highlighted throughout the review, and brief suggestions for further research, particularly through the use of new molecular techniques, will be included in a final paragraph.

Potential carbon sources for microbial communities within seagrass sediments

Organic carbon concentrations in vegetated marine sediments have been reported to exceed by 2 - 10 fold those in shelf and deltaic sediments (Duarte *et al.*, 2004), advocating the importance of marine vegetation as a carbon sink. In seagrass sediments, there appears to be a low accumulation of particulate organic carbon [POC] (Holmer and Nielsen, 1997; Holmer *et al.*, 2006), perhaps as deposition is low, or turnover rates are high (Holmer and Nielsen, 1997). However, a high accumulation of dissolved organic matter [DOC] has been reported (Holmer and Nielsen, 1997), with concentrations in sediment porewater 25% higher in seagrass-colonized compared to non-vegetated sediments (Koepfler, 1993). It is important to establish the source(s) of this extra carbon, as different compounds may be remineralized to carbon dioxide at different rates by the microbial community.

Stable isotope analyses have revealed that the carbon within seagrass sediments is generally from four discrete origins, although the extent to which each source contributes varies between beds of different seagrass species (Holmer *et al.*, 2004) and between locations (Boschker *et al.*, 2000). The carbon within seagrass sediments may originate from the seagrasses themselves, through exudation and decomposition (Ziegler and Benner, 1999), or the source may in fact be algae or seston. The relative importance of differing carbon sources within seagrass beds is largely unknown (Homer *et al.*, 2001). Research findings to date are discussed below, enabling the specific gaps in understanding to be identified.

Seagrass-derived carbon

A potential source of carbon to sediment microbial communities is that exuded from the root/rhizome system. The proportion of carbon fixed in the leaves exuded from roots and rhizomes has been reported as 6-17 % (Moriarty *et al.*, 1986), 8-18% (Hansen *et al.*, 2000) and 5.4 and 7% (Holmer *et al.*, 2001), and Moriarty *et al.* (1986) concluded that all of the exuded carbon was utilized by bacteria growing in the sediments. However, Boschker *et al.* (2000) reported that carbon fixed by seagrasses does not enter sediment to major extent, and is neither used by bacteria, nor accumulated in the sediment organic matter. The contradictory findings reported by Boschker *et al.* (2000) may be explained by the difference in study site and seagrass species. The studies reporting significant levels of root exudation studied tropical seagrass sediments, whereas Boschker *et al.* (2000) examined sediments of temperate seagrass species. Carbon exuded from seagrass roots and rhizomes may differ between seagrass species and/or climates, and this is therefore an area that requires further research.

In seagrass sediments, decomposition is likely to be quantitatively more important as a seagrass-derived source of organic matter than exudation. Living seagrass tissues are not grazed extensively (Zieger and Benner, 1999), therefore litter and particulate detritus derived from seagrasses is abundant in many coastal ecosystems (Peduzzi and Herndl, 1991). It has been reported that 50.3% of seagrass net primary production is decomposed within the system (Duarte and Cebrián, 1996), and the aerobic consumption of carbon from leaf detritus alone has been reported to represent 17% of annual seagrass production (Mateo and Romero, 1997). Seagrass detritus has been suggested to be a major carbon source for bacteria in *Posidonia oceanica* seagrass beds (Holmer *et al.*, 2004). However, although detritus is likely an important carbon source, sources not derived directly from the seagrasses may contribute significantly more to organic matter in seagrass sediments.

Non-seagrass-derived carbon

Research based on carbon loss data indicates only a small fraction of seagrass production actually fuels the seagrass ecosystem (Mateo and Romero, 1997), and seagrass material may have limited importance as a bacterial carbon source (Boschker *et al.*, 2000). Macroalgae, epibenthic and epiphytic algae have been shown to be major contributors in seagrass systems, contributing 40 - 90% of gross primary production (Pollard and Moriarty, 1991). There is evidence that benthic bacteria may respond to

algal biomass in seagrass sediments (Danovaro *et al.*, 1994), and Boschker *et al.* (2000) report that benthic algal production was likely the main source of carbon for bacterial growth in *Zostera* spp. seagrass sediments. Specifically, in anthropogenically impacted *P. oceanica* meadows, bacteria have been reported to shift to macroalgal and seston carbon sources, as opposed to detrital sources (Holmer *et al.*, 2004). This shift to macroalgal sources may be explained by the invasion of seagrass beds by thin-leaved macroalgae during nutrient enrichment, which compete with seagrasses (Holmer *et al.*, 2004), potentially becoming the dominant carbon source for sediment microbes. Seston has also been reported as an important carbon source in non-anthropogenically impacted *P. oceanica* meadows (Gacia *et al.*, 2002), and in the faster growing seagrass, *Cymodocea nodosa* (Holmer *et al.*, 2004). Although seston and algal carbon sources do not originate directly from seagrasses, their levels may be enhanced by the presence of seagrasses. Epiphytic algae would obviously not be present without the seagrass, and seagrass beds dissipate waves, trapping particles and preventing resuspension, increasing seston settlement (Holmer *et al.*, 2004). Therefore, whether directly or indirectly, seagrasses increase carbon deposition within sediments, indicating seagrass beds have the potential to be important carbon sinks.

Carbon utilization by the microbial community within seagrass sediments

The utilization of carbon within seagrass sediments by the microbial community determines the extent of organic matter accumulation, and consequently the degree to which seagrass beds can be regarded as carbon sinks. It is important to first discuss the abundance and biomass of the microbial community within seagrass sediments, as greater abundances or biomasses would indicate a greater cycling of carbon. Detrital material is likely the most important seagrass-derived carbon source for the microbial community in seagrass sediments, and its subsequent breakdown by microorganisms is a vital component of carbon cycling, therefore decomposition is discussed second. Sulphate reduction is the dominant anaerobic respiration process in marine sediments (Welsh, 2000), and sulphate reducers are especially important for the final stages of carbon remineralization within seagrass sediments (Larkum *et al.*, 2006). Therefore, sulphate reducing bacteria will be discussed last.

Microbial abundance and biomass

Bacterial activities have been reported as higher in seagrass-colonized compared to nearby non-vegetated sediments (Hansen *et al.*, 2000). From this it can be elucidated that higher bacterial biomass and abundance will be expected, and consequently a higher utilization of carbon within seagrass colonized, compared to non-vegetated sediments, although this is yet to be shown experimentally. Danovaro *et al.* (1994) reported that bacterial biomass in seagrass colonized sediments represented 30% of total living carbon and 8.4% of total organic carbon, although the findings were not compared to bacterial biomass in the adjacent bare sediment, so it is not clear if the high biomass was simply representative of the location. Studies to determine the factors influencing bacterial communities within seagrass sediments have reported seasonal variations, with highest bacterial biomass, density and abundance typically during late spring (Danovaro *et al.*, 1994; Danovaro and Fabiano, 1995; Danovaro, 1996; Glazebrook *et al.*, 1996; James *et al.*, 2006). Danovaro and Fabiano (1995)

positively correlated bacterial biomass within seagrass sediments with temperature, suggesting this is the likely the cause for seasonal variations. Danovaro and Fabiano (1995) also reported inter-annual variations in bacterial biomass within seagrass sediments, and attributed the findings to differences in organic matter composition.

Studies of microbial communities in seagrass sediments have focused on the *Bacteria*, with the *Archaea*, *Fungi*, protists and viruses being largely ignored. Viral densities in marine waters exceed those of bacteria (Weinbauer and Peduzzi, 1994), with $10^8 - 10^9$ viruses cm^{-3} typical in nearshore surface sediments (Suttle, 2005), yet their presence within seagrass sediments has not been researched. Bacteriophages cause lysis of bacterial cells, catalyzing the movement of nutrients from organisms to the dissolved organic matter pools (Suttle, 2005). Viral lysis of bacteria within seagrass sediments would result in a release of DOC into the sediment nutrient pools, which is a possible explanation for the high DOC concentrations compared to non-vegetated sediments. This is an area that requires further research.

Decomposition

Litter and particulate detritus within seagrass sediments are broken down into simpler compounds largely via bacterial decomposition (Peduzzi and Herndl, 1991). During the decomposition process, dissolved monomeric carbohydrates are reported to leach out of the material for the first 7.5 days, 92% of which are rapidly used by the microbial community (Peduzzi and Herndl, 1991). Within the first 24 hours 20% of detrital mass is reported to be lost before rates slow (Blum and Mills, 1991), suggesting the initial leaching process may be responsible for a high loss of detrital mass. The microbial community studied featured several shifts during decomposition, initially featuring uniform bacterial coverage before changing within 14 days to a seven times more abundant and heterogeneous bacterial assemblage (Peduzzi and Herndl, 1991). After 21 days leaf surfaces began to break down and a protozoan community developed, reaching maximum density at 2 months (Peduzzi and Herndl, 1991). Studies of decomposition have been conducted within laboratories and results may not truly represent natural decomposition processes, meaning further field based studies are required. However, the decomposition process clearly supports a diverse and changeable microbial community, suggesting the breakdown of organic molecules into simpler compounds occurs through a series of microbial processes.

Sulphate reducing bacteria

The final stages of decomposition are largely carried out by sulphate reducers, which are important mediators of the final remineralization of organic carbon to carbon dioxide (Larkum *et al.*, 2006). Sulphate reducers are predominant bacteria in coastal sediments which oxidize organic matter through the reduction of sulphate to sulphide (Jørgensen, 1982). In marine sediments, sulphate reducers can account for more than 50% of total carbon oxidation (Welsh, 2000). Sulphate reduction has been reported to be increased in seagrass inhabited sediments compared to non-vegetated sediments (Isaksen and Finster, 1996; Holmer and Nielsen, 1997; Küsel *et al.*, 1999; Holmer *et al.*, 2001), probably due to increased carbon load (Jensen *et al.*, 2007), with the exception of *Thalassia hemprichii* sediments, where levels were the same as in non-vegetated

sediments (Holmer *et al.*, 2001). The increased sulphate reduction rates within seagrass colonized compared to non-vegetated sediments indicates higher remineralization rates, and a greater release of carbon dioxide.

Studies have reported positive relationships between root-rhizome biomass and sulphate reduction rates (Pollard and Moriarty, 1991; Holmer *et al.*, 2001; Holmer *et al.*, 2006), suggesting sulphate reducers are more abundant on seagrass roots and rhizomes than in the surrounding bulk-sediment. However, Jensen *et al.* (2007) report that sulphate reducing *Deltaproteobacteria* contributed <2% to root associated bacterial communities, but 12 and 23% to bacterial communities in the surrounding bulk-sediment. Jensen *et al.* (2007) suggest the roots appear to select for a distinct bacterial community, potentially by inhibiting the growth of sulphate reducers, or preferentially enhancing the growth of possible nitrogen fixing symbionts. Although this appears to contradict studies reporting increased sulphate reduction rates associated with seagrass roots and rhizomes compared to surrounding bulk-sediment, this may not be the case. Sulphate reduction rates have been reported as up to eleven fold higher on seagrass roots and rhizomes compared to vegetated bulk-sediment rates (Blaabjerg and Finster, 1998; Hansen *et al.*, 2000), suggesting sulphate reducers were present in higher numbers on roots and rhizomes in Jensen *et al.*'s (2007) study, although as a smaller proportion of the community relative to other microorganisms.

Sulphate reduction typically does not regenerate enough nutrients within seagrass sediments to meet seagrass nutrient demand, suggesting seagrasses rely on other mineralization processes or the uptake of nutrients from the water column (Holmer *et al.*, 2001). A range of microbes, in addition to sulphate reducers, within the sediment may be important for the remineralization of carbon, including for example, denitrifying bacteria (Larkum *et al.*, 2006) and aerobic microorganisms (Jørgensen, 1982). Research into the diversity of microbes present, and their roles in the transformation of organic carbon, needs to be conducted to truly understand carbon cycling within seagrass sediments.

The fates of carbon within seagrass sediments

It is important to discuss the ultimate fates of carbon within seagrass sediments following utilization by the microbial community to assess carbon burial, and establish the importance of seagrass beds as carbon sinks. Total carbon burial has been reported as significant in vegetated sediments (Duarte *et al.*, 2004), and carbon deposition within a *P. oceanica* meadow has been reported as $198 \text{ g C m}^{-2} \text{ yr}^{-1}$, with only $15.6 \text{ g C m}^{-2} \text{ yr}^{-1}$ being returned via remineralization within the sediment, suggesting the majority is accumulated as organic matter (Gacia *et al.*, 2002).

Rates of remineralization may depend primarily on the carbon source, and differences between meadows should be considered. For example, in more impacted meadows, *P. oceanica* seagrass beds have been shown to shift to seston and macroalgae carbon sources, as opposed to detrital sources, and this leads to an increase in remineralization rates (Holmer *et al.*, 2004). To encourage a higher accumulation of

organic matter, human impact on seagrass meadows should consequently be minimized. In the seagrass *C. nodosa*, rates of remineralization were higher than in *P. oceanica*, and carbon sources were primarily seston and detritus, as opposed to solely detritus, suggesting seston is more labile and easily decomposed (Holmer *et al.*, 2004). This suggests the carbon source is of primary importance when estimating rates of remineralization within seagrass meadows. Overall, it is clear seagrass beds do accumulate organic matter, although the exact extent to which requires further research.

Further research

The extent to which the differing carbon sources contribute within different seagrass systems requires further investigation, and the ease with which the various carbon sources can be broken down assessed to establish turnover rates by the microbial community. Microbial communities within seagrass sediments require further research to confirm taxa present, and their relative abundances, to enable an understanding of how organic carbon in seagrass sediments is being utilized. Varied study locations and seagrass species should be chosen, and researchers should perform the same analyses on adjacent non-vegetated sediment to determine which (if any) differences in the microbial community are specifically due to the presence of seagrass. Ecological parameters, such as shoot density, temperature and organic content should also be measured, to allow research findings to be compared meaningfully between sites.

The analysis of seagrass sediment microbial communities should be carried out utilizing the newly available culture-independent techniques, as it is now known traditional culture methods significantly underestimate microbial abundances, and potentially diversity, by >99% (Béjà, 2004). The diversity of microbial taxa may be measured using community fingerprinting analyses, utilizing techniques such as denaturing gradient gel electrophoresis [DGGE]. DNA must first be extracted from the sediments, which can now be efficiently achieved using commercial soil DNA extraction kits (Luna *et al.*, 2006), and amplified using the polymerase chain reaction [PCR]. PCR products can then be analysed using DGGE. DGGE is used to provide, on a polyacrylamide gel, a profile representing the diversity of a microbial community from a specific environment (Marzorati *et al.*, 2008). DGGE is a relatively well-established molecular tool, which has high reliability and reproducibility (Marzorati *et al.*, 2008), meaning results from studies utilizing different seagrass species and study locations can be effectively compared. The abundance of the microbial community in seagrass sediments may be measured using epifluorescence microscopy, which is a reproducible technique enabling the enumeration of all groups of marine microbes (Munn, 2004). By conducting further research into microbial communities within seagrass sediments, better understanding of the utilization of organic matter once it has entered the sediment, and consequently better understanding of the ultimate fates of the carbon will be facilitated.

Concluding remarks

Carbon cycling within seagrass sediments is poorly understood, probably because the microbial role in this process has not been well researched. Of potential carbon inputs

in seagrass sediments, it is likely detrital matter, seston and algae are the dominant carbon sources for sediment microbial communities, although the significance of each input varies between seagrass species and is dependent on the degree to which the bed is anthropogenically impacted (Holmer *et al.*, 2004). Bacterial activities are enhanced in seagrass sediments (Hansen *et al.*, 2000) suggesting a higher cycling of carbon, and higher activity levels are probably a direct result of increased carbon input compared to non-vegetated sediments. However, bacterial biomass and abundance have not been measured directly and compared to figures from non-vegetated sediments. Differences in the abundance and biomass of other microbial groups within seagrass colonized compared to non-vegetated sediments have not yet been researched.

Detrital matter within seagrass sediments supports a diverse assemblage of microorganisms, and the composition of the microbial community varies throughout the decomposition process (Peduzzi and Herndl, 1991). The breakdown of detrital matter into simpler compounds probably supports the abundant sulphate reducer community, which are involved in the final stages of carbon remineralization (Larkum *et al.*, 2006). The roles of other bacterial groups in the remineralization process have not been researched. Ultimate carbon remineralization rates are low in comparison to the high input of organic matter in seagrass sediments (Gacia *et al.*, 2002), suggesting a large volume of organic matter is accumulated, implicating seagrass beds as important carbon sinks. However, further investigation is needed to fully understand the roles of the microbial community in the carbon cycling process, to establish the true fates of organic matter in seagrass sediments.

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