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Invited feature

Landscape configuration modulates carbon storage in seagrass sediments

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A B S T R A C T

Climate change has increased interest in seagrass systems as natural carbon sinks and recent studies have estimated the carbon stocks associated with seagrass meadows. However, the factors that affect their variability remain poorly understood. This paper assesses how landscape-level attributes (patch size and matrix composition) influence carbon storage in seagrass sediments. We quantified the organic carbon (C_{org}) content and other geochemical properties ($\delta^{13}C$ and particle size) in surface sediments of continuous *Posidonia oceanica* meadows, patchy meadows interspersed with rocky-algal reefs and patchy meadows on sedimentary bottoms. We also took samples of potential carbon sources for isotopic composition determination. Our results indicate that the continuous meadows accumulated larger amounts of C_{org} than patchy meadows, whether embedded in a rock or sand matrix. The C_{org} from continuous meadows was also more ^{13}C enriched, which suggests that a high proportion of the carbon was derived from plant material (autochthonous sources); in contrast in patchy meadows (especially in a sand matrix), lower $\delta^{13}C$ values indicated a higher contribution from allochthonous sources (mainly suspended particulate organic matter, SPOM). These findings suggest that the sediment of continuous meadows stores more C_{org} in than that of patchy meadows. This is probably due to the increased contribution from seagrass leaves, which are much more refractory than SPOM. In general, certain landscape configurations, and especially patchiness, appear to reduce the carbon storage capacity of seagrasses. Since the current decline of seagrass is leading to habitat fragmentation, our results increase the argument for the promotion of effective measures to preserve the integrity of these natural carbon sinks.

1. Introduction

The urgent need to reduce atmospheric CO_2 levels as an attempt to mitigate climate change has led to considerable interest in quantifying the capacity of natural systems to trap and store carbon. Vegetated coastal habitats have been reported to present a relatively high carbon storage potential (Mcleod et al., 2011; Pendleton et al., 2012; Duarte et al., 2013), despite the small proportion (<2%) of the surface they occupy (Duarte et al., 2005). These ecosystems, particularly mangroves, saltmarshes and seagrass beds, have a disproportionately high contribution to carbon sequestration, since, unlike terrestrial ecosystems, they store large amounts of organic carbon (C_{org}) in their sediments, which accounts for more than 50%–70% of all carbon stored in ocean sediments (Nellemann et al., 2009).

Among these ecosystems, seagrass beds contribute the most to carbon storage in relation to their global area (Duarte et al., 2005). Recent estimates indicate as much as 19.9 Pg C is stored in the first metre of seagrass sediment worldwide (Fourqurean et al., 2012), while their carbon accumulation rates range from 48 Tg C yr^{-1} to 112 Tg C yr^{-1} (Duarte et al., 2005; Kennedy et al., 2010). This high capacity is partly the result of their high primary production, combined with the refractory nature of seagrass tissues (Mateo and Romero, 1997). Seagrass canopies are also highly efficient at trapping particles and associated carbon from outside the ecosystem, and this key mechanism contributes to the importance of seagrasses as carbon sinks (Gacia and Duarte, 2001; Hendriks et al., 2008; Kennedy et al., 2010). Moreover, since seagrass canopies promote regular sediment accretion, seagrass carbon storage potential is maintained over time, unlike carbon-saturated terrestrial soils (Mcleod et al., 2011).

Many recent studies, mindful of the significant contribution of

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seagrasses to the carbon budget of the oceans, have attempted to quantify the carbon stocks and carbon storage potential of seagrass beds (Duarte et al., 2010; Kennedy et al., 2010; Fourqurean et al., 2012; Greiner et al., 2013; Lavery et al., 2013; Serrano et al., 2014). Those studies highlight the high variability in carbon accumulation in seagrass sediments. Species identity and canopy traits, as well as abiotic habitat characteristics such as depth, sediment properties and water turbidity, have been suggested to affect this variability (Greiner et al., 2013; Lavery et al., 2013; Serrano et al., 2014; Samper-Villarreal et al., 2016); however, our understanding of the factors that regulate such variation is still very limited (Nellemann et al., 2009; Duarte et al., 2010; Serrano et al., 2014) and the influence of other factors (e.g. the surrounding habitats and the spatial complexity of habitats) has rarely been considered.

In general terms, the carbon stored in seagrass sediments depends on the amount of carbon deposited and the proportion of this bulk carbon that is not remineralised. The C_{org} deposited in seagrass sediments comes from different sources, and its origin could play a critical role in both processes. A proportion of the carbon deposited is produced in the meadow itself (Hemminga and Mateo, 1996; Papadimitriou et al., 2005; Kennedy et al., 2010), including the contribution from below-ground organs (roots, rhizomes and, in some genera, leaf sheaths) and that from above-ground tissues (leaves and, eventually, their epiphytes) that are not exported outside the meadow (Romero et al., 1992; Hyndes et al., 2014). Other sources are allochthonous materials, such as suspended particulate organic matter (SPOM), macroalgae, land-derived detritus and to a lesser extent the macrofauna inhabiting the meadows (Kennedy et al., 2004).

The oxygen concentration in the pore water of seagrass sediment is generally low, and less than 10% of the total organic material entering the sediment decomposes (Gacia et al., 2002). The different sources of C_{org} typically have different decomposition rates. Long-term carbon sinks have been associated with refractory materials with C/N ratios that no longer exhibit changes over time (Mateo et al., 2006). In most seagrass species, this applies mainly to the carbon derived from below-ground tissues, especially in the Mediterranean species *Posidonia oceanica* (Mateo and Romero, 1997), but it also applies to seagrass leaves with intermediate decomposition rates (Mateo et al., 2006). Meanwhile, epiphytes and allochthonous materials, such as SPOM and macroalgal detritus, are more labile (Mateo and Romero, 1997; Cebrian, 2002; Trevathan-Tackett et al., 2015). Therefore, shifts in the relative proportions of C_{org} sources with different decomposition rates could determine the amount of carbon stored in seagrass sediments.

The contributions of the different carbon sources to the C_{org} accumulated in seagrass sediments vary widely (Kennedy et al., 2004; Papadimitriou et al., 2005). In most cases, SPOM appears to be the main contributor, followed by autochthonous sources (Gacia et al., 2002; Kennedy et al., 2004; Papadimitriou et al., 2005). However, little is known about the factors that modulate the relative importance of the different sources. Specifically, recent findings suggest that the configuration of the coastal seascape influences the magnitude of carbon fluxes among its habitats (Hyndes et al., 2014) probably thereby affecting the carbon stored in sediments.

Seagrass beds exist naturally and form either homogeneous landscapes (large, continuous meadows) or heterogeneous landscapes, in the form of patches of varying shapes and sizes interspersed with unvegetated areas of sand or rocky-algal reefs (Robbins and Bell, 1994; Jackson et al., 2006). These patterns are driven by natural processes, which are either physical (e.g. hydrodynamics), geological (e.g. sediment transport) or biological (e.g. growth rate and expansion of rhizomes) (Fonseca and Bell, 1998; Hovel, 2003; Mills and Berkenbusch, 2009). Anthropogenic disturbances, such as eutrophication and physical removal, constitute additional factors that can lead to fragmentation of seagrass habitats (Macreadie et al., 2009; Montefalcone et al., 2010). Landscape ecology has made a major contribution to the knowledge of seagrass ecosystem dynamics (Pittman et al., 2011); yet the interaction between landscape attributes and carbon storage remains largely unexplored. This is despite the fact that understanding these processes is crucial for improving global carbon sink estimates and future projections (Nellemann et al., 2009; Ricart et al., 2015a).

In order to explore the variability in seagrass carbon storage, we assessed the influence of landscape configuration on the carbon content and carbon sources of seagrass sediments. To this end, we adopted a patch matrix model approach (Boström et al., 2011), with *P. oceanica* seagrass meadows as the focal habitat, to compare continuous meadows with patchy meadows interspersed among rocky reefs with macroalgal cover (patches in a rock matrix) and patchy meadows on sedimentary bottoms (patches in a sand matrix). We hypothesised that landscape configuration would influence the relative importance of the sediment C_{org} sources, with autochthonous sources contributing most in continuous meadows and allochthonous sources contributing most in seagrass patches, with differences associated with the matrix type. This variability would have implications for the total amount of carbon stored in the different landscape configurations.

2. Materials and methods

2.1. Study sites

The present study was performed at six locations along the coasts of Catalonia and the Balearic Islands, in the NW Mediterranean (Fig. 1). The locations were selected because of their similar geomorphological conditions (e.g. depth range, shape and exposure) and the presence of the different seagrass landscape configurations. The continuous meadows were larger than 100 × 100 m, while the seagrass patches measured about 2 × 2 m. All the landscape configurations were at similar depths (5–8 m) and at a maximum distance of 50 m from each other at all the sites.

2.2. Sampling

Sediments were collected manually by inserting PVC cylinders (20 cm long; 4 cm internal diameter). At each location, five replicate cores were randomly taken from the continuous meadows and one core was taken from the centre of each of five randomly selected patches in a rock matrix and five patches in a sand matrix.

For the elemental and isotopic composition analysis of potential carbon sources, detached detrital leaves of *P. oceanica* and detrital macroalgae were collected using a suction device in a 40 × 40 cm quadrate near the site of each core sample. In addition, five living shoots of *P. oceanica* were retrieved in order to obtain epiphytic material (see below). Moreover, at each location, 2 litres of seawater were collected from 1 m below the surface, in triplicate, and filtered into prewashed and precombusted (450 °C, 4 h) Whatman GF/F filters within 2 h of collection for SPOM elemental and isotopic analysis. All the samples were kept frozen at −20 °C until analysis in the laboratory.

2.3. Laboratory processing

In the laboratory, the upper 2 cm of each sediment core was sectioned and weighed before and after drying at 60 °C for 48 h. Each sample was then split into two subsamples: one was retained for grain size analysis; the other was dry-sieved through a