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Mangrove carbon sink. Do burrowing crabs contribute to sediment carbon storage? Evidence from a Kenyan mangrove system

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ABSTRACT

Mangrove ecosystems are acknowledged as a significant carbon reservoir, with a potential key role as carbon sinks. Little however is known on sediment/soil capacity to store organic carbon and the impact of benthic fauna on soil organic carbon (SOC) stock in mangrove C-poor soils. This study aimed to investigate the effects of macrobenthos on SOC storage and dynamic in mangrove forest at Gazi Bay (Kenya). Although the relatively low amount of organic carbon (OC%) in these soils, they resulted in the presence of large ecosystem carbon stock comparable to other forest ecosystems. SOC at Gazi bay ranged from 3.6 kg m^{-2} in a Desert-like belt to 29.7 kg m^{-2} in the *Rhizophora* belt considering the depth soil interval from 0 cm to 80 cm. The high spatial heterogeneity in the distribution and amount of SOC seemed to be explained by different dominant crab species and their impact on the soil environment. A further major determinant was the presence, in the subsoil, of horizons rich in organic matter, whose dating pointed to their formation being associated with sea level rise over the Holocene. Dating and soil morphological characters proved to be an effective support to discuss links between the strategies developed by macrobenthos and soil ecosystem functioning.

1. Introduction

Over the last decades, there has been a strong interest in understanding how factors, such as vegetation and climate, control organic carbon accumulation in soils and sediments, and whether this process could mitigate CO_2 impacts on climate change (Jobbágy and Jackson, 2000).

Mangrove forests are ecosystems thriving in the intertidal belt, on sediments made waterlogged and saline by regular flooding. Mangrove forests cover roughly 137,760 km^2 along the coasts of the world (Giri et al., 2011) and accumulate 26.1 Tg of organic carbon annually (Breithaupt et al., 2012). Many authors argue that they rank among the most carbon-rich forest soils in the tropics (Chmura et al., 2003; Donato et al., 2011; Fujimoto et al., 1999; Kristensen et al., 2008; Matsui, 1998).

Kristensen et al. (2008) reviewed data on mangrove sediment carbon incorporation rates. They observed that carbon burial rates estimated using a bottom-up approach (Duarte et al., 2005) referred to sediments showing an average carbon content of 8.5%, while a compilation of carbon content of world mangrove sediments produced a much lower average, close to 2.2% (Kristensen et al., 2008).

Sedimentation of carbon-rich mud is often assumed as the main process of carbon burial in mangrove forests, and sediment accretion rate is used as a proxy for overall C sequestration (Chmura et al., 2003). Sediment accretion rate increases from the high to the low intertidal zone (Alongi et al., 2005); intertidal mudflats, often lying seawards to mangrove forests, may actually accumulate more sediment and carbon than the forest themselves (Sanders et al., 2010a,b). A second major allochthonous component is the continuous exchange with the large carbon reservoir of the ocean, as daily tides drive inwelling and outwelling of organic matter (Bouillon et al., 2003; Dittmar et al., 2006).

Several autochthonous components of mangrove carbon cycle remain unaccounted for (see Kristensen et al., 2008 for a review). The main such components are root-to-soil C transfer and the role of macrobenthos (Cannicci et al., 2008; Kristensen et al., 2008; Nagelkerken et al., 2008).

Sesarmid and ocipodid crabs are the major bioturbating and bioengineering components of the mangrove fauna, through their feeding and digging activities (Cannicci et al., 2008; Kristensen et al., 2008; Lee, 1998). Sesarmids dig burrows down to 2 meter depth and store leaf litter, mangrove propagules and other organic material from different sources (Dahdouh-Guebas et al., 1997; Dye and Lasiak, 1987; Micheli, 1993; Micheli et al., 1991; Robertson and Daniel, 1989; Skov and Hartnoll, 2002; Smith et al., 1991; Sousa and Dangremond, 2011). Their burrows then work as traps, shielding organic materials from flushing by ebb tides (Lee, 2008) and enhancing retention of organic C within the system (Kristensen et al., 2008). These

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leaf-consumers remove, through consumption or burial, between 28% and 79% of annual leaf-litter fall, according with the characteristics of the considered mangrove (Robertson, 1986, 1991; Robertson and Daniel, 1989; Twilley et al., 1997). Despite their being considered mainly herbivorous, sesarmids can exploit different food sources, as mud, bacteria or dead animals, in order to enrich their diet in nitrogen, as mangroves are nitrogen-poor environments (Skov and Hartnoll, 2002; Thongtham and Kristensen, 2005). Exploiting diversified food sources, they can possibly bury also other kinds of organic material (Sousa and Dangremond, 2011).

Ocipodid crabs are mainly represented, in mangrove systems, by the pantropical genus *Uca*. Although they often share habitats with sesarmids, they rely on different food sources (Macnae, 1968; Jones, 1984; Dahdouh-Guebas et al. 2002). They are filter feeders (Icely and Jones, 1978; Ribeiro and Iribarne, 2011) that are able to exploit food sources from the sediment, such as bacteria, benthic microalgae and meiofauna (Reinsel, 2004). As filter feeders they feed on the sediment surface, never burying organic material, as common for sesarmids. While filtering, they plough the top sediment layer, inducing oxidation and changes in biogeochemical properties, influencing such phenomena as bacterial and algal eutrophication (Bartolini et al., 2011; Kristensen and Alongi, 2006). Ocipodid burrows are typically less deep than the ones of sesarmids, but they can reach a density of 100 per square metre of forest or sand/mudflat ground (Cannicci et al., 2009; Geist et al., 2012; Hartnoll et al., 2002; Penha-Lopes et al., 2009). Burrows are essential as breeding sites (Mautz et al., 2011; Milner et al., 2010), as shelter during high tide (Booksmythe et al., 2012; Crane, 1975) and for thermoregulation during low tide activity (Edney, 1961), while fiddler crabs behave as central-place foragers (Crane, 1975; Zeil et al., 2006). Through burrow digging and maintenance, ocipodids enhance oxygen flux into the waterlogged sediment, facilitating oxidation and enhancing nutrient availability, sediment bacterial communities (Kristensen and Alongi, 2006) and biogeochemical processes (Holguin et al. 2001; Kristensen et al., 2008). Crabs also transfer biomass to the sediment via their exuviae and faeces, though there is lack of data about this process, as remarked by Alongi (2002, 2009); see also Eong, (1993). These clear differences in feeding and burrowing behaviour of the two burrow-builder crab families likely lead to different effects on sediment properties (Kristensen and Alongi, 2006) and carbon storage. However, to our knowledge, this latter topic has not been yet studied (Lee, 2008) and represents one of the main topics of this paper.

Published data on belowground carbon storage in mangrove ecosystems have recently increased (Donato et al., 2011; Fujimoto et al., 1999; Sanders et al., 2010a,b). Most of these studies show, however, the same sort of bias noted by Kristensen et al. (2008), as they analyse mangroves growing on carbon-rich sediments. Though there is no definite assessment of the relative importance of C-rich and C-poor sediments in world mangrove ecosystems, evidence of mangroves growing on soils with low C content continuously emerges. In the ecosystem studied by Sanders et al. (2010a,b), the soil C pool amounts to 23.5–24.8 kg m^{-2}, much lower than reported by other authors. Recently, both Tue et al. (2011) and Ranjan et al. (2011) report on mangroves growing on sediments with low C content.

Most data on belowground C storage have been gathered through a “sedimentological” approach, sampling mangrove substrata with piston corers and analysing them by depth slices (Sanders et al., 2010a,b). However, the ability of mangrove sediments to support rooted plants, combined with the identification of numerous surface-related process, such as addition of organic matter, transfer of elements and mineral weathering, allows to consider mangrove substrates as pedogenised sediments (e.g. soils; see Joffe, 1936; Paton et al., 1995; Ferreira et al., 2007a; Soil Survey Staff, 2010). Thus they can be described and sampled by standard pedological procedures, as for examples by opening soil profiles. Soil profiles supply information on such morphological characters as redoximorphic features, shape and size of biological channels, horizon development and organic matter distribution, indicative of surface-related processes and of macrobenthos activity.

The main objective of this cross-disciplinary study was to assess the contribution of key bioturbators to soil organic matter dynamics. For this purpose, specific aims were set as: a) the quantification of soil C storage in Gazi bay, a mangrove ecosystem forest thriving on C-poor soils; b) the evaluation of crab biomass distribution in the mangrove forest; c) the identification of the contribution of key-bioturbators to carbon storage, by a combined pedological and biological approach.

2. Material and methods

2.1. Study area

Gazi Bay (4° 22′ S, 39° 30′ E) is a semi-enclosed, shallow bay about 40 km South of Mombasa in Kwale district, Kenya (Fig. 1). The climate of the Kenyan coast is typically monsoonal, influenced by the moist southeast monsoon from March to September and by the dry northeast monsoon from October to March; rain occurs in March–May and, to a lesser extent, October and November. Total annual precipitation fluctuates between 1000 and 1600 mm, showing a bimodal distribution pattern. Air is hot and humid, with an average temperature of about 28 °C and little seasonal variation; relative humidity is about 95%, due to the close proximity to the sea (Kitheka, 1996).

A mangrove forest, up to 3.3 km across and with an area of about 6.61 km^2, surrounds the northern shores of the bay (Matthijs et al., 1999). The mangrove forest receives low freshwater and sediment inputs. Tidal amplitude ranges from about 1.4 m to 4 m at neap and spring tides, respectively, generating significant flows across the bay. The large *Thalassia* seagrass beds (7 km^2), lying southwards and seawards from the mangroves, likely act as a trap of nutrients (Kitheka, 1996).

2.2. Sampling

A transect was established across the intertidal zone; as a strong relationship was found between tidal flooding intervals and vegetation (Fig. 1) four distinct mangrove compartments were defined as stations.

The “Desert-like belt” (DES1 and DES2 representative soil profiles) is only flooded at the highest spring tides, about 5 days per month, and is mostly bare (Fig. 1). The “*Avicennia* belt” (AV1 and AV2 profiles), bounded by high spring tide and high neap tide levels, is covered by a fairly closed canopy of *Avicennia marina* forest with a Leaf Area Index (LAI) of 1.18 (Robert et al., 2009; Schmitz et al., 2008). The Upper Eulittoral belt is bounded by high neap tide and average sea levels; *Ceriops tagal* (CER), is the dominant specie but a pure open forest (LAI 0.23) of *A. marina* is also present (AV3). Although *Avicennia* forests in both zones are of the basin scrub-type (Middelburg et al., 1996), the Upper eulittoral belt trees are smaller (mean height of 2 m) compared to those in the *Avicennia* belt (Robert et al., 2009; Schmitz et al., 2008). The “*Rhizophora* belt” (RHI), dominated by *Rhizophora mucronata*, lies below average sea level and, being daily inundated, has nearly permanently saturated soils.

Sampling took place in October 2009. Triplicate soil profiles were sampled both according to soil genetic horizons, which were distinguished by features dependent on pedogenesis (Soil Survey Staff, 2010), and to fully represent fixed depth intervals, set as 0–10, 10–20, 20–40 and 40–80 cm. Further samples were collected by auger to check soil spatial variability for each belt. Descriptions of 7 representative soil profiles (DES1, DES2, AV1, AV2, AV3, CER, RHI), are presented. Samples for bulk density (BD) were collected for the fixed depth intervals with a 123.15 cm^3 ($h = 5$ cm and $r = 2.8$ cm) steel cylinder.

2.3. Estimation of crab biomass and matter stored in sesarmid burrows

For each belt, five 2 × 2 m random quadrats were sampled to assess the density of crab populations. Different sampling techniques were