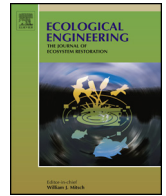




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# Decomposition as a regulator of carbon accretion in mangroves: a review

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### ABSTRACT

The production and decomposition of litter in mangroves plays a significant role in the nutrient and organic carbon cycles. These can be highly variable both spatially and temporally as a result of numerous factors including tidal range, forest type, abundance and type of herbivorous fauna, temperature, and microbial activity. Mangroves also play an important role in blue carbon sequestration, with their status as carbon sinks crucial in mitigating against greenhouse gas-induced climate change. Blue carbon is a term used to describe the carbon captured by oceans and coastal ecosystems. We review and discuss the current available knowledge regarding sources of organic matter (OM) in mangroves as well as the roles of benthic macrofauna, water and microbial activity in the decomposition of OM in order to gain a better understanding of the decompositional processes that take place. Macrofauna break down and bury litter, thereby improving litter quality, in turn increasing decomposition rates via leaching and microbial activity. Microbial decomposition in mangroves is slow as a result of phenolic concentrations in the litter. A build-up of phenolic compounds inhibits microbial activity leading to the accumulation of OM in mangroves. Although knowledge has improved, there are still gaps in the information available and we still have an incomplete picture of the decompositional process in mangroves, and in particular the formation of blue carbon stores, necessitating further research.

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## 1. Introduction

Mangrove forests are highly productive ecosystems that occur in the intertidal zones of the tropics and sub-tropics (Bouillon et al., 2008a; Keuskamp et al., 2015; Mitsch and Gosselink, 2015). These intertidal forests play an important role in coastal ocean biogeochemistry as they act as nutrient filters between land and sea (Sanders et al., 2010a; Bouillon et al., 2008a; Castillo et al., 2017). Their nutrient cycles are closely linked with those found in the adjacent water (Alongi, 1996). Mangroves also play a significant role in the total organic carbon (TOC) oceanic cycle (Sanders et al., 2010b) as they have the capacity to efficiently trap, uptake and recycle suspended litter in the water column (Twilley et al., 1986; Kristensen et al., 1994; Middleburg et al., 1996; Sanders et al., 2012).

Decomposition is an important process that controls the flux of carbon and nutrients in mangroves (McKee and Faulkner, 2000). Due to the imbalance between rates of organic matter (OM) production and decomposition, mangroves and other vegetated coastal

ecosystems represent an important global carbon sink (Donato et al., 2011; Yuan et al., 2015). As such, mangroves are receiving growing attention in the climate change debate in relation to their capacity for so-called “blue carbon” sequestration. In this context, the estimated 30–50% reduction in mangrove coverage reported in recent decades (Donato et al., 2011) is a significant concern.

The magnitude and fate of OM in mangroves is highly variable both temporally and spatially because they are regulated by numerous factors such as soil type and texture, tidal range and elevation, bioturbation intensity, forest type, abundance of herbivorous fauna, redox state, temperature and rainfall (Middelburg et al., 1996; Ashton et al., 1999; Sukardjo and Alongi, 2013).

In this report, we review and evaluate the current knowledge regarding the decomposition of OM in mangrove ecosystems. We will discuss the various sources of OM and review the different decomposition processes that take place in mangroves, including leaching, litter grazing by macroinvertebrates and microbial decomposition, with an emphasis on carbon, nitrogen and phosphorous cycles. Developing a more comprehensive understanding of decomposition processes in these systems is vital given their important role in sequestering blue carbon, and potentially mitigating against climate change.

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## 2. Sources of organic matter in mangroves

There are a range of sources that contribute to the OM found in mangroves. The two primary sources are litter fall from trees, which is composed primarily of leaves, propagules, fallen tree stems and branches along with subsurface roots (Tam and Wong, 1998; Bouillon et al., 2004; Kristensen et al., 2008). Organic matter inputs also consist of production by micro- or macro-algae, phytoplankton production in the local water column (autochthonous inputs) and marine or riverine material such as seagrasses (allochthonous inputs) (Bouillon et al., 2004; Kristensen et al., 2008).

### 2.1. Primary productivity

The primary means of estimating the input rate of OM in mangroves is using primary production (Kristensen et al., 2008). Litter production is one of the three main components of net forest primary productivity and therefore a useful indicator of primary productivity (Mfilinge et al., 2005; Sukardjo and Alongi, 2013). It is estimated that litter fall from mangroves equates to approximately 30%–60% of net primary production in forest ecosystems (Ashton et al., 1999; Alongi et al., 2005; Malhi et al., 2011; Alongi, 2014); with global average litter fall rates of  $38 \text{ mol C m}^{-2} \text{ yr}^{-1}$  (Kristensen et al., 2008). However, production rates can vary widely throughout the globe with the highest rates observed in tropical regions (lowest latitudes), and rates decreasing linearly with increasing latitude (sub-tropical regions; Twilley et al., 1992). Litter production also varies between species (Hossain and Hoque, 2008) along with percentage contribution between leaves, fruits, flowers, stipules and twigs which can also vary seasonally (Mfilinge et al., 2005; Hossain and Hoque, 2008; Kamruzzaman et al., 2017).

Litter production can also be dependent upon flood duration. A study conducted by Krauss et al. (2006) identified that *L. racemosa* distributed more biomass to leaves and stems than to roots with greater flood duration, as opposed to *A. germinans*, which distributed more biomass to its roots. *R. mangle* appeared to be unaffected by flood duration.

Relying solely on litter fall may give a skewed estimate of primary production as mangroves can also be efficient at trapping suspended material from the water column, trapping on average 30% of sediment (Victor et al., 2004) with records as high as 80% (Furukawa et al., 1997). Other sources of primary productivity in mangroves are known to vary substantially; microphytobenthos, phytoplankton and benthic macroalgae rates of productivity are reported to range between 7 and  $73 \text{ mol C m}^{-2} \text{ year}^{-1}$ ,  $0.7\text{--}21 \text{ mol C m}^{-2} \text{ year}^{-1}$ , and  $110\text{--}118 \text{ mol C m}^{-2} \text{ year}^{-1}$  respectively (Kristensen et al., 2008). Ray and Shahraki (2016), in their survey of an Indian and Iranian mangrove system also showed that the contribution from different carbon sources may show significant seasonal variation.

## 3. The role of benthic macrofauna in organic matter decomposition

Mangrove forests are an important habitat for a diverse community of benthic fauna which are typically dominated by burrowing decapods such as grapsid crabs, fiddler crabs and sesarmine crabs (Kristensen et al., 2008; Kristensen, 2008; Bouillon et al., 2008b; Mfilinge and Tsuchiya, 2008). The macrofauna are important biotic agents in the regulation of mangrove productivity (Lee, 1999). The foraging and feeding activity of the macrofauna are reported to influence the rate of OM export, decomposition, and nutrient cycling (Lee, 1999; McKee and Faulkner, 2000; Middleton and McKee, 2001; Bosire et al., 2005; Mfilinge and Tsuchiya, 2008;

Bouillon et al., 2008b; Kristensen and Alongi, 2006; Kristensen et al., 2008; Kristensen, 2008).

Due to their dominance, a large majority of studies conducted on macrofauna in mangroves have focused on crabs and in particular, sesarmid and fiddler crabs. Crabs have been identified as ecosystem engineers due to the fact that the construction of their burrows modify physical structures, substance chemistry and transport conditions which alter the availability of resources for microbial, faunal and plant communities (Schories et al., 2003; Kristensen, 2008).

### 3.1. Macrofauna feeding activities

Although previously believed to be of negligible influence, macrofauna substantially reduce litter export through litter consumption (Lee, 1999; Kristensen et al., 2008; Mfilinge and Tsuchiya, 2008). A study conducted by Robertson (1986) identified that sesarmine crabs could remove at least 28% of litter produced in mixed *Rhizophora* forests through consumption and burial in their burrows. Invertebrates have been found to triple surface litter decomposition rates in intertidal areas (Middleton and McKee, 2001). This influence is likely due to the fact that the majority of their diet is composed of leaf litter. Malley (1978) identified that the stomach contents of the sesarmine crab was more than 95% by volume mangrove leaf fragments.

Camilleri (1992) identified macrofauna as a primary link in the mangrove forest food web. Their study determined that feeding on detritus directly influences the rate of decomposition and that macrofauna have the ability to increase the rate of leaf litter turnover by as much as 75 times, than if they weren't present. Additionally, through analyzing the stomach and rectum contents of *Sesarma erythrodractyla* crabs Camilleri (1992) identified that crabs have a preference for partially aged *Rhizophora stylosa* and *Ruguiera gymnorhiza* litter. Mfilinge and Tsuchiya (2008) later built on these findings and identified a preference for aged or slightly senescent litter which is believed to be a result of lower C/N ratio and higher nutritional value in aged leaves or lower tannin content as it is known to be aversive to detritivores (Bosier et al., 2005).

Crab feeding activities have also been found to affect the quality of litter. When litter is consumed by macrofauna, the plant tissues are broken down, simplifying the structure and the chemical composition and in turn freeing plant cell contents cellulose and hemicellulose from degradation-resistant materials such as lignin (Camilleri, 1992) which facilitates degradation by microorganisms (Camilleri, 1992; Lee, 1999; ; Bosier et al., 2005). Macrofauna and in particular sesarmine crabs also ensure a continuous supply of particulate organic matter (POM) through the production of fecal material which is further decomposed by microorganisms or exported from the mangrove environment (Camilleri, 1992; Lee, 1999).

### 3.2. Macrofauna foraging activities

Crab foraging activities also influence decomposition. Middleton and McKee (2001) identified that crabs plaster leaves on the walls of their burrows and in doing so increase the rate of decomposition by 2.4 times when compared to litter on the soil surface. This increase in decomposition is likely due to the increase in pore water exchange and sediment chemistry (Lee, 1999).

Additionally, bioturbation affects sediment topography and biogeochemistry through the modification of particle size distribution, redox conditions, drainage and OM and nutrient content (Kristensen, 2008). Crab burrows can affect ground water flow and sediment chemistry, all of which influence the decomposition of OM (Lee, 1999). The effect is likely to vary depending on the species since each species has different burrowing techniques resulting

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