

Leaf transport in mimic mangrove forests and seagrass beds

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ABSTRACT: Mangrove forests and seagrass beds are thought to exchange particulate organic material, especially in the form of leaves. However, relatively little is known about the trapping capacity of mangrove above-ground roots and seagrass plants for leaf segments. We aimed to identify the major factors controlling the leaf-trapping capacity of mangroves and seagrasses in a flume study. For mangroves, we found that higher density mangrove roots enhanced trapping capacity whereas the presence of waves strongly reduced the trapping capacity. The latter might be explained by a reduced average collision time (i.e. the time a leaf was attached to a root structure) in the presence of waves. The ability for seagrass beds to trap leaves was dominated by the length/type of vegetation and the absence/presence of waves. Overall, our results suggest that mangroves—via their roots—have a more efficient trapping mechanism than seagrass beds. Mangrove roots extend through the entire water column the majority of the time, which enhances trapping capacity. In contrast, seagrass beds require particulate organic material to become entangled within the predominantly submerged shoots, making trapping dependent on the degraded state of the leaf and the water depth. Our results give an indication of parameters which could be used in a model of trapping capacity of these ecosystems. As leaves are associated with nutrients, we have identified factors which will help to determine what parameters affect the nutrient retention or export of ecosystems. These include density of roots, hydrodynamic conditions (absence/presence of waves), location of initial deposition, degradation stage and type of leaf.

KEY WORDS: Particulate organic material · Nutrients · Trapping capacity · Hydrodynamics · Flume experiment

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INTRODUCTION

Ecosystems are open to exchange materials with adjacent environments (Polis et al. 1997, Lovett et al. 2005). This is particularly true for mangrove forests and seagrass beds, which are often found in proximity to each other in the tropical coastal seascape (Ogden & Gladfelter 1983, Moberg & Rönneback 2003). Both systems are subjected to large tidal exchanges that facilitate the movement of particulate organic matter (POM) and dissolved nutrients from one ecosystem to another, or to deeper water (Lee

1995, Bouillon & Connolly 2009, Davis et al. 2009). POM can be classified as leaves, seeds, roots and other detachable parts of a plant. Of major importance is the nutrient potential of POM, i.e. how much of its associated nutrients can be made available to other ecosystems and organisms (Odum & Heald 1975, Bird et al. 1998, Polis et al. 1997). POM originating from ecosystems such as mangrove forests and/or seagrass beds is potentially an important source of nutrients for adjacent keystone organisms and their associated species (Alongi 1990, Lee & Dunton 2000, Granek et al. 2009).

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Mangrove forests are intertidal ecosystems with large variability in the tree and root formation. Mangrove tree species can range from pioneering species such as *Avicennia* sp. (1 to 2 m tall) which has pneumatophores vertically extending from the ground, to *Rhizophora* sp. (5 to 40 m tall) with characteristic prop or stilt roots that can extend horizontally directly from the trunk (Giesen et al. 2006). Mangrove ecosystems can typically tolerate flow velocities of 0.02 to 0.2 m s⁻¹ and wave heights of 0.15 to 0.25 m (Quartel et al. 2007). In contrast, tropical seagrass species can range from the smallest *Halophila* sp. (leaf length 2 cm) to the largest *Enhalus* sp. (leaf length 30 cm) (Duarte 1991). The ecosystem can experience higher hydrodynamic energy than mangrove forests, flow velocities of 0.0004 to 1.5 m s⁻¹ and wave heights of 0.1 to 0.32 m (de Boer et al. 2000, Masini et al. 2001). Further, the extensive roots systems of many seagrass plants can reduce sediment erosion and facilitate sedimentation (Agawin & Duarte 2002, Gacia et al. 2002).

Because of their shape and density in the water column, mangrove roots and pneumatophores can trap POM (Alongi 1990, Lee 1995). Mangrove trees can decrease the water velocity and attenuate waves, causing calmer hydrodynamic conditions that facilitate trapping (Wolanski et al. 1998, Massel et al. 1999, Quartel et al. 2007). Factors such as density, species, root shape, and biomass as well as intertidal position of the mangrove forest can vary greatly (Friess et al. 2012). These factors affect the hydrodynamics and consequently the trapping capacity. Consequently, the interior of mangroves has greater trapping capacity compared with the seaward edges (Friess et al. 2012). Seagrass beds can also trap particles of POM inside the seagrass canopy (Terrados & Duarte 2000, Agawin & Duarte 2002, Vonk et al. 2008). Trapping results directly from the physical structure of the meadow or from settling induced by changes in the hydrodynamic conditions, which are related to plant/root density, root type and leaf characteristics (Fonseca & Cahalan 1992, Agawin & Duarte 2002, Newell & Koch 2004, Uku & Bjork 2005, Hendriks et al. 2008). Once particulate material is deposited within seagrass beds, a high percentage will remain in place as the plants in the meadow limit re-suspension (e.g. see Terrados & Duarte 2000, Wilkie et al. 2012).

The majority of the studies on POM trapping in mangrove forests and seagrass beds focus on small detrital material (Terrados & Duarte 2000, Agawin & Duarte 2002, Wilkie et al. 2012). Large forms of particulate matter, for example mangrove and seagrass leaves, are a mobile source of POM in the coastal

ocean (Hemminga et al. 1994, Davis et al. 2009). Mangrove forests and tropical seagrass can trap POM in the form of floating leaves (Alongi & Christoffersen 1992, Hemminga et al. 1994, Lee 1995, Kitheka 1997, Rivera-Monroy et al. 1998, Koch & Madden 2001, Bouillon & Connolly 2009). Changes in the water content of leaves through trapping or degradation can also affect their movement although this has only been verified for seeds (Chang et al. 2008). However, relatively little data are available on trapping capacity and transport velocities of various types of leaves in mangrove forests and seagrass meadows. Furthermore we are unaware of how changes in hydrodynamics, such as the presence of waves or increased velocity, can change the trapping capacity of these ecosystems.

To facilitate physical modelling of large POM exchange in the tropical coastal seascape, we used flume experiments to quantify the effects of plant/root density, current velocity, and the absence/presence of waves on the movement of leaves in mimic mangrove forests and seagrass meadows. Moreover, we measured settling velocities to determine the collision time needed for leaves to settle down and how increased moisture content of the leaf may affect its trapping potential. We investigated the following hypotheses regarding the physical trapping of POM within these ecosystems: (1) Higher density seagrass canopies and mangrove roots will increase trapping potential; (2) Longer leaf length will enhance the trapping capacity of mimic mangroves and seagrass ecosystems; (3) Addition of waves to the flow will generate an unbalanced leaf movement, creating a lower likelihood that a leaf will become trapped; (4) Mangroves will have greater trapping potential than seagrass because of their extension through the whole water column. Verifying these hypotheses will provide us with parameters that allow us to model what factors in different ecosystems will affect the transportation of leaves through the ecosystems.

MATERIALS AND METHODS

Flume experiments

By means of a flume study, we quantified the retention of fresh mangrove and seagrass leaf segments by mimicking seagrass canopies and mangrove forests for a variety of hydrodynamic conditions. The experiments were conducted in the racetrack flume (17.5 m long, 0.6 m width and water depth of 0.3 m) at the Royal Netherlands Institute of Sea Research (NIOZ),

Yerseke, Netherlands, in May 2012. The design of the flume allows uniform flow conditions, and generates normal velocity profiles. The fresh leaves were transported in a cool box from Pari Island, Indonesia to NIOZ. The leaves were randomly selected from healthy plants and trees; care was taken to ensure leaves selected were the oldest fully-grown with uniform physical appearance. Leaves were either used immediately in the experiment or kept refrigerated until use. The hydrodynamic conditions tested included 2 current velocities (0.1 and 0.2 m s⁻¹) and 2 wave conditions (none and 0.1 m high, 1 s period waves). These conditions are similar to those typically reported in the literature for mangrove creeks and seagrass meadows (de Boer et al. 2000, Masini et al. 2001, Quartel et al. 2007). For our experiments, we did not investigate extreme tides or a storm, which would have increased the velocities and wave heights; our proposition was to look at the transportation under normal conditions.

Transport was measured for the following leaf segments: 0.1 and 0.3 m length, 0.02 m width and 0.0009 m thickness of fresh *Enhalus acoroides* leaves (seagrass); and 0.2 m length, 0.05 m width and 0.0008 m thickness of *Rhizophora apiculata* leaves (mangrove). In a 2.4 m² (4 m length × 0.6 m width) area of the flume, 2 densities of mangrove roots were mimicked: 4.5 roots m⁻² (low density) and 9 roots m⁻² (high density) using bamboo canes (~0.1 m diameter, ~0.8 m length uncut) (similar to Van der Stocken et al. 2013). A 1.2 m² (2 m length × 0.6 m width) seagrass meadow was mimicked using highly flexible plastic strips (0.2 m tall and 0.02 m wide). Two leaf densities were tested: 200 leaves m⁻² (low density) and 400 leaves m⁻² (high density) (Folkard 2005). Both densities of mangrove roots and seagrass canopies were similar to physical properties of the ecosystems found in the field sites where we did the settling velocity experiments: 6 to 11 mangrove roots m⁻² and 170 to 510 seagrass leaves m⁻². Within the flume section, mangrove roots were randomly distributed over the available space. The mimic canopy was fully submerged in the flume, leaving 0.14 m depth of water overlying the seagrass canopy to mimic an incoming/outgoing tide, i.e. when POM transport may be expected to be highest.

Ten replicates were completed for each combination of parameters for a total of 48 treatments: 2 flow velocities (0.1 and 0.2 m s⁻¹), 2 wave conditions (waves and no waves), 3 leaf lengths/types (0.1 and 0.3 m seagrass leaves and 0.2 m mangrove leaves), 2 mimicked ecosystems (mangrove forest and seagrass meadow) and 2 densities (high and low) for each

mimic ecosystems. For the mangrove forest treatments, individual leaves were released onto the water surface; throughout this experiment all leaves remained on the surface of the water. In the seagrass meadow treatments, individual leaves were released either onto the water surface or at the bottom within the mimicked seagrass canopy. In the mimic mangrove forest treatments, leaves were initially also released on the bottom. However, all leaves floated to the surface of water. Hence this aspect was not investigated in the mangrove experiments.

In total, 240 leaves were observed. We measured the time for leaves to move out of the system and we counted the number of collisions between released leaves and mimicked mangrove roots or seagrass stalks. We also recorded the total time the leaves were stalled due to collisions with mimicked mangrove roots or seagrass material. Preliminary long-term flume runs showed no leaf release once the stall time exceeded 2 min. Hence, if the stall time exceeded 2 min, we considered them to be trapped indefinitely, meaning that to be released, a change in current direction would need to occur. Consequently, the trapping capacity for each system was determined as the percentage of leaves that stayed on a root or within a seagrass bed for >2 min.

Leaf settling velocity experiments

Five fresh seagrass leaves 0.1 m and 0.3 m long were taken from the seagrass bed in Koh Chong Lat Noi bay, on the island of Koh Yao Yai, South Thailand (7° 54' 28" N, 98° 35' 12" E). We also collected five 0.2 m long mangrove leaves from the mangrove forest at the same location. Collected leaves were all green without imperfections in the leaf structure. The leaves were directly transported to the marine laboratory in a cool box. Epiphytes were removed from the collected mangrove and seagrass leaves where they occurred. The leaves (5 each of 0.1 and 0.3 m seagrass leaves and 0.2 m mangrove leaves) were placed into a net bag of mesh size <0.5 mm that allowed for small organisms to migrate in and out, but dispelled larger marine animals such as crabs. At the mangrove forest a metal stake was placed into the substrate. The 3 net bags (i.e. 1 with mangrove and 2 with seagrass leaves) were then secured to the pole at a height of 0.05 m. These net bags were collected from the sampling sites after 5 d and leaves were used for measuring settling velocities.

Settling velocity (m s⁻¹) was measured using a settling chamber, which is a 0.3 m tall cylinder container

filled with water to a depth of 0.3 m. To determine settling velocities, the stopwatch was started when the leaf was placed into the surface of the water and stopped once the entire leaf was deposited on the bottom of the chamber. The time taken was recorded in seconds. Each 5 d degraded leaf was measured in this way, giving 5 replicates for 3 classes (0.1 and 0.3 m seagrass leaves and 0.2 m mangrove leaves). A 5 d degradation period was chosen because we found that at this time period leaves displayed rapid physical degradation.

Statistical analysis

We used ANOVA for analyzing cumulative collision time versus 2 seagrass densities, presence/absence of waves and leaf type in a mangrove forest (1-way ANOVA). A 2-way ANOVA was tested for trapping capacity versus presence/absence of waves in a mangrove forest. Lastly a 3-way ANOVA was used to test travelling times versus 2 velocities, absence/presence of waves and leaf length in the seagrass bed. One-way ANOVA was also used for the settling velocity versus leaf type. Prior to testing, normality in the data was assessed using a D'Agostino-Pearson test. Least squares difference (LSD) post-hoc testing was performed following ANOVA. All statistical testing was completed using the R programming platform (R Development Core Team 2012).

RESULTS

Flume experiment—mangrove forest

The trapping capacity of the high-density mangrove forests, estimated as the percent of leaves that remained trapped on a root for more than 2 min, was higher in the absence of waves ($68 \pm 4.4\%$) than in the presence of waves ($33 \pm 7.3\%$) (2-way ANOVA, $p = 0.0004$, $F = 17.3$, $n = 120$; Fig. 1). The trapping capacity in high density mangroves was also significantly higher than in low density mangroves (2-way ANOVA, $p = 0.02$, $F = 6.2$, $n = 240$; Fig. 1), but the effect of vegetation density (trapping capacity $\sim 20\%$) was smaller than that of waves ($\sim 30\%$). No interactions were found between high and low densities of roots and the absence/presence of waves.

Cumulative collision time was reduced in the presence of waves compared with absence of waves (1-way ANOVA, $p < 0.00001$, $F = 20.4$, $n = 240$; Fig. 2). Among leaf types, the 0.3 m long seagrass leaves had

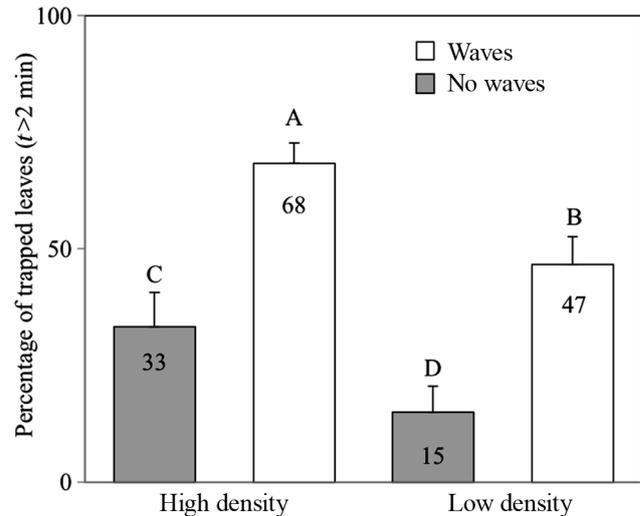


Fig. 1. Percentage of trapped leaves (>2 min) in high- and low-density mangrove root mimics with and without waves. Percentages (numeric values in boxes) were calculated from 240 experiments ($n = 60$ for each treatment). Data are means ($+1$ SE) ($n = 6$ leaves per run). Letters denote significant differences (LSD test, $p = 0.05$)

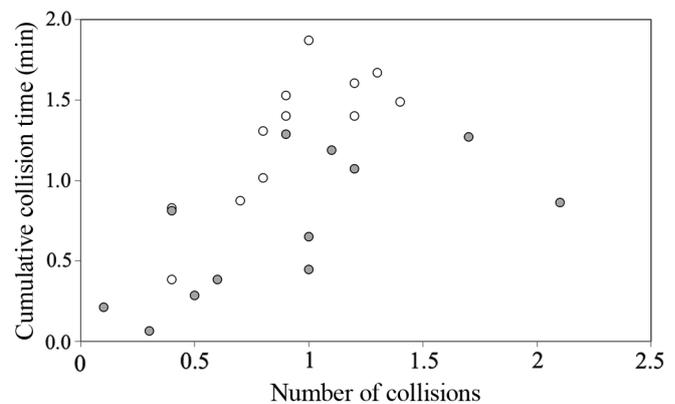


Fig. 2. Relationship between number of collisions and cumulative collision time (min) for a single leaf for experiments with waves (grey circles) and without waves (white circles). In total, 240 leaves were observed ($n = 120$ for each treatment). Data are means of 10 flume runs. Cumulative collision times for wave and no wave conditions were significantly different (1-way ANOVA, $p < 0.00001$, $F = 20.4$, $n = 240$), but number of collisions was not significant

the highest number of collisions as well as the longest collision time in the mimicked mangrove roots (Fig. 3). Seagrass leaves of 0.3 m length collided with the mangrove roots one or more instances the majority of the time ($93 \pm 3.9\%$) (Fig. 3). The 0.1 m long seagrass leaves and 0.2 m long mangrove leaves had fewer collisions. There was a positive relationship between the mean number of collisions and the cumulative collision time (minutes). A little more than half ($58 \pm 8.3\%$) of these leaves (0.1 and 0.2 m) had more than

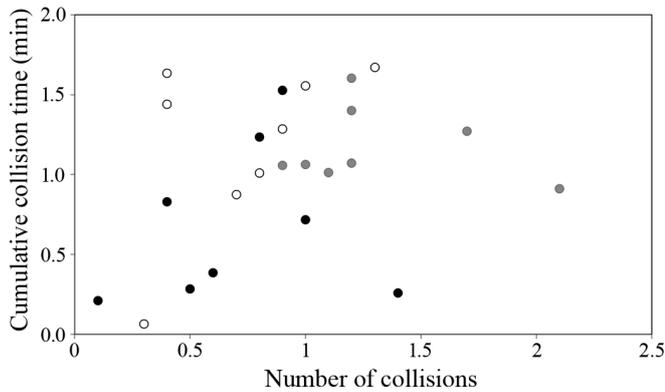


Fig. 3. Relationship between the number of collisions and cumulative collision time (min) for 0.2 m long mangrove leaves (white circles) and 0.1 and 0.3 m seagrass leaves (black and grey circles, respectively). Data are means of $n = 10$ runs ($n = 80$ for each treatment). Mangrove leaves (0.2 m) and seagrass leaves (0.1 m) showed a reduced cumulative collision time compared to seagrass leaves (0.3 m) (1-way ANOVA, $p = 0.0003$, $F = 8.3$, $n = 240$)

one collision with the mangrove roots. The cumulative collision time values for 0.2 m long mangrove leaves and 0.1 m long seagrass leaves were significantly lower than that of 0.3 m long seagrass leaves (1-way ANOVA, $p = 0.0003$, $F = 8.3$, $n = 240$; Fig. 3).

Flume experiment—seagrass bed

In the mimicked seagrass canopy experiments, all leaves released on the water surface moved over the meadow with no collisions. Higher velocity currents decreased travelling time significantly: 0.04 s versus 0.07 s (3-way ANOVA, $p < 0.00001$, $F = 486.6$, $n = 240$), however traveling time was not affected by the presence/absence of waves (3-way ANOVA, $p = 0.3$, $F = 1.1$, $n = 240$). On the bottom of the seagrass canopy, leaf type generated the greatest difference in travelling time (3-way ANOVA, $p = 0.0004$, $F = 9.2$, $n = 240$; Fig. 4). This difference was due to 0.3 m leaves becoming trapped for >2 min in 3 out of 4 conditions (Fig. 4). In the presence of waves, travelling time for leaves was shorter: 0.9 min versus 1.5 min (3-way ANOVA, $p = 0.02$, $F = 6$, $n = 240$; Fig. 4). Velocity did not change travelling time for leaves in the seagrass canopy (3-way ANOVA, $p = 0.5$, $F = 0.5$, $n = 240$; Fig. 4). Testing with a 3-way ANOVA revealed that there were no interactions between vegetation length/type, absence/presence of waves and current velocity. No significant difference was shown between the different densities of seagrass canopies (1-way ANOVA, $p > 0.5$, $F = 0.06$, $n = 480$), therefore the data was pooled for the high and low densities.

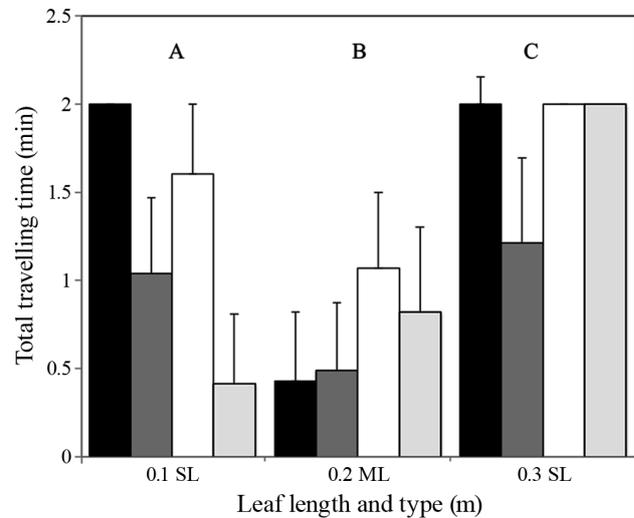


Fig. 4. Total travelling time for leaves of different lengths through the bottom of the seagrass beds for 4 conditions and 3 combinations of leaf lengths and types: 0.1 m seagrass leaves (SL), 0.2 m mangrove leaves (ML) and 0.3 m seagrass leaves. Boxes refer to the following conditions: no waves and 0.1 $m s^{-1}$ velocity (black), waves at 0.1 $m s^{-1}$ velocity (dark grey), no waves at 0.2 $m s^{-1}$ velocity (white), and waves at 0.2 $m s^{-1}$ velocity (light grey). Density was pooled for the figures. In total 240 leaves were observed ($n = 80$ of 0.1 m seagrass, $n = 80$ of 0.2 m mangrove and $n = 80$ of 0.3 m seagrass leaves). Travel times are means ($+1$ SE) for $n = 10$ runs. Letters denote significant differences (LSD test, $p = 0.05$)

Settling velocity

Mean settling velocities of 5 d degraded mangrove leaves (0.2 m: $0.02 m s^{-1}$) and seagrass leaves (0.1 m: $0.011 m s^{-1}$; 0.3 m: $0.01 m s^{-1}$) in the settling chamber with standing sea water showed no significant differences between leaf origin ($p = 0.002$, $F = 10.4$, $n = 5$; Fig. 5).

DISCUSSION

These experiments provide data for some important model parameters affecting the export of POM from mangrove forest and seagrass beds. Models for mangrove structure and dynamics such as FORMAN, KiWi and MANGRO and hydrodynamic models (for example Delft 3D) would be able to utilize this data for greater understanding of spatio-temporal changes in mangrove forests. Trapping capacity of mimicked mangrove roots was strongly dependent on the density of the roots and presence of waves (Fig. 1). Smaller leaves (0.1 m seagrass leaves and 0.2 m mangrove leaves) did not have prolonged collisions with mangrove roots, and therefore had shorter collision

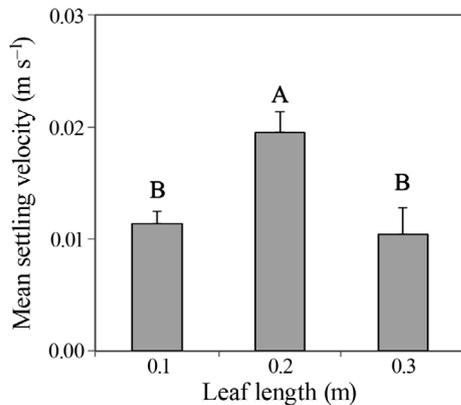


Fig. 5. Mean (+1 SE) settling velocities for different lengths of degraded leaves. Lengths of 0.1 and 0.3 m correspond to the seagrass leaves; 0.2 m, mangrove leaves; letters denote significant differences ($p = 0.002$, $F = 10.4$, $n = 5$ of each leaf type; 1-way ANOVA, LSD test)

times than the longer 0.3 m seagrass leaves (Figs. 2 & 3). Results from the seagrass canopy experiments indicated that leaves are trapped only if they come in contact with the bed, and the rate of trapping within seagrass canopies was determined largely by the length and/or type of vegetation (Fig. 4).

Prior studies have found that the hydrodynamics within a mangrove have a strong influence on dissolved and particulate matter transportation. For example, Wolanski et al. (1998) released a tracer into the upper areas of a mangrove swamp. After 15 d the tracer was still trapped within the edge of the forest. Wave action within mangrove forests decreases from the seaward edge of the mangrove forest towards the landward edge (Koch et al. 2009). Wolanski et al. (1998) showed that particles became trapped in the inner mangrove. Our results are in agreement: we found that trapping capacity increased (from 15–33% to 47–68%; Fig. 1) in the absence of waves (i.e. within the mangroves).

The dispersal of leaves could also be related to the tide cycle, where leaves released at high tide may become stranded above the high tide line—as Allen & Krauss (2006) and Clarke (1993) found for mangrove propagules. We found that smaller leaves were less likely to be trapped by mangrove roots, suggesting that small leaf fragments—e.g. broken by degradation or animals (e.g. crabs)—will have a greater chance of transporting nutrients to other systems. For this experiment we used a simplistic structure of mangrove roots; however, root density and shape has huge variability within mangroves forests depending on location and species. We did not establish transportation for leaves at the bottom of the mangrove roots, which

can be moved by either hydrodynamics or biological aspects such as crabs. Movement of leaves into the sediment has ecological importance and should be the focus for future work. The present work is limited to physical transport with tidal flow, as can be applied in a flume setup.

The capacity of the seagrass canopy to trap POM depended on the initial location where the leaf was released: i.e. on the surface of the water column or within the seagrass canopy. The flexible seagrass canopy did not hinder leaves that floated on the surface. However, if leaves became entangled within the seagrass canopy, they were more likely to be trapped. Settling velocities of 0.01 to 0.02 m s⁻¹ indicate that in shallow water, short collisions are sufficient to cause degraded leaves to settle. Previous work has shown that seagrass canopies can reduce the re-suspension of small particles from within a meadow by approximately 98% (Terrados & Duarte 2000). Thus, once seagrass leaves are deposited within beds, they likely will not be remobilized. Gacia et al. (2002) showed that particulate organic carbon (POC) in seagrass bed sediment can be made up of 43% of *Posidonia oceanica* material. In Kenya, up to 30% of sediment POC was made up from *Thalassia hemprichii* derived particulate matter (Hemminga et al. 1994). In our experiment, the seagrass canopy occupied two-thirds of the water column. This canopy will undoubtedly increase the trapping efficiency compared to seagrass species with very small canopies. Furthermore, tide height at the time of leaf release would affect trapping potential. For example, a spring tide would reduce trapping even with species of seagrass with long leaves if plants are completely submerged. In our experiment we mimicked the incoming/outgoing tide, as POM exchange may be expected to be highest during these periods.

To gain greater insight into the trapping capacity of mangrove forests and seagrasses canopies, further information should be obtained regarding the different types of leaves (both terrestrial and marine). It would be insightful to establish how different types of leaves are trapped and then transported through the bottom of a seagrass bed or mangrove forests. Chang et al. (2008) found that the longer a seed was in water, the higher the water content, and this decreased the seed's buoyancy. A similar mechanism may occur in leaves. Biofilms that form on leaves can change the physical surface of the leaf by making it more tacky (Lindow & Brandl 2003, Bogino et al. 2013). However, in our mimic ecosystems we did not have any biofilms on the roots or canopies (to our knowledge), which may have reduced trapping capacity by reducing this

stickiness. Leaves or roots with a higher potential for biofilm colonisations may have a greater trapping potential. Storm events could result in the simultaneous shedding of many leaves. The transport of a cohort of leaves may change the retention capacity of the ecosystems. This was however outside the scope of the current study.

Both seagrass beds and mangrove forests have different distributions and species assemblage in clear zonation patterns. In addition, differences in density among various species related to zonation potentially affect leaf trapping capacity. For example, in mangrove forests many species at the seaward edge such as *Avicennia* sp. and *Rhizophora* sp. can have extensive horizontal and vertical roots plus pneumatophores (Giesen et al. 2006). These roots and pneumatophores will increase leaf trapping, but their location at the seaward edge means they may experience a relatively high wave action (Giesen et al. 2006, Koch et al. 2009). In contrast, landward mangroves may have a lower root and pneumatophore density but also less exposure to wave action (Giesen et al. 2006, Koch et al. 2009). The present study suggests wave action has a stronger effect on leaf trapping than root density, but it requires further research to fully understand the spatial aspects of root density and wave exposure for leaf trapping. Further, many pioneer seagrass species such as *Halodule* sp. and *Halophila* sp. at the edge of the seagrass bed have smaller leaves and therefore lower trapping potential. We recommend that future work should concentrate on degradation and nutrient-release rates of trapped leaves, and what this means for nutrient retention in the mangrove forest or seagrass bed. Data on trapped degraded leaves would allow us to understand the time scale of nutrient release from leaves. New research should focus on how anthropogenic and natural impacts reduce the density or change the zonation of mangrove forests and seagrass beds. Modelling efforts should focus at the landscape scale and especially take into account how ecosystem fragmentation affects trapping capacity, nutrient retention and nutrient outwelling to adjacent ecosystems or the adjacent estuary.

CONCLUSIONS

Our research indicates that mangrove roots have a more efficient mechanism for trapping leaves than seagrass beds because their roots and pneumatophores extend through much of the water column the majority of the time. In contrast, seagrass beds require

POM to become entangled within the bed. Thus, trapping is dependent on the state of the leaf (degraded and non-degraded) and the water depth. These results give an initial idea of what processes need to be parameterized when modelling the transportation of POM from and between ecosystems: density of roots, hydrodynamic conditions (absence/presence of waves), location of initial deposition, degradation stage and type of leaf. In the present study we primarily concentrate on the physical transport of POM with tidal flow rather than biological transport. Further work is required to understand how biological aspects such as movement by organisms or bacterial degradation may affect leaf litter transportation. Finally, this work strengthens the viewpoint that the POM-trapping capacity of mangrove forests and seagrass beds could have a significant effect on the potential of retaining nutrients in leaves within the ecosystem. Importantly, understanding the trapping capacity of mangrove forests and seagrass beds also supports modeling of outwelling from ecosystems to estuaries in the tropical coastal seascape.

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LITERATURE CITED

- Agawin NSR, Duarte CM (2002) Evidence of direct trapping by a tropical seagrass meadow. *Estuaries* 25:1205–1209
- Allen JA, Krauss KW (2006) Influence of propagule flotation longevity and light availability on establishment of introduced mangrove species in Hawaii. *Pac Sci* 60:367–376
- Alongi DM (1990) Effect of mangrove detrital outwelling on nutrient regeneration and oxygen fluxes in coastal sediments of the central Great Barrier Reef lagoon. *Estuar Coast Shelf Sci* 31:581–598
- Alongi DM, Christoffersen P (1992) Benthic infauna and organism–sediment relations in a shallow, tropical coastal area: influence of outwelled mangrove detritus and physical disturbance. *Mar Ecol Prog Ser* 81:229–245
- Bird KT, Johnson JR, Jewett-Smith J (1998) In vitro culture of the seagrass *Halophila decipiens*. *Aquat Bot* 60:377–387
- Bogino PC, de las Mercedes OM, Sorroche FG, Giordano W (2013) The role of bacterial biofilms and surface components in plant–bacterial associations. *Int J Mol Sci* 14: 15838–15859
- Bouillon S, Connolly RM (2009) Carbon exchange among tropical coastal ecosystems. In: Nagelkerken I (ed) *Ecological connectivity among tropical coastal ecosystems*. Springer, Dordrecht, p 45–70
- Chang ER, Veeneklaas RM, Buitenwerf R, Bakker JP, Bouma TJ (2008) To move or not to move: determinants of seed retention in a tidal marsh. *Funct Ecol* 22:720–727
- Clarke PJ (1993) Dispersal of grey mangrove (*Avicennia*

- marina*) propagules in southeastern Australia. *Aquat Bot* 45:195–204
- Davis SE, Lirman D, Wozniak JR (2009) Nitrogen and phosphorus exchange among tropical coastal ecosystems. In: Nagelkerken I (ed) *Ecological connectivity among tropical coastal ecosystems*. Springer, Dordrecht, p 9–43
- de Boer WF, Rydberg L, Saide V (2000) Tides, tidal currents and their effects on the intertidal ecosystem of the southern bay, Inhaca Island, Mozambique. *Hydrobiologia* 428: 187–196
- Duarte CM (1991) Seagrass depth limits. *Aquat Bot* 40: 363–377
- Folkard AM (2005) Hydrodynamics of model *Posidonia oceanica* patches in shallow water. *Limnol Oceanogr* 50: 1592–1600
- Fonseca MS, Cahalan JA (1992) A preliminary evaluation of wave attenuation by four species of seagrass. *Estuar Coast Shelf Sci* 35:565–576
- Friess DA, Krauss KW, Horstman EM, Balke T, Bouma TJ, Galli D, Webb EL (2012) Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. *Biol Rev* 87:346–366
- Gacia E, Duarte CM, Middelburg JJ (2002) Carbon and nutrient deposition in a Mediterranean seagrass (*Posidonia oceanica*) meadow. *Limnol Oceanogr* 47:23–32
- Giesen W, Wulffraat S, Zieren M, Scholten L (2006) Mangrove guidebook for Southeast Asia. FAO, Bangkok
- Granek EF, Compton JE, Phillips DL (2009) Mangrove-exported nutrient incorporation by sessile coral reef invertebrates. *Ecosystems* 12:462–472
- Hemminga MA, Slim FJ, Kazungu J, Ganssen GM, Nieuwenhuize J, Kruyt NM (1994) Carbon outwelling from a mangrove forest with adjacent seagrass beds and coral reefs (Gazi Bay, Kenya). *Mar Ecol Prog Ser* 106:291–301
- Hendriks IE, Sintes T, Bouma TJ, Duarte CM (2008) Experimental assessment and modeling evaluation of the effects of the seagrass *Posidonia oceanica* on flow and particle trapping. *Mar Ecol Prog Ser* 356:163–173
- Kitheka JU (1997) Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. *Estuar Coast Shelf Sci* 45:177–187
- Koch MS, Madden CJ (2001) Patterns of primary production and nutrient availability in a Bahamas lagoon with fringing mangroves. *Mar Ecol Prog Ser* 219:109–119
- Koch EW, Barbier EB, Silliman BR, Reed DJ and others (2009) Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. *Front Ecol Environ* 7:29–37
- Lee KS, Dunton KH (2000) Effects of nitrogen enrichment on biomass allocation, growth, and leaf morphology of the seagrass *Thalassia testudinum*. *Mar Ecol Prog Ser* 196:39–48
- Lee SY (1995) Mangrove outwelling: a review. *Hydrobiologia* 295:203–212
- Lindow SE, Brandl MT (2003) Microbiology of the phyllosphere. *Appl Environ Microbiol* 69:1875–1883
- Lovett GM, Jones CG, Turner M, Weathers KC (eds) (2005) *Ecosystem function in heterogeneous landscapes*. Springer, New York, NY
- Masini RJ, Anderson PK, McComb AJ (2001) A *Halodule*-dominated community in subtropical embayment: physical environment, productivity, biomass, and impact of dugong grazing. *Aquat Bot* 71:179–197
- Massel SR, Furukawa K, Brinkman RM (1999) Surface wave propagation in mangrove Forests. *Fluid Dyn Res* 24: 219–249
- Moberg F, Rönnback P (2003) Ecosystem services of the tropical seascape: interactions, substitutions and restoration. *Ocean Coast Manag* 46:27–46
- Newell RIE, Koch EW (2004) Modeling seagrass density and distribution in response to changes in turbidity stemming from bivalve filtration and seagrass sediment stabilization. *Estuaries* 27:793–806
- Odum E, Heald EJ (1975) The detritus-based food web of an estuarine mangrove community. In: Cronin LE (ed) *Estuarine research*, Vol 1. Academic Press, New York, NY, p 265–286
- Ogden JC, Gladfelter EH (1983) Coral reefs, seagrass beds and mangroves: their interactions in the coastal zones of the Caribbean. *UNESCO Rep Mar Sci* 23:133
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28: 289–316
- Quartel S, Kroon A, Augustinus PGEF, Van Santen P, Tri NH (2007) Wave attenuation in coastal mangroves in the Red River Delta, Vietnam. *J Asian Earth Sci* 29:576–584
- R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org/
- Rivera-Monroy VH, Madden CJ, Day JW, Twilley RR, Vera-Herrera F, Alvarez-Guillén H (1998) Seasonal coupling of a tropical mangrove forest and an estuarine water column: enhancement of aquatic primary productivity. *Hydrobiologia* 379:41–53
- Terrados J, Duarte CM (2000) Experimental evidence of reduced particle resuspension within a seagrass (*Posidonia oceanica* L.) meadow. *J Exp Mar Biol Ecol* 243:45–53
- Uku J, Bjork M (2005) Productivity aspects of three tropical seagrass species in areas of different nutrient levels in Kenya. *Estuar Coast Shelf Sci* 63:407–420
- Van der Stocken T, De Ryck DJR, Balke T, Bouma TJ, Dahdouh-Guebas F, Koedam N (2013) The role of wind in hydrochorous mangrove propagule dispersal. *Biogeosciences Discuss* 10:895–925
- Vonk JA, Kneer D, Stapel J, Asmus H (2008) Shrimp burrow in tropical seascape meadows: an important sink for litter. *Estuar Coast Shelf Sci* 79:79–85
- Wilkie L, O'Hare MT, Davidson I (2012) Particle trapping and retention by *Zostera noltii*: a flume and field study. *Aquat Bot* 102:15–22
- Wolanski E, Nhan NH, Spagnol S (1998) Sediment dynamics during low flow conditions in the Mekong river estuary, Vietnam. *J Coast Res* 14:472–482