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Mangrove leaf transportation: Do mimic *Avicennia* and *Rhizophora* roots retain or donate leaves?

L. G. Gillis[1,*], M. Zimmer[1], T. J. Bouma[2]

[1]Mangrove Ecology, Leibniz Center for Tropical Marine Ecology (ZMT), 28359 Bremen, Germany
[2]Department of Spatial Ecology, Royal Netherlands Institute for Sea Research (NIOZ), 4401 NT Yerseke, The Netherlands

ABSTRACT: Mangrove forests are typically located in the catchment areas of the terrestrial zone and can be adjacent to oceanic ecosystems (e.g. seagrass beds and coral reefs). These forests are thought to provide ecosystem services by retaining particulate organic matter such as detrital leaves that can facilitate nutrient-sensitive seagrass beds and coral reefs. However, there is a scarcity of knowledge about the mechanisms that control leaf retention. In this study, using a flume and mimic mangrove roots, we aimed to identify the physical (hydrodynamics, root density and type) and biological (size and decay state of the leaf) parameters that control the retention of leaves within these mangrove forests. Our study found that the majority (83 to 92%) of decaying leaves were retained within *Rhizophora* and *Avicennia* mimic roots. Only the mimic *Rhizophora* roots trapped fresh fragmented leaves (25%); other drivers such as fragment size, root density and presence of waves showed a significant difference in trapping leaves. These results suggest that the zonation of tree species and the hydrodynamics acting on roots can play an important role in the leaf-trapping capacity of a mangrove forest. This information may be used in planning for conservation and restoration of these forests, especially with respect to facilitating the establishment and expansion of connected ecosystems. However, further work in the field under more realistic hydrodynamic conditions is needed to verify the results of this flume experiment.

KEY WORDS: Mangrove forest · Connectivity · Ecosystem engineer · Flume · Hydrodynamics · Nutrients · Seascape · Particulate organic matter

INTRODUCTION

Ecosystems such as mangrove forests that straddle the interface between the terrestrial and the oceanic zones can experience a strong exchange of particulate organic matter (POM) with the ocean and connected ecosystems (Nagelkerken 2009, Adame & Lovelock 2011). Mangroves are typically found in catchment areas adjacent to the ocean, and this location allows them to receive and retain POM from external (terrestrial and oceanic) as well as internal (mangrove forest) sources. They are often found in proximity to or connected to seagrass beds and coral reefs in the tropical coastal seascape, and therefore may have an important ecosystem function as a buffer for excess nutrient inputs (Ogden & Gladfelter 1983, Moberg & Rönnbäck 2003, Gillis et al. 2014a). This role in retaining POM is important as it provides an essential ecosystem service to oligotrophic systems, and may facilitate the establishment and expansion of seagrass beds and coral reefs (Gillis et al. 2014a). Thus, it is critical to understand how mangrove forests retain or outwell POM such as detrital leaves, and how the retention of POM is affected by various abiotic and biotic variables (e.g. macro- and micro-organisms, hydrodynamics, root type, density of trees).

Mangrove forests support a high diversity of organisms (Benner & Hodson 1985, Twilley et al. 1997) and are one of the most productive ecosystems on the

*Corresponding author: lucy.gillis@leibniz-zmt.de

planet (Bouillon et al. 2008, Nagelkerken et al. 2008, Lee et al. 2014). For many mangrove-associated organisms, senescent leaves are a major food source (Nagelkerken et al. 2008, Gatune et al. 2012, Zagars et al. 2013). These organisms utilize the nutrients and energy retained in the leaves for growth and reproduction (Alongi 2014). The mangrove forest food web is composed of a mixture of arboreal and sediment flora and fauna that can actively and efficiently cycle POM, even though mangrove leaves can contain high levels of potentially toxic tannins (Alongi 2014). A change in detritus palatability and usability primarily occurs through decay (via micro-organisms) and fragmentation (via macro-organisms, e.g. crabs) (Zimmer 2008). Freshly shed versus decaying leaves, as well as intact versus fragmented leaves, will have different physical attributes such as buoyancy and cohesiveness. Recent work has highlighted the controlling physical parameters of fresh detrital leaf movement using mimic mangrove roots (Gillis et al. 2014b). Nevertheless, relative little is known about how alterations in the shape and buoyancy of decaying leaves may affect how the leaf is transported or trapped within the mangrove forest and how leaves interact with different mangrove root structures and densities.

In order to understand how leaves are transported through mangrove roots, variability in the physical root structures that mangrove species typically exhibit must be considered (Giesen et al. 2006). For example, prop or stilt roots from *Rhizophora* spp. (0.5 to 24 m tall) extend through the entire water column (Giesen et al. 2006), whereas pencil roots associated with *Avicennia* spp. (3 to 14 m tall) extend vertically from the bottom, but not always through the entire water column (although this strongly depends on the tidal regime; Giesen et al. 2006). These various root structures differ in their leaf-trapping mechanisms (Alongi 1990, Lee 1995): prop roots can potentially trap both floating fresh detritus and negatively buoyant decaying leaves, whereas pencil roots (when not extended through the entire water column) mainly trap negatively buoyant decaying leaves. Previous studies have examined leaf and seed movements through mimic *Rhizophora* roots (Van der Stocken et al. 2013, Gillis et al. 2014b); however, to date no studies have included comparisons among different root structures, e.g. between *Avicennia* and *Rhizophora* mimic roots. This an important knowledge gap, since root structures may interact with leaf characteristics e.g. thicker roots (which have a greater surface area) may form a more effective barrier to the movement of whole leaves compared to the trapping capacity of thinner roots for fragmented leaves. In addition to the importance of root structures in understanding leaf trapping, hydrodynamic forcing on the detrital leaves must also be considered.

The physical structure of mangrove trees and their associated roots will also alter the hydrodynamics of the water flow through the forest (Gillis et al. 2014b). Mangrove forests are typically exposed to wave heights of 0.15 to 0.25 m, although they can tolerate higher waves during storms and even small tsunamis (Quartel et al. 2007). Mangrove trees can attenuate waves, resulting in calmer hydrodynamic conditions within the forest that facilitate trapping of detrital leaves (Wolanski et al. 1998, Massel et al. 1999, Quartel et al. 2007). Factors such as tree density, tree species, root shape and standing biomass as well as the intertidal position of the mangrove forest can vary greatly among and between species (Friess et al. 2012). These factors affect the hydrodynamics, and accordingly, the retention capacity of the forest so that interior mangroves may be expected to have a greater trapping capacity for internally produced material and landward supplies compared to the seaward edges (Friess et al. 2012). Retaining and accumulating such internally produced materials is important, as it enables mangroves to act as a sink of dissolved nutrients. The dominance of the mangrove species associated with specific root types (i.e. pencil or prop roots) and their distribution will also interact with the hydrodynamic forces acting on the trees. To date, only *Rhizophora* mimic roots have been studied in relation to hydrodynamic forces acting upon leaf transportation, and only using fresh mangrove and seagrass detrital leaves (Gillis et al. 2014b).

In this study, we aimed to tease apart the various abiotic and biotic parameters that influence the ability of mangrove forests to either retain or outwell detrital leaves to other ecosystems such as seagrass beds or coral reefs. Specifically, our goal was to answer 4 main questions: (1) Do changes in the physical structure of leaves affect the trapping potential of these leaves; (2) Does the presence or absence of waves alter the movement of decaying vs. fresh detritus; (3) Does increasing the density of roots increase their trapping capacity; and (4) How do different types of roots differ in their trapping capacity? By answering these questions, we can gain a greater understanding of the mangrove forests function as a nutrient source or nutrient buffer for connected ecosystems.

MATERIALS AND METHODS

Flume experiment

By means of a flume study, we quantified the retention of fragmented decaying and fresh detrital *Rhizophora mucronata* leaves in the presence and absence of waves (with constant flow velocity) by mimicking prop and pencil roots of mangrove forests. The experiment was conducted in a racetrack flume (17.5 m long, 0.6 m wide, 0.3 m water depth) at the Royal Netherlands Institute of Sea Research (NIOZ), Yerseke, in November 2014 (Fig. 1). The design of the flume allows uniform flow conditions and generates normal velocity profiles. A conveyor belt at the long side of the flume, opposite the measuring section, generates unidirectional flow; regular waves of varying heights and periods can be generated with a wave paddle in front of the measuring section, and the waves can then be superimposed onto a current (Fig. 1) (Paul & Gillis 2015).

Fresh *Rhizophora mucronata* leaves were collected from healthy trees in Zanzibar by gently shaking branches so that only senescent leaves fell; these were collected and transported in a coolbox to Yerseke in October 2014. To obtain fresh detrital leaves, we air-dried the freshly collected leaves to stop further decay. Each individual leaf was then carefully torn apart to resemble fragmented leaves found in the field in Zanzibar. For decaying leaves, our aim was to obtain an intermediate state of litter decay. To achieve this, we placed fresh leaves in plastic bags and kept them at a constant temperature of 20°C for 3 wk before the start of the experiment.

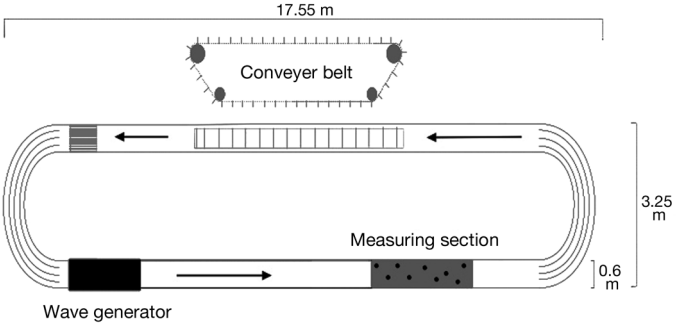


Fig. 1 Flume setup (Paul et al. 2012). Black filled circles in the measuring section represent the mimic mangrove roots made out of bamboo cane (not to scale) that were inserted into the sediment. The conveyor belt (on the side opposite the measuring section) lies on top of the water surface generating unidirectional flow; regular waves of varying heights and periods can be generated with a wave generator (black rectangle) in front of the measuring section

Each individual decayed leaf was then carefully torn apart to resemble the same leaf surface area as the fresh detrital leaves. Both fresh and decaying detritus were then soaked in fresh water for 24 h before the start of the experiment.

The hydrodynamic conditions tested consisted of 2 wave conditions (0 vs. 0.1 m height, 1 s period waves) and 1 current velocity (0.1 m s^{-1}). These conditions are similar to those typically reported in the literature for mangrove forests (Quartel et al. 2007, Friess et al. 2012). We did not try to mimic extreme tides or storms, which would have increased the velocities and wave heights; our goal was to study leaf transportation under average conditions.

Transportation was measured for the following leaf segments both for fresh and decaying detritus: whole leaves (leaf area: 0.007 m^2), half leaves (0.004 to 0.005 m^2) and quarter leaves (0.002 to 0.003 m^2). In a 2.4 m^2 test section of the flume (4 m long × ~0.6 m wide), 2 types of mangrove roots were investigated: pencil (*Avicennia*) and prop (*Rhizophora*) roots. We simulated 2 different densities of mangrove roots: 4.5 roots m^{-2} (low density) and 9 roots m^{-2} (high density), using bamboo canes. The density and size of the *Rhizophora* mimic roots were similar to those found at sites in Indonesia (Gillis et al. 2014b), and *Avicennia* mimic roots had the same physical properties as those found in Zanzibar. For prop roots, we used canes of ~0.1 m diameter and ~0.8 m length (Van der Stocken et al. 2013, Gillis et al. 2014b); for pencil roots, we used canes of ~0.025 m diameter, ~0.1 m length. Within the flume section, mangrove roots were randomly distributed over the available space. The simulated prop roots extended through the entire water column, whilst the pencil roots were fully submerged in the flume, leaving ~0.2 m depth of water overlying them.

Ten replicates were completed for each combination of parameters for a total of 48 treatments (480 leaves in total): 1 flow velocity (0.1 m s^{-1}); 2 wave conditions (presence or absence of waves); 2 mimicked roots (prop or pencil); 2 densities (high or low); 6 leaf types (whole, half, quarter of both decaying and fresh) for each type of mimic root. Leaves were released at the starting point, 0.25 m from the test section; fresh detrital leaves were placed on the water surface whilst decaying leaves (which were negatively buoyant) were placed on the sediment surface.

We measured the time it took for leaves to move out of the system and counted the number of collisions between released leaves and mimic mangrove roots. We also recorded the total time the leaves were

stalled due to collisions with the mimic roots. Preliminary long-term flume runs (Gillis et al. 2014b) showed no leaf release once stall time exceeded 2 min; hence, once leaves were trapped for >2 min we considered them to be trapped indefinitely, i.e. in order to be released, a change in current direction would have to occur. Consequently, the trapping capacity for each system was determined as the percentage of leaves that stayed on a root for >2 min.

Fresh detrital leaf-settling experiment

In order to determine how many days were required for fresh detrital mangrove leaves to become negatively buoyant, 5 of each size (whole, half and quarter) of the fresh detrital leaves without imperfections in leaf structure were placed into a settling chamber (0.4 m tall cylindrical container filled with artificial seawater to a depth of 0.3 m). Settling chambers were monitored during 2 periods each day. No settling velocity experiments were conducted for decaying leaves, as these were already negatively buoyant.

Organic carbon and total nitrogen retained in the system

Fresh and decaying detrital leaves were analyzed for total organic carbon (TOC, %) and total nitrogen (TN, %). Leaf material samples were ground for homogenization, then analyzed by means of elemental analysis isotope ratio mass spectrometry (EA-IRMS) using a Thermo Finnigan Flash 1112. Using the number of leaves trapped, we then approximated the equivalent TOC and TN (g) retained within the system for both fresh and decaying detrital leaves; this was then normalized to represent g m^{-2}.

Statistical analysis

Prior to testing, normality of the data was assessed using a D'Agostino-Pearson test. We used ANOVA to analyze the trapping capacity of decaying versus fresh detrital leaves in *Avicennia* and *Rhizophora* mimic roots (2-way ANOVA) and fresh leaf-settling velocities (1-way ANOVA). No significant difference was found between the trapping capacity of *Rhizophora* and *Avicennia* roots, thus we pooled the results of the decaying leaves. A 3-way ANOVA was used to analyze average collision time of decaying leaves through *Rhizophora* and *Avicennia* roots versus hydrodynamics (presence and absence of waves), leaf shape (whole, half and quarter) and mangrove root density (high and low). Lastly, a 3-way ANOVA was used to test travelling time of fresh detrital leaves through *Rhizophora* roots versus hydrodynamics (presence and absence of waves), leaf shape (whole, half and quarter) and mangrove root density (high and low). Tukey's post hoc test was performed following ANOVA. All statistical analysis was completed using the R programming platform (R Development Core Team 2012).

RESULTS

Trapping of decaying versus fresh detrital leaves

Both *Avicennia* and *Rhizophora* mimic mangrove roots showed remarkably similar trapping capacity for decaying leaves (2-way ANOVA, $p > 0.05$, $F = 4.9$, n = 240; Fig. 2). Mimic *Avicennia* roots did not trap any fresh detrital leaves, whilst mimic *Rhizophora* roots trapped approx. (mean ± SE) 25 ± 8% of fresh detrital leaves (2-way ANOVA, $p < 0.05$, $F = 10.98$, n = 240; Fig. 2). Trapping of decaying leaves in mimic *Avicennia* roots was equivalent to 11.5 g m^{-2} of TOC and 0.081 g m^{-2} of TN; *Rhizophora* mimic roots trapped 3.4 g m^{-2} of TOC and 0.02 gm^{-2} of TN in fresh detrital leaves, and 12.3 g m^{-2} of TOC and 0.076 g m^{-2} of TN in decaying leaves.

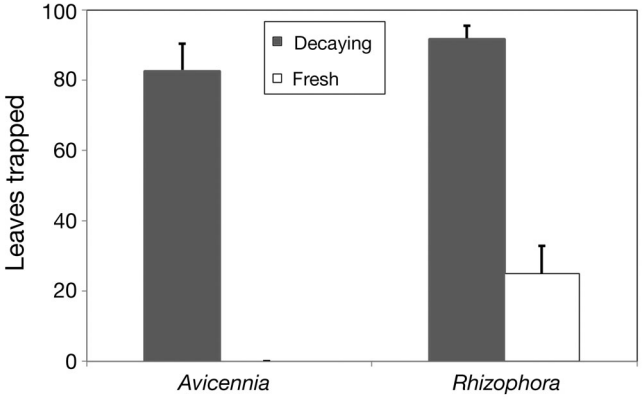
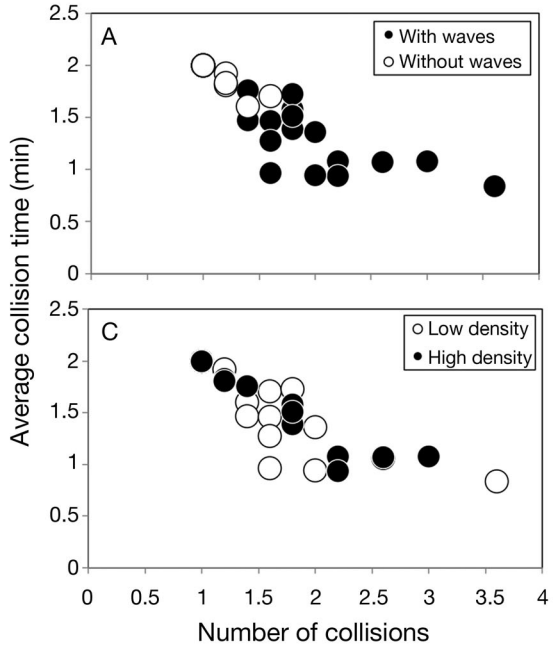


Fig. 2. Mean (±SE) percentage of fresh and decaying leaves trapped (>2 min) in mimic *Avicennia* and *Rhizophora* roots. Percentages were calculated from 480 runs (n = 120 for each treatment, 10 leaves run^{-1}). A significance difference was seen between fresh leaves trapped and root type (2-way ANOVA, $p < 0.05$)



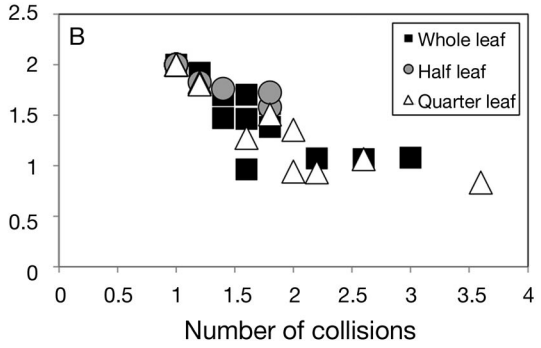


Fig. 3. Number of collisions of leaves versus average collision time of leaves with mimic *Avicennia* and *Rhizophora* roots, showing (A) a single decaying leaf for runs with and without waves, (B) runs using whole, half and quarter leaves and (C) runs using low- and high-density mangrove roots for all hydrodynamic conditions and leaf types. In total, 240 leaves were observed: 120 for (A) and (C); 80 for (B). Data are means of 10 flume runs. Average collision times were significantly different for presence vs. absence of waves and leaf shape (whole, half and quarter) (3-way ANOVA, $p < 0.05$)

Table 1. Three-way ANOVA of controlling factors and interactions for decaying mangrove leaf collisions with *Avicennia* and *Rhizophora* mimic roots. Data reflect interactions between waves (presence or absence), leaf type (whole, half or quarter) and mangrove root density (low or high). ns: not significant. Means followed by a similar superscript letter are not significantly different at $p > 0.05$

Source	df	MS	*F*	p	n	Average collision time (min)(mean ± SE)	No. of collisions (mean ± SE)
Wave	1	15.52	77.71	<0.05	120		
Presence						1.4^{a} ± 0.06	1.8 ± 0.1
Absence						1.95^{b} ± 0.02	1.1 ± 0.03
Leaf	2	3.25	16.27	<0.05	80		
Whole						1.57^{a} ± 0.07	1.58 ± 0.1
Half						1.93^{b} ± 0.03	1.13 ± 0.07
Quarter						1.58^{a} ± 0.07	1.58 ± 0.1
Density	1	0.078	0.39	ns	120		
High						1.71^{a} ± 0.09	1.43 ± 0.09
Low						1.68^{a} ± 0.05	1.43 ± 0.08
Wave × Leaf	2	2.1	10.52	<0.05			
Wave × Density	1	0	0.001	ns			
Leaf × Density	2	0.18	0.88	ns			
Wave × Leaf × Density	2	0.37	1.86	ns			

Driving forces of movement of decaying leaves

Average collision time was reduced in the presence of waves for decaying leaves compared to that in the absence of waves (3-way ANOVA, $p > 0.05$, Fig. 3A, Table 1). The presence of waves also resulted in more collisions compared to the no-wave condition (Table 1). Leaf fragment size also showed a significant difference for average collision time of decaying leaves (3-way ANOVA, $p > 0.05$; Fig. 3, Table 1). Tukey's post hoc test showed that half leaves had the least number of collisions but the highest average collision time compared to the average collision time of whole or quarter decaying leaves, which also had a greater number of stops. Density of the mimic roots showed no significant difference in average collision time of leaves (3-way ANOVA, $p < 0.05$; Fig. 3, Table 1). There was a significant interaction between the presence and absence of waves and size of decaying leaves (3-way ANOVA, $p > 0.05$; Fig. 3,

Table 1). Without waves, 90% of whole, 100% of half and 94% of quarter leaves stopped at the first collision and remained there for 2 min. In the presence of waves, average collision time was reduced for whole and quarter leaves, and 87% of half leaves remained on their first collision with a root for 2 min.

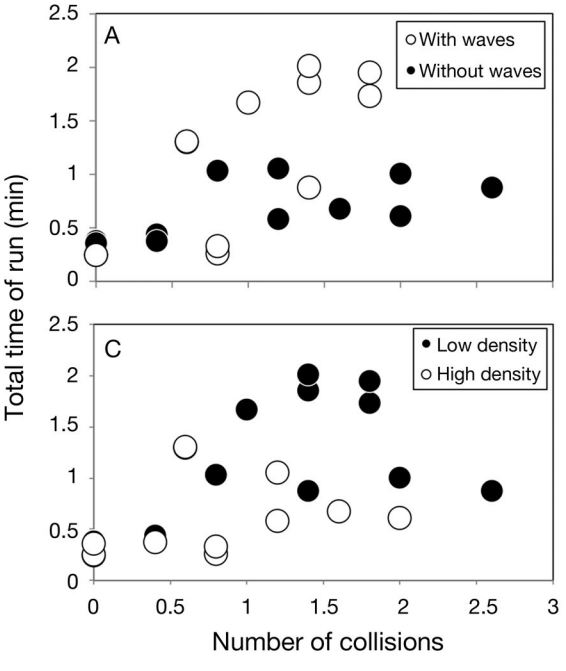
Travel time of fresh detrital leaves through mimic *Rhizophora* roots

Since fresh detrital leaves did not always collide with mimic *Rhizophora* roots, we analyzed total travelling time of the leaves rather than average collision time. A significant difference was seen with changes in hydrodynamic conditions, (absence and presence of waves) (3-way ANOVA, $p < 0.05$; Fig. 4A, Table 2). Post hoc testing showed that in the absence of waves, fresh detrital leaves had longer total travel time than in the presence of waves; however, under both hydrodynamic conditions, leaves had a similar number of collisions (Fig. 4A, Table 2). The different leaf sizes showed a significant difference between total travelling time (3-way ANOVA, $p > 0.05$; Fig. 4B, Table 2). Further post hoc testing for size of detrital leaf showed that there was a significant difference between quarter leaves and both half and whole leaves (Fig. 4B, Table 1), with quarter leaves having 50% of the total travelling time compared to half and whole leaves (Fig. 4B, Table 2).

Number of collisions per type of leaf showed a positive relationship with leaf fragment size, whereby whole leaves had more collisions than half and quarter leaves, and half leaves had a higher number of collisions than quarter leaves (Fig. 4B, Table 2). A significant difference was found between the 2 different mimic root densities and total travelling time (3-way ANOVA, $p > 0.05$; Fig. 4C, Table 2). Tukey's post hoc test indicated that high-density mangrove roots caused a longer travelling time for detrital leaves than low-density roots (Fig. 4C, Table 2). In addition, a difference was seen in the number of collisions, where leaves travelling through high-density roots had almost double the number of collisions compared to leaves travelling through low-density roots (Fig. 4C, Table 2). A significant interaction was also found between density of roots and presence/absence of waves (3 way ANOVA, $p > 0.05$; Table 2). This interaction was seen for conditions without waves plus high density of roots, where leaves had a significantly higher total travelling time compared to all the other variables (Table 2).

Fresh detrital leaf settling velocity

The fresh mangrove leaves took between 3 and 7 d to become negatively buoyant in the 0.3 m settling chamber containing artificial seawater. There was no significant difference in the mean settling velocities



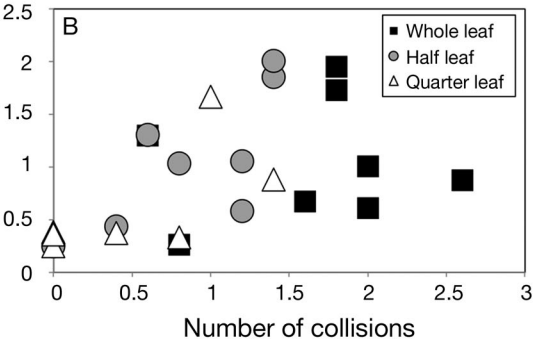


Fig. 4. Number of collisions of leaves versus total time of runs for *Rhizophora* mimic roots, showing (A) a single fresh leaf for runs with and without waves, (B) whole, half and quarter leaves, and (C) low- and high-density mangrove roots for all hydrodynamic conditions and leaf types. In total, 120 leaves were observed: 60 for (A) and (C); 40 for (B). Data are means of 10 flume runs. Total time of runs were significantly different for presence vs. absence of waves, leaf shape (whole, half and quarter) and high vs. low density (3-way ANOVA, $p < 0.05$)

Table 2. Three-way ANOVA of controlling factors and interactions for total travelling time of fresh mangrove leaves through *Rhizophora* mimic roots. Data reflect statistically significant interactions between waves (presence or absence), leaf type (whole, half or quarter) and mangrove root density (low or high). ns: not significant. Means followed by a similar superscript letter are not significantly different at $p > 0.05$

Source	df	MS	*F*	p	n	Total travelling time (min) (mean ± SE)	No. of collisions (mean ± SE)
Wave	1	7.55	20.26	<0.05	60		
Presence						0.65^{a} ± 0.12	1.01 ± 0.15
Absence						1.15^{b} ± 0.12	0.97 ± 0.12
Leaf	2	3.08	8.26	<0.05	40		
Whole						1.05^{a} ± 0.12	1.65 ± 0.18
Half						1.07^{a} ± 0.13	0.88 ± 0.13
Quarter						0.58^{b} ± 0.09	0.45 ± 0.12
Density	2	9.81	26.34	<0.05	60		
High						1.18^{a} ± 0.11	1.21 ± 0.14
Low						0.61^{b} ± 0.08	0.77 ± 0.11
Wave × Leaf	2	0.074	0.19	ns			
Wave × Density	1	7.38	19.81	<0.05			
Leaf × Density	2	0.091	0.24	ns			
Wave × Leaf × Density	2	0.14	0.38	ns			

of fresh detrital leaves (quarter: 1.2×10^{-6}, half: 1.2×10^{-6}, whole: 4.9×10^{-7} m s^{-1}; 1-way ANOVA, $p > 0.05$, $F = 0.78$, $n = 5$).

DISCUSSION

The most important finding of this experiment was that both *Avicennia* and *Rhizophora* mimic roots retained the majority of fragmented decaying leaves. Given that detrital leaves will quickly degrade and potentially become trapped, this finding is highly relevant. It means that nutrient-rich detrital leaves will be retained and be available as a food source for micro- and macro-organisms, and the nutrients in this decaying material will not be exported to connected ecosystems such as seagrass beds and coral reefs. In addition, *Avicennia* roots did not trap any fresh detrital leaves, whilst *Rhizophora* roots trapped ca. 24 ± 8%. This has implications in that *Rhizophora*-dominated zones of the mangrove forests will retain more leaves and thus more particulate nutrients. Finally, we clearly identified the physical parameters that control the ability of mangrove roots to trap fragmented decaying and fresh detrital leaves—notably, the presence of waves, size of leaves and density of the roots.

Decaying leaves were generally always trapped by both *Avicennia* and *Rhizophora* mimic roots. Detrital leaves decay upon physico-chemical processing and through microbial activity, or are fragmented by macrofauna (Nagelkerken et al. 2008). Consumption of these detrital leaves can also play an important role in nutrient cycling (Alongi et al. 1993, Nagelkerken et al. 2008). Thus, it is vital to general ecosystem functioning and the health of the mangrove forest that detritus is retained within the mangrove forest. At the same time, retaining this nutrient source within the mangrove system protects adjacent oligotrophic ecosystems, such as seagrass beds and coral reefs, from eutrophication. The higher proportion of trapped decaying leaves may be due to their reduced buoyancy, as these leaves sink to the ground and adhere to the sediment or roots (Lindow & Brandl 2003, Gatune et al. 2012, Bogino et al. 2013). Decaying leaves did not show any interaction with morphology or density of roots. We expected to see a difference between the various widths of the roots and trapping capacity, but since the decaying leaves did not move from their initial position for the majority of runs, they did not encounter a root. In the instance of fresh floating detrital leaves, we only examined one depth, such that that only *Rhizophora* roots were emerging whilst *Avicennia* roots were submerged. Future studies should seek to clarify how *Avicennia* trees (which have thinner roots) have altered trapping capacities at different depths, which would be more similar to a natural system such as mimicking a tidal cycle.

Mimic *Avicennia* roots only trapped decaying leaves that had sunk to the bottom, but no fresh detrital leaves that were floating at the water surface, because their roots did not extend through the entire water column. Given that many mangroves are in

tidal zones, and therefore the water column depth varies depending on the time of cycle, our estimate of the trapping of fresh detrital leaves by *Avicennia* is likely to be an underestimation. As the tide flows out from the mangrove forest and the depth becomes shallower, *Avicennia* roots would extend further through the water column and therefore also trap fresh detrital leaves. However, thin *Avicennia* roots might form a less effective barrier for fresh detrital leaves than the thicker *Rhizophora* roots. Most importantly, although we cannot quantify the exact effect of the tides, it is obvious that the structure of *Avicennia* roots would result in less effective leaf trapping than that of *Rhizophora*. Mangrove zonation patterns in northern Australia, eastern Africa, Malaysia and Indo-Pacific regions generally indicate that *Avicennia* trees are prevalent at the lowest elevations, typically at the frontal oceanic edge of the forest, whilst *Rhizophora* trees typically occur at a higher elevation in the tidal prism (Smith 2013). Our results provide a greater understanding of leaf retention in terms of the functioning of mangrove zonation for these regions and species density. We found that fresh *Rhizophora mucronata* leaves started sinking after 3 to 7 d, and were well retained by *Rhizophora* roots, especially at high root density. Hence, it is likely that any fresh senescent *Rhizophora* leaves shed from trees would be trapped and sink to the bottom upon becoming detrital before reaching the *Avicennia* zone. This would allow them to be partly decomposed and fragmented by microbes and crabs (Allen & Krauss 2006). However, it should be noted that in other global regions, *Avicennia* species are not limited to the ocean edge of the forest—they can be found in the highest intertidal zones, and *Rhizophora* trees can be found in the lowest (Smith 2013); thus, the trapping capacity of the trees may differ significantly depending on specific zonation patterns within the forest.

We found that waves reduced the trapping capacity of fragmented decaying and fresh detrital mangrove leaves, which is in line with previous flume studies regarding fresh detrital leaves and tracer experiments (Wolanski et al. 1998, Gillis et al. 2014b). Waves decrease exponentially from the seaward edge of mangrove forests to the inner forest; this decrease is related to the distance through the mangroves and the density of mangrove trees and roots (Barbier et al. 2008, Quang Bao 2011). Consequently, the importance of waves in decreasing the retention of detrital leaves will only be of significance to trees that are located close to the ocean or bay where wave action is highest (Massel et al. 1999, Koch et al. 2009). Leaves that are released in the center of the forest or towards the landward edge would experience reduced wave action, and would probably be retained within the forest. We only investigated a single flow condition in our study, but flow conditions in mangrove forests may be quite variable, depending on the time of month or tidal cycle (Quartel et al. 2007, Friess et al. 2012). We recommend that further work should also investigate the potential development of different flow regimes (such as skimming or recirculation flows) forming around emerged or above submerged mangrove roots. The trapping potential of roots may be significantly altered at different tidal periods due to the potential changes in flow regimes or changes in current direction, facilitating the release of leaves or propagules from roots (Stieglitz & Ridd 2001). Studies have already been completed on these flows (Folkard 2011, Adhitya et al. 2014, Paul & Gillis 2015), but did not consider rigid structures or the trapping capacity of POM. Previous studies found no significant difference in the trapping capacity of whole leaves under different flow velocities (0.1 and 0.2 m s^{-1}) and mimic *Rhizophora* roots (Gillis et al. 2014b), but flow conditions as mentioned above may have a greater influence on smaller particles.

CONCLUSIONS

Our results provide valuable information on the role of mangrove forests in retaining and exporting detrital leaves. This information could be used in the conservation and restoration of these forests, especially with respect to facilitating the establishment and expansion of connected ecosystems such as seagrass beds or coral reefs. The restoration of mangrove trees with different types of roots could prove important, especially when nutrient retention or donation are among the ecosystem services required in a given area.

We investigated each root type separately rather than in combination. Further work should seek to clarify how different types of mangrove roots might interact with each other and how they could alter wave evolution and flow velocity. It would also be useful to investigate how the position of leaf fall within the array of mangrove roots and within different configurations of root structures alters the movement of detrital leaves. In this study, we mainly examined transportation within an array, and this might be an underestimation of the trapping capacity. Establishing how hydrodynamics, root structure and leaf characteristics interact with each other could be incorpo-

rated into models such as FORMAN, KiWi and MANGRO, and hydrodynamic models such as Delft 3D, in order to gain a more complete understanding of the dynamics of the mangrove ecosystem.

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