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Impact of landscape structure on propagule dispersal in mangrove forests

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ABSTRACT: Although many riparian and semi-aquatic plant species disperse via water currents, little is known about how this process interacts with the landscape matrix. In mangroves, the dense aerial root network could act as a strong dispersal barrier for the morphologically diverse propagules found in these trees. In this study, we combined field and laboratory experiments to test the effect of root density, propagule morphology and hydrodynamic variables on retention rates and trajectories of the propagules of 4 common species. Overall, flume experiments showed that larger propagules were more frequently retained than smaller ones. For the larger propagules, retention rates increased with increasing obstacle density in the landscape matrix. In elongated propagules, intraspecific variation was linked to floating orientation. Experimental wave action and increased water flow velocity reduced retention. Dispersal in the field was constrained by major tidal currents and experiments confirmed less retention of smaller propagules, which moved farther than larger ones. Overall, our results reveal that the pronounced morphological variation in mangrove propagules interacts with the landscape matrix, contributing to strong differences in dispersal capacity among species and morphotypes. These results may help to explain observed mangrove distribution patterns, including zonation at local, regional and global scales. Additionally, given that many mangrove biotopes are currently strongly threatened by human pressure and fragmentation, this information is important as an input variable for dispersal models that aim to predict dispersal patterns at multiple scales and species responses to environmental change.

KEY WORDS: Retention · Hydrochory · Flume tank · Tidal system · Community structure

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INTRODUCTION

In general, propagules (i.e. dispersal units) of passively dispersing organisms have a low probability of reaching a suitable destination, and this probability strongly decreases with increasing spatial scale (Clobert et al. 2012). Besides the dilution effect associated with dispersal over wider areas, the main causes explaining the failure of propagules to complete their mission are interactions with the landscape matrix. Geomorphology, currents and other landscape elements constitute barriers that may constrain, delay or prevent dispersal altogether. For instance, Baums et al. (2006) showed that for the reef building coral *Acropora palmata*, topographically induced gyres in the Mona Passage between the Dominican Republic and Puerto Rico act as a seasonal filter for larval dispersal, determining population connectivity and structure. Davies & Sheley (2007) demonstrated that high vegetation can strongly limit the dispersal

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distance of wind-dispersed seeds. Mangrove systems provide excellent examples of fragmented populations that are dependent on dispersal for exploiting the availability of suitable local and remote locations. These ecosystems, however, are also notorious for their impenetrable nature. Specialized mangrove growth forms with aerial roots generate dense networks of branches and roots that allow for persistence in a harsh environment with a high disturbance regime. At the same time, the root network is also likely to interfere with hydrochorous transport of mangrove propagules, affecting both emigration and immigration. Although the complexity of the landscape matrix and the interplay with morphological propagule traits and hydrodynamic variables have been shown to influence hydrochorous dispersal in wetland plants (Schneider & Sharitz 1988, Chang et al. 2008, Nilsson et al. 2010), it is unknown whether this process is important for mangrove propagules. Past studies have revealed that the interaction of dispersing mangrove propagules with salt-marsh vegetation can facilitate recruitment (McKee et al. 2007, Peterson & Bell 2012). The efficiency of such physical structures in trapping hydrochorous propagules increases with propagule size (Sousa et al. 2007) and depends on structural differences in vegetation (Peterson & Bell 2012). In addition, higher water levels can strongly reduce or completely overcome the trapping capacity of vegetation structures, with potential effects on deposition patterns (Peterson & Bell 2012). Besides the interaction with physical structures, water flow direction, water depth and propagule traits have been linked to long-term community dynamics (Rabinowitz 1978b). Rabinowitz (1978b) showed that smaller propagules are transported farther inland than larger ones, but the final deposition pattern depends on site-specific conditions (rainfall, overland runoff, tidal regime) (Sousa et al. 2007). Although these studies indicate that propagules interact with the landscape matrix, the effect of propagule traits and hydrodynamic variables on the process of retention and dispersal has, to our knowledge, never been studied for mangroves using a combined experimental (i.e. under controlled conditions) and field based approach.

In this study, we empirically tested the impact of root density, propagule morphology, water flow velocity and waves on the retention and the dispersal distance and direction of mangrove propagules. Therefore, we mimicked mangrove root complexes in a controlled experimental flume tank while manipulating velocity and wave action (*ex situ*). Additionally, we conducted release–recapture experiments in a natural macrotidal mangrove system (*in situ*). In the experimental treatments, different root densities were mimicked and multiple water flow velocities applied. Waves were induced as an additional hydrodynamic variable. We hypothesized that (1) retention of propagules would increase with increasing root density; (2) larger propagules would be more easily retained than smaller ones; (3) propagule retention would decrease with increasing water flow velocity; and (4) wave action would reduce propagule retention. Finally, we assessed the impact of mangrove roots and tidal forces on the dispersal behaviour of the propagules of 2 mangrove species by measuring the dispersal distance and direction in a release–recapture experiment in a natural mangrove system. Here, we hypothesized that (5) the dispersal trajectories of different propagule types in a natural system would be constrained by the interplay between propagule morphology, root density (dispersal distance) and hydrodynamics (dispersal distance and direction).

MATERIALS AND METHODS

Flume experiment

Retention rates and dispersal characteristics of propagules in a mangrove forest environment were studied in a flume facility for a variety of barrier densities and hydrodynamic conditions. The racetrack flume at the Royal Netherlands Institute for Sea Research (see Bouma et al. 2005 for a detailed description) was adjusted with a wooden frame (6 m long, 0.6 m wide and 0.3 m high), of which the bottom and top were covered with poultry netting through which bamboo sticks were inserted to mimic tree stems and vertical stilt roots (Fig. 1). The 2 layers of poultry netting ensured that bamboo sticks were kept in place against the force of the water current. Bamboo sticks (0.04 and 0.06 m diameter) were more or less regularly interspersed over the whole length of the construction, mimicking 3 different root densities (10, 20 and 30 roots m^{-2}). Dispersal behaviour was studied for propagules of 4 species: *Rhizophora mucronata*, *Ceriops tagal*, *Heritiera littoralis* and *Xylocarpus granatum* (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m524p095_supp.pdf). In general, propagules of the first 2 species float horizontally after release from the parent tree and progressively change to a vertical position as the density distribution of their tissue changes (Davis 1940, Rabinowitz 1978a). Hence, for these species,

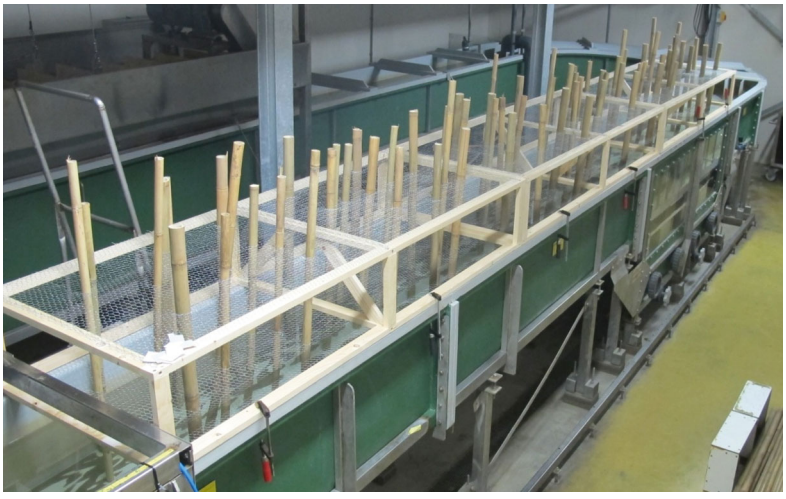

Fig. 1. Mimicked mangrove roots used in our flume experiments. Bamboo sticks (0.04 and 0.06 m diameter) were more or less regularly interspersed over the whole length of the construction, mimicking 3 different root densities (10, 20 and 30 roots m^{-2}). For technical details of the flume, see Bouma et al. (2005)

both horizontally and vertically floating propagules were used. For *X. granatum*, only one fruit (containing 8 seeds) was available. We therefore opted to use the seeds, allowing us to have more replications and to have 2 distinct morphological groups: elongated propagules for *C. tagal* and *R. mucronata*, and the more compact propagules of *H. littoralis* (ellipsoidal, with a dorsal sail) and *X. granatum* seeds (angular, pyramidal). All propagules were sampled in Gazi Bay, Kenya (39° 30′ E, 04° 25′ S) on 28 March 2012. We considered the propagules mature when they readily fell when slightly touched. For *H. littoralis*, propagules were collected at neap tide under a parent tree in the high intertidal area. We checked all propagules for damage, which may alter their buoyancy over the course of the experiment. Root densities of 10 and 30 roots m^{-2} were combined with a water flow velocity of 0.1 m s^{-1}, and the 20 roots m^{-2} density were combined with 3 water flow velocities (0.05, 0.10 and 0.15 m s^{-1}). Water flow velocities were chosen based on the range of water flow conditions in a natural mangrove habitat (Kitheka 1996, 1997). This experimental setup allowed us to study both the effect of various water flow velocities at the same root density, and the effect of different root densities at a constant water flow velocity.

Waves were induced as an additional hydrodynamic variable in one of the treatments (0.10 m s^{-1} water flow velocity and 30 roots m^{-2}) to test the effect of waves on the retention capacity of mangrove roots. Small-scale water surface waves were created by using 6 Knf LABOPORT Mini Diaphragm vacuum pumps at the bottom of the flume (one at each 1 m interval of the test section).

Dispersal velocities through the mimicked mangrove forest were calculated by measuring the time it took propagules to travel through the artificial root system. To interpret the data, we imposed the following rules: (1) a propagule was considered as 'retained' when it was stuck for >3 min, and not touching the walls of the flume; (2) measurements for a propagule that was hindered by the walls of the flume were not considered in the results and were repeated; and (3) when a propagule was retained during 5 subsequent trials, it was labeled 'stranded' (i.e. not able to cross the dispersal barrier).

Field experiment

Field experiments were conducted in a mangrove forest in Gazi Bay (Fig. 2). The tidal regime in this area is semi-diurnal, with ebb currents being stronger than flood currents, and with a macrotidal range of 3.5 m (Kitheka 1996, 1997). Here, 4 plots (1 plot per intertidal location) were selected along an intertidal transect, covering typical stands of the most abundant species and root types: landward *A. marina* zone (AML), *C. tagal* zone (CT), *R. mucronata* zone (RM) and creekward *A. marina* zone (AMC). Average root density and height were measured in the CT and RM intertidal zones. In the CT zone, average root density was 28.8 roots m^{-2} (6 plots of 1 m^2), with an average height of 11.1 ± 5.7 cm (n = 173). For RM, average root height was 16.2 ± 1.5, 6.2 ± 2.4 and 5 ± 2.6 roots m^{-2} at 0, 0.5 and 1 m above the ground (4 plots of 1 m^2), respectively. For the AML and AMC zone, data on root density for the same study site was retrieved from Dahdouh-Guebas et al. (2004). In these zones, root densities range between 4 and 250 roots m^{-2}, and 44 and 1950 roots m^{-2}, respectively. In each plot (1 × 1 m), we placed 30 *C. tagal* and 30 *R. mucronata* propagules at low tide. The propagules were collected from neighbouring *R. mucronata* and *C. tagal* trees, marked with white waterproof paint and numbered, in order to link them to their initial release location. At 1, 2 and 4 d after their release, propagules were retrieved by systematically covering the area within a radius of ~500 m during spring tide (9 to 13 March 2012). Limits of the search area were situated well beyond the zone

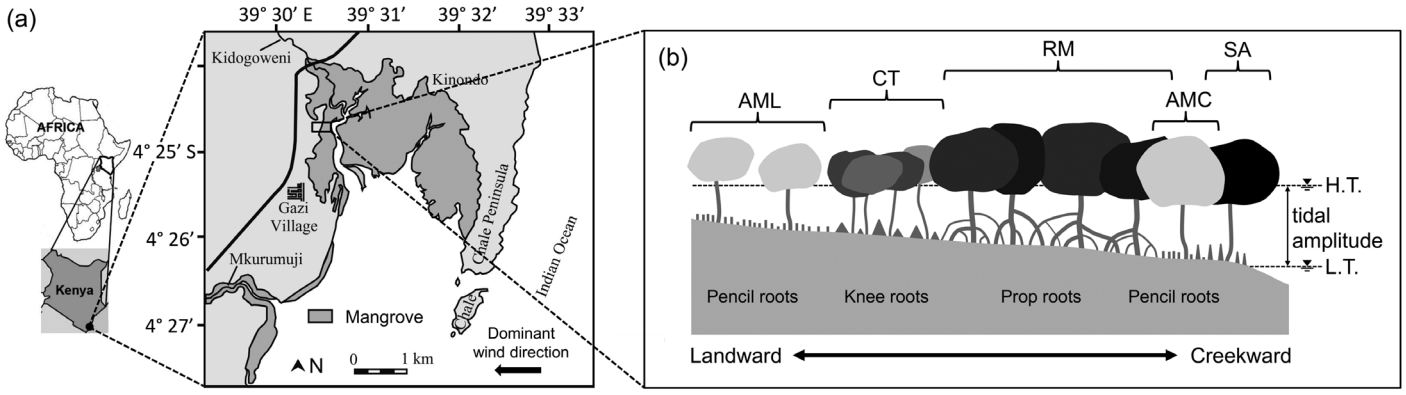

Fig. 2. (a) Study area (Gazi Bay, Kenya; 39° 30′ E, 04° 26′ S) where field experiments were conducted and (b) species zonation along our intertidal transect. AML: *Avicennia marina* landward; CT: *Ceriops tagal*; RM: *Rhizophora mucronata*; AMC: *A. marina* creekward; SA: *Sonneratia alba* (SA was not considered in our study, but is shown for completeness). H.T.: high tide water level; L.T.: low tide water level

in which no more propagules were recovered. The intensity of searching was constant with distance from the release locations, thereby excluding a potential effort-related bias. The experiment was conducted around spring tide (9 to 13 March 2012), as both high and low tide water levels within this period were most extreme, and hydroperiods in the various mangrove zones were the longest. Under these conditions, the interaction of dispersing propagules with the landscape matrix could be studied for all mangrove tree species and root types present over the whole intertidal range, since seawater then also enters the most landward trees of the mangrove forest.

For all recovered propagules, the dispersal distance and direction were measured, using a compass and distometer (Leica DISTO A5, maximum range: 200 m). The distometer relies on line of sight. Hence, for propagules that dispersed beyond the maximum ranges of the distometer, the geographical coordinate was recorded with a Garmin GPSMAP 62 and the dispersal distance calculated via the spherical law of cosine:

$$d = \arccos[\sin(\varphi_1)\sin(\varphi_2)+\cos(\varphi_1)\cos(\varphi_2)\cos(\Delta\lambda)]\cdot R \quad (1)$$

where φ is the latitude, λ the longitude, and R = 6 370 000 m (Earth's radius). The dispersal direction was approximated using the formula for the initial bearing (i.e. forward azimuth):

$$\theta = \arctan 2\begin{bmatrix}\sin(\Delta\lambda)\cos(\varphi_2), \cos(\varphi_1)\sin(\varphi_2)-\\ \sin(\varphi_1)\cos(\varphi_2)\cos(\Delta\lambda)\end{bmatrix} \quad (2)$$

Resulting values were converted to degrees and the modulo function was used to ensure that all angles were between 0 and 360 degrees (www.movable-type.co.uk/scripts/latlong.html).

Data analysis

Potential effects of the categorical variables root density and propagule type on the fraction of retained (1) and non-retained (0) propagules were investigated using a generalized linear model (GLZ) with a logit link function and binomial error distribution. To test the potential effect of water flow velocity on the fraction of retained and non-retained propagules, a GLZ was constructed, including water flow velocity and propagule type as categorical predictors. The potential effect of surface waves was assessed via a GLZ, with surface waves as a predictor variable. The effects of day, propagule type, release location and the multiple interaction terms on dispersal distance in our field experiment were tested using factorial ANOVA, followed by a Tukey post-hoc analysis for pairwise comparison. A general linear model (GLM) was constructed, including day, propagule type, release location and the multiple interactions of these predictor variables. All statistical tests were performed in Statistica 8.0 (StatSoft). Non-significant interaction terms were removed from the models. We tested for significant directionality in the dispersal direction data of our field study using the Rayleigh test of uniformity in Oriana 4.01.

RESULTS

Flume tank experiments on propagule retention

Root density and propagule type. A complete overview of dispersal velocities and proportions of stranded propagules for all propagule types and experimental treatments is provided in Table 1. Overall,

Table 1. Characteristics of the 4 mangrove propagule types used (*Ceriops tagal, Rhizophora mucronata, Heritiera littoralis, Xylocarpus granatum*), retention data and dispersal velocities for the various conditions simulated in the flume experiment. Retained: stuck for >3 min, not touching flume walls; stranded: stuck for >3 min for ≥5× independently. Mean propagule dispersal velocity excludes stranded propagules. (–) Not applicable or no data

Species			*C. tagal*		*R. mucronata*		*H. littoralis*	*X. granatum* seed
Morphology			Elongated		Elongated		Ellipsoidal	Angular/Pyramidal
Floating orientation			Horizontal	Vertical	Horizontal	Vertical	–	–
n			20	19	20	15	10	2×8
Mean length ± SD (cm)			24.38 ± 2.68	24.69 ± 2.21	41.03 ± 6.63	44.93 ± 5.23	–	–
Mean mass ± SD (g)			8.25 ± 1.76	8.27 ± 1.36	64.70 ± 16.39	81.60 ± 24.84	33.33 ± 6.59	48.06 ± 10.15
Mean density ± SD (g cm^{-3})			994.20 ± 9.62	1023.28 ± 4.88	1001.80 ± 8.47	1018.08 ± 5.86	617.42 ± 28.38	870.00 ± 35.32
Water velocity (cm s^{-1})	**Root density (roots m^{-2})**	**Ripples**	**% of propagules retained | stranded**					
5	20	No	80 | 40	0 | 0	100 | 100	84.6 | 84.6	40 | 5	6.25 | 0
10	10	No	70 | 10	0 | 0	75 | 55	20 | 0	0 | 0	0 | 0
10	20	No	80 | 30	0 | 0	95 | 80	33.3 | 0	15 | 0	0 | 0
10	30	No	85 | 55	15.8 | 0	95 | 90	53.3 | 23.1	25 | 0	12.5 | 0
10	30	Yes	80 | 0	–	–	–	–	–
15	20	No	85 | 30	15.8 | 0	95 | 70	38.5 | 0	10 | 0	12.5 | 0
Water velocity (cm s^{-1})	**Root density (roots m^{-2})**	**Ripples**	**Mean propagule dispersal velocity ± SD (cm s^{-1})**					
5	20	No	3.66 ± 1.01 (n = 12)	5.14 ± 0.49 (n = 19)	–	3.93 ± 1.36 (n = 14)	4.85 ± 0.27 (n = 2×10)	4.69 ± 0.52 (n = 2×8)
10	10	No	6.39 ± 1.60 (n = 18)	10.69 ± 1.11 (n = 19)	6.31 ± 1.44 (n = 9)	7.54 ± 1.36 (n = 15)	8.49 ± 0.57 (n = 2×10)	8.66 ± 0.44 (n = 2×8)
10	20	No	6.08 ± 2.57 (n = 16)	10.64 ± 1.08 (n = 19)	6.05 ± 2.72 (n = 3)	10.00 ± 1.55 (n = 15)	9.56 ± 0.74 (n = 2×10)	9.91 ± 0.59 (n = 2×8)
10	30	No	5.06 ± 1.31 (n = 9)	9.22 ± 2.01 (n = 19)	7.35 ± 1.83 (n = 2)	8.37 ± 1.34 (n = 12)	8.37 ± 0.80 (n = 2×10)	8.46 ± 0.88 (n = 2×8)
10	30	Yes	4.28 ± 1.30 (n = 15)	–	–	–	–	–
15	20	No	7.61 ± 2.71 (n = 16)	13.10 ± 1.10 (n = 19)	6.71 ± 1.68 (n = 5)	14.36 ± 1.68 (n = 15)	12.81 ± 1.19 (n = 2×10)	13.48 1.09 (n = 2×8)

the probability to get retained or stranded in roots depended on propagule type (GLZ, $p < 0.0001$). Propagules of *H. littoralis* and *X. granatum*, and of the vertically floating *C. tagal* and *R. mucronata*, did not get stranded in any of the treatments. Of the vertically floating *R. mucronata* propagules, however, between 23.1 and 69.2% were retained, depending on root density and water flow. Root density had a significant effect on the fraction of retained and stranded propagules (GLZ, $p \leq 0.01$), with increasing numbers of propagules being retained or stranded with increasing root density. Detailed results of the GLZ analyses are provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m524p095_supp.pdf.

Water flow velocity. The GLZ including water flow velocity and propagule type identified significant effects of propagule type on the fraction of retained and stranded propagules (GLZ, $p < 0.0001$). Water flow velocity had a significant effect on the fraction of stranded propagules (GLZ, $p = 0.002$), with fewer propagules being stranded with increasing water flow velocity. Water flow velocity had no significant effect on the fraction of retained propagules (GLZ, $p > 0.1$). There was no significant interaction effect. Detailed results of this GLZ are summarized in Table S2 in the Supplement.

Wave action. Wave action reduced the fraction of stranded propagules (GLZ, $p < 0.01$) but not the fraction of retained propagules (GLZ, $p = 0.678$).

Dispersal distance and direction in a natural mangrove system

Of all propagules released, 68 and 95% were respectively recovered for *C. tagal* and *R. mucronata* on the first day (after 1 high tide), 53 and 84% on the second day (after 3 high tides), and 48 and 85% on the third day (after 5 high tides).

Reconstructed dispersal distance distributions were leptokurtic, with the majority of propagules having been transported over short distances (from a few meters to <50 m) (Fig. 3). However, a number of propagules were transported farther than 50 m (31.6% of *C. tagal* and 11.8% of *R. mucronata* propagules; after 5 high tides) and a few farther than 100 m (7.0% of *C. tagal* and no *R. mucronata* propagules; after 5 high tides). One of the *C. tagal* propagules was retrieved at 320 m from its release location after 5 high tides. Dispersal distances differed among propagule types (factorial ANOVA, $F_{1.495}$ = 10.279, p = 0.001). Propagules of *C. tagal* were transported farther from the release site (41.30 ± 52.44 m) than *R. mucronata* propagules (21.86 ± 21.71 m) but dispersal distance also depended on release location (factorial ANOVA, $F_{3.495}$ = 4.547, p = 0.004). Dispersal distances were shorter in the AMC zone than in the RM zone. A GLM revealed significant effects of day, propagule type and release location on dispersal distance ($F_{23.495}$ = 4.13, p < 0.00001, adjusted r^2 = 0.12; Table S3 in the Supplement).

Dispersal direction data showed a clear bimodal distribution that corresponded with the bidirectionality of tidal action in this area (Fig. 4). The average of all dispersal direction data (both species, all zones, all days) was used as a threshold to distinguish the 2 main dispersal direction groups (group 1: >218.2° and <38.2°; group 2: <218.2° and >38.2°) (Table S4 in the Supplement). One group of dispersal directions was towards the south (grand mean after 5 high tides is 176.8°), i.e. towards the inlet of the bay, while a second dominant dispersal direction was inland, more or less perpendicular to the creek (grand mean after 5 high tides is 279.6°). Overall, Rayleigh's tests showed significant directionality in all zones and for all species (all p < 0.05), with the exception of the *C. tagal* propagules released in the RM zone, presumably due to the low number of recovered propagules (n = 3).

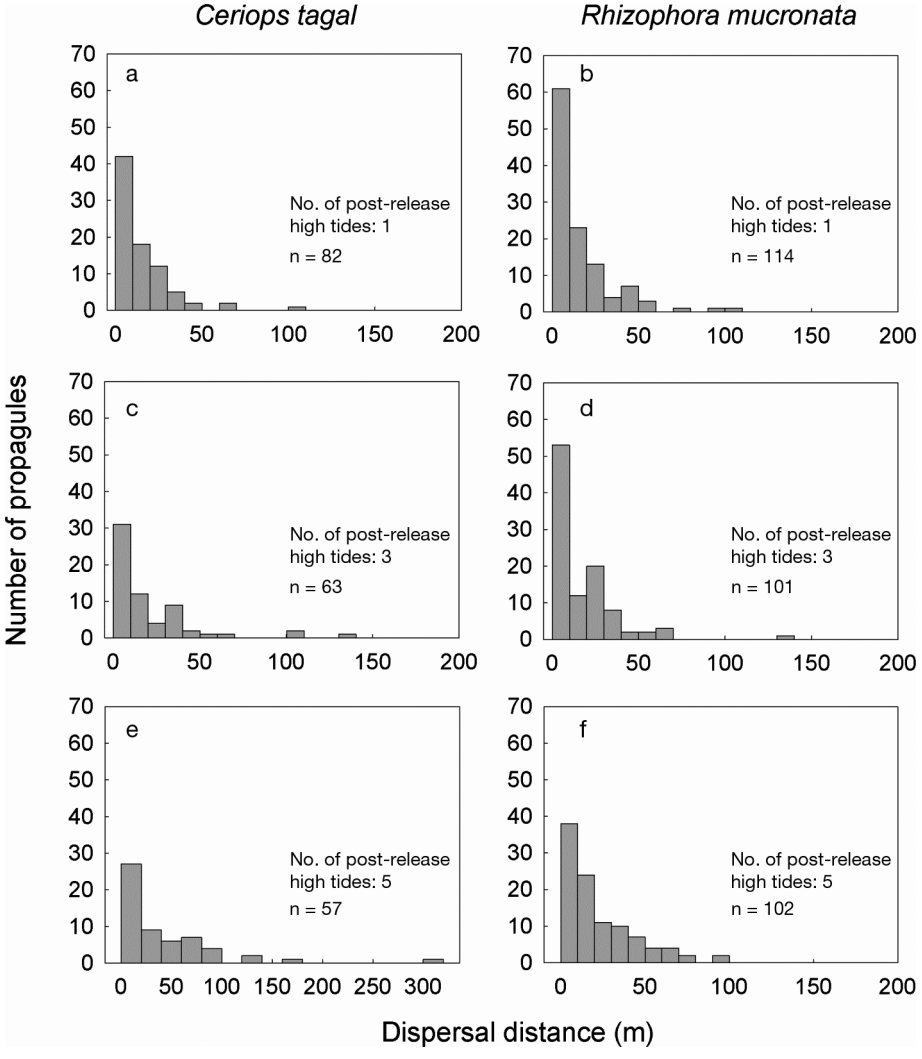

Fig. 3. Dispersal distances of *Ceriops tagal* and *Rhizophora mucronata* propagules along a transect in the mangrove forest of Gazi Bay (Kenya). Propagules were released in 4 different plots covering typical stands of the most abundant root types in a natural macrotidal mangrove system. Propagules were searched for at 1 d (1 high tide), 2 d (3 high tides), and 4 d (5 high tides) after their release. The intensity of searching was constant with distance from the release locations, excluding a potential effort-related bias. Hence, the decreasing number or propagules recovered is distance-related

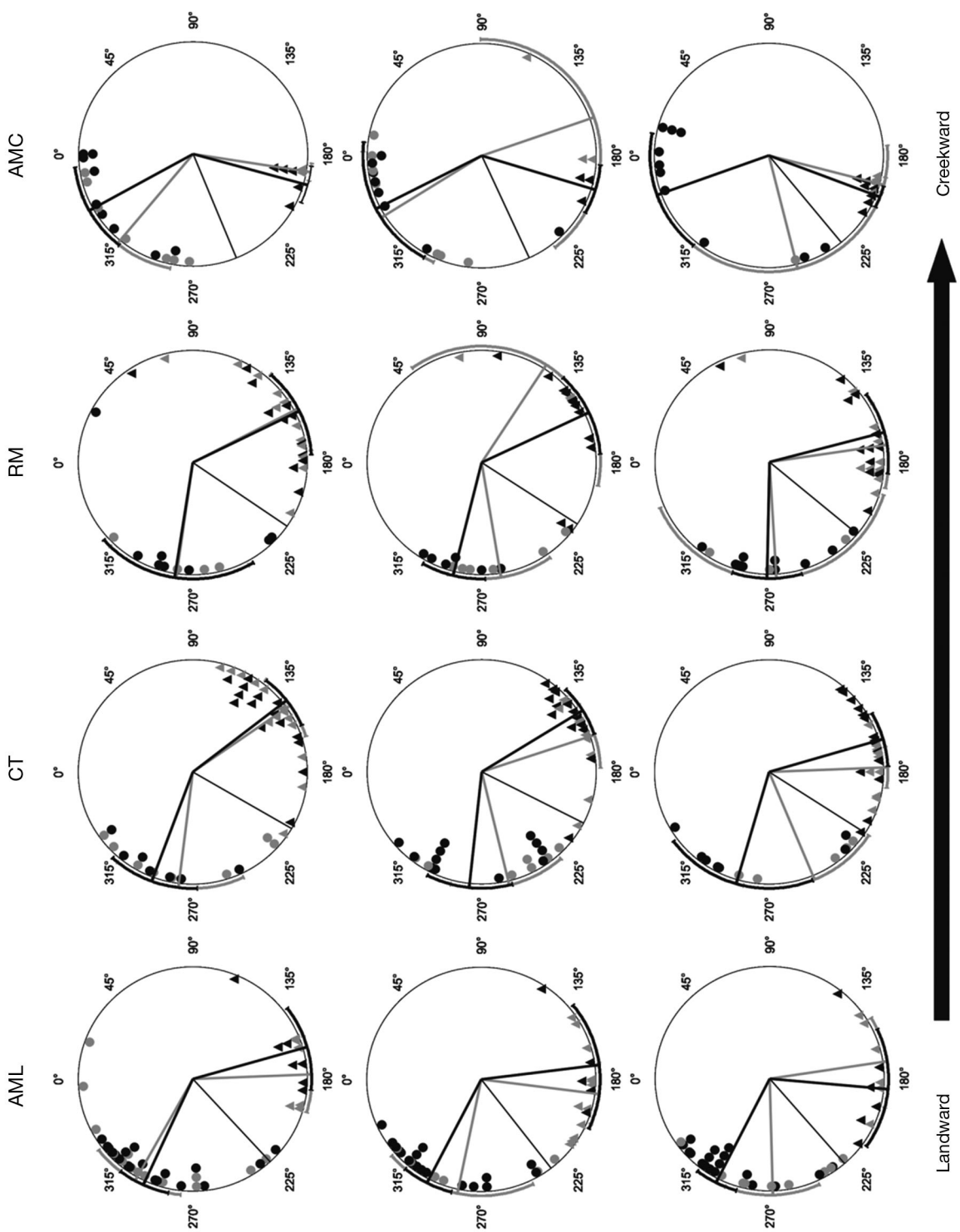

Fig. 4. Circular representation of dispersal directions of the *Ceriops tagal* (grey symbols) and *Rhizophora mucronata* (black symbols) propagules released at the various mangrove species zones along our transect (AML: *Avicennia marina* landward; CT: *C. tagal*; RM: *R. mucronata*; AMC: *A. marina* creekward). For each of the 2 species, 30 propagules were released at low tide on 9 March 2012 and retrieved on 10 March 2012 (after 1 high tide), 11 March 2012 (after 3 high tides) and 13 March 2012 (after 5 high tides). Based on the clear bimodal nature of the data, 2 groups of dispersal directions were defined using the average dispersal directions of all data—group 1: >218.2° and <38.2° (circles); group 2: <218.2° and >38.2° (triangles). Bold lines from the centre to the periphery represent averages for the dispersal direction groups; intervals outside the periphery are 95% CIs. Thin lines represent the grand mean

DISCUSSION

Current advances in predicting gene flow and range expansion in plants are hampered by a lack of knowledge on interactions between dispersing propagules and the landscape matrix. This problem is of particular importance for mangrove systems, where propagules have to navigate through a maze of roots and stems before being dispersed over long distances.

As expected, the fraction of retained and stranded propagules increased with increasing propagule size. This empirically supports our field observations, where the smaller *C. tagal* propagules on average dispersed farther than the larger *R. mucronata* propagules. Similar effects of size-related interactions with the landscape matrix on dispersal distances were found in a natural mangrove system in Panama (Sousa et al. 2007). Results from our flume study revealed the additional importance of buoyancy orientation. Both in *C. tagal* and *R. mucronata*, horizontally floating propagules were more likely to get stuck in the landscape matrix. This is due to the fact that the vertically floating propagules floated parallel to the root mimics used in our flume experiment. Hence, they experienced less obstruction as compared to their horizontally floating counterparts. Of course, at specific moments over the tidal cycle when water depth is lower than the height of a dispersing propagule, friction with the substrate may slow down or hamper dispersal.

Fractions of retained and stranded propagules also increased with increasing root density. This agrees with the findings of Peterson & Bell (2012) on the retention of *A. germinans* propagules by salt-marsh plants. In their experiment, differences in propagule retention were explained by structural differences (lateral obstruction) in vegetation. In a flume study on the sorting of seeds in riparian systems, it was reported that sorting became more effective with increasing stem density (Chambert & James 2009).

Besides propagule traits, hydrodynamic variables such as surface waves also influence the interaction of dispersing propagules with the landscape matrix. Flume experiments using waterlogged seeds of 3 salt-marsh species (*Plantago maritima*, *Suaeda maritima* and *Elytrigia atherica*) demonstrated that surface waves in combination with water flow can strongly reduce the number of retained seeds (Chang et al. 2008). This agrees with measurements on the retention of mangrove leaves by mangrove roots and seagrass beds (Gillis et al. 2014), and is supported by our flume study on the transport of mangrove propagules. These results suggest that wind-generated waves or larger waves during storms could impact dispersal and propagule deposition patterns via the dislodgement of retained propagules. Especially at the edge of a mangrove forest, where wave energy has not yet dissipated, the effect of waves on the transport of propagules may be important. Additionally, our flume study shows that increasing water flow velocity facilitates transport through a barrier. The most likely explanation for this is that when propagules travel too slowly, they will more easily get stuck or get delayed due to low kinetic energy. Several studies have focused on water flow through mangrove forests (Wolanski et al. 1980, Mazda et al. 1995, Furukawa et al. 1997, Aucan & Ridd 2000) and all reported rather limited water flow velocities (ca. 0 to 0.10 m s^{-1}) due to high friction. This agrees with our measurements in the flume and the high retention rates in the field. Although not investigated in our study, the potential importance of turbulence due to water–plant interactions is recognized, as this may also affect the retention process.

Dispersal distances in our field experiment were generally short, often not more than several meters, and the majority of propagules were retrieved within a few tens of meters from their release location after 5 high tides. This typical leptokurtic distribution of dispersal distances is in accordance with other studies, where propagule movement in mangrove systems was found to be restricted to short distances from the parent tree (Chan & Husin 1985, McGuinness 1997, Sousa et al. 2007).

The number of recovered propagules was high. The propagules that were not retrieved in our experiments might have been consumed by herbivorous crabs (De Ryck et al. 2012) or dispersed beyond the range of our search area. Predation vulnerability at our study site was found to be higher for *C. tagal* than for *R. mucronata* propagules (De Ryck et al. 2012), which may explain the lower recovery of *C. tagal* propagules in all plots. Also, the smaller *C. tagal* propagules might have dispersed over longer distances. The lower recovery of propagules from both species released in the AMC and RM zone very likely reflects proximity to open water. While the distance to open water, and hence barrier width, is shorter at these creekward sites compared to higher, more inland locations, the creekward sites experience higher water depths and longer hydroperiods. Hence, the overall time period within which water currents can influence the deposition pattern of propagules in these locations is longer. In the RM zone, predation might also partly explain unrecovered propagules,

since high predation rates were reported in this location by De Ryck et al. (2012). A recent study in Gazi Bay showed that propagule predation rate is positively correlated with crab density and that crab density is negatively correlated with pneumatophore density (Van Nedervelde et al. 2015); however, it is unknown to what degree the density distribution of herbivorous crabs across the intertidal range correlates with and contributes to the spatial variation in propagule recovery and seedling establishment, since predation pressure also depends on the nutritional value of propagules (Van Nedervelde et al. 2015).

Consistent with earlier work in tidal systems (Schneider & Sharitz 1988, Sousa et al. 2007), dispersal in the field was found to be highly directional. Additionally, the data revealed a clear bimodality, reflecting dominant tidal currents. One dispersal direction corresponded with the direction of strong incoming tides, while the other dispersal direction reflected the south-southeastward ebb component. The inland component is in accordance with Rabinowitz' Tidal Sorting Hypothesis, stating that smaller propagules are transported farther inland than larger ones (Rabinowitz 1978b). Conversely, Sousa et al. (2007) found that propagule dispersal directions were predominantly from higher to lower elevations. They recognize, however, that their findings may be typical for the Caribbean, where the tidal range is small and seasonal rainfall high, so that sheet flow runoff may dominate the effect of tidal currents; this is in contrast to our study site. The slight westward deviation in the southward dispersal direction of the creekward plots (Fig. 4) may reflect the effect of easterly winds during the period of our field study (Van der Stocken et al. 2013).

We recognize that the structure of natural landscape matrices may be more complex than the one simulated in our flume experiments. *Rhizophora* stilt roots, for example, are characterized by high spatial complexity, which may retain vertically floating propagules equally well as horizontally floating ones. Also, propagules can be retained by young seedlings or in the crown of trees (pers. obs.). However, our findings clearly demonstrate that root density, propagule traits and hydrodynamic variables affect the ability of propagules to navigate through a landscape matrix. Interestingly, the decreasing fraction of retained and stranded propagules with decreasing root density as found in our flume experiment suggests that temporal variations in water height may reduce barrier density and hence retention (Schneider & Sharitz 1988). As such, windows of lower retention, and hence higher long distance dispersal (LDD) potential, may exist (Fig. 5). The duration and frequency of these windows would then depend on the structure of the landscape matrix, the tidal system and the geomorphologic features of the coastline. In the case of mangrove forests consisting of several mangrove taxa varying in architecture and stature that have overlapping distributions, the net retention curve at a certain location would consist of the sum of the average species-specific retention curves. Also, stochastic events such as storms, during which water velocities and wave energy may be higher than normal, could have a disproportionate effect on dispersal and establishment. To study the role of such events, similar release–recapture dispersal experiments could be set up just before a major storm is anticipated.

As the interaction between dispersing propagules and physical barriers determines the proportion of propagules available for local replenishment as well as the amount of propagules that could be dispersed over long distances, it may play an important role in the explanation of mangrove distributions at local, regional and global scales. Whether or not dispersal is effective therefore also depends on the longevity of propagule viability and buoyancy, as well as on oceanographic distance (sensu Wood et al. 2014) to suitable habitat fragments.

Although speculative, our findings may also help to explain variation in mangrove zonation patterns (Sousa et al. 2007, Peterson & Bell 2012). In our study area in Gazi Bay, for example, trees of species with the most compact propagules (e.g. *A. marina*, *H. littoralis*, *X. granatum*) are typically found growing in high shore locations of the mangrove forest, while *C. tagal* and *R. mucronata* trees dominate the middle and creekward sides of the forest. Correlations between zonation and dispersal potential have been studied earlier by Clarke et al. (2001), who postulated that in northern Australia, dispersal potential alone does not correspond with zonation, and that zonation may be driven much more by traits related to establishment. Species zonation has been linked to various environmental factors, such as predation (Smith 1987) or differences in flood tolerance (McKee 1993, Ye et al. 2003). Evidence for a correlation between zonation and establishment related factors also follows indirectly from this study. Around spring tides, for example, propagules of *C. tagal* and *R. mucronata* may occasionally be transported to backshore areas, although mature individuals of these species do not occur there. The same explanation applies to *H. littoralis* and *X. granatum* whose local

presence is restricted to the upper intertidal zones, despite the fact that their propagules can easily reach sites in the lower intertidal area. However, while factors such as soil salinity, inundation period, competition with other species and physiological traits determine establishment, dispersal traits and aspects such as the interaction of propagules with the landscape matrix control the distribution of viable propagules over suitable and unsuitable locations. Compact propagules, for example, may be beneficial for the

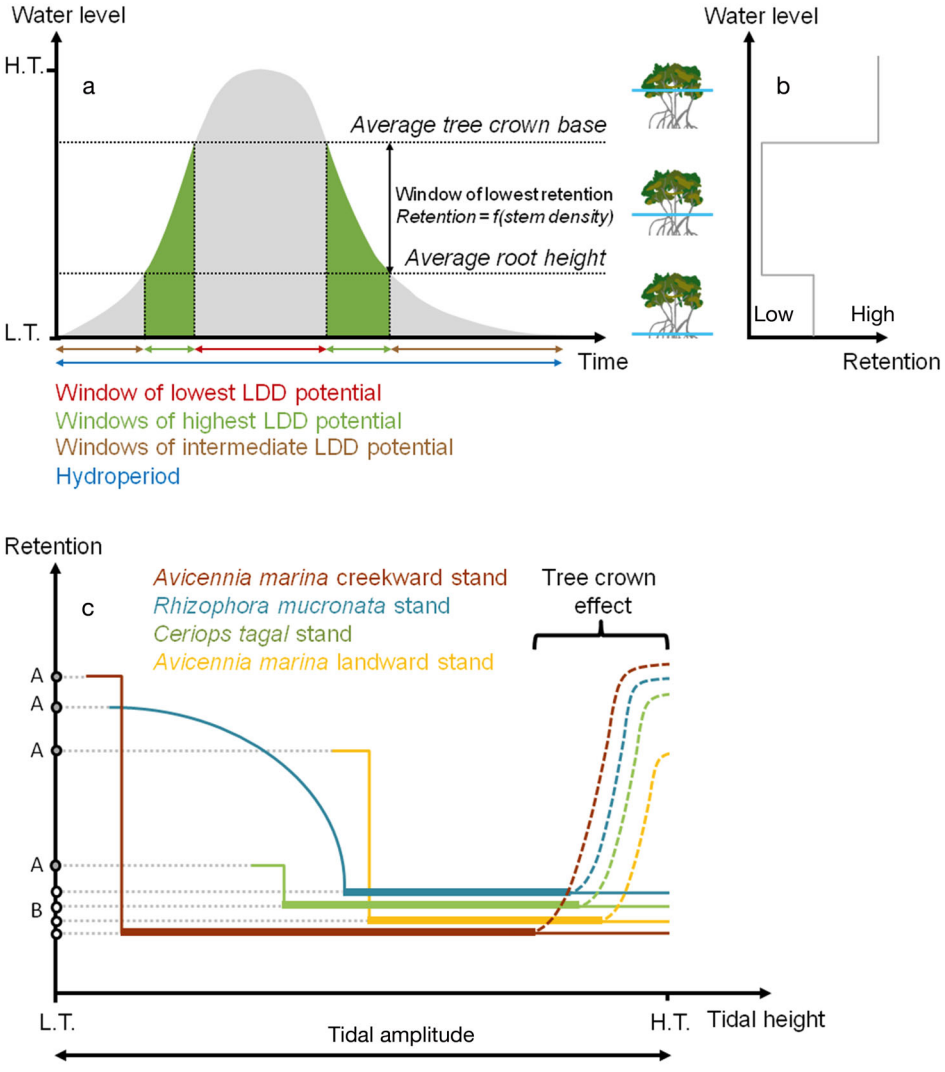

Fig. 5. Synthetic model showing temporal variation in dispersal barrier density over a tidal cycle. (a,b) Periods with water levels in the range between the average root height and tree crown base represent windows of lower retention and higher (long distance) dispersal (LDD) potential. Tidal currents can be asymmetric, which may influence the effect of incoming and outgoing tides. (c) We applied the concept of windows of higher and lower retention to our field study transect (also see Fig. 2b). The model illustrates the variation in retention over the range of the tidal amplitude, from low water (L.T.) to high water (H.T.). Water enters the creekward side of the forest, inundating the creekward *Avicennia marina* stand. Initially, barrier density is high (A), and falls back to the stem density (B) as soon as the water level exceeds average root height (i.e. window of lower retention and higher LDD potential). The same process accounts for the variation in retention in other species zones, with interspecific differences in root height and hydroperiod. Occasionally, water may exceed the average tree crown base, strongly increasing retention. The width and frequency of these windows of lower retention are a function of intertidal position and topography. Trees in the inland zone of a mangrove forest will experience shorter hydroperiods than trees on the more creekward or seaward side. This is true over the daily tidal cycle, but also over the monthly tidal cycle, with some areas only being inundated around spring tides. For example, the landward *A. marina* stand in our field experiment is beyond the reach of the water line, except around spring tides; thus, dispersal potential is much lower compared to that in our *Rhizophora mucronata* site. Local (micro)topography and characteristics of the tidal regime may add complexity to the graphs

colonization of suitable high-shore habitat locations (Rabinowitz 1978b), but may also facilitate the export of propagules from backshore species separated from open water by dense physical barriers.

In conclusion, larger mangrove propagules were more frequently retained than smaller ones, which implies that smaller propagules may contribute disproportionately to dispersing propagule cohorts, particularly over larger distances. However, we cannot exclude the potential existence of a selective pressure against LDD. Increasing obstacle density in the landscape matrix increases the number of propagules retained, and hence influences the proportion of propagules available for dispersal over longer distances. We have shown that hydrodynamic variables such as waves and high water flow can facilitate the transport of propagules through a landscape matrix. As such, dispersal distance distributions (i.e. dispersal kernels) and deposition patterns (including dispersal direction) are determined by propagule traits, hydrodynamic conditions and the nature of the landscape matrix. The interaction of these factors influences the probabilities of propagules leaving the local habitat, and hence may determine the proportions of propagules available for local replenishment and LDD. To validate whether our flume results are representative of actual situations in the field, future studies are needed to estimate the size and composition of propagule assemblages at different distances from the coast. Our study clearly demonstrates that knowledge on the retention process should be considered when constructing dispersal models. Finally, future studies should investigate the degree to which variation in dispersal capacity contributes to observed distribution patterns including zonation at local, regional and global scales.

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