

Size does matter, but not only size: Two alternative dispersal strategies for viviparous mangrove propagules

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ARTICLE INFO

Article history:

Received 14 September 2011

Received in revised form 21 June 2012

Accepted 23 June 2012

Available online 16 July 2012

Keywords:

Ceriops tagal

Rhizophora mucronata

Long-distance dispersal

Hydrochory

Predation

Propagule density

Propagule size

Tracking

Vivipary

Root-growth

ABSTRACT

We studied the propagules of two widespread mangrove species, *Ceriops tagal* and *Rhizophora mucronata*, that are similar in shape but differ in other morpho-anatomical features (average length is 23.1 ± 2.2 cm and 44.4 ± 4.3 cm, resp., $n = 180$). We hypothesized the propagules of both species to have a different hydrodynamic behavior and establishing capacity, resulting in a different dispersal strategy. More specifically, we hypothesized that *C. tagal* propagules have a larger dispersal capacity than those of *R. mucronata*. The dispersal strategies of *C. tagal* and *R. mucronata* propagules were elucidated through a combination of a propagule tracking ($n = 180$ per species), predation ($n = 20$ per species) and root-growth experiment ($n = 120$ per species), carried out in the field. *C. tagal* and *R. mucronata* adopted two different dispersal strategies. *C. tagal* releases a large number of propagules and disperses fast, having a slender morphology and low density (average ρ : 985.29 ± 19.02 g L⁻¹), as well as a high agility (smaller size) when dispersing through dense root systems. *C. tagal* propagules have a theoretical advantage to disperse over longer distances over the thicker, longer and denser *R. mucronata* propagules (average ρ : 1003.92 ± 8.52 g L⁻¹; $t = 8.90$, $p < 0.0001$, $n = 197$). *C. tagal* have, however, lower establishment chances due to slower root-growth, desiccation sensitivity and smaller size. In contrast to *Ceriops'* tactic of releasing high numbers of propagules and fast dispersal, *R. mucronata* has adopted a dispersal tactic of survival. Fewer propagules are released, but they are more resistant to predators due to their larger size and they can anchor themselves faster due to quicker root-growth (Mann–Whitney U : $p < 0.0001$, $n_{Ct} = 59$, $n_{Rm} = 57$). Overall, propagule characteristics of both species result in different and alternative dispersal strategies on a local scale, contradicting our initial hypothesis. On a global scale, we hypothesize this might lead to a similar capacity for long-distance dispersal, ending in successful establishment.

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1. Introduction

Mangrove forests, characteristic for (sub)tropical coastal zones, form unique ecosystems of high ecological and economical importance (Donato et al., 2011). Multiple adaptations, such as aerial roots, salt exclusion/secretion and vivipary, have developed which provide the needed tools and, therefore, resilience to survive in the extreme and highly dynamic intertidal environment (Tomlinson, 1994). (True) vivipary is a rare phenomenon among plants. The embryo grows, without any dormancy period, first out of the seed coat and then out of the fruit, while still attached to the parent

tree (Tomlinson, 1994). After germination, hydrochorous propagules part from the parent tree as a seedling that can either plant in the shadow of their parent or propagate to nearby locations and thereby replenish existing stands. Occasionally, propagules may take advantage of estuarine, coastal and ocean currents to disperse over long distances and, if still viable, (re)colonize remote and suitable habitats (Duke et al., 1998). Both local establishment and the potential for long distance dispersal long-distance dispersal, in the sense of propagule movement over oceanic expanses), have important implications for mangrove ecology. They are at the base of forest structure and dynamics, new populations and genetic diversity and differentiation (Sousa et al., 2003; Ceron-Sousa et al., 2005).

As most mangrove species are typically water dispersed by buoyant propagules, these dispersal units take advantage of estuarine, coastal and ocean currents in order to replenish existing stands and to colonize new suitable habitats (Duke et al., 1998). However,

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propagules do not disperse uniformly as their dispersal ability is expected to result from a combination of factors interacting with various propagule properties. Biotic properties determining the spatiotemporal distribution of propagules include propagule characteristics such as buoyancy, size, shape, weight, longevity and speed of root-growth, as well as external factors deriving from the mangrove formation, mainly above-ground root complexes, predation on propagules and propagule numbers allowing predator saturation (Rabinowitz, 1978; Clarke et al., 2001; Cannicci et al., 2008). Additionally, microtopography, wind and hydrodynamics are equally important abiotic factors influencing propagule dispersal and establishment (Minchinton, 2001; Stieglitz and Ridd, 2001; Di Nitto et al., 2008).

In the field of mangrove ecology, studies on propagule dispersal characteristics arose over the years, yet there is still an apparent scientific gap with respect to the actual dispersal and recruitment mechanisms and the role of vegetation and abiotic factors (e.g. hydrodynamics, wind) on propagule dispersal. Most research focus has been on the effect of (a)biotic factors on propagule growth and survival (Delgado et al., 2001; Kitaya et al., 2002; Cannicci et al., 2008). Citing Duke et al. (1998), 'if a species is present, the environment must be suitable for it, but the opposite does not apply', we emphasize the importance of the period between the abscission of a mature propagule and early growth of the seedling. Given the complexity of propagule dispersal dynamics, it is timely to conduct experiments that would ultimately benefit modeling propagule dispersal within its biogeographical context. In addition, understanding the process of seed dispersal is important for conservation of mangrove forests against the background of natural and human induced threats (e.g. sea-level rise, climate extremes, salinity fluctuations, clear-felling, siltation).

The aim of this study was to describe the dispersal behavior of viviparous and hydrochorous mangrove propagules in a macrotidal environment based on field experiments and observations. Therefore, in our analysis, we dealt with both propagule characteristics (size, buoyancy and palatability) and environmental characteristics influencing propagule dispersal (soil texture, root structure, predator presence and tidal position) integrated in three types of *in situ* experiments: (i) a tracking experiment in which we quantified and evaluated dispersal distance and dispersal direction of propagules, (ii) a predation experiment in which we studied propagule predation by crabs, (iii) a root-growth experiment to evaluate root-growth initiation and speed of root-growth. The predation experiment (ii) gives explanatory power to the observations we made in the tracking experiment (i), which together with experiment (iii) enables us to make an hypothesis about the dispersal capabilities of *Cerriops tagal* and *Rhizophora mucronata* propagules.

We hypothesized that species differ in suitability for long-distance dispersal due to differences in density, size and morphology of their propagules. Subsequently, the propagules of *C. tagal* were hypothesized to be the best dispersers due to their slender morphology, resulting in lower retention in the root complex and thus faster dispersal speed than *R. mucronata* propagules. Furthermore, position of the parent tree in the low intertidal zones (e.g. along the creek border) and capacity to initiate root growth rapidly once stranded are hypothesized to be factors increasing the possibility for successful long-distance dispersal of mangrove propagule.

2. Methods

2.1. Study area

The study was performed in Gazi Bay (39°30'E, 4°25'S) at the Kenyan coast, about 50 km south of Mombasa. This shallow, open

estuary is fed by two seasonal rivers, the Kidogoweni and the Mkurumuji, and has a total area of 600 ha of mangrove forest (Neukermans et al., 2008) dominated by *R. mucronata* Lamk., *Avicennia marina* (Forsk.) Vierh. and *C. tagal* (Perr.) C.B. Robinson. In this bay, a clear zonation is observed, meaning that monospecific bands or mixed zones of mangroves are found along the intertidal area, perpendicular to the topographic gradient. Our study was conducted in stands where *A. marina* is found both in the landward and seaward mangrove fringe with, in between, pure *R. mucronata* stands landward of the seaward *A. marina* zone, followed by pure *C. tagal* stands (Fig. 1). The bay is subjected to a semi-diel tide system with a mean variation in tidal amplitude of 2.5–3 m (Obura, 2001). These tides, which are one of the primary drivers of water circulation, are asymmetric with a relative stronger ebb than flood flow (Kitheka, 1997). Because the bay has a mean depth of less than 5 m, inundation of the intertidal area is quick and short (3–4 h) resulting in high flushing rates. Annual rainfall in Kenya has a bimodal distribution: the 'long-rains', coinciding with the southeast monsoon (late March–July), and the 'short-rains', coinciding with the northeast monsoon (October–November). The Kenyan coast is very humid and warm with mean annual air temperatures of 22–30°C and a mean relative humidity between 65 and 81% (Kenya Meteorological Department, Mombasa, Kenya).

2.2. Studied species

Propagules of *C. tagal* and *R. mucronata*, two mangrove species of the Rhizophoraceae, were used in the experiments carried out for this research. Like most mangroves, the viviparous propagules of *C. tagal* and *R. mucronata* are hydrochorous. Propagules of these two dominant mangrove species share a number of structural and phenological features, but are still sufficiently different in terms of shape and weight to expect a different hydrodynamic behavior. Both species have oblong torpedo-like shaped propagules, but those of *R. mucronata* are more robust, larger and heavier than those of *C. tagal*.

2.3. Sample collection

Mature propagules were (haphazardly) picked from adult trees to avoid exposure to the osmotic effects of tidal water after abscission. We consider propagules mature when (i) the cotyledon is bright reddish yellow (*Cerriops*) or brownish yellow (*Rhizophora*) and (ii) the propagule readily sheds from the tree when shaken. After collection and consecutive removal of damaged/abnormal propagules (e.g. insect damage and unusual growth forms), length and mass of each propagule was determined. All propagules were marked and numbered with a white, non-toxic varnish to be able to distinguish dispersing propagules in tracking experiments. Density of 200 propagules (100 of each species) was measured based on the water displacement method of the wood density field protocol of Chave (2005), where the volume of propagules is obtained by immersing the propagule in a waterfilled container standing on a digital scale. Subsequently, the measured mass of displaced water is equal to the propagules volume. Density differences between species were checked using a Student's *t*-test for independent samples in Statistica 7.0 (StatSoft Inc., Tulsa, OK, USA). To establish the relative magnitude of the differences between means of the density, we calculated the 'effect size', also known as 'strength of association', by means of the Eta-squared value (η^2). Cohen (1988) fixed interpretation of the Eta-squared values on 0.01 (small effect), 0.06 (moderate effect) and 0.14 (large effect).

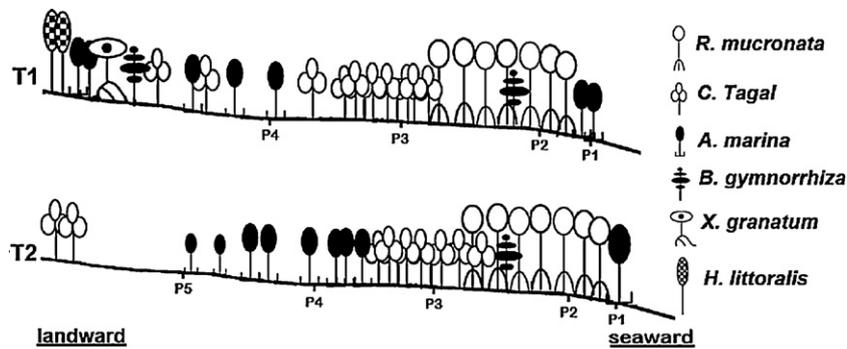


Fig. 1. Overview of the two transects (T1 and T2) used in the tracking experiments with their respective assemblages (from landward to seaward side of the intertidal zone): *Rhizophora mucronata*, *Ceriops tagal*, *Avicennia marina*, *Bruguiera gymnorrhiza*, *Xylocarpus granatum* and *Heritiera littoralis*. Adapted from Dahdouh-Guebas et al. (2004).

2.4. Tracking experiment

Along two transects from low to high intertidal zone (T1 and T2, Fig. 1), plots were chosen in five different vegetation assemblages: seaward *A. marina* (P1), *R. mucronata* (P2), *C. tagal* (P3), landward *A. marina* (P4) and unvegetated landward zone (P5). For all plots, (i) height above datum (HAD) was calculated using tracing paper and Mombasa tide tables (Di Nitto et al., 2008), (ii) an indicative slope value was given (slight slope or no slope – the slope never exceeded 10° except for creek sides), (iii) soil texture was identified by means of standard field characterization methods (Globe, 2005), whereas (iv) vegetation structure (canopy cover and root density) were quantified by making use of the cover estimate scales of the Braun-Blanquet method (e.g. Westhoff Maarel, 1973) (Table 1). In each plot, 40 propagules (20 of each species) were released in horizontal position at low tide (February, 2009), five days before spring tide. Released propagules were searched repeatedly for a period of two weeks (and again, once, after five months), therefore adopting a systematic searching method of circling around each plot screening about two meters to the left/right while moving through the forest. In the more densely vegetated plots (P1, P2 and P3) the searching diameter is around 20 m, because of the difficult search conditions (*i.e.* very dense and high aerial root systems and muddy substrate), while in the most landward plots the searching diameter extends well over 30 m (P4) or 140 m (T2P5). The search diameter is, although sometimes around 20 m, adequate to interpret and discuss the dispersal of propagules in respect to the long-distance dispersal capacity of propagules, because of the total package of experiments we performed. For each propagule found (i) dispersal direction (in degrees north), (ii) distance from the centre of the release point, (iii) orientation on the ground and (iv) health status of the propagule were noted. To see whether we

recovered a significantly different number of *C. tagal* and *R. mucronata* propagules on the two transects, as well as across the two transects and between different plots of the same transect, non-parametric Mann-Whitney *U* and Kruskal-Wallis tests were carried out (Statistica 7.0 – StatSoft Inc., Tulsa, OK, USA). To test whether propagules dispersed uniformly or in a certain direction we used circular statistics (*V*-test) in EASY-STAT 2.3 (Marco Vannini c/o Università degli Studi di Firenze, 26/04/1993) to visualize dispersal directions per plot, per transect and per day.

2.5. Predation experiment

Nine plots, all chosen within five meters from the plots used for the tracking experiment and equivalent in soil structure, type of root complex and crab density, have been used to fix 10 propagules to a one meter long twine tied close to the ground around roots and stems. Horizontal positioning of the propagules at low tide was ensured through the length of the twine and manual disentangling of the twines after high tides. The propagules were monitored 1, 2, 3, 4, 6, 8, 10 and 14 days after the start of the experiment. Two possible outcomes were expected: (i) the propagule remains untouched and in good condition and (ii) the propagule gets predated. Predation is defined here as the slightest damage caused by animals on an intact propagule. Propagules were considered 'non-viable' if (i) the epicotyl had been eaten, (ii) at least half of the hypocotyl had been eaten or (iii) the propagule had been pulled into a crab burrow (Bosire et al., 2005). The results of this experiment give explanatory power to our tracking experiment in such a way that they can partly explain what happened to the unrecovered propagules.

Table 1
Vegetation and environmental characteristics of the two transects used in the tracking experiment. HAD: height above datum; slope [slight (S) or flat (F)]; vegetation assemblage (AmL: landward *Avicennia marina*; Ct: *Ceriops tagal*; Rm: *Rhizophora mucronata* and AmS: seaward *Avicennia marina*; sand: open sandy area); Braun-Blanquet^a (BB) canopy cover and Braun-Blanquet^a root density.

Transect	Plot	Position	HAD (m)	Slope	Soil texture	Vegetation assemblage	BB canopy cover	BB root density
T1	P4	Landward	2.91	F	Sand	AmL	2a	2 m
	P3		2.77	S	Silty-clay	Ct	5	2b
	P2		2.50	S	Silty clay-loam	Rm	4	3
	P1	Seaward	2.05	S	Sandy-clay	AmS	4	2 m
T2	P5	Landward	3.23	F	Sand	Sand	R	R
	P4		2.89	F	Sand	AmL	2	1
	P3		2.73	F	Silty-clay	Ct	5	2b
	P2		2.28	S	Silty clay-loam	Rm	4	3
	P1	Seaward	1.62	S	Sandy-clay	AmS	2b	2 m

^a Braun-Blanquet scale: R: rare, <5% cover; +: small amount of individuals (e.g. aerial roots), <5% cover; 1: large amount of individuals, <5% cover; 2 m: very large amount of individuals (>50), <5% cover; 2a: 5–12.5% cover; 2b: 12.5–25%; 3: 25–50%; 4: 50–75%; and 5: 75–100%.

2.6. Root-growth experiment

120 *C. tagal* and 120 *R. mucronata* propagules were planted in an upright position in a *C. tagal* and *R. mucronata* stand, respectively. At different moments in time (2, 4, 6, 8, 10 and 12 days after planting), twenty propagules of each species were taken out of the soil, with great care not to break newly formed roots. The number of roots as well as the root lengths of each propagule was measured. Subsequently, the speed of root-growth was calculated using:

$$v_r = \frac{\sum_{i=1}^{n(\Delta t)} (l_i) \Delta t}{\Delta t}$$

where $n(\Delta t)$ = number of roots after time interval Δt ; l_i = length of root i (cm); $\Delta t = t_f - t_i$ = time interval between end of experiment and first root-growth initiation ($t_i = 6$ and 8 for *C. tagal* and *R. mucronata*, respectively). A Mann–Whitney U test was used to test for difference in speed of root-growth between *C. tagal* and *R. mucronata* propagules after root-growth initiation.

3. Results

3.1. Propagule characteristics

The propagules of *C. tagal* and *R. mucronata* propagules used in the tracking propagules had an average mass of 7.28 ± 1.2 g and 68.5 ± 10.6 g ($n = 180$), an average length of 23.1 ± 2.2 cm and 44.4 ± 4.3 cm, respectively. There was a highly significant difference in densities ($t(197) = 8.90$, $p < 0.0001$) for *C. tagal* (average = 985.29 g L⁻¹, SD = 19.02, $n = 100$) and *R. mucronata* (average = 1003.92 g L⁻¹, SD = 8.52, $n = 100$) propagules released on transect 1. Based on the Eta-squared ($\eta^2 = 0.29$), the magnitude of the difference in densities between the two species was very large.

3.2. Tracking experiment

The tracking experiment showed that predation and the number of propagules we recovered daily on the two transects were similar between transects in all respective plots (e.g. T1P1 and T2P1) (Mann–Whitney U). The main observation on the number of recovered propagules over time is that many more *R. mucronata* than *C. tagal* propagules were recovered on both transect 1 (Mann–Whitney U : $p < 0.0001$, $n = 80$) and transect 2 (Mann–Whitney U : $p < 0.0001$, $n = 100$). Often over 70% of *C. tagal* propagules disappeared after only a few days [e.g. P3 (Table 2)], whereas *R. mucronata* propagules were found back much more easily. Furthermore, differences in the number of recovered propagules are found between plots of transect 1 for *R. mucronata* (Kruskal–Wallis: $p = 0.002$, $n = 80$) and transect 2 for *C. tagal* (Kruskal–Wallis: $p = 0.003$, $n = 100$) and *R. mucronata* (Kruskal–Wallis: $p = 0.002$, $n = 100$): a higher number of *R. mucronata* than *C. tagal* propagules were found back in the most outermost seaward and landward plots (P1, P4 and P5) of both transects. Most predation is observed in P2 and P3 for both *C. tagal* and *R. mucronata* propagules (Table 2). The amount of predation in these plots is an underestimation of the real amount of predation, because not all propagules could be recovered. Since the dispersal of and predation on the propagules of the two transects (T1 and T2) shows a high similarity, we only show the results of the tracking experiment for transect 1 (Table 2).

As expected, *C. tagal* and *R. mucronata* propagules dispersed in similar directions during the tracking experiment. In general, directions of their dispersal differ from day to day with a tendency of landward or along-shore-directed dispersal, especially in the most landward plots (data not shown). In the most seaward plot (P1) only landward-directed dispersal is observed, since the propagules

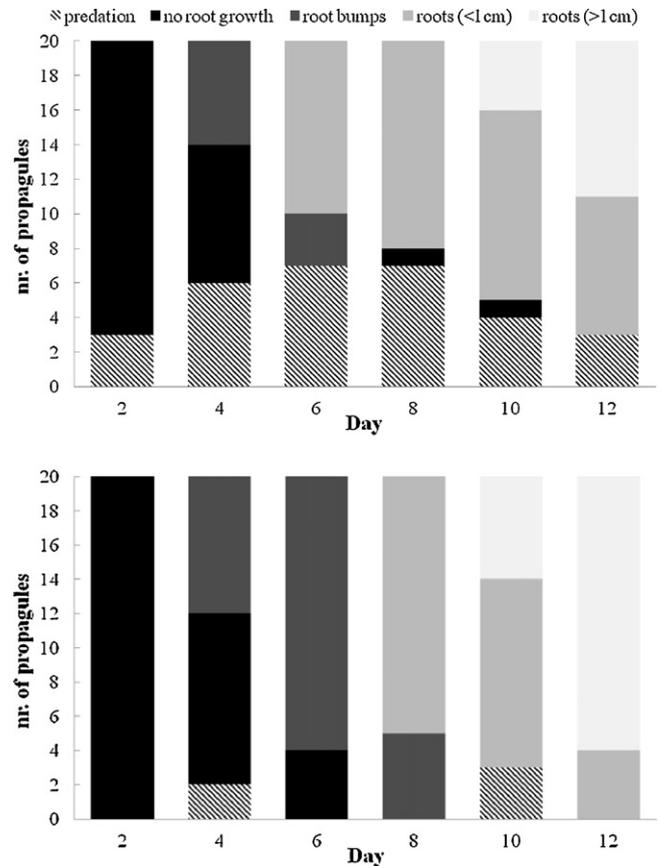


Fig. 2. Root growth of *C. tagal* ($n = 120$) and *R. mucronata* ($n = 120$) propagules after 2, 4, 6, 8, 10, 12 days (in groups of twenty), planted in their respective parental zones.

dispersing in the seaward directions could not be found back. In the most landward plots (P4 and P5) the largest dispersal distances are observed for both species, with *R. mucronata* and *C. tagal* propagules observed to disperse up to 60 m and 146 m, respectively. In other plots (P1, P2 and P3), the dispersal distance has an upper limit due to the maximum searching perimeter of 30 m radius.

3.3. Predation experiment

As the results of the tracking experiment suggest (Table 2), the predation experiment showed that there is no predation at all in the most extreme seaward and landward plots (P1 and P4, Table 3). On the other hand, the number of propagules that were predated is very high in P3 and P2 of transect 1, with a high number of *C. tagal* propagules completely consumed.

3.4. Root-growth experiment

Once planted in the soil, *C. tagal* propagules tend to have a quicker root-growth initiation than *R. mucronata* propagules (Fig. 2). Root-growth initiation of *C. tagal* propagules occurred after 6 days, while *R. mucronata* propagules only after 8 days. However, once roots emerged at the radicle end of a *R. mucronata* propagule, they grew much faster than roots of *C. tagal* propagules (Mann–Whitney U : $p < 0.0001$, $n_{Ct} = 59$, $n_{Rm} = 57$) (see Table 4). Furthermore, root-growth initiation between propagules of the same species is synchronized. Almost every propagule, planted for an equal period of time, was found in the same stage of root develop-

Table 2
Number of *Cerriops tagal* and *Rhizophora mucronata* propagules over time (expressed in number of days since release) that are dispersed [with (P) and without predation (N)], not dispersed [with (P) and without (N) predation], not found^a, completely eaten, recovered or predated for the four plots of transect 1 (Fig. 1) ($n = 20$ per plot, per species). Water level above datum at high tide is given (in decimeters) at each respective day, as well as the p -values of Kruskal–Wallis tests (significant values in bold). Plots are ordered from land to sea.

	Plot 4				Plot 3				Plot 2				Plot 1				KW												
Day	1	2	3	5	6	8	14	1	2	3	5	6	8	14	1	2	3	5	6	8	14	1	2	3	5	6	8	14	
Water level (dm)	2	5	8	9	8	8	7	4	7	9	1	9	9	7	7	9	12	13	12	12	11	11	14	16	18	17	17	17	17
<i>Cerriops tagal</i>																													
Dispersed/N	6	12	7	1	2	3	3	3	4	2	0	0	0	0	4	1	1	1	0	0	0	0	1	2	2	1	1	0	$p < 0.05$
Dispersed/P	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	3	0	0	0	0	0	0	$p = 0.56$
Not dispersed/N	14	1	0	0	0	0	0	5	2	0	0	0	0	0	5	1	0	0	0	0	0	12	3	1	0	0	0	0	$p = 0.93$
Not dispersed/P	0	0	0	0	0	0	0	0	0	0	2	1	1	1	2	0	0	0	0	1	0	5	1	0	0	0	0	0	$p = 0.19$
Not found	0	7	13	19	18	17	17	12	14	18	18	18	18	18	6	13	12	14	15	14	14	0	15	16	17	18	18	19	$p = 0.12$
Whole prop. eaten	0	0	0	0	0	0	0	0	0	0	0	1	1	1	3	5	6	5	5	5	6	0	0	1	1	1	1	1	$P < 0.0001$
# Recovered	20	13	7	1	2	3	3	8	6	2	2	2	2	2	14	7	8	6	5	6	6	20	5	4	3	2	2	1	$p = 0.12$
# Predated	0	0	0	0	0	0	0	0	0	0	2	2	2	2	5	5	7	5	5	6	6	8	1	1	1	1	1	1	$p < 0.001$
<i>Rhizophora mucronata</i>																													
Dispersed/N	1	13	14	10	2	3	3	2	8	7	2	3	3	2	1	11	12	11	9	8	7	1	8	8	9	8	8	7	$p = 0.22$
Dispersed/P	0	0	0	0	0	0	0	1	2	3	5	4	6	5	0	1	1	1	2	2	2	0	0	0	0	0	0	0	$p < 0.0001$
Not dispersed/N	19	5	5	4	0	0	0	12	6	0	0	0	0	0	18	4	5	2	3	2	2	17	9	7	6	6	6	6	$p < 0.05$
Not dispersed/P	0	0	0	0	0	0	0	0	0	2	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$p < 0.01$
Not found	0	2	1	6	18	17	17	5	3	7	10	10	9	9	1	4	2	6	6	8	9	2	3	5	5	6	6	7	$p = 0.42$
Whole prop. eaten	0	0	0	0	0	0	0	0	1	1	1	1	1	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$p < 0.0001$
# Recovered	20	18	19	14	2	3	3	15	17	13	10	10	11	11	19	16	18	14	14	12	11	18	17	15	15	14	14	13	$p = 0.42$
# Predated	0	0	0	0	0	0	0	1	3	6	8	7	8	9	0	1	1	1	2	2	2	0	0	0	0	0	0	0	$p < 0.0001$

^a 'Not found' includes propagules that were washed to the sea, completely eaten within one day or overlooked while searching.

Table 3
The number of *C. tagal* and *R. mucronata* propagules over time (expressed in nr. of days since release) that are predated on the soil surface or after being dragged into a crab hole and the number of propagules that are not only predated but completely eaten as well as the number of propagules that were not predated at all for the four plots of transect 1 (Fig. 1) ($n = 10$ per plot, per species). The significant p -values of Kruskal–Wallis tests are indicated in bold. Plots are ordered from land to sea.

	Plot 4							Plot 3							Plot 2							Plot 1							KW
	Day																												
	1	2	3	4	6	8	14	1	2	3	4	6	8	14	1	2	3	4	6	8	14	1	2	3	4	6	8	14	
<i>Ceriops tagal</i>																													
On surface	0	0	0	0	0	0	0	6	2	2	4	4	2	2	0	6	4	4	6	4	2	0	0	0	0	0	0	0	$p < 0.0001$
In crab hole	0	0	0	0	0	0	0	0	8	2	0	0	0	0	0	0	2	2	2	2	0	0	0	0	0	0	0	0	$p < 0.05$
Whole prop. eaten	0	0	0	0	0	0	0	0	4	14	14	14	16	18	0	2	2	2	2	8	14	0	0	0	0	0	0	0	$p < 0.001$
No predation	20	20	20	20	20	20	20	14	6	2	2	2	2	0	20	12	12	12	10	6	4	20	20	20	20	20	20	20	$p < 0.0001$
<i>Rhizophora mucronata</i>																													
On surface	0	0	0	0	0	0	0	0	2	2	4	6	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$p < 0.0001$
In crab hole	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	$p = 1$
Whole prop. eaten	0	0	0	0	0	0	0	6	8	10	10	8	10	10	8	10	10	12	12	12	12	0	0	0	0	0	0	0	$p < 0.0001$
No predation	20	20	20	20	20	20	20	14	10	8	6	6	6	6	12	10	10	8	8	8	8	20	20	20	20	20	20	20	$p < 0.0001$

Table 4
Characteristics of *Ceriops tagal* (*Ct*) and *Rhizophora mucronata* (*Rm*) propagules with their respective hypothesized effect on long-distance dispersal (LDD) and establishment (positive effect, + or negative, –), propagule (prop.); numbers (nrs.); root-growth rates: the average of the root-growth speed of propagules after 12 days (see Section 2).

Property	<i>Ct</i>			<i>Rm</i>		
	Relative value	Reference	Effect on LDD	Relative value	Reference	Effect on LDD
Occurrence	Landward		–	Seaward		+
Prop. nrs	High	Observed	+	Low	Observed	–
Average prop. size	Small	23.1 cm ($n = 120$)	+	Large	44.4 cm ($n = 120$)	–
Average prop. density	Lower	985.29 g L ⁻¹ ($n = 100$)	+	Higher	1003.92 g L ⁻¹ ($n = 100$)	–
Buoyant period		>30 days (observed)		High	Median = 70 days; max = 150 days (Drexler, 2001)	+
Displacement velocity	Faster	Observed	+	Slower	Observed	–
Predation vulnerability	Higher	See Table 3	–	Lower	See Table 3	+
Property	<i>Ct</i>			<i>Rm</i>		
	Relative value	Reference	Effect on establishment	Relative value	Reference	Effect on establishment
Root-growth initiation	Faster	6 days	+	Slower	8 days	–
Root-growth rate	Lower	0.34 cm/day ($n = 17$)	–	Faster	1.71 cm/day ($n = 20$)	+

4. Discussion

Our results indicate that propagules dispersing within the dense *C. tagal* and *R. mucronata* forest (inner mangrove P2 and P3) are subjected to high predation by crabs and high root retention, but still have a larger probability of long-distance dispersal compared to the landward regions, because of their more seaward intertidal position. The high density of stilt roots in *R. mucronata* stands and knee roots in the seaward *C. tagal* stands, along with the muddy soils found in these two vegetation zones, restrict dispersal through obstruction and retention of propagules. The landward *C. tagal* zone is separated from the creek by the dense root system of the seaward *R. mucronata* forest, which diminishes the potential for long-distance dispersal of propagules in the more landward plots. The probability for long-distance dispersal of propagules dispersing from the landward and inner mangroves could, however, be increased by a seaward, more unidirectional flow, leading all propagules (unless obstructed) towards the main tidal stream or the ocean. Firstly, this could be brought about by sheet flow (freshwater runoff that is generated by rainfall, here, from high to low intertidal areas) (Sousa et al., 2007). Our dispersal experiments were done in the middle of the dry season, when there is no seaward sheet flow. Secondly, the chance for long-distance dispersal can be enhanced by the presence of small creeks, which originate through withdrawal of tidal water. We released several propagules near a small creek in the landward region at ebb tide. They readily dispersed through the inner mangrove zone, via this small drainage creek, to the main creek, which ultimately gives access to the bay area and the ocean.

We used the results from the predation experiment to estimate the percentage of the propagules that reached the open sea in the tracking experiment and could thus go on a long-distance dispersal mission for each plot. For both *C. tagal* and *R. mucronata* propagules, we estimated that in the seaward P1, 99% were washed to the sea, while in the landward P4 and P5 a maximum of 10% were washed to the sea because of the barrier of dense mangrove root complexes that exists between the landward zone and the creek. Since predation percentages in the dense mangrove plots P3 and P2 are different for *C. tagal* and *R. mucronata*, we estimate that a maximum of 20% and 30% of *C. tagal* propagules and 20% and 50% of *R. mucronata* propagules reached the sea, respectively.

We conclude that the most seaward fringe is expectedly the most suitable for successful long-distance dispersal. Although an open vegetation in a more landward region also allows great dispersal distances, a low survival rate was observed due to quick desiccation. Propagules released in these mangrove fringes were not subjected to predation but the larger *R. mucronata* propagules were slightly hindered by the density of *A. marina* pneumatophores in the seaward zone. Nevertheless, propagules were recovered several 100 m downstream of transect 1 further suggesting that the major part of the released propagules, that could not be found back drifted away over long distances. Clarke (1993) mentions a possible magnitude of tens of kilometers, while Komiyama et al. (1992) found dispersal distances of stranded propagules up to 1210 m for *R. mucronata* propagules directly released in a river. Our observations of vast numbers of *C. tagal* and *R. mucronata* propagules quickly dispersing out of the main creek, and away from the mangrove forest along the coastline, further suggest that dispersal distance can easily reach tens of kilometers (De Ryck et al., unpublished data). Colonization of remote islands, which have never been part of a continental coast with mangrove cover, provides circumstantial evidence that this effective long-distance dispersal (at a regional spatial scale) is operational. Our results show however that this is not the common fate of the bulk of propagules. The strategy of Rhizophoraceae in developing this costly, large and fairly low

abundance diaspore (as compared to most tree seed numbers), which often does not overcome predation sufficiently and which usually disperses over short distances only, with a fairly limited longevity under common environmental conditions (Komiyama et al., 1992; Drexler, 2001), requires a renewed scrutiny.

Hydrochorous, viviparous propagules of *C. tagal* and *R. mucronata* do not have a common dispersal strategy, but alternative ones. *C. tagal* and *R. mucronata* developed two different dispersal strategies (Table 4). The one of *C. tagal* consists of releasing a large number of propagules, thereby locally saturating the predators (Dahdouh-Guebas et al., 1998), fast dispersal movement (low density and slender morphology) and high agility (small size) when dispersing through dense root systems. *C. tagal* propagules have a theoretical advantage to disperse over longer distances over *R. mucronata* propagules, but lower establishment chances due to slower root-growth, desiccation sensitivity and smaller size. *R. mucronata*, on the other hand, has adopted a dispersal tactic of survival. A small number of propagules (with respect to *C. tagal* propagules) are released, but they are more tolerant to predation due to their larger size. Being bigger also provides them with a larger immediate water and nutrient supply. We hypothesize that *R. mucronata* propagule characteristics are inherently less suitable for long-distance dispersal, with a slower dispersal, but more suitable to disperse over a longer period and to establish fast upon arrival at a suitable site. This is realized by a higher desiccation tolerance than *C. tagal* propagules, a higher probability for establishment due to its large size, more starch reserves and faster root-growth. In the literature, this situation is referred to as a competition/colonization trade-off. If this trade-off is seed mass based, the largest propagule is expected to be the best competitor while the smallest propagule is the best colonizer or disperser (Turnbull et al., 1999). Smaller seeds tend to disperse better, but establish and germinate less well, and produce smaller seedlings both within and between species (Turnbull et al., 1999; Lahoreau et al., 2006; Skarpaas et al., 2011). This competition/colonization trade-off is acknowledged by our results that *C. tagal* propagules dispersed further and quicker than *R. mucronata* propagules. To have a more direct proof of the relative dispersal speed between *C. tagal* and *R. mucronata* propagules we released fresh propagules (20 propagules of *C. tagal* and *R. mucronata* each) in an along shore current of Gazi Bay, followed for approximately twenty meters and counted at an imaginary finish line. In two consecutive experiments, eight and nine out of ten *C. tagal* propagules were faster than the ten propagules of *R. mucronata*, indicating that the smaller propagule is indeed the faster disperser under identical conditions. Taken together, predation resistance, faster root-growth and a better starting position in the intertidal area of the larger *R. mucronata* propagules result in a pattern of slow but possibly longer dispersal period with the possibility of quick establishment when a propagule arrives at a suitable site. *C. tagal* has many dispersing propagules but with a more limited probability per propagule to develop into a seedling, while *R. mucronata* has fewer dispersing propagules but the ones that start the long-distance dispersal journey are more likely to establish successfully. Despite different morphological characteristics of propagules of both species, the alternative dispersal strategies resulted in a similar capacity for dispersal (possibly also long-distance dispersal), within the distance range studied, ending in successful establishment.

We found that size does influence dispersal success in the two studied species, both positively and negatively at the same time, but not only size. Other propagule and environmental characteristics such as palatability, buoyancy, number of released propagules and tidal position influence the long-distance dispersal capacity of mangrove species as well. Extensive tracking experiments with propagules of diverse mangrove species are useful to clarify dispersal characteristics, but have the disadvantage of being labor

intensive and difficult to interpret, due to the low numbers of propagules that are found back. An interesting next step to get a better understanding of the long-distance dispersal capacity of mangroves could be to fit propagules with a detectable device, since it could be the only way to understand propagule movement, to do complementary genetic studies, within and between populations, and propagule dispersal modeling.

Acknowledgements

The Flemish Interuniversity Council, the 'Vrije Universiteit Brussel', the Laboratorium of Plant Biology and Nature Management, and the Fund for Scientific Research Flanders financed this project. We thank the many lab and field assistants: Amani Said, Hamisi Ali Kirauni, Abu Hamisi Jambia, Rafael De Schutter and Timothy Sierens. Also Dr. Hans Beeckman from the Royal Museum of Central Africa (RMCA), and Dr. Jared Bosire and Dr. James Gitundu Kairo from Kenyan Marine Fisheries and Research Institute (KMFRRI) are acknowledged for the guidance, cooperation and logistical support.

Author contributions: Dennis De Ryck originally formulated the idea along with Nico Koedam. Dennis De Ryck, Farid Dahdouh-Guebas, Diana Di Nitto, Nele Schmitz and Nico Koedam conceived and designed the experiments. Dennis De Ryck conducted field-work/experiments and analysed the data. Dennis De Ryck and Nele Schmitz performed statistical analysis. Dennis De Ryck wrote the manuscript, with paragraphs from Farid Dahdouh-Guebas, Diana Di Nitto, Elisabeth Robert, Tom Van der Stocken. All authors, except the first author, gave editorial advice.

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