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Towards an unknown fate: The floating behaviour of recently abscised propagules from wide ranging Rhizophoraceae mangrove species

Nathalie Tonné[a,b,*], Hans Beeckman[b], Elisabeth M.R. Robert[a,b], Nico Koedam[a]

[a] Ecology and Biodiversity, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium
[b] Laboratory of Wood Biology and Xylarium, Royal Museum for Central Africa (RMCA), Leuvensesteenweg 13, B-3080 Tervuren, Belgium

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ABSTRACT

The persistence of a mangrove ecosystem depends on the potential of its propagules to disperse. In case of the Rhizophoraceae mangrove species, propagules are elongated cylinder-shaped seedlings that have an initial ability to float upon abscission from the parent tree. During the hydrochoric dispersal period, propagule traits (*e.g.* volume and density) change over time, which in parallel influences propagule buoyancy behaviour. Recently abscised, mature propagules of three rhizophoracean mangrove species (*Bruguiera gymnorrhiza* (L.) Sav., *Ceriops tagal* (Perr.) C.B. Rob., *Rhizophora mucronata* Lam.) were submitted to a three-month floating experiment to investigate the timing and pattern in their buoyancy behaviour linked to changes in propagule density. Anatomical analyses of the aerenchymatous tissues complemented the floatation data. Initial propagule density (between 0.96 (*C. tagal*) and 0.99 g cm^{-3} (*B. gymnorrhiza* and *R. mucronata*)) was on slightly lower than that of seawater and increased over time in all species but at dissimilar rates. Intra-individual density increased from the plumule- towards the radicle end, and corresponded with a decrease in proportion of intercellular surface area per unit area. The interplay between propagule traits and surface water conditions determine the fate of each propagule and its capacity to escape the local forest and reach open water. The combination of techniques used and hence combination of data obtained in this study, contribute to an increased understanding of mangrove forest dynamics: the potential and the limits therein to expand the species range or to replenish existing populations with new recruits.

1. Introduction

Worldwide, mangrove forests are lost at a high rate due to the conversion of mangrove areas to other land uses such as aquaculture, agriculture and urban development (FAO, 2007; Polidoro et al., 2010). Their loss and fragmentation imperil mangrove-dependent fauna (Duke et al., 2007; Polidoro et al., 2010; Barbier et al., 2011) and are associated with the loss of mangrove-associated ecosystem services (*e.g.* nursery grounds for diverse animal groups, timber, protection against coastal erosion (Alongi, 2002)). Mangroves may recover naturally without human intervention or with minimal intervention when required (Lewis, 2011), but when they fail to do so, mangrove restoration and afforestation projects are frequently initiated. This particularly happened after the 2004 Indian Ocean tsunami. However, the effectiveness of such projects is not always guaranteed (Erftemeijer and Lewis, 1999) mostly because environmental conditions, species-specific needs and the hydrology of the site had not been taken into account when extensively planting seedlings. Additionally, the persistence of a mangrove ecosystem has been shown to equally depend on the potential for its dispersal units or propagules (mangrove fruits, seeds or seedlings) to disperse and colonise new and suitable areas, and on the success of propagule establishment, growth and survival (Lewis, 2011; Di Nitto et al., 2013). Dispersal-related factors are important in the light of, amongst others, gene flow between isolated populations and forest rejuvenation both on short and longer distances from the parent tree. The knowledge on such factors is most relevant for understanding biogeographical range structure and for complementing the existing knowledge used in mangrove restoration and conservation projects.

In case of rhizophoracean mangrove tree species, the water-dispersed propagules are seedlings which develop directly from the embryo without a dormancy period while they are still attached to the parent tree (*i.e.* true vivipary) (Tomlinson, 1986; Elmqvist and Cox, 1996). Rhizophoracean mangrove propagules

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[*] Corresponding author at: Ecology and Biodiversity, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium.
E-mail address: Nathalie.Tonne@vub.be (N. Tonné).

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typically are elongated and cylinder-shaped hypocotyls, topped by a short plumule (embryonic shoot) and with a radicle (embryonic root) below pointing towards the soil while on the parent tree (Tomlinson, 1986; Sousa et al., 2007). Upon maturity, the propagules detach from the parent tree and fall. Whether they have the opportunity to disperse with the tidal water, depends on various factors such as their location within the mangrove zonation and potential obstacles (like pneumatophores and crab holes) on their way to the open water (Sousa et al., 2007; Van der Stocken et al., 2015a).

All mangrove propagules have the initial ability to float (Tomlinson, 1986) but differences in propagule floating behaviour exist (Rabinowitz, 1978b; Clarke et al., 2001; Sousa et al., 2007; Kadoya and Inoue, 2015). Propagule dispersal is an interplay between various biotic (*e.g.* propagule shape, density and floating orientation) and abiotic factors (*e.g.* wind, water currents, seawater surface salinity and temperature) (Van der Stocken et al., 2013, 2015b). Concerning propagule floating behaviour, the elongated rhizophoracean mangrove propagules form a special and complex case. Besides floating horizontally and sinking, they can also adopt intermediate floating orientations such as prone and vertically hanging at the water surface, or touching the bottom in a vertical fashion after having sunk. This differential buoyancy behaviour is thought to be related to differences in density along the length of the propagules from the plumule- towards the radicle end (Davis, 1940). The dynamics and gradients herein have been briefly touched upon (*e.g.* Robert et al., 2015) but not yet investigated extensively within the context of mangrove propagule dispersal ability. From an anatomical perspective, volume and density and thus propagule buoyancy are influenced by the intercellular spaces in the aerenchymatous cortex and pith tissues of the propagules (Tomlinson, 1986; Robert et al., 2015; Tonné et al., 2016). Insights in these dynamics and gradients, both in space and time, contribute to establishing a link between anatomy and abovementioned dynamics in propagule buoyancy.

Long distance dispersal (LDD – here understood as propagule movement over oceanic expanses) has received much attention in the literature as regards dispersal distances (*e.g.* Drexler, 2001; De Ryck et al., 2012; Di Nitto et al., 2013; Lo et al., 2014) and factors related to or influencing propagule stranding (*e.g.* Rabinowitz, 1978a; Sousa et al., 2007; Peterson and Bell, 2012). However, the dispersal period within the mangrove forest right after propagule abscission and preceding LDD on the open water, is an equally important phase in the dispersal process influencing the eventual fate of each propagule (*e.g.* Kadoya and Inoue, 2015; Robert et al., 2015). Environmental conditions differ along the mangrove zonation (Matthijs et al., 1999; Bengen and Dutton, 2004; Robert et al., 2009; Medellu et al., 2012) and together with the heterogeneous mangrove landscape matrix they influence the onset of the dispersal trajectory of propagules. In addition, propagule traits such as mass and density gradually change over time (Robert et al., 2015) which in turn affects the influence of prevailing local environmental conditions on propagule dispersal. When propagules reach the open seawater after abscission, dispersal over several kilometres is possible, and this certainly after already two ebb tides (Van der Stocken et al., 2013).

The aim of this study was to gain an understanding of the dynamics in the density of elongated mangrove propagules linked to their floating orientation, as well as in the change in density gradient over time along the length of the propagules. We therefore monitored the buoyancy behaviour of three mangrove species of Rhizophoraceae (*Bruguiera gymnorrhiza* (L.) Sav., *Ceriops tagal* (Perr.) C.B. Rob. and *Rhizophora mucronata* Lam.) during the first three months after abscission. The specific aims were to determine (1) the initial density of the different rhizophoracean mangrove propagules and their floating position upon reaching a body of water immediately after detachment, (2) the density gradient along the length of the propagules as a function of floating orientation, and (3) the timing and pattern of change in the density of the different propagules during the dispersal process. Supporting anatomical analyses of the aerenchymatous hypocotyl tissues complemented the floatation data. By combining the data on floating behaviour with data on temperature and salinity of surface water in and near mangrove forests from literature and *in situ* diurnal point measurements, we in addition examined how water conditions and changes herein can affect the (initial) floating dynamics of the propagules of different species and hence their potential to disperse, away from the parent tree, and to reach open water.

2. Materials and methods

2.1. Studied species

The hydrochorous mangrove propagules of *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Rhizophora mucronata* mangrove species (hereafter Bg, Ct and Rm respectively) were considered in this study. We have chosen these species because they are the most common along the coast of East Africa, which is latitudinally the core of their range, and also the most common representatives for the pantropical mangrove family Rhizophoraceae in this biogeographical area. All three species belong to the tribe Rhizophoreae within the family Rhizophoraceae (Tomlinson and Cox, 2000), implying an ontologically similar development. The propagules all have a similar shape (*i.e.* elongated cylinder-shaped propagules) with a function in LDD important in the biogeographical range of the species (Tomlinson, 1986; Tomlinson and Cox, 2000).

2.2. Propagule collection

Collection of Ct, Rm and Bg mangrove propagules was done on 25th April and 5th May, 2015 at Menai Bay (6°18′S, 39°22′E) and on 26th April, 2015 at Bumbwini (5°56′S, 39°12′E), both on Unguja, the main island of the Zanzibar Archipelago in Tanzania. Mature and healthy propagules were collected according to availability from adult trees (propagules were sampled from at least five trees, to take into account species-specific tree fecundity) by softly shaking branches or whole trees, and collecting the released propagules in order to avoid their exposure to the osmotic effects of the tidal water after abscission. The GPS coordinates of every parent tree were recorded (Garmin GPSMAP 64S, Garmin (Europe) Ltd., Hampshire, UK), and the propagules were labelled with a permanent marker. Propagules which showed signs of decay were discarded. In total, 14 healthy propagules of Bg, 117 of Ct, and 42 of Rm were collected.

On the very same day of the collection, the initial buoyancy behaviour of a subset of the propagules (14 Bg, 99 Ct, 39 Rm propagules) was determined in a large basin filled with seawater on the SUZA campus (the State University of Zanzibar, Unguja, Tanzania) (25th April, 2015), or in the seawater near the mangrove forest (26th April, 2015). Water temperature and salinity were 28 °C and 17‰, and 30 °C and 24‰ respectively. After collection and before transport, the propagules were loosely stored in humid cloths, outside of the direct sunlight and with sufficient space between them to allow aeration.

The propagules were transported to Belgium by airplane on 8th May, 2015, wrapped in humid towels. Upon arrival, the propagules were immediately placed in bins with water of mean seawater salinity (32.5‰), attained by mixing fresh water with commercial NaCl, in order to acclimatise during three days at ambient conditions (air temperature approximately between 25 and 30 °C). One to two air pumps per bin allowed aeration of the water.

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During the period between the field collection of the propagules and the propagule floating experiment (see Section 2.3.), a small number of the propagules of Bg developed a little tap root of less than 5 mm. The majority of the Ct and Rm propagules had small root bumps or small roots (less than 5 mm). Root development before dispersal or even abscission is not uncommon under natural conditions. Propagules of *Ceriops* and *Rhizophora* for example, already develop root bumps during development when still attached to the parent tree (Juncosa, 1982; Robert et al., 2015), although this does not occur in propagules of *Bruguiera* (Juncosa, 1984). Root formation can occur in abscised propagules which fall on the mangrove floor and stay in contact with the substrate for a relatively long period of time (Robert et al., 2015), for example during a neap tide or on locations where tidal inundation is infrequent. The root bumps and roots ceased development in all species upon initiation of the floating experiment.

2.3. *Floating experiment*

After an acclimation period of three days, the initial floating orientation (*i.e.* the angle at which the propagule was floating at the water surface, or the angle at which it was standing on the bottom) of each propagule was determined (11th May, 2015). For this, the propagules were put in an aquarium (tank) which was filled with de-ionised freshwater mixed with commercial NaCl to reach mean seawater salinity (32.5‰) (*i.e.* experimental seawater). On the aquarium as well as on a separate plastic flexible plate, angles between 0 and 90° were drawn with a resolution of 5° which allowed us to accurately determine the floating angle of each propagule. The temperature of the water in the aquarium was logged throughout the experiment at one-minute intervals by means of a Hobo UTBI-001 TidbiT v2 Water Temperature Data Logger (Onset, Bourne, USA). Salinity was measured three to four times per week using a handheld refractometer (VWR, Leuven, Belgium) and kept constant throughout the experiment. During the recording of propagule floating orientation, we accurately noted the time to be able to retrieve the exact water temperature from the Hobo datalogger and hence determine the density of the water at that moment.

Also determined for the first time were the following propagule traits: length, mass, volume and density (*i.e.* initial measurements). The hypocotyl length and the mass of every propagule were measured with a measuring tape (0.1 cm resolution) and an electronic precision balance (LP 1502, VWR series, Leuven, Belgium; 0.01 g resolution) respectively. In case of curved propagules (Rm only), the inner as well as the outer side of the hypocotyl curve were measured. The volume of each propagule was determined in freshwater by means of the water displacement method (Chave, 2005; Hughes, 2005), by using a second electronic precision balance (Acculab Atilon ATL 4202-I, Sartorius, Gottingen, Germany; 0.01 g resolution). Volume measurements took a few seconds (less than 5 s) per propagule, and buoyancy was unchanged after the measurement. The volume together with the temperature of the fresh water, which was assessed with a HI 145-20 Digital Thermometer (Hanna Instruments, Woonsocket, USA; 0.1 °C resolution), allowed to accurately calculate the density of each propagule.

2.4. *Propagule sampling*

After the acclimation period, we monitored the floating orientation of the propagules three to four times per week, for a period of three months from 11th May until 12th August, 2015. This experimental period included the weeks after abscission, but equally allowed us observing propagule floating behaviour during longer time periods (which reflect durations for LDD).

During the three experimental months, we sampled a range of floating orientations – as wide as possible and as allowed by the collection of propagules – per species. At the same time, we attempted to sample at least the following floating orientations: horizontally (S0) and vertically floating at the water surface (S90), propagules lying horizontally on the bottom (B0) and touching the bottom vertically (B90). Propagules with a vertical orientation (S90 or B90) had their radicle end pointing down. Orientations S0 and B0 included propagules with an angle smaller than 10° (between 0° and 9°), orientations S90 and B90 included angles larger than 80° (between 81° and 90°). During sampling, propagule length, mass and volume, and therewith the density, were determined for a second time (*i.e.* final measurements), in order to compare these propagule traits with the initial measurements and hence find a possible pattern in those traits as a function of floating orientation.

After the measurements, the hypocotyl of every propagule was divided into five segments of equal length. Of each segment, we measured and calculated the mass, volume and density. The difference in density between the experimental seawater and each segment was calculated. For a subset of the propagules (Bg n = 9; Ct n = 86; Rm n = 22) and after having done the aforementioned measurements, we additionally checked the buoyancy behaviour of every segment separately in the experimental seawater.

2.5. *Sample preparation and light microscopy*

Exploratory anatomical analysis was done on the hypocotyl segments of two Ct (S0 and S90), one Bg (S90) and two Rm (S90 and B90) propagules, which were sampled according to the *Propagule sampling* procedure outlined above (Section 2.4.). The propagule segments were preserved in a mixture of 35% ethanol and glycerol (1:1 ratio) until sectioning. Of the Bg and Ct propagule segments (segment 1–5), transverse sections were made (three per segment) with a thickness of 15–25 μm using a sliding microtome (Sledge GSL1, Zürich, Switzerland (Gärtner et al., 2014)). The segments of Rm (segment 1–5, in the middle) were soaked with polyethylene glycol (PEG) 1500 (Rotipuran® Ph. Eur., Carl Roth, Germany) for five days at 60 °C, and subsequently sectioned with a sliding microtome (Microm HM 440E, GMI, Minnesota, USA) at 12–20 μm thickness (three sections per segment).

All sections were put on a labelled microscope slide and bleached with commercial bleach for a few minutes in order to remove phenolic compounds (Gärtner and Schweingruber, 2013), and subsequently rinsed well with demineralised water. They were double stained with a mixture of Safranin O (0.35 g in 35 ml of 50% ethanol) and Alcian Blue (0.65 g in 65 ml water) for circa one minute. Surplus stain was removed with demineralised water before the sections were dehydrated by successively rinsing them with 50%, 75% and 96% ethanol. Finally, they were embedded with a few drops of Euparal (Carl Roth, Germany), covered with a cover glass and a weight, and dried overnight in an oven at 60 °C. Of every section of each segment, three images of the inner cortex and pith at highest magnification (400×) were made with a camera connected to a microscope (Olympus UC30 and Olympus BX60 respectively, Olympus Europa Holding GmbH, Hamburg, Germany), using the image analysis software programme CellB̂ (Olympus Europa Holding GmbH, Hamburg, Germany).

2.6. *Data and anatomical analyses*

The difference in propagule length, mass, volume and density between the start of the floating experiment (11th May, 2015) and harvest (*i.e.* between initial- and final measurements) was tested for all the propagules of each species, except for those which were immediately sampled on 11th May. Data which were normally distributed and had comparable variances were tested using the

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paired *t*-test (0.05 significance). When one of the assumptions was violated, differences between initial and final measurements were tested using the nonparametric Mann-Whitney Wilcoxon test (by specifying in R that the data are paired). Interspecific differences in length, weight, volume and density (for initial and final measurements) between all species were tested using the Kruskal-Wallis test, as in all cases one of the assumptions for doing ANOVA was violated. After, pairwise interspecific differences were identified using the Mann-Whitney Wilcoxon test. All the above-mentioned statistical analyses were conducted using R (version 3.2.3; R Core Development Team, 2015).

The images of the sections of the propagule segments were analysed in ImageJ 1.50i (Wayne Rasband, National Institute of Health, Bethesda, Maryland, USA). The surface area of the images was determined, after which the number of intercellular spaces was counted and the surface area of every space was measured. Subsequently, the total intercellular surface area per unit area (by summing the surface area of each intercellular space) and the percentage intercellular space per unit area of the image were calculated. The data were analysed in Microsoft Office Excel 2007 (Microsoft Corporation, Washington, USA).

2.7. Buoyancy behaviour simulations

We examined how the buoyancy behaviour of propagules right after abscission would be influenced by changing environmental conditions by combining the data of propagule density (obtained during the *Floating experiment*, Section 2.3) with information on surface temperature and surface salinity of water flowing through (*e.g.* rivers, streams) and near (*e.g.* coastal water) mangrove forests as well as still water (*e.g.* pools) within mangrove forests. We therefore calculated, based on the initial density of the propagules, the percentage of the propagules that would float and thus would be able to disperse away from the parent tree, for a given combination of surface water temperature (SWT) and salinity (SWS) which can be observed over the day and tidal cycle in a native mangrove system. Calculations were performed in Microsoft Office Excel 2007 (Microsoft Corporation, Washington, USA). The same procedure was repeated using the final density of the propagules determined at harvest (see Section 2.4., *Propagule sampling*), and compared with the results based on initial propagule density.

Data on SWT and SWS were obtained in mangrove forests in Gazi Bay (Kenya) and Chwaka Bay (Unguja, Zanzibar, Tanzania) (Table 1), both belonging to the Western Indian Ocean biogeographical province (*sensu* Spalding et al., 2007). In Chwaka Bay, a non-estuarine embayment, water-related data was collected bimonthly during the day at spring low tide by Lugendo et al. (2005) along a trajectory from inside the mangrove forest via creeks and channels, towards the seaward side of the forest on intertidal mudflats, seagrass beds and open water. In Gazi Bay, *in situ* point measurements of SWT and SWS were taken over the day and tidal cycle in February 2016 in three characteristic mangrove settings. Temperature of the surface water (5 cm depth) was measured using a HI 145-20 Digital Thermometer (Hanna Instruments, Woonsocket, USA), and the salinity was measured using a handheld refractometer (VWR, Leuven, Belgium).

3. Results

3.1. Propagule floating behaviour

In the field, immediately after the abscission from the respective parent tree, all tested propagules (14 Bg, 99 Ct and 39 Rm) floated at the surface of the water, with the exception of two individuals (one Bg and one Ct) which were touching the bottom in a vertical fashion with the radicle end pointing down (B90). Of the floating propagules, the majority was floating horizontally at the water surface (S0) in Ct and Rm (100% and 79% respectively), while in Bg the majority was floating prone or vertically hanging (64%) (Fig. 1).

The initial density of all propagules, with the exception of two Bg propagules, was lower than that of the experimental seawater (32.5‰) in the aquarium tank, but differences existed in the density between species. Propagules of Bg and Rm had a comparable density (0.99 ± 0.01 g cm^{-3} and 0.99 ± 0.02 g cm^{-3} respectively), which were both significantly higher than that of Ct (0.96 ± 0.03 g cm^{-3}) (Tables 2 and 3). Hence, at the start of the actual floating experiment, almost all propagules of all studied species floated at the water surface. Their evolution in floating orientation over time is illustrated in Fig. 1. The initially predominant floating orientation of the Bg propagules was prone or vertically hanging at the water surface (S90) (86%), while the majority of the Ct and Rm propagules (96% and 61% respectively) floated horizontally at the water surface (S0). The remainder of the Ct and Rm propagules floated in a prone position between S0 and S90. None of the propagules was floating with its plumule end pointing down.

The density of almost all propagules significantly increased over time resulting in a buoyancy pattern which was most pronounced by the propagules of Rm (Fig. 1C): the Rm propagules which initially floated horizontally (S0) at the water surface, gradually dropped their radicle end to change to a vertical hanging position (S90). The time frame in which they changed orientation, ranged from 2 to 35 days (mean period = 9.3 days; n = 18). During S90 floating, the plumule end of the propagules reached above the water surface. This evolution was also observed in propagules of Ct (mean period = 11 days; n = 12).

Only in Rm propagules, an evolution from a vertically hanging (S90) to a vertically standing (B90) orientation was observed (Fig. 1C). At the start of this transition, which took less than one week, the Rm propagules touched the water surface with only the very tip of their plumule end and alternated between the S90 and B90 position (Fig. 1C). After the propagules had definitively reached the bottom (B90), the few propagules which were not yet sampled then gradually started dropping their plumule end and stood prone on the bottom (Fig. 1C).

Propagules of Bg and Ct changed floating orientation more slowly than those of Rm, hence both former species adopted a wider variety of floating angles between S0° and S90° (Fig. 1A–B: "S prone"). Over time, about 20% of the Ct propagules started wandering around a certain prone floating angle, alternating between a slightly larger and slightly smaller angle. The period in which they exhibited this behaviour, ranged from 6 to 65 days (mean period = 33.4 days; n = 22). By the end of the floating experiment, none of the Bg propagules had adopted the S0 floating orientation, none of the Ct propagules had reached the bottom, and none of the Rm propagules was observed lying flat on the bottom (B0) (Fig. 1).

Average propagule length changed over the course of the experiment: it non-significantly increased in Bg and Rm, and significantly increased in Ct. Propagule mass on average significantly decreased in Bg and Ct, while it significantly increased in Rm. In all species, average propagule volume significantly decreased and density significantly increased (Table 3).

3.2. Density pattern along the propagule

With minor exceptions for Bg and Rm (2/14 and 3/42 respectively), the density of the propagules increased along their length from the plumule end towards the radicle end. In Ct, a larger proportion (28/117) of propagules did not exactly follow this increasing trend in density down to the radicle end (*e.g.* segment 1 was sometimes slightly denser than segment 2), but the differences were minor and the overall density trend was yet valid (Fig. 2C). The

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Table 1
Temperature and salinity of the surface water (SWT and SWS respectively) along a trajectory from within the mangrove forest towards the open water. In case of Chwaka Bay, the mean values (±SD) are based on data collected by Lugendo et al. (2005). In case of Gazi Bay, the data are based on ground-truthing measurements (range from minimum to maximum) over eight days and around spring tide which is expected to give differences in SWT and SWS due to newly reached areas high in the intertidal which had been exposed to air and evaporation throughout the inter-spring tide period.

Chwaka Bay, Unguja, Zanzibar, Tanzania (trajectory landward → seaward)					
Observational period: bimonthly during one year (November 2001–October 2002)					
	Mangrove creeks	Mangrove channel	Mud/sand flat	Seagrass beds in bay	Seagrass beds in ocean
SWT (°C)	26.3 (2.5)	26.8 (3.0)	27.6 (2.2)	28.1 (2.1)	27.3 (2.4)
SWS (‰)	30.9 (6.9)	29.9 (8.6)	32.2 (5.8)	33.8 (5.4)	35.5 (1.9)

Gazi Bay, Kenya (trajectory landward → seaward)			
Observational period: eight consecutive days (February 2016)			
	Permanent tidal creek	Shallow tidal creek or pool	Bay
SWT (°C)	27.2–31.4	26.9–36	27.5–33.1
SWS (‰)	33–41	36–43	34–39

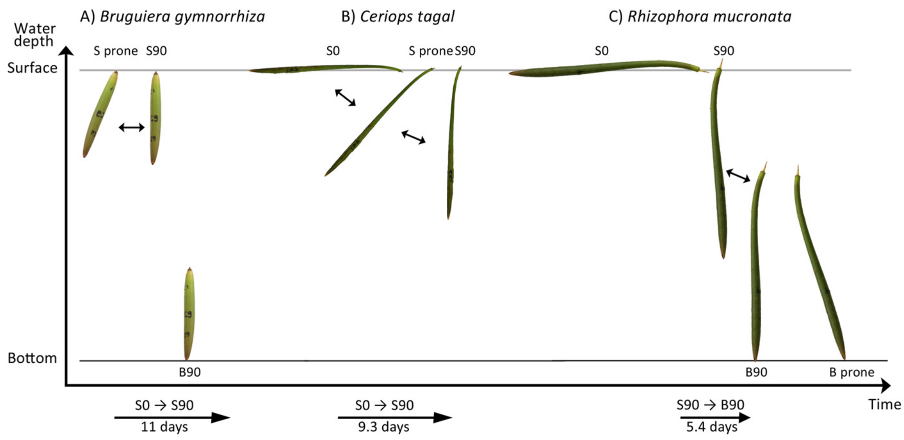

Fig. 1. The consecutive floating orientations adopted by the propagules of (A) *Bruguiera gymnorrhiza*, (B) *Ceriops tagal* and (C) *Rhizophora mucronata* over time during the experimental period. Propagules of *B. gymnorrhiza* and *C. tagal* sometimes wandered around a certain floating orientation, alternating between a slightly smaller or larger angle (double arrows). The timelines below the figures depict the average number of days it took for propagules to make the transition between two particular floating orientations. S and B: indicate surface and bottom of water column respectively; 0, 90 and prone: refer to a horizontally, vertically and prone orientation respectively (colour online only).

Table 2
The non-parametric Kruskal-Wallis tests identified (non-)significant interspecific differences in the traits propagule length, weight, volume and density. W indicates the value of the non-parametric Mann-Whitney Wilcoxon test statistic in R to identify the pairwise differences (as in all cases, one of the assumptions for parametric testing was violated); the corresponding *p*-value is also indicated. IL: inner hypocotyl length, OL: outer hypocotyl length.

	Bg/Ct	Ct/Rm	Bg/Rm
Initial measurements			
Length	W = 17; p < 0.0001	IL: W = 96.5; p < 0.0001 OL: W = 98.5; p < 0.0001	IL: W = 0; p < 0.0001 OL: W = 0; p < 0.0001
Weight	W = 740; p-value = 0.0002	W = 0; p < 0.0001	W = 3; p < 0.0001
Volume	W = 733; p-value = 0.0003	W = 0; p < 0.0001	W = 3; p < 0.0001
Density	W = 755; p < 0.0001	W = 238.5; p < 0.0001	W = 81; p-value = 0.0670
Final measurements			
Length	W = 16.5; p < 0.0001	IL: W = 100.5; p < 0.0001 OL: W = 102; p < 0.0001	IL: W = 0; p < 0.0001 OL: W = 0; p < 0.0001
Weight	W = 733; p-value = 0.0003	W = 3; p < 0.0001	W = 0; p < 0.0001
Volume	W = 729; p-value = 0.0003	W = 3; p < 0.0001	W = 0; p < 0.0001
Density	W = 0; p < 0.0001	W = 55.5; p-value = 0.0069	W = 1399.5; p-value = 0.1100

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Table 3
Intraspecific differences between mean initial (“I”; upper row) and final (“F”; lower row) measurements (±SD) of propagule length, mass, volume and density of all propagules, except of those which were sampled at the start of the experiment. The two values for the average hypocotyl length in *Rhizophora mucronata* represent the outer (left) and inner length (right) respectively. As in some cases one of the assumptions for the paired *t*-test was violated, the Mann-Whitney Wilcoxon test was performed in all cases: a – significant difference, b – non-significant difference.

		Bruguiera gymnorrhiza (n = 10)	*Ceriops tagal* (n = 86)	*Rhizophora mucronata* (n = 27)	
Length ± SD (cm)	I	12.2 ± 4.0	24.6 ± 3.8	33.2 ± 3.9	32.9 ± 4.0
	F	12.3 ± 4.0 ^{b}	24.7 ± 3.8 ^{a}	33.2 ± 3.9 ^{b}	33.0 ± 4.0 ^{b}
Weight ± SD (g)	I	14.28 ± 6.31	7.46 ± 2.06	49.48 ± 13.75	
	F	14.05 ± 6.22 ^{a}	7.40 ± 2.06 ^{a}	49.90 ± 13.80 ^{a}	
Volume ± SD (cm^3)	I	14.70 ± 6.32	7.77 ± 2.12	49.77 ± 13.37	
	F	13.99 ± 6.25 ^{a}	7.48 ± 2.06 ^{a}	49.02 ± 13.39 ^{a}	
Density ± SD ($g\ cm^{-3}$)	I	0.99 ± 0.01	0.96 ± 0.03	0.99 ± 0.02	
	F	1.01 ± 0.00 ^{a}	0.99 ± 0.01 ^{a}	1.02 ± 0.01 ^{a}	

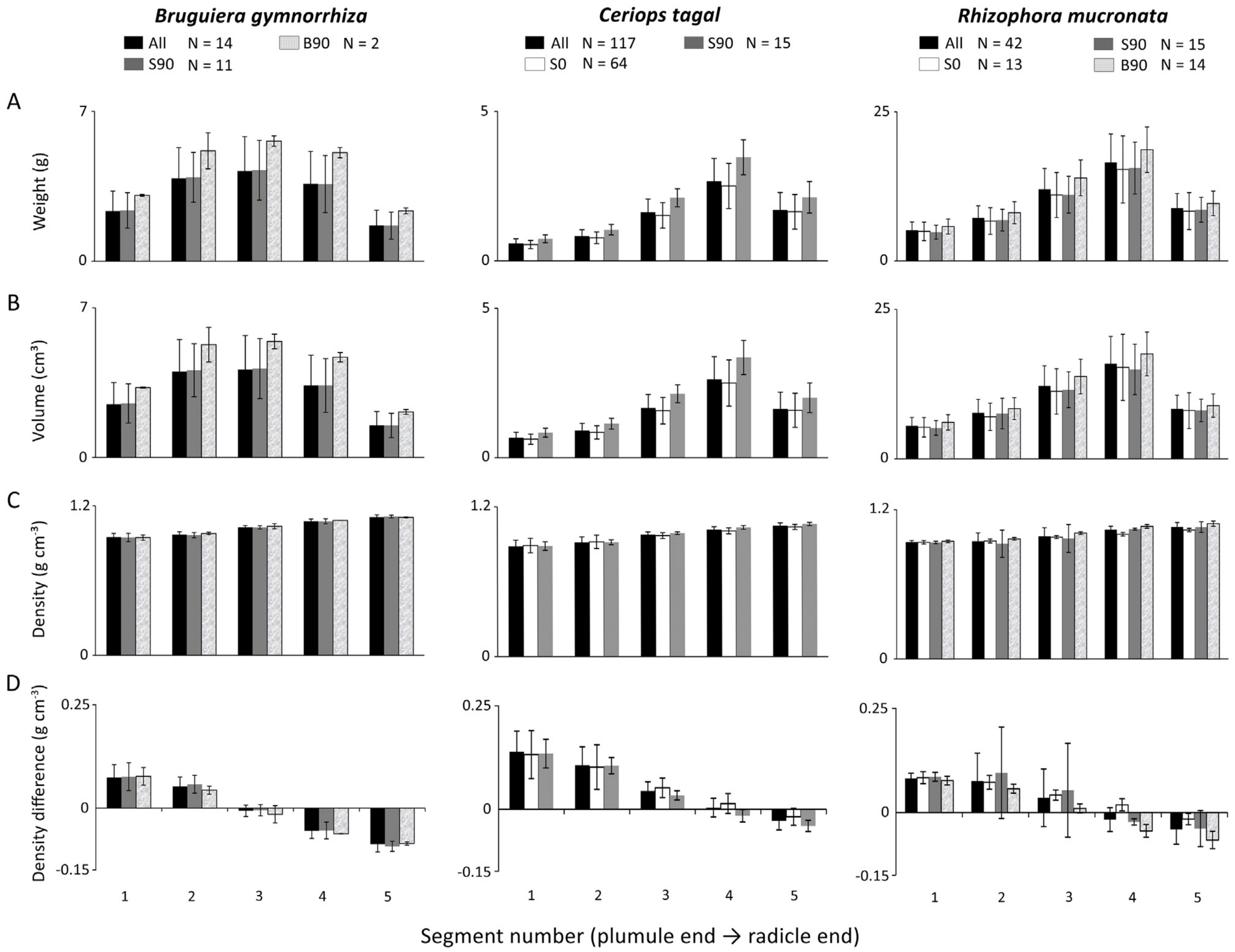

Fig. 2. Average (A) weight, (B) volume and (C) density (±SD) of each of the five propagule segments at harvest per species, and average (D) density difference (±SD) at harvest between the experimental seawater and each propagule segment. Propagule segments are numbered 1–5, according to the length of the propagule from the plumule- towards the radicle end. Legend: black: all propagules; white, grey and pattern: propagules adopting the S0, S90 respectively B90 floating orientation at harvest.

weight and volume of the segments did not follow the same trend as the density. In Bg, the middle segment was generally the heaviest and had the largest volume, while in Ct and Rm this was the fourth segment (Fig. 2A–B). Irrespective of the species and floating orientation, the plumule segment had a lower density than the experimental seawater, while the radicle segment had a higher density (Fig. 2C). Analogous to the plumule segment, segment 2 was also lighter than the experimental seawater, and the same was true for segment 3 in case of Ct. Regarding segment 3 and 4 in Bg and Rm, and segment 4 in case of Ct, the difference in density with the experimental seawater was dependent on the floating orientation, but in general the following was valid: the larger the floating angle, the more hypocotyl segments starting from the radicle end had a density which was higher than that of the experimental seawater (Fig. 2D).

In the majority of cases (more than 93%), the observations from the buoyancy test on a subset of the propagule segments agreed with the calculated difference in density between the experimental seawater and each segment. As such, we observed that segment 1 (plumule segment) and 2 floated, and segment 5 (radicle segment) sank in all cases irrespective of the species. Segment 3 floated in all cases in Ct, and segment 4 sank in all cases in Bg. Segment 3 in case

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of Bg and Rm, and segment 4 in case of Ct and Rm, floated or sank depending on the floating orientation.

3.3. Light microscopy

Light microscopy on the microsections of the Bg, Ct and Rm propagule segments revealed that the intercellular spaces were predominantly situated in the inner cortex and the pith. The cells in the outer cortex were compactly arranged with fewer intercellular spaces.

Along the length of the Bg propagule, we observed a gradual change in the morphology and organisation of the inner cortex cells from radially elongated and loosely arranged respectively (segment 1, plumule end) to roundish and more compactly arranged (segment 5, radicle end) (Fig. 3A). The morphology and organisation of the inner cortex cells along the length of the Ct propagules and irrespective of floating orientation, was different to that of Bg: near the plumule end the inner cortex cells were isodiametrical and orderly arranged (segment 1); towards the radicle end the cells became predominantly radially elongated and were loosely arranged (segment 5) (Fig. 3B). Within the propagules of Rm and irrespective of the floating orientation (S90 vs. B90), the cellular morphology and organisation of the inner cortex of segment 1 was similar to that of the Ct propagules, *i.e.* roundish and orderly arranged cells (Fig. 3C). In segment 3 and 5 the cells of the inner cortex were equally roundish, but they were more compactly arranged compared to segment 1 (Fig. 3C). Trichosclereids (*i.e.* branched sclerenchymatous idioblasts (Foster, 1956)) occurred scattered throughout the cortex and pith tissues of the Rm propagules, while sclereid clusters occurred in the outer cortex (Fig. 3C). In all three species, the pith was composed of roundish cells interspersed with intercellular spaces.

In both the inner cortex and pith tissues, we observed a decreasing trend in density of intercellular spaces per unit area and proportion of intercellular surface area per unit area, along the length of the propagules (from plumule- to radicle end). An example of the analysis is shown in Table 4. This trend held for all species, irrespective of the floating orientation.

The proportions of intercellular surface area per unit area were on average higher in the horizontally floating Ct propagule (S0) compared to the vertically floating one (S90) (data not shown). This pattern was less clear in the Rm propagules with orientation S90 and orientation B90 (data not shown).

3.4. Buoyancy behaviour simulations

Based on the SWS and SWT data from native mangrove systems (Chwaka Bay, Zanzibar (Lugendo et al., 2005) and Gazi Bay, Kenya) (Table 1), combined with the initial propagule densities, we estimated that more than 90% of the propagules of all species would float immediately after abscission, under most circumstances and along the trajectory from within the mangrove forests towards the open water. During heavy rains, the salinity in the mangrove creeks of Chwaka Bay can be temporarily lowered to a naturally occurring 5‰ (without a change in the SWT) (Lugendo et al., 2005), which would cause the percentage of floating propagules to decrease to 71% and 74% for Bg and Rm, respectively. The percentage of floating Ct propagules would remain unaffected by such salinity decrease (99% remained floating at the water surface irrespective of the surface water salinity conditions). Occasionally, evaporation can cause the salinity of tidal pools in the mangrove forest to increase to 63.5‰. The percentage of floating propagules would then be 100% in all species.

Using the final densities of the propagules at harvest (different sampling moments throughout the experimental period), we estimated that the percentage of floating Rm propagules would decrease depending on the combination of SWT and SWS (the percentage of floating propagules ranged between 64% and 88%). The majority (more than 90%) of the Bg and Ct propagules on the other hand, would remain lighter than the seawater and continue floating. Only when the salinity was lowered to 5‰ (without a change in the SWT), the percentage of floating Ct propagules would start decreasing to 84%. Also in Bg and Rm, the percentage of floating propagules would then decrease to 21% and 31% respectively. An increase in salinity of tidal pools to 63.5‰, would cause 100% of the Bg and Ct propagules to stay afloat, and more than 95% of the Rm propagules.

4. Discussion

4.1. Propagule density

The idea that elongated propagules of the family Rhizophoraceae have a density adjusted to that of seawater was coined by Guppy (1906), and is confirmed by our results on propagules of *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Rhizophora mucronata*: all species had an initial density close to that of seawater (seawater with a salinity of 32.5‰ has a density around 1.02 g cm^{-3}). Hence, the great majority of all propagules floated after detachment from the parent tree, but the initial floating orientation differed between species: propagules of Ct and Rm initially floated horizontally, whereas those of Bg floated prone or vertically hanging at the water surface (*sensu* Clarke et al., 2001). Similar initial propagule densities were found for Bg, Ct and Rm propagules collected in Kenya (De Ryck et al., 2012; Van der Stocken et al., 2015b) and for propagules of *R. stylosa* Griff. collected in Japan (Kadoya and Inoue, 2015). The ecological significance of the differences in buoyancy behaviour upon abscission between homologous structures and whether these different buoyancies are equally effective in terms of LDD, however, remains insufficiently comprehended. We would expect these differences to result in differential dispersal distances and colonisation potentials, because interspecific differences in floating orientation upon abscission can influence the potential of propagules to escape from the local forest (*e.g.* horizontally and vertically floating propagules are differentially retained by the root network of adult mangrove and external factors such as wind and water currents affect them variously (Van der Stocken et al., 2015a)).

Over time, propagule density increased in all studied species, and this was in line with the findings of Robert et al. (2015) on propagules of Ct and Rm. The observed non-random evolution in propagule floating orientation for Ct and Rm (Fig. 1) is consistent with an increase in propagule density along the hypocotyl starting from the radicle end and with the reported buoyancy behaviour of propagules of *R. harrisonii* Leechm. (Rabinowitz, 1978b), *R. mangle* L. (Davis, 1940) and Ct (Clarke et al., 2001; Robert et al., 2015).

On average, the propagules of Bg and Ct floated longer than those of Rm which started sinking earlier. The Rm propagules in our study had initiated small roots at the start of the floating experiment which may have influenced the speed with which propagule density and hence floating orientation changed over time, likely preparing the propagules for establishment once they strand on a suitable habitat patch. Vertically oriented *Rhizophora* propagules may even establish in water that is deeper than the propagule itself (Cheeseman, 2012).

Besides interspecific differences, also intraspecific differences in floating patterns exist, emphasising the dynamic nature of the dispersal process in Rhizophoraceae mangrove propagules. An example of this is the changing density of Bg propagules. The observations of Kadoya and Inoue (2015) herein were opposite to ours and opposite to the floating patterns observed by Guppy (1906) and

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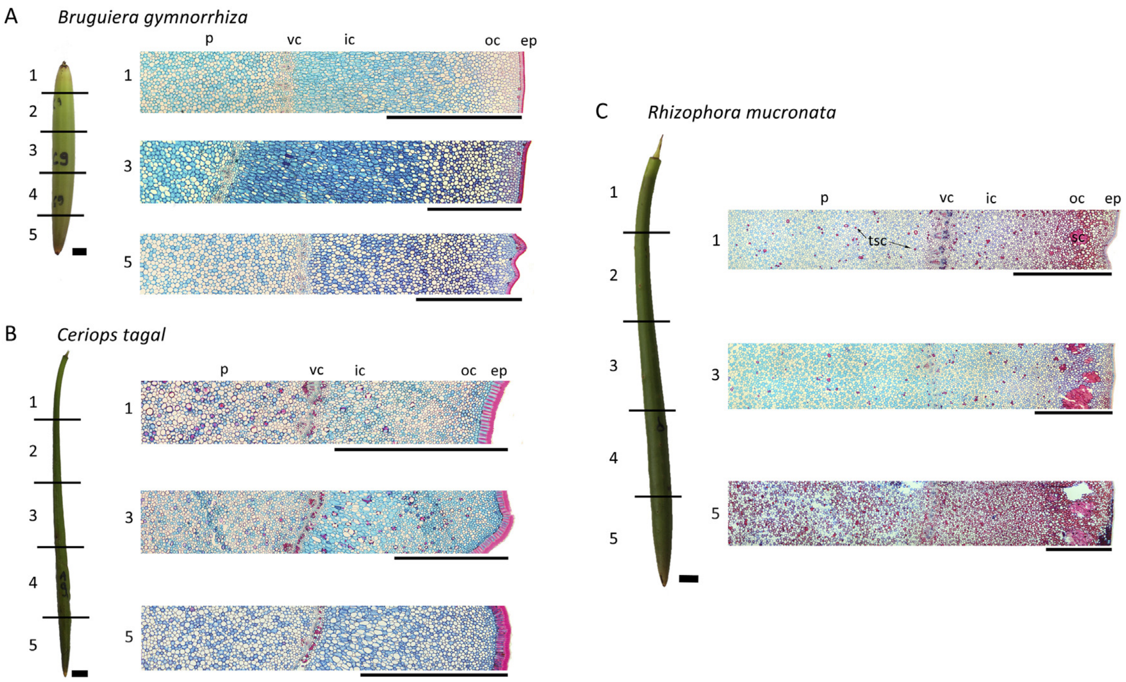
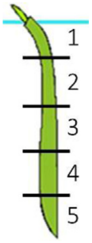
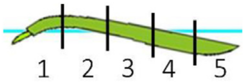
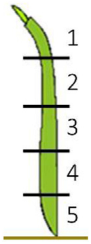


Fig. 3. Propagules of (A) *Bruguiera gymnorrhiza*, (B) *Ceriops tagal* and (C) *Rhizophora mucronata* were divided into five segments (1–5) during *Propagule sampling* (see Section 2.4). On the right of each propagule, the corresponding microsections of segment 1, 3 and 5 are shown. The colours of the sections refer to unlignified cells (blue – Alcian Blue) and lignified cells or phenolic substances (red – Safranin O). Abbreviations: p: pith; vc: vascular cylinder; ic: inner cortex; oc: outer cortex; tsc: trichosclereids; sb: sclereid clusters; ep epidermis. Scale bars propagules: 1 cm; scale bars microsections: 1 mm (colour online only).

Table 4
The intra-individual gradient in the average number of intercellular spaces per unit area and the proportion of intercellular surface area per unit area in both the cortex and pith tissues, along the length of the propagules of *Bruguiera gymnorrhiza*, *Ceriops tagal* and *Rhizophora mucronata* from segment 1 to segment 5 (*i.e.* from the plumule- towards the radicle end).

		Cortex		Pith	
		Average number of intercellular spaces (mm^{-2})	Proportion intercellular surface area (%)	Average number of intercellular spaces (mm^{-2})	Proportion intercellular surface area (%)
Bruguiera gymnorrhiza – vertically floating (S90)					
	Segment 1	514	13.40	918	3.25
	Segment 2	257	10.03	454	1.14
	Segment 3	339	9.79	325	1.09
	Segment 4	372	5.15	454	1.28
	Segment 5	511	4.19	722	0.80
Ceriops tagal – horizontally floating (S0)					
	Segment 1	1050	31.92	1172	23.41
	Segment 2	911	21.07	1340	21.86
	Segment 3	407	7.41	968	11.03
	Segment 4	293	6.32	957	7.15
	Segment 5	593	11.77	593	2.56
Rhizophora mucronata – vertically standing (B90)					
	Segment 1	525	27.10	593	33.07
	Segment 2	490	28.34	393	27.46
	Segment 3	339	23.19	268	21.69
	Segment 4	268	18.56	154	15.67
	Segment 5	297	18.64	175	12.98

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Clarke et al. (2001) for this species. The Bg propagules collected in Japan initially sank after detachment due to their slightly higher density (1.05 g cm^{-3}). Already within 72 h after submergence, their density gradually decreased and the propagules started floating. The authors did however not provide any specifications on the temperatures and salinities of the water in their study. The variable findings regarding the density of Bg propagules likely reflect different dispersal mechanisms (short and long distance dispersal – SDD and LDD; SDD – here understood as local propagule movement near the parent tree, within the mangrove forest) inherent to Bg. Further, discrepancies between our results and those of Kadoya and Inoue (2015) might be due to differences in propagule collection location within the mangrove forest (mid-intertidal vs. along a river), study methodologies, but also differences in ecological setting and genetic composition between the mangrove populations cannot be excluded.

4.2. Within-propagule density gradient

The notion of the existence of a gradient in density along the length of elongated rhizophoracean mangrove propagules was already coined by Davis (1940), and was supported by our floatation results on the propagule segments and the supporting anatomical analyses. As the proximal part of the propagules (near the plumule end) contains a higher number of intercellular spaces compared to the distal part (at the radicle end) (Table 4), it can hold more air, positively influencing the buoyancy behaviour of the entire propagule. The persistence of this internal density gradient over time would allow the lighter proximal part of the propagule, containing the plumule, to remain upward and (mostly) in contact with the air during stranding and establishment, while the denser distal part from which the taproot (in case of Bg) or lateral roots (in case of Ct and Rm) emerge, would stay in contact with the soil as required for establishment. This within-propagule density gradient and hence overall propagule configuration, would also facilitate withstanding tidal buffeting and wind action for the settling propagule (Tonné et al., 2016).

We observed air bubbles escaping from the conspicuous lenticels of some Rm propagules, floating horizontally as well as prone at the water surface, and therefore assume that (at least) a part of the intercellular spaces in the inner cortex is in connection with the atmosphere through lenticels. Even though lenticels consist mainly of water repellent, loose filling tissue that has numerous intercellular spaces (Evert, 2006), the escaping of air suggests that water enters the propagule to fill the space that was left by the outgoing air. Like *Rhizophora mucronata* and *R. mangle* (Roth, 1965), propagules of Ct also have conspicuous lenticels along their hypocotyl length, while Bg propagules have lenticels mainly on their distal end (Tonné et al. submitted). Lenticels may form part of the mechanism causing the increase in propagule density and the loss of buoyancy. Yet, it remains a challenge to unravel the exact mechanism, anatomical as well as physiological, driving the transition from one propagule floating orientation to another and the associated loss of propagule buoyancy.

Prone floating propagules of Ct and Bg were sensitive to ‘wandering’ around a certain floating angle. Re-orientation during floating appears to be common in elongated mangrove propagules, and is suggested to be due to the interactive effects between salinity and time (Clarke et al., 2001). Throughout our experiment, salinity was kept constant. Hence, water temperature was the only variable that fluctuated. No pattern could be detected however, between the variation in water temperature and the propagule wandering behaviour, indicating that water temperature alone does not explain this behaviour. Besides density, also propagule mass and volume affect propagule floating behaviour through their influence on the inertia of the propagule. Compared to the relatively large and heavy propagules of Rm, propagules of Ct and Bg are smaller and have a lower average mass and volume (Table 3), making them less inert and more susceptible to the upward forces of the water (*i.e.* upward buoyancy (Hughes, 2005)) and thus more readily exhibit wandering behaviour. This in turn influences the extent to which external forces can act upon them during dispersal (*e.g.* wind and water current), and thereby also the speed and direction of dispersal (Van der Stocken et al., 2013). Finally, metabolic activities of the propagules (*e.g.* respiration) and the influence of temperature on the air in the aerenchymatous tissues should equally be taken into account in light of (varying) propagule buoyancy.

4.3. Propagule buoyancy behaviour

We clearly demonstrated that propagule buoyancy is a highly dynamic process that is determined by various propagule traits (*e.g.* density, anatomy and propagule morphology) and conditions of the water body (*e.g.* SWT and SWS). In most tropical locations, with the exception of the equatorial zone, propagule release has been significantly linked to rainfall during the wet season (Van der Stocken, 2015). At the moment of release however, environmental and water conditions (tidal inundation, rainfall, water temperature and salinity and their combinations) are random, rendering it difficult to exactly predict propagule floating behaviour and potential dispersal trajectories.

Since initial propagule density after abscission is not very different from seawater density, it allows the propagules to disperse under a wide range of SWT-SWS combinations. Most propagules will float upon encountering a water body or, after landing on the mangrove floor, can be carried away by the incoming and outgoing tides. After abscission, the fate of each propagule can be broadly categorised into two options. (1) Part of the propagules will gain more in density or at a faster rate, thereby exceeding water density and limiting their dispersal capabilities. These propagules stick around, and can settle and contribute to local forest rejuvenation and patch dynamics. (2) Another part of the propagules will maintain a density that is sufficiently low to allow dispersal to other parts of the forest (*e.g.* more inland or upstream along a river) or to embark on a LDD trajectory once they have overcome potential obstacles (*e.g.* stilts roots, pneumatophores, crab burrows and litter accumulation). In Gazi Bay for example, propagules of all three studied species have been found in considerable numbers in the water body beyond the mangrove limit (Van der Stocken et al., 2013), indicating that propagules have the potential to ‘escape’ from the local mangrove system. These numbers however, are not necessarily proportional to the fecundity on an individual and forest basis, although fecundity is a determining factor in propagule dispersal. During LDD other, previously mentioned factors come into play that influence the dispersal trajectory of the propagule.

Clarke et al. (2001) defined ‘floaters’ as propagules with variable buoyancy but of which more than 50% remain buoyant after 15 days of enforced dispersal. According to this definition, our observations, which covered three months, indicate that Bg and Ct species are long-term floaters in seawater and seem to have a greater ability to embark on LDD than Rm.

Most observations indicate that rhizophoracean mangrove propagule dispersal is generally limited to rather short distances (*e.g.* several meters for propagules of Rm and Ct (McGuinness, 1996; Van der Stocken et al., 2015a), less than 10 m for *R. mangle* propagules (Sousa et al., 2007) and up to 60 m and 146 m for Rm and Ct propagules respectively (De Ryck et al., 2012)), and thus that dispersal distances of elongated propagules fit a unimodal leptokurtic distribution (Van der Stocken et al., 2015a; Sousa et al., 2016). However, this does not mean that LDD can or does not happen, especially when propagules are moved to or directly fall into tidal creeks or open seawater, and the importance of such events should

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be highlighted. The present-day biogeographical distributions of the different *Rhizophora* species for example, represent historical events of vicariance and LDD (Lo et al., 2014). In the study of Ngeve et al. (2016), both genetic data and probabilistic estimates from numerical propagule dispersal models indicate that *R. racemosa* G. Mey. propagules are able to disperse distances of about 100 km along the West-African coast of Cameroon. It was calculated that this distance of 100 km can be covered in 6–12 days, considering an ocean current velocity of 1–2 $m\,s^{-1}$.

In the Zanzibar Channel, between mainland Tanzania and Unguja Island, the average ocean current velocity is between 0.05 and 0.3 $m\,s^{-1}$ depending on the time of the year and monsoon season (Zavala-Garay et al., 2015). Considering an ocean current velocity between 0.05 and 0.3 $m\,s^{-1}$ and that the starting position of the propagules is the open water, the distance dispersed after one month would be between 130 and 778 km. After two months a distance between 264 and 1581 km would be covered, and between 393 and 2359 km after three months. When propagules reach open water during the northeast monsoon season (December–February), the predominant dispersal direction would be in the southward direction. During the southwest monsoon season (April–November), propagules would rather be dispersed in the northward direction.

Complex oceanographic features such as eddies, like in the Mozambique Channel between mainland Mozambique and Madagascar (Ternon et al., 2014), may also hamper the passive dispersal and dispersal trajectories (direction and speed) of biological material, and hence can cause these living structures to spend a longer time on geographical distance. Convergent oceanic currents near the Cameroon Estuary Complex for example, have been proposed to form a barrier for gene flow between this area and two areas south from this oceanic convergence zone (Ngeve et al., 2016).

Propagule viability is a limiting factor in successful dispersal under natural as well as experimental conditions, as it decreases with time (*sensu* Nathan, 2006). Drexler (2001) for example, followed the buoyancy behaviour of *R. apiculata* and *R. mucronata* propagules up to 150 days. The author observed that the floating period until sinking averaged 15 and 53 days respectively (maximum floating period was 89 and 150 days respectively), but that viability of sunken propagules upon planting was lower than 50% in both species. Data on propagule viability data is limiting, but necessary to assess the effectiveness of propagule dispersal when it takes place over a certain distance for a certain amount of time.

5. Conclusion

This study has shown that after abscission, the rhizophoracean mangrove propagule population does not have one single assigned fate nor a single dispersal strategy. Rather, we interpret that the density of propagules close to that of seawater and the dynamics herein are an evolutionary adaptation to the intertidal mangrove environment, making different scenarios of SDD as well as LDD possible, and hence defining the fate of every single propagule. In this context, we also wish to refer to Nathan et al. (2008) who define polychory as seed dispersal by multiple dispersal vectors. In our case water is the only vector, but its vector-function changes over time both diurnally and seasonally. Further, the wandering behaviour and lenticels call for investigation of the metabolic processes in dispersing propagules and for the trigger to switch from arrested development to establishment.

Taking into account species-specific dynamics in propagule density (over time as well as along propagule length) and other propagule- and dispersal-related factors in dispersal models, will help in acquiring a comprehensive picture of potential species-specific dispersal distances and directions important for forest rejuvenation, and the identification of potential source and sink populations of gene flow (through propagules). Such knowledge in turn is valuable to assess mangrove population response in light of global change and concomitant sea level rise as well as the potential of natural expansion of a certain mangrove population.

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