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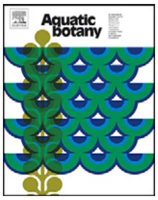

Size does matter, but not only size: Two alternative dispersal strategies for viviparous mangrove propagules

Dennis J.R. De Ryck[a,b,*], Elisabeth M.R. Robert[a,c], Nele Schmitz[a,c], Tom Van der Stocken[a,b], Diana Di Nitto[a,b], Farid Dahdouh-Guebas[a,b], Nico Koedam[a]

[a] Laboratory of Plant Biology and Nature Management (APNA),Vrije Univiversiteit Brussel (VUB), Pleinlaan 2, B-1050 Brussels, Belgium
[b] Laboratory of Systems Ecology and Resource Management, Université Libre de Bruxelles (ULB), Avenue F.D. Roosevelt 50, B-1050 Brussels, Belgium
[c] Laboratory for Wood Biology and Xylarium, Royal Museum for Central Africa (RMCA), Leuvensesteenweg 13, B-3080 Tervuren, Belgium

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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.

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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* Corresponding author at: Vrije Universiteit Brussel (VUB), Laboratory of Plant Biology and Nature Management (APNA), Pleinlaan 2, B-1050 Brussels, Belgium. Tel.: +32 6293433.
E-mail address: dderyck@vub.ac.be (D.J.R. De Ryck).

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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 *Ceriops 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 (*Ceriops*) 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).