BIOLOGICAL AND ENVIRONMENTAL DRIVERS OF MANGROVE PROPAGULE DISPERSAL:

A FIELD AND MODELING APPROACH

Tom Van der Stocken

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A FIELD AND MODELING APPROACH

Thesis submitted in the fulfilment of the requirements
for the degree of Doctor of Philosophy in Sciences
of the Vrije Universiteit Brussel
and the Université Libre de Bruxelles

by

Tom Van der Stocken

2015

Cover picture: Brian Gratwicke

Dedicated to Dr. Ronald Nuyts †

One of the most passionate and dedicated people I have met,
brilliant and highly skilled teacher in mathematics
with a rare sense of responsibility.

One person with passion
is better than forty people merely interested

— E. M. Forster

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The various parts of this research project consist of a collaboration between the Laboratory of Plant Biology and Nature Management (APNA) of the Vrije Universiteit Brussel (VUB, Brussels, Belgium), the laboratory of Systems Ecology and Resource Management (SERM) of the Université Libre de Bruxelles (ULB, Brussels, Belgium), the Kenya Marine and Fisheries Research Institute (KMFRI, Mombasa, Kenya), the Netherlands Institute for Sea Research (NIOZ, Yerseke, the Netherlands), the Departamento Ecología Funcional of the Instituto de Ecología (INECOL, Xalapa, Mexico), and the Jet Propulsion Laboratory (JPL, Pasadena, USA). This research was funded by the Flemish Interuniversity Council (VLIR-UOS), the VUB, the ULB, the Company of Biologists (COB) through the Society for Experimental Biology (SEB), the European Commission (EU Marie-Curie IRSES CREC 247514), the Belgian National Science Foundation, the Fonds de la Recherche Scientifique (FNRS; MIS 1765914) and JPL.

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I am a mind
floating in an ocean of confusion

— Modified from Caroline B. Cooney
















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SUMMARY

Mangrove ecosystems function at the edge of land and sea, often covering large intertidal areas along (sub)tropical coastal regions worldwide but also in a wide array of other topographical settings. Once or twice a day, tides move seawater in and out, consecutively submerging and exposing the intertidal surface, while freshwater now and then, at moments of heavy rainfall, may enter the system from the land. Mangroves can live in these highly dynamic and demanding environmental conditions via a series of remarkable adaptations such as aerial roots (pneumatophores), specialized cells in their leaves to excrete salt and the production of buoyant seeds and fruits (propagules) that disperse at the ocean surface (*i.e.* hydrochory). With their dense root networks, mangroves present a natural breeding ground and nursery for juvenile fish and provide shelter to many other animal species, rendering mangrove systems ecologically invaluable. From a socio-economical point of view, these forests sustain fisheries, provide firewood and wood for charcoal and construction. They may offer coastal protection to natural disasters such as storm surges and under certain conditions against tsunami. Despite their ecological and economical value, about 40 % of original mangroves have been lost worldwide during the last 50 years due to excessive exploitation and development. Deforestation, degradation and conversion to other land uses like intensive shrimp farming and agriculture have reduced and fragmented these ecosystems at an alarming rate. Climate change, probably most pronouncedly via changes in sea level, poses another important threat.

In this dissertation we investigate some understudied but important aspects of the dispersal process in mangroves, with as the main objective the reduction of parameter and model uncertainty. In this way more reliable predictions of dispersal patterns and long-term population dynamics under different climate change scenarios can be expected.

Meta-analysis of peer-reviewed literature on propagule release timing for mangroves reveals phenological complementarity between the northern and southern hemispheres, with a peak in propagule fall corresponding to the boreal and austral summers, respectively. Additionally, the data show strong positive correlations between mangrove propagule release and rainfall, with 72 % of compiled data reporting release during the wet season. At higher latitudes than the equatorial zone, propagule release is also correlated with temperature. In the equatorial zone (*i.e.* 10° N to 10° S), propagules fall from parent trees throughout most of the year, showing no pronounced production peaks, and no significant correlation with rainfall or temperature.

Dispersal experiments in the field and in a flume racetrack show that the pronounced morphological variation in propagules produced by different mangrove species explains interaction with the landscape matrix, contributing to strong differences in dispersal capacity among species and morphological types. Retention rates increase with propagule size and obstacle density in the landscape matrix, while waves and increasing water velocity reduce retention. Besides the interaction with the landscape matrix, dispersal in the forest is constrained by major tidal currents.

Results suggest that in open water, propagule traits (density, morphology, and floating orientation) determine the effect of water and wind currents on dispersal dynamics. This has important implications for inter- and intraspecific variation in dispersal patterns and the likelihood of reaching suitable habitat patches within a propagule's viable period. The low-density propagules of *Heritiera* *littoralis* are most affected by wind, while the high-density vertically floating propagules of *Ceriops tagal* and *Bruguiera gymnorrhiza* are least affected. *Avicennia marina*, and horizontally floating *Rhizophora mucronata* and *C. tagal* propagules behaved similarly. Morphological propagule traits, such as the dorsal sail of *H. littoralis*, explain another part of the interspecific differences. Within species, differences in dispersal velocities can be explained by differences in density and for *H. littoralis* also by variations in the shape of the dorsal sail. Hence, from a very same origin, propagules of different species could be expected to follow different trajectories, depending on the balance between hydrochory and pleustochory.

We introduce the concept of Biological Window of Opportunity (BWO), *i.e.* the timeframe during which effective dispersal can take place. This window begins at the end of the obligate dispersal period and extends until the end of the maximum flotation period or the maximum viability period, depending on whichever is shortest.

These insights allow for parameterization of dispersal models. Ideally, the position of the propagule producing species in the intertidal ecotone is included, because this defines access to the dispersal vector, with barriers to be traversed.

Finally, we initiate, develop and explore the potential of a model to predict passive dispersal at or near the ocean surface. In this model we integrate knowledge on the dispersal vectors at play and use the highest resolution global oceanographic and wind current data that is currently available. By performing runs for a particularly complex marine area relevant to our study, the Mozambique Channel, we establish that wind can strongly influence the dispersal trajectory of propagules, with considerable implications for long-term biogeographic patterns. Morphological features may facilitate or counteract hydrochorous dispersal, depending on the relative interaction of water and wind currents. Hence, under strong onshore wind conditions, the vertically floating propagules of *Rhizophora mucronata, Ceriops tagal* and *Bruguiera gymnorrhiza* have a higher probability for long distance dispersal as compared to for example *Heritiera littoralis* propagules.

We provide novel insight relevant to the biogeography of mangroves and to the drivers of distribution patterns. There is a potential applicability in any other system where propagules are dispersed passively at or near the ocean surface. Additionally, our results hold important considerations for conservation and management and will help to assess the potential of natural expansion of current mangrove fragments, as well as to explain and predict current and future distributions of mangrove forests.

SAMENVATTING

Mangrovewoud-ecosystemen zijn steeds terug te vinden op de grens tussen land en zee, langs een grote diversiteit van subtropische en tropische kusten. Een of twee maal per dag worden de mangrovewouden overstroomd door zout water bij hoogtij, maar bij hevige regenval kan er ook vanuit het land instroom van zoetwater zijn. Mangrovebossen kunnen deze zeer dynamische en dus moeilijke omstandigheden overleven door een reeks unieke aanpassingen: ze hebben lange luchtwortels – groeiend van de stam naar de grond – of ademwortels (pneumatoforen) die boven de grond uitsteken voor extra ademhaling; ze bezitten gespecialiseerde klieren in de bladeren die overtollig zout kunnen uitscheiden; en ze hebben drijvende zaden of vruchten die worden verspreid via oceaanstromen (*i.e.* hydrochorie), die zelfs al kunnen kiemen aan de ouderboom (*i.e.* viviparie). Deze kustwouden hebben een onschatbare ecologische waarde aangezien hun dens wortelstelsel dienst doet als broedgronden en kraamkamers voor vissen, en bescherming biedt voor vele andere dieren. Socio-economisch gezien onderhouden deze kustwouden de lokale visserij, leveren brandhout, houtskool en constructiehout, en nog vele andere producten. Fysisch gezien beschermen mangroves de kustzone door met hun uitgebreid wortelcomplex sediment vast te houden en ze vormen als geheel een belangrijke buffer tegen stormvloed en de eerder zeldzame maar verwoestende tsunami's. Ondanks hun ecologische en economische waarde, zijn mangrovewouden in de laatste 50 jaren wereldwijd al 40 % van hun oorspronkelijke oppervlakte verloren, veelal ten gevolge van overmatige exploitatie en kustontwikkeling. Met een alarmerende snelheid worden mangroves gefragmenteerd en gereduceerd door ontbossing, degradatie en omzetting naar andere landgebruiken zoals garnaalkwekerijen en landbouw. De klimaatsverandering is een bijkomende bedreiging die zich vooral zal manisfesteren door zeespiegelstijgingen.

In dit doctoraat onderzoeken we enkele belangrijke aspecten van het verspreidingsproces van mangroves waarvan belangrijke aspecten tot op heden niet of onderbestudeerd zijn. Het hoofddoel van dit werk is het verminderen van de parameter- en modelonzekerheden, waardoor meer betrouwbare voorspellingen van verspreidingspatronen en populatiedynamieken op langere termijn onder de verschillende scenario's van klimaatsverandering mogelijk worden.

We verzamelen alle wetenschappelijke literatuur die het tijdstip beschrijft waarop propagulen van de ouderboom loskomen. Door alle gegevens samen te brengen in een meta-analyse, komt een fenologische complementariteit tussen het noordelijk en zuidelijk halfrond aan het licht met een respectievelijke piek in propaguleval tijdens de noordelijke en zuidelijke zomer. 72 % van de propaguleval vind plaats in het regenseizoen wat duidt op een sterke positieve correlatie tussen propaguleval en regenval. Op hogere noordelijke of zuidelijke breedtegraden dan de equatoriale zone, is propaguleval ook gecorreleerd met de temperatuur. In de equatoriale zone (d.w.z. 10° NB tot 10° ZB) is er geen uitgesproken seizoenaliteit in propaguleval of correlatie met regenval en temperatuur, maar vallen propagulen het hele jaar door van de ouderbomen.

Verspreidingsexperimenten in het veld en de experimentele opzetting van de 'flume' tonen grote verschillen in interactie met de landschapsmatrix voor propagulen van verschilende soorten. Dit impliceert sterke verschillen in verspreidingscapaciteit tussen soorten en morfologische types. De mate van retentie (*i.e.* het tegenhouden) van propagulen in het mangrovesysteem neemt toe met de grootte van de propagulen en obstakeldensiteit in de landschapsmatrix, terwijl golven en toenemende watersnelheid de retentie doen afnemen (*i.e.* ervoor zorgen dat propagulen makkelijker het systeem kunnen verlaten). Naast de interactie met de landschapsmatrix, is verspreiding in het veld sterk bepaald door getijdenstromingen.

De resultaten geven aan dat de verspreidingsdynamiek van mangroves in open water sterk bepaald wordt door de interactie tussen water- en windstromingen, en de specifieke eigenschappen van propagulen (densiteit, morfologie, en drijforiëntatie). Dit heeft belangrijke gevolgen voor de inter- en intraspecifieke variatie in verspreidingspatronen, en de kans op het bereiken van geschikte habitatplekken binnen de levensvatbare periode van een propagule. De propagulen van *Heritiera littoralis* met hun lage densiteit worden het sterkst beïnvloed door de wind, terwijl de verticaal drijvende propagulen van *Ceriops tagal* en *Bruguiera gymnorrhiza* met een hoge densiteit het minst worden beïnvloed door de wind. De dynamiek van propagulen van *Avicennia marina* en de horizontaal drijvende propagulen van *Rhizophora mucronata* en *C. tagal*, worden evenveel beïnloed door wind. De specifieke propagulemorfologie van *H. littoralis* met zijn dorsale zeil, verklaart een ander deel van de interspecifieke verschillen. Verschillen in verspreidingssnelheden binnen een soort kunnen verklaard worden door densiteitsverschillen, en voor *H. littoralis* ook door variaties in de vorm van het dorsale zeil. Als propagulen van verschillende soorten op eenzelfde plaats worden vrijgelaten kunnen ze verschillende trajecten volgen, afhankelijk van het aandeel hydrochorie en pleustochorie.

We introduceren het concept van een 'Biologisch Window of Opportunity' (BWO), dat het tijdsvenster aangeeft waarbinnen de effectieve verspreiding kan plaatsvinden. Dit tijdsvenster begint aan het einde van de verplichte verspreidingsperiode, en eindigt – afhankelijk van de periode die het kortst is – ofwel aan het einde van de maximale drijfperiode, ofwel aan de maximale levensvatbaarheidsperiode.

Deze inzichten laten een parametrisatie van verspreidingsmodellen toe. Idealiter zouden ook de positie van propagule-producerende soorten van de kustecotoon (of grensstrook) mee opgenomen moeten worden, omdat deze de aanwezigheid van de verspreidingsvector en de te overwinnen hindernissen bepaalt.

We hebben tevens een model ontwikkeld voor het voospellen van de passieve verspreiding van propagulen aan het wateroppervlak van oceanen (let wel, het gaat om statistische probabiliteiten, gegeven de stochastiek die inherent is aan het verspreidingsproces en de bepalende factoren zoals oceaan- en windstromingen). In dit model integreren we de belangrijkste verspreidingsvectoren alsook wereldwijde oceanografische en windgegevens met de hoogste resolutie die momenteel beschikbaar is. Door het model toe te passen op een bijzonder complex maar voor ons ook relevant marien gebied – het Kanaal van Mozambique – hebben we kunnen vaststellen dat de wind het traject van drijvende propagulen sterk kan beïnvloeden, met aanzienlijke gevolgen voor de biogeografische patronen van mangroves op langer termijn. Morfologische karakteristieken van propagulen kunnen hydrochorie vergemakkelijken of tegenwerken, afhankelijk van de relatieve interactie tussen wind- en waterstromingen. Vandaar dat onder sterke landwaartse wind, de verticaal drijvende propagulen van *R. mucronata*, *C. tagal* en *B. gymnorrhiza* een hogere kans hebben om ver verspreid te worden in vergelijking met bijvoorbeeld propagulen van *H. littoralis*.

We komen tot nieuwe en relevante inzichten die de verspreidingspatronen en biogeografie van mangroves kunnen helpen verklaren. Deze inzichten zijn toepasbaar in andere mariene systemen waar propagulen passief aan het wateroppervlak verspreid worden. De resultaten hebben bovendien belangrijke implicaties voor natuurbehoud en -beheer waarbij een inschatting van de potentiële natuurlijke uitbreiding van mangrovefragmenten gemaakt kan worden, belangrijke bronpopulaties, evenals het verklaren en voorspellen van de huidige en toekomstige verspreidingsgebieden.

RÉSUMÉ

Les mangroves sont des écosystèmes situés entre terre et mer, couvrant de grandes étendues intertidales le long des régions côtières (sub)tropicales dans un ensemble de situations topographiques différentes. Une ou deux fois par jour, les marées amènent l’eau de mer qui submerge alors la surface intertidale, tandis que de l’eau douce peut occasionnellement entrer dans le système lors d’intenses épisodes pluvieux. Les mangroves parviennent à vivre dans cet environnement très dynamique et exigeant grâce à une série d’adaptations remarquables telles des racines aériennes (pneumatophores), des cellules spécialisées qui secrètent le sel hors des feuilles, et la production de graines et fruits flottants (les propagules) qui se dispersent à la surface de l’océan (par le mécanisme d’hydrochorie). Avec leur réseau racinaire dense, les mangroves forment un vivier naturel pour les poissons et offrent une protection à beaucoup d’autres animaux, créant ainsi un système d’une valeur écologique inestimable. D’un point de vue socio-économique, ces forêts soutiennent des pêcheries, fournissent du bois de feu et de construction ainsi que du charbon de bois. Elles offrent également une protection contre les catastrophes naturelles tels les tempêtes et sous certaines conditions les raz-de-marée. Malgré leur valeur écologique et économique, environ 40 % de la surface originelle des mangroves a été détruite durant ces 50 dernières années à cause d’une exploitation et d’un développement excessif. La déforestation, la dégradation et la conversion vers d’autres types d’utilisation des sols tels l’élevage intensif de crustacés et l’agriculture ont réduit et fragmenté ces écosystèmes à un rythme alarmant. Les changements climatiques, et en particulier l’élévation du niveau de la mer, constituent également une menace. Il est donc impératif d’arriver à une connaissance approfondie et intégrée de la reproduction, de la croissance et des mécanismes de dispersion de ces plantes afin de développer des stratégies scientifiquement fondées de préservation et de gestion.

Dans cette thèse, nous analysons certains aspects clés – sous-étudiés – du mécanisme de dispersion des mangroves, en ayant comme objectif principal de réduire l’incertitude des paramètres et des modèles. Ce faisant nous pourrons générer des prédictions plus fiables des *patterns* de dispersion et de la dynamique des populations sous différents scénarios de changements climatiques.

Une méta-analyse de la littérature scientifique concernant le timing d’émission des propagules de mangroves révèle une complémentarité phénologique entre les hémisphères nord et sud, avec un pic de chute de propagules correspondant aux étés boréaux et austraux respectivement. Les données démontrent également des corrélations positives entre l’émission des propagules et la pluviométrie: 72 % des données faisant état d’émission de propagules lors de la saison des pluies. Sous les latitudes non-équatoriales, l’émission de propagules est corrélée avec la température. Dans la zone équatoriale (de 10° N à 10° S), les propagules chutent pendant la majeur partie de l’année, sans pic de production marqué, et sans corrélation significative avec la pluviométrie ou la température.

Des expériences de dispersion sur le terrain et en laboratoire (à l’aide d’un *flume racetrack*) démontrent que la grande variation morphologique des propagules produites par différentes espèces de mangroves explique l’interaction avec la matrice paysagère, contribuant à des fortes différences de capacité de dispersion entre espèces et entre types morphologiques. Le taux de rétention augmente avec la taille des propagules et la densité des obstacles dans la matrice paysagère, tandis que les vagues et une vélocité de l'eau plus élevée réduisent la rétention. Sur le terrain, la dispersion est aussi contrainte par les marées.

Les résultats suggèrent qu'en eau libre, les caractéristiques des propagules (densité, morphologie et orientation de la flottaison) déterminent l'effet des courants aquatiques et éoliens sur la dynamique de dispersion. Ceci impacte la variation inter- et intra-spécifique des *patterns* de dispersion ainsi que la probabilité d'atteindre des habitats adéquats pendant la période de viabilité des propagules. Les propagules peu denses de *Heritiera littoralis* sont les plus sensibles au vent, tandis que les propagules denses et flottantes de *Ceriops tagal* et *Bruguiera gymnorrhiza* sont les moins impactées. *Avicennia marina*, et les propagules flottantes de *Rhizophora mucronata* et *C. tagal* ont un comportement similaire. Des traits morphologiques des propagules, telle la voile dorsale de *H. littoralis*, expliquent une partie des différences interspécifiques. La différence intra-spécifique des vélocités de dispersion peut être expliquée par des différences de densité, ainsi que par des variations de la forme de la voile dorsale chez *H. littoralis*. Ainsi à partir d'un point de départ commun, des propagules de différentes espèces vont suivre des trajectoires différentes, en fonction de la relation entre hydrochorie et pleustochorie.

Nous proposons le concept de 'Biological Window of Opportunity', décrivant le laps de temps durant lequel une dispersion effective peut être réalisée. Cette fenêtre débute à la fin de la période obligatoire de dispersion et s'étend jusqu'à la période de flottaison maximale ou jusqu'à la période de viabilité maximale.

Ces constats permettent une paramétrisation des modèles de dispersion, si les positions des espèces produisant des propagules dans l'ecotone intertidal sont inclues, car celles-ci définissent l'accès au vecteur eau ou la longueur de la zone à obstacles à traverser.

Nous générons, développons et finalement le potentiel d'un modèle de dispersion passive au niveau de la surface de l'océan. Dans ce modèle nous intégrons les connaissances concernant les vecteurs de dispersion en nous utilisons des données océanographiques et éoliennes au niveau global, à la plus haute résolution présentement disponible. En appliquant le modèle à une zone marine particulièrement complexe et pertinente pour notre étude – le canal du Mozambique – nous démontrons que le vent peut fortement influencer la trajectoire de dispersion des propagules, ceci ayant des conséquences à long terme considérables pour les patterns biogéographiques. Les caractéristiques morphologiques peuvent faciliter ou contrecarrer la dispersion hydrochorique, en fonction de l'interaction relative des courants marins et éoliens.

Ainsi lors de conditions de vent venant de la mer, les propagules à flottaison verticale de *Rhizopohora mucronata, Ceriops tagal* et *Bruguiera gymnorrhiza* ont une probabilité de dispersion à longue distance (LDD) plus élevée comparée aux propagules de *Heritiera littoralis* par exemple.

Nous fournissons ainsi des informations nouvelles quant à la biogéographie des mangroves et quant aux forces motrices façonnant les *patterns* de distribution. Il y a de surcroît un potentiel d'applicabilité à d'autres systèmes dans lesquels des propagules sont dispersées passivement à la surface de l'océan. Nos résultats mènent en outre à d'importantes considérations portant sur la préservation et la gestion des forêts de mangroves, et contribuent à évaluer le potentiel d'expansion naturelle des fragments de mangroves actuelles, ainsi qu'à expliquer et prévoir la répartition actuelle et future des forêts de mangrove.

ZUSAMMENFASSUNG

An der Grenze zwischen Land und Meer erstrecken sich Mangroven Ökosysteme oft über weite Gebiete an subtropischen und tropischen Küsten weltweit. Ein bis zweimal pro Tag werden die Mangrovenwälder überschwemmt mit Salzwasser aus dem Meer, während vom Land Süßwasser durch starke Regenfälle in das System gelangen kann. Mangroven können unter diesen dynamischen und dadurch schwierigen Umständen leben mit Hilfe von speziellen Anpassungen wie Luftwurzeln (Pneumatophoren), Zellen in den Blättern die überschüssiges Salz ausscheiden können und die Produktion schwimmfähiger Samen und Früchte, die über die Meeresoberfläche des Ozeans verbreitet werden (Hydrochorie). Auf Grund ihres dichten Wurzelsystems dienen Mangroven als Brutplatz und Aufzuchtsstätte für junge Fische und sie bieten vielen anderen Tierarten Schutz, was Mangroven ökologisch unentbehrlich macht. Sozio-ökonomisch betrachtet sind Mangrovenwälder wichtig für die Fischerei, liefern Feuer- und Bauholz und Holz für Kohle. Außerdem schützen sie die Küste bei Naturkatastrophen wie Sturmfluten und unter bestimmten Umständen auch bei Tsunamis. Trotz ihres hohen ökologischen und ökonomischen Werts sind etwa 40 % der Mangrovenwälder weltweit verloren gegangen in den letzten 50 Jahren auf Grund von Übernutzung und Küstenentwicklung. Abholzung, Degradierung und die Umwandlung zu anderen Nutzungsformen wie Garnelenzucht und Landwirtschaft haben diese Ökosysteme stark reduziert und fragmentiert. Klimawandel, vor allem das Ansteigen des Meeresspiegels, stellt eine weitere Bedrohung dar. Daher ist tiefgründiges und integriertes Wissen über Fortpflanzung, Wachstum und Verbreitungsmechanismen dieser Pflanze von größter Wichtigkeit, um eine wissenschaftliche Basis für Naturschutz und Management-Strategien zu schaffen.

In dieser Dissertation beschäftigen wir uns mit einigen wenig erforschten aber sehr wichtigen Aspekten des Verbreitungsprozesses von Mangroven mit dem Ziel Parameter- und Modellunsicherheiten zu verringern. Dadurch werden zuverlässigere Voraussagen über Verbreitungsmuster oder langfristige Populationsfluktuationen unter verschiedenen Klimawandelszenarios möglich.

Eine Meta-Analyse wissenschaftlicher Literatur über den Zeitpunkt an dem die Ableger vom Mutterbaum fallen zeigte, dass sich die Nord- und Südhalbkugel phänologisch ergänzen. Die höchste Ableger- Abgabe findet jeweils im nördlichen und südlichen Sommer statt. Außerdem weisen die Daten eine positive Korrelation zwischen der Freigabe von Mangrovenpropagationsformen und Niederschlag auf. Von den zusammengestellten Daten melden 72 %, dass die Freisetzung in der Regenzeit auftritt. In höheren nördlichen und südlichen Breitengraden als die Äquatorialzone spielt Temperatur ebenfalls eine Rolle. In der Äquatorialzone (d.h. 10° N bis 10° S) fallen die Ableger die meiste Zeit des Jahres mit keiner markanten Hochsaison und ohne signifikanten Zusammenhang mit Temperatur oder Niederschlag von den Bäumen.

Verbreitungsexperimente im Freiland und in einer experimentellen Rutschanlage zeigen, dass Propagationsformen verschiedener Arten sehr unterschiedlich mit der Landschaftsmatrix interagieren. Dies sorgt für große Unterschiede im Ausbreitungsvermögen zwischen Arten und morphologischen Typen. Die Rückhalterate nimmt zu mit der Größe der Ableger und der Hindernisdichte in der Landschaftsmatrix, während Wellen und steigende Wassergeschwindigkeit die Retention reduzieren. Neben der Interaktion mit der Landschaftsmatrix spielen bei der Verbreitung im Freiland die Gezeiten eine große Rolle.

Die Ergebnisse legen nahe, dass in offenen Gewässern die Eigenschaften der Propagationsformen (Dichte, Morphologie und Schwimmausrichtung) den Effekt von Wasser und Windströmung auf die Verbreitungsdynamik bestimmen. Dies hat wichtige Auswirkungen auf die inter- und intraspezifische Variation in Verbreitungsmustern und die Wahrscheinlichkeit ein passendes Habitat innerhalb der Lebenspanne des Ablegers zu finden. *Heritiera littoralis*, die eine geringe Dichte besitzt, wurde am meisten durch Wind beeinflusst, während die vertikal schwimmenden *Ceriops tagal* und *Bruguiera gymnorrhiza* mit einer hohen Dichte am wenigsten beeinträchtigt wurden. *Avicennia marina* und die horizontal schwimmenden *Rhizophora mucronata* und *C. tagal* Propagationsformen verhielten sich ähnlich. Die Eigenschaften der Ableger, wie zum Beispiel das Rückensegel der *H. littoralis*, erklärte einen weiteren Teil der interspezifischen Abweichungen. Unterschiede in der Verbreitungsgeschwindigkeit innerhalb der Arten lassen sich durch Abweichungen in der Dichte und für *H. littoralis* auch durch Abweichungen der Form des Rückensegel erklären. Abhängig vom Anteil Hydrochorie und Pleustochorie können Propagationsformen unterschiedlicher Arten, die an der gleichen Stelle losgelassen werden, an sehr unterschiedlichen Orten ankommen.

Wir führen das Konzept des 'Biological Window of Opportunity' (BWO) ein, das die Zeitspanne angibt in der die Verbreitung stattfinden kann. Dieses Zeitfenster beginnt am Ende der obligatorischen Dispersionsperiode und endet entweder zum Ende der maximalen Schwimmperiode oder zum Ende der maximalen Lebensfähigkeitsperiode, je nachdem welche kürzer ist.

Diese Einsichten machen eine Parametrisierung von Verbreitungsmodellen möglich. Im Idealfall sollten auch die Standorte der Ableger-produzierenden Arten der Küstenökotone mit einbezogen werden, da diese den Ausbreitungsvektor mit den zu überwindenden Hindernissen zum Wasser definieren.

Abschließend haben wir ein Modell entwickelt, um die passive Verbreitung an oder nahe der Meeresoberfläche von Ozeanen zu prognostizieren. In diesem Modell integrieren wir die wichtigsten Verbreitungsvektoren sowie Daten zur globalen Ozeanografie und Windströmungen in der höchsten Auflösung die derzeit verfügbar ist. Durch unser Modell anzuwenden auf ein besonders komplexes aber für uns wichtiges Gebiet, der Kanal von Mozambik, haben wir feststellen können, dass Wind die Verbreitung der Propagationsformen stark beeinflussen kann, was wiederum erhebliche Langzeitfolgen für die Biogeografie der Mangroven hat. Morphologische Eigenschaften können Hydrochorie erleichtern oder erschweren, abhängig vom relativen Zusammenspiel von Wasser- und Windströmungen. Daher haben die Propagationsformen der *Rhizophora mucronata, Ceriops tagal* und *Bruguiera gymnorrhiza* bei auflandigem Wind eine höhere Chance weit verbreitet zu werden im Vergleich zu beispielsweise Ablegern von *Heritiera littoralis*.

Wir kommen zu neuen und wichtigen Erkenntnissen über die Verbreitungsmuster und Biogeografie von Mangroven. Diese Einsichten können in allen marinen Systemen angewandt werden in denen Propagationsformen passiv über die Meeresoberfläche verbreitet werden. Zudem beinhalten diese Resultate wichtige Implikationen für Naturschutz und -verwaltung und können helfen eine Einschätzung der potenziellen natürlichen Ausweitung der gegenwärtigen Mangrovenfragmente zu erstellen und helfen die heutige und zukünftige Verbreitung der Mangroven zu erklären und vorauszusagen.

ABBREVIATIONS

AEP	Atlantic East Pacific
AMC	*Avicennia marina* creekward zone
AML	*Avicennia marina* landward zone
ANOVA	Analysis of Variance
BWO	Biological Window of Opportunity
CT/Ct	*Ceriops tagal*
EC	Equatorial Current
ECCO	Estimating the Circulation and Climate of the Ocean
ECMWF	European Center for Medium-Range Weather Forecasts
EACC	East African Coastal Current
EICC	East India Coastal Current
GIS	Geographic Information System
GLM	General Linear Model
GLZ	Generalized Linear Model
GW	Great Whirl
H.T.	High Tide
IWP	Indo-West Pacific
KWA	Kenya Wildlife Service
LDD	Long Distance Dispersal
LH	Lakshadweep high
LL	Lakshadweep low
LLC	Longitude/Longitude/Polar-cap
L.T.	Low Tide
MAHT	Monthly Average High Temperature
MALT	Monthly Average Low Temperature
MAR	Monthly Average Rainfall
MFP	Maximum Flotation Period
MIT	Massachusetts Institute of Technology

MVP	Maximum Viability Period
ODP	Obligate Dispersal Period
RM/Rm	*Rhizophora mucronata*
SA	*Sonneratia alba*
SC	Somali Current
SDD	Short Distance Dispersal
SEC	South Equatorial Current
SECC	South Equatorial Counter Current
SMC	Summer Monsoon Current
UTC	Coordinated Universal Time
WICC	West India Coastal Current
WMC	Winter Monsoon Current
3D	Three-dimensional

CHAPTER 1

GENERAL INTRODUCTION[1],

OBJECTIVES AND THESIS OUTLINE

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[1] Sections of this chapter have been taken and modified from *A framework of biophysical factors contributing to mangrove propagule dispersal at multiple scales* by Tom Van der Stocken*, Alison K. S. Wee*, Dennis J. R. De Ryck, Daniel A. Friess, Farid Dahdouh-Guebas, Nico Koedam, Edward L. Webb (unpublished manuscript) *Equal contribution

Abstract

In many parts of the world mangrove forests are degraded and fragmented as a result of anthropogenic impact. Currently, effective management strategies are hampered by a lack of knowledge on the factors that determine dispersal and deposition patterns of seeds and fruits. While a number of case studies highlight the importance of individual cues or traits affecting this key ecological process, the interplay of different drivers of mangrove dispersal and colonization remains largely unknown. This study presents a first integrated overview of the interactions between different factors that contribute to the fate of dispersing mangrove propagules. We consolidated the biological and physical components of mangrove propagule dispersal and organized these components into a three-part mechanistic framework (propagule source, propagule dispersal and propagule establishment), centered around the dispersal process. Long-term studies of propagule dispersal and establishment under different environmental conditions are important to better understand and predict the magnitude and directionality of mangrove dispersal fluxes over different spatial scales. Insight in the process of dispersal and underlying mechanisms will allow a greater biological realism of dispersal models and hence the prediction of long-term population dynamics and biogeographic range shifts under changing environmental conditions.

Mangroves - Seafaring taxa in the (sub)tropics

Few landmarks on earth are more effective dispersal barriers than the great oceans. Yet some species, like the great explorers of the 15th and 16th centuries, take the risk of crossing the seven seas by relying on a set of unique adaptations. Perhaps the most iconic of these seafaring taxa are mangrove trees and shrubs. Mangroves are formations thriving at the edge of sea and land in the world's (sub)tropical regions (Fig. 1.1). Life in intertidal areas requires a series of morphological and ecophysiological adaptations like aerial roots (*i.e.* pneumatophores), vivipary and the hydrochorous dispersal of propagules (*i.e.* dispersal units), making mangrove vegetation structurally and functionally unique. Despite their economical value via the important ecosystem services they provide *e.g.* sources of wood, natural fish nurseries, and protection of coastal areas (Alongi 2002, Balmford *et al.* 2002, Walters *et al.* 2008), mangroves are threatened globally by land conversion and habitat degradation (Valiela *et al.* 2001), resulting in increasingly fragmented and degraded mangrove habitats (Fahrig 2003, Duke *et al.* 2007) (Fig. 1.2).

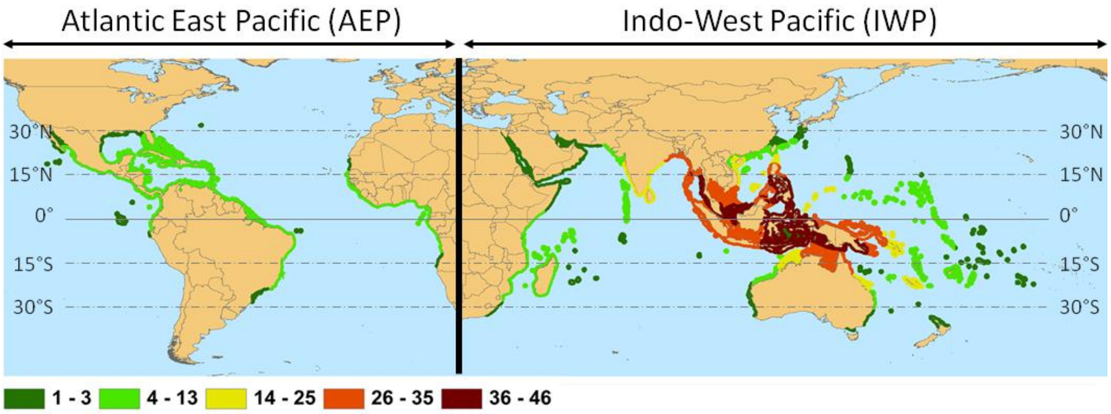

Figure 1.1: Two major biogeographical regions – Atlantic East Pacific (AEP) and Indo-West Pacific (IWP) – and species richness (color code) for mangroves (modified after Polidoro *et al.* 2010). Mangroves are found along coastal areas of 123 countries, with the extreme range limits reaching 32.28° N (Bermuda) and 38.45° S (East Australia), respectively (Spalding *et al.* 2010). The AEP biogeographical region holds 12 species, while 62 species are found in the IWP with a peak diversity around South-East Asia. Total global mangrove area ranges from 137760 km² (Giri *et al.* 2011) to 152000 km² (Spalding *et al.* 2010), and once covered more than 200000 km² (Spalding *et al.* 2010). Global annual decrease of mangrove area due to human activities was 0.66 % during the 2000-2005 period (FAO 2007) and an estimated loss of more than 35 % since the early 1980s (Duke *et al.* 2007).

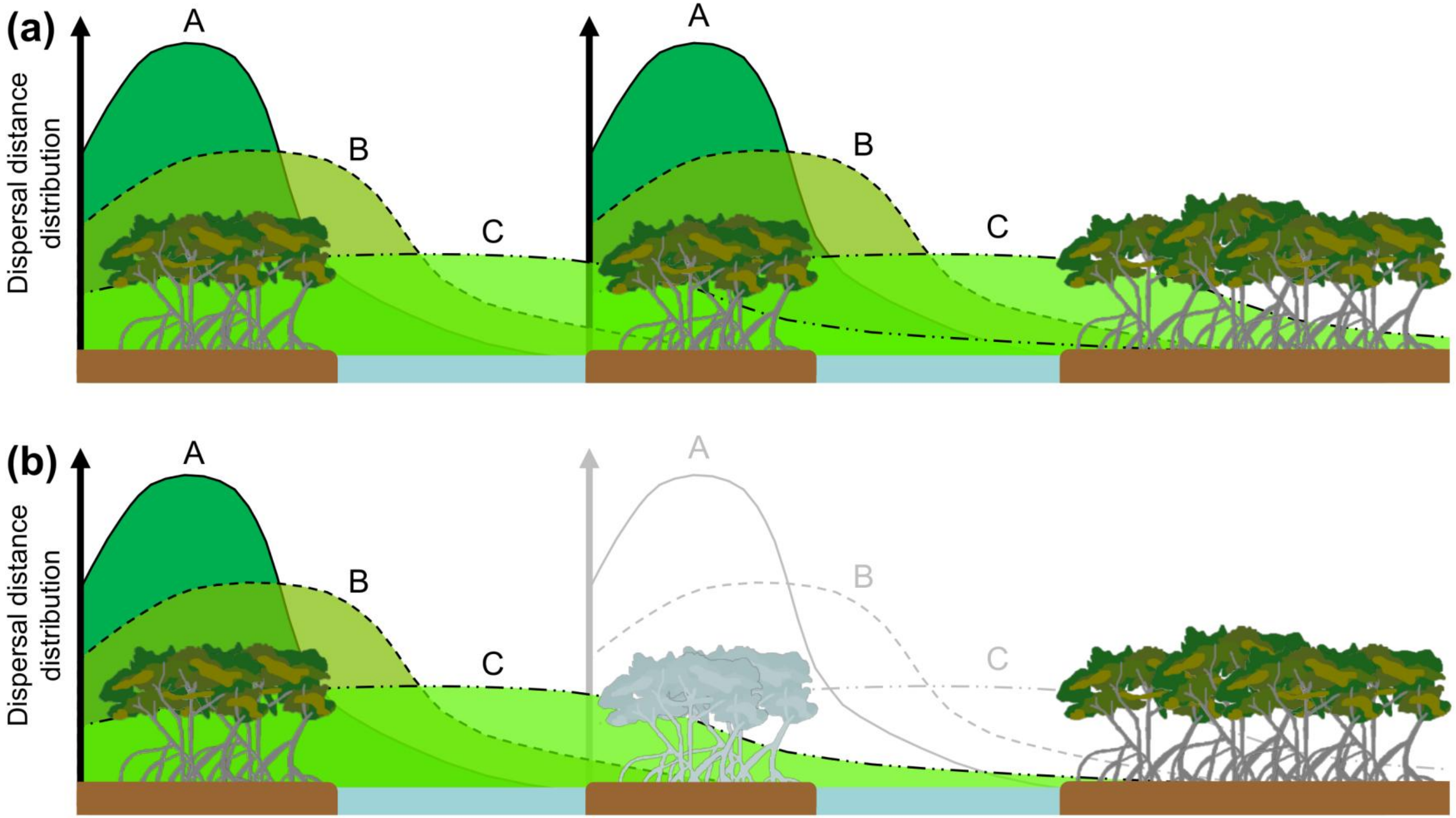

Figure 1.2: Fictive dispersal kernels for three species (A, B and C) to illustrate the potential impact of mangrove habitat fragmentation and degradation on connectivity and colonization potential. (a) Remote habitat fragments can be connected through a network of populations within the dispersal range (kernel, *i.e.* frequency distribution of dispersal distance) of a species. While suitable habitat is beyond the long distance dispersal component (*i.e.* the tail) of the kernel of species A, the two other species can reach the rightmost location, either directly (species C) or in a stepping stone manner (species B and C). (b) If, in the central location of the figure, environmental conditions become unsuitable due to human impact, species C is the only species that could potentially reach the rightmost habitat.

Over the coming decades, climate change will pose an important additional threat, probably most pronouncedly via changes in sea level (Gilman *et al.* 2008). Additionally, the response of mangroves to environmental change is difficult to predict since the tolerance to increased disturbance and resistance to environmental stress expected under climate change, is likely to be site-specific and will depend on the interplay of different processes and their time scale. In this context, dispersal plays an important role by allowing for gene flow between isolated populations and colonizing suitable habitat, as well as forest rejuvenation, age structure and responses to environmental change. Yet, for mangroves, the mechanisms of dispersal remain poorly understood with little and often scattered data on propagule and dispersal vector properties, hampering the reconstruction and prediction of the frequency and the likely trajectories of natural dispersal events.

Importance of dispersal

In mangroves, propagule dispersal mainly occurs through passive dispersal of buoyant propagules at the ocean surface (*i.e.* hydrochory). Mangrove propagules show a wide variety of morphologies (Fig. 1.3) and may be seedlings (*i.e.* the viviparous propagules of the family Rhizophoraceae), semi-germinated cryptoviviparous fruits (*e.g. Avicennia*), single-seeded fruits (*e.g. Heritiera*) or multiple-seeded fruits (*e.g. Sonneratia* and *Xylocarpus*).

Mangrove communities occur in intertidal areas with little hydrodynamic energy (Tomlinson 1994). Though the temporary flooding by seawater or brackish water is a characteristic feature of these systems, making a sharp boundary with beach forests *sensu* Primavera and Sadaba (2012), the tidal amplitude may be very small in some regions. Mangroves tend to have a naturally discontinuous distribution along coastlines. They are found in estuaries, river deltas, back-barrier and less-exposed coastal shores (Spalding *et al.* 2010). The exchange of propagules among mangrove biotopes is an important component of mangrove ecology and biogeography, and therefore key to conservation. In addition to pollen flow, propagule dispersal could maintain demographic connectivity among naturally fragmented mangrove populations. Also, the magnitude of dispersal fluxes may determine the natural potential for recovery of highly degraded sites (Palumbi 2003) and is critical in the management decision for assisted regeneration (*e.g.* reforestation).

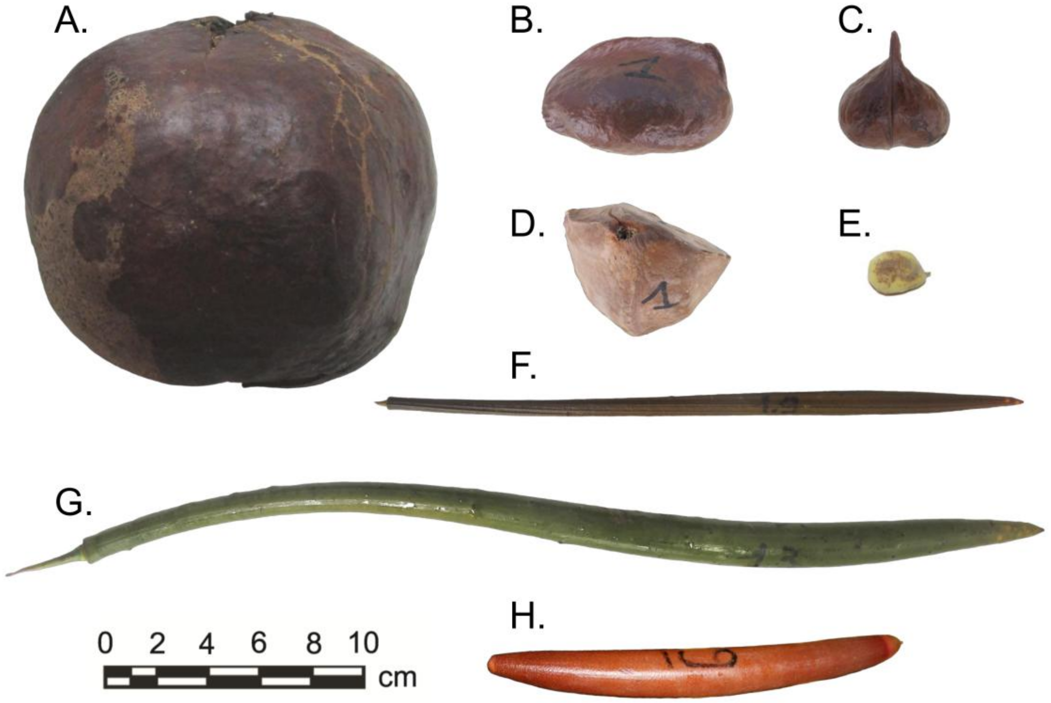

Figure 1.3: Overview of the mangrove propagules considered in this work. Propagules are from the following mangrove species: (A) *Xylocarpus granatum* (fruit); (B-C) *Heritiera littoralis*; (D) *X. granatum* (seed); (E) *Avicennia marina*; (F) *Ceriops tagal*; (G) *Rhizophora mucronata*; and (H) *Bruguiera gymnorrhiza*.

Methodological approaches to study dispersal

Empirical measurements of propagule dispersal in mangroves (*i.e.* the phase between propagule release and establishment) are difficult to obtain due to the large spatial and temporal scales involved, which results in important methodological challenges and logistic constraints (Nathan 2001). Therefore, most research on mangrove propagule dispersal has been componential, focusing on specific parts of the dispersal process. Direct observations of the process at its full spatio-temporal scale is lacking altogether.

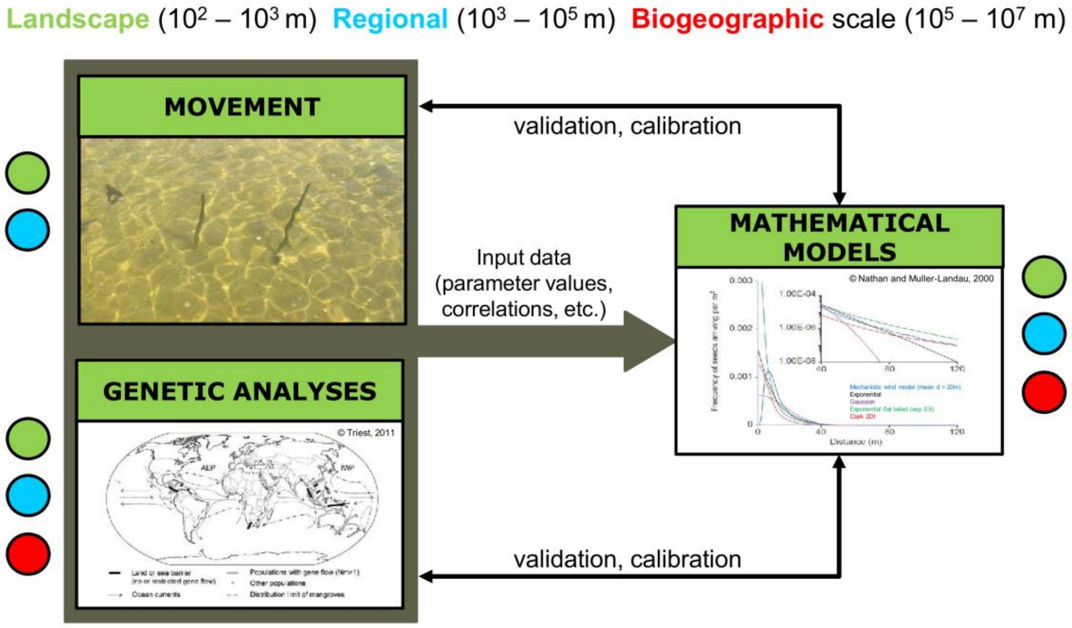

Figure 1.4: Major methodological groups to study and describe dispersal patterns (see Nathan 2001, Nathan *et al.* 2003) and the spatial scales at which they can be applied. Definitions of the different spatial scales are taken from Nathan *et al.* (2008). Ideally, to allow for optimal descriptions and quantifications of dispersal patterns, the various methodological approaches are combined.

Various methods have been proposed over the years to measure dispersal kernels in plants, though the quantification of the tail (long distance dispersal; LDD) remains challenging (Nathan and Muller-Landau 2000). Nathan (2001) postulated three major methodological approaches for the study of LDD: (1) Eulerian[2] and Lagrangian[3] movement and redistribution methods; (2) short- and long-term genetic analyses; and (3) mathematical models (Fig. 1.4). These methods are also summarized and discussed in more detail by Nathan *et al.* (2003). A number of field methods to study dispersal have also been outlined by Bullock *et al.* (2006). Even though the genetic methodological approach is not the main focus of this study, it is a relevant complementary tool to study dispersal and deposition patterns in natural

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[2] *i.e.* observing marked or unmarked propagule(s) from a fixed point in space while time passes

[3] *i.e.* the observer follows the marked or unmarked propagule(s) through space and time, and hence obtains information on its dispersal behavior at each point along its total trajectory between release and end location.

environments. Therefore, the next section shortly considers the value of the genetic approach. The two other methodological approaches (movement and modeling) constitute the core methodology in this study, and are illustrated throughout the various chapters.

Genetic analyses

Since it is difficult to empirically measure and track LDD, genetic analysis can be a useful tool to assess dispersal patterns in mangroves. Successful inter-population dispersal events leave behind a genetic trail that can be detected with population genetics and phylogeographic studies[4]. According to the one-migrant-per-generation rule, occasional LDD events across populations could maintain sufficient gene flow to counteract the effects of genetic drift and prevent genetic differentiation (Wright 1931, Slatkin 1987). Therefore, an assessment of genetic connectivity among populations can provide insight on both historical and contemporary spatial patterns and magnitude of propagule dispersal.

Over the past two decades, population genetic studies of mangroves have focused largely on phylogeography. These studies advanced our understanding on speciation events (Duke *et al.* 1998, Dodd and Afzal-Rafii 2002) and biogeography of mangroves (see Triest 2008). Unfortunately, the descriptive nature and the lack of hypothesis testing in phylogeographical studies left information on life histories, dispersal ecology and most importantly how genetic or demographic connectivity is forged and maintained, much to be desired. The few exceptions to this provided invaluable evidence on how local, fine-scale geomorphology (Geng *et al.* 2008), regional ocean currents (Pil *et al.* 2011, Wee *et al.* 2014) and land-barriers (Takayama *et al.* 2013) may influence the dispersal patterns of mangrove propagules. In addition, Dodd *et al.* (2002) have also presented indirect evidence of historical trans-oceanic propagule dispersal that reduced the genetic divergence of *Avicennia germinans* populations

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[4] Genetic analysis can also provide direct estimates of pollen or seed dispersal through parentage analysis, though such an approach is difficult to apply in high density populations or to detect LDD (pers. comm. Olivier Hardy).

from the East and West Atlantic, demonstrating the presence of historical trans-oceanic dispersal connecting mangroves from both sides of the Atlantic. These studies demonstrate the merits of hypothesis-oriented genetic studies and the usefulness of genetic studies in advancing our knowledge of mangrove dispersal ecology. It is however not a straightforward interpretation from population genetic patterns and phylogeography to the process of dispersal. Using genetic data to inform dispersal research requires well delineated hypotheses.

In this particular respect, seascape genetics – which couples empirical genetic patterns and simulations of dispersal probability based on biophysical models – could be a valuable research avenue to uncover dispersal events that may otherwise be difficult to detect on a landscape level (Selkoe *et al.* 2010). Discordances between data reveal regions where dispersal alone does not capture connectivity (Riginos and Liggins 2013). Recent oceanographic studies have shown that even connectivity of marine populations along straight coastlines can be patchy and stochastic due to turbulence and nonlinearity in prevailing ocean currents (Siegel *et al.* 2008, Watson *et al.* 2010). Hence, the explicit inclusion of ocean circulations is very useful in interpreting complex genetic structure of coastal and marine organisms (Waters 2008, White *et al.* 2010, Wee *et al.* 2014).

Spatial scale of mangrove propagule dispersal

An overview of dispersal distances in mangroves reported in peer-reviewed literature is summarized in Table 1.1. While the consideration of buoyancy and viability features of mangrove propagules as well as the wide distribution patterns of many mangrove species, often on remote oceanic islands, clearly indicate long distance dispersal (LDD), current empirical evidence of confirmed LDD events and its frequency in mangroves is limited. Instead, as in other organisms, the vast majority of scientifically reported dispersal events were limited to local (hundreds of meters) and intermediate scales (several km) (Table 1.1).

An important aspect within this context, is which dispersal events are considered short distance dispersal (SDD) and LDD (Nathan *et al.* 2003). Various definitions have been used by different authors (*e.g.* Higgins *et al.* 2003b, Muller-Landau *et al.* 2003, Nathan *et al.* 2003, Kinlan *et al.* 2005, Soons and Ozinga 2005, Trakhtenbrot *et al.* 2005). Generally, as summarized in Nathan (2005), LDD is defined as dispersal beyond a certain threshold distance or as dispersal beyond a distance that is considerably longer than that of most other individuals of the population (*i.e.* the mean or median). However, the definition of LDD is very case-specific and arbitrary (Nathan *et al.* 2003). In this study, we rather focus on 'candidates' for LDD, *i.e.* those propagules that overcome the different dispersal barriers (*e.g.* retention) and filters (*e.g.* predation) within the local system and succeed in leaving the local habitat, rather than measuring (effective) LDD *per se*.

The spatial scale of dispersal is typically described using dispersal kernels, *i.e.* a frequency distribution of dispersal distances. Although dispersal distances vary widely across species, these distributions are usually leptokurtic (*i.e.* having a positive excess kurtosis or sharpness of the peak) (Harper 1977, Portnoy and Willson 1993, Willson 1993, Kot *et al.* 1996, Cain *et al.* 2000, Nathan and Muller-Landau 2000, Levin *et al.* 2003), with a pronounced peak representing frequent dispersal at or close to the parent's location, followed by a quick decline at intermediate distances and an elongated tail capturing sporadic dispersal over long distances. Leptokurtic dispersal kernels have also been shown for mangroves. Empirical and genetic evidence for various species of the Rhizophoraceae family consistently showed that the distance of dispersed propagules from the parent tree fits a unimodal leptokurtic distribution (*e.g.* Komiyama *et al.* 1992, McGuinness 1997, Geng *et al.* 2008, Van der Stocken *et al.* 2015a).

The leptokurtic distribution is most pronounced in viviparous species. For *Kandelia candel*, Yamashiro (1961) found that most of the marked propagules did not disperse farther than 50 m. However, there were several caveats to this study: (1) the fate of 88 % of the propagules used in the experiment is unknown; (2) lost propagules were assumed to have dispersed beyond the boundaries of the study area and (3) the role of predation in propagule loss was not considered (Yamashiro 1961). An interesting large-scale study has been conducted by Steinke and Ward (2003), in which 4500 drift cards with similar buoyancy as *Avicennia marina* propagules were dropped from an aircraft into the sea. Although the majority of the recovered cards (12.42 % in total) were found stranded within 1 km of the dropping point, a few cards were found more than 5 to 24 km from their release point, and one card even as far as about 700 km (Steinke and Ward 2003), though issues of propagule viability may constrain the effectiveness of dispersal at this scale.

Better data on LDD is available for *Avicennia* spp.. *Avicennia marina* propagules in southeastern Australia have been observed 20 km from the nearest source, even though buoyancy data suggests that most propagules should strand close to their maternal parent (Clarke and Myerscough 1991). Dispersal distances were tested in more detail subsequently, by releasing three samples of 100 propagules each at 500 meter intervals in two creeks (Clarke 1993). Most propagules stranded 10-500 m from the source, three propagules were recovered at more than 10 km from the estuary and one at more than 50 km (Clarke 1993). Dispersal distances of the same order of magnitude can be derived from the data of Gunn and Dennis (1973) who found *A. marina* propagules at the Gulf coast of Texas, with the nearest mangrove forest situated at multiple kilometers distance. However, all data give conservative values, as long as full recovery (*i.e.* 100 %) is not realized.

It is clear that dispersal is generally limited to locations close to the source tree, and that dispersal over a few kilometers is "undertaken" by only a few propagules (Table 1.1). Additionally, these distances are species-specific, and the fate of a dispersing propagule depends on a wide range of environmental factors, such as propagule and vector properties, and dispersal barriers.

Table 1.1: Summary of dispersal distances in mangroves found in peer-reviewed literature.

Species	**Dispersal distance**	**Methodological group**	**Specific methods**	**Reference**
Avicennia germinans	Trans-Atlantic	Genetic analysis	Amplified fragment length polymorphism (AFLP) molecular analysis	Dodd *et al.* (2002), See also Nettel and Dodd (2007)
	< 10 times the distance of *Laguncularia racemosa*	Eulerian movement	Marked propagules	Sousa *et al.* (2007)
Avicennia marina	≤ 1 km; a few > 5 km and > 24 km; 1 at 700 km	Eulerian movement	4500 drift cards with similar buoyancy as propagules dropped from an aircraft into the sea	Steinke and Ward (2003)
	Multiple kilometers	Eulerian movement	Observations of stranded propagules on beaches	Gunn and Dennis (1973)
	Close to their maternal parent, some > 20 km	Eulerian movement and flotation data	Observations of stranded propagules on beaches and inferences from flotation data	Clarke and Myerscough (1991)
	10-500 m > 0-10 m; 3 prop. > 3 km; 1 prop. > 50 km	Eulerian movement	Marked propagules	Clarke (1993)
	up to 60 m	Eulerian movement	Marked propagules	Breitfuss *et al.* (2003)
Ceriops tagal	76% ≤ 1 m; 91% ≤ 3 m	Eulerian movement	Marked propagules	McGuinness (1997)
	max. 146 m	Eulerian movement	Marked propagules	De Ryck *et al.* (2012)
	max. 2958 m	Eulerian movement	Marked propagules	Van der Stocken *et al.* (2013)

Kandelia candel	9.4 m	Genetic analysis	Combined application of highly polymorphic nuclear and chloroplast SSR markers	Geng *et al.* (2008)
	18.8 m	Modeling	Modified two-component normal model composed of two kinds of normal distribution with short and long variances	Geng *et al.* (2008)
	≤ 50 m	Eulerian movement	Marked propagules	Yamashiro (1961)
Laguncularia racemosa	≥ 85 m	Eulerian movement	Marked propagules	Sousa *et al.* (2007)
Rhizophora apiculata	Extensive distances	Longevity data	Based on longevity data	Drexler (2001)
Rhizophora mangle	Trans-Atlantic, trans-Pacific	Genetic analysis	cpDNA and nuclear microsatellite analysis on 36 populations across the Atlantic East Pacific and South Pacific	Takayama *et al.* (2013)
	≤ 1 km; some > 2 km	GIS	Hand-counting propagules within quadrats on beaches, and aerial photographs and satellite imagery classification	Sengupta *et al.* (2005)
	< 200 time the distance of *Laguncularia racemosa*	Eulerian movement	Marked propagules	Sousa *et al.* (2007)
Rhizophora mucronata	< 20 m; a few > 50 m	Eulerian movement	Marked propagules	Chan and Husin (1985)
	< 300 m; max. 1210 m	Eulerian movement	Marked propagules	Komiyama *et al.* (1992)
	max. 60 m	Eulerian movement	Marked propagules	De Ryck *et al.* (2012)
	max. 2783 m	Eulerian movement	Marked propagules	Van der Stocken *et al.* (2013)

Number of propagules available for establishment

A questions one encounters when studying dispersal processes is 'how many propagules are available for successful establishment close and remote?'. A starting point would be the question 'what is the number of propagules produced by a mangrove tree, *i.e.* fecundity, and when considering larger scales, by the population of a specific species?'. Of the viable propagule pool, a certain amount may be removed by predation and parasitism (both in the pre- and post-dispersal phase, but also during dispersal) or lose viability naturally before reaching a suitable site for establishment. Other factors such as the interaction of propagules with the landscape matrix (*i.e.* retention) are important as well, particularly when interested in the number of propagules available for long distance dispersal (LDD). While aspects as retention and viability will be considered later in this work, we shortly devote a section on fecundity and predation for completeness. Remobilization after initial establishment appears to be rare (but not impossible) in our opinion (personal observation within our team), since in floating populations of propagules, one rarely finds rooting individuals.

Fecundity

Fecundity (*i.e.* the rate of propagule production) is a determining factor of the magnitude of dispersal, as it dictates the amount of propagules available for dispersal. At an individual level, fecundity contributes to the definition of the dispersal kernel – the spatial distribution of seeds around their source (Clark *et al.* 1999). While more propagules will not increase the probability for LDD of a specific propagule, a higher number of propagules will increase the overall potential for LDD, as there are more potential candidates. At the population level, the net population propagule productivity is a product of population size and the average individual fecundity (*i.e.* fitness or average number of descendants) minus pre-release mortality due to for example predation, pests or diseases. Hence, fecundity is a key factor in population dynamics (Howe and Miriti 2004). All else being equal, species with higher fecundity potentially have a larger number of emigrants compared to species with lower fecundity, and may contribute to a higher number of dispersal events, more long-distance colonization (Higgins and Richardson 1999, Henle *et al.* 2004) and higher demographic connectivity.

High fecundity is a typical pioneer strategy (Swaine and Whitmore 1988) which can be observed in pioneer mangrove genera such as *Sonneratia* (Lythraceae), *Avicennia* (Acanthaceae) and *Laguncularia* (Combretaceae) (Friess *et al.* 2012). *Sonneratia* produces fruits that contain more than 100 seeds that are released once the fruit disintegrates after prolonged immersion in saline or brackish water (Ball and Pidsley 1995). Large-crop *Avicennia marina* trees produce between 422 and 5210 propagules per tree annually, though this number is likely to vary with tree age and geographical location (Clarke 1992). In contrast, non-pioneer *Rhizophora* spp. (Rhizophoraceae) exhibit relatively low fecundity due to high investment in tissue of high quality propagules. Amarasinghe and Balasubramaniam (1992) found that *Rhizophora mucronata* trees produce a lower biomass of reproductive parts than *A. marina* trees located within the same estuary. From the point of view of resilience to climate change and fragmentation, high fecundity may be advantageous by increasing the number of candidates for colonizing suitable habitat (Levine and Murell 2003) including the probability of stochastic LDD (Corlett and Westcott 2013), and increase survival rate due to saturation of predators such as crabs (Lindquist *et al.* 2009).

Net population propagule production may be affected by factors that vary in time such as freshwater input, length of drought period, nutrient influx (Amarasinghe and Balasubramaniam 1992), herbivory rates (Anderson and Lee 1995) and pre-release propagule predation (Clarke 1995). Additionally, fecundity can vary across years, as the rate of propagule production can be modulated by natural disturbances such as tropical storms and hurricanes (Alleman and Hester 2011). For example, Proffitt *et al.* (2006) found that propagule production of *R. mangle* trees dropped significantly following the 2004 Hurricane Charley in Florida.

Propagule predation and parasitism

Previous work has shown that propagule predation can have important negative effects on realized net propagule production of populations. When predation is sufficiently high it could even lead to completely failed recruitment with no viable propagules available for dispersal (Robertson *et al.* 1990, Clarke 1992). Predation has been most commonly attributed to two sources: insect infestation on developing seeds or fruits, and post-release damage by grapsid and sesarmid crab herbivory (Dahdouh-Guebas *et al.* 1997, Cannicci *et al.* 2002, Cannicci *et al.* 2007). Pre-dispersal propagule predation is a common phenomenon in mangroves. In a global study, covering 41 localities and 3299 propagules, Farnsworth and Ellison (1997) reported a total predation rate of 23.3 % and a mean level of 28.3 % for all species and locations. Propagule predation rates for species considered in this work, are shown in Table 1.2. Recently, Van Nedervelde *et al.* (2015) showed that predation is positively correlated with crab density, which in turn depends on tree and root density. Additionally, predation rates seem to be strongly linked to the nutritional value of the propagules (Van Nedervelde *et al.* 2015), suggesting important differences in predation pressure among mangrove species.

Table 1.2: Overview of propagule predation values for the mangrove species studied in this work. For detailed information on the study site(s), experimental period and the number of propagules considered, the reader is referred to the respective source(s).

Species	Predation (%) (±SD, if available)	Location	Source
Avicennia marina	50 (± 40)	Global study (41 sites)	Farnsworth and Ellison (1997)
	96.0 (± 1.8)	Queensland (Australia)	Smith (1987)
	65-90.4	Queensland (Australia)	Robertson *et al.* (1990)
Ceriops tagal	24.9 (± 23.0)	Global study (41 sites)	Farnsworth and Ellison (1997)
	71.7 (± 4.3)	Queensland (Australia)	Smith (1987)
	10.2-12	Queensland (Australia)	Robertson *et al.* (1990)
	0-100	Gazi Bay (Kenya)	De Ryck *et al.* (2012)
Rhizophora mucronata	33.7 (± 31.2)	Global study (41 sites)	Farnsworth and Ellison (1997)
	0-75	Gazi Bay (Kenya)	De Ryck *et al.* (2012)
Xylocarpus granatum seed	22.4 (± 8.6)	Kosrae (Federated States of Micronesia)	Allen *et al.* (2003)
	77.7-90.7	Queensland (Australia)	Robertson *et al.* (1990)
Heritiera littoralis	76.4-98	Queensland (Australia)	Robertson *et al.* (1990)
Bruguiera gymnorrhiza	27.5 (± 35)	Global study (41 sites)	Farnsworth and Ellison (1997)
	59.0 (± 6.4)	Queensland (Australia)	Smith (1987)
	54.2-80.5	Queensland (Australia)	Robertson *et al.* (1990)

Predation and parasitism levels seem to be highly variable across sites, depending on the composition of local predator and parasite assemblages, mangrove propagule density, tidal level and the species and, potentially, genetic composition of mangrove stands (Farnsworth and Ellison 1997, Dahdouh-Guebas *et al.* 2011). The actual impact of predation on propagule mortality depends on the amount and the type of damage on the propagule (Cannicci *et al.* 2008). Although predation in some species might increase buoyancy of propagules by introducing air-filled space, and thus may contribute to higher dispersal potential, this advantage is counteracted by the various impairments it causes, such as premature release from the parent tree (Clarke 1992) and damage or decay of propagules (Farnsworth and Ellison 1997, Minchinton 2006).

Buoyancy and maximum flotation period (MFP)

In Mangroves, a broad range of morphological adaptations to hydrochory can be found, including a corky testa (*Sonneratia* spp., *Xylocarpus* spp. and *Nypa fruticans* Wurumb.; see also Das and Ghose 2003), a fibrous mesocarp (*Heritiera* spp.), aerenchyma tissue within the hypocotyl (*Rhizophora* spp.), fine hairs that trap air bubbles (*Osbornia octodonta* F. Muell. and *Acanthus* spp.), and a pericarp that potentially traps air before it is shed (*Avicennia* spp.) (Tomlinson 1994, Saenger 2002). Fine hairs of *Avicennia* propagules often encourage clumping of propagules, which may also facilitate flotation and 'rafting'. These flotation-aids confer buoyancy and may be linked to the buoyancy behavior of the propagules.

Buoyancy traits and flotation period, in particular, are important determinants of potential dispersal distance. In mangroves, propagule flotation period is often used as a proxy for dispersal potential across species (Clarke *et al.* 2001, Ye *et al.* 2004, Allen and Krauss 2006). Currently, interspecies contrasts of hydrochorous dispersal potential are complicated due to variation in the methodology used in different studies. For example, Clarke *et al.* (2001) performed a flotation experiment using fourteen mangrove species over a total duration of only fifteen days, after which viability was assessed. Given that propagules often remain viable for a much longer time period, the duration of the study did not allow to reliably quantify relative differences in flotation period. Other studies have focused on MFP without checking for viability (Table 1.3). This is problematic, because non-viable propagules often continue to float even though they can no longer establish and grow. Hence, long-term studies are needed to determine the MFPs and viability of the propagules. This combination of information constitutes the desired basis for estimating effective LDD events.

Table 1.3: Summary of existing literature on mangrove propagule flotation periods and viability. The flotation periods recorded here refer to propagules floating in sea water (± 35 ‰), except for those from Ye *et al.* (2004), which were floating in 15 ‰ saline water. Obligate dispersal period (ODP) refers to the post-release period during which a propagule is yet to initiate root-growth. –: no data available; av.: average.

Species	**Maximum flotation period (MFP)**		**Obligate dispersal period (ODP) (Days)**	**Maximum viability period (MVP)**		**Pattern for loss of viability**	**References**
	Days	**Percentage floating at MFP**		**Days**	**Percentage viable at MVP**		
Acanthus ilicifolius	–	–	3	< 11	–	–	Ye *et al*. (2004)
Aegialitis annulata	10	5	10 (av.)	120	15	–	Clarke *et al*. (2001)
Aegiceras corniculatum	5	5	8 (av.)	120	28	–	Clarke *et al*. (2001)
Avicennia germinans and *Avicennia bicolor*	82	100	–	80	65	Logarithmic	Rabinowitz (1978a)
Avicennia marina	15	100	4 (av.)	240	4	Logarithmic	Clarke and Myerscough (1991); Clarke (1993); Clarke *et al*. (2001)
Avicennia germinans	365	–	–	365	100	–	Gunn and Dennis (1999)
Bruguiera exaristata	15	95	8 (av.)	120	75	–	Clarke *et al.* (2001)
Bruguiera gymnorrhiza	31	–	14 (av.)	210	100	–	Clarke *et al.* (2001); Steele (2006)
Bruguiera parviflora	5	20	8 (av.)	120	28	–	Clarke *et al.* (2001)
Bruguiera sexangula	63	10	–	63	–	–	Allen and Krauss (2006)
Ceriops decandra	15	80	8 (av.)	120	37	–	Clarke *et al.* (2001)

Ceriops tagal	15	95	14 (av.)	120	20	–	Clarke *et al.* (2001)
Cynometra iripa	15	100	23 (av.)	120	22	–	Clarke *et al.* (2001)
Excoecaria agallocha	208	–	2	210	5	–	Ye *et al*. (2004); Steele (2006)
Heritiera littoralis	150	–	23 (av.)	210	5	–	Clarke *et al.* (2001); Ye *et al.* (2004); Steele (2006)
Laguncularia racemosa	90	5	8	–	–	–	Rabinowitz (1978a); Clarke *et al.* (2001)
Lumnitzera littorea	214	–	–	210	10	–	Steele (2006)
Lumnitzera racemosa	–	–	12	< 20	–	–	Ye *et al*. (2004)
Pelliciera rhizophorae	107	44	30	107	45	Exponential	Rabinowitz (1978a)
Rhizophora apiculata	89	–	–	89	–	Exponential	Drexler (2001)
Rhizophora harrisonii	104	90	≈ 40	–	–	–	Rabinowitz (1978a)
Rhizophora mangle	260	–	–	210	62	–	Allen and Krauss (2006); Steele (2006)
Rhizophora mucronata	150	–	–	150	–	–	Drexler (2001)
Rhizophora stylosa	75	–	14	210	55	–	Clarke *et al.* (2001); Steele (2006)
Xylocarpus granatum	60	–	–	210	80	–	Steele (2006)
Xylocarpus moluccensis	214	–	–	210	20	Logarithmic	Steele (2006)
Xylocarpus mekongensis	15	100	4 (av.)	120	82	–	Clarke *et al.* (2001)

There is substantial variation in MFP across mangrove species, ranging from almost no flotation in *Aegiceras corniculatum* (L.) (Clarke *et al.* 2001) to more than 104 days in *Rhizophora harrisonii* Leechm. (Rabinowitz 1978a) and 150 days in *H. littoralis* (Ye *et al.* 2004). Gunn and Dennis (1999) reported a floating period of > 1 year for *A. germinans* with 100 % of the seeds being viable. In combination with a high fecundity, low susceptibility to retention due to its compact propagules (Van der Stocken *et al.* in press-a), and the formation of roots during dispersal (Rabinowitz 1978a), the success of this species may not be surprising. The MFP of species that best retain their flotation ability over time are more difficult to determine due to the long observation windows required. Consequently, MFP of long floating species are either unknown or based on rough estimates (Table 1.3). For example, Allen and Krauss (2006) performed linear extrapolations, in which they estimated the MFP of *R. mangle* propagules up to a maximum of 302 days. Although the large propagules of *Rhizophora* species potentially have a high MFP (Clarke *et al.* 2001, Rabinowitz 1978a), there is little support for an extrapolation of the MFP based on a linear trend. Also, clear differences in MFP may be present within one species. For example, *A. marina* was found to have populations of floaters and sinkers (Steinke 1986). A final example, acknowledging the need for more extensive experiments, is the flotation potential of *H. littoralis* propagules, which could have one of the longest flotation periods among mangrove propagules, due to its very low density (613 g L^{-1}, Van der Stocken *et al.* 2013) and a hard woody epicarp (Tomlinson 1994). However, the MFP has never been confidently quantified, with only Ye *et al.* (2004) stating that it is more than 150 days.

The impact of salinity on buoyancy

Salinity significantly affects the buoyancy characteristics of mangrove propagules, including flotation period, orientation, viability and root initiation. Flotation experiments that included salinity treatments showed that, consistent across species and populations, propagules floated longer and postponed root growth under higher ambient salinities. In Rhizophoraceae, viviparous propagules largely retain a horizontal orientation under higher salinities (Rabinowitz 1978a, Clarke *et al.* 2001). Also, shedding of the pericarp of *Avicennia* propagules, which signals the initiation of root growth, occurs earlier in brackish water than in seawater (Clarke and Myerscough 1991), which may be an adaptation to indicate the arrival in a suitable environment. Since retaining the pericarp facilitates flotation, *Avicennia* propagules sink earlier in brackish water. Delayed root initiation in higher salinity was also observed in *Laguncularia racemosa*, *Heritiera littoralis* and *Acanthus ilicifolius* L. (Ye *et al.* 2004). Furthermore, despite the fact that seawater prevents fungal growth better than freshwater (Alleman and Hester 2011), prolonged flotation in seawater still reduces propagule viability (Rabinowitz 1978a). Secondary propagule dispersal (*i.e.* regaining buoyancy after an initial sinking) is more frequently observed under higher salinity for *A. germinans* (Alleman and Hester 2011) and lower salinity in *A. marina* (Clarke and Myerscough 1991). This difference may be linked to species-specific physiological responses to varying salinity levels, as secondary buoyancy was thought to be related to the rate of respiration of cotyledonary reserves (Steinke 1986, in Clarke and Myerscough 1991). In conclusion, these studies showed that the overall trend of increased sinking, root initiation, shedding of the pericarp and a vertical orientation of propagules under lower salinities could be adaptive in the sense that brackish and freshwater conditions could signal suitable conditions for mangrove establishment after dispersal.

Propagule obligate dispersal period

Apart from the MFP, a minimum dispersal period (or obligate dispersal period, ODP),may be present in mangrove propagules. This ODP represents the period after release during which a propagule is not yet able to initiate root-growth. This mechanism of delayed germination by means of dormancy[5] may increase the dispersal potential of propagules by postponing the establishment of propagules. Additionally, variation in ODP among propagules could potentially represent an evolutionary risk spreading strategy from the perspective of the parents, which could ensure that at least a fraction of propagules can grow to reproduce (Childs *et al.* 2010). However, the duration of the ODP and the trigger(s) that break(s) the dormant phase of a propagule are currently unknown. Currently, the only reliable ODP data are available for *Laguncularia racemosa* (Rabinowitz 1978a) because this experiment made

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[5] We introduce the term '*delayed* dormancy', since in contrast to "normal dormancy", the dormant phase is preceded by a period of metabolic activity.

the important distinction between ODP and the minimum time required for root initiation following ODP and after stranding. It should be mentioned here that root development of propagules may be delayed by water turbulence and tidal action (*e.g.* McMillan 1971, Delgado *et al.* 2001), extending the dispersal period. Despite the clear definition, ODP has been variably quantified experimentally. Clarke *et al.* (2001), for example, considered the time until the growth of the first root of 1 mm as the ODP, irrespective of the fact that the propagules were floating (the first 15 days of the experiment) or planted (after 15 days). Rabinowitz (1978a) calculated ODP as the period of time for the seedling to establish. However, it is not clear which criteria were considered to define establishment.

As such, there is a need to standardize these measurements, improving knowledge and insight in propagule traits within and between species. Acquiring reliable ODP data is a prerequisite to identify the time frame in which dispersal and establishment can occur. Additionally, knowledge on variation in dormancy via ODP among species can shed new light on the evolution of dispersal in mangroves and the role of risk spreading strategies mediating population persistence and expansion in mangroves. Finally, these data are necessary to parameterize realistic simulation models of mangrove population dynamics and may help to inform mangrove restoration programs by allowing them to select propagules that have reached the right age for planting.

Propagule viability

Besides physical factors such as vector properties, both the total dispersal distance (total distance along the dispersal trajectory and, to a lesser extent, the realized dispersal distance (Euclidean distance between origin and destination) is determined by the combination of propagule viability and the flotation time of the propagule, whichever is shorter. For instance, *Bruguiera sexangula* (Lour.) Poir. propagules can remain viable up to 63 days upon submersion in seawater, but only 5 % will still be floating by then (Allen and Krauss, 2006). In this case, the flotation period will be the determining factor for dispersal distance. Overall, in most mangroves evidence suggests that maximum viability is as long as, if not more than, the flotation period (Table 1.3). Therefore, dispersal distance will be primarily limited by the flotation period. The longest viability was recorded for *Avicennia marina* – most propagules were viable after 5 months with some maintaining viability up to 7 months in seawater (Clarke 1993). Due to the tendency for propagules to rot in seawater, viability was observed to be longer in freshwater (Rabinowitz 1978a). The proportion of propagules that loses viability over time varies across species. The loss of viability was observed to be exponential in *Pelliciera rhizophorae* Pl. and Tr. and *Rhizophora apiculata* BL., and logarithmic in *Avicennia* spp. and *Xylocarpus moluccensis* (Lamk.) Roem.. Based on these reservations, it is clear that it is impossible to assess the dispersal potential of mangroves without knowing both MFP and propagule viability decay curves. Hence, future work should focus to fill in these knowledge gaps. Additionally, it would be worth to investigate whether selection for prolonged viability in sea water is linked to specific taxa such as pioneer species that dominantly rely on colonization for their regional persistence.

The biological window of opportunity for dispersal

The combination of ODP, MFP and variation in the decay of propagule viability over time results in a limited window of opportunity during which propagule dispersal could – but not necessarily will – lead to successful establishment in a new site. Any propagules that arrive at a suitable site outside of this window will not be able to germinate and establish regardless of the suitability of local conditions. As shown in Figure 1.5, this window of opportunity begins at the end of the ODP and extends until the end of the MFP (Fig. 1.5 a) or the maximum viability period (MVP) (Fig. 1.5 b), depending on whichever is shortest. Dispersal events that terminate at destination[6] within this time frame are regarded as ecologically meaningful, as the deposited propagules are viable and can initiate establishment. Subsequent successful establishment at a new location then depends on whether requirements for establishment are met, *i.e.* the presence of an inundation-free period, the presence of roots which are long enough to resist hydrodynamic forces, and preferentially even longer roots to withstand high energy events (see Balke *et al.* 2011).

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[6] The word 'destination' carries the connotation of a premeditated final location, which is of course absent in biological dispersal.

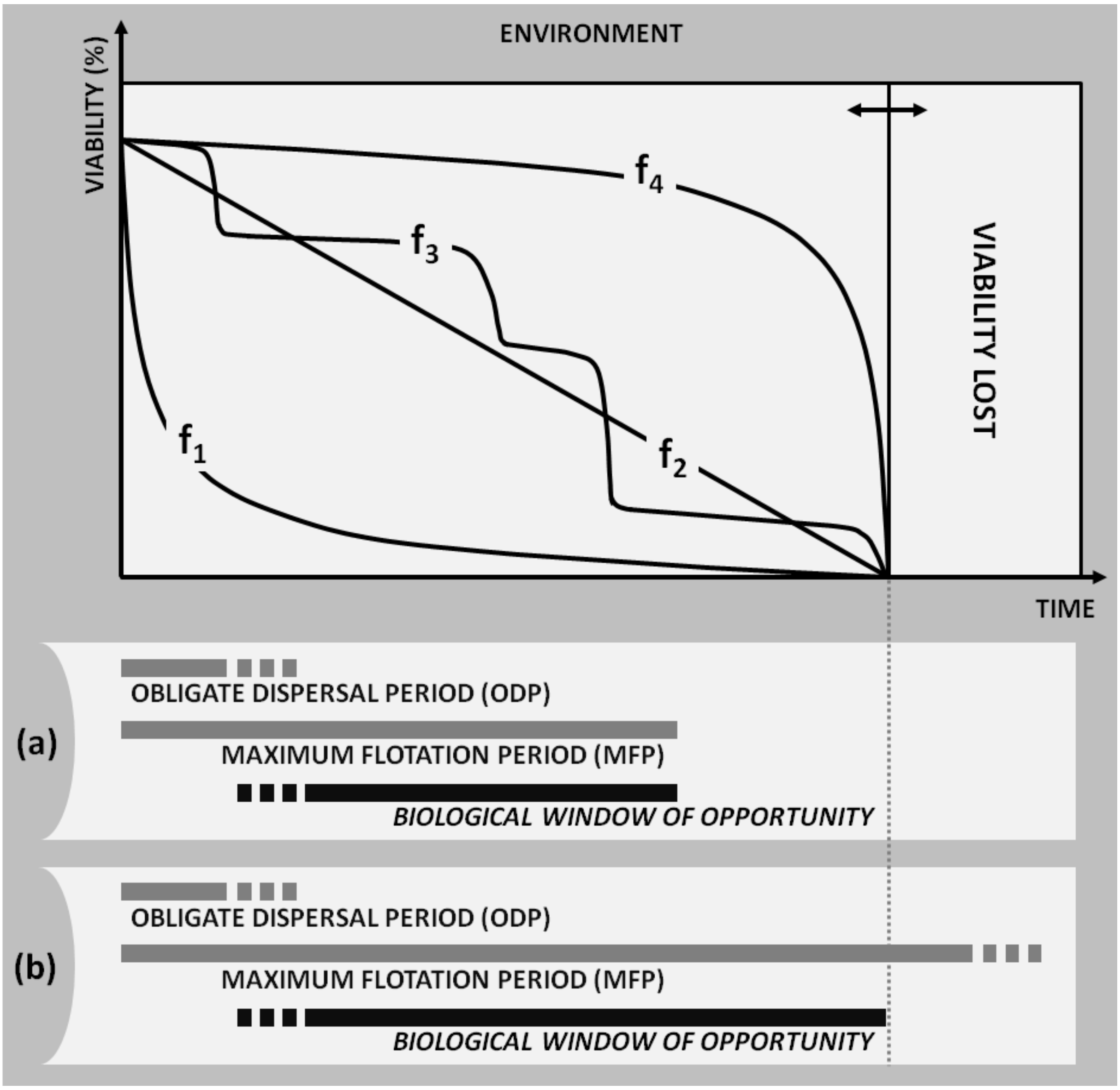

Figure 1.5: A schematic representation of the biological window of opportunity (BWO) for viable propagules to be dispersed. This figure shows the interaction between three drivers – maximum flotation period (MFP), obligate dispersal period (ODP) and viability – in determining dispersal distance. Propagules lose viability after release. Depending on the species, the proportion of viable propagules decreases in an exponential (f1) or logarithmic (f4) manner. We hypothesize that the proportion of viable propagules can also decrease in a linear (f2) or stepwise (f3) manner. The BWO refers to the time frame between (a) the end of the ODP and the MFP or (b) the maximum viability period (MVP), depending on whichever is shortest. Beyond the maximum viability period (MVP) among a population of propagules (indicated with the vertical line in the figure), connectivity cannot be established even if a propagule is deposited into a suitable habitat.

Establishment conditions

Typically, only coastal intertidal areas qualify as suitable areas for mangrove establishment. Yet, even if a propagule manages to strand in such a locality, strong spatial heterogeneity in local conditions may still act as an important filter for establishment. Both biotic and abiotic conditions can limit establishment in a variety of ways.

Krauss and coworkers (2008) provided a comprehensive overview of the biotic factors (*e.g.* herbivory, seedling growth rates) and abiotic factors (*e.g.* temperature, carbon dioxide, salinity, light, nutrients, flooding, sea-level rise) that influence establishment and early development of seedlings. Stranded propagules have to be able to survive long inundation periods, withstand hydrodynamic drag forces (Balke *et al.* 2011, Friess *et al.* 2012), tolerate high salinity (Jayatissa *et al.* 2008) and overcome herbivory (Delgado *et al.* 2001) in order to establish. Finally, if other mangrove propagules or trees or other types of vegetation are present, a propagule must be able to survive local competitive interactions. Overall, a propagule does not only have to arrive in a suitable area (regional scale) within a window of opportunity dictated by temporal constraints (MFP and MVP), it also needs a favorable combination of propagule traits suitable to survive under the given local conditions for settlement. General requirements for all species include an inundation-free period after stranding for rapid root fixation, the presence of sufficiently long roots to withstand tidal and wave action, and even longer roots to outlive removal of sediment around the seedling due to mixing or erosion of the upper sediment layer (Balke *et al.* 2011). However, propagules of different species also differ in their ability to cope with post-dispersal challenges such as propagule predation, high salinity and inundation (Delgado *et al.* 2001, Jayatissa *et al.* 2008). Propagules and seedlings of pioneer species, such as *Avicennia* spp., *Sonneratia* spp. and *Laguncularia racemosa*, possess traits to facilitate establishment at the pioneer zone of the mangroves, including shade intolerance, lack of seed dormancy, high tolerance to salinity and regular inundation as well as resistance to wave action (Friess *et al.* 2012).

As successful establishment is the final step for effective dispersal, the biophysical factors dictating propagule establishment will have a considerable influence over long-term dispersal patterns.

OBJECTIVES AND THESIS OUTLINE

Thus far, no attempt has been made to reconstruct a general framework of propagule dispersal in mangroves. Such a framework could fill an important void in our current understanding of mangrove dynamics across spatial and temporal scales (population dynamics, biogeographic distribution patterns) in the light of environmental change. Similar synthetic frameworks have been previously established for other taxonomic groups, such as wind-dispersed plants (Nathan *et al.* 2011), microorganisms and viruses (*e.g.* Brown and Hovmøller 2002, Kellog and Griffin 2006), and wind- and animal-vector mediated dispersal of freshwater invertebrates (*e.g.* Bilton *et al.* 2001, Vanschoenwinkel *et al.* 2008, Figuerola *et al.* 2010).

The **MAIN OBJECTIVE** of this work is to contribute to currently understudied aspects of the mangrove propagule dispersal process which will reduce parameter and model uncertainty (*sensu* Higgins *et al.* 2003a), and hence allow for more reliable predictions of dispersal patterns and long-term population dynamics under different climate change scenarios. Although – in my opinion – the dispersal phase does not include propagule release nor establishment processes, some aspects related to these life stages such as fecundity and phenology (the timing of propagule release in particular) are considered, since they constitute important input components (when and how do propagules enter the dispersal phase?). Using a conceptual framework we assess the relative importance of intrinsic (biological) and extrinsic (environmental) factors that determine dispersal and gene flow in mangroves, starting from (1) the source population, (2) the dispersal process from source to destination and (3) the establishment of propagules at the destination (Fig. 1.6). We focus on how variability in the constituents of dispersal – the heterogeneous and dynamic features of coastal areas and the diverse propagule traits of mangrove flora – may be reflected in important variation in the magnitude, directionality and seasonality of dispersal dynamics among species and localities as well as in variation in establishment success.

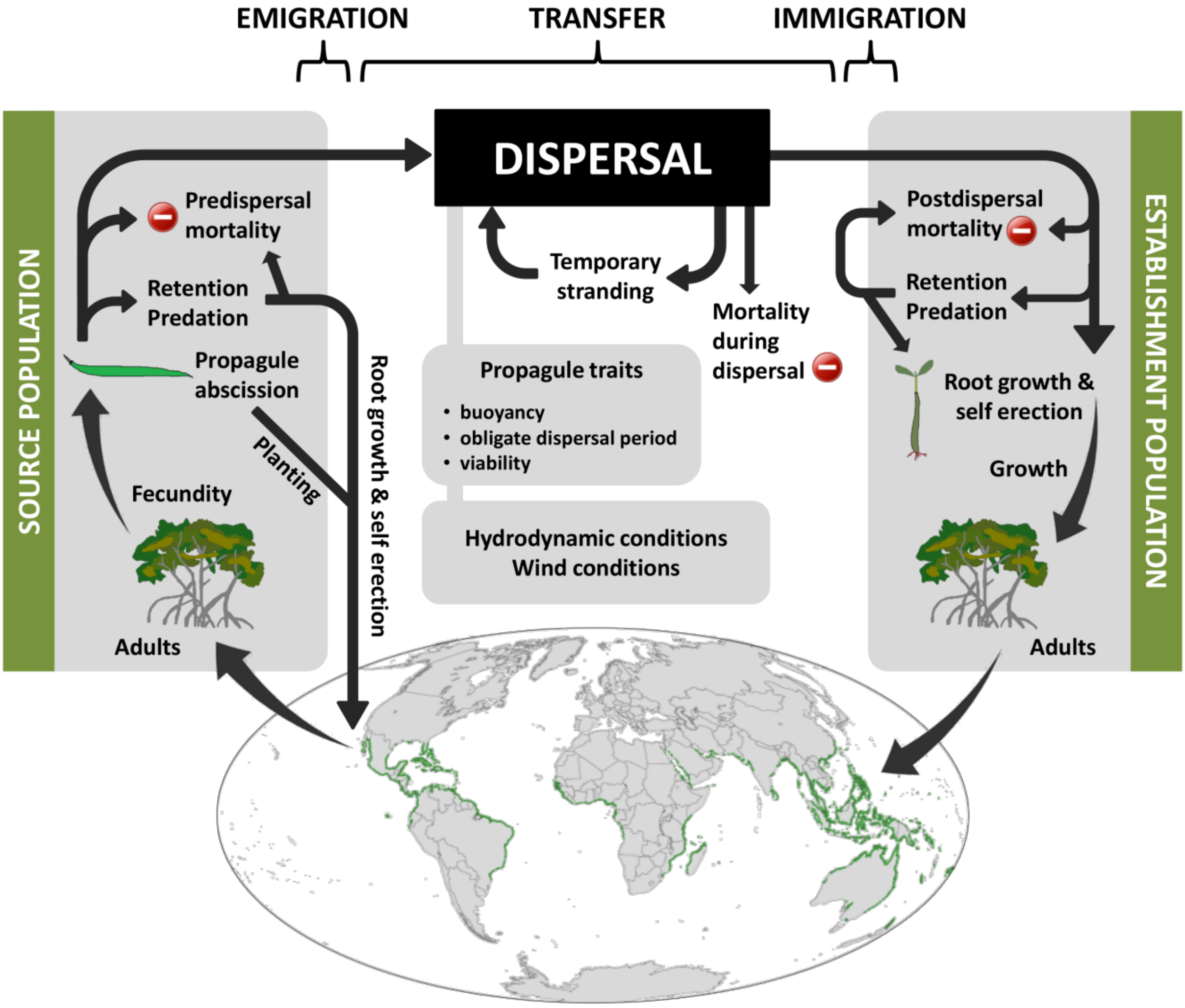

Figure 1.6: Schematic representation of the life-cycle of a mangrove tree. Knowledge on the factors involved in the dispersal process is incomplete, mainly due to methodological challenges. The source and establishment population on the world map should be interpreted within the context of long distance dispersal (LDD) events, rather than as a punctual event or case study.

In **CHAPTER 2** – *LATITUDINAL PATTERN IN THE TIMING OF MANGROVE PROPAGULE RELEASE: A META-ANALYSIS OF GLOBAL DATA* – we performed a meta-analysis of peer-reviewed literature on propagule release timing for mangroves and examine latitudinal patterns in this data, as well as correlations with the climate variables rainfall and temperature.

In **CHAPTER 3** – *IMPACT OF LANDSCAPE STRUCTURE ON PROPAGULE DISPERSAL IN MANGROVE FORESTS* – we combined field and laboratory experiments to test the effect of root density, propagule morphology and hydrodynamic variables on retention rates and trajectories in the propagules of four common species.

In **CHAPTER 4** – *THE ROLE OF WIND IN HYDROCHOROUS MANGROVE PROPAGULE DISPERSAL* – we combined *in situ* (field) and *ex situ* (flume tank) dispersal experiments to understand water and wind current contributions to dispersal potential as well as to estimate real dispersal ranges due to immediate response to tidal currents.

In **CHAPTER 5** – *INTERACTION BETWEEN WATER AND WIND AS A DRIVER OF PASSIVE DISPERSAL IN MANGROVES* – we built further on CHAPTER 4, and use mangrove propagules with a wide variety of morphological features to investigate the interaction between water and wind operating on these features as a driver of passive dispersal.

In **CHAPTER 6** – *MODELING MANGROVE PROPAGULE DISPERSAL TRAJECTORIES USING HIGH RESOLUTION ESTIMATES OF OCEAN SURFACE WINDS AND CURRENTS* – we present preliminary results of a dispersal model, which, using the highest resolution global oceanographic and wind data now available, allows for statistical probabilistic estimates of the nature and shape of actual dispersal routes. Multiple mangrove localities in the Mozambique Channel were selected to investigate how the interaction of ocean surface and wind currents determines the fate of dispersal units with different morphologies and floating orientations. The case of the Mozambique Channel was selected for its reported oceanographic complexity.

I end this dissertation with **CHAPTER 7** – *CONCLUSION AND PERSPECTIVES* – in which I collate the findings of the different chapters and discuss their relevance and applicability in dispersal ecology. Additionally, I formulate recommendations for future research with the overall goal of improving dispersal model parameters and predictions of dispersal patterns and potential biogeographical range shifts under future environmental changes.

CHAPTER 2

LATITUDINAL PATTERN IN THE TIMING OF MANGROVE PROPAGULE RELEASE: A META-ANALYSIS OF GLOBAL DATA

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Abstract

Despite widespread recognition that phenological events may shift under changing climatic conditions with potential impact on the patterns of dispersal and deposition, phenology is often neglected in dispersal research. In this study, we performed a meta-analysis of peer-reviewed literature on propagule release timing for mangroves, which are among the most threatened ecosystems in the tropics. Most of the available data is related to *Avicennia marina*, *Avicennia germinans* and *Rhizophora mangle*. Our study demonstrates phenological complementarity between the northern and southern hemispheres, with a peak in propagule fall corresponding to the boreal and austral summers, respectively. We found strong positive correlations between mangrove propagule release and rainfall, with 72 % of data reporting release during the wet season, except in the southernmost latitudes. At higher latitudes than the equatorial zone, propagule release was also correlated with temperature. In the equatorial zone, propagules fall from parent trees throughout most of the year, showing no pronounced production peaks, and no significant correlation with rainfall or temperature. Considering current and future climate change, it is important to increase the spatial coverage and temporal resolution of available data on mangrove propagule release which currently does not allow for robust and realistic model parameters and hampers the biological realism of dispersal models and predictions of species responses to environmental changes. Hence, researchers worldwide are encouraged to study phenological events such as propagule release for different mangrove species over periods that are long enough to allow for understanding its response to external drivers such as rainfall.

Introduction

Over the last years, the phenology of plant species has received increasing attention in ecology, especially because of growing evidence of phenological shifts due to climate change and its importance in assessing the vulnerability of a particular species (Kramer *et al.* 2000, Cleland *et al.* 2007, Körner and Basler 2010). Most studies have focused on species in temperate zones, where plant phenologies have been correlated with photoperiod and temperature (Huang *et al.* 2001, Menzel *et al.* 2005, Vitasse and Basler 2013), although plant phenologies are very likely controlled by complex interactions among biotic and abiotic factors (Wolkowich *et al.* 2014). In tropical areas, on the other hand, where photoperiod and temperature show less seasonal variability, phenology was reported to be mainly controlled by precipitation and soil water availability (Singh and Kushwaha 2005, Couralet *et al.* 2013). Since anthropogenic activities will increasingly influence these factors, insight in the environmental cues that underlie plant phenology is important for predicting the survival and growth of individuals, the reproductive success of populations and species interactions under shifting climatic conditions (Cleland *et al.* 2007). Furthermore, phenological data, particularly on the timing of seed release, is important in dispersal studies, since in combination with temporal variations in the characteristics of the main dispersal vectors, it determines dispersal and deposition patterns (Greene 2005, Savage *et al.* 2010, Savage *et al.* 2012), and hence connectivity. In marine metapopulations where dispersal takes place through larval stages, 'timing' has been raised as a key component in understanding connectivity (Carson *et al.* 2010).

In mangrove ecosystems, which have been strongly reduced over the last decades due to changes in land use, dispersal is a key mechanism in predicting long-term community structure and biogeographical range shifts under current changing climatic conditions. Additionally, it can help beneficial alleles to spread among populations fueling local adaptation (Levine and Murrell 2003). Hence, there is a strong need for good empirical data and mechanistic models to reconstruct and predict the frequency and the likely trajectories of natural dispersal events, to assess the vulnerability of populations to extinction and the likelihood of successful range expansion. However, while the dispersal behaviour of individual mangrove propagules (*i.e.* dispersal units) and the interaction of the dispersal vectors at play have been studied recently (Van der Stocken *et al.* 2013, Van der Stocken *et al.* in 2015b), relatively little is known about the temporal dynamics of propagule release and its environmental drivers, hampering the biological realism of model predictions. Such knowledge is essential given the temporal variation of dispersal vectors properties (strength and direction) which may condition the sites of propagule arrival.

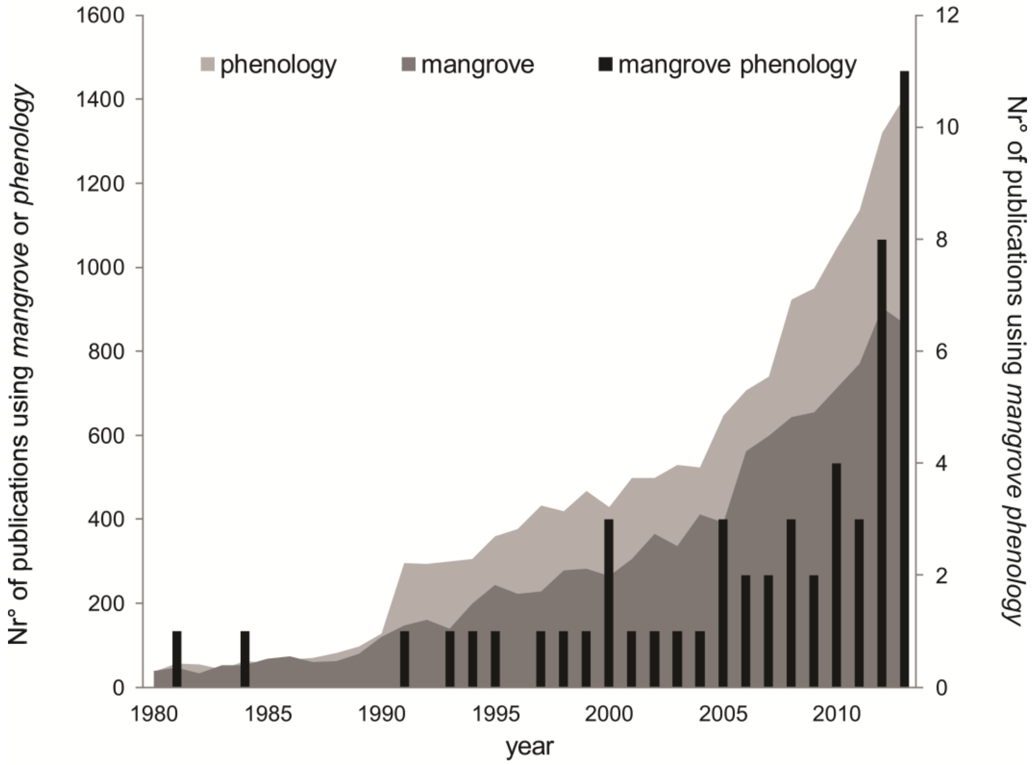

Figure 2.1: Number of publications from 1980 through 2013 extracted from the Web of Knowledge database with 'phenology' (light grey), 'mangrove' (dark grey), and 'mangrove phenology' (black bars) in the title, keywords or abstract. There is a rapid increase in the number of publications (left y-axis) on phenology and mangroves, but the number of publications on mangrove phenology, though increasing (right y-axis) is still limited.

Mangrove phenology has received increasing attention (Fig. 2.1) because these ecosystems represent a crucial component of primary production in many tropical and subtropical coastal regions (Bouillon *et al.* 2008). Their role in providing valuable nutrients that support coastal and marine systems has been frequently reported (Odum and Heald 1975, Aburto-Oropeza *et al.* 2008). However, phenological data are mostly restricted to a particular species and cover time periods that are too short to detect long-term phenological patterns and responses to (changes in) environmental factors such as rainfall and temperature. Additionally, the drivers mentioned earlier for tropical plant seed phenology (such as soil water availability) are not expected to be merely transposable to mangroves in their particular waterlogged marine environment. They present an important research subject for phenology in view of the wide latitudinal range of many species. Therefore, long-term repetitive recordings of mangrove phenological events are needed, as well as a quantitative knowledge of their interaction with potential environmental drivers. Here, we assembled most available data on mangrove propagule release timing to assess current knowledge, intending to answer the following questions: (1) Is there a latitudinal pattern in mangrove propagule release timing?; (2) Is mangrove propagule release coupled with climate features such as rainfall and temperature?; (3) What is the ecological and biogeographical importance of temporal patterns in propagule release and how may shifts in environmental seasonality affect the potential for long distance dispersal, and hence dispersal patterns and the connectivity among mangrove populations worldwide? To our knowledge, this is the first study in which patterns of mangrove propagule release are considered at a global scale.

Material and methods

Data sources

Peer-reviewed journal articles on mangrove phenology were searched for using Web of Knowledge. As a keyword, 'phenology' was used and on the outcome of this search, 'mangrove' was used as an additional search operator. The remaining articles were screened for information on the timing of propagule release. Additionally, to ensure that our study includes most of the relevant publications that mention the timing of propagule release, we intensively screened the reference lists of the manuscripts found and searched for missing literature. We continued this procedure until no new data on propagule release was found. We highlight that the list of mangrove plants is a best professional combination of several sources defining which species actually can be qualified as a 'mangrove', including the original list published by Tomlinson (1994), the World Register of Marine Species at www.marienspecies.org (Appeltans *et al.* 2012), as well as selected species published in between (Duke 2006, Giesen *et al.* 2007). This was the most comprehensive list we could possibly create without going into the debate as to what is a mangrove and what not, which is beyond the scope of this study. We recorded information on the timing of propagule release, the study area, its latitude and longitude, and the season (dry or wet) in which the propagules were released. The information on propagule release was drawn from the text, figures or tables. Data on propagules per se (*e.g.* dry weight) are not considered in this study because the way in which data were presented often did not allow for such detailed information. We used a binary scale (1-0), marking the months when most propagules were reported (1) and the other months (0). We used the reporting of mature propagules as a proxy for release, when release was not mentioned explicitly. This allows for the separation of months when the bulk of propagules were released from months where propagule release was limited or absent. If geographical coordinates were not reported, this data was retrieved from searching the study site using Google Earth based on specifications on the locality in the source publication. A special effort was done to retrieve data for West Africa, but as yet no data were found which could be used in this analysis.

Data on three environmental variables – monthly average rainfall (MAR), monthly average low temperature (MALT) and monthly average high temperature (MAHT) – were extracted from the World Weather Online database (www.worldweatheronline.com) using published location information, for correlation with timing of propagule release. Data on the global distribution of mangroves was taken from the Mangrove Reference Database and Herbarium (Massó i Alemán *et al.* 2010).

To investigate the potential existence of global latitudinal patterns in the timing of propagule release, monthly binarized data were summed per latitudinal range groups (20 to 37° S, 10 to 20° S, 10° S to 10° N, 10 to 20° N, 20 to 28° N) and normalized by dividing by the total number of reported propagule release data per latitudinal range group. Unfortunately, the size of the dataset does not allow for meaningful statistical analysis when increasing the number of latitudinal bands. The value 37° S is 1-2° from the absolute mangrove southern latitudinal range limit (38.45° S, East-Australia), while the northern latitudinal limit of mangrove forests is 32.28° N (Bermuda) (Spalding *et al.* 2010).

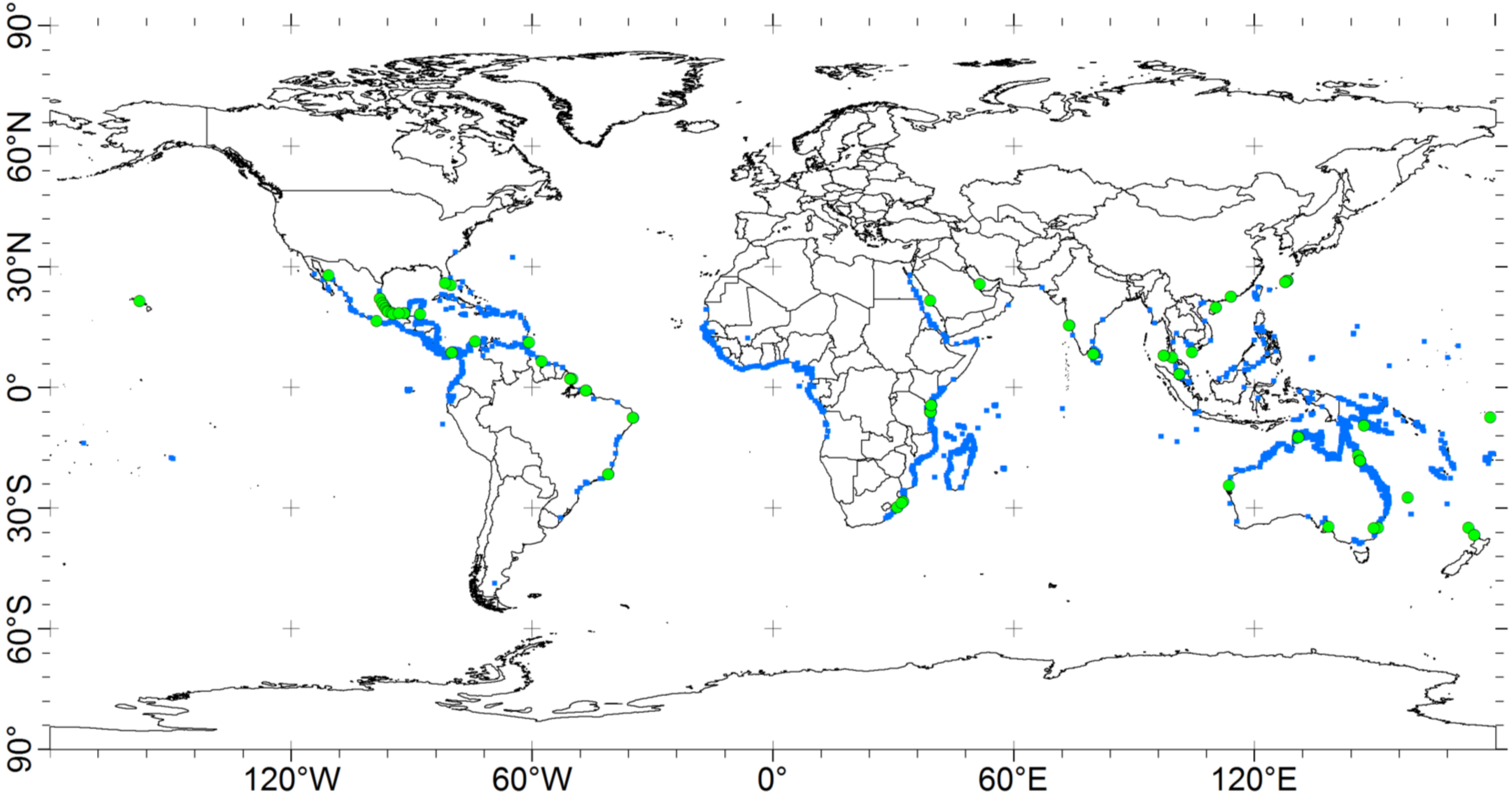

Figure 2.2: Geographic locations (green circles) from which phenological data is included in this meta-analysis. Global mangrove distribution is shown in blue (Mangrove Reference Database and Herbarium, Massó i Alemán *et al.* 2010). Most data comes from study sites in Australia and Central America. No data was reported for West Africa. Map source: ESRI, WorldPlateCarree.mdx (ArcGIS 10).

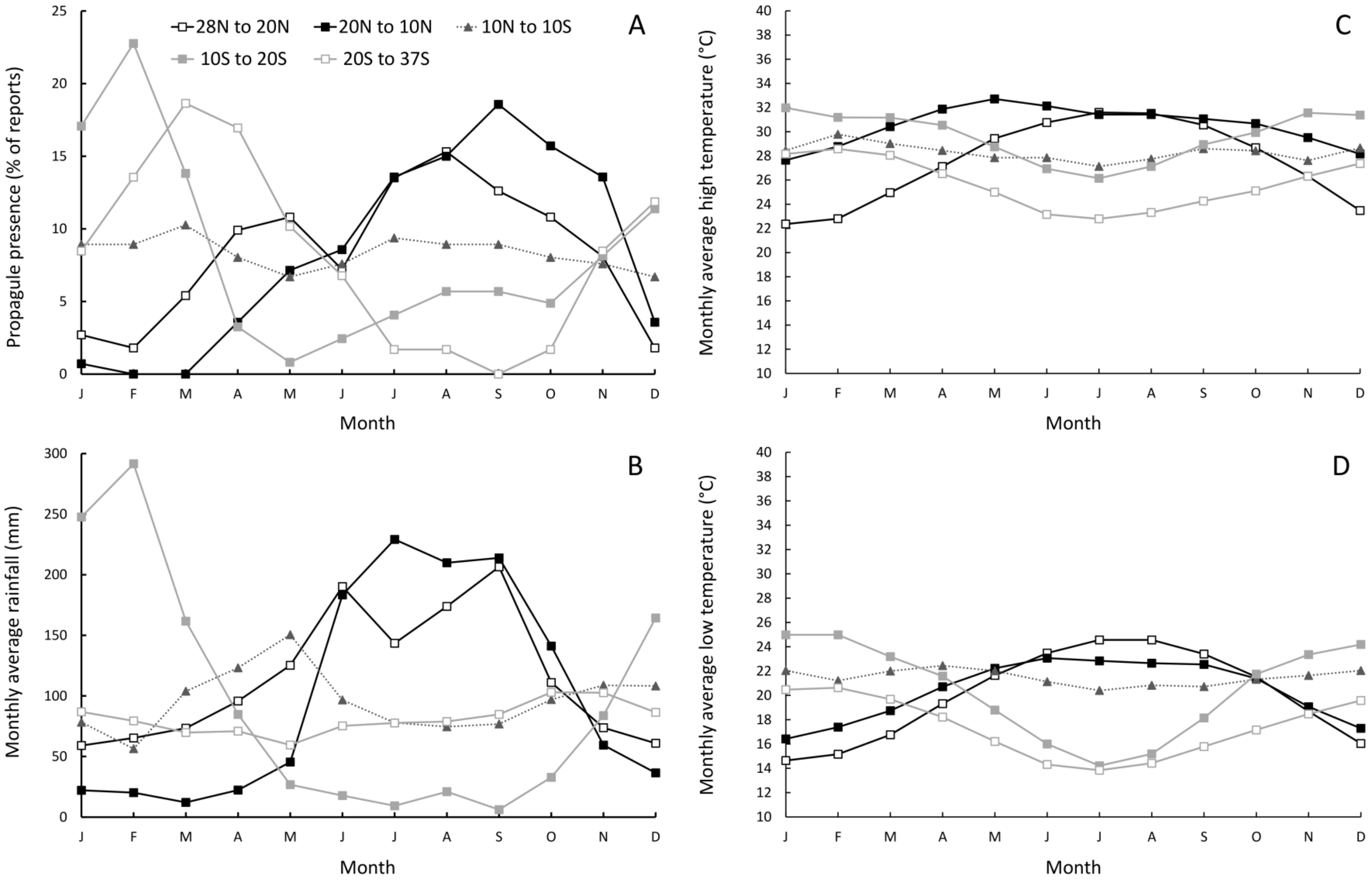

Figure 2.3: Latitudinal pattern in (A) propagule release timing (% of reports), (B) monthly average rainfall (MAR), (C) monthly average high temperature (MAHT), and (D) monthly average low temperature (MALT). Climatological data was extracted from World Weather Online (http://www.worldweatheronline.com) for each reported study site and averaged per latitudinal range group.

Data analysis

Using the Microsoft Office Excel 2007 Software, we calculated the percentage of data per latitudinal range group, the relative abundance of the various mangrove specied studies, and the percentage of reported data per country. This allows us to track knowledge gaps at the level of species and study site. We computed coefficients and corresponding P-values of Pearson correlations between reported propagule release data (hence normalized and expressed as a percentage of reports per latitudinal range group) and climatological variables, using Matlab R2014a. Statistica 8 (StatSoft, Inc) was used to test for autocorrelation between the climatological variables. Due to significant autocorrelation between these environmental variables, no multiple regression analysis was conducted. To illustrate and discuss the importance of phenological data in the study of propagule dispersal and deposition patterns, release locations were plotted for the Indian Ocean area relative to ocean surface current circulation in the southwest and northeast monsoon season. Ocean surface circulation patterns were taken from Shankar *et al.* (2002) and for the Mozambique Channel from Ternon *et al.* (2014). The respective maps were created using ArcGIS 10.

Results

Our literature search yielded 61 peer-reviewed manuscripts published in the period 1971-2013, containing relevant data on propagule release timing, covering 170 data lines (Table 2.4). Altogether, 47 species of 25 genera were covered by these references, *i.e.* more than 65 % of known mangrove species (Polidoro *et al.* 2010). Geographical locations of mangrove propagule fall studies are shown in Figure 2.2. Most data correspond to *Avicennia marina* (14.1 %), *Avicennia germinans* (10.6 %), *Rhizophora mangle* (10.6 %), *Laguncularia racemosa* (6.5 %), and *Rhizophora mucronata* (5.3 %). Considering the genera, most data are available on *Avicennia* species (27.6 %), followed by *Rhizophora* (25.9 %), *Bruguiera* (9.4 %), *Laguncularia* (6.5 %), *Sonneratia* (6.5 %) and *Ceriops* (5.9 %). Most data comes from mangrove sites in Australia (31.18 % of all data), Mexico (18.82 % of all data) and Brazil (7.06 % of all data), *i.e.* three countries that together with Indonesia and Nigeria account for 48 %

of the global mangrove area (FAO 2007). To our knowledge no published data are available for West-Africa (Fig. 2.2).

Table 2.1: Coefficients and P-values of Pearson correlations between propagule release (% of reports) and monthly averages of the climatological variables rainfall, high temperature and low temperature, for each latitudinal range group. All data. *(P < 0.05), **(P < 0.01), ***(P < 0.001), n.s. (non significant).

Latitudinal range group	n	Monthly average rainfall (mm) (MAR)		Monthly average high T (°C) (MAHT)		Monthly average low T (°C) (MALT)	
		r	P	r	P	r	P
28N to 20N	25	0.73	**	0.91	***	0.92	***
20N to 10N	31	0.83	***	0.43	n.s.	0.72	**
10N to 10S	47	-0.62	*	0.11	n.s.	-0.35	n.s.
10S to 20S	48	0.94	***	0.58	*	0.70	*
20S to 37S	19	-0.41	n.s.	0.78	**	0.63	*

Overall, for the northern latitudes (> 10° N, 32.9 % of all data) propagule fall peaks during the boreal summer and is reduced during the boreal winter (Fig. 2.3 A). For southern latitudes (< 10° S, 39.4 % of all data), the pattern is complementary, with abundant propagule fall in the austral summer (*i.e.* boreal winter) and lower amounts during the austral winter (*i.e.* boreal summer). Close to the equator (10° N to 10° S, 27.6 % of all data), propagule release is reported for the whole year. In the southern hemisphere, the peak in propagule fall shifts with decreasing latitude, with propagules released about a month later in the extreme southern latitudes (20 to 37° S, 11.2 % of all data) compared to lower latitudes (10 to 20° S, 28.2 % of all data). Though less clear, this one-month shift is present as well in the northern latitudes.

For all data, 72 % of the propagules are released during the wet season, 16 % in the dry season, while 12 % show no clear seasonality. Latitudinal propagule release patterns seem to correlate with MAR data (Fig. 2.3 A-B, Table 2.1), with highly significant positive correlations in the northern latitudes and between 10° S and 20° S. In the southernmost latitudes (20° S to 37° S) this correlation is not significant. Positive correlations were found as well between propagule release and MALT and MAHT (Fig. 2.3 C-D, Table 2.1). In the equatorial latitudinal range (10° N to 10° S) the correlation with temperature is not significant. Pearson coefficients are slightly higher for correlation with MALT than compared to MAHT (Table 2.1). Not unexpectedly, a significant correlation was found between the climatological variables MALT and MAHT ($r = 0.72$, $P < 0.000001$), MALT and MAR ($r = 0.64$, $P < 0.000001$), and MAHT and MAR ($r = 0.45$, $P < 0.001$).

Table 2.2: Coefficients and P-values of Pearson correlations between propagule release (% of reports) and monthly averages of the climatological variables rainfall, high temperature and low temperature, for each latitudinal range group. *Avicennia* data. *($P < 0.05$), **($P < 0.01$), ***($P < 0.001$), n.s. (non significant).

Latitudinal range group	n	Monthly average rainfall (mm) (MAR)		Monthly average high T (°C) (MAHT)		Monthly average low T (°C) (MALT)	
		r	P	r	P	r	P
28N to 20N	7	0.84	***	0.63	*	0.73	**
20N to 10N	10	0.64	*	-0.06	n.s.	0.40	n.s.
10N to 10S	15	-0.30	n.s.	0.49	n.s.	0.03	n.s.
10S to 20S	4	0.92	***	0.62	*	0.79	**
20S to 37S	11	0.15	n.s.	0.58	*	0.66	*

Table 2.3: Coefficients and P-values of Pearson correlations between propagule release (% of reports) and monthly averages of the climatological variables rainfall, high temperature and low temperature, for each latitudinal range group. *Rhizophora* data. *($P < 0.05$), **($P < 0.01$), ***($P < 0.001$), n.s. (non significant).

Latitudinal range group	n	Monthly average rainfall (mm) (MAR)		Monthly average high T (°C) (MAHT)		Monthly average low T (°C) (MALT)	
		r	P	r	P	r	P
28N to 20N	6	0.89	***	0.83	***	0.88	***
20N to 10N	11	0.86	***	0.63	*	0.83	***
10N to 10S	14	-0.04	n.s.	0.47	n.s.	0.09	n.s.
10S to 20S	9	0.83	***	0.47	n.s.	0.57	n.s.
20S to 37S	3	0.19	n.s.	0.69	*	0.50	n.s.

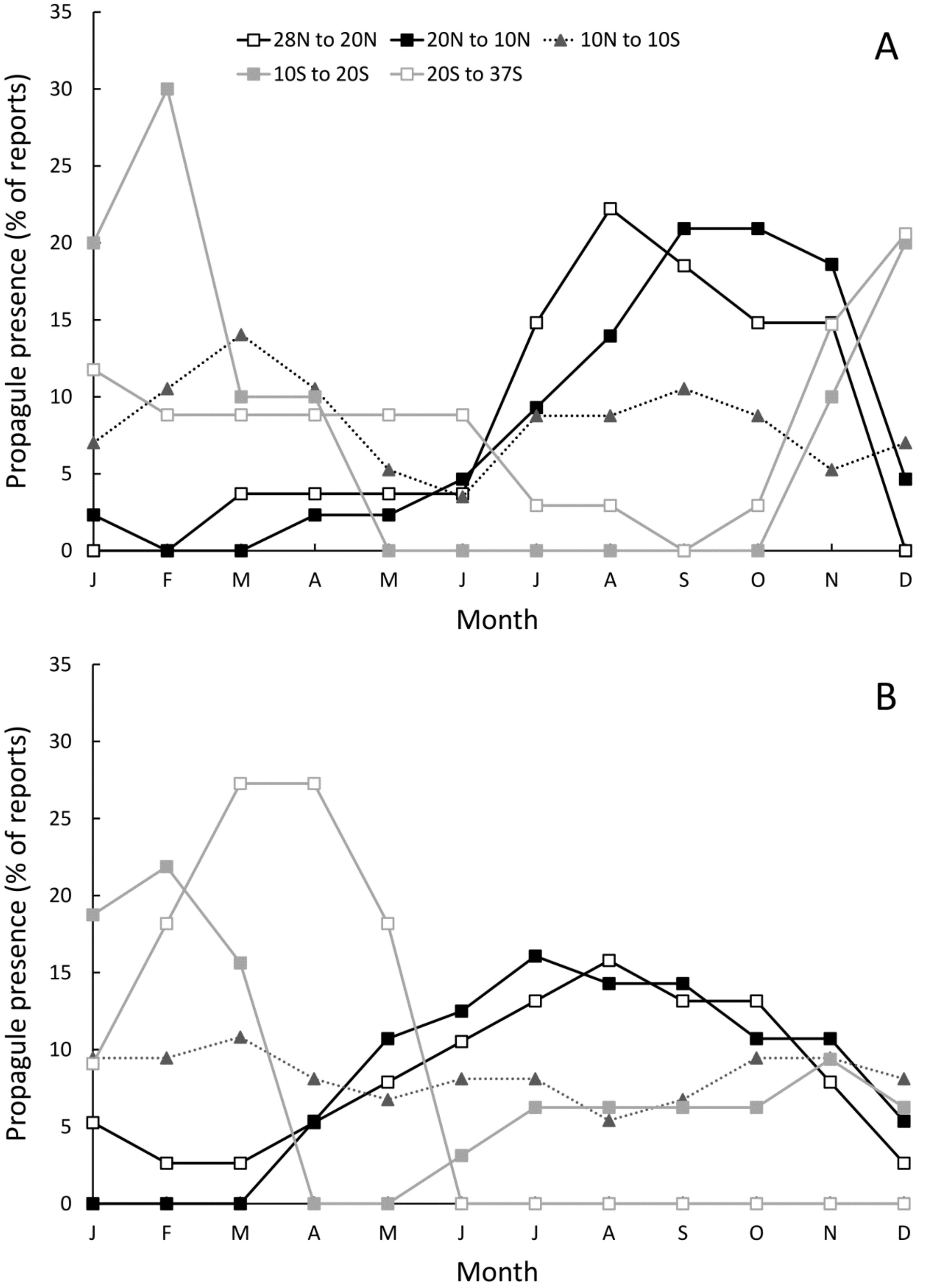

Figure 2.4: Latitudinal pattern in propagule release timing (% of reports) for (A) *Avicennia* and (B) *Rhizophora*.

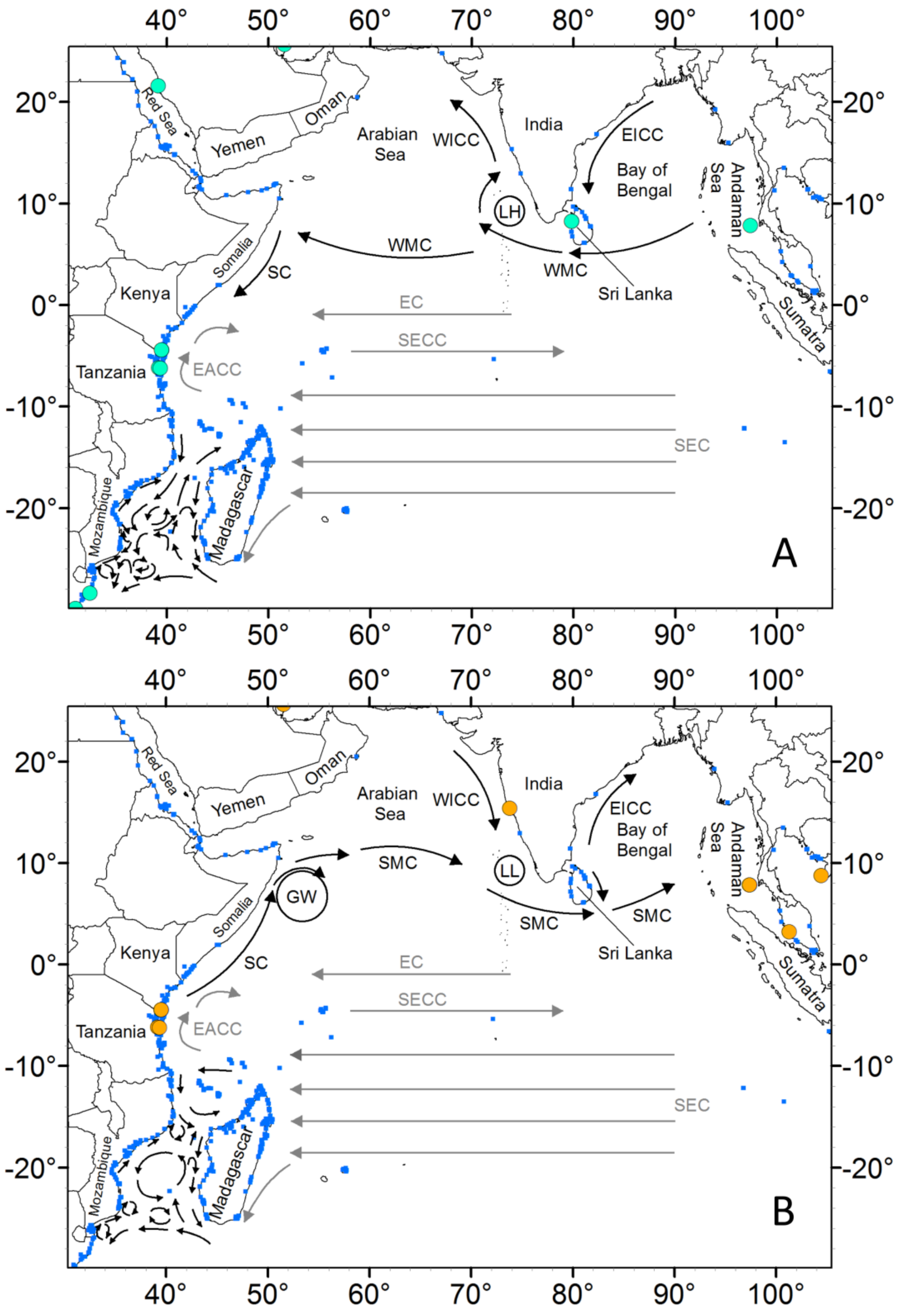

Figure 2.5: Surface currents in the Indian Ocean during (A) the southwest (May-September) and (B) the northeast (November-February) monsoon (modified from Shankar *et al.* 2002, circulation in the Mozambique Channel after Ternon *et al.* 2014), locations where propagule release has been reported during these respective seasons (colored circles), and the distribution of mangroves (blue areas, after the Mangrove Reference Database and Herbarium, Massó i Alemán *et al.* 2010). Seasonally variable currents (black arrows) are distinguished from stable circulation (grey arrows). SC, Somali Current; EC, Equatorial Current; SMC, Summer Monsoon Current; WMC, Winter Monsoon Current; EICC, East India Coastal Current; WICC, West India Coastal Current; SECC, South Equatorial Counter Current; EACC, East African Coastal Current; SEC, South Equatorial Current; LH, Lakshadweep high; LL, Lakshadweep low; and GW, Great Whirl. Map source: ESRI, WorldPlateCarree.mdx (ArcGIS 10).

These latitudinal patterns and correlations with rainfall and temperature also apply as a pattern within and among genera (Fig. 2.4, Tables 2.2 and 2.3). Pearson correlation is significant between propagule release and rainfall for both *Avicennia* (Table 2.2) and *Rhizophora* (Table 2.3), except in the southernmost latitudes where the correlation was found to be significant with temperature. In the equatorial zone (10° N to 10° S) correlations with climatic variables were not significant (Tables 2.2 and 2.3).

The biogeographic distribution of mangroves relative to the ocean surface currents in the Indian Ocean and the geographical locations of the reported propagule release during the winter (northeast monsoon, November-February) and summer (southwest monsoon, May-September) is depicted in Figure 2.5. Clear differences in ocean surface current circulation patterns can be seen between the respective seasons, some currents showing a complete reversal of direction, such as for example the Somali Current (Fig. 2.5). Pronounced changes in current direction can be seen in the waters surrounding India. Also, notice the complex configuration and dynamics of ocean surface currents in the Mozambique Channel (see Ternon *et al.* 2014).

Discussion

The data here encompasses several species and an ample range in longitudinal and latitudinal variation. Not all species have been studied along their biogeographical range, which would be the optimal to study the timing of propagule release. However, the data produced so far do show interesting latitudinal patterns and correlations with climatological variables that may shift under future climate change. Error in observation or reporting is probably limited because of the coverage of data, but new data may further increase validity of patterns. Interpretation is somewhat complicated by the local variation in the distribution ranges of the species due to the extension on the eastern coasts and contraction on the western coasts caused by the shape of the continents and the circulation pattern of sea currents of the world (Quisthoudt 2012). For example, in the Americas, mangrove distribution along the Pacific coasts is less extensive than along the Atlantic coasts.

Latitudinal patterns and correlations with rainfall and temperature

Our data revealed clear latitudinal patterns. While propagules seem to be released throughout the year in the equatorial zone, there is a clear alignment between propagule fall and boreal and austral summers as northern and southern latitudes increase, respectively. This is in accordance with the hypothesis that light and temperature are important seasonal cues for plant growth and development. In mangroves, day length and air temperature have been proposed as cues (Leach and Burgin 1985, Saifullah *et al.* 1989, Duke 1990, Navarrete and Olivia-Rivera 2002). However, it is unclear to what extent these variables dictate the timing of life-history events and how environmental variables may influence phenology altogether. Also, different species may have different responses to changes in the same environmental variable, and spatio-temporal variations in resource availability may result in different timing in phenology (Wilczek *et al.* 2010). This may explain why, in contrast to the findings of Sharma *et al.* (2012), Bernini and Rezende (2010) found no significant correlation between seasonal litter fall and rainfall, mean air temperature or wind speed.

Our database shows that for 72 % of reported data, propagules are released during the wet season. Indications for this correlation can be seen as well in Figures 2.3 A-B and it is supported by significant positive Pearson correlation coefficients (Tables 2.1-2.3). Rainfall has been suggested earlier as a phenological driver in mangroves. Arreola-Lizárraga *et al.* (2004), for example, found that 86 % of the seasonal variability in litterfall was explained by rainfall, sea level and the rainfall/evaporation ratio. It is unclear, however, in which way this environmental factor influences the timing of propagule release. Also in Farascan (Saudi Arabia), propagule release is related to rainfall (pers. comm. Marco Fusi). Pronounced increases in propagule fall have been reported during strong winds and typhoons (Kamruzzaman *et al.* 2013a, 2013b), but since strong rains and high wind speeds often occur together, it is difficult to distinguish the potential effect of these environmental variables and underlying mechanisms. On the other hand, as mangroves thrive in the intertidal zone along tropical and subtropical coasts, rainfall can strongly regulate phenology via changes in substrate salinity. For example, litterfall, productivity and structure of mangrove forests have been linked with ground water salinity (López-Portillo and Ezcurra 1989, Agraz Hernández *et al.* 2011).

Latitudinal propagule release patterns also showed significant positive correlation with MALT and MAHT (Tables 2.1-2.3), which supports earlier findings on interdependence with monthly mean air temperature (Lu and Lin 1990). Interestingly, the correlation with MALT and MAHT becomes more pronounced and significant towards higher northern and southern latitudes, compared to latitudes closer to the equator. This is expected given the increasing seasonality in these climatic variables with increasing latitude. Hence, while propagule release patterns are increasingly linked with MALT and MAHT towards mangrove latitudinal range limits, they seem to be more related to rainfall between 20° N and 20° S. Based on our data, propagule release is more connected to temperature than rainfall in the southernmost latitudes of the mangrove range.

It has been suggested that propagules are released during periods when environmental factors are optimal for the growth and development of seedlings (Duke *et al.* 1984), which may be species- and site-specific. While factors such as rainfall, temperature, wind and soil salinity have received some attention separately, it is most likely that phenological patterns are regulated by two or more factors. By using principal component analysis, for example, López Portillo and Ezcurra (1985) found that water level, evaporation, temperature and insolation were highly intercorrelated, and synthesized it in a principal component axis accounting for 82 % of environmental variability. This axis was directly correlated with leaf fall and inversely correlated with propagule fall. However, there was no correlation between litterfall and local rainfall, suggesting that continental runoff is more important than local rainfall.

While large-scale studies found no clear latitudinal patterns in propagule release and correlations with climatic factors (Duke 1990), our results demonstrate strong interconnectedness with latitude, rainfall and temperature. Although, phenological patterns are likely to be also controlled by factors other than the major climatic variables which we have considered, our findings suggests that important phenological processes in mangroves are driven by climatic conditions. Current data hampers the examination of (synergetic) effects of these and other environmental cues on propagule release. Hence, it remains to be seen which other factors are at play as more species and sites are studied, registering propagule fall from the beginning to the end.

Climate change and implications for dispersal

Over the last decades, long distance dispersal (LDD) has received major attention as a mechanism for the survival of plant populations under changing climatic and environmental conditions (Higgins and Richardson 1999, Johst *et al.* 2002, Corlett and Westcott 2013). In mangroves, understanding the mechanisms of dispersal and predicting dispersal patterns is important given the increasing fragmentation and encroachment by non mangrove landcover (Fahrig 2003, Duke *et al.* 2007) which threaten the biodiversity mangroves sustain. Obtaining data on dispersal patterns and connectivity is an important challenge in LDD research (Nathan 2001) that can be partly tackled by combining genetic and modeling studies that could yield reliable estimations of actual patterns and to predict the potential impact of future scenarios. Species-specific characteristics such as propagule size, density, buoyancy, morphology, and longevity have been provided by various authors (Clarke and Myerscough 1991, Tomlinson 1994, Clarke *et al.* 2001, Drexler 2001, Allen and Krauss 2006), and studies on dispersal vectors and establishment processes have also been carried out (Balke *et al.* 2011, Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b). Nevertheless, an important variable in great need is the timing of propagule release.

For aerial dispersal of spores, it was shown recently that small changes in the timing of their release can significantly influence the area of deposition and thus the probability of establishment and survival (Savage *et al.* 2010, Savage *et al.* 2012). In mangroves, the interaction between the timing of propagule release and the changes in the direction and strength of key dispersal vectors define the traveling course of the propagule, and are thus essential to predict propagule deposition patterns. Wind strength and direction vary on short time scales, and, depending on the propagule morphology and floating orientation, determine the fate of a propagule (Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b). Flood and ebb currents alternate on a daily basis with monthly changes in tidal amplitude. At high tide, propagules will migrate away from the source while at low tide they may accumulate in the locality, thus increasing the possibility of establishment (Van der Stocken *et al.* 2015a). Finally, seasonal variation in ocean currents (Ffield *et al.* 1997, Sengupta *et al.* 2005), such as the alignment with seasonal monsoons (Shankar *et al.* 2002, Heron *et al.* 2006) may also condition the sites of propagule arrival.

Additionally, our findings suggests that the effect on phenological shifts of altered rainfall patterns under climate change (Thornton *et al.* 2014) may have more impact on forest structure than previously thought. This is especially important given the shifts in the seasonal magnitude, timing and duration of tropical rainfall under global climate change (Feng *et al.* 2013) and projected changes in climatic events such as monsoons, due to perturbations in the radiative budget (Collins *et al.* 2013). Changes in rainfall and temperature patterns may shift the timing of mangrove propagule release, while changes in monsoonal variation also control ocean surface circulation (Fig. 2.5). Shift in the timing of phenological events relative to changes in the strength and direction of dispersal vectors could strongly affect propagule dispersal and deposition patterns with consequences for long-term population dynamics and biogeographical signals. Hence, we stress the need for more data to investigate the causal nature of these environmental variables for phenological processes in different species and localities.

Conclusion

Our results show clear latitudinal patterns in propagule release timing and strong positive correlations with rainfall and temperature. This suggests that phenological shifts under changing climatic conditions, relative to temporal changes in dispersal vector properties may influence propagule dispersal and deposition patterns with consequences for long-term population dynamics and biogeographical ranges. However, more data is needed to better understand the multiplicity of putative environmental drivers that control plant phenology and the time scales (*i.e.* circadian, seasonal) on which they operate. Moreover, it will enable the construction of mixed models including multiple drivers which may best account for the observed phenological patterns, and reliable predictions in response to climate change (Wolkovich *et al.* 2014). Since phenology can be species- and site-specific (Wium-Andersen 1981, Sasekumar and Loi 1983, Amarasinghe and Balasubramaniam 1992), possibly the best way is to gather long-term global information through global monitoring programs in which local communities are engaged and trained by mangrove scientists that collect data regularly and share it in a global database that can be used by scientists and educators, similar to

Project BudBurst. Additionally, a global dataset of long-term phenological events would aid in assessing species abilities to shift with climate change (Cleland *et al.* 2012).

Acknowledgements

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Table 2.4: Reported information on mangrove and mangrove-associate propagule release or mature propagule presence. Mangrove and mangrove-associate species names were copied as published in the respective references, whereas families are indicated with respect to APGIII (APGIII 2009,Chase and Reveal 2009). Longitude and latitude are given in decimal degrees.

Species	**Family**	**Propagule fall period**	**Study Area**	**Latitude (°)**	**Longitude (°)**	**Reference**
Acanthus ilicifolius L.	Acanthaceae	Jan.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Aegialitis annulata R. Br.	Plumbaginaceae	Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Aegiceras corniculatum (L.) Blanco	Primulaceae	Jan.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Avicennia alba Blume	Acanthaceae	Jul.-Nov.	South Banjar Forest Reserve, Kuala Selangor, Malay Peninsula	3.25	101.30	Sasekumar and Loi (1983)
Avicennia bicolor Standl.	Acanthaceae	Jul.-Oct.	Isthmus of Panama	8.67	-80.00	Rabinowitz (1978a)
Avicennia germinans (L.) Staern	Acanthaceae	Jul.-Nov.	Cannon Island, Florida	25.96	-81.71	Peterson and Bell (2012)
Avicennia germinans (L.) Staern	Acanthaceae	Jul.-Nov.	Pueblo Viejo, Tamiahua mudflat basin, Mexico	22.09	-97.86	López Portillo and Lara Domínguez (unpubl. data)
Avicennia germinans (L.) Staern	Acanthaceae	Aug.-Nov.	Tuxpan mudflat basin, Mexico	20.92	-97.32	López Portillo and Lara Domínguez (unpubl. data)
Avicennia germinans (L.) Staern	Acanthaceae	Aug.-Nov.	Tecolutla, Nautla mudflat basin, Mexico	20.33	-96.90	López Portillo and Lara Domínguez (unpubl. data)
Avicennia germinans (L.) Staern	Acanthaceae	Jul.-Oct.	El Llano, La Mancha mudflat basin, Mexico	19.57	-96.39	López Portillo and Lara Domínguez (unpubl. data)

Avicennia germinans (L.) Staern	Acanthaceae	Aug.-Nov.	Mandinga mudflat basin, Mexico	19.05	-96.08	López Portillo and Lara Domínguez (unpubl. data)
Avicennia germinans (L.) Staern	Acanthaceae	Aug.-Nov.	Alvarado mudflat basin, Mexico	18.76	-95.78	López Portillo and Lara Domínguez (unpubl. data)
Avicennia germinans (L.) Staern	Acanthaceae	Sep.-Nov.	Sontecomapan mudflat basin, Mexico	18.54	-95.03	López Portillo and Lara Domínguez (unpubl. data)
Avicennia germinans (L.) Staern	Acanthaceae	Aug.-Nov.	Ostión mudflat basin, Mexico	18.18	-94.64	López Portillo and Lara Domínguez (unpubl. data)
Avicennia germinans (L.) Staern	Acanthaceae	Aug.-Oct.	Isthmus of Panama	8.67	-80.00	Rabinowitz (1978a)
Avicennia germinans (L.) Staern	Acanthaceae	Jul.-Aug.	Las Guásimas, eaStaern coast of the Gulf of California, Mexico	27.87	-110.70	Arreola-Lizárraga *et al.* (2004)
Avicennia germinans (L.) Staern	Acanthaceae	Jul.-Nov.	Boca Chica, Lagina de Términos, Yucatan, Mexico	18.47	-91.78	Day *et al.* (1987)
Avicennia germinans (L.) Staern	Acanthaceae	Apr.-Nov.	Estero Pargo, Lagina de Términos, Yucatan, Mexico	18.47	-91.78	Day *et al.* (1987)
Avicennia germinans (L.) Staern	Acanthaceae	Sep.-Jan.	Laguna de Mecoacán, Tabasco, Mexico	18.42	-93.17	López-Portillo and Ezcurra (1985)
Avicennia germinans (L.) Staern	Acanthaceae	Sep.-Dec.	Chengue Bay, Tayrona Natural Park, Colombia	11.33	-74.13	Rodriguez-Ramirez *et al.* (2004)
Avicennia germinans (L.) Staern	Acanthaceae	Nov.-Apr.	Onverwagt, Guyana	6.45	-57.63	Chale (1996)
Avicennia germinans (L.) Staern	Acanthaceae	Mar. Apr.	Bragança, Pará, North Brazil	-0.84	-46.64	Mehlig (2001), Carvalho (2002); Santos (2005), Table 3 in: Menezes *et al.* (2008)

Avicennia germinans (L.) Staern	Acanthaceae	Oct.-Dec.	do Paraíba do Sul River, SoutheaStaern Brazil	-21.60	-41.05	Bernini and Rezende (2010)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	May-Sep.	Al-Khor mangrove lagoon on the eaStaern coast of Qatar, Arabian Gulf	25.67	51.58	Hegazy (1998)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Mar.-Apr.	Ras Hatiba, Saudi Arabian Red Sea coast	21.60	39.15	Saifullah *et al.* (1989)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Jul.-Oct.	Erumathivu, Sri Lanka	8.25	79.83	Amarasinghe and Balasubramaniam (1992)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Oct.-Feb.	Kala Oya, Sri Lanka	8.25	79.83	Amarasinghe and Balasubramaniam (1992)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Jul.-Sep.	Phuket Island, Thailand	7.85	97.42	Wium-Andersen and Christensen (1978)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Mar.-May	Gazi Bay, Kenya	-4.42	39.50	Wang'ondu *et al.* (2010)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Apr.-Jun.	Gazi Bay, Kenya	-4.42	39.50	Ochieng and Erftemeijer (2002)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Feb. Mar.	Chwaka Bay, Unguja Island, Zanzibar	-6.17	39.20	Shunula and Whittick (1999)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Mar.-May	Maruhubi, Unguja Island, Zanzibar	-6.20	39.37	Shunula and Whittick (1999)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Feb.-Mar.	Port Moresby, Papua New Guinea	-9.53	147.28	Duke (1990)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Nov.-Feb.	Darwin Bay, northern Australia	-12.43	130.87	Woodroffe *et al.* (1988)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Dec.-Jan.	Darwin Harbour, northern Australia	-12.43	130.85	Coupland *et al.* (2005)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Feb.-Apr.	Cairns, Queensland	-16.95	145.78	Duke (1990)

Avicennia marina (Forssk.) Vierh.	Acanthaceae	Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	May-Jun.	Carnarvon, weStaern Australia	-24.47	113.68	Duke (1990)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	May-Aug.	Brisbane River, Queensland, Australia	-27.40	158.14	Mackey and Smail (1995)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Mar.-Jun.	St. Lucia estuary, South Africa	-28.37	32.42	Steinke and Ward (1988)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Mar.-Apr.	Mgeni River estuary, Durban, South Africa	-29.88	31.00	Naidoo (1989)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Nov.-Feb.	Adelaide, South Australia	-34.70	138.47	Duke (1990)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Nov.-Dec.	central and south coast of New South Wales, Sydney region, Australia	-35.00	150.78	Clarke and Myerscough (1991)
Avicennia marina (Forssk.) Vierh.	Acanthaceae	Nov.-Dec.	central and south coast of New South Wales, Jervis Bay, Australia	-35.03	149.67	Clarke and Myerscough (1991)
Avicennia marina (Forssk.) Vierh. var. *australasica* (Walp.) Moldenke	Acanthaceae	Dec.-Jan.	Rangaunu Harbour, New Zealand	-34.95	173.25	May (1999)
Avicennia marina (Forssk.) Vierh. var. *resinifera* (Forst.) Bakh (low mangroves)	Acanthaceae	Nov.-Apr.	Tuff Crater, Shoal Bay, Waitemata Harbour, Auckland, New Zealand	-36.80	174.75	Woodroffe (1982)
Avicennia marina (Forssk.) Vierh. var. *resinifera* (Forst.) Bakh (tall mangroves)	Acanthaceae	Dec.-Feb.	Tuff Crater, Shoal Bay, Waitemata Harbour, Auckland, New Zealand	-36.80	174.75	Woodroffe (1982)
Avicennia officinalis L.	Acanthaceae	Jun.-Jul.	Mandovi-Zuari Estuaries, Central West Coast of India	15.44	73.80	Wafar *et al.* (1997)

Avicennia schaueriana Stapf and Leechman	Acanthaceae	Dec.-Mar.	Pernambuco, north-east Brazil	-7.66	-34.84	Nadia *et al.* (2012)
Avicennia schaueriana Stapf and Leechman ex Moldenke	Acanthaceae	Jun.-Jul. and Sep. and Dec.-Apr.	Bragança, Pará, north Brazil	-0.84	-46.64	MPEG Herbarium, Santos (2005), Table 3 in: Menezes *et al.* (2008)
Barringtonia racemosa (L.) Spreng.	Lecythidaceae	Dec.-Apr.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Bruguiera cylindrica (L.) Bl.	Rhizophoraceae	Oct.-Jun.	Phuket Island, Thailand	7.85	97.42	Wium-Andersen and Christensen (1978)
Bruguiera cylindrica (L.) Bl.	Rhizophoraceae	Nov.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Bruguiera exaristata Ding Hou	Rhizophoraceae	Jan.-Feb.	Darwin Bay, northern Australia	-12.43	130.87	Woodroffe *et al.* (1988)
Bruguiera exaristata Ding Hou	Rhizophoraceae	Feb.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Jul.	Ohura Bay, Okinawa, Japan	26.52	128.08	Hardiwinoto *et al.* (1989)
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Oct.-May	Okinawa, Japan	26.52	128.08	Nakasuga and Itoo (1983), in: Hardiwinoto *et al.* (1989)
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Apr.-Aug.	Okinawa Island, Japan	26.18	127.67	Kamruzzaman *et al.* (2013b)
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Jun.-Sep.	Chwaka Bay, Unguja Island, Zanzibar	-6.17	39.20	Shunula and Whittick (1999)
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Jun.-Nov.	Maruhubi, Unguja Island, Zanzibar	-6.20	39.37	Shunula and Whittick (1999)
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Jan.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Feb.-Jun.	St. Lucia estuary, South Africa	-28.37	32.42	Steinke and Ward (1988)

Bruguiera gymnorrhiza (L.) Lam.	Rhizophoraceae	Feb.-Apr.	Mgeni River estuary, Durban, South Africa	-29.88	31.00	Naidoo (1989)
Bruguiera parviflora (Roxb.) Wight and Arn. Ex Griff.	Rhizophoraceae	Jan.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Bruguiera sexangula (Lour.) Poir.	Rhizophoraceae	Sep.	Changning River, Hainan Island, China	19.85	110.40	Lu and Lin (1990)
Bruguiera sexangula (Lour.) Poir.	Rhizophoraceae	Sep.	He-Gang, Hainan Island, China	19.85	110.40	Lu and Lin (1990)
Bruguiera sexangula (Lour.) Poir.	Rhizophoraceae	Aug.-Sep.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Camptostemom schultzii Mast.	Malvaceae	Mar.-Apr.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Ceriops australis (C.T. White)	Rhizophoraceae	Oct.-Nov.	Darwin Harbour, northern Australia	-12.43	130.85	Coupland *et al.* (2005)
Ceriops decandra (Roxb.) Ding Hou	Rhizophoraceae	Dec.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Ceriops tagal (Perr.) C. B. Rob.	Rhizophoraceae	Mar.-Jun.	Chwaka Bay, Unguja Island, Zanzibar	-6.17	39.20	Shunula and Whittick (1999)
Ceriops tagal (Perr.) C. B. Rob.	Rhizophoraceae	Jan.-Feb. and Jul.-Sep.	Maruhubi, Unguja Island, Zanzibar	-6.20	39.37	Shunula and Whittick (1999)
Ceriops tagal (Perr.) C. B. Rob.	Rhizophoraceae	Oct.-Feb.	Darwin Bay, northern Australia	-12.43	130.87	Wium-Andersen and Christensen (1978)
Ceriops tagal (Perr.) C. B. Rob.	Rhizophoraceae	Jan.	Phuket Island, Thailand	7.85	97.42	Woodroffe *et al.* (1988)
Ceriops tagal (Perr.) C. B. Rob.	Rhizophoraceae	Mar.	South Africa	-29.88	31.00	T. D. Steinke, pers. comm. (in Duke *et al.*, 1984)
Ceriops tagal (Perr.) C. B. Rob.	Rhizophoraceae	Mar.-May	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Ceriops tagal var. *australis* C. T. White	Rhizophoraceae	Oct.-Jan.	Darwin Bay, northern Australia	-12.43	130.87	Woodroffe *et al.* (1988)

Ceriops tagal var. a*ustralis* C. T. White	Rhizophoraceae	Dec.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Conocarpus erectus L.	Combretaceae	May-Aug.	Barra de Tecoanapa, Guerrero, Mexico	16.50	-98.75	Tovilla and de la Lanza (1999)
Conocarpus erectus L.	Combretaceae	Jan.-Dec.	Pernambuco, north-east Brazil	-7.66	-34.84	Nadia *et al.* (2012)
Cynometra iripa Kostel	Fabaceae	Dec.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Diospyros ferrea var. *geminata* (R. Br.) Bakh.	Ebenaceae	Sep.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Dolichandrone spathacea (L.f.) K. Sch.	Bignoniaceae	Nov.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Excoecaria agallocha L.	Euphorbiaceae	Jan.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Heritiera littoralis Ait.	Malvaceae	Sep.-Dec.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Kandelia candel L.	Rhizophoraceae	Apr.-May	Ohura Bay, Okinawa, Japan	26.52	128.08	Hardiwinoto *et al.* (1989)
Kandelia candel L.	Rhizophoraceae	Apr.-May	Okinawa, Japan	26.52	128.08	Hardiwinoto (1988), in: Hardiwinoto *et al.* (1989)
Kandelia candel L.	Rhizophoraceae	Mar.-May	Okinawa, Japan	26.52	128.08	Nakasuga and Itoo (1983), in: Hardiwinoto *et al.* (1989)
Kandelia candel L.	Rhizophoraceae	Mar.-May and Jul.-Sep.	Mai Po Marshes fringing Deep Bay, northwest Hong Kong	22.52	114.08	Lee (1989)
Kandelia obovata (L.) Druce	Rhizophoraceae	Apr.-May	Manko Wetland,southern part of Okinawa Island, Japan	26.18	127.67	Sharma *et al.* (2012)

Kandelia obovata (S., L.)	Rhizophoraceae	Mar.-May	Okinawa Island, Japan	26.18	127.67	Kamruzzaman *et al.* (2013a)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Jun.-Sep.	Pueblo Viejo, Tamiahua mudflat basin, Mexico	22.09	-97.86	López Portillo and Lara Domínguez (unpubl. data)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Jun.-Nov.	Tecolutla, Nautla mudflat basin, Mexico	20.33	-96.90	López Portillo and Lara Domínguez (unpubl. data)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Jul.-Oct.	Mandinga mudflat basin, Mexico	19.05	-96.08	López Portillo and Lara Domínguez (unpubl. data)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Aug.-Nov.	Alvarado mudflat basin, Mexico	18.76	-95.78	López Portillo and Lara Domínguez (unpubl. data)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Jul.-Nov.	Sontecomapan mudflat basin, Mexico	18.54	-95.03	López Portillo and Lara Domínguez (unpubl. data)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Jul.-Nov.	Boca Chica, Lagina de Términos, Yucatan, Mexico	18.47	-91.78	Day *et al.* (1987)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Apr.-Nov.	Estero Pargo, Lagina de Términos, Yucatan, Mexico	18.47	-91.78	Day *et al.* (1987)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Jul.-Nov.	Ostión mudflat basin, Mexico	18.18	-94.64	López Portillo and Lara Domínguez (unpubl. data)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Aug.-Nov.	Isthmus of Panama	8.67	-80.00	Rabinowitz (1978a)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	May-Aug.	Pernambuco, north-east Brazil	-7.66	-34.84	Nadia *et al.* (2012)
Laguncularia racemosa (L.) C. F. Gaertn. f.	Combretaceae	Feb.-Apr.	do Paraíba do Sul River, southeaStaern Brazil	-21.60	-41.05	Bernini and Rezende (2010)
Lumnitzera littorea (Jack) Voight.	Combretaceae	Feb.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)

Lumnitzera littorea (Jacq.)	Combretaceae	Nov.-Apr.	Phuket Island, Thailand	7.85	97.42	Wium-Andersen and Christensen (1978)
Lumnitzera racemosa (L.) C. F. Gaertn. f.	Combretaceae	Mar.-Apr.	South Africa	-29.88	31.00	T. D. Steinke, pers. comm. (in Duke *et al.*, 1984)
Lumnitzera racemosa (L.) C. F. Gaertn. f.	Combretaceae	Jan.-May	Bragança, Pará, north Brazil	-0.84	-46.64	Mehlig (2001), Silva (2005), Table 3 in: Menezes *et al.* (2008)
Lumnitzera racemosa Willd.	Combretaceae	Feb.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Nypa fruticans Wurumb.	Arecaceae	Feb.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Osbornia octodonta F. Muell.	Myrtaceae	Feb.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Pelliciera rhizophorae Triana and Planch.	Pellicieraceae	Jul.-Sep.	Isthmus of Panama	8.67	-80.00	Rabinowitz (1978a)
Pemphis acidula J. R. and G. Forst	Lythraceae	Dec.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Rhizophora × lamarckii Montr.	Rhizophoraceae	Jan.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Rhizophora × lamarckii Montr.	Rhizophoraceae	Jul.-Nov.	Missionary Bay, Hinchinbrook Island, northeaStaern Australia	-18.27	146.24	Williams *et al.* (1981)
Rhizophora apiculata Bl.	Rhizophoraceae	Apr.-Jun.	Mandovi-Zuari Estuaries, Central West Coast of India	15.44	73.80	Wafar *et al.* (1997)
Rhizophora apiculata Bl.	Rhizophoraceae	May-Nov.	Mekong Delta, Ca Mau Province, southern Vietnam	8.78	104.45	Clough *et al.* (2000)
Rhizophora apiculata Bl.	Rhizophoraceae	Jun.-Jul.	Phuket Island, Thailand	7.85	97.42	Christensen and Wium-Andersen (1977)

Rhizophora apiculata Bl.	Rhizophoraceae	Apr.-Jul.	Tura Island, Trang Province, southern Thailand	7.36	99.51	Bunyavejchewin and Nuyim (1998)
Rhizophora apiculata Bl.	Rhizophoraceae	Nov.-Mar.	Missionary Bay, Hinchinbrook Island, north-eaStaern Australia	-18.27	146.24	Williams *et al.* (1981)
Rhizophora apiculata Bl.	Rhizophoraceae	Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Rhizophora apiculata or R. mucronata	Rhizophoraceae	Jan.-Dec.	South Banjar Forest Reserve, Kuala Selangor, Malay Peninsula	3.25	101.30	Sasekumar and Loi (1983)
Rhizophora harrisonii Leechman	Rhizophoraceae	Jan.-Dec.	Isthmus of Panama	8.67	-80.00	Rabinowitz (1978a)
Rhizophora mangle L.	Rhizophoraceae	Aug.-Oct.	Fairchild Tropical Garden, Miami, Florida	25.46	-80.22	Gill and Tomlinson (1971)
Rhizophora mangle L.	Rhizophoraceae	Apr.-Oct.	Pueblo Viejo, Tamiahua fringe, Mexico	22.09	-97.86	López Portillo and Lara Domínguez (unpubl. data)
Rhizophora mangle L.	Rhizophoraceae	Jun.-Nov.	Oahu Island, Hawaii	21.43	-157.77	Cox and Allen (1999)
Rhizophora mangle L.	Rhizophoraceae	Jan.-Dec.	Tuxpan fringe, Mexico	20.92	-97.32	López Portillo and Lara Domínguez (unpubl. data)
Rhizophora mangle L.	Rhizophoraceae	Jan. and Jul.-Nov.	Tecolutla, Nautla fringe, Mexico	20.33	-96.90	López Portillo and Lara Domínguez (unpubl. data)
Rhizophora mangle L.	Rhizophoraceae	Jul.-Sep.	El Llano, La Mancha fringe, Mexico	19.57	-96.39	López Portillo and Lara Domínguez (unpubl. data)
Rhizophora mangle L.	Rhizophoraceae	May-Nov.	Mandinga fringe, Mexico	19.05	-96.08	López Portillo and Lara Domínguez (unpubl. data)
Rhizophora mangle L.	Rhizophoraceae	Jun.-Dec.	Alvarado fringe, Mexico	18.76	-95.78	López Portillo and Lara Domínguez (unpubl. data)

Rhizophora mangle L.	Rhizophoraceae	May-Dec.	Sontecomapan fringe, Mexico	18.54	-95.03	López Portillo and Lara Domínguez (unpubl. data)
Rhizophora mangle L.	Rhizophoraceae	Jul.-Nov.	Boca Chica, Lagina de Términos, Yucatan, Mexico	18.47	-91.78	Day *et al.* (1987)
Rhizophora mangle L.	Rhizophoraceae	Apr.-Nov.	Estero Pargo, Lagina de Términos, Yucatan, Mexico	18.47	-91.78	Day *et al.* (1987)
Rhizophora mangle L.	Rhizophoraceae	Jul.-Sep.	Quintana Roo, Mexico	18.20	-87.85	Navarette and Oliva-Rivera (2002)
Rhizophora mangle L.	Rhizophoraceae	Jul.-Dec.	Ostión fringe, Mexico	18.18	-94.64	López Portillo and Lara Domínguez (unpubl. data)
Rhizophora mangle L.	Rhizophoraceae	May-Jul.	Bon Accord Lagoon, southwest Tobago	11.17	-60.76	Juman (2005)
Rhizophora mangle L.	Rhizophoraceae	Jan.-Dec.	Isthmus of Panama	8.67	-80.00	Rabinowitz (1978a)
Rhizophora mangle L.	Rhizophoraceae	Jan.-Apr.	Caeté river, Bragança district, Pará, Brazil	-0.84	-46.64	Menezes (1997); Mehlig (2001); Carvalho (2002); Mehlig (2006); Table 3 in: Menezes *et al.* (2008)
Rhizophora mangle L.	Rhizophoraceae	Oct.-Mar.	Pernambuco, north-east Brazil	-7.66	-34.84	Nadia *et al.* (2012)
Rhizophora mangle L.	Rhizophoraceae	Jan.-May	do Paraíba do Sul River, southeaStaern Brazil	-21.60	-41.05	Bernini and Rezende (2010)
Rhizophora mucronata Lam.	Rhizophoraceae	Apr.-Jun.	Mandovi-Zuari Estuaries, Central West Coast of India	15.44	73.80	Wafar *et al.* (1997)
Rhizophora mucronata Lam.	Rhizophoraceae	Aug.-Nov.	Erumathivu, Sri Lanka	8.25	79.83	Amarasinghe and Balasubramaniam (1992)

Rhizophora mucronata Lam.	Rhizophoraceae	Oct.-Dec.	Kala Oya, Sri Lanka	8.25	79.83	Amarasinghe and Balasubramaniam (1992)
Rhizophora mucronata Lam.	Rhizophoraceae	Jun.-Jul.	Ao Nam Bor mangrove forest, Phuket Island, Thailand	7.85	97.42	Wium-Andersen (1981)
Rhizophora mucronata Lam.	Rhizophoraceae	Nov.-May	Gazi Bay, Kenya	-4.42	39.50	Wang’ondu *et al.* (2013)
Rhizophora mucronata Lam.	Rhizophoraceae	Jan.-Mar.	Chwaka Bay, Unguja Island, Zanzibar	-6.17	39.20	Shunula and Whittick (1999)
Rhizophora mucronata Lam.	Rhizophoraceae	Jan.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Rhizophora mucronata Lam.	Rhizophoraceae	Mar.-May	Richards Bay, South Africa	-28.83	32.03	Steinke and Ward (1988)
Rhizophora mucronata Lam.	Rhizophoraceae	Feb.-Apr.	Mgeni River estuary, Durban, South Africa	-29.88	31.00	Naidoo (1989)
Rhizophora racemosa G.F.W. Meyer	Rhizophoraceae	Mar.-Apr. and Sep.-Oct. and Dec.	Bragança, Pará, north Brazil	-0.84	-46.64	MPEG Herbarium, Table 3 in: Menezes *et al.* (2008)
Rhizophora stylosa Griff.	Rhizophoraceae	May-Aug.	Manko Wetland, Okinawa Island, Japan	26.18	127.67	Sharma *et al.*(2011)
Rhizophora stylosa Griff.	Rhizophoraceae	Dec.-Mar.	Darwin Bay, northern Australia	-12.43	130.87	Woodroffe and Moss (1984)
Rhizophora stylosa Griff.	Rhizophoraceae	Jun.-Nov.	Darwin Harbour, northern Australia	-12.43	130.85	Coupland *et al.* (2005)
Rhizophora stylosa Griff.	Rhizophoraceae	Jan.-Mar.	Missionary Bay, Hinchinbrook Island, north-eaStaern Australia	-18.27	146.24	Williams *et al.* (1981)
Rhizophora stylosa Griff.	Rhizophoraceae	Jan.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)

Rhizophora stylosa Griff. (*no mature propagules collected)	Rhizophoraceae	Jan.-Mar.	Vaitupu, Tuvalu	-7.47	178.70	Woodroffe *et al.* (1988)
Scyphiphora hydrophyllacea Gaertn. f.	Rubiaceae	May-Jul.	Ao Nam Bor mangrove forest, Phuket Island, Thailand	7.85	97.42	Wium-Andersen (1981)
Scyphiphora hydrophyllacea Gaertn. f.	Rubiaceae	Feb.-Mar.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Sonneratia alba J. Smith	Lythraceae	May.-Jun. and Sep.-Oct.	Mandovi-Zuari Estuaries, Central West Coast of India	15.44	73.80	Wafar *et al.* (1997)
Sonneratia alba J. Smith	Lythraceae	Feb.-Mar.	South Banjar Forest Reserve, Kuala Selangor, Malay Peninsula	3.25	101.30	Sasekumar and Loi (1983)
Sonneratia alba J. Smith	Lythraceae	Jun.-Sep.	Gazi Bay, Kenya	-4.42	39.50	Wang'ondu *et al.* (2013)
Sonneratia alba J. Smith	Lythraceae	Jan. and Jul.-Oct.	Chwaka Bay, Unguja Island, Zanzibar	-6.17	39.20	Shunula and Whittick (1999)
Sonneratia alba J. Smith	Lythraceae	Nov.-Jan. and Jun.-Aug.	Maruhubi, Unguja Island, Zanzibar	-6.20	39.37	Shunula and Whittick (1999)
Sonneratia alba J. Smith	Lythraceae	Jul.-Sep.	Darwin Harbour, northern Australia	-12.43	130.85	Coupland *et al.* (2005)
Sonneratia alba J. Smith	Lythraceae	Jan.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Sonneratia caseolaris (L.) Engl.	Lythraceae	Jul.-Oct.	Shenzhen City, Guangdong Province, China	22.55	114.10	Tam (2007), in Chen *et al.* (2009)
Sonneratia caseolaris (L.) Engl.	Lythraceae	Jun.-Jul.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Sonneratia caseolaris (L.) Engl.	Lythraceae	Dec.	NE Australia	-18.27	146.22	Duke *et al.* (1984)

Sonneratia caseolaris (L.) Engl.	Lythraceae	Mar. and Aug.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Xylocarpus australasicus Ridl.	Meliaceae	Dec.-Feb.	NE Australia	-18.27	146.22	Duke *et al.* (1984)
Xylocarpus granatum Koenig.	Meliaceae	Jun.-Sep.	NE Australia	-18.27	146.22	Duke *et al.* (1984)

CHAPTER 3

IMPACT OF LANDSCAPE STRUCTURE ON PROPAGULE DISPERSAL IN MANGROVE FORESTS

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Abstract

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

Introduction

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

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

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

Material and methods

Flume experiment

Retention rates and dispersal characteristics of propagules in a mangrove forest environment were studied in a flume facility for a variety of barrier densities and hydrodynamic conditions. The racetrack flume at the Royal Netherlands Institute for Sea Research (see Bouma *et al.* 2005 for a detailed description) was adjusted with a wooden frame (6 m long, 0.6 m wide and 0.3 m high), of which the bottom and top were covered with poultry netting through which bamboo sticks were inserted to mimic tree stems and vertical stilt roots (Fig. 3.1). The 2 layers of poultry netting ensured that bamboo sticks were kept in place against the force of the water current. Bamboo sticks (0.04 and 0.06 m diameter) were more or less regularly interspersed over the whole length of the construction, mimicking 3 different root or stem densities (10, 20 and 30 roots[1] m^{-2}). Dispersal behaviour was studied for propagules of 4 species: *Rhizophora mucronata*, *Ceriops tagal*, *Heritiera littoralis* and *Xylocarpus granatum* (Fig. 3.2). In general, propagules of the first 2 species float horizontally after release from the parent tree and progressively change to a vertical position as the density distribution of their tissue changes (Davis 1940, Rabinowitz 1978a). Hence, for these species, both horizontally and vertically floating propagules were used. For *X. granatum*, only one fruit (containing 8 seeds) was available. We therefore opted to use the seeds, allowing us to have more replications and to have 2 distinct morphological groups: elongated propagules for *C. tagal* and *R. mucronata*, and the more compact propagules of *H. littoralis* (ellipsoidal, with a dorsal sail) and *X. granatum* seeds (angular, pyramidal). All propagules were sampled in Gazi Bay, Kenya (39° 30' E, 04° 25' S) on 28 March 2012. We considered the propagules mature when they readily fell when slightly touched. For *H. littoralis*, propagules were collected at neap tide under a parent tree in the high intertidal area. We checked all propagules for damage, which may alter their buoyancy over the course of the experiment. Root densities of 10 and 30 roots m^{-2} were combined with a water flow velocity of 0.1 m s^{-1} and the 20 roots m^{-2} density with 3 water flow velocities (0.05, 0.10 and 0.15 m s^{-1}). Water flow velocities were chosen based on the

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[1] throughout the text, 'roots m^{-1}' is also used for 'root or stem mimic density' in the flume

range of water flow conditions in a natural mangrove habitat (Kitheka 1996, 1997). This experimental setup allowed us to study both the effect of various water flow velocities at the same root density, and the effect of different root densities at a constant water flow velocity.

Figure 3.1: Mimicked mangrove roots used in our flume experiments. Bamboo sticks (0.04 and 0.06 m diameter) were more or less regularly interspersed over the whole length of the construction, mimicking 3 different root densities (10, 20 and 30 roots m^{-2}). For technical details on the flume, see Bouma *et al.* (2005).

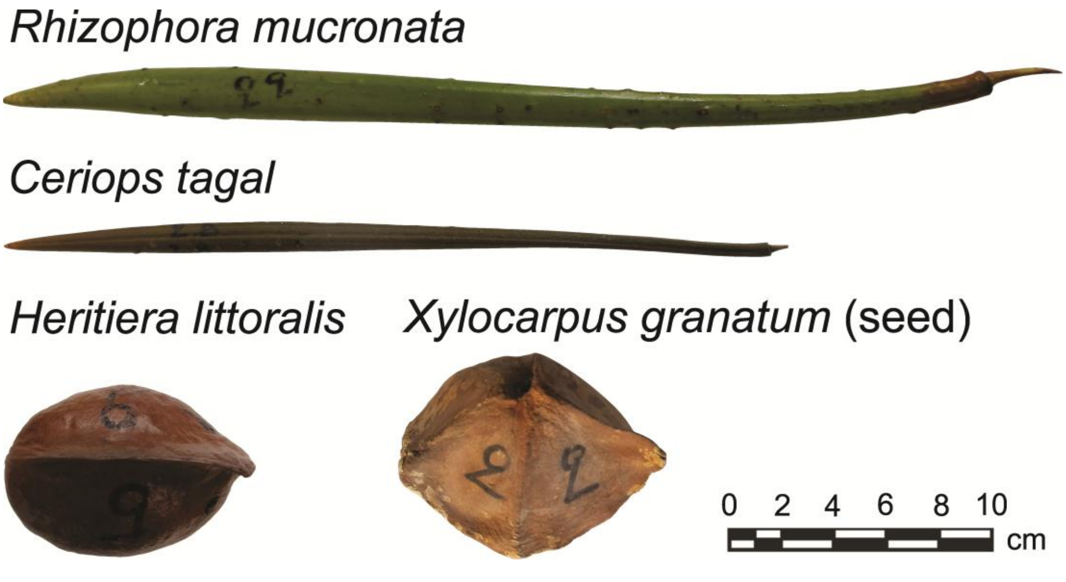

Figure 3.2: Photograph of dispersal propagules of the four studied species.

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

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

Field experiment

Field experiments were conducted in a mangrove forest in Gazi Bay (Fig. 3.3). The tidal regime in this area is semi-diurnal, with ebb currents being stronger than flood currents, and with a macrotidal range of 3.5 m (Kitheka 1996, 1997). Here, 4 plots (1 plot per intertidal location) were selected along an intertidal transect, covering typical stands of the most abundant species and root types: landward *A. marina* zone (AML), *C. tagal* zone (CT), *R. mucronata* zone (RM) and creekward *A. marina* zone (AMC). Average root density and height were measured in the CT and RM intertidal zones. In the CT zone, average root density was 28.8 roots m^{-2} (6 plots of 1 m^2), with an average height of 11.1 ± 5.7 cm (n = 173). For RM, average root height was 16.2 ± 1.5, 6.2 ± 2.4 and 5 ± 2.6 roots m^{-2} at 0 , 0.5 and 1 m above the ground (4 plots of 1 m^2), respectively. For the AML and AMC zone, data on root density for the same study site was retrieved from Dahdouh-Guebas *et al.* (2004). In these zones, root densities range between 4 and 250 roots m^{-2}, and 44 and 1950 roots m^{-2}, respectively. In each of the four plots (each plot being 1 × 1 m), we placed 30 *C. tagal* and 30 *R. mucronata* propagules at low tide. The propagules were collected from neighbouring *R. mucronata* and *C. tagal* trees, marked with white waterproof paint and numbered, in order to link them to their initial release location. It should be stressed that the marking with paint does not influence propagule buoyancy as tested in a control experiment by De Ryck (2009). One, 2 and 4 days after their release, propagules were retrieved by systematically covering the area within a radius of about 500 m during spring tide (9 to 13 March 2012). Limits of the search area were situated well beyond the zone in which no more propagules were recovered. The intensity of searching was constant with distance from the release locations, thereby excluding a potential effort-related bias. The experiment was conducted around spring tide (9 to 13 March 2012), as both high and low tide water levels within this period were most extreme, and hydroperiods in the various mangrove zones were the longest. Under these conditions, the interaction of dispersing propagules with the landscape matrix could be studied for all mangrove tree species and root types present over the whole intertidal range, since seawater then also reaches the most landward trees of the mangrove forest.

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

$$\mathrm{d} = \arccos\left[\sin(\varphi_1)\sin(\varphi_2) + \cos(\varphi_1)\cos(\varphi_2)\cos(\Delta\lambda)\right] \cdot \mathrm{R} \tag{1}$$

where φ is the latitude, λ the longitude, and R = 6370 000 m (Earth's radius). The dispersal direction was approximated using the formula for the initial bearing (*i.e.* forward azimuth):

$$\theta = \arctan 2\left[\sin(\Delta\lambda)\cos(\varphi_2), \cos(\varphi_1)\sin(\varphi_2) - \sin(\varphi_1)\cos(\varphi_2)\cos(\Delta\lambda)\right] \tag{2}$$

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

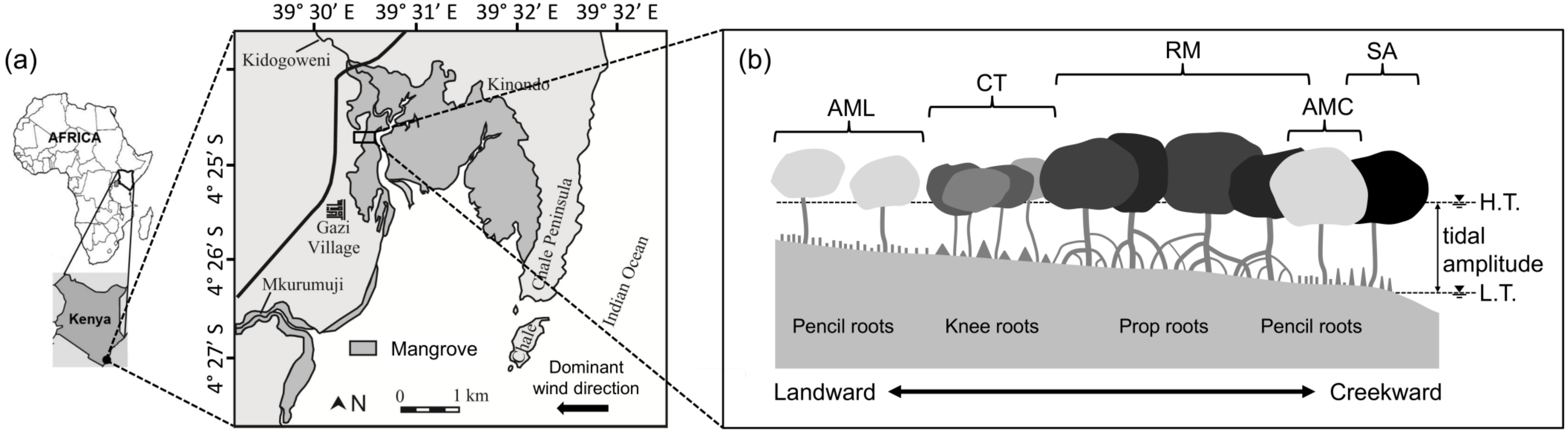

Figure 3.3: (a) Study area (Gazi Bay, Kenya; 39° 30' E, 04° 26' S) where field experiments were conducted and (b) species zonation along our intertidal transect. AML: *Avicennia marina* landward, CT: *Ceriops tagal*, RM: *Rhizophora mucronata*, AMC: *A. marina* creekward, SA: *Sonneratia alba* (SA was not considered in our study, but is shown for completeness). H.T.: high tide water level, L.T.: low tide water level.

Table 3.1: Characteristics of the 4 mangrove propagule types used (*Ceriops tagal*, *Rhizophora mucronata*, *Heritiera littoralis*, *Xylocarpus granatum*), retention data and dispersal velocities for the various conditions simulated in the flume experiment. Retained: stuck for > 3 min, not touching flume walls; stranded: stuck for > 3 min for ≥ 5 × independently. Mean propagule dispersal velocity excludes stranded propagules. (–) Not applicable or no data. Ripples are small-scale perturbations of the water surface, often called 'capillary waves', having a wavelength that is typically less than a few centimeters.

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

Data analysis

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

Results

Flume measurements on propagule retention

Root density and propagule type. A complete overview of dispersal velocities and proportions of stranded propagules for all propagule types and experimental treatments is provided in Table 3.1. Overall, the probability to get retained or stranded in roots depended on propagule type (GLZ, $P < 0.0001$). Propagules of *H. littoralis* and *X. granatum*, did not get stranded in any of the treatments, neither did the vertically floating *C. tagal* and *R. mucronata* propagules. Of the vertically floating *R. mucronata* propagules, however, between 21.3 and 69.2 % were retained, depending on root density and water flow. Root density had a significant effect on the fraction of retained and stranded propagules (GLZ, $P \leq 0.01$), with increasing numbers of propagules being retained or stranded with increasing root density. Detailed results of the GLZ analyses are provided in Table 3.2.

Table 3.2: Result of the generalized linear model for the effect of root density (10, 20 and 30 roots m^{-2}) and propagule type (both categorical predictors) on the fraction of retained (resp. stranded) and non-retained (resp. not stranded) propagules. Water flow velocity was 0.10 m s^{-1}. Bold denotes statistical significance at P < 0.05, * P ≤ 0.0001. (–) Not applicable or no data. GLZ results our shown with (left) and without (right) interaction term.

	Retained		Stranded	
Intercept	**0.0005**	*	*	*
Root density	**0.010**	**0.002**	0.147	**0.001**
Propagule type	*	*	*	*
Propagule type × Root density	0.994	–	0.774	–

Table 3.3: Result of the generalized linear model for the effect of water flow velocity (0.05, 0.10 and 0.20 m s^{-1}) and propagule type (both categorical predictors) on the fraction of retained (resp. stranded) and non-retained (resp. not stranded) propagules. Root density was 0.20 roots m^{-2}. Bold denotes statistical significance at P < 0.05, * P ≤ 0.0001. (–) Not applicable or no data. GLZ results our shown with (left) and without (right) interaction term.

	Retained		Stranded	
Intercept	0.068	0.100	*	*
Water flow velocity	0.566	0.101	0.085	**0.002**
Propagule type	*	*	*	*
Propagule type × Water flow velocity	0.484	–	0.297	–

Water flow velocity. The GLZ including water flow velocity and propagule type identified significant effects of propagule type on the fraction of retained and stranded propagules (GLZ, P < 0.0001). Water flow velocity had a significant effect on the fraction of stranded propagules (GLZ, P = 0.002), with fewer propagules being stranded with increasing water flow velocity. Water flow velocity had no significant effect on the fraction of retained propagules (GLZ, P > 0.1). There was no significant interaction. Detailed results of this GLZ are summarized in Table 3.3.

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

Dispersal distance and direction in a natural mangrove system

Of all propagules released, 68 and 95 % were respectively recovered for *C. tagal* and *R. mucronata* on the first day (after 1 high tide), 53 and 84 % on the second day (after 3 high tides), and 48 and 85 % on the third day (after five high tides). The number of recovered propagules for both species for each of the release locations, are summarized in Table 3.4.

Table 3.4: Number of *Ceriops tagal* (Ct) and *Rhizophora mucronata* (Rm) propagules retrieved for each of the different release locations.

	AML		CT		RM		AMC	
	Ct	Rm	Ct	Rm	Ct	Rm	Ct	Rm
Day 1	20	26	22	22	16	20	9	14
Day 2	18	23	17	26	9	18	10	11
Day 3	15	25	15	22	14	24	6	17

Table 3.5: Result of the general linear model for the effect of day, propagule type, release location and the multiple interaction terms on dispersal distance of mangrove propagules in a natural mangrove system. Bold denotes statistical significance at $P < 0.05$, * $P \leq 0.0001$

	SS	Df	MS	F	P
Intercept	221788.0	1	221788.0	340.4986	*
Day	24487.3	2	12243.7	18.7970	*
Propagule type	6695.4	1	6695.4	10.2791	**0.0014**
Release location	8885.7	3	2961.9	4.5472	**0.0037**
Day × Propagule type	9415.4	2	4707.7	7.2275	**0.0008**
Day × Release location	14407.6	6	2401.3	3.6865	**0.0014**
Propagule type × Release location	606.1	3	202.0	0.3102	0.8180
Day × Propagule type × Release location	11339.6	6	1889.9	2.9015	**0.0086**
Error	322424.3	495	651.4		

Reconstructed dispersal distance distributions were leptokurtic, with the majority of propagules having been transported over short distances (from a few meters to < 50 m) (Fig.

3.4). However, a number of propagules were transported farther than 50 m (31.6 % of *C. tagal* and 11.8 % of *R. mucronata* propagules; after 5 high tides) and a few farther than 100 m (7.0 % of *C. tagal* and no *R. mucronata* propagules; after 5 high tides). One of the *C. tagal* propagules was retrieved at 320 m from its release location after 5 high tides. Dispersal distances differed among propagule types (factorial ANOVA , $F_{1.495} = 10.279$, $P = 0.001$). Propagules of *C. tagal* were transported farther from the release site (41.30 ± 52.44 m) than *R. mucronata* propagules (21.86 ± 21.71 m) but dispersal distance also depended on release location (factorial ANOVA, $F_{3.495} = 4.547$, $P = 0.004$). Dispersal distances were shorter in the AMC zone than in the RM zone. A GLM revealed significant effects of day, propagule type and release location on dispersal distance ($F_{23.495} = 4.13$, $P < 0.00001$, adjusted $r^2 = 0.12$; Table 3.5).

Dispersal direction data showed a clear bimodal distribution that corresponded with the bidirectionality of tidal action in this area (Fig. 3.5). The average of all dispersal direction data (both species, all zones, all days) was used as a threshold to distinguish the 2 main dispersal direction groups (group 1: > 218.2° and < 38.2°; group 2: < 218.2° and > 38.2°) (Table 3.6). One group of dispersal directions was towards the south (grand mean after 5 high tides is 176.8°), *i.e.* towards the inlet of the bay, while a second dominant dispersal direction was inland, more or less perpendicular to the creek (grand mean after 5 high tides is 279.6°). Overall, Rayleigh's tests showed significant directionality in all zones and for all species (all $P < 0.05$), with the exception of the *C. tagal* propagules released in the RM zone, presumably due to the low number of recovered propagules ($n = 3$).

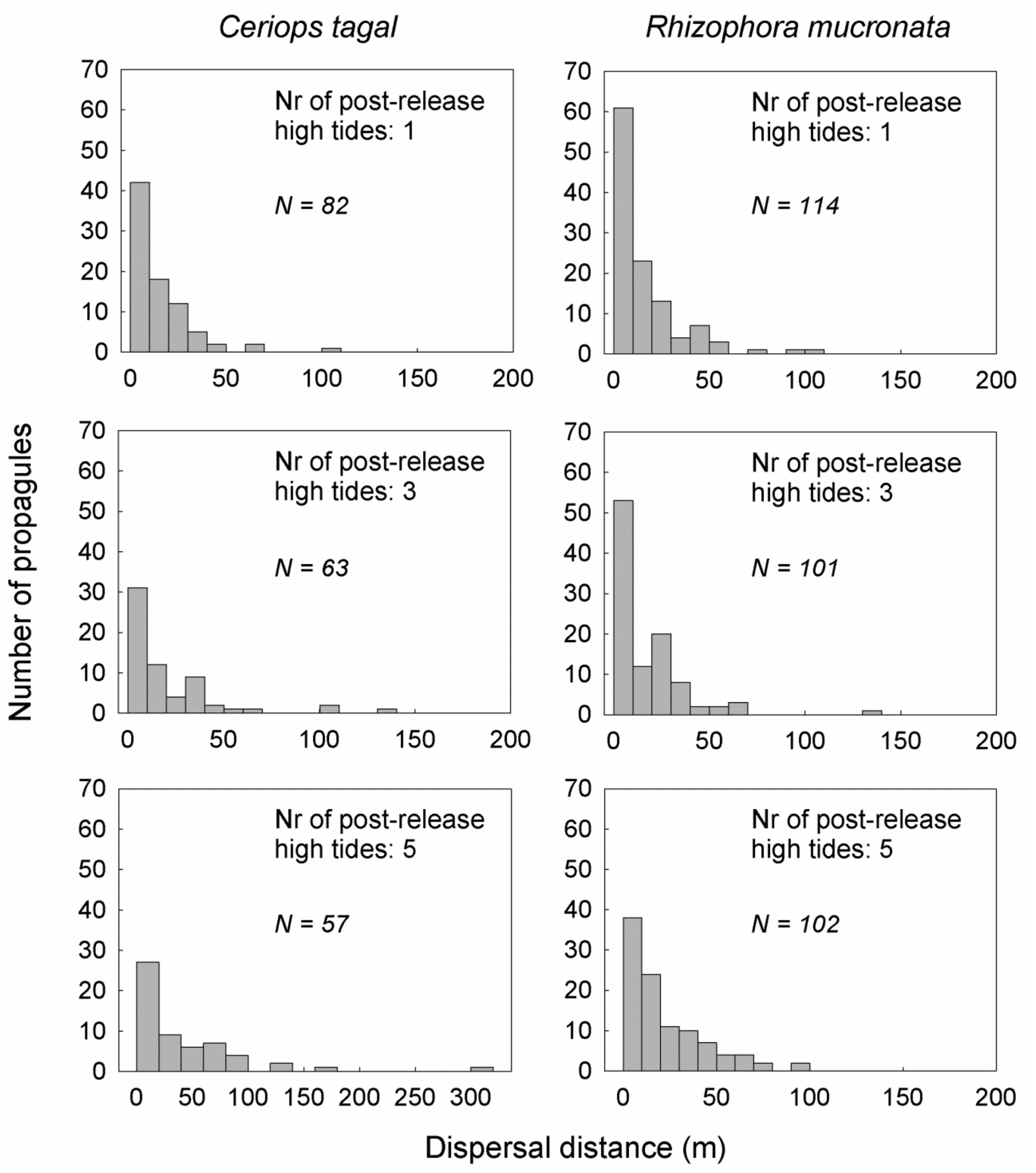

Figure 3.4: Dispersal distances of *Ceriops tagal* (left) and *Rhizophora mucronata* (right) propagules along a transect in the mangrove forest of Gazi Bay (Kenya). Propagules were released in 4 different plots covering typical stands of the most abundant root types in a natural macrotidal mangrove system. Propagules were searched for 1 day (1 high tide), 2 days (3 high tides), and 4 days (5 high tides) after their release. The intensity of searching was constant with distance from the release locations, excluding a potential effort-related bias. Hence, the decreasing number of propagules recovered is distance-related.

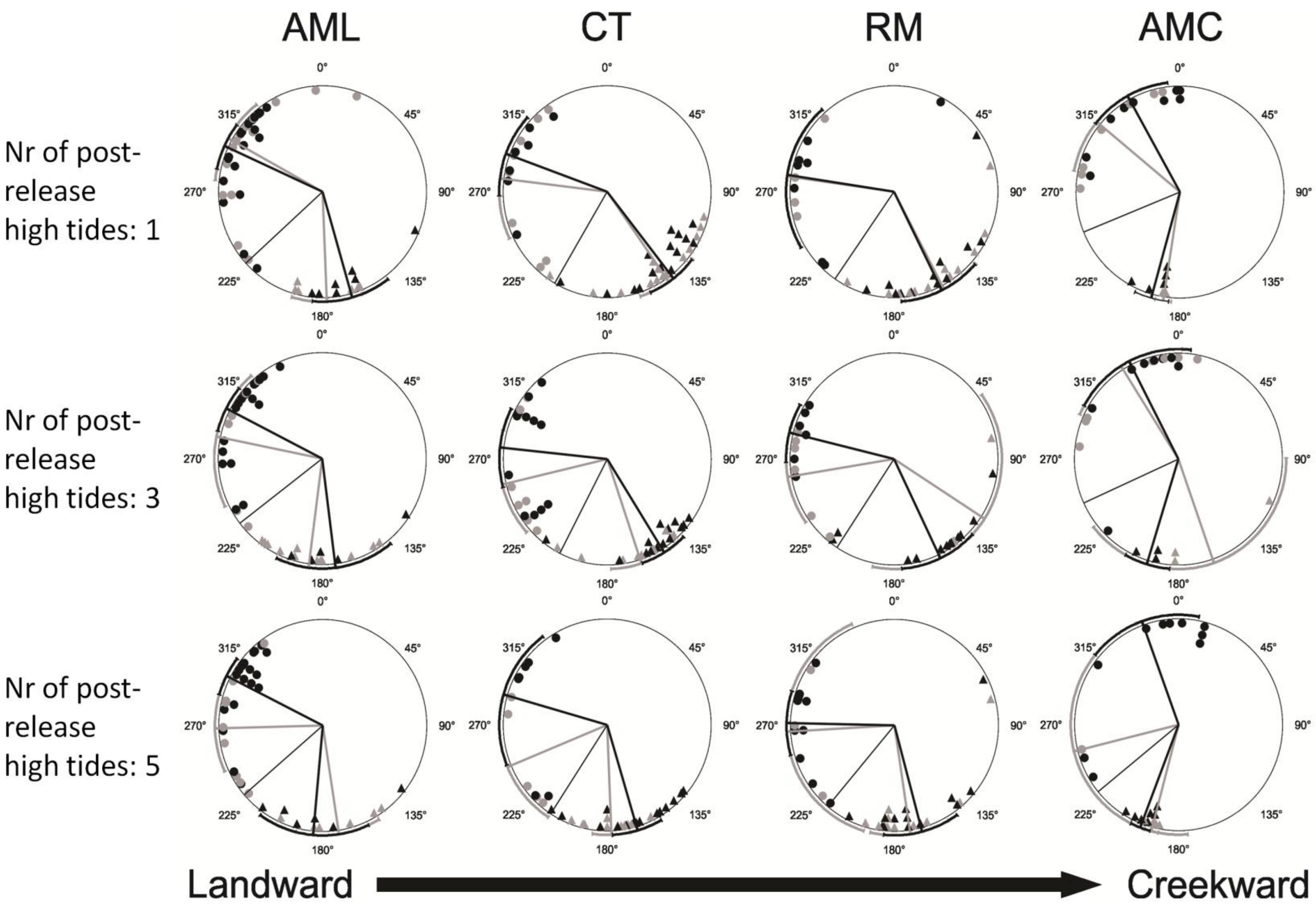
AML
CT
RM
AMC
Nr of post-release high tides: 1
Nr of post-release high tides: 3
Nr of post-release high tides: 5
0°
45°
90°
135°
180°
225°
270°
315°
Landward
Creekward

Figure 3.5: Circular representation of dispersal directions of the *Ceriops tagal* (grey symbols) and *Rhizophora mucronata* (black symbols) propagules released at the various mangrove species zones along our transect (AML: *Avicennia marina* landward; CT: *C. tagal*; RM: *R. mucronata*; AMC: *A. marina* creekward). For each of the 2 species, 30 propagules were released at low tide on 9 March 2012 and retrieved on 10 March 2012 (after 1 high tide), 11 March 2012 (after 3 high tides) and 13 March 2012 (after 5 high tides). Based on the clear bimodal nature of the data, 2 groups of dispersal directions were defined using the average dispersal directions of all data – group 1: > 218.2° and < 38.2° (circles); group 2: < 218.2° and > 38.2° (triangles). Bold lines from the centre to the periphery represent averages of the dispersal direction groups; intervals outside the periphery are the 95 % CIs. Thin line represents the grand mean.

Table 3.6: Basic circular statistics for the propagules recovered in our field experiments after 5 high tides (day 3). In total, 30 *Ceriops tagal* (Ct) and 30 *Rhizophora mucronata* (Rm) propagules were released in four different plots along an intertidal transect – AML: *Avicennia marina* landward, CT: *Ceriops tagal*, RM: *Rhizophora mucronata*, AMC: *A. marina* creekward. A clear bimodal directionality was found in the dispersal movement of both the *C. tagal* and *R. mucronata* propagules (Fig. 3.5). We used the average of all dispersal direction data to group the data into two groups on which circular statistics were applied. Bold denotes statistical significance at P < 0.05, * P ≤ 0.0001; (–) Not applicable or no data.

	GROUP 1 (> 218.2° and < 38.2°)								GROUP 2 (< 218.2° and > 38.2°)							
	AML		CT		RM		AMC		AML		CT		RM		AMC	
	Ct	Rm	Ct	Rm	Ct	Rm	Ct	Rm	Ct	Rm	Ct	Rm	Ct	Rm	Ct	Rm
Nr. of obs.	9	19	5	7	3	11	1	10	6	6	10	15	11	13	5	7
Mean angle (°)	268.5	296.8	247.6	286.0	266.6	271.2	–	340.2	171.4	185.2	177.8	163.5	171.5	165.1	194.6	200.8
SD	29.9	23.6	27.9	40.2	32.2	25.0	–	48.5	21.5	28.6	14.0	24.4	31.5	33.8	3.0	5.8
Rayleigh test (p)	*	*	**0.01**	**0.008**	0.1	*	–	**0.005**	**0.001**	**0.004**	*	*	*	*	**0.001**	*

Discussion

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

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

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

Besides propagule traits, the interaction of dispersing propagules with the landscape matrix is determined by hydrodynamic variables such as surface waves. Flume experiments using waterlogged seeds of three salt-marsh species (*Plantago maritima*, *Suaeda maritima* and *Elytrigia atherica*) demonstrated that surface waves in combination with water flow can strongly reduce the number of retained seeds (Chang *et al.* 2008). This is in alignment with measurements on the retention of mangrove leaves by mangrove roots and seagrass beds

(Gillis *et al.* 2014), and is supported by our flume study on the transport of mangrove propagules. These results suggest that wind-generated waves or larger waves during storms could impact dispersal and propagule deposition patterns via the dislodgement of retained propagules. Especially at the edge of a mangrove forest, where wave energy has not yet dissipated, the effect of waves on the transport of propagules may be important. Additionally, our flume study shows that increasing water flow velocity facilitates transport through a barrier. The most likely explanation for this is that when propagules travel too slowly they will more easily get stuck or get delayed due to low kinetic energy. Several studies have focused on water flow through mangrove forests (Wolanski *et al.* 1980, Mazda *et al.* 1995, Furukawa *et al.* 1997, Aucan and Ridd 2000) and all reported rather limited water flow velocities (*ca.* 0 to 0.10 m s^{-1}) due to high friction. This agrees with our measurements in the flume and high retention rates in the field. Although not investigated in our study, the potential importance of turbulence due to water-plant interactions is recognized, as this may also affect the retention process.

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

The number of recovered propagules was high. The propagules that were not retrieved in our experiments might have been consumed by herbivorous crabs (De Ryck *et al.* 2012) or dispersed beyond the range of our search area. Predation vulnerability at our study site was found to be higher for *C. tagal* than for *R. mucronata* propagules (De Ryck *et al.* 2012), which may explain the lower recovery of *C. tagal* propagules in all plots (Table 3.4). Also, the smaller *C. tagal* propagules might have dispersed over longer distances and some propagules may have been overlooked, if for example covered with mud or leaf litter. The *C. tagal* propagules generally are more difficult to recover, because of their smaller size, and their dark brown-reddish color. The lower recovery of propagules from both species released in the AMC and RM zone (Table 3.4) very likely reflects proximity to open water. While the distance to open water is shorter, and hence the barrier width narrower, as compared to higher, more inland locations, these creekward sites experience higher water depths and a longer hydroperiod. Hence, the overall time period within which water currents can influence the deposition pattern of propagules in these locations is longer. In the RM zone, predation may as well explain part of the propagules that were not recovered, since high predation rates were reported in this location by De Ryck *et al.* (2012). A recent study in Gazi Bay showed that propagule predation rate is positively correlated with crab density and that crab density is negatively correlated with pneumatophore density (Van Nedervelde *et al.* 2015). However, it unknown to what degree the density distribution of herbivorous crabs across the intertidal range correlates with and contributes to the spatial variation in propagule recovery and seedling establishment, since predation pressure also depends on the nutritional value of propagules (Van Nedervelde *et al.* 2015).

Consistent with earlier work in tidal systems (Schneider and Sharitz 1988, Sousa *et al.* 2007), dispersal in the field was found to be highly directional. Additionally, the data revealed a clear bimodality, reflecting dominant tidal currents. One dispersal direction corresponded with the direction of strong incoming tides, while the other dispersal direction reflected the south-southeastward ebb-component. The inland component is in accordance with Rabinowitz' Tidal Sorting Hypothesis, stating that smaller propagules are transported farther inland than larger ones (Rabinowitz 1978b). Conversely, Sousa *et al.* (2007) found that propagule dispersal directions were predominantly from higher to lower elevations. They recognize, however, that their findings may be typical for the Caribbean, where, in contrast to our study site, the tidal range is small and seasonal rainfall high, so that sheet flow runoff may dominate the effect of tidal currents. The slight westward deviation in the southward dispersal direction of the creekward plots (Fig. 3.5) may reflect the effect of easterly winds during the period of our field study (Van der Stocken *et al.* 2013).

We recognize that the structure of natural landscape matrices may be more complex than the one simulated in our flume experiments. *Rhizophora* stilt roots, for example, are characterized by high spatial complexity which may retain vertically floating propagules equally well as horizontally floating ones, and roughness of the tree and root surface may yield higher friction as compared to the bamboo sticks. Also, propagules can be retained by young seedlings, but also by the crown of trees at high water near spring tide, when water

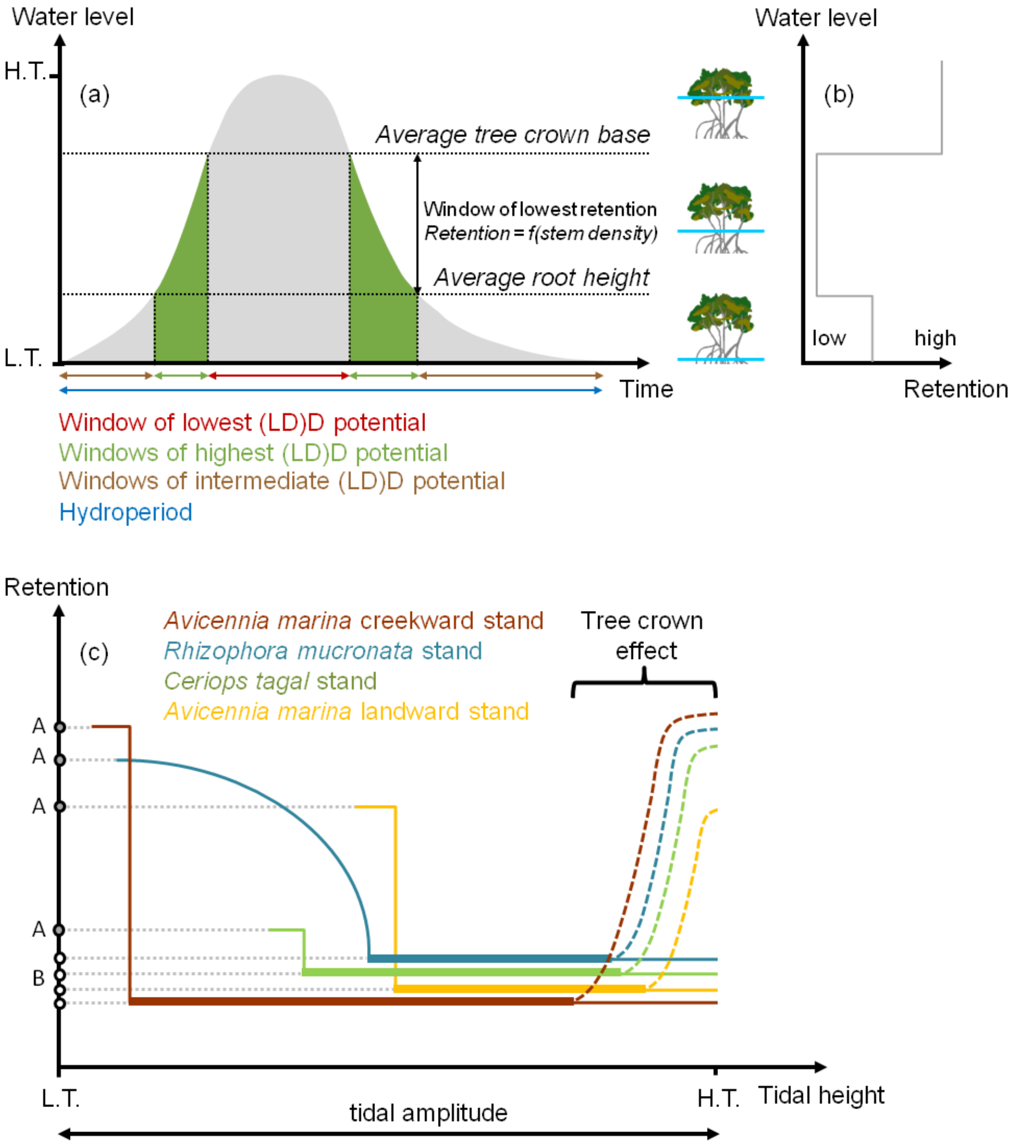

Figure 3.6: Synthetic model showing temporal variation in dispersal barrier density over a tidal cycle. (a-b) Periods with water levels in the range between the average root height and tree crown base represent windows of lower retention and higher (long distance) dispersal (LDD) potential. Tidal currents can be asymmetric, which may influence the effect of incoming and outgoing tides. (c) We applied the concept of windows of higher and lower retention to our field study transect (see also Fig. 3.3 b). The model illustrates the variation in retention over the range of the tidal amplitude, from low water (L.T.) to high water (H.T.). Water enters the creekward side of the forest, inundating the creekward *Avicennia marina* stand. Initially, barrier density is high (A), and falls back to the stem density (B) as soon as the water level exceeds average root height (*i.e.* window of lower retention and higher LDD potential). The same accounts for the variation in retention in other species zones, with interspecific differences in root height and hydroperiod. Occasionally, water may exceed the average tree crown base, strongly increasing retention (pers. obs.). The width and frequency of these windows of lower retention are a function of intertidal position and topography. Trees in the inland zone of a mangrove forest will experience shorter hydroperiods than trees on the more creekward or seaward side. This is true over the daily tidal cycle, but also over the monthly tidal cycle, some areas only being inundated near spring tide. For example, the landward *A. marina* stand in our field experiment is beyond the reach of the water line, except around spring; thus, dispersal potential is much lower compared to that in our *Rhizophora mucronata* site. Local (micro)topography and characteristics of the tidal regime may add complexity to the graphs.

level may submerge part of the canopy (pers. obs.; Fig. 3.6). However, our findings clearly demonstrate that root density, propagule traits and hydrodynamic variables affect the ability of propagules to navigate through a landscape matrix. Interestingly, the decreasing fraction of retained and stranded propagules with decreasing root density as found in our flume experiment suggests that if we extrapolate to the actual field situation, temporal variations in water height (over the course of the tidal cycle; Fig. 3.6 a) may reduce barrier density and hence retention, similar to the findings of Schneider and Sharitz (1988). The typical physiognomy of mangrove trees with a high root density close to the surface and a dense canopy cover, brings about a higher retention at these heights as compared to mid-height where barrier density is determined by the spatial distributions of the tree stems alone (Fig. 3.6 b). As such, windows of lower retention, and hence higher long distance dispersal (LDD) potential, may exist (Fig. 3.6 a and 3.6 c). The duration and frequency of these windows would then depend on the structure of the landscape matrix, the tidal system and the geomorphologic features of the coastline. In the case of mangrove forests consisting of several mangrove taxa varying in architecture and stature that have overlapping distributions, the net retention curve at a certain location would consist of the sum of the average species-specific retention curves. Also, stochastic events such as storms, during which water velocities and wave energy may be higher than normal, could have a disproportionate effect on dispersal and establishment. To study the role of such events, similar release-recapture dispersal experiments could be set up just before a major storm is anticipated.

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

Although speculative, our findings may also help to explain variation in mangrove zonation patterns (Sousa *et al.* 2007, Peterson and Bell 2012) (Fig. 3.7). In our study area in Gazi Bay, for example, trees of species with the most compact propagules (*e.g. A. marina*, *H. littoralis* and *X. granatum*) are typically found in high shore locations of the mangrove forest, while *C. tagal* and *R. mucronata* trees dominate the middle and creekward sides of the forest. The creekward *Avicennia* trees, being older than their landward counterparts (pers. comm. F. Dahdouh-Guebas), may represent relicts from the earliest stages of the mangrove forest, when conditions in the more landward zones may not have been favourable yet for establishment, for example due to soil texture and composition. While the larger propagules of *C. tagal* and *R. mucronata* may occasionally be transported to more inland areas around spring tide or during storm surges, their absence in these zones indicates the importance of establishment related factors such as soil salinity, inundation period and competition with other species, as well as physiological traits. Correlations between zonation and dispersal potential have been studied earlier by Clarke *et al.* (2001), who postulated that in northern Australia, dispersal potential alone does not correspond with zonation, and that zonation may be driven much more by traits related to establishment. Species zonation has been linked to various environmental factors, such as predation (Smith 1987) or differences in flood tolerance (McKee 1993, Ye *et al.* 2003). Evidence for a correlation between zonation and establishment related factors also follows indirectly from this study. Around spring tides, for example, propagules of *C. tagal* and *R. mucronata* may occasionally be transported to backshore areas, though mature individuals of these species do not occur there. The same explanation applies to *H. littoralis* and *X. granatum* whose local presence is restricted to the upper intertidal zones, despite the fact that their propagules can easily reach sites in the lower intertidal area. However, while factors such as soil salinity, inundation period, competition with other species, and physiological traits determine establishment, dispersal traits and aspects such as the interaction of propagules with the landscape matrix control the distribution of viable propagules over suitable and unsuitable locations. Compact propagules, for example, may be beneficial for the colonization of suitable high-shore habitat locations (Rabinowitz 1978b), but may also facilitate the export of propagules from backshore species separated from open water by dense physical barriers.

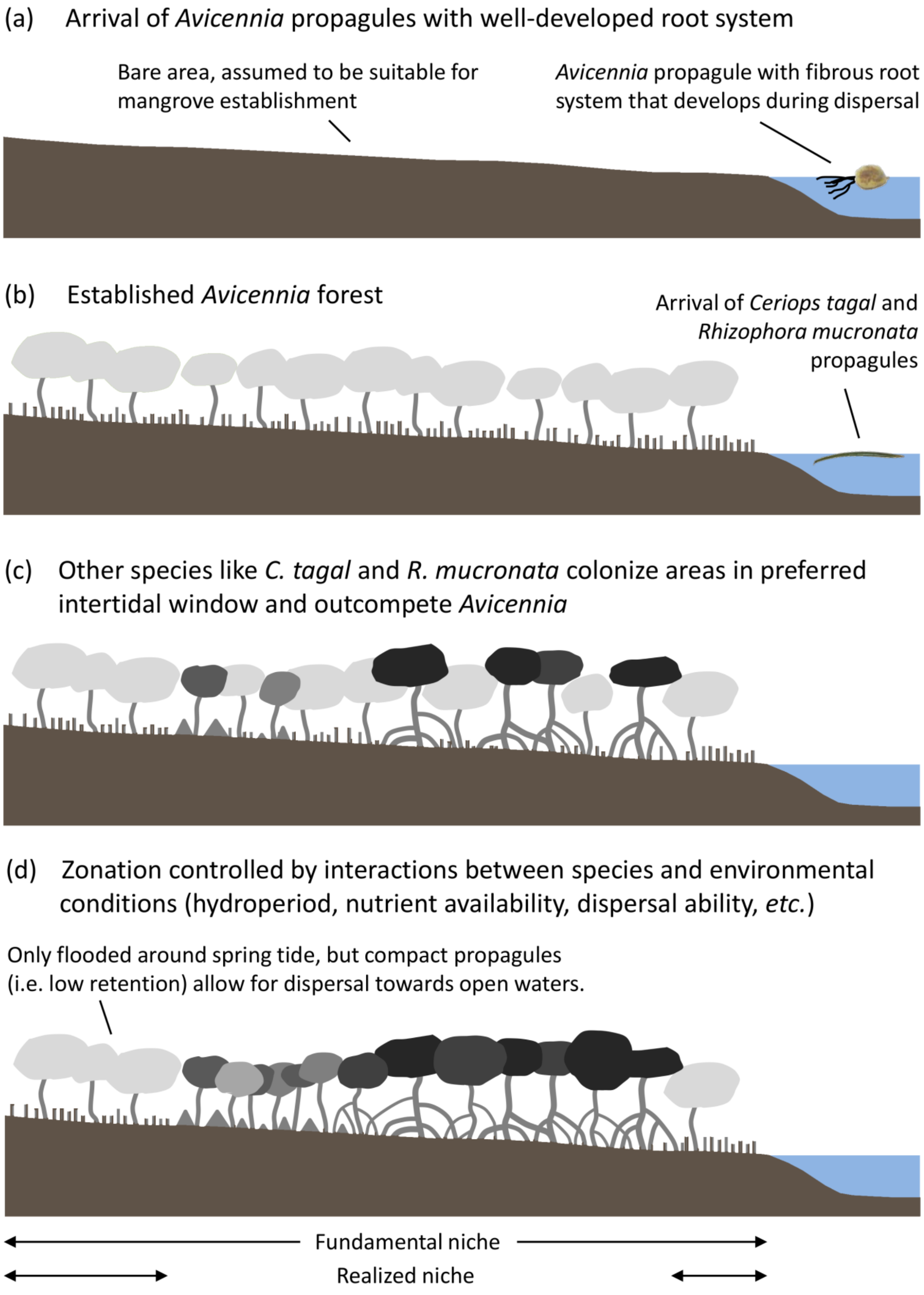

Figure 3.7: Speculative illustration of how the mangrove zonation in Gazi Bay (Kenya) may have formed over time. Standing in landward areas, *Avicennia marina* may take advantage of its compact propagules to overcome the dense barrier that separates it from the open water. Conversely, these compact propagules may colonize areas that are beyond the reach of species with larger propagules. However, the presence of propagules of other species such as *Rhizophora mucronata* and *Ceriops tagal* in these landward zones but the absence of juveniles and mature trees of these species in indicates the importance of establishment related factors such as soil salinity, inundation period and competition with other species, as well as physiological traits.

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

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CHAPTER 4

THE ROLE OF WIND IN HYDROCHOROUS MANGROVE PROPAGULE DISPERSAL

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Abstract

Although wind has been recognized to be an important factor in the dispersal of hydrochorous mangrove propagules, and hence in the quantification of (meta)population dynamics, the species-specific sensitivity to wind effects has not been studied. We combined dispersal experiments in the field and under controlled conditions (flume tank) to understand water and wind current contributions to dispersal potential as well as to estimate real dispersal ranges due to immediate response to tidal currents (two outgoing tides). This was done for 4 species with propagules differing in morphological and buoyancy properties (*i.e. Rhizophora mucronata, Ceriops tagal, Heritiera littoralis* and *Xylocarpus granatum*). The flume experiments revealed that the influence of wind depends on propagule density (and hence its buoyancy characteristics) and that typical morphological characteristics of the dispersal unit are additionally important. *Heritiera littoralis* propagules were influenced most, due to their low density and 'sailboat-like' structure. The *X. granatum* fruits appeared to be little influenced by ambient wind conditions, explained by the smooth spherical shaped surface of which only a small part sticks above the water surface. Although the seeds of *X. granatum* are of a similar size class as *H. littoralis* propagules, they are (like the *X. granatum* fruits) largely submerged due to their high density, hence catching less wind than *H. littoralis* propagules. A differential effect of wind was found within elongated propagules, which directly follows from the floating orientation of the propagules. Contrary to the horizontally floating propagules, wind had little effect on the dispersal trajectory of the vertically floating propagules. To validate the flume results, propagules of *C. tagal* and *R. mucronata* were released during outgoing tide in a tidal creek in Gazi Bay (Kenya), followed by observation of their dispersal distance and direction, while knowing the actual dominant wind direction. In line with the flume results, this study showed that wind plays an important role in the dispersal distance of the propagules. The present study provides important mechanistic insight in the effect of wind on hydrochorous mangrove propagule dispersal, thereby yielding an essential step towards the construction and optimization of dispersal models.

Introduction

A series of publications have stressed the importance of dispersal in the evolution of plant population structure and composition (*e.g.* Duke *et al.* 1998, Cain *et al.* 2000, Nathan and Muller-Landau 2000, Caswell *et al.* 2003, Nathan *et al.* 2003, Bowne and Bowers 2004, Clobert *et al.* 2012), where other reports emphasized the fundamental need to study long distance dispersal (LDD) as a crucial mechanism for understanding and predicting the adaptability of species to cope with environmental and climate change (*e.g.* Pitelka *et al.* 1997, Higgins and Richardson 1999, Nathan 2001, Johst *et al.* 2002, Doyle *et al.* 2003). The spatial distribution of mangroves on a regional and global scale has been studied extensively (*e.g.* Ridley 1930, van der Pijl 1982, Duke *et al.* 1998), and the determining role of dispersal in spatiotemporal changes of species distribution is a well-endorsed subject (Duke 1992, Clarke *et al.* 2001, Sousa *et al.* 2007). Some authors used marked propagules (*i.e.* dispersal units) to investigate dispersal distances (Yamashiro 1961, Komiyama *et al.* 1992, Clarke 1993, McGuinness 1997, Breitfuss *et al.* 2003, Sousa *et al.* 2007, De Ryck *et al.* 2012). Though most propagules were found to disperse over only short distances (up to tens of meters), some propagules dispersed over extensive ranges. Clarke (1993), for example, recovered 3 *Avicennia marina* propagules at more than 10 km and 1 propagule at more than 50 km. For *Rhizophora mucronata*, Komiyama *et al.* (1992) found a maximum dispersal distance of 1210 m. Nevertheless, the dynamics and controlling factors of mangrove propagule dispersal have remained understudied, mostly due to the difficulty of the quantification of (long-distance) dispersal (Nathan 2001). Such knowledge is however essential in defining realistic dispersal kernels and improving existing dispersal models, and thus for predicting the dispersal route of mangrove propagules. This knowledge may in turn improve the success of future restoration projects.

Mangrove propagules are hydrochorous, meaning that the hydrodynamics of tides and (ocean) currents constitute the dominant dispersal vector. Dispersal dynamics are further defined by the characteristics of the propagule itself, such as buoyancy, longevity and morphology (Tomlinson 1994, Clarke and Myerscough 1991, Clarke *et al.* 2001, Drexler 2001, Allen and Krauss 2006). Recently, Di Nitto *et al.* (2013) used a finite-volume advection-diffusion model to investigate the effect of these variables on the fate of dispersing propagules of the mangrove species *Rhizophora mucronata* Lamk., *R. apiculata* BL., *Ceriops tagal* (Perr.) C.B. Robinson and *Avicennia officinalis* L. in the Pambala-Chilaw Lagoon Complex (Sri Lanka). Until present, the study of Di Nitto *et al.* (2013) presents the only model that investigates mangrove propagule dispersal based on hydrodynamics and including trapping agents (retention by vegetation). Di Nitto *et al.* (2013) found that wind has a significant influence on the final distribution pattern of mangrove propagules, using a wind drag function of 3 % wind speed on the surface currents in the model she applied. However, wind-induced dispersal was imposed uniformly on all species as a hydrodynamic component (Di Nitto *et al.* 2013) and consequently, though recognized to be important, species-specific differential behaviour was not taken into account.

The role of prevailing wind conditions generally received only minor attention in existing hydrochorous dispersal studies, but those studies that are available point at the potential importance of species-specific effects. For example, for a set of non-mangrove seeds it was shown that seed transport and sorting by hydrochory is strongly influenced by wind, depending on the seed density and shape (Chambert and James 2009). Stieglitz and Ridd (2001) investigated the dispersal of buoyant propagules of *R. stylosa* Griff*., Bruguiera gymnorrhiza* (L.) Lamk*., Xylocarpus mekongensis* Pierre and *Heritiera littoralis* Dryand. in the Normanby River estuary (Australia). Besides the main finding that the distribution of these propagules is characterized by a density-driven secondary circulation of water during the tropical dry season, wind-generated waves or wind-drift seemed to have a negligible influence on their drift path (Stieglitz and Ridd 2001). That is, despite their distinct shapes and sizes, especially the 'sail' of *H. littoralis*, propagules which enhances wind-driven dispersal (Tomlinson 1994), the dispersal path within the estuary was found to be similar for all propagules (Stieglitz and Ridd 2001).

This study aims at investigating the importance of morphological propagule traits and buoyancy behaviour in understanding the role of wind in hydrochorous mangrove propagule dispersal. This was studied by determining the dispersal behaviour of propagules under different hydrodynamic and wind conditions, both in a flume tank (controlled conditions), as well as in the field (natural conditions). We hypothesized that the influence of wind will be more pronounced for: (1) propagules with lower density; (2) propagules with high surface roughness; (3) horizontally floating propagules compared to vertically oriented ones, in the case of elongated dispersal units. The main goal of our field experiment was to investigate the frequency distribution of dispersal distances under natural conditions as a first rough validation of the flume results. Knowing the dominant wind direction at the moment of the *in situ* experiment, we were able to study the role of wind in determining the shape of the dispersal distance distribution. Additionally, a collaboration was set up with local fishermen to get an idea of which species and how many propagules reach the open sea (Indian Ocean), and thus potentially start an LDD journey.

Material and Methods

Studied species

The hydrochorous propagules of *C. tagal*, *R. mucronata*, *H. littoralis* and *X. granatum* Koen. (the fruit as a whole, as well as the separate seeds) were considered in this study (see Table 4.1), and are representatives of the most common mangrove propagule morphological types worldwide, with the exception of *Avicennia marina* (Forssk.) Vierh. type of propagule. We chose these species because *C. tagal* and *R. mucronata* (both Rhizophoraceae) are widely present in our study area and have typical viviparous propagules. Vivipary means that the embryo first protrudes through the seed coat and then out of the fruit, while still attached to the parent tree (Tomlinson 1994). The propagules of both of these species are typically elongated (torpedo-shaped), of which *C. tagal* propagules are the smaller and more slender ones (Table 4.1). *Heritiera littoralis* propagules (Sterculiaceae) were interesting to study because of their distinctive morphology, with a raised (dorsal) sail (Tomlinson 1994) and very low density. They have a hydrophobic, woody epicarp and a fibrous mesocarp (Tomlinson 1994). We added the cannonball-like fruits (*i.e.* 5 to 20 seeds encapsulated in a woody pericarp) as well as the angular shaped seeds of *X. granatum* (Meliaceae) to our study, since both fruits and seeds of this species can disperse in the mangrove habitat, with the trees often lining mangrove channels. This species selection allowed us to investigate the role of wind in the dispersal of two distinct morphological groups of dispersal units: torpedo-shaped propagules of *C. tagal* and *R. mucronata* vs. ellipsoidal and angular shaped dispersal units for the propagules of *H. littoralis* and the seeds of *X. granatum*, respectively (see Table 4.1).

Sample collection

Mature and healthy propagules of *C. tagal, R. mucronata* and *X. granatum*, were (randomly) picked from adult trees to avoid exposure to the osmotic effects of tidal water after abscission. We consider propagules mature when (1) the cotyledon is bright reddish yellow (*Ceriops*) or brownish yellow (*Rhizophora*) and (2) the propagule readily sheds from the tree when shaken. Lastly, freshly fallen *H. littoralis* propagules (seeds), were collected at neap tide under a parent tree in the high intertidal area.

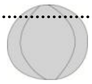
The length, volume (using the water displacement method *cf.* Chave 2005), mass and density of all propagules were measured and calculated before the start of the experiments. All propagules we used were checked for any damage that may modify surface roughness or significantly influence buoyancy behaviour throughout the duration of the experiments.

Flume study

The importance of floating orientation in the quantification of the contribution of wind in hydrochorous dispersal was analyzed in a flume setup, using 20 horizontally and 20 vertically floating *C. tagal* propagules. We did not consider vertically floating propagules of *R. mucronata* here, since the length of the propagules exceeded the depth of the flume tank, thereby hampering vertical free flow. Furthermore, 20 horizontally floating *R. mucronata* propagules were used to look for differences between the dispersal speed of the two viviparous mangrove species, as well as 10 seeds of *H. littoralis*, and one fruit (unopened) and 8 individual seeds (after opening of the fruit) of *X. granatum* as the more compact counterparts of the two viviparous species.

Various hydrodynamic and wind conditions for mangrove propagule dispersal were simulated in a 17.5 m long and 0.6 m wide (Fig. 4.1 a) oval race-track flume tank, which allowed uniform flow conditions. The flume was filled with sea water (salinity of 34 ‰, temperature of 13.6 °C and a water density of 1025.52 g l^{-1}) and the water-depth in the flume was kept constant at 0.35 m.

Table 4.1: Propagule characteristics and dispersal speed under various hydrodynamic and wind conditions. All values are averages over the distance range from 1m to 4m, so excluding the first and last meter. * n = 18; † mean over 3rd meter; ‡ mean over 5th meter; ¥ 1 propagule, 1 run.

Species		***H. littoralis***	***X. granatum***		***R. mucronata***	***C. tagal***	
Morphology floating orientation		ellipsoidal –	angular/pyramidal –	"cannonball" –	elongated horizontal	elongated horizontal	elongated vertical
Position relative to water surface (dotted line)							
n		10	8	1	20	20	20
Run/propagule		1	1	5	1	1	1
Mean length (cm)		–	–	–	41.03 ± 6.63	24.38 ± 2.68	24.69 ± 2.21
Mean mass (g)		33.11	46.80	892.72	65.70 ± 16.39	8.25 ± 1.76	8.27 ± 1.36
Mean density ($g\ l^{-1}$)		613.58 ± 27.94	870.66 ± 27.89	890.05	994.20 ± 9.62*	1001.80 ± 8.47	1023.28 ± 4.88
	Wind						
$v_w = 0 \times 10^{-2}$ m s^{-1}	S/O	7.83 ± 1.45 †	5.62 ± 1.24 †	0.04 †¥	5.46 ± 1.53 †	5.91 ± 1.20 †	3.12 ± 1.52 †
$v_w = 15 \times 10^{-2}$ m s^{-1}	N	15.99 ± 0.63	15.68 ± 1.27	14.99 ± 0.68 ‡	15.02 ± 0.82 †	15.78 ± 0.79	15.70 ± 0.41
	S	27.12 ± 5.37	20.92 ± 0.65	16.92 ± 0.64 ‡	23.17 ± 1.40	24.29 ± 0.86	17.66 ± 1.81
	O	–	–	–	9.35 ± 0.96 †	9.88 ± 0.82	13.77 ± 1.51
$v_w = 30 \times 10^{-2}$ m s^{-1}	N	29.45 ± 2.07	29.56 ± 0.91	27.74 ± 1.24 ‡	28.29 ± 1.63 ‡	29.86 ± 1.26	30.03 ± 0.58
	S	38.10 ± 2.06	33.91 ± 1.06	29.66 ± 0.92 ‡	32.72 ± 0.90	35.72 ± 0.79	30.74 ± 1.28
	O	19.84 ± 3.70	26.06 ± 0.44	26.74 ± 1.43 †	22.84 ± 2.66	26.98 ± 1.32	28.70 ± 1.04

A uniform free flow current velocity of 15×10^{-2} m s^{-1} and 30×10^{-2} m s^{-1} was generated with a conveyer belt. These velocities reflect natural water flow velocities in the studied mangrove creek (see field study), *i.e.* the Kidogoweni Creek (Kitheka *et al.* 2003). By using a smooth flume bottom, the water velocity gradient is steep (*i.e.* high currents at the bed because of low roughness). This simulates deeper water, where the upper decimeter of the profile has uniform current velocities.

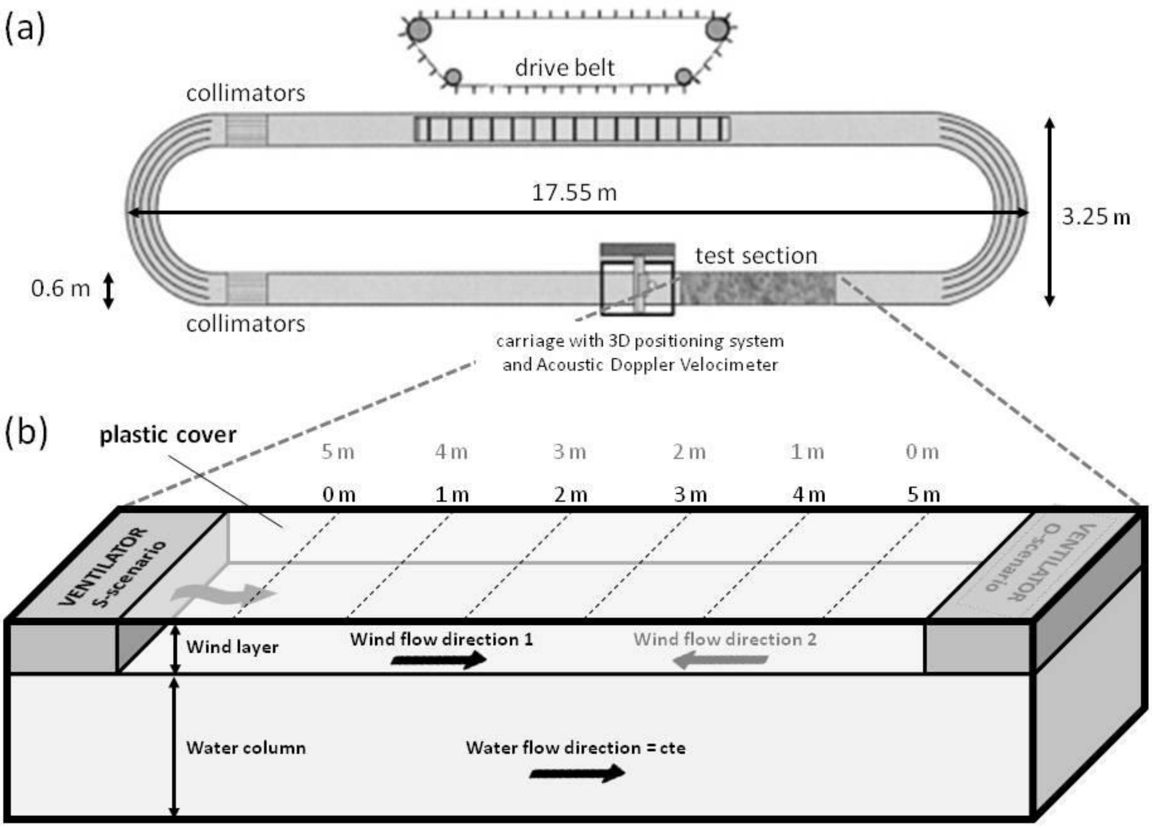


Figure 4.1: Schematic representation of (a) the racetrack flume (modified from Bouma *et al.* 2005) and (b) a detailed depiction of the experimental flume section. Fig. b: the position of the ventilator is indicated in dark grey (left: S-scenario; right: O-scenario). The wind flow direction 1 represents the S-scenario (black arrows, numbers and text), where the O-scenario setup is shown as wind direction 2 (grey arrows, numbers and text). Dispersal time was measured at intervals of one meter (see dotted lines).

For the wind experiment, an industrial ventilator was installed on top of the flume to create a wind layer over the water surface (Fig. 4.1 b). Current velocities in all wind scenario's were calibrated to ensure water current velocities to be identical in all experimental scenarios (*i.e.*

15×10^{-2} m s^{-1} and 30×10^{-2} m s^{-1}). To ensure a constant wind speed, a test section of 5 m in front of the ventilator was covered with a plastic roof and tested for leakage over the whole length of the experimental setup. The mean wind speed was 2.6 ± 0.13 m s^{-1}, which is the average of 3 wind speed measurements along the experimental setup (0 m, 2.5 m and 5 m). These wind speeds represent open sea winds, ranging from 'calm' to 'high wind' on the Beaufort scale, which is also the range of wind conditions at the moment of our field experiments (www.wunderground.com). Wind speeds in the flume experiments were measured using a velociCalc TSI anemometer (model 8384-M-GB). For both current velocities we applied an air flow in the same direction of the water flow (*i.e.* S-scenario), the opposite direction (*i.e.* O-scenario), as well as a scenario without wind (*i.e.* N-scenario) (Fig. 4.1).

Flow velocity measurements were taken before the start of each experiment by an Acoustic Doppler Velocimeter or ADV (Nortek AS, Oslo, Norway) placed on a 3D positioning system. The velocity data were stored using the Vectrino Plus Version 1.16 software programme (NIOZ, Yerseke, The Netherlands) connected with the ADV.

Propagules were consecutively released at location 0 m (Fig. 4.1 b) along the flume tank, through a small fist-size hole in the plastic cover, and traveling times were recorded using a stopwatch after passing each meter marking (0 m to 5 m).

Data analysis of flume experiment

Mean dispersal velocities for each species were calculated using Matlab R2011b. To avoid perturbations in the velocity profile, due to the closeness to the ventilator for example, we excluded the first and last meter of the total experimental dispersal distance. For the *R. mucronata* propagules, only the 3rd meter was considered, after investigating whether or not the propagule was in equilibrium with the acting water and wind forces, based on the propagule velocity profiles. Due to its significantly higher density compared to the other dispersal units (Table 4.1), the *X. granatum* fruit needed more time (or dispersal distance) to reach a stable velocity (equilibrium of forces). Therefore the dispersal velocity for this dispersing unit was calculated only over the 5th meter of the section for the N-scenario and S-scenario and over the 3rd meter in the case of the O-scenario. The latter was decided as being the most representative dispersal velocity in this specific case, enabling the fruit to reach equilibrium with the moving water body, and precautionarily excluding possible instabilities (such as turbulent wind flow) in the last meter caused by the wind force acting in opposite direction.

To test for significant differences in dispersal velocity between propagule types, unpaired t-tests and Mann-Withney U tests were conducted, when data was normally and not normally distributed, respectively. Normality was tested using the Lilliefors test. All tests were done using Statistica 8.0 (Statsoft).

Field study

The field study was conducted in the mangrove forest of Gazi Bay (39° 30' E, 4° 26' S), a shallow, tropical coastal-water system located about 46 km south of Mombasa (Fig. 4.2). The total mangrove forest area is about 6.5 km², comprising all 10 East-African mangrove species: *R. mucronata*, *C. tagal*, *A. marina* (Forssk.) Vierh., *Sonneratia alba* J. Smith, *B. gymnorrhiza*, *H. littoralis*, *X. granatum*, *Lumnitzera racemosa* Willd., *X. moluccensis* (Lamk.) Roem, and *Pemphis acidula* Forst. (nomenclature according to Tomlinson 1994). The region is drained by two tidal creeks, Kidogoweni in the north-western part and Kinondo in the eastern part. While Kidogoweni Creek receives freshwater from the Kidogoweni River, Kinondo Creek lacks a direct freshwater input (Kitheka 1996, 1997). River discharge is important during the wet season and occasionally reaches up to 5.0 and 17.0 $m^3 s^{-1}$ for the Kidogoweni and Mkurumuji Rivers, respectively (Kitheka 1997). The bay experiences semi-diurnal tides with a tidal range of about 3 m (Obura 2001) and an ebb-dominant asymmetry (Kitheka 1996, 1997). From a (long-distance) dispersal perspective, it is crucial to note that the bay is open to the Indian Ocean through a relatively wide (3500 m) entrance in the South. Although, a coral reef zone structurally separates the northern end of the Bay from the Indian Ocean, the reef has a series of narrow channels and only emerges at low spring tide (Kitheka 1996). 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 (Oct.-Nov.) (Kenya Meteorological Department, Mombasa, Kenya). The wind is characterized by an eastern component and is predominantly onshore (Meteorological Department 1964, EADAP 1994).

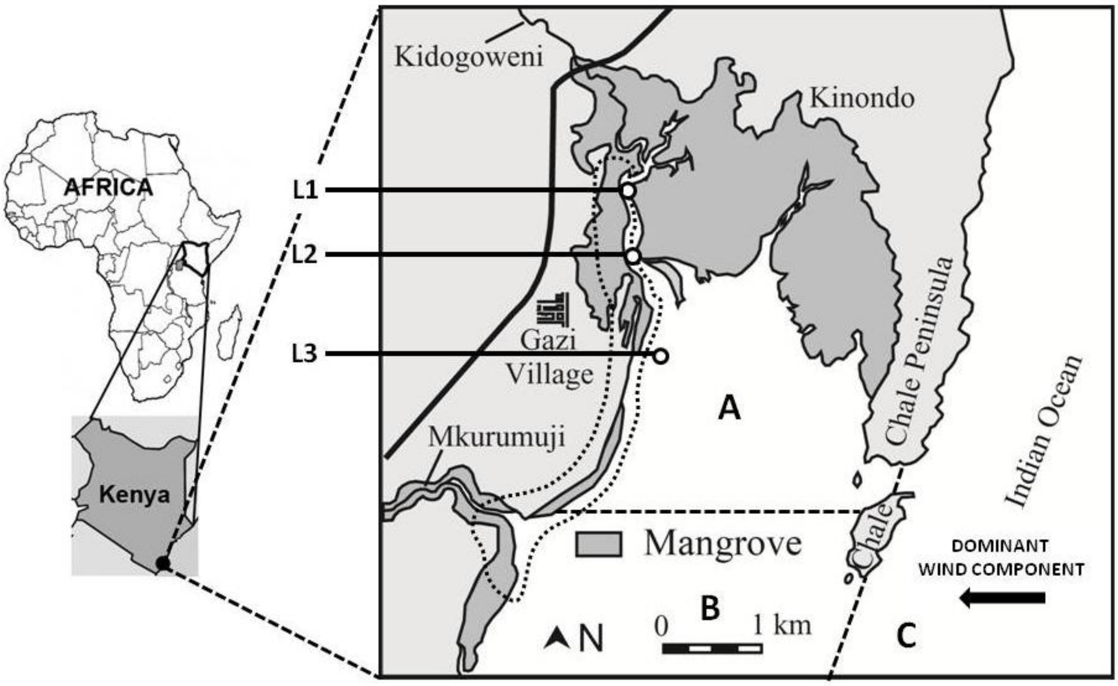


Figure 4.2: Schematic depiction of our study area (Gazi Bay), with an indication of the three locations at which propagules were dropped in our field experiment (L1 to L3). The dotted contour represents the area where propagules were sought 12h after having been released. The zones were local fishermen recovered propagules whilst fishing are indicated with A, B and C, separated by bold dotted lines.

On February 27th, 3 days after spring tide, three groups of 200 *C. tagal* and 100 *R. mucronata* propagules were released at three different locations (L1, L2 and L3) along the Kidogoweni Creek (Fig. 4.2), at the start of outgoing tide at L1 and L2 and at less than one hour later at L3. The different numbers of *C. tagal* and *R. mucronata* propagules per site reflect availability in the field at the moment of propagule collection. L1 and L2 are located in the centre of the Creek, whereas L3 is located 300 m offshore. In order to distinguish the propagules from each group and identify the original dropping location at the end of the experiment, we used white (non-toxic) waterproof paint to encode all propagules with one, two or three stripes, respectively. The white marks also increased the visibility and thus the number of propagules we found back after their release, especially in densely forested areas along the coastline (dark grey area within the dotted contour in Fig. 4.2) and in natural hydrodynamic traps where large amounts of organic material such as leaf litter accumulate.

Furthermore, all propagules were given a number to facilitate easy processing of dispersal distance information.

After a period of 12 hours (two ebb-tides since the start of the experiment), we walked the entire southern coastline, starting 100 m upstream from dropping location L1 and ending about 300 m south of the Mkurumuji river mouth (dotted contour in Fig. 4.2). The limits of this area are based on the absence of painted propagules upstream and downstream of this region, using a buffer of 100 m. We crossed the Creek several times to screen parts of the eastern coastline, where no painted propagules were recovered. A Garmin GPSMAP 62 was used to determine the geographical coordinates of the location for each found propagule. We repeated this search one week later.

Data analysis of field experiment

The dispersal distance *d* was calculated for each propagule using the spherical law of cosine and the obtained longitude-latitude data:

$$d = \arccos\ \left[\sin(Y_1)\sin(Y_2) + \cos(Y_1)\cos(Y_2)\cos(X_1 - X_2)\right] * R \qquad (1)$$

with (X_1, Y_1) and (X_2, Y_2) the longitude and latitude of the stranding location and the dropping location, respectively, and R = 6370 000 m (Earth's radius). Although this formula may underestimate the absolute dispersal distance of some propagules, ignoring the shape of the coastline and the Creek's nonlinear shape (plan view), it yields a reliable proxy. Dispersal distance frequency plots were made subsequently for each dropping location separately.

In order to test if there is a significant difference between the dispersal distance distributions of *C. tagal* and *R. mucronata* propagules in our field experiment, a Mann-Withney U test was used. All statistical tests were completed using Statistica 8.0 (Statsoft).

Fishermen data

As a proxy for propagules that leave the system to the open ocean, and possibly embark on LDD, we asked local fishermen to keep a logbook. In this logbook they wrote down the amount of propagules they found in their nets, as well as the zone in which the recoveries were done. Three zones were delineated: within the Bay (zone A), a transitional zone (zone B) and the Indian Ocean (zone C) (Fig. 4.2). However, observations were randomly gathered during their fishing trips. Consequently, we do not know which zones were screened at which date. These data are therefore only a rough indication of LDD.

Results

Flume study

Inter-specific differential effect of wind. When no wind was added to the experimental setup, all propagules dispersed at almost the exactly same speed as the water current (Fig. 4.3, Table 4.1). At the current speed of 30 × 10^{-2} m s^{-1}, only the dispersal speed of the horizontal *R. mucronata* propagules (28.3 × 10^{-2} m s^{-1}) and the *X. granatum* fruit (27.7 × 10^{-2} m s^{-1}) was on average slightly below the current velocity. As a consequence, the mean speed of horizontal *C. tagal* propagules was 1.57 × 10^{-2} m s^{-1} higher than that of the horizontal *R. mucronata* dispersal units (t = 3.39, df = 38, P = 0.002, n = 40). In general, for all species, the detailed velocity profile showed an acceleration phase, which was proportionally more pronounced depending on the density of the dispersing unit (data not shown). Nevertheless, this phase was negligibly short in all cases and consequently hard to detect in resulting figures (Fig. 4.4).

When wind was added, both in the same direction and opposite to the water flow, horizontally floating *C. tagal* and *R. mucronata* propagules showed quasi identical dispersal velocities, although *C. tagal* moved at a slightly higher speed in all cases using a 30 × 10^{-2} m s^{-1} water flow velocity (Fig. 4.3, Table 4.1). The average speed of horizontal *C. tagal* propagules was 3 × 10^{-2} m s^{-1} and 4.14 × 10^{-2} m s^{-1} higher than for horizontal *R. mucronata* propagules, under the S-scenario (t = 11.23, df = 38, P < 0.001, n = 20) and O-scenario (t =

6.24, df = 38, P < 0.001, n = 20), respectively. These differences were smaller when the water flow velocity was set at 15 × 10^{-2} m s^{-1}, where horizontal *C. tagal* propagules on average moved at a speed of 1 × 10^{-2} m s^{-1} (S-scenario, t = 3.04, df = 38, P = 0.004, n = 20) and 0.5 × 10^{-2} m s^{-1} (O-scenario, t = 1.89, df = 38, P = 0.066, n = 20) faster than the horizontal *R. mucronata* counterparts.

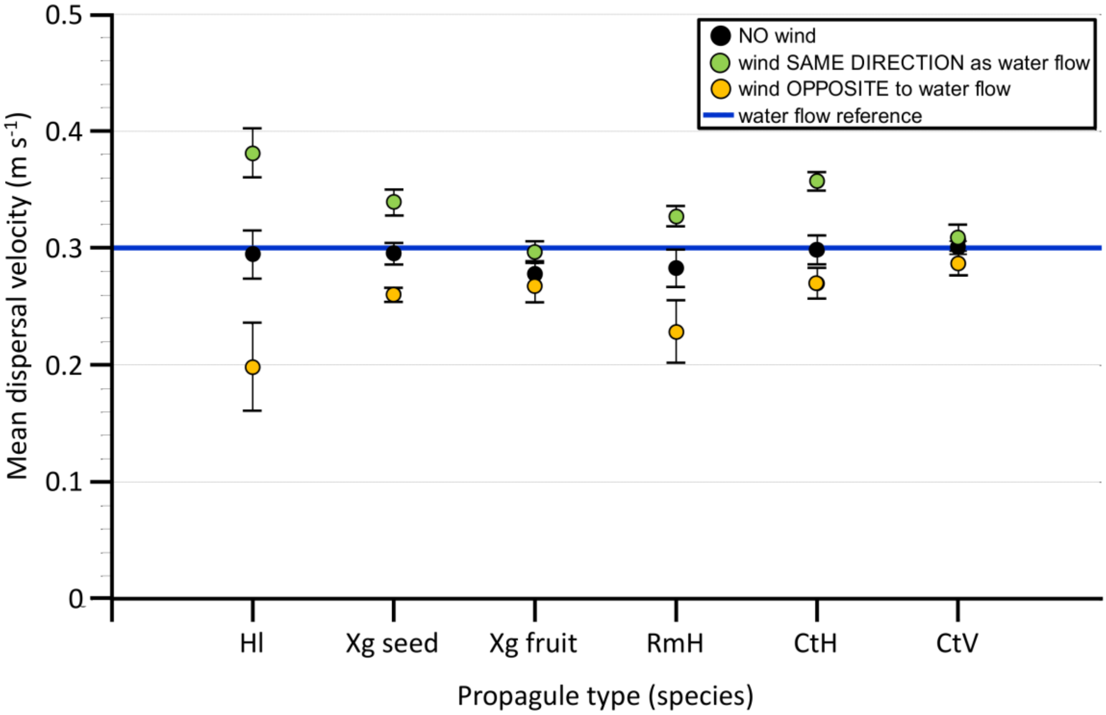


Figure 4.3: Mean dispersal velocities for all species used in the flume study, for the N-scenario (black circles), the S-scenario (grey circles) and the O-scenario (open circles). Vertical bars indicate standard deviations. The water flow velocity is added as a reference (dotted line). Hl: *Heritiera littoralis* propagules; Xg seed and fruit: seed and fruit of *Xylocarpus granatum*, respectively; RmH: *Rhizophora mucronata* propagules; CtH and CtV: horizontally and vertically floating *Ceriops tagal* propagules, respectively.

Although the results of *X. granatum* seeds were very similar to those of horizontally floating *C. tagal* and *R. mucronata* propagules, the *X. granatum* fruit seems to be least influenced by prevailing wind forces, dispersing at 16.92 ± 0.64 × 10^{-2} m s^{-1} under the S-scenario and at 15 × 10^{-2} m s^{-1} current velocity. For 30 × 10^{-2} m s^{-1} water speed, the *X. granatum* fruit dispersed at a speed of 29.66 ± 0.92 × 10^{-2} and 26.74 ± 1.43 × 10^{-2} m s^{-1} in the S- and O-scenario, respectively. The *H. littoralis* propagules are most influenced by prevailing wind conditions, dispersing at 38.10 ± 2.06 × 10^{-2} m s^{-1} in the S-scenario and at 19.84 ± 3.70 × 10^{-2} m s^{-1} in the O-scenario. If the water flow velocity was set at 15 × 10^{-2} m s^{-1} and wind in the same direction was added to the system, *H. littoralis* propagules reached a mean velocity of 27.12 ± 5.37 × 10^{-2} m s^{-1}. For the O-scenario and a 15 × 10^{-2} m s^{-1} current velocity, both *H. littoralis* and *X. granatum* propagules showed a static behaviour or moved against the water flow.

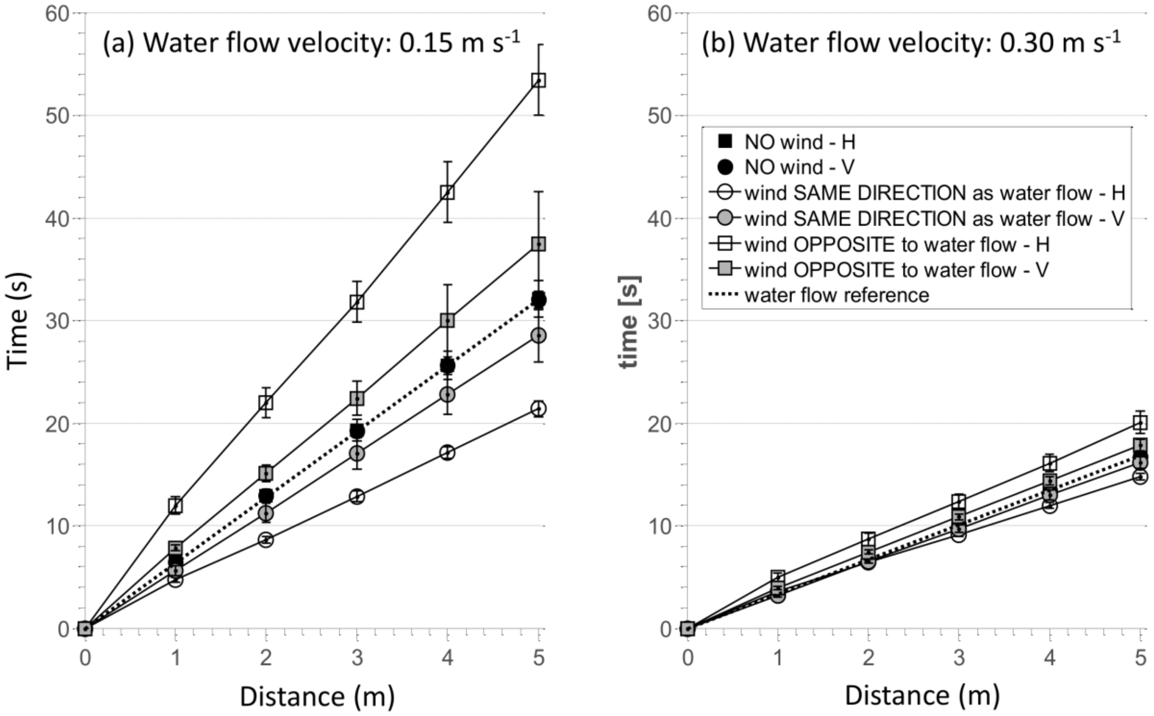


Figure 4.4: Dispersal velocity profile of horizontally (open symbols, H) and vertically (grey symbols, V) floating *Ceriops tagal* propagules, for the S-scenario (circles), O-scenario (rectangles) and for the scenario in which was not considered (black symbols). The water flow velocity (dotted line) is added as a reference. All wind scenario's were tested using a water flow velocity of (a) 0.15 m s^{-1} and (b) 0.30 m s^{-1}. Vertical bars indicate standard deviations.

Inter-specific differences most clearly follow from the scenario in which only wind was considered (no water current). In line with all other scenarios, the dispersal speed of *X. granatum* seeds (5.62 ± 1.24 × 10^{-2} m s^{-1}) approaches that of horizontally floating *C. tagal* (5.91 ± 1.20 × 10^{-2} m s^{-1}) and *R. mucronata* (5.46 ± 1.53 × 10^{-2} m s^{-1}) propagules. *Heritiera littoralis* propagules are most influenced by prevailing wind, dispersing at 7.83 ± 1.45 × 10^{-2} m s^{-1}, while the *X. granatum* fruit has a dispersal speed of 0.04 × 10^{-2} m s^{-1}, being influenced by the wind conditions only to a limited degree.

Figure 4.5 shows the increase of the dispersal speed $\Delta v(\%)$ for all propagules, for both the 15 × 10^{-2} m s^{-1} (black) and the 30 × 10^{-2} m s^{-1} (grey) water current velocity scenario, with $\Delta v(\%)$ calculated as:

$$\Delta v(\%) = \left(\frac{\bar{v}_{prop,S} - \bar{v}_{prop,N}}{\bar{v}_{prop,N}} \right) \times 100 \qquad (2)$$

Herein, $\bar{v}_{prop,S}$ and $\bar{v}_{prop,N}$ are the average dispersal velocity of the propagule under the S-scenario and the N-scenario, respectively. The value of $\bar{v}_{prop,N}$ is close to the water current velocity (see above). A general downward trend in the influence of wind with increasing density can be observed (*e.g.* negative slope of the trendlines) (Fig. 4.5). The slope of the trendline for the 15 × 10^{-2} m s^{-1} water current velocity scenario is more negative than the one for the 30 × 10^{-2} m s^{-1} scenario. Hence, the slope of the trendline is negatively correlated to the speed of the water current. Additionally, the difference between each datapoint (each dot in figure) and its projection on the trendline, from this point onward termed 'residual', decreases with increasing water current velocity.

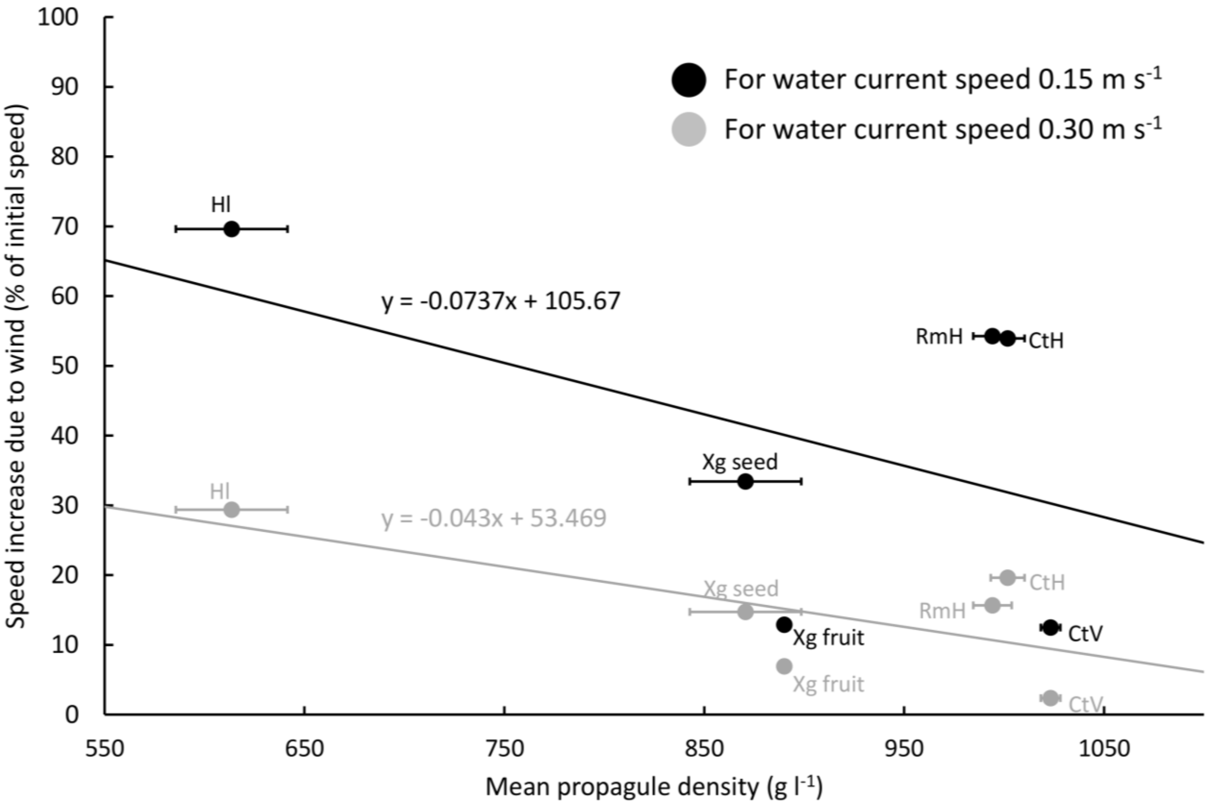


Figure 4.5: Speed increase due to wind (only for the S-scenario) in relation to propagule density, for a water current velocity of 0.15 m s^{-1} (black) and 0.30 m s^{-1} (grey).

Intra-specific differential effect of wind. Intra-specific differences are negligible, which is shown by the low standard deviations of the results in Table 4.1. However, differences occur at the level of floating orientation, which can be seen both from Figure 4.3 and Figure 4.4, as well as the velocities in Table 4.1. From the data in Figure 4.4 it follows that the horizontally floating propagules (open symbols) were significantly more influenced by equidirectional wind conditions than their vertically floating counterparts (grey symbols) ($t = 14.83$, $df = 38$, $P < 0.001$, $n = 20$ for the S-scenario; Mann-Whitney U, $P < 0.001$, $n = 20$ for the O-scenario). The role of wind appears to be less explicit when the water flow velocity was higher (Fig. 4.4 a vs. Fig. 4.4 b) ($t = 14.80$, $df = 38$, $P < 0.001$, $n = 20$ for the S-scenario; $t = -4.56$, $df = 38$, $P < 0.001$, $n = 20$ for the O-scenario). When no wind was added (black symbols), no significant differences existed among the horizontally and vertically floating propagules for a current velocity of 15×10^{-2} m s^{-1} ($t = 0.45$, $df = 38$, $P = 0.65$, $n = 20$) and 30×10^{-2} m s^{-1} (Mann-Whitney U, $P = 0.65$, $n = 20$), all floating at the same speed as the water.

Field study

Of the propagules dropped at L1, 22.5 % (n = 200) and 39 % (n = 100) of the *C. tagal* and *R. mucronata* propagules were found back, respectively. For L2, recoveries reached 32.5 % (n = 200) and 63 % (n = 100) of the released *C. tagal* and *R. mucronata* propagule batch, respectively, where for L3 this was 24 % (n = 200) and 50 % (n = 100). In total, for all dropping locations, 26.33 % of *C. tagal* propagules (n = 600) and 50.67 % of *R. mucronata* propagules (n = 300) have been recovered. The systematically lower retrieval of *C. tagal* propagules as compared to the number of *R. mucronata* propagules is very likely due to the fact that the darker colored and slender *C. tagal* propagules are less visible in the field.

The dispersal distance distributions for the propagules of both species dropped at location L1, L2 and L3 are shown in Figure 4.6. For L1, the mean dispersal distance for *C. tagal* propagules was 1156 ± 170 m and 1217 ± 211 m for *R. mucronata* propagules. No substantial inter-specific differences can be seen between the distribution in dispersal distances of both species (Fig. 4.6 a). For the propagules dropped at L2, one can recognize two different distance ranges over which propagules dispersed (Fig. 4.6 b): a first group (G1) of propagules with a shorter mean dispersal distance (140 ± 50 m for *C. tagal* and 189 ± 63 m for *R.*

mucronata) and a second group (G2) that dispersed much longer distances (1871 ± 236 m for *C. tagal* and 1683 ± 203 m for *R. mucronata*) (Mann-Whitney U, $P < 0.0001$, $n_{G1} = 33$, $n_{G2} = 94$, 1 outlier of Ct in G2 not taken into account). No significant difference exists among the dispersal shadow of both species (Mann-Whitney U, $P = 0.0920$, $n_{Ct} = 64$, $n_{Rm} = 63$). The maximum dispersal distance was 2958 m, reached by a *C. tagal* propagule (treated as an outlier, and hence not included in the calculation of the mean dispersal distance; outliers were detected using the Two sided Grubbs Test using a parameter value of 0.01 instead of 0.05). For L3, a similar scenario is observed similar to the L2 scenario, with two clearly distinct groups in terms of dispersal distance (Mann-Whitney U, $P < 0.0001$, $n_{G1} = 75$, $n_{G2} = 23$) and no significant difference between the dispersal frequency distribution of both species (Mann-Whitney U, $P = 0.11$, $n_{Ct} = 65$, $n_{Rm} = 63$) (Fig. 4.6 c). The average dispersal distance of the first group was 861 ± 97 m and 901 ± 136 m for *C. tagal* and *R. mucronata*, respectively. Individuals of the second group reached more remote areas from the dropping location (L3), 2483 ± 178 m for *C. tagal* and 2543 ± 101 m for *R. mucronata*. The maximum dispersal distance here was 2783 m.

Environmental settings where the propagules were recovered differ widely, though for L1 and L2, most propagules were recovered along the high water line south-southwest of L2, and in an adjacent forest. While the propagules on the shore were concentrated near the high water mark, the propagules in the forest were lying distributed over an area from the border of the Creek up to about 90 meters inland, lying mainly amongst roots of *R. mucronata* trees. Propagules dropped at L3 stranded on the beach, west of L3, up to the mouth of Mkurumuji River. Where the shore and beach mainly consist of bare sand, outcrops of fossil coral reef are quite extensive in some places. In these areas, propagules were collected in small pools in the dead coral's surface, under loose debris of old coral, behind fallen palm tree trunks and between extensive amounts of leaf litter in hydrodynamic traps near the high water mark.

Fishermen data

Within the Bay (zone A), 4 and 19 propagules of *C. tagal* and *R. mucronata* were found, respectively. In the transition zone (zone B), 2 and 31 propagules, and in the Indian Ocean

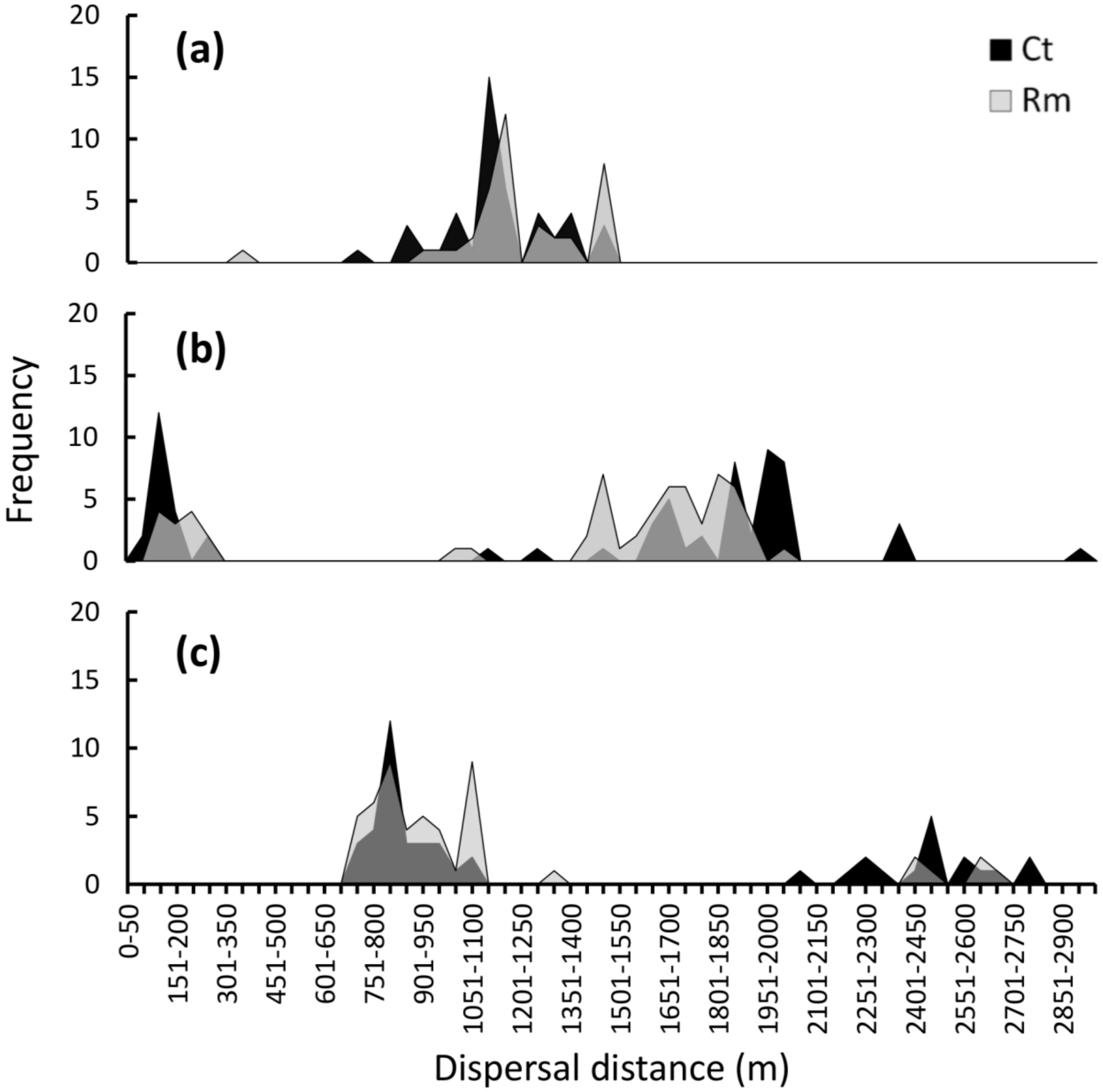


Figure 4.6: Dispersal distance distribution (number of propagules) for *Ceriops tagal* (black) and *Rhizophora mucronata* (grey) propagules used in the release-recapture experiment in the field, for propagules dropped (a) at location L1; (b) at location L2; and (c) at location L3. Locations are indicated in Figure 4.2.

(zone C), 5 and 119 propagules of these species were found, respectively. The fishing nets used within the bay are 50 m in length, and 3 m wide, with a mesh size that varied from 1.3 (middle part) to 5 cm (outer part). Beyond the coral reef (zone C), fishing nets were 70 m long and 9 m wide, and had a mesh size of 1.3 cm. Although the exact coordinate of each individual measurement is not known, hampering the study of spatial patterns, this low-cost method provides valuable data on the potential for LDD for species present in this mangrove habitat.

Discussion

To our knowledge, this is the first study to address the role of wind in hydrochorous mangrove propagule dispersal, focusing on propagule density and morphological characteristics of propagules, as well as on their floating orientation.

In the presence of wind, dispersal velocities significantly differed among species and buoyancy orientation of propagules. Thus, in agreement with our hypothesis (1) the influence of wind is more pronounced for dispersal units with a lower density. Propagules with a lower density will have a larger proportion of their volume above the water surface, which allows the wind force to exert more influence. *Heritiera littoralis* propagules floating *on* the water surface are most influenced by prevailing wind conditions, yielding significantly higher velocities when the wind is equidirectional to the water current, but strongly limiting the dispersal range when the wind acts opposite or under a certain angle to the dominant water flow. Among elongated propagules, the density distribution of a propagule must be taken into consideration, since it determines the propagule floating orientation and thus indirectly the degree to which the fate of the propagule is influenced by the wind. This is consistent with our hypothesis (3), that vertically oriented propagules are influenced significantly less than their horizontally floating counterparts. The surface roughness becomes gradually more important as the body of a propagule protrudes above the water surface. Therefore, hypothesis (2) is rejected in the particular case where a significant part of a propagule's volume is submerged.

Thus, significant differences exist among species when studying the role of wind in hydrochorous mangrove propagule dispersal, which is especially interesting in meta-population dynamics, genetic exchange and more specifically for defining dispersal kernels and dispersal model output.

Flume study

Our study answers the need for a better understanding of the dispersal mechanisms, which – along with establishment processes – present a valuable additive for existing (individual based or particle) models. Models, such as the FORMAN, KIWI and MANGRO model, constitute a standard (ecological) tool in modeling population dispersal (Werner *et al.* 2001). More specifically, they are being used to investigate the long-term evolution of Neotropical mangrove forest development, including the effects of natural and human-induced disturbances (*e.g.* Berger *et al.* 2006, Berger *et al.* 2008). Though these IBMs and the advection-diffusion hydrodynamic model of Di Nitto *et al.* (2013) are of great value in studying mangrove forest evolution and propagule dispersal, no particle-based model has been constructed in order to study the hydrochorous dispersal of mangrove propagules. Although it is assumed that finite-volume and particle tracking models should yield comparable results when properly used (Zhang and Chen 2007), this study shows that, despite mangrove propagules being passive dispersal units, species-specific differential effects of wind on propagule dispersal exist. In collaboration with Deltares, knowledge from this study will be used in the Delft3D-PART model, allowing particles (mangrove propagules) to be followed as individuals (Lagrangian) with user-defined properties. This in order to improve dispersal modeling output from the Delft3D-WAQ model (Di Nitto *et al.* 2013) in which propagules were assumed to react similarly on wind conditions.

In our study, we investigated the dispersal behaviour of *C. tagal* and *R. mucronata*, as well as *H. littoralis* and *X. granatum* propagules, under various water flow velocities and wind conditions. When wind was ignored in the experimental treatment, the dispersal velocity equaled the current speed for all propagule types, which can be explained from a purely physical point of view, where energy is transferred to the propagule until equilibrium with the water body is reached. The time to reach this equilibrium depends both on the mass of the dispersing unit, as well as on the energy of the water flow. The latter may explain why, in the case of a 30×10^{-2} m s^{-1} water flow velocity, the average velocity of *R. mucronata* dispersal units and the *X. granatum* fruit was lower than that of *C. tagal* propagules (Table 4.1), very likely being a direct consequence of the length of the test-section (5 m), meaning that these dispersal units did not have the time to reach a steady state, where they did in the 15×10^{-2} m s^{-1} water flow scenario. When wind was considered in the experiment, *H.*

littoralis propagules were by far the most strongly influenced dispersal units, which follows directly from their low density, as well as the presence of a dorsal sail acting as a sail. This may be advantageous when the wind is parallel and in the same direction as the water flow, but strongly limits the dispersal range when wind is opposite or acts under a certain angle. In their study, Stieglitz and Ridd (2001) mentioned that wind-drift seemed to have a negligible effect in the Normanby Bay at the moment of their observations. No details are given for the wind speed and direction in their study, but low wind speeds and differences in floating behaviour might be explanatory. Floating capacity of propagules (buoyancy) evolves through time (unpublished data), changing the portion of the propagule above the water surface.

In order to compare morphological groups, we also considered *X. granatum* seeds. Though their size is most comparable to that of *H. littoralis* propagules, their dispersal speed values differ widely. This is explained by the higher density of *X. granatum* seeds compared to the lighter *H. littoralis* propagules and the absence of a sail. Where the latter float on top of the water column, the *X. granatum* seeds are submerged mostly, with only a small portion of the seed sticking out of the water body, and consequently catching less wind. The dispersal unit that was least influenced by the wind, was the *X. granatum* fruit. Its high mass requires more time to reach the equilibrium speed, but once this equilibrium state is reached, the wind has little influence on the small portion of the smooth and spherical surface that rises little above the water surface.

The elongated propagules of *C. tagal* and *R. mucronata* showed comparable results, though the *R. mucronata* propagules on average were slightly slower due to a higher mass. An interesting difference was found between horizontally and vertically floating propagules of *C. tagal*, where in all experimental setups, the vertically oriented propagules were significantly less influenced by the acting wind forces.

In general, the influence of wind is negatively correlated with propagule density (Fig. 4.5). Nevertheless, the propagule's shape and surface roughness may not be ignored. The emerging surface of *X. granatum* fruits, for example, is part of a sphere with low surface roughness. Consequently, the wind has very little grip on its emerging surface. *H. littoralis* propagules, on the other hand, catch more wind, since an important part of their emerging volume (*e.g.* dorsal sail) extends in the z-direction (positive upward). The origin and magnitude of residuals can be explained from this point of view. The decrease of the trendline's slope in Figure 4.5 with increasing water current velocity can be explained by the fact that the net force of wind on all propagules becomes relatively less important. Consequently, the species-specific differential effect of wind becomes less explicit, which is illustrated by the lower residuals. Although Figure 4.5 assumes equidirectional wind and water conditions, the overall relation between density and the role of wind in hydrochorous dispersal will still hold in other scenarios where wind and water forces act under a different angle. From a physical perspective, a more pronounced species-specific differential effect would be expected if both forces act under an angle α =]90,270[, that is all winds with a component that is opposite to the dominant water current.

While the dispersal of propagules, and the role of wind therein, has been treated uniformly in the hydrodynamic model of Di Nitto *et al.* (2013), the results of our study show that important differences exist among species, but also among individuals of the same species. In order to mathematically express species-specific dispersal velocities, further experiments are needed.

Field study

The dispersal range of propagules dropped at site L1 (Fig. 4.1) in the field all stranded in a range of 750 to 1500 m from the dropping location (Fig. 4.6 a). This differs from the propagules dropped at L2 and L3 (Fig. 4.6 b and 4.6 c, respectively) where two distance ranges can be identified. This can be explained by the combination of the dominant easterly wind direction during the experiment, and the presence of natural wind barriers. The creek is relatively narrow at L1, with a partial blocking of the wind by the mangrove forest, in contrast to L2 and especially L3, where the creek gradually widens and the wind can fully influence the route of the dispersing units. Knowledge from our flume study enables us to clarify the appearance of various distance ranges, assuming that for L2 and L3, the shorter distance range represents horizontally floating propagules, being directed landward by the easterly wind, while the vertically oriented propagules are less influenced by the wind and consequently strand in more remote areas. What controls the dynamics of floating orientation during dispersal has received little attention. Preliminary research has recently shown that variations in floating orientation is related to shifts in tissue density in the middle and radicle part of the propagule via changes in the quantity of air pockets (unpublished data). However, the physiological and anatomical explanation of these variations and its potential environmental drivers (water temperature, salinity, etc.) require further study.

Considering the wind conditions in our study area (estuary and strong shoreward winds), a high density (*e.g.* floating just under the water surface) is advantageous for LDD, since the wind has less influence on submerged propagules and propagules therefore follow the water currents. Long distance is understood here as leaving the local mangrove biotope (enclosed bay), reaching the open sea. For propagules with a lower density, surface roughness becomes additionally important, since these propagules have a higher volume sticking out of the water and their dispersal path is therefore more influenced by wind action. In this latter situation, the surface roughness is preferably minimal with respect to LDD. Low density and high surface roughness will increase the susceptibility to the influence of wind, and increase the chance for the propagule to be blown towards the coast, and thus reduce its chances to leave the estuary. Among elongated propagules, vertically floating propagules are the most suitable candidates for LDD in our field situation, being directed dominantly by tidal and ocean currents. Nevertheless, hydrodynamic and wind conditions in each study area must be studied carefully in relation to local landform (or topographic) characteristics, in order to determine which propagules are most advantageous in the context of LDD. For example, low density, whether or not in combination with a high surface roughness, will very likely result in longer dispersal distances if the wind direction is parallel to or away from the coast. In general, we believe that floating, but fully submersed propagules will be the best candidates for LDD. However, to study successful LDD more holistically, the buoyancy period and viability should also be considered.

Fishermen data

Although these data cannot be used to quantify LDD, they indicate that propagules can leave the local mangrove system. This is especially clear from the amount of propagules that were found in the open ocean (zone C). Differences between *C. tagal* and *R. mucronata* may be explained by the combination of species abundance and their spatial distribution. *R.*

mucronata and *C. tagal* are the most represented species in our study area (Neukermans *et al.* 2008), but both species occupy different zones along the intertidal area. Since *R. mucronata* trees are found in the most seaward zone, the dispersal barrier that separates them from the open water, is narrower as compared to the barrier that needs to be crossed by *C. tagal* propagules which are released higher in the intertidal zone (see Van der Stocken *et al.* 2015a).

Conclusion

Our study clearly indicates that the overall dispersal distances of hydrochorous mangrove propagules that leave the forest, thereby reaching open waters, is not only determined by prevailing hydrodynamic conditions but also by dominant wind forces and also reflects species-specific aspects. The degree to which wind determines a propagule's dispersal path depends on a combination of the propagule's density and floating orientation, as well as its morphology and surface roughness. The latter is especially important for propagules that have a significant part of their volume above the water surface (*i.e.* low propagule density). For example, *H. littoralis* propagules are easily steered by acting wind forces, with their dorsal sail, having a low density, thereby floating *on* the water surface. On the other hand, wind forces have a limited direct impact on *X. granatum* fruits, which are for the most part submerged due to their large density and have a smooth and spherical surface. For more elongated propagules, the floating orientation turns out to be even more important for dispersal. This follows directly from the observation of two distinct dispersal groups in our field experiments, suggesting that vertical propagules dispersed further than horizontal propagules, since the latter were most likely blown ashore by a dominant easterly wind. This can be fully explained by our wind experiments in a flume. Hence, wind should be considered as an additional dispersal vector to increase the realism of dispersal models for organisms and objects that disperse passively at or very near to the ocean surface.

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CHAPTER 5

INTERACTION BETWEEN WATER AND WIND AS A DRIVER OF PASSIVE DISPERSAL IN MANGROVES

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Abstract

Although knowledge on dispersal patterns is essential for predicting long-term population dynamics, critical information on the modalities of passive dispersal and potential interactions between vectors is often missing. Here, we use mangrove propagules with a wide variety of morphologies to investigate the interaction between water and wind as a driver of passive dispersal. We imposed 16 combinations of wind and hydrodynamic conditions in a flume tank, using propagules of six important mangrove species (and genera), resulting in a set of dispersal morphologies that covers most variation present in mangrove propagules worldwide. Additionally, we discussed the broader implications of the outcome of this flume study on the potential of long distance dispersal for mangrove propagules in nature, applying a conceptual model to a natural mangrove system in Gazi Bay (Kenya). Overall, the effect of wind on dispersal depended on propagule density (g l^{-1}). The low-density *Heritiera littoralis* propagules were most affected by wind, while the high-density vertically floating propagules of *Ceriops tagal* and *Bruguiera gymnorrhiza* were least affected. *Avicennia marina*, and horizontally floating *Rhizophora mucronata* and *C. tagal* propagules behaved similarly. Morphological propagule traits, such as the dorsal sail of *H. littoralis*, explained another part of the interspecific differences. Within species, differences in dispersal velocities can be explained by differences in density and for *H. littoralis* also by variations in the shape of the dorsal sail. Our conceptual model illustrates that different propagule types have a different likelihood of reaching the open ocean depending on prevailing water and wind currents. Results suggest that in open water, propagule traits (density, morphology, and floating orientation) appear to determine the effect of water and wind currents on dispersal dynamics. This has important implications for inter- and intraspecific variation in dispersal patterns and the likelihood of reaching suitable habitat patches within a propagule's viable period.

Introduction

In many natural ecosystems, dispersal of organisms is mediated by a variety of external agents known as vectors such as wind, water and carrier animals. However, multiple vectors do not act independently (van der Pijl 1982, Ozinga *et al.* 2004, Nathan 2007). For instance, wind may impact the flight patterns of birds transporting the seeds of wetland plants and the eggs of aquatic crustaceans. Similarly, local wind direction can constrain the transfer of genetic material through pollen by bumblebees. Insight in the multiple dispersal vectors involved in the dispersal process of a particular species is essential to realistically describe and predict dispersal trajectories (Nathan 2007). In the case of oceanic dispersal, the course of dispersing propagules (*i.e.* dispersal units) is determined by the interaction of hydrodynamics and wind. However, this interaction has remained largely understudied, constraining the realism of existing dispersal models. Considering the wide variety of morphologically distinct propagules carried at the ocean surface (Gunn and Dennis 1999), it is reasonable to assume that wind may differentially affect the dispersal patterns of these propagules. Such insight is highly relevant, especially in the context of habitat destruction and fragmentation which threaten biodiversity (Tilman *et al.* 1994, Fahrig 2003, Ewers and Didham 2006), since together with information on propagule viability it determines the probability of effective dispersal (*sensu* Nathan 2006). In this study, we use mangrove propagules with a wide variety of morphologies to test the effect of wind on hydrochorous dispersal. Mangroves appear along tropical and subtropical coasts where onshore and offshore winds could impact the fate of dispersing propagules, while the variety of morphologically distinct propagules allows us to study species-specific differential effects.

Given the seemingly infinite expanse of the world's oceans, transoceanic dispersal of mangrove tree species via specialized buoyant propagules can be considered a remarkable evolutionary achievement. Although most propagules disperse at a local scale, *i.e.* within the boundaries of the local habitat, a minority is exported to open water where they may contribute to long distance dispersal (LDD). A better understanding of dispersal distances and directions, *i.e.* dispersal patterns, is considered a priority given the increased fragmentation of natural mangrove habitats (Duke *et al.* 2007) and expected shifts of species ranges in response to global environmental change (Valiela *et al.* 2001, Gilman *et al.* 2008).

The latter requires populations to shift and settle a new population elsewhere or adapt to the new conditions. While dispersal within the local habitat drives local replenishment, LDD can be of disproportionate importance (with respect to numbers involved) by either mediating colonization of remote areas or by providing gene flow among distant populations, which can promote local adaptive potential. Additionally, rare LDD events across oceans can result in important biogeographic signals.

Dispersal distances of mangrove propagules have mostly been studied at local (hundreds of meters) and intermediate scales (several km) using marked propagules (Yamashiro 1961, Chan and Husin 1985, Breitfus *et al.* 2003, Van der Stocken *et al.* 2013). However, these release-recapture and genetic studies typically assume dispersal in a straight line from one location to another, and do not provide information on realized dispersal trajectories. At regional (10^3–10^5 m) and biogeographical (10^5–10^7 m) scales, quantifying dispersal poses methodological challenges (Nathan 2001, Nathan *et al.* 2008). Given the rare nature of LDD events, the time frame required for observation may be too long for most research programmes, while the dilution effect resulting from a low number of propagules spread over a vast expanse of water makes it practically unfeasible to intercept propagules during transport. Long-term echoes of rare dispersal events, however, can be detected in the population genetic structure (Dodd *et al.* 2002, Nettel and Dodd 2007, Marris 2014). Additionally, large-scale experiments such as the one performed by Steinke and Ward (2003), in which 4500 drift cards were dropped from an aircraft into the sea, can help to demonstrate the feasibility of LDD. Geographic variation in allele frequencies, interception of propagules or recapture patterns of artificial propagules, however, typically do not generate information about the dispersal trajectories of individual propagules. In this context mechanistic models that integrate information from ocean currents with intimate knowledge of mangrove ecology can play an important role. Although recent research shed new light on mangrove establishment requirements (Balke *et al.* 2011, Balke *et al.* 2013a, Balke *et al.* 2013b), the relative importance of many other traits that affect dispersal and mortality, remain obscure. Such knowledge, however, will not only be crucial to parameterize mechanistic models, it will also help to answer ecological questions such as to what extent the local species composition and diversity is controlled by dispersal limitation and the composition of the regional species pool (see Sutherland *et al.* 2013).

A largely neglected factor that could influence mangrove propagule dispersal dynamics is wind action (Van der Stocken *et al.* 2013). A finite-volume advection-diffusion model developed by Di Nitto *et al.* (2013) in a Sri Lankan lagoon complex suggested that wind action can affect dispersal trajectories. However, in this model, the authors applied a wind drag function uniformly on all species as a hydrodynamic component but species-specific differential effects were not considered (Di Nitto *et al.* 2013). Mangrove propagules strongly differ in propagule size, shape and density, which can affect the distribution of drag area inside and outside the water. Therefore, it is sensible to assume that the relative importance of wind versus water drag will differ strongly among species. In this study we build on our pilot study (Van der Stocken *et al.* 2013) in order to investigate general dispersal mechanisms across mangrove species. Additionally, the potential adaptive value of the dorsal sail of the mangrove species *Heritiera littoralis* in terms of promoting wind mediated hydrochorous dispersal has not yet been investigated. This notable morphological feature could facilitate or counteract hydrochorous dispersal depending on the relative direction of water and wind currents.

We used a racetrack flume adjusted with a wind generator to investigate variation in hydrochorous dispersal of mangrove propagules in response to different hydrodynamic and wind conditions. The experiment included propagules of six species and six genera, resulting in a set of morphologies that covers most variation present in mangrove propagules worldwide. In addition to the natural propagules, we used sail-less mimics of the characteristic sail-fitted propagules of *H. littoralis* to explore the potential adaptive origin of the dorsal sail in terms of its sensitivity to wind action. We hypothesized that (1) dispersal velocities are increasingly determined by wind speed and direction for propagules with decreasing density, because Archimedes' law dictates that they will have a higher proportional volume protruding from the water; (2) morphological traits that increase the wind drag outside the water, significantly enhance the effect of wind relative to the effect of water currents. The latter is expected to apply to propagules with a specific morphological feature, such as the *H. littoralis* propagules with a dorsal sail, as well as to propagules with a specific floating strategy, such as horizontally floating propagules compared to vertically floating ones. Finally, we discuss the broader implications of the outcome of this flume study on the potential for LDD, applying a conceptual model to a natural mangrove system.

Material and methods

Studied species

Species were selected to cover a wide range of morphological propagule types (Fig. 5.1, Table 5.1). The elongated (torpedo-shaped) propagules of *Ceriops tagal* (Perr.) C. B. Robinson and *Rhizophora mucronata* Lamk. (both Rhizophoraceae), strongly contrast with the ellipsoidal propagules of *Heritiera littoralis* Dryand. (Malvaceae). The raised dorsal sail (Tomlinson 1994), in combination with a very low density, ensures that *H. littoralis* propagules resemble small sailboats floating on the water surface. The cannonball-like fruits (a woody pericarp enclosing five to 20 seeds) of *Xylocarpus granatum* Koen. (Meliaceae) have much higher densities (983.64 ± 6.54 g l^{-1} compared to 726.33 ± 70.02 g l^{-1} for *H. littoralis*). As a result, the major part of their smooth spherical body remains submerged. Besides the fruit, we also considered the irregular angular-shaped pyramidal seeds of *X. granatum*, since both the fruits and seeds of this species disperse in mangrove habitats.

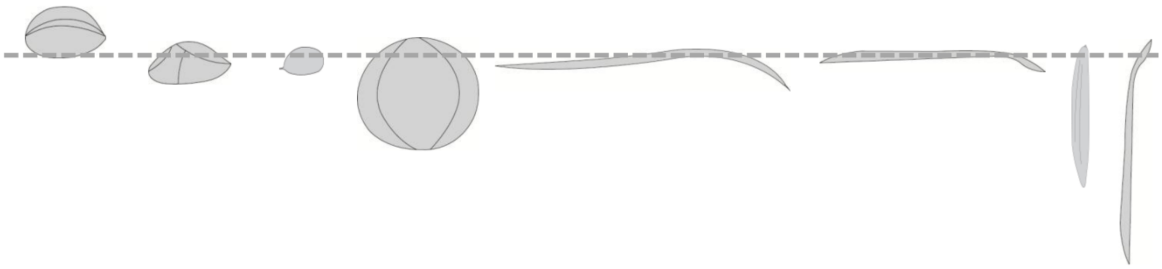

Figure 5.1: Position of the mangrove propagule types used in his study relative to the water surface (dotted line). From left to right, represented propagules are from the following mangrove species: *Heritiera littoralis*, *Xylocarpus granatum* (seed), *Avicennia marina*, *Xylocarpus granatum* (fruit), *Rhizophora mucronata*, *Ceriops tagal* (horizontally floating), *Bruguiera gymnorrhiza* and *Ceriops tagal* (vertically floating). The scale of the propagules is not the same for all drawings. For the latter, the reader is referred to the propagule mean length data in Table 5.1 and values in Tomlinson (1994).

We complemented this selection with propagules of the important pioneer species *Avicennia marina* (Forssk.) Vierh. (Acanthaceae) and the elongated *Bruguiera gymnorrhiza* (L.) Lamk. (another member of the Rhizophoraceae). *Avicennia marina* propagules are ellipsoidal to flattened ovoid, small and light, floating at the water surface. They often carry

Table 5.1: Main propagule characteristics and overview of the dispersal velocities for the various hydrodynamic and wind treatments where wind and water acted in the same direction. For general information on the various propagule types, the reader is referred as well to Fig. 1.3 and data in Tomlinson (1994).

Species	***H. littoralis***	***X. granatum* seed**	***A. marina***	***X. granatum* fruit**	***R. mucronata***	***C. tagal***	***B. gymnorrhiza***	***C. tagal***
Morphology	Ellipsoidal	Angular/Pyramidal	Ellipsoidal to flattened ovoid	Spherical ("cannonball")	Elongated	Elongated	Elongated	Elongated
Floating orientation	–	–	–	–	horizontal	horizontal	vertical	vertical
n	20	10	25	4	17	20	13	20
Mean length (cm)	–	–	–	–	36.45 ± 1.16	24.32 ± 2.14	16.02 ± 0.71	24.42 ± 3.23
Mean mass (g)	21.70 ± 0.93	58.00 ± 3.12	3.07 ± 0.10	943.51 ± 73.09	47.35 ± 2.42	7.28 ± 0.25	22.91 ± 1.57	7.08 ± 0.33
Mean density (g l^{-1})	726.33 ± 70.02	943.81 ± 17.79	968.10 ± 26.96	983.64 ± 6.54	1006.10 ± 5.76	1013.90 ± 8.04	1023.67 ± 5.23	1034.87 ± 7.20

their pericarp in the early stages of dispersal (personal observation). As for *C. tagal* and *R. mucronata*, *B. gymnorrhiza* propagules are viviparous (*i.e.* the embryo protrudes from the seed coat and the fruit, while attached to the parent tree; Tomlinson 1994) and typically elongated. *Rhizophora mucronata* has the largest propagules (36.45 ± 1.16 cm, n = 17), being much longer than *B. gymnorrhiza* propagules (16.02 ± 0.71 cm, n = 13), but having a comparable thickness. The propagules of *C. tagal* are the most slender, longer (24.37 ± 2.70 cm; n = 40) than *B. gymnorrhiza* propagules, and have a rough, warted and ribbed surface. It should be stressed here that differences in shape exist within the *C. tagal* and *R. mucronata* propagules, some being straight, while others can be bent near the plumule and the radicle. Whereas the floating orientation of *C. tagal* and *R. mucronata* propagules may vary between a horizontal and vertical position, *B. gymnorrhiza* propagules float vertically.

We used 20 horizontally and 20 vertically floating *C. tagal* propagules and 17 horizontally floating *R. mucronata* propagules. Vertically floating *R. mucronata* propagules were not considered since their length exceeded the water level in the flume, preventing vertical free flow. For *B. gymnorrhiza*, 13 vertically floating propagules were used. Furthermore, 25 *A. marina* (still carrying their pericarp) and 20 *H. littoralis* propagules were used. For *X. granatum*, we used four fruits and 10 individual seeds. All propagules were sampled in the mangrove forest of Gazi Bay, Kenya (39° 30' E, 4° 26' S). We measured the length and mass, and calculated the volume (using the water displacement method *cf.* Chave 2005) and density of all propagules. Propagules were checked for damage that could influence the buoyancy characteristics over the course of the experiments.

Propagule mimics

The potential adaptive origin of the dorsal sail in terms of its sensitivity to wind action, was tested using artificial propagules or mimics. These should be considered as *H. littoralis* propagules without dorsal sail. The mimics consisted of plastic, egg-shaped dispersal items of various sizes, which were given different densities (per type, *i.e.* per size) by filling them with different loads of pebbles (see Table 5.2). Using a special silicone glue, the mimics were made waterproof to prevent their density from changing over the course of the experiments.

Table 5.2: Characteristics of the egg-shaped mimics that were used to simulate *Heritiera littoralis* propagules without dorsal sail.

	Mass (g)	**Density (g l^{-1})**
SIZE A Length: 6 cm Height: 4 cm	8.12	159.20
	9.52	186.68
	21.91	429.55
	45.71	897.40
SIZE B Length: 9 cm Height: 5.5 cm	20.63	160.19
	23.42	182.97
	54.70	420.78
	115.76	883.66
SIZE C Length: 10 cm Height: 7 cm	42.12	160.67
	47.39	180.42
	112.27	428.92
	240.66	905.79

Flume study

A 17.5 m long and 0.6 m wide oval flume facility (Royal Netherlands Institute for Sea Research, NIOZ, Yerseke, The Netherlands) adjusted with an industrial ventilator was used to study the effect of wind on the dispersal velocity of hydrochorous mangrove propagules. This experimental set-up allowed for repetitions under controlled hydrodynamic and wind conditions. The flume was filled with seawater that was pumped directly from the sea next to the research institute. Water salinity and temperature were 35 ‰, and 9.6 °C, respectively, yielding a water density of 1027.05 g l^{-1}. Water depth in the flume was kept constant at 0.36 m during the experiment. Using a conveyer belt, a unidirectional free flow current was generated. The smooth bottom (negligible bottom friction) of the flume ensures a steep water velocity gradient, simulating deeper water. An industrial ventilator was modified to allow for multiple wind speeds. To ensure wind speeds to be constant over the course of the experiments, the test section was covered with a plastic ceil and tested for leakages.

At each one-meter interval of the test section (5 m), wind speeds were measured with a velociCalc TSI anemometer (model 8384-M-GB) at three positions over the width of the flume (in the middle and at 0.15 m from both sides of the flume), *i.e.* 15 measurements in total. Water flow velocity measurements were taken with an Acoustic Doppler Velocimeter (ADV, Nortek AS, Oslo, Norway) placed on a 3D-positioning system.

We imposed 16 combinations of wind and hydrodynamic conditions: a unidirectional water flow (0.15 m s^{-1} and 0.30 m s^{-1}) without wind; a unidirectional water flow (0.15 m s^{-1} and 0.30 m s^{-1}) in combination with a low (*ca.* 2.5 m s^{-1}), medium (*ca.* 4.5 m s^{-1}) and high (*ca.* 6 m s^{-1}) wind speed in the same and opposite direction of the water flow; a low, medium and high wind speed without water flow. Water flow velocities and wind speeds were chosen to reflect conditions in a natural mangrove habitat, based on measurements by Kitheka *et al.* (2003) and archived weather data from Mombasa (Kenya) (see Fig. 5.2).

Propagules were released one by one at the start (0 m) of the test section and traveling times were recorded at each one-meter interval using a stopwatch. The first two meters of the test section were used for the propagules to reach an equilibrium dispersal velocity, and were not included in the calculations. Dispersal velocities were calculated, by dividing the time needed to travel over the last three meters of the test section (*i.e.* precautionarily excluding the first two meters to avoid possible instabilities which may be present near the ventilator). For the opposite wind treatments, calculations were made over the first three meters.

Conceptual model

A conceptual model for the potential of LDD for mangrove propagules in nature was constructed. We discuss the LDD potential of propagules released in Gazi Bay under different combinations of onshore *vs.* offshore water and wind currents (hypothetical scenarios). We do this both for propagules that are known to be affected by wind and for those that are relatively unaffected.

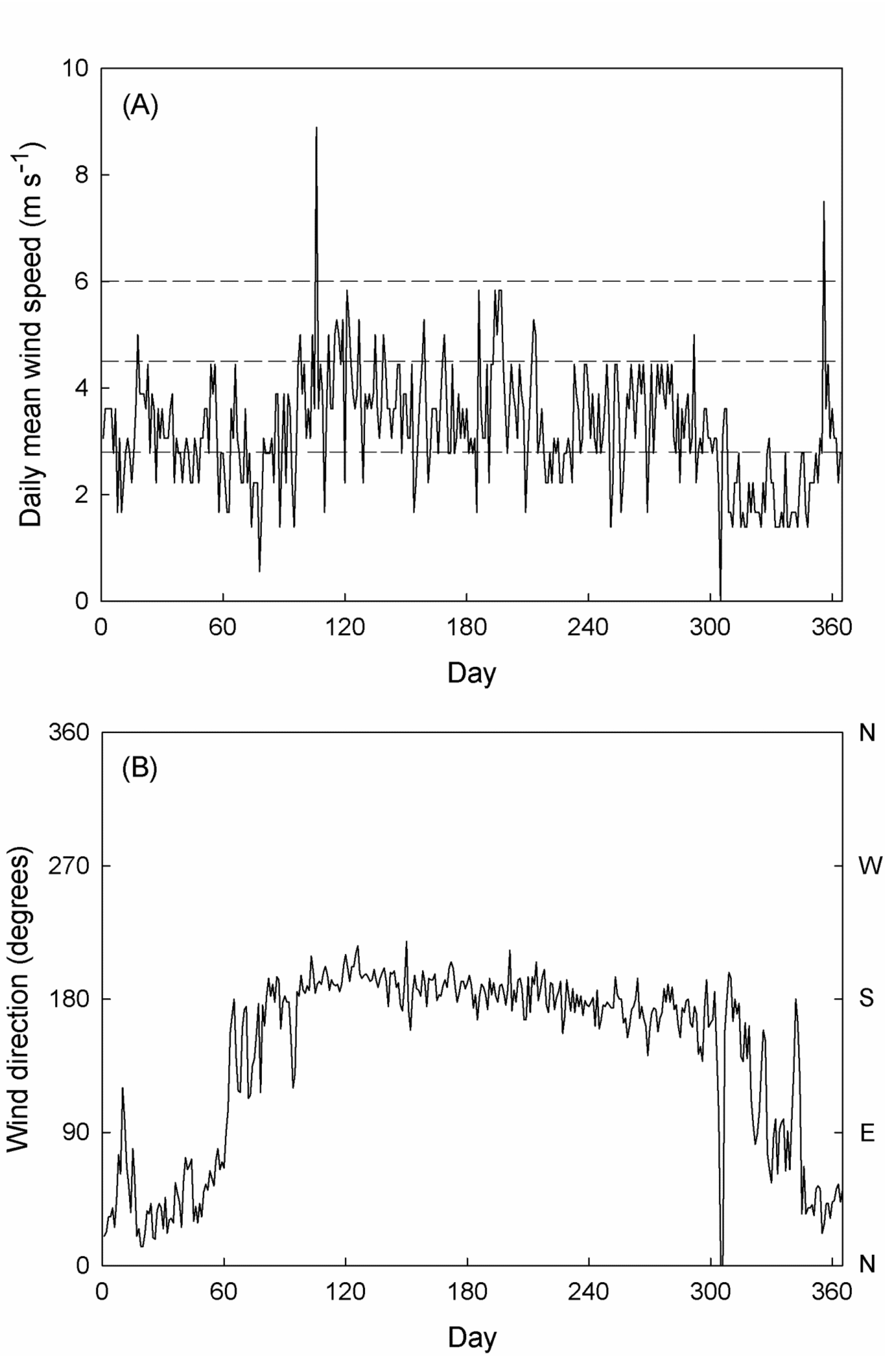

Figure 5.2: Archived data on (A) wind speed and (B) wind direction, measured 3-hourly in Mombasa (www.wunderground.com). Data is presented over a one-year period, from 1 January 2013 to 1 January 2014. Dotted lines in (A) indicate wind speeds used in our flume study.

Data analysis

We conducted factorial Analysis of Variance (ANOVA) followed by pairwise Tukey post-hoc tests to investigate differences in dispersal velocity among and within species, for various combinations of wind speed (7 levels) and water flow velocity (3 levels). Interactive effects were tested with a general linear model (GLM) with propagule density, wind speed and water flow velocity as continuous predictors for dispersal velocity. The GLM also contained the multiple interactions of these predictor variables. For investigating the effect of *H. littoralis'* dorsal sail in the wind-mediated hydrochorous dispersal process, dispersal velocity trend lines were calculated for the multiple mimics. These trend lines were then used to estimate dispersal velocities for densities of the natural *H. littoralis* propagules. Consequently, differences between the measured and estimated dispersal velocities served as a proxy for the contribution of the dorsal sail in the effect of wind. All statistical tests were performed in Statistica 8.0 (StatSoft, Inc.).

Results

Relevant propagule characteristics (morphology, floating orientation, mean length, mass and density) are summarized in Table 5.1 and Figure 5.1. Mean propagule mass and densities ranged from 3.07 ± 0.10 g (*A. marina*) to 943.51 ± 73.09 g (*X. granatum* fruit), and from 726.33 ± 70.02 g l^{-1} (*H. littoralis*) to 1034.87 ± 7.20 g l^{-1} (vertically floating *C. tagal* propagules), respectively.

The average wind speed during the low (L), medium (M) and high (H) wind speed treatments was 2.77 ± 0.23 m s^{-1}, 4.53 ± 0.38 m s^{-1} and 6.03 ± 0.08 m s^{-1}, respectively. For the treatment where the wind direction was opposite to the water flow, wind speeds were slightly different since the ventilator had to be translocated and the construction with the ceil rebuilt: 2.68 ± 0.06 m s^{-1} (L), 4.55 ± 0.19 m s^{-1} (M) and 6.03 ± 0.05 m s^{-1} (H). Water flow velocities were 0 m s^{-1}, 0.16 ± 0.02 m s^{-1} and 0.31 ± 0.03 m s^{-1}.

The effect of wind on dispersal velocities was strongly different among propagule types in the treatment without water flow (factorial ANOVA, $P < 0.0001$, $F_{6.341} = 442.48$, adjusted $R^2 =$

0.93) as well as under the 0.15 m s^{-1} (factorial ANOVA, $P < 0.0001$, $F_{7.715} = 46.17$, adjusted $R^2 = 0.98$) and 0.30 m s^{-1} (factorial ANOVA, $P < 0.0001$, $F_{7.829} = 28.54$, adjusted $R^2 = 0.96$) water flow velocity treatment. *Heritiera littoralis* propagules responded stronger to imposed wind speeds than other propagule types (Fig. 5.3). Interestingly, in the treatment with the high water flow velocity and low wind speed in the same direction, *H. littoralis* propagules were the only propagule type of which the dispersal velocity was strongly affected by wind action. They showed higher dispersal velocities than all other propagule morphotypes (One-way ANOVA, $P < 0.0001$, $F_{1.126} = 317.80$, adjusted $R^2 = 0.714$). The dispersal velocity of the vertically floating *C. tagal* and *B. gymnorrhiza* propagules were equally affected by wind action in all water flow velocity treatments (0 m s^{-1}: One-way ANOVA, $P = 0.0706$, $F_{1.61} = 3.39$; 0.15 m s^{-1}: One-way ANOVA, $P = 0.8847$, $F_{1.186} = 0.02$; 0.30 m s^{-1}: One-way ANOVA, $P = 0.4006$, $F_{213} = 0.71$). In all wind speed treatments these propagule types were less affected by wind than the other propagule types (Fig. 5.3). Wind equally affected the dispersal velocities of the horizontally floating propagules of *C. tagal* and *R. mucronata* under all water flow velocity conditions (0 m s^{-1} : One-way ANOVA, $P = 0.1830$, $F_{1.109} = 1.80$; 0.15 m s^{-1}: One-way ANOVA, $P = 0.4734$, $F_{1.219} = 0.51$; 0.30 m s^{-1} : One-way ANOVA, $P = 0.2032$, $F_{1.255} = 1.63$). The effect of wind on the dispersal velocity of *A. marina* propagules is similar to that on the dispersal velocity of the horizontally floating propagules of *C. tagal* and *R. mucronata* (Fig. 5.3), while the fruit of *X. granatum* generally shows dispersal velocities that are higher than that of the vertically floating *C. tagal* and *B. gymnorrhiza* propagules, but lower than that of all the other propagule types. The *X. granatum* seeds experience less influence from wind than *H. littoralis*, but slightly more than *A. marina* and the horizontally floating *C. tagal* and *R. mucronata* propagules.

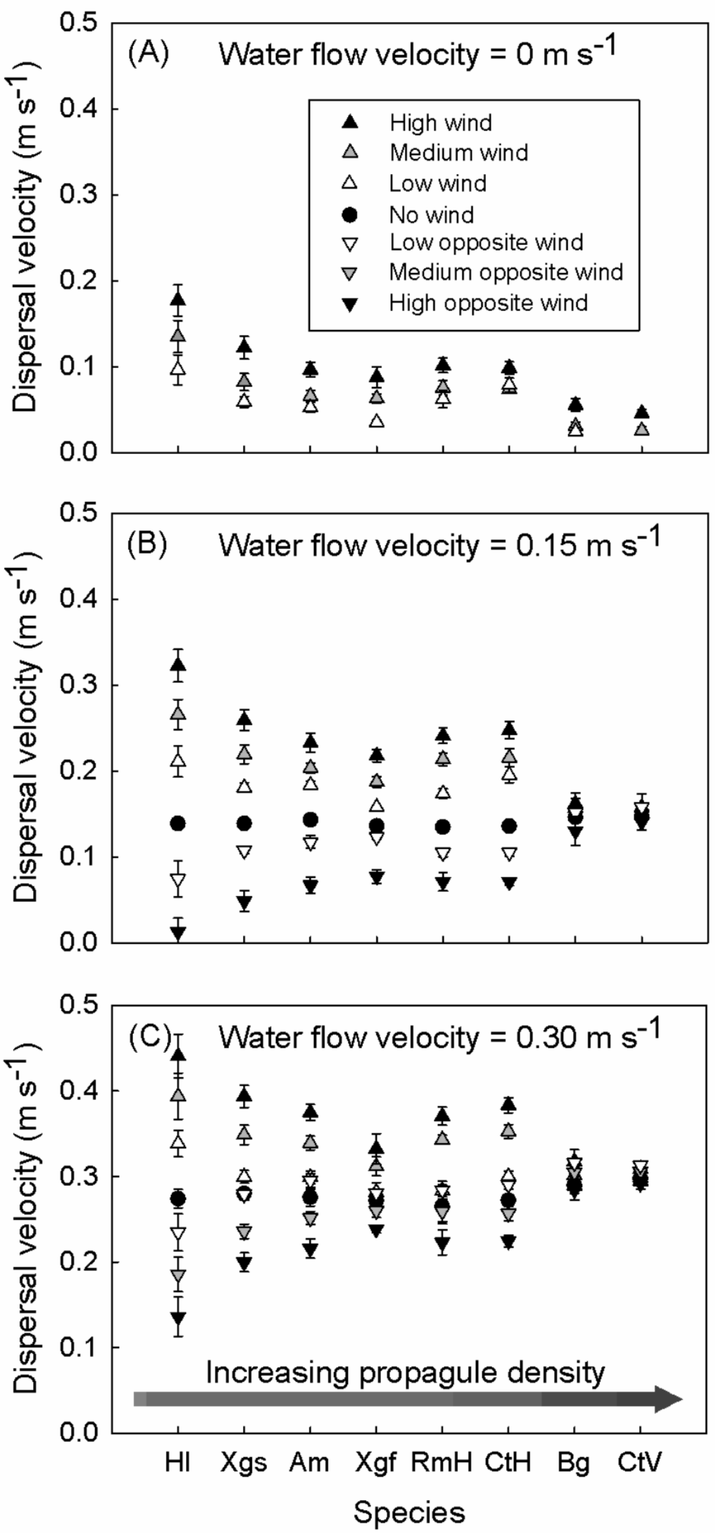

Figure 5.3: Dispersal velocities (y-axis) of the propagules used in this study (x-axis), under various wind conditions for three different water flow velocities: (A) 0 m s^{-1}, (B) 0.15 m s^{-1} and (C) 0.30 m s^{-1}. Dispersal units on the x-axis are ranked from lowest (left) to highest (right) density, as indicated by the arrow. Hl: *Heritiera littoralis*; XgS: *Xylocarpus granatum* seed; Am: *Avicennia marina*; Xgf: *X. granatum* fruit; RmH: horizontally floating *Rhizophora mucronata*; CtH: horizontally floating *Ceriops tagal*; Bg: *Bruguiera gymnorrhiza*; CtV: vertically floating *C. tagal*.

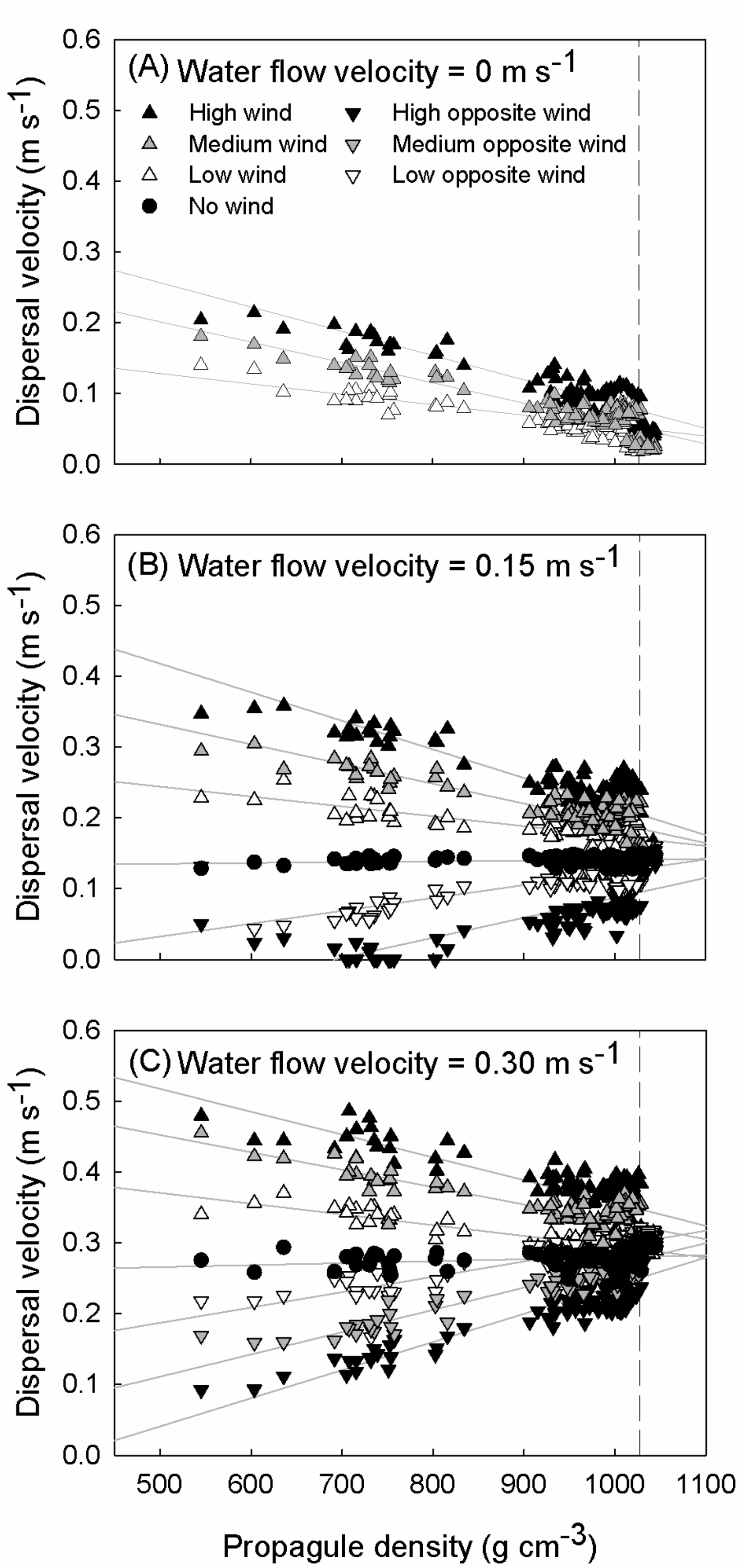

Figure 5.4: Dispersal velocities (y-axis) for all propagules used in this study, as a function of propagule density (x-axis), under various wind conditions for three different water flow velocities: (A) 0 m s^{-1}, (B) 0.15 m s^{-1} and (C) 0.30 m s^{-1}. Regression lines are plotted in light grey. The vertical dashed line indicates the water density (1027.05 g l^{-1}).

Table 5.3: Results of the general linear model for the effect of propagule density, wind speed, water flow velocity and the multiple interaction terms on dispersal velocity of mangrove propagules. Significant interactions (P < 0.05) are indicated in bold.

	Dispersal velocity Parameter	Dispersal velocity Std. Err.	Dispersal velocity t	Dispersal velocity P
Intercept	**0.052799**	**0.012695**	**4.1591**	**0.000033**
Propagule density	**-0.000042**	**0.000013**	**-3.1476**	**0.001670**
Wind speed	**0.063756**	**0.002795**	**22.8076**	**<0.00001**
Water flow velocity	**0.679794**	**0.051423**	**13.2197**	**<0.00001**
Propagule density × Wind speed	**-0.000052**	**0.000003**	**-17.7135**	**<0.00001**
Propagule density × Water flow velocity	**0.000231**	**0.000054**	**4.3131**	**0.000017**
Wind speed × Water flow velocity	0.018042	0.011387	1.5844	0.113259
Propagule density × Wind speed × Water flow velocity	**-0.000032**	**0.000012**	**-2.7403**	**0.006192**
Error	**1.04**			

Table 5.4: Result of the general linear model for the effect of propagule density, wind speed, water flow velocity and the multiple interaction terms on dispersal velocity of mangrove propagules. Significant interactions ($P < 0.05$) are indicated in bold.

	SS	Df	MS	F	P
Intercept	0.008978	1	0.008978	17.2985	**0.000033**
Propagule density	0.005142	1	0.005142	9.9077	**0.001670**
Wind speed	0.269978	1	0.269978	520.1850	**<0.00001**
Water flow velocity	0.090702	1	0.090702	174.7615	**<0.00001**
Propagule density × Wind speed	0.162847	1	0.162847	313.7676	**<0.00001**
Propagule density × Water flow velocity	0.009655	1	0.009655	18.6025	**0.000017**
Wind speed × Water flow velocity	0.001303	1	0.001303	2.5103	0.113259
Propagule density × Wind speed × Water flow velocity	0.003897	1	0.003897	7.5094	**0.006192**
Error	1.040084	2004	0.000519		

The GLM (F = 5494.98, $P < 0.001$, adjusted $R^2 = 0.95$) showed both significant main effects of density, water flow velocity and wind speed on dispersal velocity as well as interactive effects (Tables 5.3 and 5.4). The model included two significant two-way interactions as well as a significant three-way interaction. Overall, water flow velocity and (positive, in line with water flow velocity) wind speed promoted dispersal velocity, while negative wind speeds decreased dispersal velocity. Particularly lower density propagules were most sensitive to the wind treatments. Depending on the direction of the water flow vs. air flow, propagules exhibited acceleration (same direction) or deceleration (opposite direction) of their dispersal velocity (Figs 5.3 and 5.4). Significant interaction terms in the model support the interpretation of the effect of water flow velocity and wind speed being dependent on propagule density (Tables 5.3 and 5.4).

Overall, *H. littoralis* propagules with a sail responded stronger to wind than the egg-shaped mimics with a similar density but without such structures (Fig. 5.5). An indication of the contribution of the dorsal sail in the total dispersal velocity is summarized in Table 5.5.

Table 5.5: Contribution of the dorsal sail of *Heritiera littoralis* in the total dispersal velocity (%). Densities of natural propagules were inserted in the regression line formulas for the mimicked sail-less *H. littoralis* propagules. As such, a proxy was obtained for their dispersal velocity in case they would not have a sail.

		Wind speed		
		L	**M**	**H**
Water flow velocity (m s^{-1})	**0**	38.57 ±14.37	29.82 ± 9.32	22.53 ± 7.52
	0.15	11.25 ± 7.43	13.24 ± 4.97	17.29 ± 4.69
	0.30	6.66 ± 3.84	5.77 ± 5.74	5.87 ± 5.41

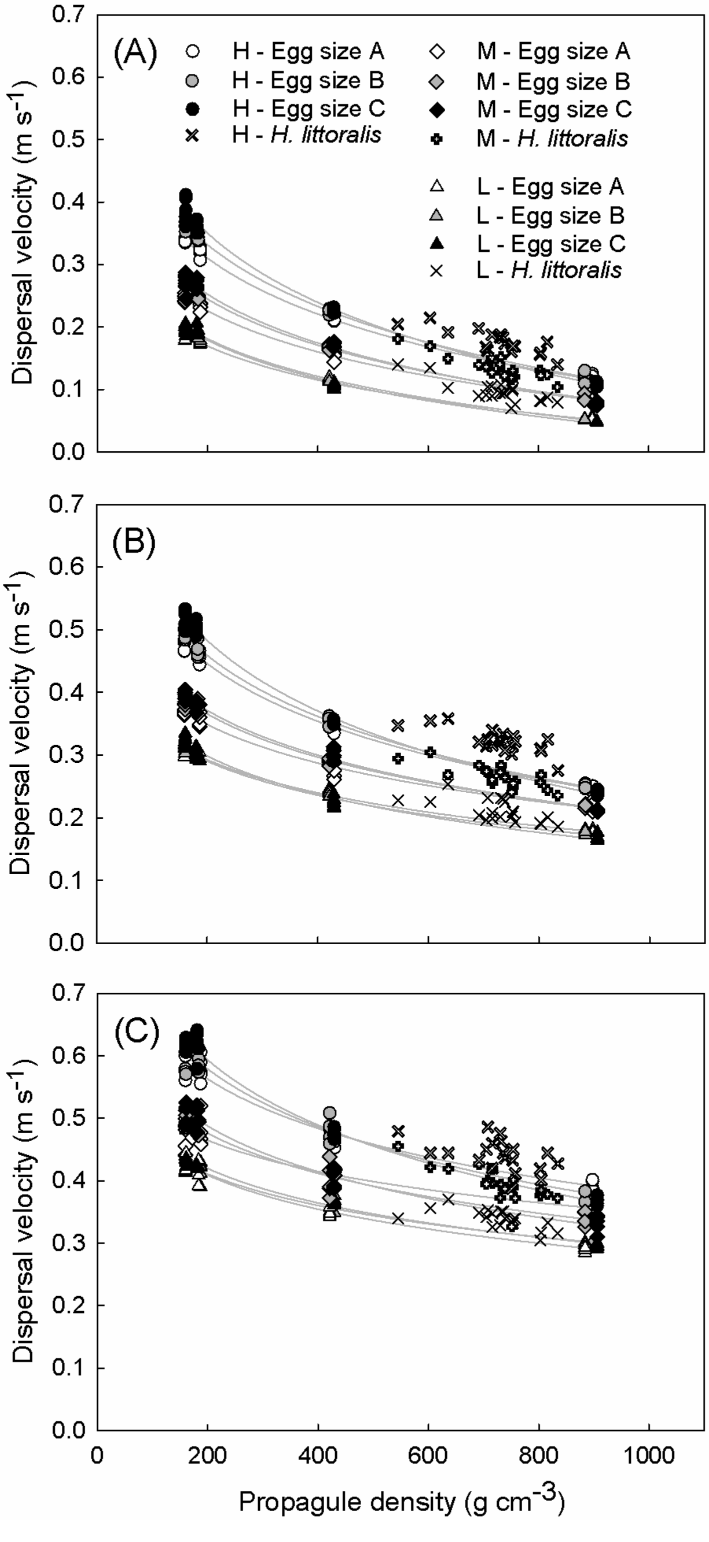

Figure 5.5: Dispersal velocities of sail-less egg-shaped propagule mimics and natural *Heritiera littoralis* propagules under various wind conditions for three different water flow velocities: (A) 0 m s^{-1}, (B) 0.15 m s^{-1} and (C) 0.30 m s^{-1}. Mimics of three different sizes with three different densities for each size were used (see Table 5.2). These mimics were used to simulate *H. littoralis* propagules without apical sail. Multiple wind speeds were imposed (L: low = 2.77 ± 0.23 m s^{-1}; M: medium = 4.53 ± 0.38 m s^{-1}; H: high = 6.03 ± 0.08 m s^{-1}) to the propagules. Trend lines were added for the mimics (light grey) for comparison with the natural propagules.

Discussion

Predicting dispersal trajectories requires substantial knowledge on the multiple dispersal vectors involved (Nathan 2007, Nathan *et al.* 2008). Although the idea that wind action may modulate hydrochorous dispersal is widely held (Clarke 1993, de Lange and de Lange 1994, Stieglitz and Ridd 2001, Di Nitto *et al.* 2013, Sarneel *et al.* 2014), the concept has rarely been tested for mangrove propagules (but see Van der Stocken *et al.* 2013). The present study considers a wide range of natural wind and hydrodynamic conditions and includes propagule morphotypes that cover most variation present in mangrove propagules worldwide as well as mimics, allowing for a generic across-species understanding of which factors control dispersal.

The role of propagule density

In the absence of wind, all propagules dispersed at velocities close or equal to the water flow velocity (Fig. 5.3, the treatment with a 0 m s^{-1} water flow and 'No wind' was not considered since no dispersal vectors act on the propagules in that case). Only the horizontally floating *C. tagal* and *R. mucronata* propagules and the fruits of *X. granatum* seemed to disperse slightly slower. This may be due to a lower drag force at the propagule surface-water contact because of their smooth surface and streamlined shape. Adding wind to the experimental set-up, however, resulted in important changes in the relative dispersal velocities of different propagule types (Fig. 5.3). In all treatments the propagules of *H. littoralis* were most influenced by wind, while the dispersal velocity of the vertically floating *B. gymnorrhiza* and *C. tagal* propagules were least influenced. Differences in propagule density appear to be a crucial determinant for the effect of wind on dispersal trajectories (Fig. 5.4, Table 5.3). This can be explained by Archimedes' law, since lower density propagules (*H. littoralis* propagules) will have a higher proportion of their volume protruding above the water surface than higher density propagules (*cf.* vertically floating *C. tagal* and *B. gymnorrhiza* propagules). This proportion determines the area on which ambient wind forces can exert a drag force. Propagules with a density close to that of the water such as the vertically floating *C. tagal* and *B. gymnorrhiza* propagules do not protrude from the water and hence are largely unaffected by direct wind action (Fig. 5.3). Similar effects of propagule density are confirmed by the GLM. Significant interaction terms show that the effects of wind and water speed are confounded by propagule density. Unlike seeds in other systems (Chang *et al.* 2008, Chambert and James 2009) mangrove propagules do not differ in terms of water saturation (dry or waterlogged). Hence, this cannot influence their density and their buoyancy behaviour. The floating orientation of *C. tagal* and *R. mucronata*, however, can change with time (Clarke *et al.* 2001) resulting in a different susceptibility to wind. Whether these species can change their floating capacity after drying or after sinking and re-exposure is currently unknown. Long-term flotation experiments could shed new light on this process. Additionally, estimates of the overall fecundity and knowledge on the proportions of vertically and horizontally floating propagules at the moment following abscission would be beneficial for the quality of dispersal models.

Average water temperature and salinity values for coastal tropical water are different from those of the water used in our flume study. Additionally, water properties may change considerably over the course of a propagule's dispersal trajectory. Taking an average water temperature of 20 °C and a salinity of 36 ‰ for tropical coastal water, the water density would be 1025.55 g l^{-1} instead of 1027.05 g l^{-1} in our flume study. We think that the effect on the emerged propagule portion would be minor, and the impact on the effect of wind negligible. For propagules with a density close to that of the water, changes in water temperature and salinity may affect the threshold between sinking or floating. However, for the purpose of this study, we deliberately focused on propagules that float. Sunken propagules under tropical water conditions would not have been taken into account.

Impact of propagule morphology

Pronounced variation in dispersal velocities were found among the twenty *H. littoralis* propagules studied, depending on the wind treatment. While variations in density, which range from 545.12 to 834.22 g l^{-1}, may explain part of this variation, the presence of a dorsal sail increased the effect of wind (Fig. 5.5, Table 5.5). *Heritiera littoralis* propagules with a well developed sail that is symmetrical to the transversal plane, typically float with their sail perpendicular to the wind (see Fig. 5.6), while propagules with an asymmetrical sail show stable orientations at sub-orthogonal (*i.e.* < 90°) attack angles. Propagules with an underdeveloped sail are less affected by wind forces. Considering the presence of similar sail-like structures in the seafaring colonial cnidarian animals *Physalia physalia* (L.) (Iosilevskii and Weihs 2009) and *Velella velella* (L.) (Francis 1991), it is sensible to assume that the sail of *H. littoralis* consists of an adaptive trait to make use of wind forces and compete with other mangrove species which lack such adaptations. This dispersal process with a strong sailing component should be called 'pleustochory' rather than mere hydrochory (*cf.* Boland 2014).

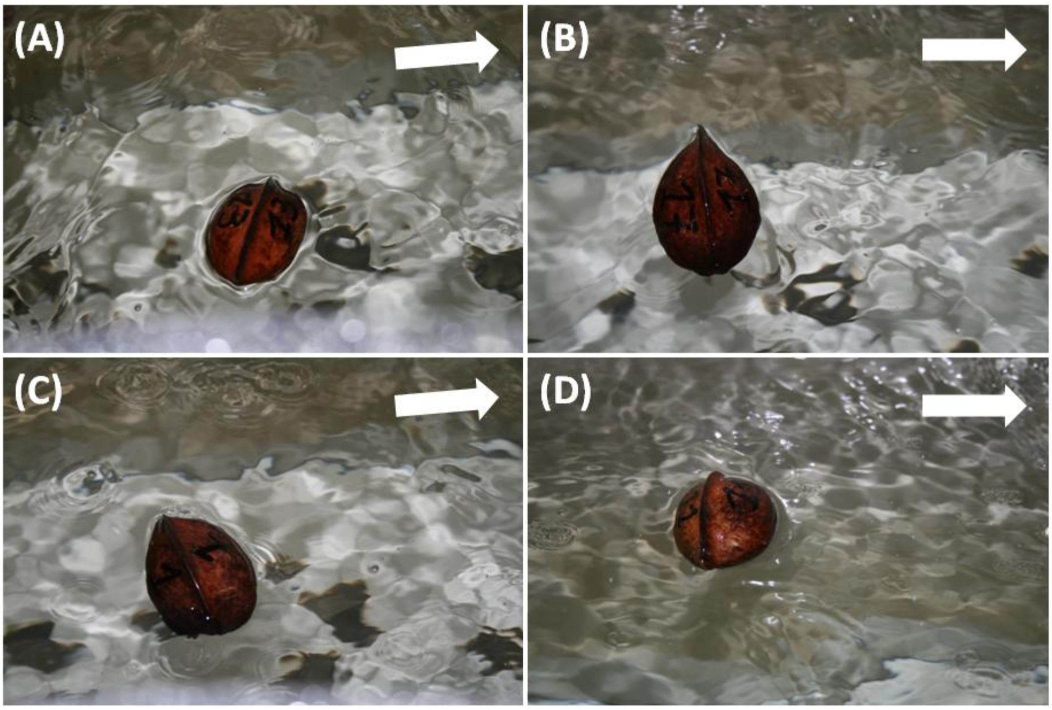

Figure 5.6: Four different *Heritiera littoralis* propagules in the race-track flume. Water and wind currents are from left to right in all photographs (white arrow). All four propagules have a well-developed sail that is symmetrical to the transversal plane. During dispersal, and wind speeds being high enough, propagules typically have their sail oriented perpendicular to the wind force.

Morphological traits were not studied in the other mangrove species. However, the small standard deviations make it reasonable to assume that morphological trait variation within these species will be of minor importance. Conversely, some of our findings suggest that differential effects of wind among species could be explained by morphological features. For example, while *X. granatum* fruits dispersed faster than the vertically floating *C. tagal* and *R. mucronata* propagules, they moved slower than the other propagule types. Since balance of the propagules with ambient dispersal vectors was ensured, the lower dispersal velocity of these fruits may result from a lower drag force at the propagule surface-water contact, but may at least partly result from the smooth spherical shape of the propagules which results in reduced mechanical friction. Similarly, the angular shaped *X. granatum* seeds have a rougher above-water surface which, via higher mechanical friction, may explain the stronger effects of wind on their dispersal velocity than the other dispersal units (except *H. littoralis*).

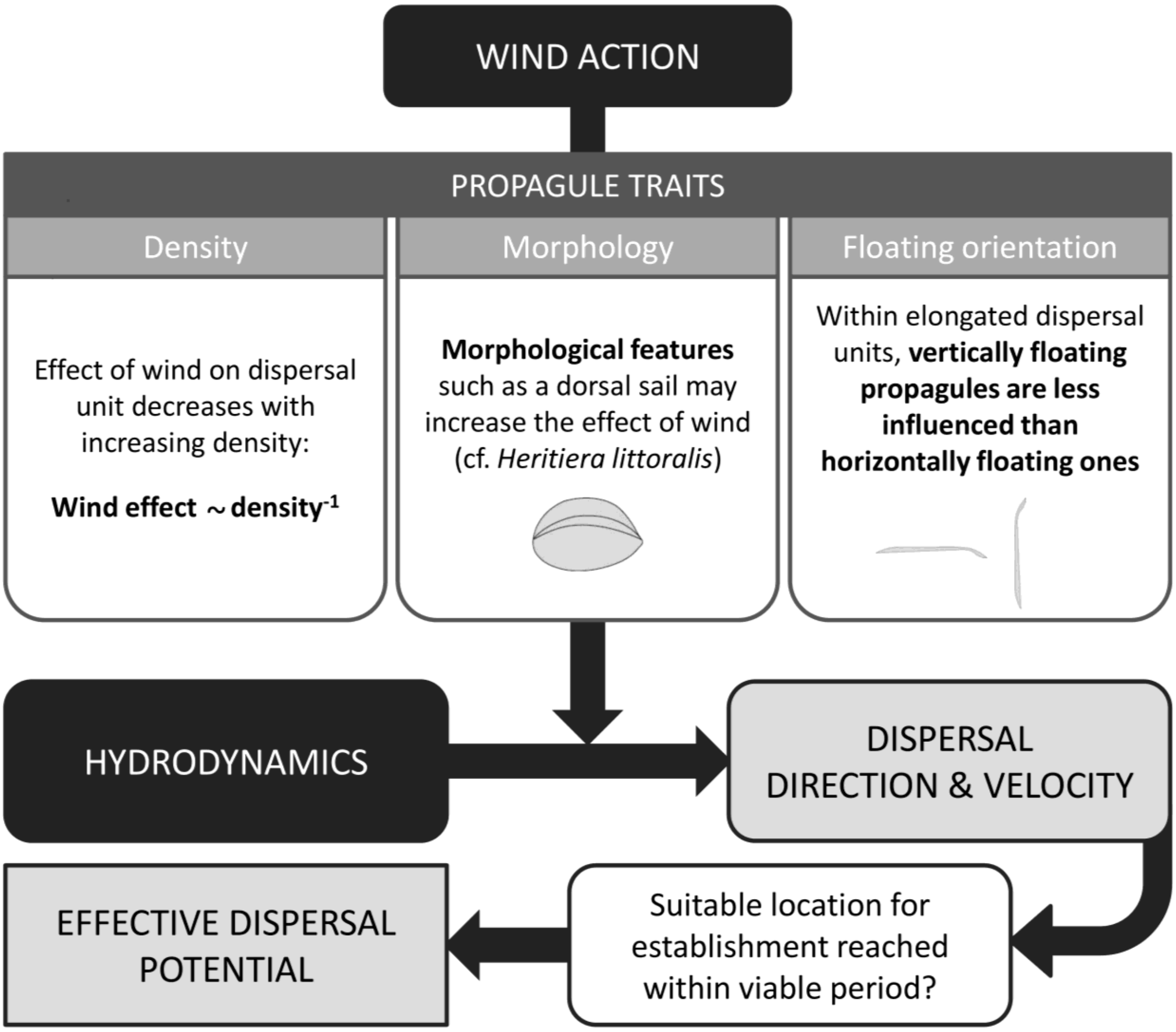

Figure 5.7: Diagram indicating how hydrodynamic and wind forces determine the dispersal direction and velocity of propagules, and in combination with the viable period of these propagules determine effective dispersal potential. The effect of wind depends on multiple propagule traits.

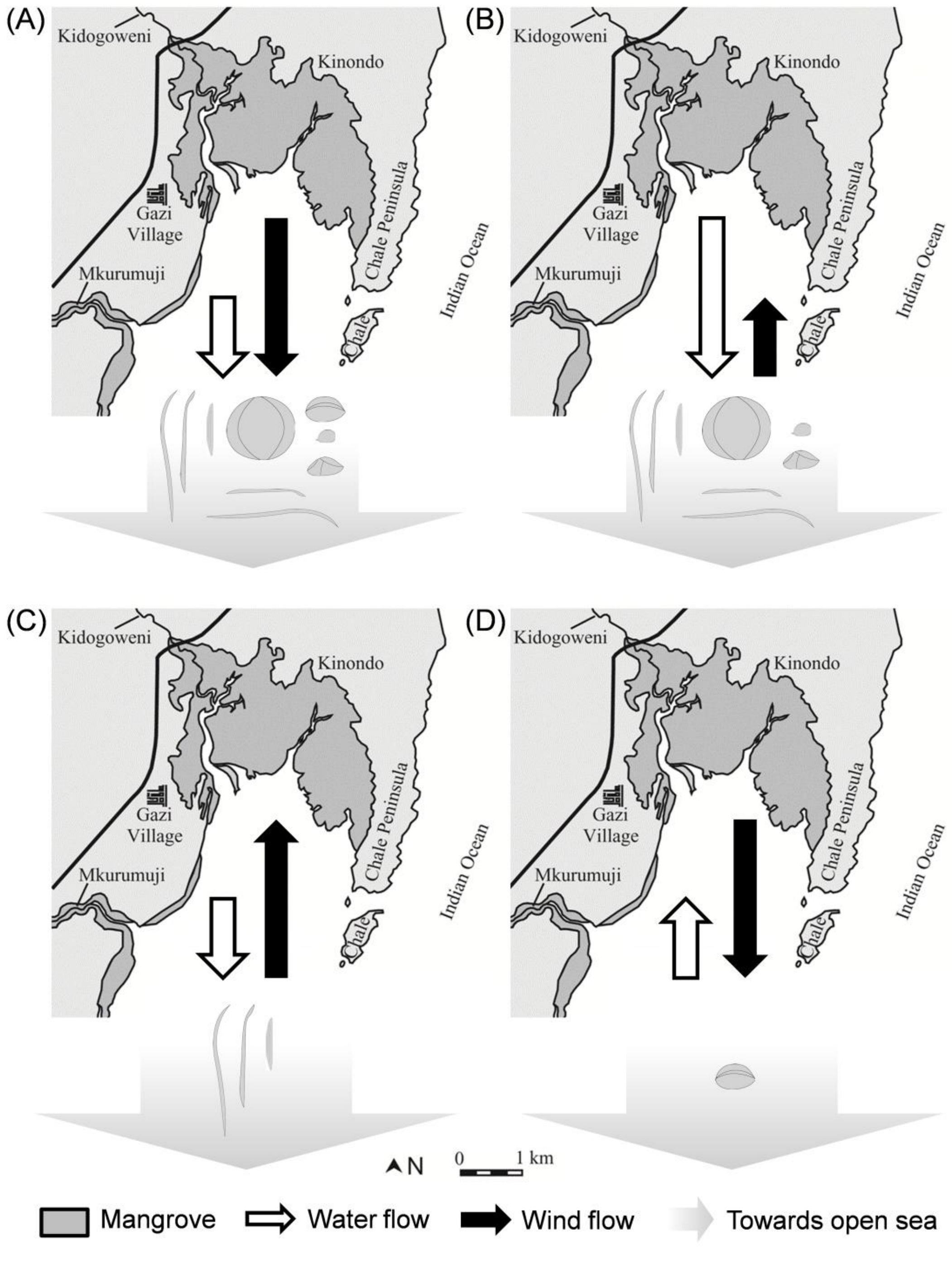

Figure 5.8: Conceptual representation of how the interplay between water and wind currents may influence the potential for long distance dispersal of mangrove propagules in Gazi Bay (Kenya). When both dispersal vectors are parallel and in the same direction (A), towards the open ocean, all propagules could leave the local system. In case of strong offshore ocean currents and onshore winds, all propagules with the exception of *H. littoralis*, will be able to escape (B). When offshore water currents are weak, strong onshore winds may constitute an important barrier for propagules that float at or on the water surface, hindering them from reaching the ocean (C). Deeply submerged propagules are less affected. When ocean currents are onshore and offshore winds are strong, only *H. littoralis* propagules will be able to embark on LDD (D). The map of Gazi Bay is modified after Dahdouh-Guebas *et al.* (2002).

Implications on dispersal patterns

Habitat destruction and fragmentation, as well as climate change alter the spatial configuration of suitable and unsuitable habitats (Trakhtenbrot *et al.* 2005). Therefore, knowledge on dispersal distances and direction, LDD in particular, is essential as it allows to assess and predict the probability of propagules to reach and colonize remote habitat fragments (Higgins and Richardson 1999, Nathan *et al.* 2008). Evidence for the ability of species to disperse over long distances via ocean currents dates back to the flotation experiments of Darwin (1859), but challenges related to direct observations and the stochasticity associated with LDD hamper the quantification and prediction of such events (Nathan 2006), and constrain the realism of dispersal models. As stressed by Nathan (2006) the best way to tackle this problem is to focus on the mechanisms involved. For passive dispersers at the ocean surface, the most straightforward factor to consider when predicting dispersal patterns is hydrodynamics. However, in this study we clearly demonstrate that in such systems, wind can modulate dispersal trajectories depending on propagule density and specific morphological features. Besides average dispersal patterns and the probability of propagules to leave the local habitat and embark on LDD, it determines the likelihood of propagules to reach a suitable location within their viable period, *i.e.* the potential of effective dispersal (Fig. 5.7). The implications of our findings for the potential of LDD are schematically illustrated for a mangrove system in Gazi Bay, Kenya (Fig. 5.8). When outgoing water flow coincides with (strong) northerly winds (Fig. 5.8 A), or when the outgoing water currents are strong compared to southerly winds (Fig. 5.8 B), all propagule types could reach the open ocean. However, *H. littoralis* propagules would disperse slowly or be prevented from leaving the local system as its dorsal sail allows prevailing wind forces to counteract the effect of hydrodynamics. When outgoing water flow is weak and strong winds act from the south, the elongated vertically floating propagules would be the only propagule types able to reach the Indian ocean and embark on LDD (Fig. 5.8 C). A low density and specific morphological features may render some propagules more efficient at reaching the Indian Ocean when strong northerly winds overrule the effect of onshore water flow (Fig. 5.8 D). For the mangrove system depicted in Figure 5.8, the average daily wind direction from 1 January 2013 to 1 January 2014 is shown in Figure 5.2. While wind predominantly comes from the northeast from early December to late February, wind comes from the south during most of the year. This strongly limits the opportunity for most propagule types to leave this mangrove system. However, they may do so during windows of lower wind speeds.

Conclusion

In conclusion, our study demonstrates that propagule density and morphology exert strong control on the way wind influences the dynamics of hydrochorous propagules floating at the surface of oceans and seas. For realistically predicting dispersal patterns, hydrochorous dispersal models should include species-specific differential effects of wind based on propagule traits. Additionally, information on both the floating and viable period of propagules is needed, since these factors represent temporal constraints to the potential of effective dispersal. Viable propagules that sink before reaching a suitable site, or propagules that reach a suitable location but are no longer viable, do not contribute to effective dispersal. Eventually, the present species-specific results on propagule dispersal properties will have consequences for long-term population dynamics, biogeographical ranges, connectivity patterns, and phenomena such as the failure of species to fully exploit their potential ranges based on niche models (Randin *et al.* 2013).

Acknowledgements

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CHAPTER 6

MODELING MANGROVE PROPAGULE DISPERSAL TRAJECTORIES USING HIGH RESOLUTION ESTIMATES OF OCEAN SURFACE WINDS AND CURRENTS

Unpublished manuscript

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Abstract

Mangrove forests are systems that provide ecosystem services and thrive at the edge of sea and land in the (sub)tropical areas of the world. They rely on floating propagules (*i.e.* seeds and fruits) of which the dispersal trajectories are determined by ocean currents and winds. Quantifying connectivity of mangrove patches is an important conservation concern. However, current estimates of connectivity fail to integrate the link between ocean currents at different spatial scales and dispersal trajectories. Overall, this research aims to integrate interactions between propagule and vector properties and assess the role of these factors in determining effective dispersal in this enigmatic group of ocean faring trees. Here, we used high-resolution estimates of ocean currents and surface winds from meteorological and oceanographic analyses, in conjunction with experimental data on propagule and dispersal vector properties, to model dispersal trajectories of mangrove propagules in the Mozambique Channel. Model output shows the effect of oceanographic features such as eddy activity and tidal motion and meteorological features such as storms and wind bursts on dispersal tracks, influencing the probability of a propagule to reach a suitable habitat within its viable period. In spite of the complex pattern of ocean surface currents and winds, some propagules are able to cross the Mozambique Channel. Our results demonstrate that wind, via morphological features, can facilitate or counteract hydrochorous dispersal depending on the relative interaction of water and wind currents, and hence determine the potential for long distance dispersal (LDD). Under onshore wind conditions, for example, the sailboat-like *H. littoralis* propagules have little chance to embark on LDD, in contrast to the vertically floating propagules of *Rhizophora mucronata*, *Ceriops tagal* and *Bruguiera gymnorrhiza*. Wind-sensitive propagules, on the other hand, may embark on LDD under the influence of offshore winds, when other propagule types are hindered from LDD by onshore water currents. The results will help to assess the potential of natural expansion of current mangrove fragments and help to explain and predict current and future distributions of mangrove forests.

Introduction

Despite several decades of study, dispersal questions continue to be an important element in current research agendas given the increasing fragmentation of natural land- and seascapes due to anthropogenic impacts (Fahrig 2003, Kokko and López-Sepulcre 2006, Chen *et al.* 2011). In a changing world, dispersal is a key process for organisms allowing for dynamic distribution ranges. Additionally, it can help beneficial alleles to spread among populations fueling local adaptation (Levine and Murrell 2003). Hence, there is a strong need for good empirical data and mechanistic models to reconstruct and predict the frequency and the likely trajectories of natural dispersal events, to assess the vulnerability of populations to extinction and the likelihood of successful range expansion. This is also true for mangroves, which despite their high socio-economical and ecological importance (Walters *et al.* 2008), are among the most fragmented and threatened habitats on the planet (Valiela *et al.* 2001, Duke *et al.* 2007, Gilman *et al.* 2008).

Mangroves are a phylogenetically diverse group of plants (APGIII 2009, Chase and Reveal 2009) with roughly similar growth forms that have emerged via convergent evolution and which disperse along ocean currents. Because mangroves have patchy distributions, they are very reliant on LDD to allow for range expansion and range shift. Despite a large body of research on mangrove dispersal at local and regional scales, relatively little is known about the dominant dispersal trajectories of floating propagules driven by oceanic currents and about variation in LDD capacity of different species. Information on connectivity and dispersal is limited to indirect estimates from population genetic studies (Triest 2008, Wee *et al.* 2014) and a number of propagule mark-release-recapture studies (De Ryck *et al.* 2012, Van der Stocken *et al.* 2013). It is clear, however, that, in order to get an integrated understanding of dispersal fluxes of mangrove propagules, empirical observations need to be complemented with detailed models that include realistic parameters that capture the behavior of individual propagules and the temporal dynamics of the dispersal vectors. Recent research has now shown that the striking variety of different propagule morphologies that is produced among mangrove genera, is likely to be reflected in differences in dispersal strategies (Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b). Combined with recent high-resolution estimates of ocean surface winds and currents, this provides unique opportunities to investigate how the interaction of ocean currents and wind determine passive dispersal dynamics and the potential of LDD. Mechanistic dispersal models can play an important role to predict the response of species distributions under environmental change and inform conservation management actions (Nathan *et al.* 2008, Travis *et al.* 2012). Parameterization of such models, however, requires an intimate knowledge of the dispersal autoecology of dispersing propagules, while mark-release-recapture data and population genetic estimates of gene flow can be used to validate model predictions (Van Dyck and Baguette 2005, Nathan *et al.* 2008, Bonte *et al.* 2012).

In this study, we develop a dispersal model to examine how the interaction of water and wind determines the dispersal trajectories of propagules at the ocean surface. We use surface winds from the 0.14° European Center for Medium-Range Weather Forecasts (ECMWF) atmospheric operational model analysis starting in 2011 and surface currents from a high-resolution (0.02° horizontal and 1-m near-surface-vertical grid spacing) ocean simulation provided by the Estimating the Circulation and Climate of the Ocean, Phase II (ECCO2) project (Menemenlis et al. 2008). The high-resolution ECCO2 simulation incorporates realistic tidal and atmospheric forcing and provides unprecedented opportunities to model propagule dispersal. While important aspects of the dispersal process such as the interaction of the dispersal vectors have recently been explored under both field and controlled conditions (Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b), the current study builds further on this knowledge to allow for robust quantifications and generalization to increase the biological realism in our dispersal model.

We hypothesize that wind can strongly influence the dispersal route of hydrochorous propagules, and in some cases might control whether or not propagules are able to leave the local system and embark on LDD. Thus far, the mechanistic link between ocean currents, surface winds, and variable propagule traits has not been explored or evaluated. We discuss the outcome of our model in the larger framework of mangrove propagule dispersal and dispersal ecology in general.

Material and methods

Estimates of ocean surface winds and currents

Ocean surface winds are from the European Centre for Medium-Range Weather Forecasts (ECMWF) operational atmospheric model analysis starting in 2011, which is made available on a model grid with 0.14° horizontal spacing, that is, 15 km or less. We use 10-m meridional and zonal wind velocity[1], made available at 6-hourly intervals (hour 0, 6, 12, and 18 UTC). We linearly interpolate these winds to hourly intervals, to match the ocean model output, and extrapolate them to 0.1 m above the ocean surface, using the following formula:

$$v_{wind,2} = v_{wind,1} \times \left(\frac{z_2}{z_1} \right)^a \qquad (1)$$

where $v_{wind,1}$ and $v_{wind,2}$ are the wind velocity (m s^{-1}) at height z_1 (= 10 m) and z_2 (= 0.1 m), respectively. The wind shear exponent a was set to 0.1, which is a generally accepted approximation above ocean surfaces. The 0.1-m height above the surface is deliberately chosen to allow for a meaningful incorporation of our water-wind interaction data (Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b) where wind speed was measured at 0.1 m as well.

Ocean surface currents are from a groundbreaking global ocean simulation that represents full-depth ocean processes with an unprecedented degree of realism (Fig. 6.1). The simulation is based on a latitude/longitude/polar-cap (LLC) configuration of the Massachusetts Institute of Technology (MIT) general circulation model (Hill *et al.* 2007). The LLC grid has 13 square tiles with 4320 grid points on each side (hereafter called LLC4320) and 90 vertical levels for a total grid count of 2.2×10^{10}. Horizontal grid spacing ranges from 0.75 km near Antarctica to 2.2 km at the Equator and vertical levels have 1 m thickness near the surface to better resolve the diurnal cycle. The simulation is initialized from a data-constrained global ocean solution provided by the ECCO2 project. From there, model resolution is gradually increased to LLC1080, LLC2160, and finally LLC4320. Configuration

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[1] Zonal velocity is the velocity along a latitude circle (*i.e.* west-east component), while meridional means along a meridian (*i.e.* north–south direction).

details are similar to those previously used by the ECCO2 project except that the LLC4320 simulation includes atmospheric pressure and tidal forcing. The inclusion of tides allows successful shelf-slope dynamics, water mass modification, and their contribution to global ocean circulation. Surface boundary conditions are from the same 0.14° ECMWF atmospheric operational model analysis that is used to provide surface wind estimates.

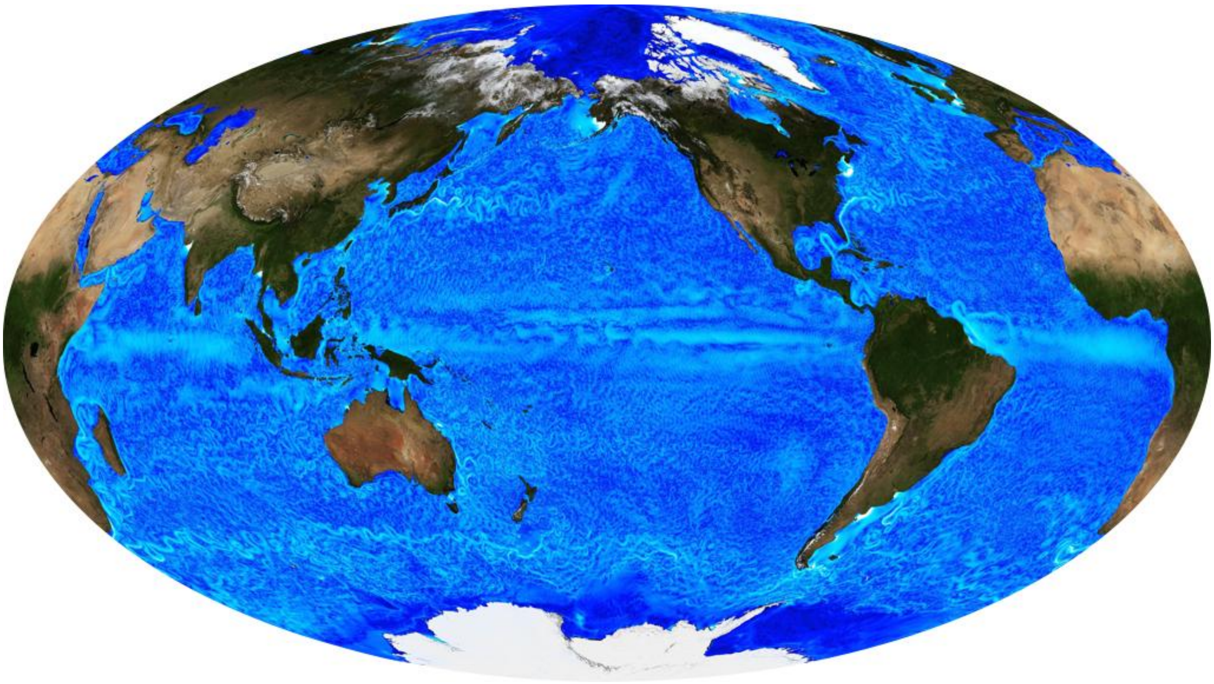

Figure 6.1: Snapshot of ocean surface current speed (darker to lighter blue gradient reflects lower to higher velocity gradient) from the LLC4320 simulation.

Another unique feature of this simulation is that we save hourly output of full 3-dimensional model prognostic variables, making it a remarkable tool for the study of ocean and air-sea exchange processes and for supporting ocean ecology studies. At the time of this study, 3 years of output was available for the LLC1080 and LLC2160 simulations, and 5 months of output (September 2011 to January 2011) for the LLC4320 simulation. The horizontal resolution and forcing strategy of the LLC4320 simulation allow it to represent ocean surface circulation in exceptional detail, including complex eddy currents which may strongly alter the dispersal track of drifting organisms (Hancke *et al.* 2014, Ternon *et al.* 2014).

Although LLC4320 initial conditions are based on an ocean-data-constrained ECCO simulation, the LLC4320 simulation itself is not data-constrained in any way. The initial conditions (from ECCO), the boundary conditions (bathymetry from Smith and Sandwell

(1997), atmospheric forcing from ECMWF analysis starting in 2011, and tidal forcing), and the MITgcm model physics are realistic. For this reason we do not use the LLC4320 simulation as truth. We use it as a way to make predictions that can be evaluated (and possibly invalidated) vs observations.

Dispersal model

Release locations. Multiple mangrove localities in the Mozambique Channel were selected to investigate how the interaction of ocean surface and wind currents determines the fate of dispersal units with different morphologies and floating orientations. The case of the Mozambique Channel was selected for its reported oceanographic complexity (Hancke *et al.* 2014, Ternon *et al.* 2014). Since release locations may be situated on land in the land-ocean model mask, an algorithm was included at the beginning of the model that calculates the minimum value of all Euclidean distances between the sample site and the centre of neighboring wet cells. The longitude and latitude of the release location are then updated and stored. Importantly, we assume that particles have reached the open water, *i.e.* the model does not take into account the role of the local landscape matrix (Van der Stocken *et al.* 2015a).

Particle propagation. At each time-step (1h), the geographical coordinate of the dispersing particle is updated based on the respective zonal (u) and meridional (v) ocean surface current and wind velocities, using the following formula:

$$v_{disp} = \left[\alpha \times (u_{wat} + v_{wat})\right] + \left[\beta \times (u_{wind} + v_{wind})\right] \tag{2}$$

wherein α and β are defined by the user to modulate the respective weight of ocean and wind currents in the overall dispersal velocity, and hence to control the interaction between both dispersal vectors. Here, we assume that α is 1, based on the data in our flume studies (Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b), where mangrove propagules were found to have dispersal velocities equal to the water flow velocity in the absence of wind. The parameter β was given different values (in percent: 0, *i.e.* only water; 1; 2; 3; 4; 5) in subsequent model runs to allow for examining the effect of wind on the potential of species to leave the local system (*i.e.* their potential of LDD) and dispersal trajectories.

Currently, the dispersal model is fully deterministic. Advection trajectories are nevertheless chaotic in that they are highly sensitive to small perturbations in the initial conditions. We will go for a probabilistic approach in the future by adding stochasticity, where the strength and direction at each time-step could be drawn from a Gaussian probability distribution.

Buoyancy assumption. Importantly, to serve the goal of this study, an infinite floating period was assumed.

All propagule dispersal modeling was conducted using Matlab R2014a.

Results and discussion

In this study, we have examined how the interaction of ocean currents and winds determine the dispersal trajectories of propagules at the ocean surface, using mangroves as an example. For this we have combined *in situ* and *ex situ* experimental data and surveys (Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b) with a detailed mechanistic simulation model and high resolution estimates of ocean surface currents and winds. Species-specific differential effects of wind were included in the model via different parameterizations of the water-wind synergies.

The different synergies between ocean currents and winds are reflected in divergent dispersal tracks (Fig. 6.2). Interestingly, our results highlight the potential of connectivity between locations at both sides of the Mozambique Channel (Fig. 6.2). This is in agreement with the findings by Hancke *et al.* (2014) who postulated that cross-channel transport between Madagascan and Mozambique shelf regions is possible in both directions. Hancke *et al.* (2014) studied dominant eddy activity in the Mozambique Channel using 82 satellite-tracked drifters, revealing a complex pattern of ocean surface circulation in this area. Our results confirm that oceanic features such as eddies can alter the dispersal trajectory of drifting organisms, as hypothesized by Ternon *et al.* (2014) and Hancke *et al.* (2014) (Fig. 6.3, see E in Fig. 6.2).

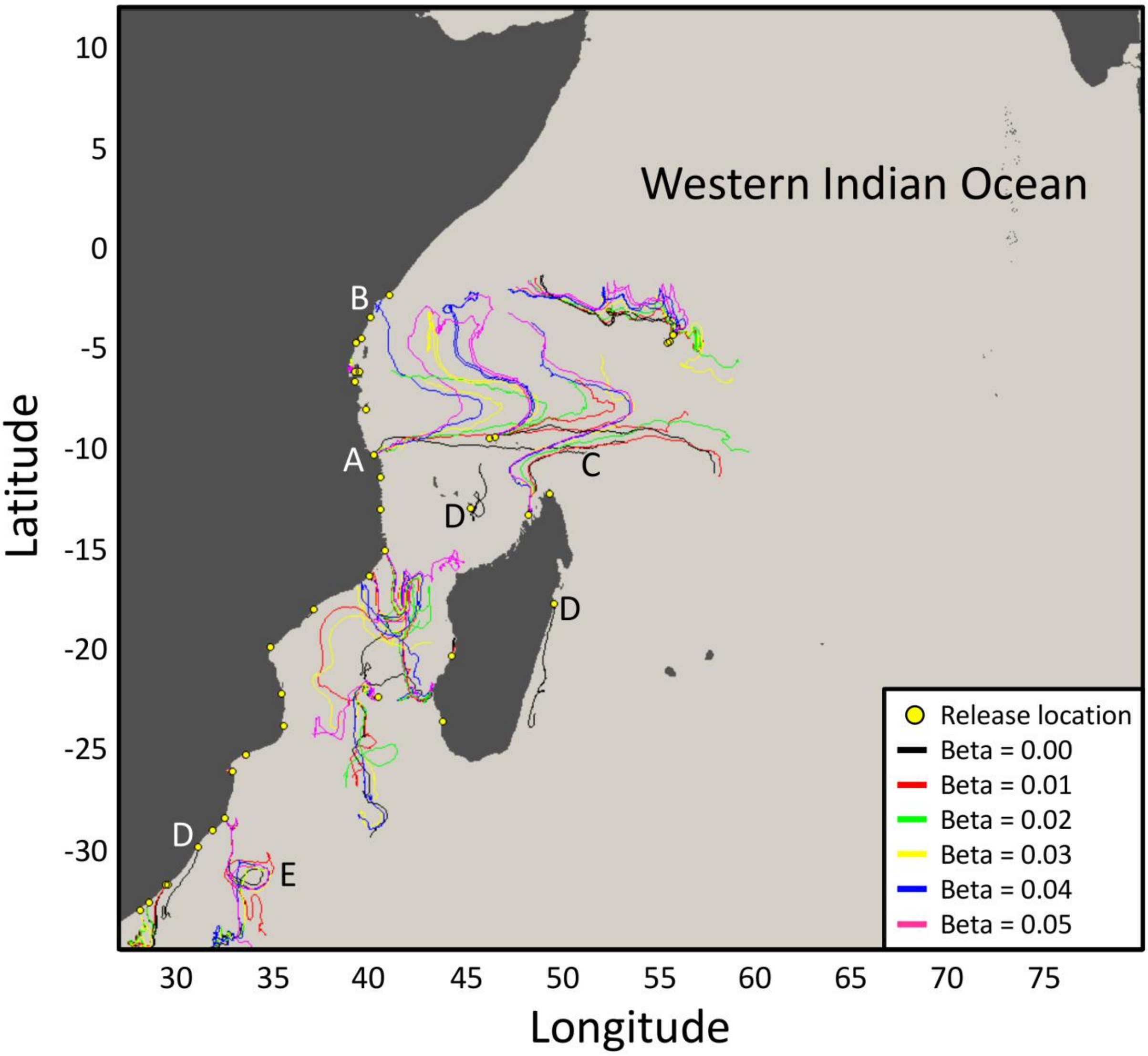

Figure 6.2: Statistical probabilistic estimate of dispersal trajectories of propagules virtually released at different locations along coastlines in the Western Indian Ocean. Dispersal period covers about 2 weeks. A clear effect of wind on dispersal routes can be seen (color code). Letters are shown to support the discussion of specific features and scenarios (see text). Dark grey: continent; Light grey: ocean. Particles were released in all release locations (yellow circles), although the scale of the figure may suggest otherwise.

This has important implications for the probability for propagules to reach a suitable habitat within their viable period. Also, viable propagules may lose buoyancy while being captured and delayed in oceanographic features such as eddies. Hence, data on propagule viability

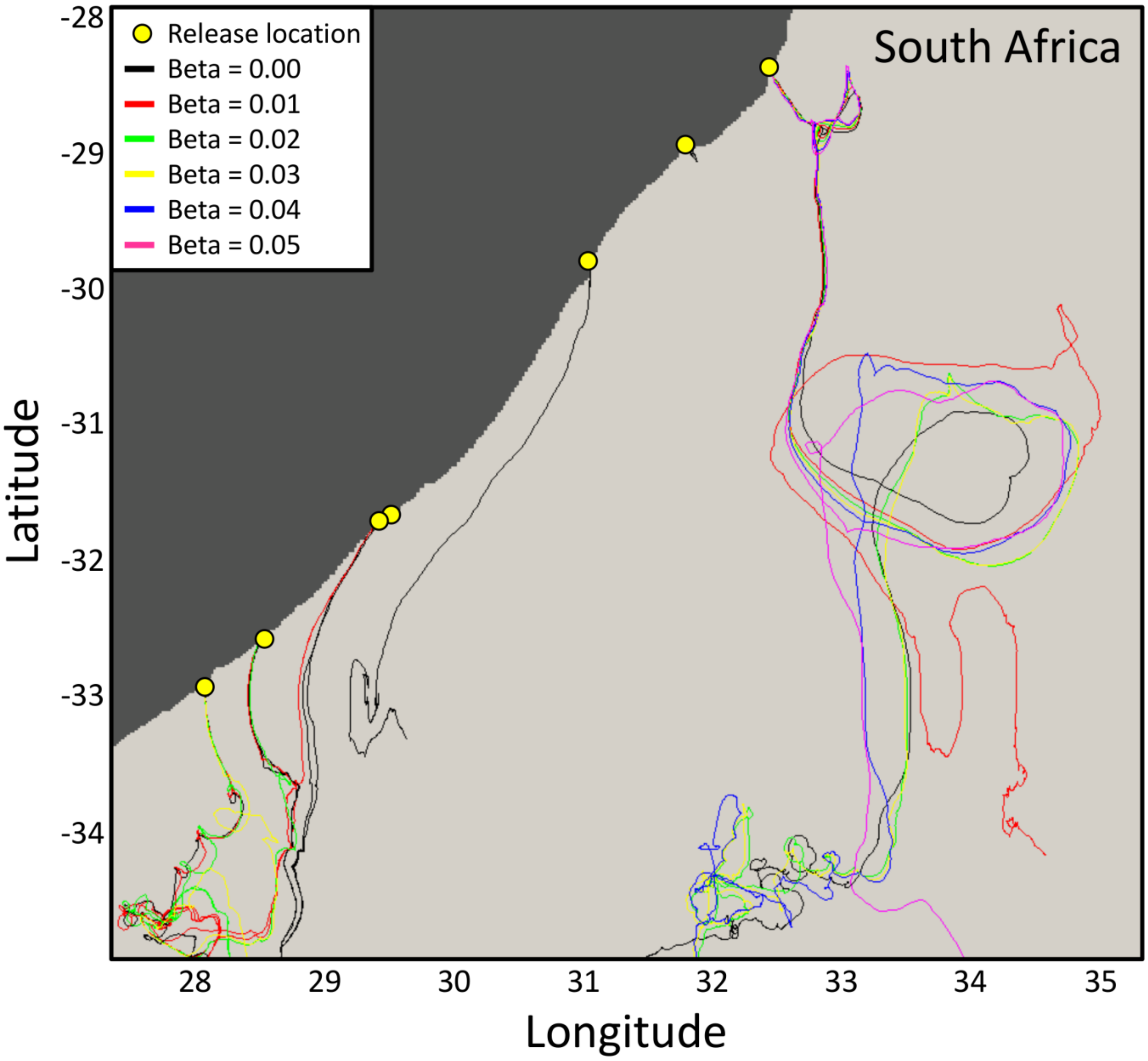

Figure 6.3: Detail of Figure 6.2, showing the effect of an anticyclonic eddy on the dispersal track of drifting propagules (right) and a situation where onshore winds counteract the potential of offshore ocean surface currents to transport propagules away from the local system (centre).

and flotation period would provide essential information to allow for more realistic estimates of effective dispersal. While data on these propagule traits is currently insufficient to allow for meaningful model parameterization, available data suggests that besides short floating propagules, an important proportion may be able to survive the delay in dispersal that is caused by eddy currents and other physical factors. In *Avicennia germinans*, for example, Gunn and Dennis (1999) reported floating periods of > 1 year with 100 % of the propagules being viable. Long floating and viable periods were also found among *Rhizophora harrisonii* Leechm. (> 104 days, Rabinowitz 1978), *R. mucronata* (> 150 days, Drexler 2001), and *Heritiera littoralis* (> 150 days, Ye *et al.* 2004). Long-term experiments to gather insight in the evolution of these propagule traits within a population of dispersing propagules could reduce parameter uncertainty (sensu Higgins *et al.* 2003) and allow for more realistic predictions of long-term biogeographic patterns.

Model results demonstrate that wind can strongly affect the overall dispersal track of a propagule. For example, propagules released in Mtwara (Tanzania, location A in Fig. 6.2) disperse to the east in the absence of wind (Fig. 6.2, locations A to C) while winds influence their dispersal direction with potential stranding on the East African coastline between Kirepwe and Lamu (Kenya, location B in Fig. 6.2). Based on the findings in our flume studies (Van der Stocken *et al.* 2013, Van der Stocken *et al.* 2015b) these results show potential genetic connectivity between A and B for species like *Heritiera littoralis*, while the vertically floating propagules of *Rhizophora mucronata*, *Ceriops tagal* and *Bruguiera gymnorrhiza* would float easterly. However, it remains to be seen if predictions are supported by genetic data in the field. Parameters such as propagule release timing may strongly affect dispersal and deposition pattern, as shown for example for wind dispersed propagules (Greene 2005, Savage *et al.* 2010, Savage *et al.* 2012). Also, the genetic structure observed today may echo genetic exchange in the past when dispersal vector properties were different (*e.g.*, paleocurrents).

Interestingly, model output shows that in some cases onshore winds could prevent propagules with specific morphological features such as *H. littoralis* to leave the local system (Fig. 6.4a, see D in Fig. 6.2), while in other cases, offshore winds could mediate hydrochorous propagules against onshore ocean surface currents (Fig. 6.4b). These findings demonstrate that morphological features could facilitate or counteract hydrochorous dispersal depending on the relative interaction of water and wind currents, and hence determine the potential for LDD as hypothesized by Van der Stocken *et al.* (2015b). Off-shore winds at the moment of propagule release, may therefore be beneficial in terms of LDD potential in the case of wind-sensitive propagules such as *H. littoralis*, while the vertically floating propagules of *R. mucronata*, *C. tagal* and *B. gymnorrhiza* have a higher probability for LDD.

In conclusion, our results demonstrate that wind can strongly influence the dispersal trajectories of hydrochorous propagules at the ocean surface. As such, species-specific wind

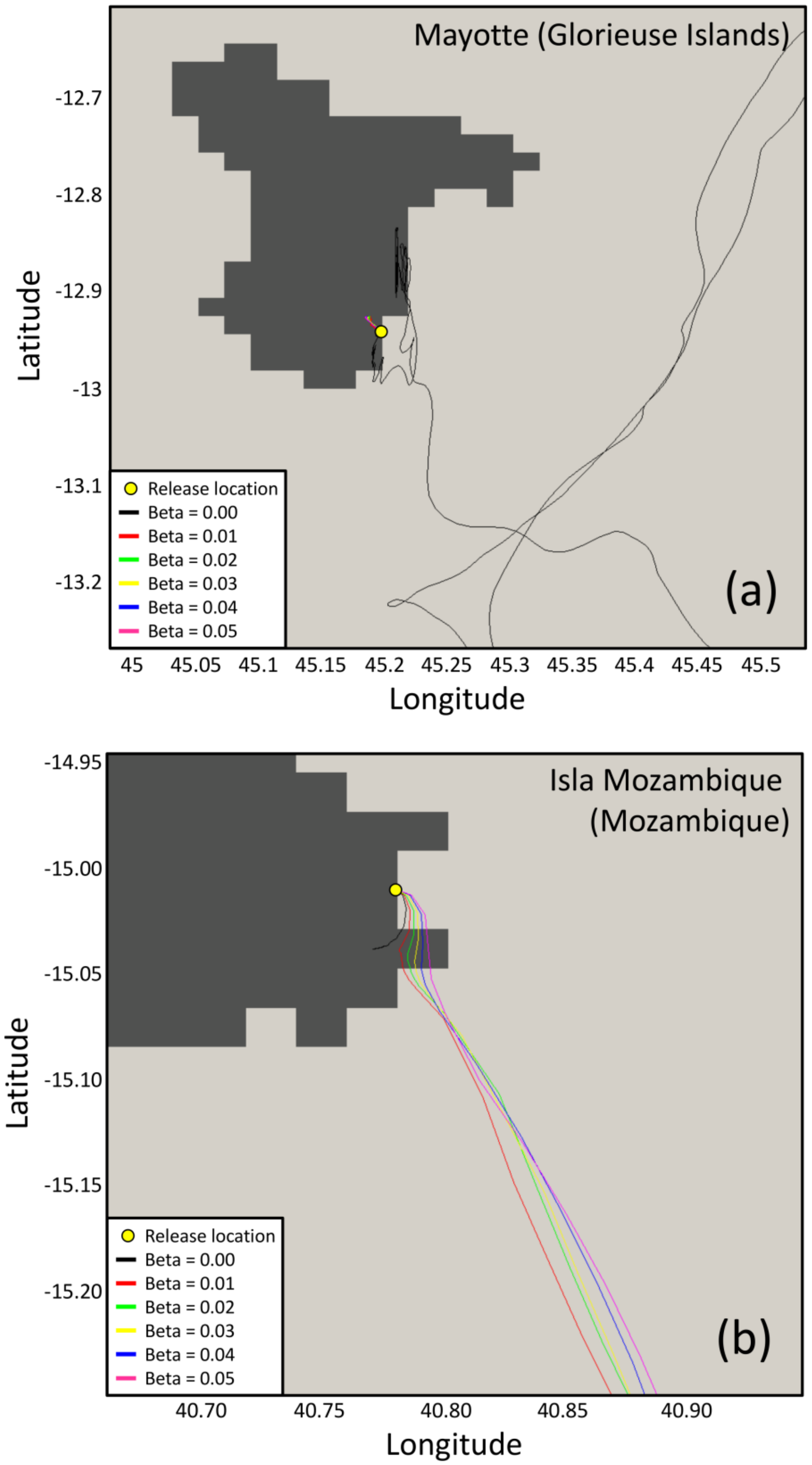

Figure 6.4: Example of how offshore and onshore winds could (a) facilitate or (b) counteract hydrochorous dispersal depending on the relative interaction of water and wind currents, and hence determine the potential for LDD.

effects should be considered in dispersal models for passive hydrochorous propagules, since it may exert pronounced control on dispersal distance and direction, and hence the potential of effective (long distance) dispersal. In a next phase, dispersal patterns of different species will be studied on a global scale and combined with available genetic data for validation.

Excellent regional and global scale studies on dispersal in marine systems have been presented recently (Paris *et al.* 2013, Simpson *et al.* 2014, Wood *et al.* 2014). However, the horizontal grid resolution of oceanographic data generally constitutes an important limitation in describing real ocean dynamics, such as mesoscale eddies, coastal currents, and tides. Also, passive and surface dispersal of mangrove propagules may strongly differ from metabolically more active animal larvae (some with active motion) that develop during dispersal, also at greater depths than the surface, requiring three-dimensional (3D) hydrodynamic models (*e.g.* Neo *et al.* 2013, Hellweger *et al.* 2014). Also, to increase the biological realism, we are in the process of expanding the model with missing empirical data on phenology and propagule traits (floating and viable period). The dispersal model bears high potential to better understand present and future species distributions and assess the potential of natural expansion of mangrove fragments under changing environmental conditions. It can contribute to explain observed patterns of genetic differentiation and apparent barriers to gene flow observed in population genetic studies, and help to understand some of the curious disjunct distributions of extant species by testing how local species composition and diversity may be controlled by dispersal limitation and interactions with the regional species pool (Sutherland *et al.* 2013). Furthermore, the model may allow to identify populations, which do contribute over-proportionately, as well as to simulate and assess effects of extreme events (*e.g.* El-Niño Southern Oscillation). Finally, this model is also relevant for ecosystems other then mangroves, where propagules are distributed by ocean surface currents, since we have the potential to modify parameters for any object that floats at the surface of the world's oceans, including plastic debris which receives increasing attention (Cózar *et al.* 2014, Jambeck *et al.* 2015). Hence, model output will increase insight into the distribution of species and the connectivity between nearby and remote habitat fragments.

Acknowledgements

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CHAPTER 7

CONCLUSION AND PERSPECTIVES

Over the last decades, **mangrove loss and fragmentation** has been increasing due to **excessive exploitation and development** (Mukherjee *et al.* 2014). Without profound and integrated knowledge on the reproduction, growth, and dispersal mechanisms of these seafaring plants, and the lack of scientifically supported conservation strategies, this decline is very likely to continue in the future. Mangrove decline has **strong implications for coastal communities, directly as well as indirectly** through the loss of biodiversity that is sustained by these tropical intertidal ecosystems. The ecosystem services offered by mangroves in a wider human context, beyond the direct link with coastal communities are equally at risk.

In this PhD project, we have studied different aspects that determine the spread of mangrove species through space, *i.e.* **the process of dispersal** (Fig. 7.1). The main objective is to provide new insight into aspects of passive dispersal (of mangroves) that have remained understudied. In doing so, I aim at constructing a global dispersal model to make statistical probabilistic estimates of dispersal patterns and detect broad-scale dispersal events.

A first question addressed the ***quantities of propagules available for dispersal and the proportion of the initial propagule batch remaining as candidates for a long distance dispersal journey?*** To answer this question we needed to know how many propagules can be produced by a tree (*i.e.* the **fecundity**) and obtain insight into the variation, both intraspecific and interspecific: within and between species, but also spatially and temporally due to for example variations in freshwater input, drought, nutrient influx (Amarasinghe and Balasubramaniam 1992) and natural disturbances such as tropical storms and hurricanes (Alleman and Hester 2011) **(CHAPTER 1)**. Data on this parameter is lacking and adds large uncertainty to current LDD research in mangroves.

Once released from the parent tree, propagules face different challenges to effectively reach open water while traveling from the point of release. Firstly, **predation**, predominantly by herbivorous crabs, removes an important part of the viable propagule batch. Predation is positively correlated with crab density, which in turn depends on tree and root density (Van Nedervelde *et al.* 2015). Additionally, predation rates seem to be strongly linked to the nutritional value of the propagules (Van Nedervelde *et al.* 2015). A high fecundity may, therefore, indeed be a good strategy, since producing more propagules increases the probability of survival per propagule due to saturation of predators such as crabs (Lindquist *et al.* 2009). It is found in pioneer species like *Avicennia* spp. (Friess *et al.* 2012), but the strategy's downside is the substantial maternal investment.

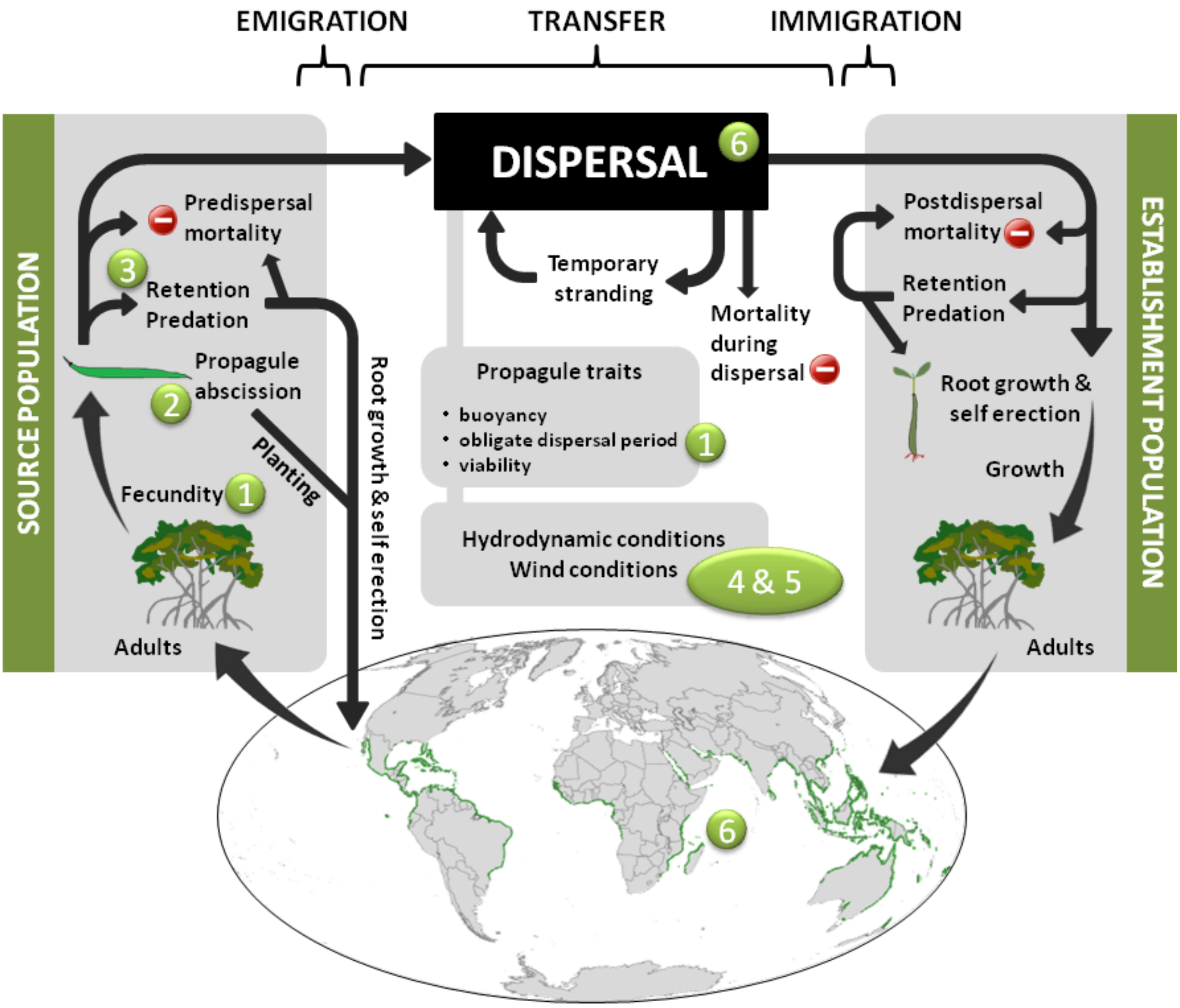

Figure 7.1: The processes and elements of mangrove dispersal: conceptual framework outlining the specific contribution of this research. Green circles and ellipsoid indicate the respective chapters.

Secondly, **retention** also lowers the size of the propagule population available for LDD (**CHAPTER 3**). Our field and flume experiments showed that for the majority of mangrove propagules, dispersal distances are generally short due to retention by the dense aerial root system. This explains the **leptokurtic** shape of the **dispersal kernel**, *i.e.* the distribution of dispersal distances. Retention, however, differs strongly among the morphologically diverse propagule types, with the compact propagules (see *Avicennia* and *Heritiera*) being much less retained compared to the larger propagules (see *Rhizophora* and *Ceriops*). Although these findings suggest that smaller propagules may contribute disproportionately to dispersing propagule cohorts, one should consider also the geographical position of the parent tree relative to the open water body. *Avicennia* trees, for example, typically grow in the more landward zones of the forest, causing their propagules to face a much wider zone of barriers as compared to for example the larger *Rhizophora* propagules that are released at the most seaward side of the forest. The landward areas also experience fewer and shorter (tidal) hydroperiods compared to the more seaward zones, and hence fewer opportunities to disperse, since water is the standard dispersal vector (*sensu* Nathan *et al.* 2008).

By means of a **flume experiment** in combination with **observations in the field**, we have proposed a **conceptual model** that illustrates how **barrier density** at a particular location varies through time, due to the vertical movement of the water surface as a consequence of tidal motion, creating **time windows of lower retention and higher LDD potential** exist **(CHAPTER 3)**. These windows of higher LDD potential are longest around spring tide when tidal amplitude is at its maximum and seawater covers considerable parts of the mangrove forest. The role of **stochastic events** such as storm surges and non-seasonal weather extremes in the context of propagule dispersal has thus far received little attention, but may be expected to have a high potential of influencing the spatial spread of propagules, and hence forest structure. Also, as postulated by Nathan *et al.* (2008) for plant dispersal in general, such events may play an important role in LDD due to increases in the vector displacement velocity. It may, therefore, be interesting to set up **release-recapture** experiments similar to those performed for this PhD, at the eve of predicted extreme meteorological events. With this kind of experiments, one should be aware that release-recapture experiments only provide information on the initial and end location of the propagules, and not on the actual dispersal trajectories. Also, although straightforward, one can only guess about the fate of non-recovered propagules which may have disappeared due to predation or due to dispersal beyond the range of the search area. However, depending on the recovery rate, it has proven to be a cost-effective way to gather valuable information on dispersal distances **(CHAPTERS 1)** and, particularly in combination with flume experiments, on interactions with the landscape matrix **(CHAPTERS 3)**.

While valuable data on **spatial characteristics of predation** has been provided recently (Van Nedervelde *et al.* 2015) and our study has added new insight on the interaction of mangrove propagules with the landscape matrix, more empirical data is needed to allow for meaningful estimations and model parameterization. Considering a single mangrove tree, and assuming that all propagules produced are viable, the number of propagules (N) available for dispersal beyond the limits of the local system (*i.e.* LDD), may be approximated using the following simple mathematical expression:

$$N_{t+1}^{LDD} = N_t^{LDD} + A - P - R \tag{1}$$

where A is the number of viable propagules abscised from the tree at time t (related to fecundity), P is the number of propagules that is no longer viable due to predation, and R is the number of propagules that is retained locally. Indeed, based on what has been mentioned earlier, this deterministic expression is not very realistic, and does not include the **environmental stochasticity** present in natural systems. Inspiration for a potential candidate for estimating propagule fluxes in and through a mangrove forest might come from matrix models (see Caswell 2001) where the probability of moving from one mangrove zone to the other would take into account the different barriers outlined earlier (predation and retention). The dispersal barriers (*e.g.* retention) and filters (*e.g.* predation) in turn depend on propagule type, the distance between the release location and open water, and the water level at time t+1. Also, one should take into account the proportion of propagules that plants directly following abscission.

For the propagules that finally reach open water (*i.e.* the number of particles released in the dispersal model) the second key question was ***which dispersal vectors are at play and how do these vectors interact?*** In many instances, propagules show morphological traits that reflect adaptations for dispersal by a specific dispersal vector. It should be noted, however, that morphological adaptations for dispersal by a particular dispersal vector does not necessarily imply dispersal by that vector (Nathan *et al.* 2008). This is nicely illustrated by plant colonization of Surtsey, a volcanic island which appeared from the ocean floor near the coast of Iceland. While it was conjectured that 78 % of plant taxa on this island detected in the decades following the island's appearance between 1963 and 1967, arrived by ocean currents, Higgins *et al.* (2003b) postulated that only one third show morphological adaptations for dispersal by water. Also, in many cases, the trajectories of dispersing organisms are **determined by the interaction between multiple dispersal vectors** (*i.e.* polychory; see for example Ozinga *et al.* 2004) **rather than one single and specific** (*i.e.* haplochory). Hence, to allow for the quantification and modeling of the total dispersal kernel (*sensu* Nathan 2007) and avoid uncertainties in model forecasts (Higgins *et al.* 2003a), it is **essential to identify all important dispersal vectors** (Nathan *et al.* 2008). In mangroves, the standard dispersal vector consists of mostly marine currents, as rendered possible by the buoyant nature of the various propagule types. However, some propagule morphological features, such as the dorsal sail of *Heritiera littoralis*, suggested that **wind** may contribute to dispersal, both in terms of velocity and direction, ultimately leading to different trajectories. In **CHAPTERS 4 and 5**, we have combined experiments in the field and under controlled conditionals in a flume, and demonstrated that wind can strongly direct the dispersal of propagules at the water surface. Therefore, this dispersal process with a great sailing component should be called **'pleustochory'[1] rather than mere hydrochory** (*cf.* Boland 2014). This adds new insight to increase the realism of existing mangrove propagule dispersal models and has important implications for LDD predictions **(CHAPTER 6)** where integrated over long timeframes the combined effects of ocean and wind currents ultimately result in very different arrival locations. Our results, for example, showed **species-specific differences** to the effect of wind, and enable to better assess the LDD potential of different propagule types and suggesting potentially diverse trajectories of 'flotillas' of propagules. This is relevant for mangroves here, but the observation contributes to the study of dispersal and **biogeographic patterns of any group of organisms of which the propagules are dispersed on and at various depths near the ocean surface**.

A third important aspect of the dispersal process that now hampers realistic mechanistic models is the timing of propagule release, *i.e.* ***when do propagules become "available" for dispersal and what is the timeframe during which effective dispersal can take place?*** One can expect, considering the **temporal variability in vector properties** (strength and direction), that knowledge on this parameter is highly relevant to model dispersal and deposition patterns, and the magnitude and frequency of LDD, as shown for example for wind dispersed propagules (Greene 2005, Savage *et al.* 2011, Savage *et al.* 2012). This

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[1] 'Pleusto-' referring to the sailing processes as in the concept 'pleuston'

phenological aspect has – to our knowledge – received no attention in the context of mangrove propagule dispersal research. Additionally, in contrast to many temperate tree species (*e.g.* Huang *et al.* 2001, Fitter and Fitter 2002, Menzel *et al.* 2005, Vitasse and Basler 2013), responses of mangrove phenology to climate change has not yet been documented. These must be preceded by establishment of the phenology under current climate conditions. Therefore, we have taken an emphatic first step in summarizing present-day available data on propagule release **(CHAPTER 2)**. At this moment, the dataset does not yet allow us to develop robust (species-specific) dispersal model parameterization, nor did we venture into taking correlation for causation. However, we found interesting **latitudinal patterns** in the timing of propagule release, as well as strong apparent responsiveness of propagule phenology to **rainfall and temperature**. This underscores the importance of this data, as it holds a high potential for understanding **impacts of climate change**, as already established in temperate plant species (Richardson *et al.* 2013). Delays in leaf abscission for *Ginkgo biloba* and *Acer palmatum* (non-mangrove species), for example, have been linked with increasing temperatures (Doi and Takahashi 2008). Considering shifts in rainfall seasonality in the tropics (Feng *et al.* 2013) and changes in atmospheric temperature, the positive correlations between mangrove phenology and these climatologic variables as found in our study, bear high potential for similar phenological shifts in mangrove species. Hence, climate change, via shifts in phenological events, may have considerable implications on long-term dispersal patterns with potential changes in the biogeographic range of mangrove species. While the global meta-analysis **(CHAPTER 2)** allows to make generalisations about the seasonality of propagule release in different species, local scale experiments may allow to explicitly analyse the relative effect of different environmental cues (hydroperiod, rainfall, wind and temperature). The response time of phenological patterns to climate change trends is another matter of uncertainty.

The timing of propagule release also sets the start of the **Biological Window of Opportunity** (BWO), *i.e.* the timeframe during which effective dispersal can take place **(CHAPTER 1)**. The BWO is an essential concept to determine the potential dispersal distance of viable propagules and hence the distribution of species. When the loss of viability is negligible, *e.g.* in floodplain plants with long propagule dormancy periods, buoyancy will be the most important determinant of dispersal distance (Edwards *et al.* 1994). In mangroves, both the

maximum flotation period (MFP) and **maximum viability period** (MVP) limit the time period available for dispersal. By the end of the MFP they are either lost at sea or deposited at a potential arrival locality. While there is a probabilistic component in dispersal research (the very basis of the concept of dispersal kernel), it must be borne in mind that a single successful dispersal event (*e.g.* **epic events**) may be at the origin of a new population at any site.

Current available data on **flotation** and **viability** periods is limited and incomplete. However, our literature survey shows that the MFP and MVP vary strongly among species. This has important implications for the shape of the dispersal kernel. For example, **dispersal kernels** of species with long-floating propagules will more likely show a longer and fatter tail (*i.e.* more LDD propagules) as compared to species with short-floating propagules. Hence, determining the BWO of different mangrove species is important to explain differences in LDD potential and species distribution. Given the different **risk costs** during dispersal (*sensu* Bonte *et al.* 2012), different **evolutionary dispersal strategies** may coexist within species, populations, and even within the same genotype. For instance, within species this could be by means of locally adapted populations, within populations by means of genetic variation, and within lineages (genotypes) by means of phenotypic variation due to phenotypic plasticity or evolutionary bet-hedging. Besides its essential need for model parameterization, meaningful buoyancy and viability experiments, *i.e.* over time periods that are long enough to capture the MFP and MVP within a population of propagules, may also allow to study the potential existence of such species-specific dispersal strategies.

In **CHAPTER 6**, we have initiated, developed and explored the potential of a **model** for passive dispersal at or near the ocean surface. In this model we integrated knowledge on the dispersal vectors at play **(CHAPTERS 4 AND 5)** and used the **highest resolution global oceanographic and wind current data** that is currently available. By performing runs for a particularly complex marine area relevant to our study, the **Mozambique channel**, we established that wind can strongly influence the dispersal trajectory of propagules, with considerable implications for **long-term biogeographic patterns**. Morphological features may facilitate or counteract hydrochorous dispersal, depending on the relative interaction of water and wind currents. Hence, under strong onshore wind conditions, the vertically floating propagules of *R. mucronata, C. tagal* and *B. gymnorrhiza* have a higher probability for LDD compared to for example *H. littoralis* propagules. The model bears high potential to better understand present and future species distributions and assess the potential of natural expansion of mangrove fragments under changing environmental conditions. It opens an exciting prospect of mirroring phylogeographic findings in mangroves. Caution is however required when interpreting the genetic structure of mangroves in the light of present-day oceanographic and wind current data. The genetic structure observed today may echo genetic exchange in the past when dispersal vector properties were different (*e.g.* **paleocurrents**). Additionally, the model can be applied to track any organism or object that disperses passively at or very near to the ocean surface, including for example plastic debris which receives increasing attention (Cózar *et al.* 2014, Jambeck *et al.* 2015).

Eventually, the model will be applied at a **global scale** (data available) and combined with connectivity estimates from **genetic studies** (available within our group). Similar studies have recently been conducted for spawning corals (Wood *et al.* 2014). At present, our dispersal model tracks particles according to the zonal (u) and meridional (v) water and wind flow velocity fields. **Biological realism** will be added by including an element of stochasticity. Propagule traits, for example, could be drawn from empirically determined trait distributions, rather than using mean values. Additionally, to better capture the probabilistic element of propagule movements, the direction of the vectors at each point in the field and at each time step can also be drawn from a theoretical Gaussian probability distribution with the direction of the vector being the most likely dispersal direction but allowing for some randomness as is characteristic for natural systems. Also, a backward version of the model to predict candidate source locations of recently formed islands, such as for example Sanibel and Caladesi Island (Florida, USA). In combination with genetic studies, both the forward and backward version of our model can be used to reveal candidate source populations for mainland sites, *i.e.* to detect examples of reverse colonization (see Bellemain and Ricklefs 2008).

Genetic samples available in the host institution VUB for *Avicennia marina* and *Rhizophora mucronata* (D. De Ryck, VUB and ULB) provide the opportunity to validate the outcome of the dispersal model. As release locations can be defined in the model, we could test whether dispersal fluxes in the model output match patterns of genetic connectivity, and under which conditions (parameter settings). In this case, the model can test the likelihood of different

LDD relationships, with an important constraint that it only allows to make statements about the consequences of relatively recent genetic exchange. Dispersal trajectories can be modeled for propagules of different species by releasing particles over the range of their biogeographical distribution. Geographic coordinates for all mangrove species are available from the Mangrove Reference Database and Herbarium (Massó i Alemán *et al.* 2010).

While most researchers currently look at neutral genetic variation, there is high potential in the **genomics approach** where analyses can be done on hundreds of loci at the same time, including loci under selection. By means of outlier detection methods, loci under selection can be detected. If linked with known proteins, recent consequences of selection pressure such as fragmentation and climate change can be traced in the genome and linked to phenotypic variation (*e.g.* **buoyancy** and other traits linked to dispersal).

Besides exploring probable intercontinental dispersal routes, the model resolution also allows to perform ***in silico* experiments** at more local scales. For instance, we could test whether wind action can provide a likely explanation for the fact that certain propagule types are more likely to reach open oceans than others, which we have shown empirically in an East African Estuary (unpublished data).

In conclusion, we have provided novel insight relevant to the biogeography of mangroves, and potential applicability in any other organism that disperses passively at or near the ocean surface. We highlighted the importance of propagule release timing and revealed some interesting latitudinal patterns and correlations with climatic factors **(CHAPTER 2)**. We combined *in situ* and *ex situ* experiments to study species-specific interactions of dispersing propagules with the landscape matrix **(CHAPTER 3)** and identified the different dispersal vectors of which the interaction strongly controls the shape of the dispersal kernel and hence the potential for LDD **(CHAPTERS 4 AND 5)**. In **CHAPTER 1**, we also proposed the BWO concept, as this defines the timeframe within which effective dispersal can take place. We recognize, that more effort is needed to shed light in the mangrove propagule dispersal black-box and to reduce parameter and model uncertainty **(CHAPTER 6)**.

Our results hold important applications for conservation and management, since realistic models (1) can help to assess to what extent range shifts of species are possible under climate change scenarios; (2) can contribute to explain observed patterns of genetic differentiation and apparent barriers to gene flow observed in population genetic studies; and (3) can help to explain some of the curious disjunct distributions of extant species by testing how local species composition and diversity may be controlled by dispersal limitation and interactions with the regional species pool (Sutherland *et al.* 2013). Additionally, coastal sustainability (including mangrove forests), which is actually at stake, is of direct interest to coastal communities, both local fisheries-based economies as well as tourism-based activities which constitute an economical lifeline in many tropical countries. In Kenya, for example, where most of the field data in this work has been collected, these economical sectors concern vulnerable sections of society, for low income communities dealing with decreasing fisheries incomes, as well as for those employed in the tourist industry. In Kenya, the tourism industry had received serious blows after the 2007-08 postelection violence and again in 2014-15 following political and international upheaval, which thus weakened local and national economy. Indeed, while tourism and the high cash flows it generates for local and national economies in certain periods appeared to be the road to follow, it is increasingly clear that healthy ecosystems (see a discussion on this concept in Temperton 2007) must be a prime concern to safeguard the future (Balmford *et al.* 2002). The quality of the coast for these multiple and alternative functions is strongly related to the health state of coastal ecosystems, amongst which mangroves are very important. Fighting shoreline erosion, the protection of mangrove resources and ecosystem services are targets which go hand in hand. The partner institutions KMFRI and particularly the Kenya Wildlife Service (KWS) have as a core mission dissemination of insights regarding environmental management. It is central in customary governance in Kenya to implement policies by consulting stakeholders. This type of governance is common practice with our direct counterparts in Kenya and ensures efficient stakeholder dissemination of relevant results at village and community level.

It has been shown extensively that mangrove recovery upon insult cannot reliably be remediated by restoration and that the resilience of this life support system depends on its potential for dispersal, rejuvenation, and expansion (*e.g.* Stevenson *et al.* 1999, Erftemeijer and Lewis 2000, Di Nitto *et al.* 2013). This implies good dispersal and realized gene flow. Though solely output and input (establishment, see Fig. 7.1) of propagules can, in places, be managed and optimized at a local level, dispersal processes are beyond any management action. By modeling ocean and wind current effects, areas which can neither contribute significantly to the dispersing propagule pool nor receive significant numbers may be recognized. Hence, our results can provide information on the *openness* of populations, *i.e.* whether populations are primarily replenished by local production (closed) or immigrants (open) (Pinsky *et al.* 2012) and as such inform management at local, regional and global scales. Populations with little or no immigrants, for example, may be of more concern as compared to populations where immigrants arrive regularly, especially when overexploitation reduces the local propagule source (*i.e.* number of mature plants). Even when rates of immigration are high, most propagules will come from the local population itself. However, considering increasing fragmentation and exploitation, immigration rates may play an important role in assessing the persistence of a population and its potential for natural recovery. In this context, knowledge on dispersal dynamics and patterns is relevant to position strongly impacted sites in the global network of mangrove populations that may act as important sources of propagules. Also, within this network, the potential of natural colonization of newly formed suitable areas can be assessed. As such, on the long-term, our dispersal model may help to define mangrove priority areas for conservation, as required by Aichi Biodiversity Target 11. This target states that "*By 2020, at least 17 per cent of terrestrial and inland water, and 10 per cent of coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes*"[2]. The present study sets the scene for future research to improve model parameterization and further enhance the reliability of model output towards management practices and conservation strategies.

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[2] https://www.cbd.int/sp/targets/

REFERENCES

Aburto-Oropeza, O., E. Ezcurra, G. Danemann, V. Valdez, J. Murray, and E. Sala. 2008. Mangroves in the Gulf of California increase fishery yields. PNAS 105: 10456-10459.

Agraz Hernández, C. M., C. G. Zaragoza, S. Iriarte-Vivar, F. J. Flores-Verdugo, and P. M. Casasola. 2011. Forest structure, productivity and species phenology of mangroves in the La Mancha lagoon in the Atlantic coast of Mexico. Wetlands Ecol. Management 19: 273-293.

Alleman, L. K., and M. W. Hester. 2011. Reproductive ecology of black mangrove (*Avicennia germinans*) along the Louisiana coast: propagule production cycles, dispersal limitations, and establishment elevations. Estuaries and Coasts 34: 1068-1077.

Allen, J. A., and K. W. Krauss. 2006. Influence of propagule flotation longevity and light availability on establishment of introduced mangrove species in Hawaii. Pacific Science 60: 367-376.

Alongi, D. M. 2002. Present state and future of the world's mangrove forests. Environmental Conservation 29: 331-349.

Amarasinghe, M. D., and S. Balasubramaniam. 1992. Net primary productivity of two mangrove forest stands on the northwestern coast of Sri Lanka. Hydrobiology 80: 37-47.

Anderson, C., and S. Y. Lee. 1995. Defoliation of the mangrove *Avicennia marina* in Hong Kong: cause and consequences. Biotropica 27: 218-226.

APG. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. Botanical Journal of the Linnean Society 161: 105-121.

Appeltans, W., S. T. Ahyong, G. Anderson, M. V. Angel, T. Artois, N. Bailly, R. Bamber, A. Barber, I. Bartsch, A. Berta, M. Blazewick-Paszkowycz, P. NBock, G. Boxhall, C. B. Boyko, S. Nunes Brandão, R. A. Bray, N. L. Bruce, S. D. Cairns, T.-Y. Chan, L. Cheng, A. G. Collins, T. Cribb, M. Curini-Galletti, F. Dahdouh-Guebas, P. J. F. Davie, M. N. Dawson, O. De Clerck, W. Decock, S. De Grave, N. J. De Voogd, D. P. Domning, C. C. Emig, C. Erséus, W. Eschmeyer, K. Fauchald, D. G. Fautin, S. W. Feist, C. H. J. M. Fransen, H. Furuya, O. Garcia-Alvarez, S. Gerken, D. Gibson, A. Gittenberger, S. Gofas, L. Gómez-Daglio, D. P. Gordon, M. D. Guiry, F. Hernandez, B. W. Hoeksema, R. Hopcroft, D. Jaume, P. Kirk, N. Koedam, S. Koenemann, J. B. Kolb, R. M. Kristensen, A. Kroh, G. Lambert, D. B. Lazarus, R. Lemaitre, M. Longshaw, J. Lowry, E. Macpherson, L. P. Madin, C. Mah, G. Mapstone, P. McLaughlin, J. Mees, K. Meland, C. G. Messing, C. E. Mills, T. N. Molodtsova, R. Mooi, B. Neuhaus, P. K. L. Ng, C. Nielsen, J. Norenburg, D. M. Opresko, M. Owsawa, G. Paulay, W. Perrin, J. F. Pilger, G. C. B. Poore, P. Pugh, G. B. Read, J. D. Reimer, M. Rius, R. M. Rocha, J. I. Saiz-Salinas, V. Scarabino, B. Schierwater, A. Schmidt-Rhaesa, K. E. Schnabel, M. Schotte, P. Schubert, E. Schwabe, H. Segers, C. Self-Sullivan, N. Shenkar, V. Siegel, W. Sterrer, S. Stöhr, B. Swalla, M. L. Tasker, E. V. Theusen, T. Timm, A. Todaro, X. Turon, S. Tylor, P. Uetz, J. Van der Land, B. Vanhoorne, L. P. Van Ofwegen, R. W. M. Van Soest, J. Vanaverbeke, G. Walker-Smith, T. C. Walter, A. Warren, G. Williams, S. P. Wilson, and M. J. Costello. 2012. The magnitude of global marine species diversity. Current Biology 22: 2189-2202.

ARREOLA-LIZÁRRAGA, J. A., F. J. FLORES-VERDUGO, and A. ORTEGA-RUBIO. 2004. Structure and litterfall of an arid mangrove stand on the Gulf of California, Mexico. Aquatic Botany 79: 137-143.

AUCAN, J., and P. V. RIDD. 2000. Tidal asymmetry in creeks surrounded by saltflats and mangroves with small swamp slopes. Wetlands Ecology and Management 8: 223-231.

BALKE, T., T. J. BOUMA, P. M. J. HERMAN, E. M. HORSTMAN, C. SUDTONGKONG, and E. L. WEBB. 2013a. Cross-shore gradients of physical disturbance in mangroves: implications for seedling establishment. Biogeosciences 10: 5411-5419.

BALKE, T., T. J. BOUMA, E. M. HORSTMAN, E. L. WEBB, P. L. A. ERFTEMEIJER, and P. M. J. HERMAN. 2011. Windows of opportunity: thresholds to mangrove seedling establishment on tidal flats. Marine Ecology Progress Series 440: 1-9.

BALKE, T., E. L. WEBB, E. VAN DEN ELZEN, D. GALLI, P. M. J. HERMAN, and T. J. BOUMA. 2013b. Seedling establishment in a dynamic sedimentary environment: a conceptual framework using mangroves. Journal of Applied Ecology 50: 740-747.

BALL, M. C., and S. M. PIDSLEY. 1995. Growth responses to salinity in relation to distribution of two mangrove species, *Sonneratia alba* and *S. lanceolata*, in Northern Australia. Functional Ecology 9: 77-85.

BALMFORD, A., A. BRUNER, P. COOPER, R. CONSTANZA, S. FARBER, R. E. GREEN, M. JENKINS, P. JEFFERISS, V. JESSAMY, J. MADDEN, K. MUNRO, N. MYERS, S. NAEEM, J. PAAVOLA, M. RAYMENT, S. ROSENDO, J. ROUGHGARDEN, K. TRUMPER, and R. K. TURNER. 2002. Economic Reasons for Conserving Wild Nature. Science 297: 950-953.

BAUMS, I. B., C. B. PARIS, and L. M. CHÉRUBIN. 2006. A bio-oceanographic filter to larval dispersal in a reef-building coral. Limnol. Oceanogr. 51: 1969-1981.

BELLEMAIN, E., and R. E. RICKLEFS. 2008. Are islands the end of the colonization road? Trends in Ecology & Evolution 23: 461-468.

BERGER, U., M. ADAMS, V. GRIMM, and H. HILDENBRANDT. 2006. Modelling secondary succession of neotropical mangroves: Causes and consequences of growth reduction in pioneer species. Perspectives in Plant Ecology Evolution and Systematics 7: 243-252.

BERGER, U., V. H. RIVERA-MONROY, T. W. DOYLE, F. DAHDOUH-GUEBAS, N. C. DUKE, M. L. FONTALVO-HERAZO, H. HILDENBRANDT, N. KOEDAM, U. MEHLIG, C. PIOU, and R. R. TWILLEY. 2008. Advances and limitations of individual-based models to analyze and predict dynamics of mangrove forests: A review. Aquatic Botany 89: 260-274.

BERNINI, E., and C. E. REZENDE. 2010. Litterfall in a mangrove in Southeast Brazil. Pan-American Journal of Aquatic Sciences 5: 508-519.

BILTON, D. T., J. R. FREELAND, and B. OKAMURA. 2001. Dispersal in freshwater invertebrates. Annual Review of Ecology and Systematics 32: 159-181.

BOLAND, J. M. 2014. Secondary Dispersal Of Willow Seeds: Sailing On Water Into Safe Sites. Modronõ 61: 388-398.

BONTE, D., H. VAN DYCK, J. M. BULLOCK, A. COULON, M. M. DELGADO, M. GIBBS, V. LEHOUCK, E. MATTHYSEN, K. MUSTIN, M. SAASTAMOINEN, N. SCHTICKZELLE, V. M. STEVENS, S. VANDEWOESTIJNE, M. BAGUETTE, K.

BARTON, T. G. BENTON, A. CHAPUT-BARDY, J. CLOBERT, C. DYTHAM, T. HOVESTADT, C. M. MEIER, S. C. F. PALMER, C. TURLURE, and J. M. J. TRAVIS. 2012. Costs of dispersal. Biological Reviews 87: 290-312.

BOUILLON, S., A. V. BORGES, E. CASTAÑEDA-MOYA, K. DIELE, T. DITTMAR, N. C. DUKE, E. KIRSTENSEN, S. Y. LEE, C. MARCHAND, MIDDELBURG, J., V. H. RIVERA-MONROY, T. J. SMITH III, and R. R. TWILLEY. 2008. Mangrove production and carbon sinks: A revision of global budget estimates. Global Biogeochemical Cycles 22: doi:10.1029/2007GB003052.

BOUMA, T. J., M. B. DE VRIES, E. LOW, G. PERALTA, and P. M. J. HERMAN. 2005. Trade-offs related to ecosystems engineering: a case study on stiffness of emerging macrophytes. Ecology 86: 2187-2199.

BOWNE, D. R., and M. A. BOWERS. 2004. Interpatch movements in spatially structured populations: a literature review. Landscape Ecology 19: 1-20.

BREITFUSS, M. J., R. M. CONNOLLY, and P. E. R. DALE. 2003. Mangrove distribution and mosquito control: transport of *Avicennia marina* propagules by mosquito-control runnels a in southeast Queensland saltmarshes. Estuarine Coastal and Shelf Science 56: 573-579.

BROWN, J. K. M., and M. S. HOVMØLLER. 2002. Aerial Dispersal of Pathogens on the Global and Continental Scales and Its Impact on Plant Disease. Science 297: 537-541.

BULLOCK, J. M., K. SHEA, and O. SKARPAAS. 2006. Measuring plant dispersal: an introduction to field methods and experimental design. Plant Ecology 186: 217-234.

BUNYAVEJCHEWIN, S., and T. NUYIM. 1998. Litterfall production in a primary mangrove, *Rhizophora apiculata* forest in southern Thailand. Thai Journal of Forestry 17: 18-25.

CAIN, M. L., B. G. MILLIGAN, and A. E. STRAND. 2000. Long-distance seed dispersal in plant populations. American Journal of Botany 87: 1217-1227.

CANNICCI, S., D. BURROWS, S. FRATINI, T. J. SMITH, J. OFFENBERG, and F. DAHDOUH-GUEBAS. 2008. Faunal impact on vegetation structure and ecosystem function in mangrove forests: A review. Aquatic Botany 89: 186-200.

CANNICCI, S., M. GOMEI, B. BODDI, and M. VANNINI. 2002. Feeding habits and natural diet of the intertidal crab *Pachygrapsus marmoratus*: opportunistic browser or selective feeder? Estuarine Coastal and Shelf Science 54: 983-1001.

CANNICCI, S., M. GOMEI, F. DAHDOUH-GUEBAS, R. RORANDELLI, and A. TERLIZZI. 2007. Influence of seasonal abundance and food quality on the feeding habits of an opportunistic feeder, the intertidal crab *Pachygrapsus marmoratus*. Marine Biology 151: 1331-1342.

CARSON, H. S., G. S. COOK, P. C. LÓPEZ-DUARTE, and L. A. LEVIN. 2011. Evaluating the importance of demographic connectivity in a marine metapopulation. Ecology 92: 1972-1984.

CARVALHO, M. L. 2002. Aspectos da produção primária dos bosques de mangue do Furo Grande, Bragança, Pará, Brasil. PhD Dissertation. University of Pará, Bragança, Pará, Brazil.

CASWELL, H. 2001. Matrix population models - construction, analysis, and interpretation. Sinauer Associates, Inc. Publishers, Sunderland, Massachussets.

CASWELL, H., R. LENSINK, and M. G. NEUBERT. 2003. Demography and dispersal: Life table response experiments for invasion speed. Ecology 84: 1968-1978.

CHALE, F. M. M. 1996. Litter production in an *Avicennia Germinans* (L.) stearn forest in Guyana, South America. Hydrobiologia 330: 47-53.

CHAMBERT, S., and C. S. JAMES. 2009. Sorting of Seeds by Hydrochory. River Research and Applications 25: 48-61.

CHAN, H. T., and N. HUSIN. 1985. Propagule dispersal, establishment and survival of *Rhizophora mucronata*. The Malaysian Forester 48: 324-329.

CHANG, E. R., R. M. VEENEKLAAS, R. BUITENWERF, J. P. BAKKER, and T. J. BOUMA. 2008. To move or not to move: determinants of seed retention in a tidal marsh. Functional Ecology 22: 720–727.

CHASE, M. W., and J. L. REVEAL. 2009. A phylogenetic classification of the land plants to accompany APGIII. Botanical Journal of the Linnean Society 161: 122-127.

CHAVE, J. 2005. Measuring Wood Density for Tropical Forest Trees: A Field Manual for CTFS Sites. Universite Paul Sabatier, Toulouse, France.

CHEN, L., Q. ZAN, L. MINGGUANG, J. SHEN, and W. LIAO. 2009. Litter dynamics and forest structure of the introduced *Sonneratia caseolaris* mangrove forest in Shenzhen, China. Estuarine, Coastal and Shelf Science 85: 241-246.

CHILDS, D. Z., C. J. E. METCALF, and M. REES. 2010. Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. Proceedings of the Royal Society B: Biological Sciences 277: 3055-3064.

CHRISTENSEN, B., and S. WIUM-ANDERSEN. 1977. Seasonal growth of mangrove trees in southern Thailand. I. The phenology of *Rhizophora apiculata* Bl. Aquatic Botany 3: 281-286.

CLARK, J. S., M. SILMAN, R. KERN, E. MACKLIN, and J. HILLE RIS LAMBERS. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80: 1475-1494.

CLARKE, P. J. 1992. Predispersal mortality and fecundity in the grey mangrove *(Avicennia marina)* in southeastern Australia. Austral. Ecology 17: 161-168.

CLARKE, P. J. 1993. Dispersal of grey mangrove (*Avicennia marina*) propagules in southeastern Australia. Aquatic Botany 45: 195-204.

CLARKE, P. J. 1995. The population dynamics of the mangrove shrub *Aegiceras corniculatum* (Myrsinaceae): fecundity, dispersal, establishment and population structure. Proc. Linn. Soc. N.S.W. 115: 35-44.

CLARKE, P. J., R. A. KERRIGAN, and C. J. WESTPHAL. 2001. Dispersal potential and early growth in 14 tropical mangroves: do early life history traits correlate with patterns of adult distribution? Journal of Ecology 89: 648-659.

CLARKE, P. J., and P. J. MYERSCOUGH. 1991. Buoyancy of *Avicennia marina* propagules in South-Eastern Australia. Aust. J. Bot. 39: 77-83.

CLELAND, E. E., J. M. ALLEN, T. M. CRIMMINS, J. A. DUNNE, S. PAU, S. E. TRAVERS, E. S. ZAVALETA, and E. M. WOLKOVICH. 2012. Phenological tracking enables positive species responses to climate change. Ecology 93: 1765-1771.

CLELAND, E. E., I. CHUINE, A. MENZEL, H. A. MOONEY, and M. D. SCHARTZ. 2007. Shifting plant phenology in response to global change. Trends in Ecology & Evolution 22: 357-365.

CLOBERT, J., M. BAGUETTE, T. G. BENTON, and J. M. BULLOCK. 2012. Dispersal ecology and evolution. Oxford University Press.

CLOUGH, B., D. T. TAN, D. X. PHUONG, and D. C. BUU. 2000. Canopy leaf area index and litter fall in stands of the mangrove *Rhizophora apiculata* of different age in the Mekong Delta, Vietnam. Aquatic Botany 66: 311-320.

COLLINS, M., R. KNUTTI, J. ARBLASTER, J.-L. DUFRESNE, T. FICHEFET, P. FRIEDLINGSTEIN, X. GAO, W. J. GUTOWSKI, T. JOHNS, G. KRINNER, M. SHONGWE, C. TEBALDI, A. J. WEAVER, and M. WEHNER. 2013. Long-term Climate Change: Projections, Commitments and Irreversibility. *In* T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P. M. Midgley (Eds.). Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

CORLETT, R. T., and D. A. WESTCOTT. 2013. Will plant movements keep up with climate change? Trends in Ecology & Evolution 28: 482-488.

COUPLAND, G. T., E. I. PALING, and K. A. MCGUINNESS. 2005. Vegetative and reproductive phenologies of four mangrove species from northern Australia. Australien Journal of Botany 53: 109-117.

COURALET, C., J. VAN DEN BULCKE, L. M. NGOMA, J. VAN ACKER, and H. BEECKMAN. 2013. Phenology in functional groups of central African rainforest trees. Journal of Tropical Forest Science 25: 361-374.

COX, E. F., and J. A. ALLEN. 1999. Stand Structure and Productivity of the Introduced *Rhizophora mangle* in Hawaii Estuaries 22: 276-284.

CÓZAR, A., F. ECHEVARRÍA, J. I. GONZÁLEZ-GORDILLO, X. ITIGOIEN, B. ÚBEDA, S. HERNÁNDEZ-LEÓN, Á. T. PALMA, S. NAVARRO, J. GARCÍA-DE-LOMAS, A. RUIZ, M. L. FERNÁNDEZ-DE-PUELLES, and C. M. DUARTE. 2014. Plastic debris in the open ocean. PNAS 111: 10239-10244.

DAHDOUH-GUEBAS, F., J. G. KAIRO, L. P. JAYATISSA, S. CANNICCI, and N. KOEDAM. 2002. An ordination study to view vegetation structure dynamics in disturbed and undisturbed mangrove forests in Kenya and Sri Lanka. Plant Ecology 161: 123-135.

DAHDOUH-GUEBAS, F., N. KOEDAM, B. SATYANARAYANA, and S. CANNICCI. 2011. Human hydrographical changes interact with propagule predation behaviour in Sri Lankan mangrove forests. Journal of Experimental Marine Biology and Ecology 399: 188-200.

DAHDOUH-GUEBAS, F., I. VAN POTTELBERGH, J. G. KAIRO, S. CANNICCI, and N. KOEDAM. 2004. Human-impacted mangroves in Gazi (Kenya): predicting future vegetation based on retrospective remote sensing, social surveys, and tree distribution. Marine Ecology Progress Series 272: 77-92.

DAHDOUH-GUEBAS, F., M. VERNEIRT, J. F. TACK, and N. KOEDAM. 1997. Food preferences of *Neosarmatium meinerti* de Man (Decapoda: Sesarminae) and its possible effect on the regeneration of mangroves. Hydrobiologia 347.

DARWIN, C. 1859. On the Origin of Species. Oxford University Press, Oxford.

DAS, S., and M. GHOSE. 2003. Seed structure and germination pattern of some Indian mangroves with taxonomic relevance. Taiwania 48: 287-298.

DAVIES, K. W., and R. L. SHELEY. 2007. Influence of neighboring vegetation height on seed dispersal: implications for invasive plant management. Weed Science 55: 626-630.

DAVIS, J. H. 1940. The ecology and geologic role of mangroves in Florida. Carnegie Institue of Washington Publications, Papers from Tortugas Laboratory 32: 304–412.

DAY, J. W., W. H. CONNER, F. LEY-LOU, R. H. DAY, and A. M. NAVARRO. 1987. The productivity and composition of mangrove forests, Laguna de Términos, Mexico. Aquatic Botany 27: 267-284.

DE LANGE, W. P., and P. J. DE LANGE. 1994. An appraisal of factors controlling the latitudinal distribution of mangrove (*Avicennia marina* var. *resinifera*) in New Zealand. Journal of Coastal Research 10: 539-548.

DE RYCK, D. 2009. Moving and settling: Experiments on the dispersal and establishment of hydrochorous propagules. Master Dissertation. Vrije Universiteit Brussel, Brussels.

DE RYCK, D. J. R., E. M. R. ROBERT, N. SCHMITZ, T. VAN DER STOCKEN, D. DI NITTO, F. DAHDOUH-GUEBAS, and N. KOEDAM. 2012. Size does matter, but not only size: Two alternative dispersal strategies for viviparous mangrove propagules. Aquatic Botany.

DELGADO, P., P. F. HENSEL, J. A. JIMENEZ, and J. W. DAY. 2001. The importance of propagule establishment and physical factors in mangrove distributional patterns in a Costa Rican estuary. Aquatic Botany 71: 157-178.

DI NITTO, D., P. L. A. ERFTEMEIJER, J. K. L. VAN BEEK, F. DAHDOUH-GUEBAS, L. HIGAZI, K. QUISTHOUDT, L. P. JAYATISSA, and N. KOEDAM. 2013. Modelling drivers of mangrove propagule dispersal and restoration of abandoned shrimp farms. Biogeosciences 10: 5095-5113.

DODD, R. S., and Z. AFZAL-RAFII. 2002. Evolutionary genetics of mangroves: continental drift to recent climate change. Trees-Structure and Function 16: 80-86.

DODD, R. S., Z. AFZAL-RAFII, N. KASHANI, and J. BUDRICK. 2002. Land barriers and open oceans: effects on gene diversity and population structure in *Avicennia germinans* L. (Avicenniaceae). Molecular Ecology 11: 1327-1338.

DOI, H., and M. TAKAHASHI. 2008. Latitudinal patterns in the phenological responses of leaf colouring and leaf fall to climate change in Japan. Global Ecology and Biogeography 17: 556-561.

DOYLE, T. W., G.F. GIROD, AND M.A. BOOKS. 2003. Modelling Mangrove Forest Migration along the Southwest Coast of Florida Under Climate Change. U.S. Geological Survey, National Wetlands Research Center.

DREXLER, J. Z. 2001. Maximum longevities of *Rhizophora apiculata* and *R. mucronata* propagules. Pacific Science 55: 17-22.

DUKE, N. C. 1990. Phenological trends with latittude in the mangrove tree *Avicennia marina*. Journal of Ecology 78: 113-133.

DUKE, N. C. 1992. Mangrove floristics and biogeography. Tropical mangrove ecosystems, pp. 63–100. American Geophysical Union, Washington, DC.

DUKE, N. C. 2006. Australia's mangroves. University of Queensland, Brisbane.

DUKE, N. C., M. C. BALL, and J. C. ELLISON. 1998. Factors influencing biodiversity and distributional gradients in mangroves. Global Ecology and Biogeography Letters 7: 27-47.

DUKE, N. C., J. S. BUNT, and W. T. WILLIAMS. 1984. Observations on the floral and vegetative phenologies of North-eastern Australian mangroves. Aust. J. Bot. 32: 87-99.

DUKE, N. C., J. O. MEYNECKE, S. DITTMANN, A. M. ELLISON, K. ANGER, U. BERGER, S. CANNICCI, K. DIELE, K. C. EWEL, C. D. FIELD, N. KOEDAM, S. Y. LEE, C. MARCHAND, I. NORDHAUS, and F. DAHDOUH-GUEBAS. 2007a. A world without mangroves? Science 317: 41-42.

DUKE, N. C., J. O. MEYNECKE, S. DITTMANN, A. M. ELLISSON, K. ANGER, U. BERGER, S. CANNICCI, K. DIELE, K. C. EWEL, C. D. FIELD, N. KOEDAM, S. Y. LEE, C. MARCHAND, I. NORDHAUS, and F. DAHDOUH-GUEBAS. 2007b. A World Without Mangroves? Science 317: 41-43.

EASTERN AFRICA DATABASE AND ATLAS PROJECT (EADAP). 1994. Database for Marine and Coastal Resources of Kenya, KMFRI, Mombasa, Kenya.

EDWARDS, A. L., and R. WYATT. 1994. Seed buoyancy and viability of the wetland milkweed *Asclepias perennis* and an upland milkweed, *Asclepias exaltata*. Bulletin of the Torrey Botanical Club 121: 160-169.

ERFTEMEIJER, P. L. A., and R. R. LEWIS. 2000. Planting mangroves on intertidal mudflats: habitat restoration or habitat conversion? ECOTONE VIII Seminar Enhancing Coastal Ecosystems Restoration for the 21st Century, pp. 156-165. Royal Forest Department of Thailand, Bangkok.

EWERS, R. M., and R. K. DIDHAM. 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biological Reviews 81: 117-142.

FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology and Systematics 34: 487-515.

FAO. 2007. The world's mangroves 1980-2005. FAO Forestry Paper 153, Rome.

FARNSWORTH, E. J., and A. M. ELLISON. 1997. The global conservation status of mangroves. Ambio 26: 328-334.

FENG, X., A. POPORATO, and I. RODRIGUEZ-ITURBE. 2013. Changes in rainfall seasonality in the tropics. Nature Climate Change: doi: 10.1038/NCLIMATE1907.

FFIELD, A., J. TOOLE, and D. WILSON. 1997. Seasonal circulation in the South Indian Ocean Geophysical Research Letters 24: 2773-2776.

FIGUEROLA, J., I. CHARALAMBIDOU, L. SANTAMARIA, and A. J. GREEN. 2010. Integral dispersal of seeds by waterfowl: effect of seed size on gut passage time and germination patterns. Naturwissenschaften 97: 555-565.

FITTER, A. H., and R. S. R. FITTER. 2002. Rapid changes in flowering time in British plants. Science 296: 1689-1691.

FRANCIS, L. 1991. Sailing downwind: aerodynamic performance of the *Velella* sail. Journal of Experimental Biology 158: 117-132.

FRIESS, D. A., K. W. KRAUSS, E. M. HORSTMAN, T. BALKE, T. J. BOUMA, D. GALLI, and E. L. WEBB. 2012. Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems. Biological Reviews 87: 346-366.

FURUKAWA, K., E. WOLANSKI, and H. MUELLER. 1997. Currents and sediment transport in mangrove forests. Estuarine and Coastal and Shelf Science 44: 301-310.

GENG, Q., C. LIAN, S. GOTO, J. TAO, M. KIMURA, M. D. S. ISLAM, and T. HOGETSU. 2008. Mating system, pollen and propagule dispersal, and spatial genetic structure in a high-density population of the mangrove tree *Kandelia candel*. Molecular Ecology 17: 4724–4739.

GIESEN, W., S. WULFFRAAT, M. ZIEREN, and L. SCHOLTEN. 2007. Mangrove guidebook for Southeast Asia. Food and Agricultural Organisation & Wetlands International, Bangkok.

GILL, A. M., and P. B. TOMLINSON. 1971. Studies on the Growth of Red Mangrove (*Rhizophora mangle* L.) 3. Phenology of the Shoot. Biotropica 3: 109-124.

GILLIS, L. G., T. J. BOUMA, W. KISWARA, A. D. ZIEGLER, and P. M. J. HERMAN. 2014. Leaf transport in mimic mangrove forests and seagrass beds. Marine Ecology Progress Series 498: 95-102.

GILMAN, E. L., J. ELLISON, N. C. DUKE, and C. FIELD. 2008. Threats to mangroves from climate change and adaptation options: A review. Aquatic Botany 89: 237-250.

GIRI, C., E. OCHIENG, L. L. TIESZEN, Z. ZHU, A. SINGH, T. LOVELAND, J. MASEK, and N. DUKE. 2011. Status and distribution of mangrove forests of the world using earth observation satellite data. Global Ecology and Biogeography 20: 154-159.

GREENE, D. F. 2005. The role of abscission in long distance seed dispersal by the wind. Ecology 86: 3105-3110.

GUNN, C. R., and J. V. DENNIS. 1973. Tropical and temperate stranded seeds and fruits from the Gulf of Mexico. Contributions in Marine Science 17: 111–121.

GUNN, C. R., and J. V. DENNIS. 1999. World guide to tropical drift seeds and fruits. Krieger Publishing Company, Malabar, Florida.

HANCKE, L., M. J. ROBERTS, and J. F. TERNON. 2014. Surface drifter trajectories highlight flow pathways in the Mozambique Channel. Deep-Sea Research II 100: 27-37.

HARDIWINOTO, S. 1988. Stand structure, litterfall and regeneration process of a mangrove forest at Oura Bay, Okinawa. PhD Dissertation. University of the Ryukyus, Okinawa, Japan.

HARDIWINOTO, S., T. NAKASUGA, and T. IGARASHI. 1989. Litter production and decomposition of a mangrove forest at Ohura Bay, Okinawa. Research Bulletins of the College Experiment Forests 46: 577-594.

HARPER, J. L. 1977. Population Biology of Plants, Academic Press, London.

HEGAZY, A. K. 1998. Perspectives on survival, phenology, litter fall and decomposition, and caloric content of *Avicennia marina* in the Arabian Gulf region. Journal of Arid Environments 40: 417-429.

HELLWEGER, F. L., E. VAN SEBILLE, and N. D. FREDRICK. 2014. Biogeographic patterns in ocean microbes emerge in a neutral agent-based model. Science 345: 1346-1349.

HENLE, K., K. F. DAVIES, M. KLEYER, C. MARGULES, and J. SETTELE. 2004. Predictors of Species Sensitivity to Fragmentation. Biodiversity and Conservation 13.

HERON, S. F., E. J. METZGER, and W. J. SKIRVING. 2006. Seasonal Variations of the Ocean Surface Circulation in the Vicinity of Palau. Journal of Oceanography 62: 413-426.

HIGGINS, S. I., J. S. CLARK, R. NATHAN, T. HOVESTADT, F. SCHURR, J. M. V. FRAGOSO, M. R. AGUIAR, E. RIBBENS, and S. LAVOREL. 2003a. Forecasting plant migration rates: managing uncertainty for risk assessment. Journal of Ecology 91: 341-347.

HIGGINS, S. I., R. NATHAN, and M. L. CAIN. 2003b. Are long-distance dispersal events in plants usually caused by nonstandard means of dispersal? Ecology 84: 1945-1956.

HIGGINS, S. I., and D. M. RICHARDSON. 1999. Predicting plant migration rates in a changing world: The role of long-distance dispersal. American Naturalist 153: 464-475.

HILL, C., D. MENEMENLIS, B. CIOTTI, and C. HENZE. 2007. Investigating solution convergence in a global ocean model using a 2048-processor cluster of distributed shared memory machines. Scientific Programming 12.

HOWE, H. F., and M. N. MIRITI. 2004. When seed dispersal matters. BioScience 54: 651-660.

HUANG, J. Z., A. SHRESTHA, M. TOLLENAAR, W. DEEN, I. RAICAN, H. RAHIMIAN, and C. J. SWANTON. 2001. Effect of temperature and photoperiod on the phenological development of wild mustard (*Sinapis arvensis* L.). Field Crops Research 70: 75-86.

IOSILEVSKII, G., and D. WEIHS. 2009. Hydrodynamics of sailing of the Portuguese man-of-war *Physalia physalis*. Journal of the Royal Society Interface 6: 613-626.

JAMBECK, J. R., R. GEYER, C. WILCOX, T. R. SIEGLER, M. PERRYMAN, A. ANDRADY, R. NARAYAN, and K. L. LAW. 2015. Plastic waste inputs from land into the ocean. Science 347: 768-771.

JAYATISSA, L. P., W. A. A. D. L. WICKRAMASINGHE, F. DAHDOUH-GUEBAS, and M. HUXHAM. 2008. Interspecific variations in responses of mangrove seedlings to two contrasting salinities. International Review of Hydrobiology 93: 700-710.

JOHST, K., R. BRANDL, and S. EBER. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. Oikos 98: 263-270.

JUMAN, R. A. 2005. Biomass, litterfall and decomposition rates for the fringed *Rhizophora mangle* forest lining the Bon Accord Lagoon, Tobago. Revista de Biologia Tropical 53: 207-217.

KAMRUZZAMAN, M., S. SHARMA, and A. HAGIHARA. 2013a. Vegetative and reproductive phenology of the mangrove *Kandelia obovata*. Plant Species Biology 28: 118-129.

KAMRUZZAMAN, M., S. SHARMA, M. KAMARA, and A. HAGIHARA. 2013b. Vegetative and reproductive phenology of the mangrove *Bruguiera gymnorrhiza* (L.) Lam. on Okinawa Island, Japan. Trees 27: 619-628.

KELLOGG, C. A., and D. W. GRIFFIN. 2006. Aerobiology and the global transport of desert dust. Trends in Ecology & Evolution 21: 639-644.

KINLAN, B. P., S. D. GAINES, and S. E. LESTER. 2005. Propagule dispersal and the scales of marine community process. Diversity and Distributions 11: 139-148.

KITHEKA, J. U. 1996. Water circulation and coastal trapping of brackish water in a tropical mangrove-dominated bay in Kenya. Limnol. Oceanogr. 41: 169-176.

KITHEKA, J. U. 1997. Coastal tidally-driven circulation and the role of water exchange in the linkage between tropical coastal ecosystems. Estuarine Coastal and Shelf Science 45: 177-187.

KITHEKA, J. U., G. S. ONGWENYI, and K. M. MAVUTI. 2003. Fluxes and exchange of suspended sediment in tidal inlets draining a degraded mangrove forest in Kenya. Estuarine Coastal and Shelf Science 56: 655-667.

KOKKO, H., and A. LÓPEZ-SEPULCRE. 2006. From Individual Dispersal to Species Ranges: Perspectives for a Changing World. Science 313: 789-791.

KOMIYAMA, A., V. CHIMCHOME, and J. KONGSANGCHAI. 1992. Dispersal patterns of mangrove propagules. Research Bulletin Fac. Agr. Gifu Univ. 57: 27-34.

KÖRNER, C., and D. BASLER. 2010. Phenology Under Global Warming. Science 327: 1461-1462.

KOT, M., M. A. LEWIS, and P. VAN DEN DRIESSCHE. 1996. Dispersal data and the spread of invading organisms. Ecology 77: 2027-2042.

KRAMER, K., I. LEINONEN, and D. LOUSTAU. 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. International Journal of Biometorology 44: 67-75.

KRAUSS, K. W., C. E. LOVELOCK, K. L. MCKEE, L. LOPEZ-HOFFMAN, S. M. L. EWE, and W. P. SOUSA. 2008. Environmental drivers in mangrove establishment and early development: A review. Aquatic Botany 89: 105-127.

LEACH, G. J., and S. BURGIN. 1985. Litter production and seasonality of mangroves in Papua New Guinea. Aquatic Botany 23: 215-224.

LEE, S. Y. 1989. Litter Production and Turnover of the Mangrove *Kandelia candel* (L.) Druce in a Hong Kong Tidal Shrimp Pond Estuarine Coastal and Shelf Science 29: 75-87.

LEVIN, S. A., H. C. MULLER-LANDAU, R. NATHAN, and J. CHAVE. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Annual Review of Ecology, Evolution and Systematics 34: 575-604.

LEVINE, J. M., and D. MURRELL. 2003. Community-level consequences of seed dispersal patterns. Annual Reviews of Ecology and Systematics 34: 349-574.

LINDQUIST, E. S., K. W. KRAUSS, P. T. GREEN, D. J. O'DOWD, P. M. SHERMAN, and T. J. SMITH. 2009. Land crabs as key drivers in tropical coastal forest recruitment. Biological Reviews 84: 203-223.

LÓPEZ-PORTILLO, J., and E. EZCURRA. 1989. Response of three mangroves to salinity in two geoforms. Functional Ecology 3: 355-361.

LU, C., and P. LIN. 1990. Studies on litter fall and decomposition of *Bruguiera sexangula* (Lour.) Poir, community on Hainan Island, China. Bulletin of Marine Science 47: 139-148.

MACKEY, A. P., and G. SMAIL. 1995. Spatial and temporal variation in litter fall of *Avicennia marina* (Forssk.) Vierh. in the Brisbane River, Queensland, Australia. Aquatic Botany 52: 133-142.

MARRIS, E. 2014. Tree hitched a ride to island. Nature 510: 320-321.

MASSÓ I ALEMÁN, S., C. BOURGEOIS, W. APPELTANS, B. VANHOORNE, N. DE HAUWERE, P. STOFFELEN, A. HAEGHEBAERT, and F. DAHDOUH-GUEBAS. 2010. The 'Mangrove Reference Database and Herbarium'. Plant Ecology and Evolution 143: 225-232.

MAY, J. 1999. Spatial variation in litter production by the mangrove *Avicenia marina* var. *australasica* in Rangaunu Harbour, Northland, New Zealand. New Zealand Journal of Marine and Freshwater Research 33: 163-172.

MAZDA, Y., N. KANAZAWA, and E. WOLANSKI. 1995. Tidal Asymmetry in Mangrove Creeks. Hydrobiologia 295: 51-58.

MCGUINNESS, K. A. 1997. Dispersal, establishment and survival of *Ceriops tagal* propagules in a north Australian mangrove forest. Oecologia 109: 80-87.

MCKEE, K. L. 1993. Soil physiochemical patterns and mangrove species distribution-reciprocal effects? Journal of Ecology 81: 477-487.

MCKEE, K. L., J. E. ROOTH, and I. C. FELLER. 2007. Mangrove recruitment after forest disturbance is facilitated by herbaceous species in the Caribbean. Ecological Applications 17: 1678-1693.

MCMILLAN, C. 1971. Environmental factors affecting seedling establisment of the black mangrove on the central Texas coast. Ecology and Freshwater Fish 52: 927-930.

MEHLIG, U. 2001. Aspects of tree primary production in an equatorial mangrove forest in Brazil. PhD Dissertation, Bremen, Germany.

MEHLIG, U. 2006. Phenology of the red mangrove, *Rhizophora mangle* L., in the Caeté Estuary, Pará, equatorial Brazil. Aquatic Botany 84: 158-164.

MENEMENLIS, D., J.-M. CAMPIN, P. HEIMBACH, C. HILL, T. N. LEE, A. NGUYEN, M. SCHODLOK, and H. ZHANG. 2008. ECCO2: High Resolution Global Ocean and Sea Ice Data Synthesis. Mercator Ocean Quaternary Newsletter: 13-21.

MENEZES, M. P. M. D., U. BERGER, and U. MEHLIG. 2008. Mangrove vegetation in Amazonia: a review of studies from the coast of Pará and Maranhão States, north Brazil. Acta Amazonica 38: 403-420.

MENZEL, A., N. ESTRELLA, and A. TESTKA. 2005. Temperature response rates from long-term phenological records. Climate Research 30: 21-28.

MINCHINTON, T. E. 2006. Consequences of pre-dispersal damage by insects for the dispersal and recruitment of mangroves. Oecologia 148: 70-80.

MUKHERJEE, N., W. J. SUTHERLAND, M. N. KHAN, U. BERGER, N. SCHMITZ, F. DAHDOUH-GUEBAS, and N. KOEDAM. 2014. Using export knowledge and modeling to define mangrove composition, functioning, and threats and estimate time frame for recovery. Ecology and Evolution 4: 2247-2262.

MULLER-LANDAU, H. C., S. A. LEVIN, and J. E. KEYMER. 2003. Theoretical perspectives on evolution of long-distance dispersal and the example of specialized pesps. Ecology 84: 1957-1967.

NADIA, T. D. L., L. P. C. MORELLATO, and I. C. MACHADO. 2012. Reproductive phenology of a northeast Brazilian mangrove community: Environmental and biotic constraints. Flora 207: 682-692.

NAIDOO, G. 1989. Seasonal plant water relations in a South African mangrove swamp. Aquatic Botany 33: 87-100.

NAKASUGA, T., and K. ITOO. 1983. Studies on the fruits, viviparous seeds and bud break of mangrove species in Japan. Res. Bull. Sub-trop. For. Univ. Ryukyus 5: 16-38.

NATHAN, R. 2001. The challenges of studying dispersal. Trends in Ecology & Evolution 16: 481-483.

NATHAN, R. 2005. Long-distance dispersal research: building a network of yellow brick roads. Diversity and Distributions 11: 125-130.

NATHAN, R. 2006. Long distance dispersal of plants. Science 313: 786-788.

NATHAN, R. 2007. Total dispersal kernels and the evaluation of diversity and similarity in complex dispersal systems. *In* A. J. Dennis, E. W. Schupp, R. J. Green and D. A. Westcott (Eds.). Seed dispersal: theory and its application in a changing world, p. 684. CAB International Publishing, Oxfordshire.

NATHAN, R., G. G. KATUL, G. BOHRER, A. KUPARINEN, M. B. SOONS, S. E. THOMPSON, A. TRAKHTENBROT, and H. S. HORN. 2011. Mechanistic models of seed dispersal by wind. Theoretical Ecology 4: 113-132.

NATHAN, R., and H. C. MULLER-LANDAU. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15: 278-285.

NATHAN, R., G. PERRY, J. T. CRONIN, A. E. STRAND, and M. L. CAIN. 2003. Methods for estimating long-distance dispersal. Oikos 103: 261-273.

NATHAN, R., F. M. SCHURR, O. SPIEGEL, O. STEINITZ, A. TRAKHTENBROT, and A. TSOAR. 2008. Mechanisms of long-distance seed dispersal. Trends in Ecology and Evolution 23: 638-647.

NAVARRETE, A. D. J., and J. J. OLIVA-RIVERA. 2002. Litter production of *Rhizophora mangle* at Bacalar Chico, southern Quintana Roo, Mexico. 18: 79-86.

NEO, M. L., P. L. A. ERFTEMEIJER, J. K. L. VAN BEEK, D. S. VAN MAREN, S. L.-M. TEO, and P. A. TODD. 2013. Recruitment constraints in Signapore's fluted giant clam (*Tridacna squamosa*) population - A dispersal model approach. Plos ONE 8: e58819. doi:58810.51371/journal.pone.0058819.

NETTEL, A., and R. S. DODD. 2007. Drifting propagules and receding swamps; genetic footprints of long–distance dispersal and Quaternary extinction along tropical coasts. Evolution 61: 958-971.

NEUKERMANS, G., F. DAHDOUH-GUEBAS, J. G. KAIRO, and N. KOEDAM. 2008. Mangrove species and stand mapping in Gazi bay (Kenya) using Quickbird satellite imagery. Journal of Spatial Science 53: 75-86.

NILSSON, C., R. L. BROWN, R. JANSSON, and D. M. MERRITT. 2010. The role of hydrochory in structuring riparian and wetland vegetation. Biological Reviews 85: 837-858.

OBURA, D. O. 2001. Kenya. Marine Pollution Bulletin 42: 64-78.

OCHIENG, C. A., and P. L. A. ERFTEMEIJER. 2002. Phenology, litterfall and nutrient resorption in *Avicennia marina* (Forssk.) Vierh in Gazi Bay, Kenya. Trees 16: 167-171.

ODUM, W. E., and E. J. HEALD. 1975. The detritus-based food web of an estuarine mangrove community. *In* J. E. Cronin (Ed.). Estuarine Research, pp. 265-286. Academic Press, Inc., New York.

OZINGA, W. A., R. M. BEKKER, S. J. H. J., and J. M. VAN GROENENDAEL. 2004. Dispersal potential in plant communities depends on environmental conditions. Journal of Ecology 92: 767-777.

PALUMBI, S. R. 2003. Population genetics, demographic connectivity, and the design of marine reserves. Ecological Applications 13: S146-S158.

PARIS, C. B., J. HELGERS, E. VAN SEBILLE, and A. SRINIVASAN. 2013. Connectivity modeling system: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environmental Modelling & Software 42: 47-54.

PETERSON, J. M., and S. S. BELL. 2012. Tidal events and salt-marsh structure influence black mangrove (*Avicennia germinans*) recruitment across an ecotone. Ecology 93: 1648-1658.

PIL, M. W., M. R. T. BOEGER, V. C. MUSCHNER, M. R. PIE, A. OSTRENSKY, and W. A. BOEGER. 2011. Postglacial north-south expansion of populations of *Rhizophora mangle* (Rhizophoraceae) along the Brazilian coast revealed by microsatellite analysis. American Journal of Botany 98: 1031-1039.

PINSKY, M. L., S. R. PALUMBI, S. ANDRÉFOUËT, and S. J. PURKIS. 2012. Open and closed seascapes: where does habitat patchiness create populations with high fractions of self-recruitment. Ecological Applications 22: 1257-1267.

PITELKA, L. F., R. H. GARDNER, J. ASH, S. BERRY, H. GITAY, I. R. NOBLE, A. SAUNDERS, R. H. W. BRADSHAW, L. BRUBAKER, J. S. CLARK, M. B. DAVIS, S. SUGITA, J. M. DYER, R. HENGEVELD, G. HOPE, B. HUNTLEY, G. A. KING, S. LAVOREL, R. N. MACK, G. P. MALANSON, M. MCGLONE, I. C. PRENTICE, and M. REJMANEK. 1997. Plant migration and climate change. American Scientist 85: 464-473.

POLIDORO, B. A., K. E. CARPENTER, L. COLLINS, N. C. DUKE, A. M. ELLISON, J. C. ELLISON, E. J. FARNSWORTH, E. S. FERNANDO, K. KATHIRESAN, N. KOEDAM, S. R. LIVINGSTONE, T. MIYAGI, G. E. MOORE, V. N. NAM, J. E. ONG, J. H. PRIMAVERA, S. G. SALMO III, J. C. SANCIANGCO, S. SUKARDJO, Y. WANG, and J. W. H. YONG.

2010. The Loss of Species: Mangrove Extinction Risk and Geographic Areas of Global Concern. Plos ONE 5: e10095, doi:10010.11371/journal.pone.0010095.

PORTNOY, S., and M. F. WILLSON. 1993. Seed dispersal curves: behavior of the tail of the distribution. Evolutionary Ecology 7: 25-44.

PRIMAVERA, J. H., and R. B. SADABA. 2012. Beach forest species and mangrove associates on the Philippines. SEAFDEC Aquaculture Department, Tigbauan, Iloilo.

PROFFITT, C. E., E. C. MILBRANDT, and S. E. TRAVIS. 2006. Red mangrove (*Rhizophora mangle*) reproduction and seedling colonization after hurricane Charley: comparisons of Charlotte Harbor and Tampa Bay. Estuaries and Coasts 29: 972-978.

QUISTHOUDT, K. 2012. Mangroves meet their limits. PhD Dissertation. Vrije Universiteit Brussel, Brussels.

RABINOWITZ, D. 1978a. Dispersal properties of mangrove propagules. Biotropica: 47-57.

RABINOWITZ, D. 1978b. Early growth of mangrove seedlings in Panama and an hypothesis concerning the relationship of dispersal and zonation. Journal of Biogeography 5: 113-133.

RANDIN, C. F., J. PAULSEN, Y. VITASSE, C. KOLLAS, T. WOHLGEMUTH, N. E. ZIMMERMANN, and C. KÖRNER. 2013. Do the elevational limits of deciduous tree species match their thermal latitudinal limits? Global Ecology and Biogeography 22: 913-923.

RICHARDSON, A. D., T. F. KEENAN, M. MIGLIAVACCA, Y. RYU, O. SONNENTAG, and M. TOOMEY. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. Agricultural and Forest Meteorology 169: 156-173.

RIGINOS, C., and L. LIGGINS. 2013. Seascape Genetics: Populations, Individuals, and Genes Marooned and Adrift. Geography Compass 7: 197-216.

ROBERTSON, A., R. GIDDINS, and T. J. SMITH. 1990. Seed predation by insects in tropical mangrove forests: extent and effects on seed viability and the growth of seedlings. Oecologia 83: 213-219.

RODRÍGUEZ-RAMÍREZ, A., J. NIVIA-RUÍZ, and J. GARZÓN-FERREIRA. 2004. Características estructurales y functionales del manglar de *Avicennia germinans* en la Bahía de Chengue (Caribe Colombiano). Bol. Invest. Mar. Cost. 33: 223-244.

SAENGER, P. 2002. Mangrove ecology, silviculture and conservation, Dordrecht, The Netherlands.

SAIFULLAH, S. M., A. K. KHAFAJI, and A. S. MANDURA. 1989. Litter production in a mangrove stand of the Saudi Arabian Red Sea Coast. Aquatic Botany 36: 79-86.

SANTOS, C. I. 2005. Fenologia de Avicennia L. em dois sítios na península de Ajuruteua, Bragança, Pará. PhD Dissertation. University of Pará, Bragança, Pará, Brazil.

SARNEEL, J. M., B. BELTMAN, A. BUIJZE, R. GROEN, and M. B. SOONS. 2014. The role of wind in the dispersal of floating seeds in slow-flowing or stagnant water bodied. Journal of Vegetation Science 25: 262-274.

SASEKUMAR, A., and J. J. LOI. 1983. Litter production in three mangrove forest zones in the Malay Peninsula. Aquatic Botany 17: 283-290.

SAVAGE, D., M. J. BARBETTI, W. J. MACLEOD, M. U. SALAM, and M. RENTON. 2010. Timing of propagule release significantly alters the deposition area of resulting aerial dispersal. Diversity and Distributions 16: 288–299.

SAVAGE, D., M. J. BARBETTI, W. J. MACLEOD, M. U. SALAM, and M. RENTON. 2012. Seasonal and diurnal patterns of spore release can significantly affect the proportion of spores expected to undergo long-distance dispersal. Microbial Ecology 63: 578-585.

SCHNEIDER, R. L., and R. R. SHARITZ. 1988. Hydrochory and regeneration in a bald cypress-water tupelo swamp forest. Ecology 69: 1055-1063.

SELKOE, K. A., J. R. WATSON, C. WHITE, T. B. HORIN, M. LACCHEI, S. MITARAI, D. A. SIEGEL, S. D. GAINES, and R. J. TOONEN. 2010. Taking the chaos out of genetic patchiness: seascape genetics reveals ecological and oceanographic drivers of genetic patterns in three temperate reef species. Molecular Ecology 19: 3708-3726.

SENGUPTA, R., B. MIDDLETON, C. YAN, M. ZURO, and H. HARTMAN. 2005. Landscape characteristics of *Rhizophora mangle* forests and propagule deposition in coastal environments of Florida (USA). Landscape Ecology 20: 63-72.

SHANKAR, D., P. N. VINAYACHANDRAN, and A. S. UNNIKRISHNAN. 2002. The monsoon currents in the north Indian Ocean. Progress in Oceanography 52: 63-120.

SHARMA, S., M. KAMRUZZAMAN, A. T. M. RAFIQUL HOQUE, K. ANALUDDIN, and A. HAGIHARA. 2011. Vegetative and Reproductive Phenology, and Litterfall Production of *Rhizophora stylosa* in Okinawa Island, Japan. International Journal of Environment 1: 21-27.

SHARMA, S., A. T. M. RAFIQUL HOQUE, K. ANALUDDIN, and A. HAGIHARA. 2012. Litterfall dynamics in an overcrowded mangrove *Kandelia obovata*, (S., L.) Yong stand over five years. Estuarine Coastal and Shelf Science 98: 31-41.

SHUNULA, J. P., and A. WHITTICK. 1999. Aspects of litter production in Mangroves from Unguja Island, Zanzibar, Tanzania. Estuarine, Coastal and Shelf Science 49: 51-54.

SIEGEL, D. A., S. MITARAI, C. J. COSTELLO, S. D. GAINES, B. E. KENDALL, R. R. WARNER, and K. B. WINTERS. 2008. The stochastic nature of larval connectivity among nearshore marine populations. Proceedings of the National Academy of Sciences of the United States of America 105: 8974-8979.

SILVA, R. M. 2005. Fenologia de Laguncularia racemosa (L.) Gaertn. f. em três bosques de manguezal na peninsula de Ajuruteua, Pará, Brasil. PhD Dissertation. University of Pará, Bragança, Pará, Brazil.

SIMPSON, S., H. B. HARRISON, M. R. CLAEREBOUDT, and S. PLANES. 2014. Long-dictance dispersal via ocean currents connects Omani clownfish populations throughout entire species range. PLoS ONE 9: e107610. doi:107610.101371/journal.pone.0107610.

SINGH, K. P., and C. P. KUSHWAHA. 2005. Emerging paradigms of tree phenology in dry tropics. Current Science 89: 964-975.

SLATKIN, M. 1987. Gene flow and the geographic structure of natural populations. Science 236: 787-792.

SMITH, T. J. 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology and Freshwater Fish 68: 266-273.

SMITH, W. H. F., and D. T. SANDWELL. 1997. Global seafloor topography from satellite altimetry and ship depth soundings. Science 277: 1957-1962.

SOONS, M. B., and W. A. OZINGA. 2005. How important is long-distance seed dispersal for the regional survival of plant species? Diversity and Distributions 11: 165-172.

SOUSA, W. P., P. G. KENNEDY, B. J. MITCHELL, and B. M. ORDÓÑEZ L. 2007. Supply-side ecology in mangroves: dor propagule dispersal and seedling establishment explain forect structure? Ecological Monographs 77: 53–76.

SPALDING, M., M. KAINUMA, and L. COLLINS. 2010. World Atlas of Mangroves. Earthscan, London.

STEELE, O. 2006. Natural and anthropogenic biogeography of mangroves in the Southwest Pacific. PhD Dissertation. University of Hawaii, Manoa.

STEINKE, T. D. 1986. A preliminary study of buoyancy behaviour in *Avicennia marina* propagules. South African Journal of Botany 52: 559-565.

STEINKE, T. D., and C. J. WARD. 1988. Litter production by mangroves. II. St Lucia and Richards Bay. South African Journal of Botany 54: 445-454.

STEINKE, T. D., and C. J. WARD. 2003. Use of plastic drift cards as indicators of possible dispersal of propagules of the mangrove *Avicennia marina* by ocean currents. African Journal of Marine Science 25: 169-176.

STEVENSON, N. J., R. R. LEWIS, and P. R. BURBRIDGE. 1999. Disused shrimp ponds and mangrove rehabilitation. *In* W. Streever (Ed.). An International Perspective on Wetland Restoration, pp. 277-297. Kluwer Academic Publishers, Dordrecht, The Netherlands.

STIEGLITZ, T., and P. V. RIDD. 2001. Trapping of mangrove propagules due to density-driven secondary circulation in the Normanby River estuary, NE Australia. Marine Ecology-Progress Series 211: 131-142.

SUTHERLAND, W. J., R. P. FRECKLETON, H. C. J. GODFRAY, S. R. BEISSINGER, T. BENTON, D. D. CAMERON, Y. CARMEL, D. A. COOMES, T. COULSON, M. C. EMMERSON, R. S. HAILS, G. C. HAYS, D. J. HODGSON, M. J. HUTCHINGS, D. JOHNSON, J. P. G. JONES, M. J. KEELING, H. KOKKO, W. E. KUNIN, X. LAMBIN, O. T. LEWIS, Y. MALHI, N. MIESZKOWSKA, E. J. MILNER-GULLAND, K. NORRIS, A. B. PHILLIMORE, D. W. PURVES, J. M. REID, D. C. REUMAN, K. THOMPSON, J. M. J. TRAVIS, L. A. TURNBULL, D. A. WARDLE, and T. WIEGAND. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101: 58-67.

SWAINE, M. D., and T. C. WHITMORE. 1988. On the definition of ecological species groups in tropical rainforests. Vegetatio 75: 81-86.

TAKAYAMA, K., M. TAMURA, Y. TATESHI, E. L. WEBB, and T. KAJITA. 2013. Strong genetic structure over the American continents and transoceanic dispersal in red mangroves *Rhizophora mangle* (Rhizophoraceae), revealed by broad-scale nuclear and chloroplast DNA analysis. American Journal of Botany.

TAM, N. F. Y. 2007. Provision of services for preparation of a management strategy for *Sonneratia* in inner deep bay areas. (Unpublished report).

TEMPERTON, V. M. 2007. The recent double paradigm shift in restoration ecology. Restoration Ecology 15: 344-347.

TERNON, J. F., M. J. ROBERTS, T. MORRIS, L. HANCKE, and B. BACKEBERG. 2014. In situ measured current structures of the eddy field in the Mozambique Channel. Deep-Sea Research II 100: 10-26.

THORNTON, P. K., P. J. ERICKSEN, M. HERRERO, and A. J. CHALLINOR. 2014. Climate variability and vulnerability to climate change: a review. Global Change Biology 20: 3313-3328.

TILMAN, D., R. M. MAY, C. L. LEHMAN, and M. A. NOWAK. 1994. Habitat destruction and the extinction debt. Nature 371: 65-66.

TOMLINSON, P. B. 1994. The Botany of Mangroves. Cambridge University Press, Cambridge.

TOVILLA, H. C., and E. G. DE LA LANZA. 1999. Ecología, produccióny aprovechamiento del mangle *Conocarpus erectus* L. en Barra de Tecoanapa Guerrero, México. Biotropica 31: 121-134.

TRAKHTENBROT, A., R. NATHAN, G. PERRY, and D. M. RICHARDSON. 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity and Distributions 11: 173-181.

TRAVIS, J. M. J., K. MUSTIN, K. A. BARTON, T. G. BENTON, J. CLOBERT, M. M. DELGADO, C. DYTHAM, T. HOVESTADT, S. C. F. PALMER, H. VAN DYCK, and D. BONTE. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. Methods in Ecology and Evolution 3: 628-641.

TRIEST, L. 2008. Molecular ecology and biogeography of mangrove trees towards conceptual insights on gene flow and barriers: A review. Aquatic Botany 89: 138-154.

VALIELA, I., J. L. BOWEN, and J. K. YORK. 2001. Mangrove forests: One of the world's threatened major tropical environments. Bioscience 51: 807-815.

VAN DER PIJL, L. 1982. Principal of dispersal in higher plants, Springer-Verlag, Berlin.

VAN DER STOCKEN, T., D. J. R. DE RYCK, T. BALKE, T. J. BOUMA, F. DAHDOUH-GUEBAS, and N. KOEDAM. 2013. The role of wind in hydrochorous mangrove propagule dispersal. Biogeosciences 10: 895-925.

VAN DER STOCKEN, T., D. J. R. DE RYCK, B. VANSCHOENWINKEL, E. DEBOELPAEP, T. J. BOUMA, F. DAHDOUH-GUEBAS, and N. KOEDAM. 2015a. Impact of landscape structure on propagule dispersal in mangrove forests. Marine Ecology Progress Series: doi: 10.3354/meps11206.

VAN DER STOCKEN, T., B. VANSCHOENWINKEL, D. J. R. DE RYCK, T. J. BOUMA, F. DAHDOUH-GUEBAS, and N. KOEDAM. 2015b. Interaction between water and wind as a driver of passive dispersal in mangroves. PLOS ONE.

VAN DYCK, H., and M. BAGUETTE. 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? Basic and Applied Ecology 6: 535-545.

VAN NEDERVELDE, F., S. CANNICCI, N. KOEDAM, J. O. BOSIRE, and F. DAHDOUH-GUEBAS. 2015. What regulates crab predation on mangrove propagules? Acta Oecologia 63: 63-70.

VANSCHOENWINKEL, B., S. GIELEN, H. VANDEWAERDE, M. SEAMAN, and L. BRENDONCK. 2008. Relative importance of different dispersal vectors for small aquatic invertebrates in a rock pool metacommunity. Ecography 31: 567-577.

VITASSE, Y., and D. BASLER. 2013. What role for photoperiod in the bud burst phenology of European beech. European Journal of Forest Research 132: 1-8.

WAFAR, S., A. G. UNTAWALE, and M. WAFAR. 1997. Litter fall and energy flux in a mangrove ecosystem. Estuarine, Coastal and Shelf Science 44: 111-124.

WALTERS, B. B., P. RONNBACK, J. M. KOVACS, B. CRONA, S. A. HUSSAIN, R. BADOLA, J. H. PRIMAVERA, E. BARBIER, and F. DAHDOUH-GUEBAS. 2008. Ethnobiology, socio-economics and management of mangrove forests: A review. Aquatic Botany 89: 220-236.

WANG'ONDU, V. W., J. G. KAIRO, J. I. KINYAMARIO, F. B. MWAURA, J. O. BOSIRE, F. DAHDOUH-GUEBAS, and N. KOEDAM. 2010. Phenology of *Avicennia marina* (Forsk.) Vierh. in a Disjunctly-zoned Mangrove Stand in Kenya. Western Indian Ocean Journal of Marine Science 9: 135-144.

WANG'ONDU, V. W., J. G. KAIRO, J. I. KINYAMARIO, F. B. MWAURA, J. O. BOSIRE, F. DAHDOUH-GUEBAS, and N. KOEDAM. 2013. Vegetative and reproductive phenological traits of *Rhizophora mucronata* Lamk. and *Sonneratia alba* Sm. . Flora 208: 522-531.

WATSON, J., S. MITARAI, D. SIEGEL, J. CASELLE, C. DONG, and J. MCWILLIAMS. 2010. Realized and potential larval connectivity in the Southern California Bight. Marine Ecology Progress Series 401: 31-48.

WEE, A. K. S., K. TAKAYAMA, T. ASAKAWA, B. THOMPSON, ONRIZAL, S. SUNGKAEW, N. X. TUNG, M. NAZRE, K. K. SOE, H. T. W. TAN, Y. WATANO, S. BABA, T. JKAJITA, and E. L. WEBB. 2014. Oceanic currents, not land masses, maintain the genetic structure of the mangrove *Rhizophora mucronata* Lam. (Rhizophoraceae) in Southeast Asia. Journal of Biogeography 41: 954-964.

WERNER, F. E., J. A. QUINLAN, R. G. LOUGH, and D. R. LYNCH. 2001. Spatially-explicit individual based modeling of marine populations: a review of the advances in the 1990s. Sarsia 86: 411-421.

WHITE, C., K. A. SELKOE, J. WATSON, D. A. SIEGEL, D. C. ZACHERL, and R. J. TOONEN. 2010. Ocean currents help explain population genetic structure. Proceedings of the Royal Society B: Biological Sciences 277: 1685-1694.

WILCZEK, A. M., L. T. BURGHARDT, A. R. COBB, M. D. COOPER, S. M. WELCH, and J. SCHMITT. 2010. Genetic and physiological bases for phenological responses to current and predicted climates. Phil. Trans. R. Soc. 365: 3129-3147.

WILLIAMS, W. T., J. S. BUNT, and N. C. DUKE. 1981. Mangrove litter fall in North-eastern Australia. II. Periodicity. Aust. J. Bot. 29: 555-563.

WILLSON, M. F. 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107/108: 261-280.

WIUM-ANDERSEN, S. 1981. Seasonal growth of mangrove trees in southern Thailand. III. Phenology of *Rhizophora mucronata* Lamk. and *Scyphiphora hydrophyllacea* Gaertn. Aquatic Botany 10: 371-376.

WIUM-ANDERSEN, S., and B. CHRISTENSEN. 1978. Seasonal growth of mangrove trees in southern Thailand. II. Phenology of *Bruguiera cylindrica*, *Ceriops tagal*, *Lumnitzera littorea* and *Avicennia marina*. Aquatic Botany 5: 383-390.

WOLANSKI, E., M. JONES, and J. S. BUNT. 1980. Hydrodynamics of a tidal creek-mangrove swamp system. Australian Journal of Marine and Freshwater Research 31: 431-450.

WOLKOWICH, E. M., B. I. COOK, and T. J. DAVIES. 2014. Progress towards an interdisciplinary science of plant phenology: building predictions across space, time and species diversity. New Phytologist 201: 1156-1162.

WOOD, S., C. B. PARIS, A. RIDGWELL, and E. J. HENDY. 2014. Modelling dispersal and connectivity of broadcast spawning corals at the global scale. Global Ecology and Biogeography 23: 1-11.

WOODROFFE, C. D. 1982. Litter production and decomposition in the New Zealand mangrove, *Avicennia marina* var. *resinifera*. New Zealand Journal of Marine and Freshwater Research 16: 179-188.

WOODROFFE, C. D., K. N. BARDSLEY, P. J. WARD, and J. R. HANLEY. 1988. Production of Mangrove Litter in a Macrotidal Embayment, Darwin Harbour, N.T., Australia. Estuarine Coastal and Shelf Science 26: 581-598.

WOODROFFE, C. D., and T. J. MOSS. 1984. Litter fall beneath *Rhizophora stylosa* Griff., Vaitupu, Tuvalu, South Pacific. Aquatic Botany 18: 249-255.

WRIGHT, S. 1931. Statistical Theory of Evolution. Journal of the American Statistical Association 26: 201-208.

YAMASHIRO, M. 1961. Ecological study on *Kandelia candel* (L) Druce, with special reference to the structure and falling of the seedlings. Hikobia 2: 209-214.

YE, Y., N. F. Y. TAM, Y. S. WONG, and C. Y. LU. 2003. Growth and physiological responses of two mangrove species (*Bruguiera gymnorrhiza* and *Kandelia candel*) to waterlogging. Environmental and Experimental Botany 49: 209-221.

ZHANG, Z., and Q. CHEN. 2007. Comparison of the eulerian and lagrangian methods for predicting particle transport in enclosed spaces. Atmospheric Environment 41: 5236-5248.

CURRICULUM VITAE

Tom Van der Stocken was born on the 16th of August 1986 in Jette, **Belgium**. He started high school at the Koninklijk Atheneum Koekelberg where he received the diploma in **Science-Mathematics 8h**, in 2004. Being passionate about the physical processes at the Earth's surface and ecology, he studied **Geography** at the Vrije Universiteit Brussel (VUB) in Brussels (Belgium). For his Master thesis he studied the routing of basal water under the **Antarctic ice sheet** and its meaning in the formation of subglacial lakes and processes of basal sliding, supervised by Prof. Philippe Huybrechts (**Ice and Climate group**, Geography Department, VUB). In that same year, he joined a research expedition to the Morteratsch Glacier in Switzerland. He took additional courses in the evolution of the biogeosphere, plant biology and biogeography at both the VUB and KULeuven. In 2010, he graduated *magna cum laude* in **Physical Geography** at the VUB. During his **PhD on dispersal ecology of plants** at the Department of **Biology** (VUB-ULB), he conducted fieldwork in Gazi Bay (Kenya) and stayed at different institutions, including the **Netherlands Institute for Sea Research** (NIOZ, Yerseke, The Netherlands) and **NASA's Jet Propulsion Laboratory** (JPL, Pasadena, USA).

LANGUAGE SKILLS

Dutch:	mother tongue
English:	full professional proficiency
French:	professional working proficiency
German:	elementary proficiency (in training)

SCIENTIFIC CONTRIBUTION (SUMMARY)

Publications in peer-reviewed international journals:	6
Oral contribution at international scientific meetings:	7
Oral contribution at international scientific meetings as first author:	3
Awards in the category 'Best Oral Presentation Talks':	3
Poster contribution at international scientific meetings:	5
Supervised bachelor and master theses:	8
Reviews performed for international scientific journals:	4

SCIENTIFIC PUBLICATIONS

ACCEPTED

1. **Van der Stocken T.**, Vanschoenwinkel B., De Ryck D.J.R., Bouma T.J., Dahdouh-Guebas F. and N. Koedam **(2015)**. Interaction between wind and water as a driver of passive dispersal dynamics: implications for potential effective dispersal. *PLoS ONE*, 10(3): e0121593. doi:10.1371/journal.pone.0121593 (IF 3.534)

2. **Van der Stocken T.**, De Ryck D.J.R., Vanschoenwinkel B., Deboelpaep E., Bouma T.J., Dahdouh-Guebas F. and N. Koedam **(2015)**. Impact of landscape structure on propagule dispersal in mangrove forests. *Marine Ecology Progress Series*. doi: 10.3354/meps11206 (IF 2.64)

3. Oste J., Robert E. M. R., **Van der Stocken T.**, De Ryck D.J.R., Quisthoudt K., Kairo J.G., Dahdouh-Guebas F., Koedam N. and N. Schmitz **(2015)**. Viviparous mangrove propagules of *Ceriops tagal* and *Rhizophora mucronata*, both Rhizophoraceae, show different dispersal and establishment strategies. *Journal of Experimental Marine Biology and Ecology*, 468: 45-54 (IF 2.475)

4. Goessens A., Satyanarayana S., **Van der Stocken T.**, Quispe Zuniga M., Mohd-Lokman H., Sulong I. and F. Dahdouh-Guebas **(2014)**. Is Matang mangrove forest in Malaysia sustainably rejuvenating after more than a century of conservation and harvesting management? *PLoS ONE*, 9(8): e105069. doi:10.1371/journal.pone.0105069 (IF 3.534)

5. **Van der Stocken T.**, De Ryck D., Balke T., Bouma T. J., Dahdouh-Guebas F. and N. Koedam **(2013)**. The role of wind in hydrochorous mangrove propagule dispersal. *Biogeosciences*, 10: 895-925, doi:10.5194/bgd-10-895-2013 (IF 3.753)

6. De Ryck D., Robert E. M. R., Schmitz N., **Van der Stocken T.**, Di Nitto D., Dahdouh-Guebas F. and N. Koedam **(2012)**. Size does matter, but not only size: two alternative dispersal strategies for viviparous mangrove propagules. *Aquatic Botany*, 103: 66-73 (IF 1.593)

SUBMITTED

7. **Van der Stocken T.**, López-Portillo J. and N. Koedam. Latitudinal pattern in the timing of mangrove propagule release: a meta-analysis of world data. Submitted in *Biotropica* (IF 2.082)

8. Triest L., Hasan S., De Ryck D.* and **T. Van der Stocken***. *Avicennia officinalis* shows regional isolation-by-distance and local clonality in the highly dynamic Sundarban mangrove forest of Bangladesh. Submitted in *Conservation Genetics* (IF 1.846) **Equal contribution*

9. De Ryck D., **Van der Stocken T.**, Koedam N., van der Ven R., Adams J. and L. Triest. Dispersal limitation of *Avicennia marina* among deep inlets of South African coastline in strong contrast to high connectivity among East African mangroves. Submitted for publication in *Marine Ecology and Progress Series* (IF 2.475)

ORAL AND POSTER CONTRIBUTIONS

ORAL

1. **Van der Stocken T.**, Vanschoenwinkel B., De Ryck D., Bouma T., Dahdouh-Guebas F. and N. Koedam **(2015)**. *Interaction between water and wind as a driver of passive dispersal in* mangroves. Annual meeting of the Society for Tropical Ecology, 7-10 April, Zürich, Switzerland.
   Best Student Oral Presentation Award - 1st runner-up

2. **Van der Stocken T.**, De Ryck D., Balke T., Bouma T., Dahdouh-Guebas F. and N. Koedam **(2013)**. *The role of wind in hydrochorous mangrove propagule dispersal.* Jongerencontactdag Vlaams Instituut voor de Zee (VLIZ), 15 February, Brugge, Belgium.
   Best Student Oral Presentation Award - 1st runner-up

3. Tonné N., Robert E.M.R. , Oste J., De Ryck D., **Van der Stocken T.**, Beeckman H. and N. Koedam **(2013)**. *The development of vascular tissue in four viviparous mangrove species.* International Symposium on Wood Structure in Plant Biology and Ecology (WSE), April 17-20, Naples, Italy.

4. **Van der Stocken T.**, De Ryck D., Di Nitto D., Kairo J. G., Dahdouh-Guebas F. and N. Koedam **(2012)**. *Biological and environmental drivers in mangrove propagule dispersal and recruitment: a field modelling approach.* Meeting on Mangrove ecology, functioning and Management (MMM3), 2-6 July 2012, Galle, Sri Lanka.
   Best Student Oral Presentation Award - 2nd runner-up

5. De Ryck D., Robert E.M.R., Schmitz N., **Van der Stocken T.**, Di Nitto D., Dahdouh-Guebas F. and N. Koedam **(2012)**. *Size does matter, but not only size: two alternative dispersal strategies for viviparous propagules.* Meeting on Mangrove ecology, functioning and Management (MMM3), 2-6 July 2012, Galle, Sri Lanka.

6. Koedam N., Mukherjee N., Ximenes A., Satyanarayana B., Kairo J. G., Bosire J. O., Mohamed M. O. S., Quisthoudt K., **Van der Stocken T.**, De Ryck D. and F. Dahdouh-Guebas **(2012)**. *Mangroves as an ecosystem – similarities and differences in a wide comparison.* Meeting on Mangrove ecology, functioning and Management (MMM3), 2-6 July 2012, Galle, Sri Lanka.

7. **Van der Stocken T.**, Oste J., Robert E. M. R., De Ryck D., Koedam N. and N. Schmitz **(2012)**. *Breaking Delayed Dormancy: Species-Specific Environmental Triggers for Mangrove Propagule Establishment.* Estuarine & Coastal Sciences Association (ECSA 50), 3-7 June 2012, Venice, Italy.
   Chairman of session on Ecosystem structure and functioning

POSTER

1. **Van der Stocken T.**, Vanschoenwinkel B., De Ryck D., Bouma T., Dahdouh-Guebas F. and N. Koedam (2015). *Interaction between water and wind as a driver of passive dispersal in*

mangroves. Jongerencontactdag Vlaams Instituut voor de Zee (VLIZ), 20 February, Brugge, Belgium

2. **Van der Stocken T.**, De Ryck D., Di Nitto D., Kairo J. G., Dahdouh-Guebas F. and N. Koedam **(2012)**. *The propagule dispersal black box - driving factors and complexities: a review.* Meeting on Mangrove ecology, functioning and Management (MMM3), 2-6 July 2012, Galle, Sri Lanka.

3. De Ryck D., **Van der Stocken T.**, Schmitz N., Robert E.M.S., Koedam N., Triest L. and F. Dahdouh-Guebas **(2012)**. *Long-distance dispersal mangroves: studied by means of genetics and tracking experiments.* Journée de la Coopération, 28 February, Université Libre de Bruxelles (ULB), Brussels, Belgium.

4. **Van der Stocken T.**, De Ryck D., Di Nitto D., Kairo J. G., Dahdouh-Guebas F. and N. Koedam **(2012)**. *Modeling hydrodynamics and sedimentation in a Kenian mangrove ecosystem.* Journée de la Coopération, 28 February, Université Libre de Bruxelles (ULB), Brussels, Belgium.

5. **Van der Stocken T.**, De Ryck D., Di Nitto D., Kairo J. G., Dahdouh-Guebas F. and N. Koedam **(2012)**. *Floating with seeds: understanding hydrochorous mangrove propagule dispersal – a field and modeling approach.* Jongerencontactdag Vlaams Instituut voor de Zee (VLIZ), 24 February, Brugge, Belgium