

VU Research Portal

Impacts of Disturbances on Species Specific Interactions between Crabs and Plants in Mangrove Ecosystems

Hardiyanta, P.S.

2015

document version

Publisher's PDF, also known as Version of record

[Link to publication in VU Research Portal](#)

citation for published version (APA)

Hardiyanta, P. S. (2015). *Impacts of Disturbances on Species Specific Interactions between Crabs and Plants in Mangrove Ecosystems*. [PhD-Thesis - Research and graduation internal, Vrije Universiteit Amsterdam]. VU University Press.

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

E-mail address:

vuresearchportal.ub@vu.nl

Chapter 4

Propagule Limitations and High Lateral Vegetative Colonization by Understory Species Suggest an Inability of Severely Disturbed Mangrove Ecosystems to Recover Naturally

Abstract

Our understanding on the mechanisms and dynamics of disturbed mangrove upon recovery after disturbance are limited and mostly related to natural disturbances. However, many mangrove ecosystems are increasingly disturbed through anthropogenic disturbance, e.g. by tree cutting. We examined whether natural recovery is possible after severe mangrove disturbance. Thereto, we measured in an Indonesian mangrove ecosystem propagule availability, propagule predation by crabs and establishment and survival rates of propagules in a field manipulation experiment. Treatments included experimental disturbance-mediated gaps with and without planted tree seedlings, with and without excluding crabs and in plots with maximum cover of mangrove trees and understory species, respectively. Biomass increment of the surviving naturally-available mangrove seedlings within the experimental gaps and lateral vegetative growth of invasive species into the gaps were compared to examine vegetation dynamics following mangrove secondary succession. The average propagule availability of mangrove trees ranged from 24.5 m⁻² in plots with maximum cover of mangrove trees to 2.6 m⁻² in the plots with experimental disturbance- gaps and to 0 in the plots with maximum cover of the invasive understory species *Derris trifoliata* and *Acanthus ilicifolius*. After one year, only 0.6 % to 0.9% of all mangrove propagules planted in the experimental gaps had survived under crab predation in the gaps, whereas 16 % of the propagules survived in absence of crab predation and no propagules survived under the canopy with maximum cover of mangrove trees or understory species. The biomass increment due to lateral vegetative growth of *Acanthus ilicifolius* and *Derris trifoliata* into the gaps (18 to 52 g DW m⁻² y⁻¹) was significantly higher compared to the biomass increment of the surviving naturally available mangrove seedlings within the experimental gaps (0.2 to 0.6 g DW m⁻² y⁻¹). We conclude that generative recovery of mangrove forest species after disturbance is almost impossible as a result of low mangrove propagule survival due to crab predation and decreased propagule availability. The vegetatively expanding understory species *Derris trifoliata* and *Acanthus ilicifolius* showed to be the better colonizers into the gaps and they constrained the establishment of mangrove tree seedlings after disturbance. Thus, lateral vegetative growth is the major driver of secondary succession dynamics in these strongly disturbed systems. Restoration management aiming to remove limitations of propagule availability and establishment and to reduce high lateral vegetative invasion of particular understory species is needed to restore severely disturbed mangrove systems.

Keywords: disturbance-mediated gaps, propagules limitation, seedlings survival rates, lateral vegetative growth, biomass increment, *Derris trifoliata*, *Acanthus ilicifolius*

1. Introduction

Disturbance is a key process in forest ecosystem dynamics allowing for secondary succession (Baldwin et al. 2001, Amir 2012). Also in mangrove forests, disturbance can significantly alter forest structure (Duke 2001, Dahdouh-Guebas et al. 2002, Clarke 2004, Cordonnier et al. 2006), faunal and floristic composition and diversity (Dye 2006, Biswas et al. 2007, Diele et al. 2012), nutrient cycles (Granek and Ruttenberg 2008, Barr et al. 2012), and primary productivity (Walter 2005, Martinuzzi et al. 2009, Rhasid et al. 2009, Aung et al. 2013). Moderate disturbances are considered important to increase biodiversity through secondary succession by facilitating the inferior competitors to flourish in the disturbance-mediated mangrove gaps (Sherman et al. 2000). Moderate disturbances such as lightning-strikes are common (Sherman et al. 2000), while severe natural disturbances are rare (Drexler and Ewel 2001, Barr et al. 2012, Diele et al. 2012, Aung et al. 2013).

Due to anthropogenic disturbances in the form of mangrove trees cutting (Burbridge 1982, Ellison 1996, Sakho et al. 2011), severe disturbance occurs increasingly in mangrove ecosystems (Valiela et al. 2001, Alongi 2002, Gilman et al. 2008, Martinuzzi et al. 2009). Mangrove tree cutting does not only create canopy gaps but also reduces the number of reproductive mature mangrove trees and potentially decreases the ability of mangrove systems to provide enough propagules to enable the system to recover naturally (Sousa and Mitchell 1999, Sherman et al. 2000). On the other hand, disturbance-mediated gaps increase light availability and therefore increase mangrove propagules recruitment and survival rates (Krauss and Allen 2003b, Clarke 2004, Walter 2005). In turn, these survival rates, and hence establishment success, is strongly controlled by crab predation (Clarke, 2002), suggesting that herbivores have great impact on recruitment. Working on 42 sites in 16 countries, Ellison (1997) found that pre-dispersal predation of mangrove propagules was ubiquitous and that in early successional stages less pre-dispersal propagule predation occurred. Other studies showed that disturbance-mediated gaps reduce mangrove propagule predation by crabs as well, further enhancing propagule recruitment and survival rates (Clarke and Kerrigan 2000, Clarke 2004).

Moreover, more severe mangrove disturbances were reported to contribute to biological invasion (Biswas et al. 2007), resulting in the dominance of ruderal species (Rhasid et al. 2009), including shade-intolerant mangrove understory species such as *Derris trifoliata*

and *Acanthus ilicifolius*, at the cost of potentially decreasing diversity within the system. In some cases, severe disturbances may even cause the system to be unable to naturally recover to a position close to its original functionality (Alongi 2002, Bosire et al. 2008). However, the mechanisms behind the temporary or permanent triumph of species that are normally considered understory species during secondary succession in disturbed mangrove ecosystems (Biswas et al. 2007, Hinrichs et al. 2009, Rhasid et al. 2009) are not yet clear. Such understanding is, however, critically needed if we aim to restore the functionality and diversity of mangrove ecosystems worldwide.

The aims of this study are therefore to determine the mechanisms allowing plant species to dominate during secondary succession in a severely disturbed mangrove ecosystem by i) examining the natural recovery potential of severely disturbed mangrove by measuring propagule availability, propagule predation, and propagule survival rates and ii) by comparing biomass increments of surviving mangrove tree seedlings vs. those by lateral vegetative growth of *Derris trifoliata* and *Acanthus ilicifolius* within the gaps. We asked whether (1) mangrove disturbance significantly decreases the availability of mangrove propagules, (2) mangrove gaps affect propagules establishment and survival (3) crab predation is a major constraint on the natural recovery of disturbed mangrove system and whether (4) biomass increment of mangrove lateral vegetative growth of *Derris trifoliata* and *Acanthus ilicifolius* is higher than biomass increment of mangrove tree seedlings in mangrove secondary succession after disturbance. We hypothesized that (1) the number of mangrove propagules available in the disturbance-mediated gaps are higher compared to those in areas with maximum mangrove tree cover; (2) the propagules establishment and survival rates are higher in the disturbance-mediated gaps compared to areas with a maximum cover of mangrove trees or ruderal understory species; (3) propagule predation by crabs decreases propagules establishment and survival rates of mangrove seedlings; and (4) biomass increment of lateral vegetative growth of *Derris trifoliata* and *Acanthus ilicifolius* into the gaps is higher compared to the biomass increment of the mangrove tree seedlings. To test these hypotheses we created 28 experimental plots in four blocks of 7 treatments. Five treatments included creating mangrove gaps of 16m² with and without planting of mangrove propagules combined with the removal and non-removal of lateral vegetative growth of *Derris trifoliata* and *Acanthus ilicifolius*, and a fifth treatment that combined planting of propagules, removal of lateral growth and mangrove crab exclusion from the plots. We also established one treatment of 16 m² within an intact undisturbed mangrove ecosystem with maximum cover of mangrove trees and one treatment of 16 m² within the disturbed mangrove with

maximum cover of *Derris trifoliata* and *Acanthus ilicifolius* as controls for net natural propagules productivity and survival rate.

2. Materials and Methods

2.1. Study sites and general experimental design

This study was performed in a disturbed mangrove system at the Segara Anakan mangrove forest (24.000 ha) in Java, Indonesia. Nine mangrove tree species and three mangrove understory species were found in this forest including the dominant mangrove tree *Bruguiera parviflora* with lower abundances of *Aegiceras corniculatum*, *Rhizophora apiculata*, *Avicennia alba*, *Sonneratia alba*, *Nypha fruticans*, *Xylocarpus granatum*, *Bruguiera gymnorhiza*, and *Rhizophora mucronata*. The most dominant ruderal understory species was *Derris trifoliata* with lesser occurrences of *Acanthus ilicifolius* and *Finlaysonia obovata*. Parts of this forest are large undisturbed intact mangrove areas, while other areas are severely disturbed. This combination of features makes this forest suitable for testing our hypotheses.

We established four blocks of permanent experimental plots. In each block, we created five gaps of 16 m² (4m X 4m) in the disturbed mangrove and we established one control plot of 16 m² within a stand of still intact mangrove with a maximum cover of mangrove trees (CMM) and one other control plot of 16 m² within a stand with a maximum cover of the ruderal understory species *Derris trifoliata* and *Acanthus ilicifolius* (CDA). Gaps were created by clearing and removing any mangrove trees and understory species from the experimental-gap plots to mimic disturbance-mediated gaps of mangrove tree cutting. The five gap treatments included (1) planting of mangrove propagules on top of natural propagule availability and growth and allowing lateral vegetative growth into the gaps (PIL), (2) planting of mangrove propagules, inclusion of natural propagule availability and growth and removal of all lateral vegetative growth (PRL), (3) No planting of mangrove propagules, but inclusion of natural propagule availability and growth and inclusion of lateral vegetative growth (NPIL), (4) no planting of mangrove propagules, inclusion of natural propagule availability and growth and removal of all lateral vegetative growth (NPRL), (5) planting of mangrove propagules, exclusion of natural propagules, removal of all lateral vegetative growth and removal and exclusion of all mangrove crab from the plots (PRLCEX). The procedure was repeated in each block. The distances between different plots were no more than 20 meters to keep similar environmental

conditions while the distances between blocks were at least 300 meters to avoid pseudo replication. We deliberately selected plot areas with similar hydrological positions with maximum tides between 30 cm to 40 cm above the soil surface to avoid biases on mangrove propagule dispersal, propagule predation rates by mangrove crabs and mangrove establishment and survival rates with regard to tidal regimes (Ball 1980, Krauss and Allen 2003a, Dahdouh-Guebas et al. 2011).

Within this design, we measured (1) propagule availability in the system by comparing the number of available propagules in experimental gaps (PIL, PRL, NPIL, NPRL and PRLCEX) vs. control plots with maximum mangrove tree cover (CMM) and cover by ruderal understory species (CDA), (2) overall propagule establishment and survival rates by comparing NPIL, NPRL, PIL, PRL to PRLCEX, CMM and CDA, (3) propagule survival and crab predation on planted propagules of specific plant species by comparing PIL, PRL and PRLCEX, (4) the outcome of colonization, establishment and growth during secondary succession by comparing the biomass increment of surviving mangrove tree seedlings to the biomass increment of lateral vegetative growth within the NPIL and PIL plots.

2.2. Treatment installation

After the gap creation, each plot was first allowed to consolidate for 14 days. Then, we collected mature propagules of 8 mangrove species including the mangrove trees *Rhizophora apiculata*, *Bruguiera parviflora*, *Rhizophora mucronata*, *Aegiceras corniculatum*, *Avicennia alba*, *Sonneratia alba*, and the understory species *Derris trifoliata* and *Acanthus ilicifolius* to be planted in a total of 12 gap-experimental plots of PIL, PRL and PRLCEX. Before planting the propagules in the PRLCEX plots, we removed all mangrove crabs found within the plots and installed 1 meter high plastic wire net around the plots to prevent mangrove crabs from entering the plots. Subsequently, within each gap-experimental plot, 32 propagules of each of the 8 different mangrove species were planted, thus reflecting natural propagule availability within this system. Planting was done in groups of 4 propagules for each species in a completely randomized design (8 columns X 8 rows) to avoid bias in the predation by mangrove crabs related to the positions of each propagule in the gaps relative to the crabs and to avoid bias in the establishment and growth of each propagule related to any environmental factors during the experiment. Due to the buoyant characteristics of *Avicennia alba*, *Derris trifoliata* and *Acanthus ilicifolius* we tethered the propagules with

transparent plastic wires in groups of 4 and tied them to a bamboo stick to keep them from being driven away by tidal currents. Due to the small size of *Sonneratia alba* seeds, we grew them 7 days before planting in groups of 4 within small pots to let the initial root attach to the soil and removed the pots before planting. We did not plant mangrove propagules in the control plots with maximum cover of either mangrove trees or understory species since it was not doable to apply a similar planting design with such high vegetation cover.

2.3. Data collection

We monitored propagule establishment and predation by mangrove crabs every day during the first two weeks of the treatment, in the third week, and at the 30th, 60th, 90th, 180th and 352nd days after planting the propagules in the plots. Propagules which had been completely consumed by the crabs were counted as predated. Decayed propagules and the dead seedlings were measured to calculate survival rate. We also measured the natural seed rain of mangrove propagules including their establishment and their survival rates within all plots. We measured lateral vegetative growth of *Derris trifoliata* and *Acanthus ilicifolius* into the gaps of PIL and NPIL plots and measured and removed them every month from the NPRL and PRL plots. We also counted the number of mangrove crabs found within the plots by direct count of 4 sub plots of total 1 m² at the beginning of the treatment and at the end of the treatment.

At the end of the experiment, i.e. after one year, we harvested all the surviving seedlings of the spontaneously established and the planted propagules in each plot, cleaned their roots from soil, harvested their leaves and put the leaves, the trunk and the roots separately in individual envelopes to have them oven dried at 70°C for 7 days for further dry weight measurement. We also harvested *Derris trifoliata* and *Acanthus ilicifolius* from each plot, cleaned their root from soil, harvested the leaves and put the leaves, the trunks and the roots in separate bags, oven dried them at 70°C for 10 days and measured their dry weight. The same procedure was repeated during the second year only until day 30 in order to examine whether there were differences in mangrove crab predation and propagule establishment between years. However, we did not collect data of biomass increment and mangrove survival rates for the end of this second year treatment due to time constraints.

2.4. Data analysis

Repeated measures (RM-)ANOVA with treatment as within-subject factor and block as between-subject factor was run to analyze differences in propagule availability, number of propagules established and relative survival rates of naturally prevailing propagules between treatments. With a similar design, differences in mangrove crab densities between PIL, PRL, NPIL, NPRL, CDA and CMM were analyzed. A repeated measures-ANOVA with a similar design, but including species identity as within-subject factor was performed to analyze differences in the relative survival rates of planted mangrove propagules in PIL, PRL and PRLCEX and in propagule predation rates in the first thirty days of the treatments by mangrove crabs between PIL and PRL plots. Finally, a repeated measures-ANOVA with a similar design but both treatment and year as within-subject factors was run to test effects of year on propagule availability. We then calculated the Generalized Eta Squared (GES) values to compare the effect size of each factor as resembled in the variance explained by each factor (Bakeman 2005). Given the large impacts of crab predation (see **Results**), an additional one-way ANOVA followed by a TukeyHSD post-hoc test was performed to analyze differences in the relative survival rates of the different mangrove species in the absence of crab predation, i.e. in the PRLCEX plots. Also, a one-way ANOVA followed by a Tukey HSD post-hoc test was run to analyze differences in crab predation among different mangrove species. In all analyses, relative survival rates were calculated per plot, assuming an exponential decrease in the number of surviving propagules. A repeated measures-ANOVA with sources of biomass increment as within-subject factor and treatment within block as between-subject factor and was performed to analyze differences in biomass increment between the different sources of survived seedlings of naturally available propagules vs. lateral vegetative growth and between the planted (PIL) and the non-planted (NPIL) gaps treatments for the first year. All analyses were done in R using (lm) and (ez) libraries.

3. Results

3.1. Tree propagule availability decreases significantly upon disturbance

Propagules of six different mangrove species reached the experimental gaps with the highest number of propagules for *Aegiceras corniculatum* (2.63 m⁻²), followed by *Bruguiera parviflora* (1.98 m⁻²) > *Ceriops tagal* (0.98 m⁻²) > *Derris trifoliata* (0.09 m⁻²) > *Nypha fruticans* (0.06 m⁻²) > *Finlaysonia obovata* (0.04 m⁻²). The number of naturally

available propagules differed significantly between treatments ($P < 0.003$) with the highest number of stranded propagules in the CMM plots, where vegetation had not been removed (Table 4.1). Most of the stranded propagules in the CMM plots were propagules of *Aegiceras corniculatum* and *Bruguiera parviflora*. On the other hand, no propagules were found under the control plots dominated by *Derris trifoliata* and *Acanthus ilicifolius*. There was no significant difference found between years ($P > 0.6$) nor was there an interaction between year and treatments ($P > 0.9$). Also between treatments where vegetation had been removed, propagule availability showed strong spatial heterogeneity. For instance, the high values for NPRL plots seem to be entirely due to *Ceriops tagal* which was abundant near one of the plots (results not shown). Given the impacts of such heterogeneity, in further analysis, we focus on the establishment and survival rates of planted propagules only.

Table 4.1. Average number (\pm SD) of naturally prevailing mangrove plant propagules and mangrove crab density.

Treatments ¹⁾	Propagules (m ⁻²)		Crabs (indv. m ⁻²)	
	Year 1	Year 2	Year 1	Year 2
CMM	16.0 \pm 13.0	19.7 \pm 8.0	24.3 \pm 9.2	26.3 \pm 2.9
NPRL	6.5 \pm 1.8	4 \pm 3.5	19.0 \pm 4.4	19.0 \pm 3.7
NPIL	1.9 \pm 1.2	0.1 \pm 0.1	13.3 \pm 3.9	16.3 \pm 5.4
PRL	1.5 \pm 0.8	0.2 \pm 0.1	18.8 \pm 2.1	19.0 \pm 2.4
PIL	0.3 \pm 0.1	0	15.5 \pm 3.7	13.5 \pm 3.1
CDA	0	0	14.0 \pm 3.3	16.3 \pm 3.8
PRLCEX	0	0	0	0

¹⁾ Treatments existed of Control of maximum mangrove trees (CMM); No planting of mangrove propagules, inclusion of natural propagule availability and growth and removal of all lateral vegetative growth (NPRL); No planting of mangrove propagules, but inclusion of natural propagule availability and growth and inclusion of lateral vegetative growth (NPIL); Planting of mangrove propagules, inclusion of natural propagule availability and growth and removal of all lateral vegetative growth (PRL); Planting mangrove propagules, allowing for natural propagule availability and growth and inclusion of lateral vegetative growth into the gaps (PIL); Control of maximum mangrove shrubs *Derris trifoliata* and *Acanthus ilicifolius* (CDA); Planting of mangrove propagules, exclusion of natural propagules, removal of all lateral vegetative growth and removal and exclusion of all mangrove crab from the plots (PRLCEX). This PRLCEX treatment also prevented naturally available propagules from entering the plots.

3.2. Propagule establishment and survival rates

Mangrove propagule establishment and seedling relative survival rates were overall very low. Soon after planting, survival decreased for all species and in most conditions (Figure 4.1). Only 6.6% of the propagules in the PIL plots and 10.5% of the propagules in the PRL plots survived the first 30 days of the experiment and after one year only 0.6% of the seedlings had survived in the PIL plots (Figure 4.1A) and 0.9% in the PRL plots (Figure 4.1B). On the other hand, mangrove propagule establishment and seedling

Propagule Limitations and High Lateral Vegetative Colonization by Understory Species Suggest an Inability of Severely Disturbed Mangrove Ecosystems to Recover Naturally

survival rates in the absence of crabs (PRLCEX) (Figure 4.1C) were significantly higher (16%) compared to PRL and PIL (Figure 4.1D). All together this indicates that crab predation strongly affects propagule survival in this system. Indeed, the RM-ANOVA on the relative survival rates of mangrove propagules showed significant differences between treatments, and mangrove species and to lesser extents between years. Moreover, all interactions except between year and treatment were significant (Table 4.2). Considerably lower Generalized Eta Squared (GES) values were found for the main effects of species identity and year (and treatment) than for the interaction between species identity and year (0.41), the latter caused by significantly ($P < 0.001$) different survival rates of *Rhizophora apiculata* and *Acanthus ilicifolius* between the first and second year. This indicates that the survival rates of mangrove propagules were driven not only by our treatments but even more strongly by mangrove species identity and differed among years. In the absence of crab predation, among 8 different mangrove species being planted in the PRLCEX, the Rhizophoraceae species, with generally larger propagules, including *Rhizophora apiculata*, *Bruguiera parviflora* and *Rhizophora mucronata* performed better than other species especially with *Rhizophora apiculata* being significantly higher survival rates compared to *Derris trifoliata* and *Acanthus ilicifolius* (Figure 4.2A).

Table 4.2. Results of a repeated-measured ANOVA on the survival rates of mangroves propagules (day 30) planted in the PIL, PRL and PRLCEX plots with block as between subject factor and treatment and mangroves as within-subject factors (n=4)

Effect	F values	P values	Generalized eta-squared values
Year	14.6	0.008	0.13
Treatment	19.0	< 0.001	0.27
Species identity	7.8	< 0.001	0.25
Year*treatment	1.0	0.3	0.01
Year* species identity	16.1	<0.001	0.41
Treatment* Species identity	3.4	< 0.001	0.24
Year* treatment* Species identity	3.3	< 0.001	0.23

3.3. Tree propagule predation by mangrove crabs

The average mangrove crab abundance across all plots was 17.4 m⁻² in the first year and 18.4 m⁻² in the second year of the experiment (Table 4.1). There were no significant differences in mangrove crab density between treatment plots ($P > 0.05$) nor between first year and second year ($P = 0.41$).

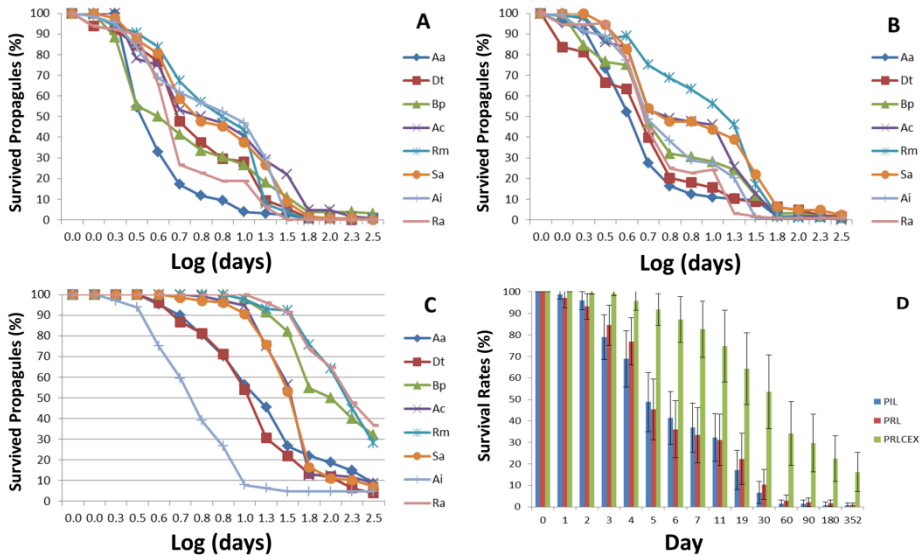


Figure 4.1. Survival rates (%) of 8 different species of mangrove seedlings planted in plots that additionally **(A)** included natural propagule availability and growth and lateral vegetative growth into the gaps (PIL), **(B)** included natural propagule availability and growth, while all lateral vegetative growth removed (PRL), **(C)** excluding natural propagules, removing all lateral vegetative growth and removing and excluding all mangrove crab from the plots (PRLCEX) and **(D)** the averages of survived propagules of PIL, PRL and PRLCEX during one year of treatment. Aa= *Avicennia alba*, Ac= *Aegiceras corniculatum*, Ai= *Acanthus ilicifolius*, Bp= *Bruguiera parviflora*, Dt= *Derris trifoliata*, Ra= *Rhizophora apiculata*, Rm= *Rhizophora mangle*, Sa= *Sonneratia alba*. Error bars= standard error of means.

Table 4.3. Results of a repeated-measured ANOVA on the predation rates of propagules planted in the PIL and PRL plots with block as between subject factor and treatment and mangroves as within-subject factors (n = 4)

Effect	F values	P values	Generalized eta-squared values
Year	0.87	0.35	0.02
Treatment	0.99	0.32	0.02
Species identity	14.52	< 0.001	0.36
Year*treatment	4.729	0.03	0.11
Year* species identity	15.59	< 0.001	0.39
Treatment* Species identity	1.34	0.24	0.03
Year* treatment* Species identity	0.81	0.56	0.02

In the treatments where crab predation had not been excluded, PRL and PIL, mangrove propagule predation rate was very high (Figure 4.2B) and substantially contributed to the low survival rates found (Figures 4.1A and 4.1B). The RM-ANOVA showed no significant difference in the relative predation rates of mangrove propagules between years ($P = 0.35$), indicating stable crab predation across time (Table 4.3). Significant differences

Propagule Limitations and High Lateral Vegetative Colonization by Understory Species Suggest an Inability of Severely Disturbed Mangrove Ecosystems to Recover Naturally

were neither found between PRL and PIL treatments ($P = 0.32$). However, a significant difference was found between different mangrove species ($P < 0.001$) and in the interactions between year and treatment ($P = 0.03$) and plant species and year ($P < 0.001$), but not between mangrove, treatment and year ($P = 0.56$). The Generalized Eta Squared values for plant identity (0.36) and the interaction between plant identity and year (0.39) were relatively high, indicating that propagule predation was driven more by differences in mangrove species identity than by treatment and year of sampling. When we analyzed the propagule predation on each mangrove species between PIL and PRL we found significantly lower predation for *Derris trifoliata* (while still having low survival rates (Figure 4.2A)) and all other mangrove species planted in the experimental plots except *Acanthus ilicifolius*. *Sonneratia alba* suffered the greatest predation (Figure 4.2B).

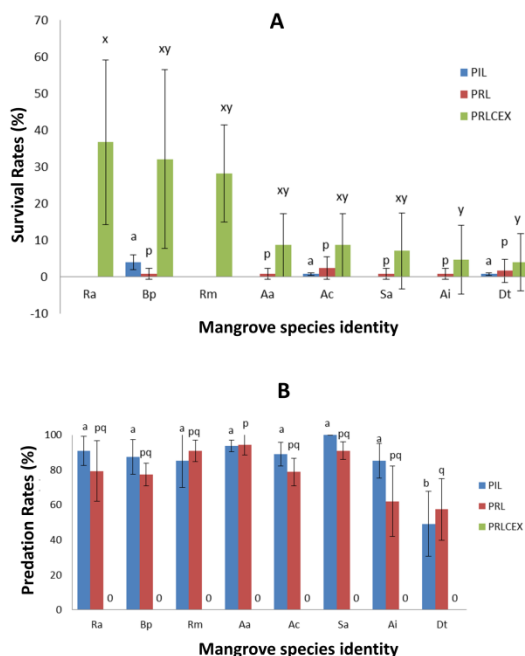


Figure 4.2. (A) Survival rates (%) of 8 mangrove species planted in the PIL, PRL and PRL CEX by the end of the first year experiment, **(B)** The averages of first and second years propagule predation rates (%) on the planted propagules of PIL and PRL plots at the 30th day of treatment. Aa= *Avicennia alba*, Ac= *Aegiceras corniculatum*, Al= *Acanthus ilicifolius*, Dt= *Derris trifoliata*. Bp= *Bruguiera parviflora*, Ra= *Rhizophora apiculata*, Rm= *Rhizophora mangle*, Sa= *Sonneratia alba*, Error bars = Standard error of means.

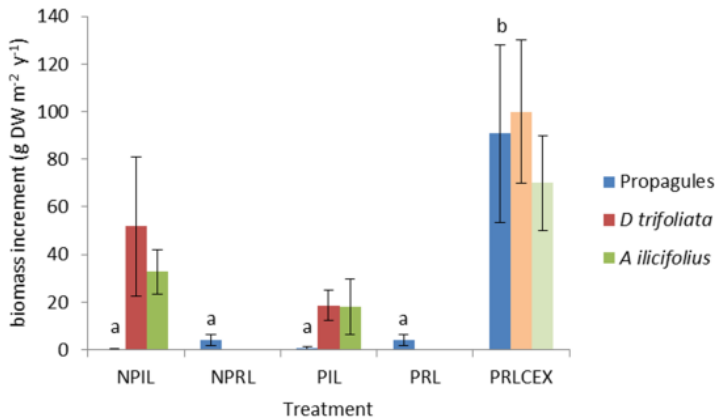


Figure 4.3. Biomass increments ($\text{g DW m}^{-2} \text{y}^{-1}$) of surviving seedlings (planted and non-planted) and of lateral vegetative growth of *Derris trifoliata* and *Acanthus ilicifolius* in the plots without planted propagules but allowing for lateral growth (NPIL), plot without planted propagules in which lateral growth was removed (NPRL), plot with planted propagules and allowing for lateral vegetative growth (PIL), plots with planted propagules in which lateral growth was growth (PRL) and plots with planted propagules where all lateral vegetative growth was removed and crabs were excluded (PRLCEX). Please note that the bars for lateral growth of *Derris trifoliata* and *Acanthus ilicifolius* in the PRLCEX plots are approximations of lateral growth that would have occurred in the absence of crab consumption. In reality, all lateral growth occurring in these plots were removed. Error bars = standard error of means.



Figure 4.4. First author standing in the midst of *Derris trifoliata* occupying the disturbed mangrove gap in the Segara Anakan mangrove forest. In the background the undisturbed mangroves stand.

3.4. Mangrove biomass increments

Biomass increment for mangrove seedlings was significantly lower ($P < 0.05$) compared to that from lateral vegetative growth of *Derris trifoliata*. Biomass increment of naturally established propagules in the treatments where lateral growth had been avoided was almost equally low (7.7 ± 7.7 g DW m⁻² and 4.0 ± 1.1 g DW m⁻² in the PRL and NPRL plots, respectively). No significant difference in biomass increment was found between *Acanthus ilicifolius* and *Derris trifoliata* or between *Acanthus ilicifolius* and natural propagules. Neither were there significant difference in biomass increment between the PIL and NPIL treatment (i.e. when comparing a situation with simulated undisturbed seed rain -by planting- to the situation with on affected seed rain). Only in the case of crab predation exclusion, biomass increments of propagules were substantially higher (Figure 4.3). In the NPIL and PIL treatments, the only treatments in which propagules and lateral growth were present, no significant difference in biomass increment between propagules and lateral growth were found.

4. Discussion

Large scale man-made mangrove disturbances in the form of mangrove trees cutting are ubiquitous and promote the occurrence of disturbance-mediated gaps. We examined to which extent and by what means natural recovery of mangrove forest is possible in these disturbance-mediated gaps. Our results indicate that natural recovery of mangrove tree species seems impossible under the current conditions due to the occupation through lateral vegetative growth of the ruderal invasive species *Derris trifoliata* and *Acanthus ilicifolius* into the disturbance-mediated gaps. The most important factor hampering tree species establishment seems to be the establishment phase with low numbers of available propagules, high propagule predation rates and low propagule survival (Clarke and Kerrigan 2002). Lateral vegetative growth is much less hindered by these conditions and allows higher biomass increments. If these conditions persist in the long run, establishment of trees following disturbance may be seriously limited in mangrove ecosystems, and they will likely be completely dominated by these understory species instead. Thus, specific nature management measures may be needed to help in the recovery of disturbed mangrove ecosystems.

4.1. Propagule limitation in the disturbance-mediated gaps

The natural recovery of mangrove forests after disturbances depends first of all on propagule availability (Lewis 2005) as provided by adjacent undisturbed mangrove trees (Roth 1992, Sherman et al. 2000, Rhasid et al. 2009). Mangrove propagule availability in the control plots with maximum mangrove trees cover (CMM) was as high as 16 to 19.7 propagules m^{-2} (Table 3.1), which is similar or higher compared to estimates from other mangrove ecosystems (Roth 1992, Sherman et al. 2000). In combination with the 8.5% of the propagules surviving crab's predation and other limitations during the first 30 days (Figure 4.1D), the surviving propagules density of 1.3 to 1.6 m^{-2} would have met the presumed requirements for an adequate natural regeneration of the mangrove forest, given the estimated seedling densities of 0.6 to 1.8 m^{-2} for mangrove forests recovering from hurricane and lightning (Roth 1992, Sherman et al. 2000) and thinning (Srivastava and Khamis 1978, Amir 2012). This suggests that in the absence of severe disturbances, propagule availability in our case study was not a limiting factor for the natural regeneration of mangrove trees.

In contrast, propagule availability in the disturbance-mediated gaps was only 2.6 m^{-2} . This number is only 16% of the available propagules found in the undisturbed mangrove forest control plots. This suggests that a strong propagule limitation occurs even at the short distance between the gaps and the experimental plots despite the buoyant characteristics of mangrove propagules in general (McGuinness 1997). We observed that the propagules of *Avicennia alba*, *Derris trifoliata*, *Acanthus ilicifolius* and of *Aegiceras corniculatum* are easily transported by the tidal current. This coincides with findings that *Ceriops tagal* and *Rhizophora mucronata* were able to disperse more than 30 meters away from their mother trees (De Ryck et al. 2012). Since the distance between the experimental gaps and the non-disturbed plots was always less than 20 meter and that the plots were in a similar tidal regime, propagule dispersal was not hampered in our study (McGuinness 1997, De Ryck et al. 2012).

Still, we found only a small number of propagules stranded in the disturbance-mediated plots (Table 4.1). Lower propagule availability in combination with heavy propagule predation by crabs, of particular importance in mangrove ecosystems, seems to be the limiting factor for natural propagule availability in the disturbance-mediated gaps as was also reflected by the strong predation on the planted propagules in plots where crab access was allowed (Figure 4.2B). The resulting density of surviving seedlings of only

0.02 m⁻² represents only 4% of the required density proposed for natural regeneration. This result confirmed the importance of herbivory (by crabs) in negatively affecting the regeneration of mangrove ecosystems (Osborne and Smith 1990, Sousa and Mitchell 1999, Bosire et al. 2005). This strong herbivory-induced limitation contrasts with the importance of herbivory in terrestrial forest secondary succession series (Fleury and Galetti 2004, Lindquist and Carroll 2004, Fleury and Galetti 2006).

4.2. Propagule recruitment vs. crab predation

Natural propagule recruitment in this system thus seems first of all severely constrained by high propagule predation by crabs. This is exemplified by the huge differences in propagule survival between the treatments with and without crab exclusion. Crab predation was particularly severe, in absolute and relative terms, during the first month after establishment. Thus, natural regeneration through naturally available propagules within the disturbance-mediated gaps seems unlikely at the current conditions.

On the other hand, lower propagule predation does not always imply high recruitment rates. For instance, *Derris trifoliata* was consumed at relatively lower rates compared to other plant species (Figure 4.2B), but still this species had lower survival rates, even without crab predation (compare Figure 4.2A and 4.2B), due to rotting. Survival rates of *Derris trifoliata* and *Acanthus ilicifolius* were lower than those of mangrove tree species with great dispersal ability due to their high seed buoyancy and high number of propagules (*Avicennia alba*, *Aegiceras corniculatum* and *Sonneratia alba*) and were particularly low compared to that of Rhizophoraceae species (*Rhizophora* and *Bruguiera*) that tend to dominate the climax vegetation in mangrove ecosystems. Despite the low natural propagule survival rates, *Derris trifoliata* prevailed in occupying the disturbance-mediated gaps and became the dominant species in the previously disturbed mangrove area (Figure 4.4) due to its strong lateral vegetative growth

4.3. Secondary succession under the pressure of propagule limitation favored lateral vegetative growth

Low recruitment rates of *Derris trifoliata* and *Acanthus ilicifolius* in the presence and absence of predation by mangrove crab (Figure 4.2A) suggest that their dominant presence in the previously disturbance-mediated gaps (Figure 4.4) was not through propagule recruitment, but through their strong lateral vegetative growth. Indeed, we

showed that biomass increment by *Derris trifoliata* and *Acanthus ilicifolius* due to lateral vegetative growth into the gaps was significantly higher compared to biomass increment of their own propagules as well as of those of mangrove trees (Figure 4.3). Likewise, lateral vegetative growth of *Derris trifoliata* and *Acanthus ilicifolius* was much less limited by crab predation. As a consequence, although propagule recruitment of *Derris trifoliata* and *Acanthus ilicifolius* was low, the total biomass increment of these species was much higher than that of naturally established mangrove tree species. Lateral vegetative growth was thus the major driver of the secondary succession dynamics in these strongly disturbed systems. This strategy, probably evolved to quickly respond to the heterogeneous -but commonly low- light conditions at the bottom of the mangrove forest floor (where we consistently observed the species), thus seems highly competitive in these disturbance-mediated gaps. Instead of considering *Derris trifoliata* an invasive species (see Biswas 2007), we thus consider it a mangrove species taking advantage of the provided opportunities within the system. If these conditions persist in the long run, mangrove tree species abundance may be seriously limited in disturbed mangrove ecosystems. In the Segara Anakan area, this seems to be the direction to which the system evolves as major proportions have now been occupied by *Derris trifoliata* and *Acanthus ilicifolius* (Figure 4.4).

4.4. Implications for future management for severely disturbed mangrove ecosystems

In line with the increasing number of mangrove disturbances, mangrove restoration projects are also increasing as well as the awareness (Ellison 2000) towards ecological restoration (Michener 1997, Kamali and Hashim 2011). However, most mangrove restoration projects so far have immediately considered planting of mangrove seedlings or propagules without first examining why natural recovery had not occurred (Bosire 2008). This practice has resulted in major failures and financial losses (Erfemeijer and Lewis 1999, Elster 2000), even if the appropriate hydrological conditions were implemented (c.f. Bosire et al. 2008, Dahdouh-Guebas et al. 2011, Kamali and Hashim 2011). Assessing the natural recovery opportunities and identification of its major constraints, as investigated in this study, are therefore mandatory before stepping into restoration after disturbances.

The long lasting human disturbance in the Segara Anakan mangrove forest has resulted in the prevalence of understory species occupying almost all of the man-made gaps at

the cost of the ability of mangrove trees to recover naturally after these disturbances. It thus seems that at severely disturbed mangrove ecosystems, understory species have a selective advantage over tree species. This may be due to dispersal and establishment limitations of tree species. In addition, data –the absence of any propagule in understory plots compared to gaps despite similar distances from tree stands- suggest a stronger predation of propagules in those conditions despite similar crab abundance and crab species composition. Once *Derris trifoliata* and *Acanthus ilicifolius* have completely covered the gaps, no natural propagule recruitment seems to be possible anymore. Even in gaps with ample light availability, propagules were able to recruit and survive sufficiently for natural recovery only in the absence of crabs. In the presence of crabs, i.e. at the natural conditions, lateral vegetative growth of the understory mangroves *Derris trifoliata* and *Acanthus ilicifolius* overrides growth of the naturally available mangrove tree seedlings. The prevalence of lateral vegetative growth of these formerly understory mangroves in turn eliminates the possibility for propagules, if there are any, to recruit and survive. This pattern occurs wherever and whenever human disturbance mediated gaps occur combined with the presence of the understory species *Derris trifoliata* and *Acanthus ilicifolius* in the ecosystem (e.g. in Bangladesh; Biswas et al. 2007).

Our result suggests that restoration projects may only be successful if either a) mangrove fields are cleared from and maintained clear from co-occurring *Derris trifoliata* and *Acanthus ilicifolius* to provide gaps for propagules recruitment or, b) planted propagules are protected from crab predation to facilitate propagule survival. Provision of gaps combined with crab exclusion (for example by planting already developed mangrove saplings rather than mangrove propagules) could thus be an ideal future restoration method to bring mangrove forest back from the severely disturbed and degenerated state.

5. Conclusions

In severely disturbed mangrove systems, propagule limitation due to low mangrove propagule recruitment and survival rates and high propagule predation by crabs hindered natural mangrove recovery. Instead, secondary succession was driven by lateral vegetative growth by understory mangrove species such as *Derris trifoliata* and *Acanthus ilicifolius*. If such conditions and processes persist in the long run, the disturbance-mediated mangrove gaps will likely to be completely dominated by these

understory mangrove at the cost of a decrease or even absence of mangrove tree species from the system. Restoration management needs to focus on securing propagules recruitment, protection against crab predation and removal of *Derris trifoliata* and *Acanthus ilicifolius* to facilitate natural succession towards mangrove forests.

References

- Alongi, D. M. 2002. Present state and future of the world's mangrove forests. *Environmental Conservation* **29**:331-349.
- Amir, A. A. 2012. Canopy gaps and the natural regeneration of Matang mangroves. *Forest Ecology and Management* **269**:60-67.
- Aung, T. T., Y. Mochida, and M. M. Than. 2013. Prediction of recovery pathways of cyclone-disturbed mangroves in the mega delta of Myanmar. *Forest Ecology and Management* **293**:103-113.
- Bakeman, R. 2005. Recommended effect size statistics for repeated measures design. *Behavior Research Methods* **37** (3):379-384.
- Baldwin, A., M. Egnotovitch, M. Ford, and W. Platt. 2001. Regeneration in fringe mangrove forests damaged by Hurricane Andrew. *Plant Ecology* **157**:149-162.
- Ball, M. C. 1980. Patterns of Secondary Succession in a Mangrove Forest of Southern Florida. *Oecologia (Berl.)* **44**:226-235.
- Barr, J. G., V. Engel, T. J. Smith, and J. D. Fuentes. 2012. Hurricane disturbance and recovery of energy balance, CO₂ fluxes and canopy structure in mangrove forest of the Florida Everglades. *Agricultural and Forest Meteorology* **153**:54-66.
- Biswas, S. R., J. K. Choudhury, A. Nishat, and M. M. Rahman. 2007. Do invasive plants threaten the Sundarbans mangrove forest of Bangladesh? *Forest Ecology and Management* **245**:1-9.
- Bosire, J. O., F. Dahdouh-Guebas, M. Walton, B. I. Crona, R. R. Lewis, C. B. Field, J. G. Kairo, and N. Koedam. 2008. Functionality of restored mangroves: A review. *Aquatic Botany* **89**:251-259.
- Bosire, J. O., J. G. Kairo, J. Kazungu, N. Koedam, and F. Dahdouh-Guebas. 2005. Predation on propagules regulates regeneration in a high-density reforested mangrove plantation. *Marine Ecology Progress Series* **299**:149-155.
- Burbridge, P. R. 1982. Management of mangrove exploitation in Indonesia. *Applied Geography* **2**:39-54.
- Clarke, P. J. 2004. Effects of Experimental canopy gaps on mangrove recruitment: lack of habitat partitioning may explain stand dominance. *Journal of ecology* **92**:203-213.
- Clarke, P. J. and R. A. Kerrigan. 2000. Do forest gaps influence the population structure and species composition of mangrove stand in northern Australia? *BIOTROPICA* **32**:642-652.
- Clarke, P. J. and R. A. Kerrigan. 2002. The effects of seed predators on the recruitment of mangroves. *Journal of Ecology* **90**:728-736.
- Cordonnier, T., B. Courbaud, and A. Franc. 2006. The effect of colonization and competition processes on the relation between disturbance and diversity in plant communities. *Journal of Theoretical Biology* **234**:1-12.
- 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 Experimental Marine Biologi Ecology* **399**:188-200.
- 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* **103**:66-73.
- Diele, K., D. M. Tran Ngoc, S. J. Geist, F. W. Meyer, Q. H. Pham, U. Saint-Paul, T. Tran, and Berger.U. 2012. Impact of typhoon disturbance on the diversity of key ecosystem engineers in a mono culture mangrove forest plantation, Can Gio Biosphere Reserve, Vietnam. *Global Planet Change*: (<http://dx.doi.org/10.1016/j.gloplacha.2012.1009.1003>).
- Drexler, J. Z. and K. C. Ewel. 2001. Effect of the 1997-1998 ENSO-related drought on hydrology and salinity in a Micronesian wetland complex. *Estuaries* **24**:347-356.
- Duke, N. C. 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystem. *Wetlands Ecology and Management* **9**:257-269.
- Dye, A. H. 2006. Persistent effects of physical disturbance on meiobenthos in mangrove sediments. *Marine Environmental Research* **62**:341-355.
- Ellison, A. M. 1996. Anthropogenic Disturbance of Caribbean Mangrove Ecosystems: Past Impacts, Present Trends, and Future Predictions. *BIOTROPICA* **28**:549-565.
- Ellison, A. M. 2000. Mangrove Restoration: Do We Know Enough? *Restoration Ecology* **8 (3)**:219-229.
- Elster, C. 2000. Reason for reforestation success and failure with three mangrove species in Colombia. *Forest Ecology and Management* **131**:201-214.
- Erfteemeijer, P. L. A. and R. R. Lewis. 1999. Planting mangrove on intertidal mudflats: habitat restoration or habitat conversion? In: *Exotone, VIIIth Seminar, Enhancing Coastal Ecosystem Restoration for the 21st Century, Ranong and Phuket, May 1999*, pp.1-11.
- Fleury, M. and M. Galetti. 2004. Effects of microhabitat on palm seed predation in two forest fragments in southeast Brazil. *Acta Oecologica* **26**:179-184.
- Fleury, M. and M. Galetti. 2006. Forest fragment size and microhabitat effects on palm seed predation. *Biological Conservation* **131**:1-13.
- Gilman, E. L., J. Ellison, N. C. Duke, and C. Field. 2008. Threats to mangrove from climate change and adaptation options: A review. *Aquatic Botany* **89**:237-250.
- Granek, E. F. and B. I. Ruttenberg. 2008. Changes in biotic and abiotic processes following mangrove removal. *Estuarine, Coastal and Shelf Science* **80**:555-562.
- Hinrichs, S., I. Nordhaus, and S. J. Geist. 2009. Status, diversity and distribution patterns of mangrove vegetation in the Segara Anakan lagoon, Java, Indonesia. *Regional Environment Change* **9**:275-289.
- Kamali, B. and R. Hashim. 2011. Mangrove restoration without planting. *Ecological Engineering* **37**:387-391.
- Krauss, K. W. and J. A. Allen. 2003a. Factors influencing the regeneration of the mangrove *Bruguiera gymnorhiza* (L) Lamk. on a tropical Pacific island. *Forest Ecol. Manage* **176**:49-60.
- Krauss, K. W. and J. A. Allen. 2003b. Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii. *Aquatic Botany* **77**:311-324.

- Lewis, R. R. 2005. Ecological engineering for successful management and restoration of mangrove forests. *Ecological Engineering* **24**:403-418.
- Lindquist, E. S. and C. R. Carroll. 2004. Differential Seed and Seedling Predation by Crabs: Impacts on Tropical Coastal Forest Composition. *Oecologia* **141**:661-671.
- Martinuzzi, S., W. A. Gould, A. E. Lugo, and E. Medina. 2009. Conversion and recovery of Puerto Rican mangroves: 200 years of change. *Forest Ecology and Management* **257**:75-84.
- McGuinness, K. A. 1997. Dispersal, Establishment and Survival of *Ceriops tagal* Propagules in a North Australian Mangrove Forest. *Oecologia* **109**:80-87.
- Michener, W. K. 1997. Evaluating Restoration Experiments: Research Design, Statistical Analysis, and Data Management Considerations. *Restoration Ecology* **5** (4):324-337.
- Osborne, K. and T. J. Smith. 1990. Differential Predation on Mangrove Propagules in Open and Closed Canopy Forest Habitats. *Vegetatio* **89**:1-6.
- Rhasid, S. H., S. R. Biswas, R. Bocker, and M. Kruse. 2009. Mangrove community recovery potential after catastrophic disturbances in Bangladesh. *Forest Ecology and Management* **257**:923-930.
- Roth, L. 1992. Hurricane and Mangrove Regeneration: Effects of Hurricane Joan, October 1988, on the Vegetation of Isla del Venado, Bluefields, Nicaragua. *BIOTROPICA* **24**(3):375-384.
- Sakho, I., V. Mesnage, J. Deloffre, R. Lafite, I. Niang, and G. Faye. 2011. The influence of natural and anthropogenic factors on mangrove dynamics over 60 years: The Somone Estuary, Senegal. *Estuarine, Coastal and Shelf Science* **94**:93-101.
- Sherman, R. E., T. J. Fahey, and J. J. Battles. 2000. Small-scale disturbance and regeneration dynamics in a neotropical mangrove forest. *Journal of ecology* **88**:165-178.
- Sousa, W. P. and B. J. Mitchell. 1999. The effect of seed predators on plant distributions: is there a general pattern in mangroves? *Oikos* **86**: 55-66.
- Srivastava, P. B. L. and D. Khamis. 1978. Progress of Natural Regeneration after Final Felling under the Current Silvicultural Practices in Matang Mangrove Reserve. *Pertanika* **1**(2):126-135.
- Valiela, I., J. L. Bowen, and J. K. York. 2001. Mangrove forests: one of the world's threatened major tropical environments. *Bio Science* **51**:807-815.
- Walter, B. B. 2005. Ecological effects of small-scale cutting of Philippine mangrove forests. *Forest Ecology and Management* **206**:331-348.