

Differences in regeneration between hurricane damaged and clear-cut mangrove stands 25 years after clearing

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Abstract The effect of human disturbance on mangrove forest may be substantially different from the effects of natural disturbances. This paper describes differences in vegetation composition and structure of five vegetation types in two mangrove areas near Darwin, Australia, 25 years after disturbance. The vegetation in clear-felled forest showed more adult *Avicennia marina* than in the hurricane-affected forest, and a virtual absence of *A. marina* juveniles and saplings. This indicates that *A. marina* will be replaced by other species in the canopy, showing a multi-phase vegetation development in mangrove forest after human disturbance. The mechanism of distur-

bance and the conditions after clearing therefore affects the vegetation composition for at least 25 years after this disturbance took place.

Keywords Regeneration · Mangroves · Long-term · Disturbance

Introduction

Mangroves are frequently disturbed. Disturbances can have a natural or artificial cause. Due to their distribution along low-latitude sea-coasts (approximately between 32° N and 38° S, Chapman, 1977) they are particularly prone to experience hurricanes and other tropical storms which can have a devastating effect on the mangrove communities. Damage ranges from crown damage to wind throw of complete areas (Hutchings & Saenger, 1987). Human disturbances vary from selective logging to total clearance for development purposes placing an ever-increasing pressure on coastal resources and habitats. The long-term effects of these disturbances are not clear.

It may take a forest several decades to regenerate after disturbance, and studies on the long-term effects of disturbances are rare (see however Guinea, 1987; McGuinness, 1992). Knowledge of the long-term effects of clearing, and the factors involved in the regeneration process can make an

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essential difference for the success of restoration and management of mangrove areas. With the increased attention for restoration issues (King, 1991; Ellison, 2000), this knowledge becomes even more important.

Various studies have been performed on the first stages of regeneration and establishment of mangroves (Sukardjo, 1987; Clarke & Allaway, 1992; Roth, 1992; Blanchard & Prado, 1995). Factors such as fruit dispersal (Clarke & Allaway, 1992; Sengupta & Middleton, 2005), predation by crab (Osborne & Smith Iii, 1990; McGuinness, 1997a) and soil properties (Ball, 1987; Duarte et al., 1998) influence the initial stage of colonisation. Although Clarke & Allaway (1992) gives a main dispersal range of a few hundred meters for *Avicennia marina*, according to Blanchard & Prado (1995), the main settlement of propagules of the *Rhizophora mangle* takes place within a few meters from the adult tree, and McGuinness (1997a) reported a main dispersal range of 3 m for *Ceriops tagal* in mangroves around Darwin. This indicates that nearby presence of well-developed mangroves may be of essential influence on the rate of re-establishment of mangroves in cleared areas.

Moreover, removal of the mangrove canopy reduces shading, affecting salinity, which in turn affects habitat suitability for invertebrates such as crab. As mangrove species vary in their sensitivity to salinity (Ye et al., 2005) and predation by invertebrates (Smith Iii, 1987b), the removal of canopy directly influences the establishment of mangroves.

This study compares the vegetation structure, rate of vegetation recovery and species composition of a hurricane-damaged and an artificially cleared mangrove area near Darwin, Northern Territory, Australia, 25 years after disturbance. The following question is addressed: “How do the stands differ in species composition, tree density and tree stem diameter?”, and the results are discussed in relation to factors that may have caused these differences. Clear felling of a forest results in complete removal of all viable plant material, whereas hurricanes only damages trees, and a part of the plant material may survive, resulting in a higher availability of propagules of a more diverse range of species in hurricane-felled

areas, compared to clear-felled areas. Therefore it was expected that re-vegetation of clear-felled forests takes longer with initially a lower number of species and a lower density of trees than hurricane-affected forest.

Material and methods

Study sites

Research was carried out in the mangrove forests of two small coastal creek systems near Darwin, Northern Territory, Australia: Ludmilla (12°23'0" S, 130°51'30" E) and Rapid Creek (12°25'0" S, 130°50'30" E). As described by McGuinness (1992; 1997b), the forest at Ludmilla (hurricane affected sites) was severely damaged by Cyclone Tracy, which passed directly over Darwin on December 24, 1974. After the cyclone only approximately 35% of the area was covered with vegetation. Even after 26 years evidence of the cyclone is visible, with dead trees covering large areas of the forest floor (McGuinness 1992, 1997a). Cyclone Tracy struck the coast while the tide was partially in, and as a consequence many mangrove seedlings and smaller saplings were protected from the worst effects (Stocker, 1976).

The downstream area of Rapid Creek (clear-cut sites) was cleared in 1969 for a housing project (Dwyer, 1980) with only a small area upstream left unaffected. The cleared area was almost completely denuded, with virtually every seedling, sapling and tree removed. The development project was terminated after Cyclone Tracy with the area being left to regenerate naturally (Guinea, 1987; McGuinness, 1992).

Based on the classification by Brocklehurst & Edmeades (1995), five different vegetation types can be distinguished in the study area: (1) *Rhizophora stylosa* and *Bruguiera* spp. closed forest, growing on tidal creek banks (*Rhizophora/Bruguiera* forest), (2) *Rhizophora/Bruguiera/Ceriops* closed forests, growing on the transition from creek bank to tidal flat (*Bruguiera/Ceriops* forest), (3) mono specific *C. tagal* low closed forest, growing on the low tidal flat (*Ceriops* forest), (4) *C. tagal/A. marina* low closed forest, growing on the high tidal flat (*Ceriops/Avicennia*

forest), and (5) mixed species low closed to open forest, growing in the hinterland (Hinterland). In the study areas the forests canopy of the hinterland reached 10 m in places, in contrast to the described 3.5 m in Brocklehurst & Edmaedes (1995).

Photo interpretation

Aerial photo interpretation was used to map the evolving forest cover. Stereo photographs were available for the hurricane-affected creek from 1975, 1978, 1983 and 1999 and for the clear-cut creek from 1969, 1978, 1983 and 1997. All aerial photographs, except for the images from the hurricane-affected creek in 1975, were scanned at high resolution and geo-referenced. The scanned images served as a background in a GIS (ArcInfo) to delineate vegetated areas. A stereo-viewer was used to better determine vegetated versus non-vegetated areas. Subsequently the percentage of vegetated area for each image was exported, and plotted against years after clearing.

Field sampling

The current vegetation structure and species composition in both creek fields was assessed using a stratified sampling scheme. In each creek two locations were selected in disturbed areas of each of the five predominant mangrove vegetation types. At each location, two plots (10 m × 10 m) were set up by randomly selecting a tree as corner point from which the plot was set up. In each plot, all trees (woody plants with a DBH > 2 cm) were identified according to Wightman (1983) and the number of individuals was counted. The DBH was measured at 1.3 m height using DBH tape.

Densities of saplings and sub-adults were extremely high in certain vegetation types. Therefore within each of these plots, three subplots (2 m × 2 m) were laid out, at 2 m from the corners. In the subplots, all woody plants with a DBH less than 2 cm were identified and the number of each species was recorded in two categories: sub-adults (individuals taller than 50 cm with a DBH less than 2 cm) and saplings (established individuals with at least two leaves,

smaller than 50 cm). All botanical nomenclature is according to Wightman (1989).

Plot elevation was determined using the inundation levels during a spring-tide. Before the spring-tide on June 4th, cotton-rope, died in water soluble food-dye, was tied between the roots and the crown of a large tree in each plot. A test showed that the food-dye washes out up to the high-tide water level. Just above this water level the food-dye accumulates, due to the upward movement of water through the cotton rope, leaving a darker stain than in the rest of the rope. This concentrated stain was used as a marker for the highest water level. During low tide, each plot was revisited, and the water depth at high tide was determined by measuring the height up to which the food-dye was washed away. The plot height was subsequently determined by subtracting the inundation level from the predicted high-tide water level from the tidal forecast charts for Darwin Harbour on that day (Anon, 1999). An analysis of variance (ANOVA) was performed with factors creek and vegetation type to determine differences in elevation above mean sea-level between creek systems.

Data processing and analysis

The similarity of the locations in each of the creeks and vegetation types was assessed using ordination. Species data on a strong environmental gradient typically displays a 'bell-shaped' ordination-response, which can be reduced by using a non-metric multidimensional scaling (NMDS) ordination (Fasham, 1977). Since mangrove forests display zonation along a strong elevation/salinity/inundation gradient, a NMDS ordination, based on Bray–Curtis dissimilarities calculated from the average number of trees per species at each location and vegetation type was performed.

ANOVA was used to compare the effects of creek system and vegetation type on the total number of trees and the average DBH for each species. For both *R. stylosa* and *Bruguiera parviflora* only *Rhizophora/Bruguiera* forest and *Bruguiera/Ceriops* forest were included, and *Lumnitzera racemosa* was only analysed for *Ceriops/Avecennia* forest. For these species no

mature individuals were observed in the other vegetation types. For some groups the data deviated from normality, and the number of trees of *C. tagal* and *R. stylosa*, and the DBH of *A. marina*, *B. exaristata* and *C. tagal* were log-transformed. Even so, variances for *B. exaristata* (analyses of number of trees), *A. marina*, *B. parviflora* and *C. tagal* (analysis of DBH) were heterogeneous (Cochran's test, $P < 0.05$). Tukey's HSD test was used to compare means after the ANOVA.

The number of species and the age structure of the population reflect the vegetation regeneration phase. To test for differences in species richness and population structure between different vegetation types and study areas, the data were summarized, and mean and variances were calculated for the relative abundances for the different species in the three size classes (adults, sub-adults and saplings). The data from the three 2 m × 2 m subplots of each 10 m × 10 m plot were averaged, extrapolated to number of individuals per 100 m² and combined with the results from the 10 m × 10 m plots. From this the relative abundance of each species per size-class was calculated for every plot.

To analyse the age structure of the population, we compared the frequencies in different DBH classes for the three most common species using histograms for each species, at each vegetation type and creek system. The total DBH range covered for each species determined the size of the DBH classes used.

Results

Photo interpretation

Figure 1 gives an overview of vegetation cover, as determined from digitised aerial photographs. In the clear-cut forest, most of the forest floor was initially covered with dead trees, clearly visible on the image. In 1978, nine years after clearing most of the dead trees were absent, and individual living trees are visible on the image, with small clusters of trees along the creek beds and on the landward margin. The 1983 images showed large areas of the clear-cut forest covered with evenly

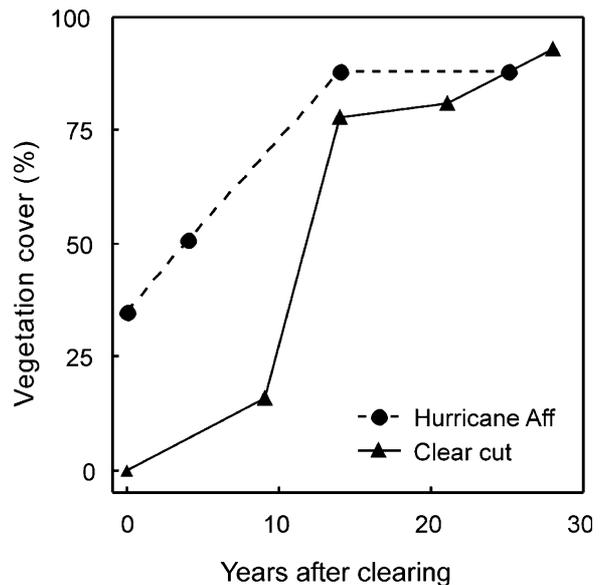


Fig. 1 Vegetation cover in Ludmilla and Rapid Creek as derived from aerial photographs. Year 0 Ludmilla = 1975; Year 0 Rapid Creek = 1969

distributed small trees and a very open canopy. The 1990 images (21 years after the clearing) show completely closed canopies, which cover about 90% of the area.

One month after Cyclone Tracy only 35% of the area of the hurricane-affected forest was covered with green vegetation. The rest was covered with defoliated trees. Four years after clearing some of the defoliated trees had resprouted and 50% of the hurricane-affected forest was covered with green vegetation. The rest was littered with dead trees between which young trees started to emerge. In 1988, 14 years after clearing, 90% of the hurricane-affected forest was covered with closed canopy vegetation. In 1999 the same areas as in 1988 were devoid of vegetation. In the field these bare areas showed crystallized salt on rocks and soil and were identified as salt flats.

Plot elevation

Differences occur in the elevation above mean sea level for different vegetation types (Fig. 2). However, no differences could be detected in plot elevation between the different creek systems (Fig. 2).

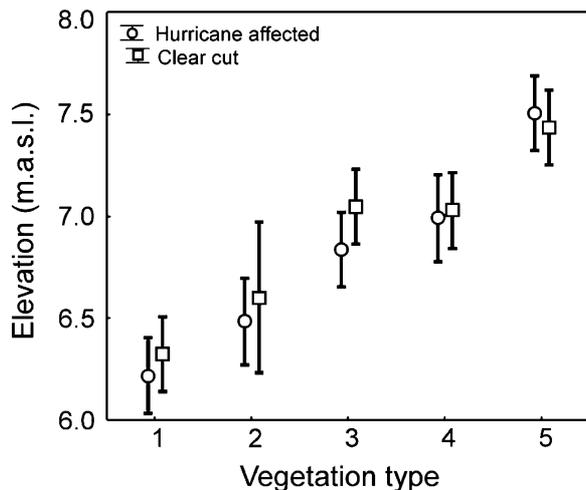


Fig. 2 Mean elevation of plots in hurricane-affected and clear-cut sites. Bars indicate 95% confidence of the mean. Vegetation types (1) *Rhizophora stylosa* and *Bruguiera* spp. closed forest, growing on tidal creek banks (*Rhizophora/Bruguiera* forest), (2) *Rhizophora/Bruguiera/Ceriops* closed forests, growing on the transition from creek bank to tidal flat (*Bruguiera/Ceriops* forest), (3) mono specific *Ceriops tagal* low closed forest, growing on the low tidal flat (*Ceriops* forest), (4) *Ceriops tagal/Avicennia marina* low closed forest, growing on the high tidal flat (*Ceriops/Avicennia* forest), and (5) mixed species low closed to open forest, growing in the hinterland (Hinterland)

Species composition and structure

A total of 1650 and 1442 mature individuals with DBH < 2 cm were measured in hurricane-affected and clear-cut forests respectively. Three of these species (i.e. *Aegialitis annulata*, *Avicennia integra* and *Camptostemon shultzii*) were present in very low numbers (9, 5 and 4 individuals respectively). These were excluded from further analyses.

The ordination showed a separation of plots according to the distribution of species and the number of individuals (Fig. 3). The first axis reflects the distribution of species and position on the tidal flat. Low values indicate the presence of species found closer towards the creek banks (*R. stylosa*, *B. parviflora*), where high values are related to presence of species that are found higher on the tidal range (*L. racemosa*, *C. tagal*). The second ordination axis is related to the number of trees present in the plot. Lower values indicate a high number

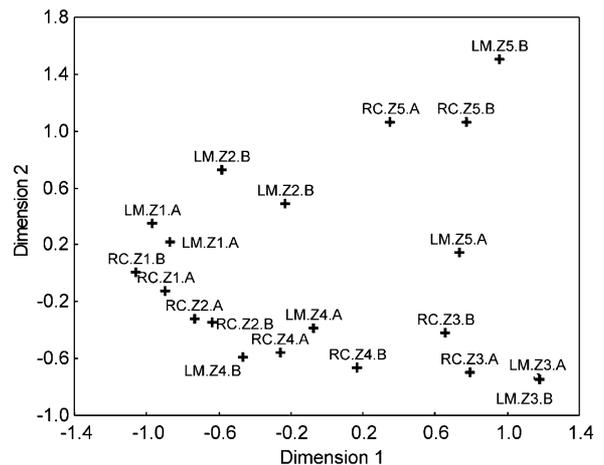


Fig. 3 Scatterplot of Bray-Curtis dissimilarities between research locations, based on total number of trees per species per locations. Coding: LM = Hurricane-affected area, RC = Clear-cut area. Z1–Z5: Vegetation types (1) *Rhizophora stylosa* and *Bruguiera* spp. closed forest, (2) *Rhizophora/Bruguiera/Ceriops* closed forests, (3) mono specific *Ceriops tagal* low closed forest, (4) *Ceriops tagal/Avicennia marina* low closed forest, and (5) mixed species low closed to open forest. A = Ludmilla, B = Rapid Creek (Stress value = 0.118)

of trees present, where high values reflect a low number of trees.

There was a good similarity in number of species and species composition of the same vegetation types between the two creeks (Fig. 3). Plots in *Rhizophora/Bruguiera* forest and *Bruguiera/Ceriops* forest in the clear-cut creek system tend to have more trees than plots in the same vegetation types in the hurricane-affected creek system. Plots in the *Ceriop* forest, in the clear-cut forest show more dominance of species lower on the tidal flat than these forests in the hurricane-affected creek system. The other vegetation types show a similar species composition and similar number of individuals between the two creek systems. An exception formed location 1 in the hinterland for the hurricane-affected area. This location had a lower value on the second axis, indicating a higher number of trees present than the other hinterland plots.

Tree density

In contrast to differences in the abundance of species between vegetation types, there were few

Table 1 Average number of mature trees and average tree diameter at breast height (mm) of mature trees (DBH > 20 mm) per 10 m × 10 m for each vegetation type (VT1–VT5: Vegetation types (1) *Rhizophora stylosa* and *Bruguiera* spp. closed forest, (2) *Rhizophora/Bruguiera/*

Ceriops closed forests, (3) mono specific *Ceriops tagal* low closed forest, (4) *Ceriops tagal/Avicennia marina* low closed forest, and (5) mixed species low closed to open forest in hurricane-affected (HA) and clear-cut (CC) forest, 25 years after clearing)

	VT 1		VT 2		VT 3		VT 4		VT 5	
	HA	CC								
Number of trees										
<i>A. marina</i>	14	24	4	44	0	2	32	43	0	2
<i>B. exaristata</i>	7	3	36	9	1	6	2	1	3	10
<i>B. parviflora</i>	2	8	6	0	0	0	0	0	0	0
<i>C. tagal</i>	1	0	6	1	204	97	18	50	16	3
<i>L. racemosa</i>	0	0	0	0	0	0	0	0	29	34
<i>R. stylosa</i>	25	15	9	3	0	0	0	0	0	0
DBH										
<i>A. marina</i>	82	59	43	50	0	35	49	35	0	43
<i>B. exaristata</i>	48	25	37	28	5	39	11	11	36	12
<i>B. parviflora</i>	18	26	24	0	0	0	0	0	0	0
<i>C. tagal</i>	10	0	39	12	30	27	33	25	29	38
<i>L. racemosa</i>	0	0	0	0	0	0	0	0	92	65
<i>R. stylosa</i>	58	86	58	29	0	0	0	0	0	0

differences between creeks (Tables 1 and 2). The only species for which differences between the two creeks occurred was *A. marina*. The difference depended on vegetation type: *A. marina* was more abundant in *Rhizophora/Bruguiera*, *Bruguiera/Ceriops* and *Ceriops/Avicennia* forest in the clear-cut creek system than in these vegetation types in the hurricane-affected creek system, but equally abundant in the other two vegetation types (Tukey's test $P < 0.05$). The number of trees of *A. marina* in the clear-cut creek system was lower in *Ceriops forest* and the hinterland than in *Rhizophora/Bruguiera forest*, which had fewer trees than *Bruguiera/Ceriops* and *Ceriops/*

Avicennia forest. *A. marina* is absent in *Bruguiera/Ceriops forest*, *Ceriops forest* and the hinterland. The number of *A. marina* trees is very low in *Bruguiera/Ceriops forest* ($n = 4$); It is highest in *Ceriops/Avicennia forest* (Tukey's test $P < 0.05$). *C. tagal* was very abundant in *Ceriops forest* in both creeks, with higher densities in hurricane-affected sites than in clear-cut sites (Tukey's test $P < 0.05$).

Diameter at breast height

For most species no differences in mean DBH occurred between creeks or vegetation types

basal area (TBA) for the six most common species in Ludmilla and Rapid Creek

Table 2 ANOVA significance of effects of creek system and vegetation type on the average number of trees (NT), average tree diameter at breast height (DBH) and total

	<i>A. marina</i>			<i>B. exaristata</i>			<i>B. parviflora</i>			
	df	NT	DBH	df	NT	DBH	df	NT	DBH	
Creek	1	***	***	1			1			
Vegetation type	4	***	***	4	**		1			
Creek × Veg. type	4	**	***	4			1			
		<i>C. tagal</i>			<i>L. racemosa</i>			<i>R. stylosa</i>		
Creek	1			1			1			
Vegetation type	4	***					1	*	*	
Creek × Veg. type	4						1		*	

* $P \leq 0.1$, ** $P \leq 0.05$, *** $P \leq 0.01$

(Tables 1 and 2). Only for *A. marina* and *R. stylosa* differences in mean DBH were found between creeks and vegetation types. The mean DBH of *A. marina* in the clear-cut creek system (*Ceriops* forest and Hinterland) was higher than in those forest types in the hurricane-affected creek system (Tukey's test $P < 0.05$). The mean DBH of *A. marina* in the clear-cut creek system (*Rhizophora/Bruguiera*, *Bruguiera/Ceriops I*, and *Ceriops* forest) and in the hurricane-affected creek system (*Rhizophora/Bruguiera* forest) was higher than the mean DBH of *A. marina* in the hinterland of the clear-cut creek system (Tukey's test $P < 0.05$). The mean DBH of *R. stylosa* was higher in *Rhizophora/Bruguiera* forest than in *Bruguiera/Ceriops* forest in the clear-cut creek system (Tukey's test $P < 0.05$). Although the ANOVA indicated a difference in mean DBH for *R. Stylosa* between creeks, Tukeys HSD test ($P < 0.05$) could not distinguish any differences.

Age and occurrence

Relative abundance of species varied between vegetation types, between size classes and between creek systems (Fig. 4). For *Rizophora/Bruguiera* forest in the hurricane-affected creek system most of the saplings were *B. exaristata*, while in the clear-cut creek system they were *B. parviflora*. In both creek systems the sub-adult and the adult class of *Rizophora/Bruguiera* forest were dominated by other species. For the hurricane-affected creek system both the adult and the sub-adult group were dominated by *R. stylosa*, whereas the adult stage in the clear-cut creek system mainly consisted of *A. marina*. The sapling and the sub-adult class in *Bruguiera/Ceriops* forest were dominated by *B. exaristata* for both creek systems. *A. marina* dominated the adult group in the clear-cut creek system, while the adult group in the hurricane-affected creek system was dominated by *B. exaristata*. *C. tagal* was the dominant species in all size classes for both creek systems in *Ceriops* forest (Fig. 3). The saplings in *Ceriops/Avicennia* forest were mainly *C. tagal*, In the clear-cut creek system *C. tagal* dominated the sub-adult stage, and the adult stage had an even mixture of *C. tagal* and

A. marina whereas the sub-adult and adult stage in the hurricane-affected creek system mainly consisted of *A. marina*.

Differences per DBH class

The DBH classes for *A. marina*, *B. exaristata* and *C. tagal* varied between vegetation types, creeks and species (Fig. 5). With increasing DBH, the number of *A. marina* trees first increased slightly, and decreased for higher DBH classes in *Rhizophora/Bruguiera* and *Bruguiera/Ceriops* forest in both creek systems. These vegetation types in the clear-cut creek system had the maximum number of trees in the 40–60 mm class. This, combined with the low relative abundance of saplings and sub-adult *A. marina* in these vegetation types, might reflect a reduced recruitment. In *Ceriops/Avicennia* forest the number of individuals decreased with increasing DBH for both creeks. This pattern was also observed in *Ceriops* forest in the clear-cut creek system, but to a lesser degree. For *B. exaristata* a decline in number of individuals was found with increasing DBH for all vegetation types except for the hinterland in the hurricane-affected creek system where the number of individuals in the three smallest DBH classes was much lower than in the other two classes. For *C. tagal* there is a decrease in the number of individuals with increasing DBH, except for the hinterland for both creeks (which had a low number of *C. tagal* saplings and no sub-adults).

Discussion

The factors that affect initial re-vegetation of denuded mangrove habitat are diverse, and vary between geographic regions. Where some authors find the effect of salinity on the establishment and survival of propagules to be of major importance (Ye et al., 2005) other authors report the presence of propagules (Sengupta & Middleton, 2005) or the predation on those (Clarke & Kerrigan, 2002) to be the main factor. We found that differences in regeneration rate between disturbed areas seem to be the result of absence of juvenile trees and saplings and probably also lack of propagules in completely

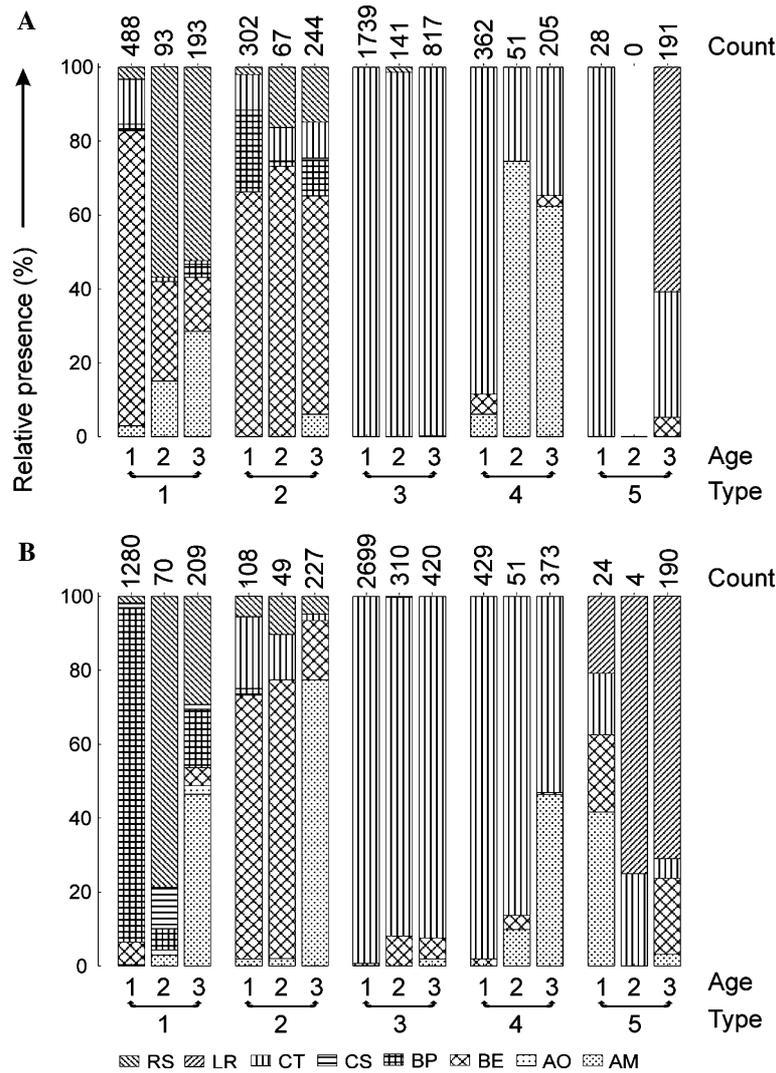


Fig. 4 Relative occurrence of each species in different size-classes for **(A)** Ludmilla and **(B)** Rapid Creek. Age classes: (1) Saplings < 50 cm, (2) sub-adult > 50 cm and DBH < 2 cm, (3) adult trees DBH > 2 cm. Vegetation types (1) *Rhizophora stylosa* and *Bruguiera* spp. closed

forest, (2) *Rhizophora/Bruguiera/Ceriops* closed forests, (3) mono specific *Ceriops tagal* low closed forest, (4) *Ceriops tagal/Avicennia marina* low closed forest, and (5) mixed species low closed to open forest. Numbers above columns indicate total number of individuals

cleared areas. The amount of vegetation cover left after clearing influences the species composition in the first decades after clearing, due to differences in predator densities, soil salinities and the availability of micro-sites suitable for establishment, combined with the availability propagules.

The observed differences between creek systems in the present study indicate a lag in vegetation development in a clear-cut creek

system compared to a hurricane-affected creek system: The re-vegetation of the hurricane-affected creek system was initially faster than in the clear-cut area. After about 10 years, the area covered by vegetation in the first reached 88%, and has hardly changed since then, whereas after 25 years the area covered by vegetation in the latter still seems to increase (Fig. 1).

A number of different factors may have caused this slower recovery in the clear-cut area. When

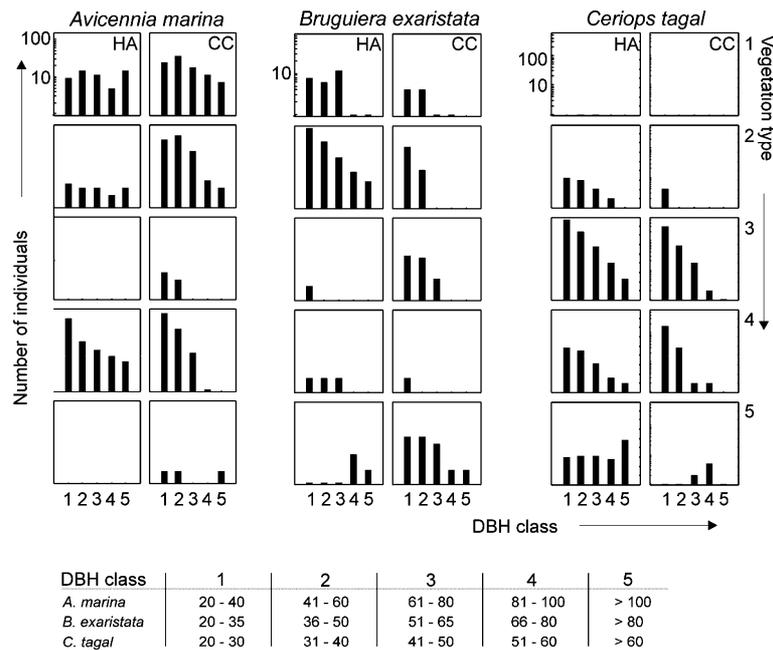


Fig. 5 Histograms of DBH classes, grouped by vegetation type, creek and species for *Avicennia marina*, *Bruguiera exaristata* and *Ceriops tagal*, with DBH in mm

‘Tracy’ hit Darwin, the tide was partially in, and the water offered some protection against the wind, leaving most of the saplings and sub-adults in the hurricane-affected creek system undamaged (Stocker, 1976). The removal of the vegetation canopy by ‘Tracy’ may have led to an increased growth of the saplings and sub-adults replacing the dead adult trees fairly quickly. Although mangrove trees can die of defoliation, a part of the trees may have survived defoliation, resulting in adult trees in the damaged areas. The affected area in the clear-cut area on the other hand was almost completely denuded, with all mature plants removed. Ten years after clearing only 16 % of the area was covered by regrowth. In the following 20 years, the clear-cut area recovered (Blanchard & Prado, 1995).

Clarke (1992) and McGuinness (1997b) showed a limited effective dispersal range for mangrove species common in the region. The difference in recovery rate in later years may therefore reflect a difference in propagule availability between clear-cut and hurricane-affected sites, due to the virtual absence of mangroves in the clear-cut area after clearing. On the other hand, as stated in McGuinness (1997a), the

circumstances during the first few months or years of the life of individuals may strongly affect the rate at which mangrove species recolonise a habitat.

Mature *A. marina* is more abundant in *Rhizophora/Bruguiera*, *Bruguiera/Ceriops* and *Ceriops/Avicennia* forests in the clear-cut area than in the same vegetation types in the hurricane-affected creek system. In the younger classes, *A. marina* is virtually absent (Fig. 4). Dwyer et al. (1980) reported that *A. marina* and *C. tagal* are the main species that managed to settle in the clear-cut area during the first years after clearing. Guinea (1987) found a significant increase in tree height for *A. marina* in the clear-cut area between 1980 and 1987, while the size of saplings and sub-adults of other species found in the survey areas stayed the same. This indicates that the prevailing conditions during the first years after clearing favoured establishment of *A. marina*, an advantage which seems to be absent under current conditions.

Absence of shade in clearings results in higher soil salinities than in covered situations (McGuinness, 1997b), particularly in the less frequently inundated areas. Although all mangroves are to a

certain extend salt tolerant when fully established, not all propagules are equally resistant (Clough, 1984). *A. marina* is characterised as the most salt tolerant of all the mangroves (Ball, 1987), and root initiation and subsequent establishment of *A. marina* is hardly hampered by extreme saline conditions (Ye et al., 2005). The absence of shade in the clear-cut area in the first few years after clearing may have caused a difference between the clear-cut area and the hurricane-affected area in the settlement and growth of different species, favouring *A. marina* in the clear-cut area.

Propagule predation is another factor that might have played a role in the higher presence of *A. marina* in the clear-cut area. Propagule predation is a major factor reducing the survival of propagules (Smith Iii, 1987a; Clarke & Kerrigan, 2002; Lindquist & Carroll, 2004). This predation has been shown to be different between mangrove species (Smith Iii, 1987a; Clarke & Kerrigan, 2002) and vary between geographic regions (Farnsworth & Ellison, 1997) but occurs globally (Farnsworth & Ellison, 1997). Globally, *A. marina* suffers most from crab predation on propagules (Farnsworth & Ellison, 1997). Smith (1987a) showed high predation rates on *A. marina* propagules in the mid-tidal range, which was subsequently confirmed by Osborne and Smith (1990). They reported that grapsid crabs (*Brachyura*, *Grapsidea*) could consume up to 100% of all *A. marina* propagules under closed canopy conditions. Predation rates on *A. marina* propagules in clearings may be lower than under closed canopy situations, as the result of the virtual absence of grapsid crabs in these clearings (Osborne & Smith Iii, 1990). When gaps are formed in the canopy of a mangrove forest, ocypodid crabs replace the grapsid crab fauna (Osborne & Smith Iii, 1990). Since ocypodid crabs do not eat mangrove propagules, this shift may have a strong influence on the regeneration capacity of mangroves (Osborne & Smith Iii, 1990). Salgado-Kent (2002) showed high propagule predation rates at Reichardt Creek (approximately 10 km from our study sites) with predation is greatest for *A. marina*, followed by *C. tagal* and *R. stylosa* propagules. Therefore the difference in initial

vegetation cover between the clear-cut area may have resulted in different grapsid crab densities, with lower predation rates on *A. marina* saplings in the clear-cut creek system than in the hurricane-affected creek system, increasing relative survival rates for *A. marina*.

This is supported by the relative abundance of *A. marina* in the canopy when compared to the understory. *A. marina* is relatively more abundant in the canopy layer than in the understory. The number of juvenile trees depends on three factors: seed/sapling production, their germination and establishment and their subsequent survival. Perret (1995) showed that fruit production of *A. marina* was second highest of all species in this study. However closure of the canopy would have resulted in an increase of the grapsid crab population and high predation rates. McGuinness (1997b) reported up to 100% for *A. marina*, a predation level supported by Salgado-Kent (2002). This causes a relatively higher survival rate of saplings of other species, compared to the adult phase. Therefore *A. marina* may eventually be replaced by other species as main canopy species in most vegetation types, except for those where it is a dominant species, e.g., *C. tagal*/*A. marina* low closed forest.

This study gives insight in differences in regeneration of mangrove forest that is either fully or only partially cleared. Naturally, low supply of propagules is a primary cause for slow re-vegetation of cleared mangrove areas. However, even when ample propagules are available, development into maturity may for several species be hampered by the absence of shading, and subsequent salination of the mudflats. Absence of shade and increased salinity seem to have favoured the settlement of *A. marina* saplings. Under full canopy cover *A. marina* sapling and juveniles are virtually absent. This indicates that *A. marina* will be replaced by other species in the canopy, showing multi-phase vegetation regeneration in mangrove forest.

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