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PNEUMATOPHORE HEIGHT AND DENSITY IN RELATION TO MICRO-TOPOGRAPHY IN THE GREY MANGROVE *AVICENNIA MARINA*

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Abstract. — Mangroves are known to stabilise coastal sediments through their above-ground aerial root complex. The results presented in this paper suggest that the grey mangrove *Avicennia marina* has the ability to adapt its pneumatophores to micro-topographical irregularities in the otherwise regularly sloping intertidal zone. The difference in height above datum (and thus in hydrological regime) in this study was as little as 15 cm higher as opposed to that for the surrounding mangrove soil. Significantly higher pneumatophore densities and total pneumatophore lengths were observed in the centre of the landward depression, and significantly lower below-ground pneumatophore length in the centre of the seaward depression. The mangrove's adaptations to these localised topographic differences are important in view of changes in intertidal hydrology, the latter being linked to changes in topography. We emphasize the need to consider the effect of topography in the intertidal environment of mangroves more closely in the future on different ecological scales (individual adaptation – regeneration of the entire population) and under different scenarios of change (direct anthropogenic impact – changes in sea level).

Key words. — *Avicennia*, aerial roots, Kenya, micro-topography.

INTRODUCTION

Mangrove species have developed many morphological and physiological adaptations that are essential for them to survive in the harsh intertidal zone in which they grow. Adaptations include aerial roots, salt balance, vivipary and hydrochory (Tomlinson 1986). Whereas most mangrove species display a choice for optimal conditions for their growth, others have developed an ability to withstand a wide range of global and local conditions (e.g., Ball 1988). Of all mangroves, *Avicennia marina* (Forssk.) Vierh. has the largest latitudinal spread (cf. Spalding *et al.* 1997), and on a regional scale, it has been shown to adapt to varying climatic conditions by adjusting its phenology (Duke 1990). This species-specific plasticity has also been found on a much larger scale, as this species displays differential population structures at different latitudes (Osunkoya & Creese 1997). Even within a particular mangrove forest *Avicennia marina* has shown to be one of the most eurytopic species along environmental

Table 1. Overview of countries or regions where a 'double' or 'disjunct' zonation of *Avicennia marina* has been observed within sites with multiple mangrove species. The number of true mangrove species for the respective country is given according to SPALDING *et al.* (1997), but may differ on a local scale. For some countries more recent corrected species numbers have been given. This overview obviously excludes references to areas where *A. marina* occurs as the sole mangrove species (e.g., monospecific stands at latitudinal distribution limits).

Country or region	Number of true mangrove species	Reference(s)
Indo-West Pacific	up to 45	MACNAE (1968)
East-Africa	11	WALTER & STEINER (1936)
Kenya	10	GALLIN *et al.* (1989), DAHDOUH-GUEBAS *et al.* (1998), MATTHIJS *et al.* (1999), DAHDOUH-GUEBAS *et al.* (2002a,b, 2004a,b)
India	28	SATYANARAYANA *et al.* (2002)
Malaysia	36	WATSON (1928)
Australia, NT	37	BUNT (1996), WOODROFFE & GRIME (1999)
Australia, QLD	37	MACNAE (1969), BUNT (1996), CLARKE (2004)

gradients, which is particularly well illustrated by the appearance of a 'double' or 'disjunct' intertidal zonation in many parts of the world (Table 1). Such a zonation has been occasionally reported as observations (JOHNSTONE 1983, SMITH 1992, OCHIENG & ERFTEMEIJER 2002), but recently DAHDOUH-GUEBAS *et al.* (2004a) described *Avicennia marina*'s clear variation in morphological and genetic characteristics between landward and seaward zones.

Apart from effects induced by the natural environment, mangroves are additionally affected by direct and indirect human-induced stresses and disturbances, some effects of which are compounded in the intertidal zone (e.g., ALONGI 2002, DAHDOUH-GUEBAS *et al.* 2004b). In the light of the response of mangroves to global climatic change, and in particular of *A. marina* to sea-level rise, this preliminary study focuses on the adaptation of the pencil-root[1] complex of *A. marina* to changes in micro-topography. DAHDOUH-GUEBAS *et al.* (2004a) demonstrated that root density and length were dependent on the intertidal zone in which the tree was growing. The objective of the present study was to investigate whether very shallow and local micro-topographic depressions (0.2 – 0.4 m) have an effect on *A. marina* pneumatophore density or on their above- and below-ground length. Our hypothesis was that there exists a trend in the density and the length of pneumatophores from the centre of a small depression (high/long) towards the edges (lower/shorter) in both landward and seaward *A. marina* zones.

MATERIAL AND METHODS

The study was conducted in the Kenyan mangrove area near Gazi (Fig. 1), for which the disjunct zonation of *Avicennia marina* has been described earlier (DAHDOUH-GUEBAS *et al.* 2002a,b, 2004a,b). The two *Avicennia* zones are located along the intertidal slope and are separated by approximately 100 m. Between these two *Avicennia* fringes, the mangrove vegetation is composed of other species, such as Rhizophoraceae. The spring tidal amplitude is about 3.5 m, and the seaward *Avicennia* zone is

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[1] Mangrove aerial roots are commonly distinguished as prop or stilt roots (e.g., *Rhizophora* spp.), knee-roots (e.g., *Bruguiera* spp.), plank and buttress roots (e.g., *Xylocarpus* spp.), peg roots (e.g., *Sonneratia* spp.), and pencil roots (see TOMLINSON 1986). Pencil roots originate from the below-ground cable root and stick out vertically from the soil, and are a typical feature of *Avicennia* species (Fig. 1).

inundated twice daily (water column may be more than 2 m high), whereas the landward zone is inundated only during spring high tides (water column < 0.5 m). For a detailed description of the study site, including remotely sensed imagery and descriptive vegetation data, see DAHDOUH-GUEBAS *et al.* (2004a). A 10 m transect was laid across a natural topographic depression within the landward *Avicennia marina* vegetation zone. An 11 m transect was used in the seaward *A. marina* vegetation zone. The landward zone was composed entirely of *A. marina*. In the seaward zone *A. marina* was the dominant (87%) species with some *Rhizophora mucronata* Lamk. and *Sonneratia alba* J. Smith. Tree spread was approximately even in both zones. At 1 m intervals along each of the transects, 1 m^2 quadrates were established ($n_{\text{landward}} = 10$; $n_{\text{seaward}} = 11$), and within each quadrate, the number of pencil roots was counted and their above-ground length was recorded. In addition, four randomly chosen pneumatophores per quadrate were excavated down to the cable root in order to measure their below-ground-length. Since there was little variation in below-ground-length, the average of the four measurements was added to each of the above-ground-length measurements to obtain the total pneumatophore length. Spearman's rank correlation coefficient (r_s) was used as described by SOKAL & ROHLF (1981) in order to correlate height above datum (and thus relative depression depth) with the variables and parameters from the root complex. The height above datum was measured using a theodolite (Nikon, Auto level AE-3G). This was done at 1 m intervals within the depressions, and at 5 m intervals between the depressions, using a reference point or benchmark. This benchmark was the maximum water height above datum (highest water line), as predicted by tide tables available from the Kenya Port Authority. We are aware that tidal predictions may be off by a few centimetres, particularly in shallow bays, but we did not attempt to measure the actual hydro-graphic height, mainly because the objective of this study emphasized the existing relative differences in height and their effect on the vegetation. All elevations were expressed as 'meters above datum', and the error of the theodolite was experimentally recorded at 3 cm.

Redox potentials of the soil were measured with a platinum-Ag/AgCl redox electrode connected to a pH/mV/T-meter (P601, Eijkelkamp, Agrisearch Equipment), as described in MATTHIJS *et al.* (1999), in order to examine the effect of long inundation periods at the centre of the depressions.

RESULTS

Maximum depth of the topographic depression was 15 cm in the landward zone (3.4 m above datum; Fig. 2a). The highest density of pneumatophores in the landward depression was 2 500 m^{-2} at the centre of the depression (Fig. 2c), but was only 200 m^{-2} outside the pit. The redox potential of the interstitial water at the centre of the landward depression was -259 mV, while values outside the depression were less reduced (-55 mV and -178 mV). Total pneumatophore length increased towards the centre of the landward depression (Fig. 2a) and the relationship with height above datum was highly significant ($r_s = 0.71$; $n = 10$; $P < 0.005$). The below-ground length decreased significantly with a lower height above datum in the landward depression ($r_s = -0.86$; $n = 10$; $P < 0.001$; Fig. 2a).

Maximum depth of the topographic depression was 44 cm in the seaward zone (1.7 m above datum; Fig. 2b). However, there was a decrease in below-ground pneumatophore length with a lower height above datum ($r_s = -0.94$; $n = 11$; $P < 0.001$; Fig. 2b). There was no significant decrease in total pneumatophore length with a lower height above datum ($r_s = 0.44$; $n = 11$; n.s.). For the seaward depression, there seems to be no relationship between pneumatophore density and the position in the depression and thus height above datum (Fig. 2b,d). The redox potential of the interstitial water of the seaward depression was most reduced half-way down the depression slope (-352 mV and -386 mV), less reduced in the deepest quadrates (-296 mV and -306 mV) and least reduced at the top margins (-155 mV and -135 mV).

DISCUSSION

The discussion of our results is made within the seasonal conditions that prevailed during out field campaign (dry season). Although we are aware that our environmental measurements of the redox potential may be different in the wet season, or when multiple measurements are performed throughout the year, we have often observed that the more stressful conditions shaping the vegetation occurs in the dry season.

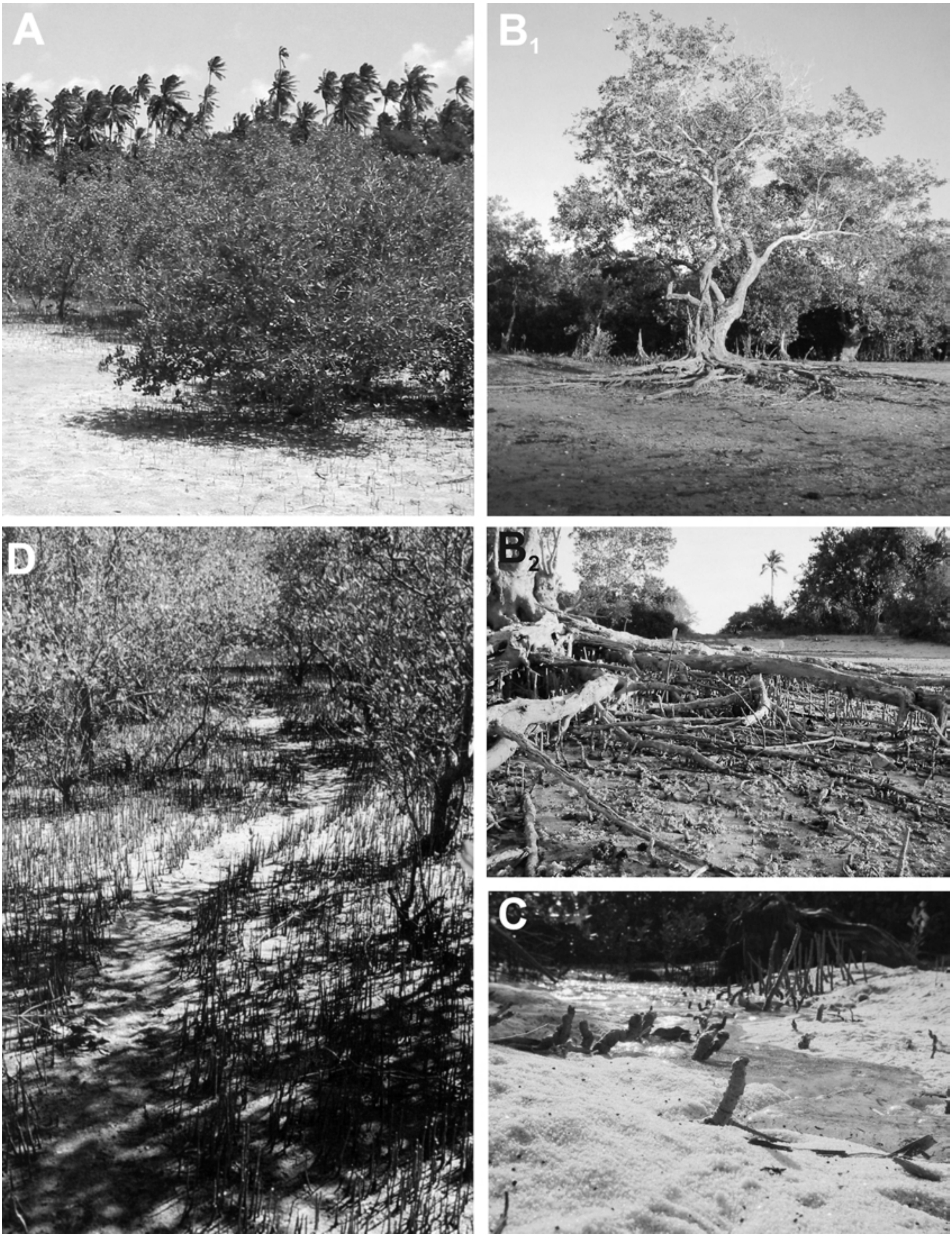

Fig. 1. (A) Physiognomy of a landward *Avicennia marina* fringe in Gazi, Kenya. (B) Overview (B1) and close-up (B2) of an *A. marina* tree uprooted by tidal and wave energy. (C) Close-up of *A. marina* pencil-roots and of the micro-topographic variations (note the pathway of the incoming tide). (C) Path amongst *A. marina* pneumatophores created by walking fisherfolk. (Photographs taken by Griet Neukermans and Farid Dahdouh-Guebas)

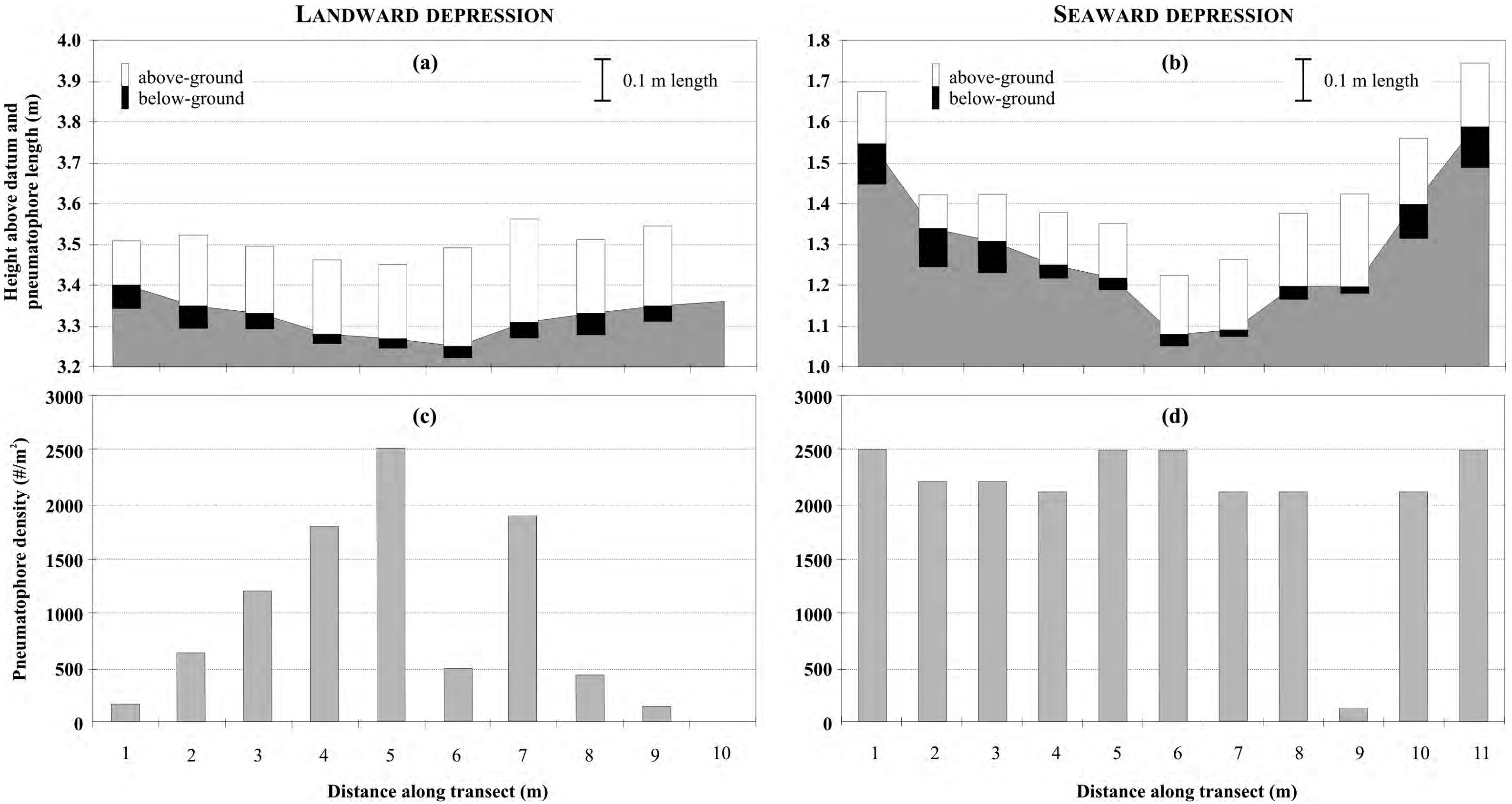

Fig. 2. (a-b) Micro-topography and above- and below-ground pneumatophore length, and (c-d) pneumatophore density for *Avicennia marina* sampled across a depression at 1 m intervals along a landward and a seaward mangrove transect.

Observed pneumatophore density and length in the topographic depressions are in line with the hypothesis that pneumatophore density and length is higher for places with longer inundation periods (DAHDOUH-GUEBAS *et al.* 2004a). The hypothesis was confirmed for pneumatophore density and total and below-ground length in the landward depression. In addition, the present study revealed the sensitivity of the root complex of *Avicennia marina* with respect to micro-topographical settings. It is notable that even shallow depressions (0.2 m and 0.4 m for the landward and seaward depression, respectively) seem to trigger the plants to adjust their root complex significantly. However, further investigations in a variety of mangrove formations are necessary to validate these results.

Decreased below-ground pneumatophore length in the landward zone can be explained by the sandy substrate being easily removed by water, making the below-ground length appear shorter. In some landward areas outside the study area, the action of water has denuded entire root complexes of *Avicennia marina* (Fig. 1B). This removal of the substrate occurs in areas that display a sparse distribution of trees and roots, and where small waves (< 1 m length along the topographical gradient) occur at spring tide. Pneumatophore length and density being higher towards the centre of the depression may be indicative of root growth toward more oxygenated surface horizons (cf. DAHDOUH-GUEBAS *et al.* 2004a).

Pneumatophores in the seaward depression generally do not reach above the high water level. Tidal fluctuations of > 2 m in our sites cannot be overcome by the height of pencil roots of *Avicennia marina* (unlike peg roots in *Sonneratia* spp., pencil roots are thin throughout their length and tend to fall over as they grow tall). An increase in density would be beneficial, but of less importance in a depression, since the pneumatophores are already entirely exposed to water, and not covered by detritus.

Even though this study was conducted in a natural *A. marina*-dominated zone with an even spread of trees, local variations in pneumatophore density may be due to tree density (both *A. marina* and other species) and cable root length (distance to tree). However, at the place of the depressions no other species were present. The pneumatophore density or length in a large majority of quadrates studied consistently displayed the hypothesized trend in both depressions.

The results suggest that the grey mangrove *Avicennia marina* has the ability to adapt its root complex to micro-topographical irregularities in the otherwise regularly sloping intertidal zone. Although this study was carried out in Kenya, a review of recent literature indicates that it may apply to other mangroves dominated by *A. marina* worldwide, where pneumatophore density, pneumatophore density range or microtopography display similarities in absolute or relative values (Table 2). Yet, differences in root density as a result of micro-topographic differences have never been reported before. The hydrological regime in this study was as little as 15 cm higher than that for the surrounding mangrove soil. The mangrove species' adaptation to this localised topographic difference is important in view of changes in intertidal hydrodynamics, the latter of which is linked to changes in topography. Apart from individual adaptation, the effects on the regeneration of the entire populations also should be considered, as substratum heterogeneity has been found to influence the recruitment of *A. marina* (MINCHINTON 2001). Changing root complexes may alter their ability to entangle mangrove propagules directly, or indirectly through woody debris (STIEGLITZ & RIDD 2001, KRAUSS *et al.* 2005).

From a human impact or management perspective, the observed results are of importance and suggest that trees will react to the creation of topographical depressions or pneumatophore destruction, both of which may occur when people make their way through the mangrove on foot (Fig. 1D). Although we do not know at what time scale the difference in pneumatophore density and length have developed, or to which extent it can be found in other mangrove formations, it is evident that the influence of microtopography merits closer attention in the future, as it may be significant on other scales of the

Table 2. Recent peer-reviewed papers referring to variations in pneumatophore density for mangrove species or to the effects of micro-topographical differences (*A. mar* = *Avicennia marina*; *B. gym* = *Bruguiera gymnorrhiza*; *R. api* = *Rhizophora apiculata*; *S. alb* = *Sonneratia alba*; *X. gra* = *Xylocarpus granatum*; n.a. = not available).

Height above datum	Pneumatophore density (number/m^2)	Species	World region	Reference
1 to 3 m	4 - 1950	*A. mar*	Kenya	Dahdouh-Guebas *et al.* (2004a)
n.a.	80 - 180	*A. mar*	Mozambique	Macia *et al.* (2003)
n.a.	56 - 1168	*A. mar*	Pakistan	Saifullah & Elahi (1992)
n.a.	200	*A. mar*	QLD, Australia	Laegdsgaard & Johnson (2001)
n.a.	*ca.* 65 - 80	*A. mar*	QLD, Australia	Skilleter & Warren (2000)
n.a.	24 - 347	*A. mar*	QLD, Australia	Harty & Cheng (2003)
n.a.	382 - 718	*A. mar*	NSW, Australia	Bishop *et al.* (2007)
6 to 13 m	389 - 1040	*A. mar*	NSW, Australia	Melville & Pulkownik (2007)
n.a.	*ca.* 20 - 85	*A. mar*	NSW, Australia	Kelaher *et al.* (1998)
n.a.	50 - 381	*A. mar*	NSW, Australia	Burchett *et al.* (1999)
n.a.	*ca.* 40 - 250	*A. mar*	New Zealand	Young & Harvey (1996)
n.a.	80 - 200	*A. mar*	New Zealand	Alfaro (2006)
-50 to +10 cm	n.a.	*B. gym* *R. api* *S. alb* *X. gra*	Micronesia	Fujimoto *et al.* (1995)

mangrove ecosystem as well (*e.g.*, vegetation structure, dispersion processes). In addition, the strength and density of the root complex of mangrove trees is worth focusing on in the light of their ability to protect coastal areas from human, meteorological and oceanographical hazards (Badola & Hussain 2005, Dahdouh-Guebas *et al.* 2005a,b). Not only for *Avicennia* spp., but also for other mangrove species there is a lack of studies relating micro-topography (rather than intertidal position and intertidal height above datum) to vegetation characteristics. We recommend that more research be focused on the interrelationships between hydrodynamics, topography and vegetation, particularly the effects of water on the mangroves' root complex, and the effect of the mangrove root complex on the water currents and on a wide range of water-related impacts, among which storm surges, sea-level rise, daily tidal action, heavy El-Niño rains and tsunamis.

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