Stressor Elements Inhibiting Natural Mangrove Regeneration along Coastlines in the Cross River Estuary, Nigeria

Ebigwai JK, Bassey, RA and Oden, GN

Department of Plant and Ecological Studies, University of Calabar, Nigeria

Abstract

The planned Assisted Regeneration Programs (ARP) in the Niger Delta is dependent on accurate profiling

of the various indigenous stressor elements inhibiting natural regeneration in the area. Twelve permanent plots established under the influence of tidal regimes for stressor elements identification were maintained for this study spanning 2016-2017. Previously altered hydrological channels were redesigned as to emptying deposits on adjoining tidal flats thereby ensuring propagule availability. Six plots had an altitude of 10m above mean sea level while the other six had less than 10m. Three plots in each group separated by altitudinal character were subjected to bi weekly removal of siltation caused by tidal regime and wave influences. The number of propagules deposited and the number germinated in each of the four groups were studied About 75.24% of the total propagule deposited for the period were observed in plots with lowered altitude while 59.1% of mangrove re growth was noted for plots where siltation removal was conducted irrespective of altitudinal discrimination. When the results were subjected to correlation analysis, the results showed a 0.71 R² between siltation removal influencing propagule regeneration than altitude differentials. The study concludes by asserting that silt deposition on the coastlines is the basic factor hindering natural mangrove regeneration in the Kwa River area of Nigeria's Niger Delta region.

Key words : Kwa River, mangrove regeneration, Niger Delta, stressor elements, siltation.

Background

The offering of various ecosystem services played by an array of indigenous mangrove species in Nigeria and the world over is currently being threatened by multifaceted factors. Factors least mentioned and addressed include propagule predation, propagule dormancy, pollinators risk/decline and regeneration capacities, amongst others. Since mangrove forests are classified based on the predominance of salt tolerant species, decline rate in species diversity and abundance caused by whatever factor(s) shrinks the mangrove habitats correspondingly. Factors decimating mangrove species in Nigeria differ significantly across spatial and temporal gradients. For instance, while the activities of oil exploration are the main drivers of mangrove species loss in Delta, Bayelsa, Rivers and Akwa Ibom states (Akani et al., 2018), the same cannot be said as the overarching criterion for its loss in Cross River state in particular. Mangrove belts are found along the shorelines bordering some communities in Bakassi, Akpabuyo, Calabar South, Calabar Municipality and Odukpani LGAs of the state, where oil exploration is minimal at

best. In fact, mangrove loss has continually been reported in areas where oil exploration and pipeline Right of Way (RoW) is virtually absent. The absence of hydrocarbon in the soil water and sediment samples in these mangrove areas is a further testimony that flooding regimes from the oil polluted zones do not overlap yet there are reported mangrove loss. Several assisted mangrove regeneration programs had failed in Africa (Suding, 2001), Asia (Brown et al., 2014) and in the Americas (Primavera and Esteban, 2008) due to paucity of knowledge on the underlying causal factors hindering natural regeneration processes. Altitude, flooding regime and wave actions, as well as alteration of normal hydrology, were later determined as basic parameters that hindered the progress of the various assisted mangrove programs. It was reported that these factors act either in synergy or solely (López-Portillo et al., 2017). The capital outlay for these failed programs was on the average fifty times (personal communication) in excess of what was eventually spent on removing the natural stressor elements years after the assisted programs had failed. In Africa, where funding for scientific enterprise is not only limited but viewed as waste, such colossal capital drain would foreclose any future endeavours in that direction. Similarly, embarking on a mangrove restoration operation without determining the identity of natural stressor elements indigenous to it would inadvertently crash. The mangrove ecosystem in Nigeria's Niger Delta is shrinking (Akani et al., 2018) prompting unending agitations and sometimes violent confrontation by local communities on multinational oil giants and on the Nigerian government. A fall out of these age long pent-up emotions is the proposals by the Nigerian government, backed by multinational oil corporations, to commence phase restoration exercises beginning with the Ogoni Oil Spill Clean Up program. It is imperative that a comprehensive and co-ordinated research work detailing localized natural stress factors in each area be documented in advance of this initiative. This would not only aid the success of the program, it would also ensure tailor-made approach and the associated value-chain advantages to each restoration environment. It is based on the foregoing that this research is conceived, to determine the indigenous stressor elements operating in the Kwa River axis of the Cross River Estuary.

Study Area

The Calabar Estuary also known as the Great Kwa Estuary is about 20km wide and 50km long and stretches from Oron on the west bank, through Parrot Island and Calabar, on the central flank down to Ikang and Bakassi in the east bank, bordering Cameroon. The twelve permanent plots are shown in Fig 1.

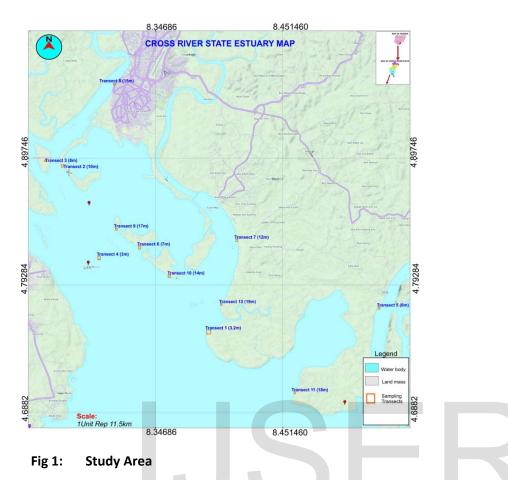


Table 1 provides plot dimension in the form of co ordinates

latitude	longitude	Plot
4.759484	8.3864152	SP 1 (3.2m)
4.756233	8.3864152	
4.756319	8.3900201	
4.759655	8.3898485	
4.759484	8.3864152	
4.891906	8.2699135	SP 2 (10m)
4.891735	8.268154	
4.893745	8.2681325	
4.893958	8.2698277	
4.891927	8.2699564	
4.897609	8.2542716	SP 3 (8m)
4.896353	8.2542984	
4.896353	8.2553874	
4.897651	8.2553284	

Table 1: Plots Co ordinates

4.897625	8.254277		
4.819654	8.2979389	SP 4 (3m)	
4.816747	8.2979818		
4.816779	8.2999774		
4.819729	8.2998487		
4.819676	8.2979926		
4.778221	8.5277487	SP 5 (6m)	
4.776489	8.5277272		
4.776511	8.5263754		
4.778221	8.5263754		
4.778179	8.5277272		
4.82786	8.3327784	SP 6 (7m)	
4.825433	8.3327999		
4.825519	8.3309116		
4.827914	8.3309438		
4.827882	8.3327248		
4.833458	8.4103404	SP 7 (12m)	
4.83148	8.4103619		
4.83148	8.4121214		
4.833458	8.4120999		
4.833468	8.4103511		
4.96021	8.3104045	SP 8 (15m)	
4.958371	8.3104045		
4.958307	8.3119709		
4.960103	8.3120353		
4.96021	8.3104045		
4.842583	8.3122995	SP 9 (17m)	
4.840701	8.3122781		
4.840701	8.3136943		
4.842433	8.3136514		
4.842433	8.312321		
4.709349	8.4590602	SP 11(18m)	
4.709371	8.4577298		
4.707767	8.4577298		
4.707735	8.4591031		
4.709339	8.459087		
4.781017	8.3980601	SP 12(19m)	
4.77952	8.3980494		
4.779466	8.3994549		

4	1.780974	8.3994334
4	1.781017	8.3980923

The study area is a characteristic Bar-built Estuary comprising about nine barrier islands with thin meandering inlets to the open sea. The area is characterized by semi-diurnal tides and extensive mud flats. The reworked deposited sediments on the tidal flats comprised mainly of oyster shells, periwinkles and clastic debris. The dominant and most frequent mangrove genus is Nypa, with Avincinnia, Rhizophora, and Laguncularia in that order making up the remainder. Table 2 provide details on each plot.

Plot	Altitude (m)	Dominant flora	Sediment estimation	Flooding episode	and duration
1	1.8	Nypa, Rhizophora	Moderate sediment load	HT& MT	8hrs/day
2	0.8	Rhizophora & Nypa	Rich sediment load	HT, MT <	17hrs/day
3	1.3	Nypa, Rhizophora &	Rich sediment load	HT, MT <	14 hrs/day
4	0.3	Rhizophora, Avincinnia	Rich sediment load	HT, MT <	24hrs/day
5	1.1	Rhizophora, Avincinnia 15hrs/day	, Laguncularia & Nypa	Rich sediment loa	ad HT, MT <
6	0.6	Rhizophora & Nypa	Rich sediment load	HT, MT <	15hrs/day
7	3.2	Nypa	scanty sediment load	НТ	5 hrs/day
8	2.6	Nypa & Avincinnia	scanty sediment load	НТ	6hrs/day
9	2.1	Nypa & Rhizophora Laguncularia	Moderate sediment load	HT & MT	8 hrs/day
10	3.9	Nypa	Moderate sediment load	HT& MT	8hrs/day
11	3.6	Nypa	scanty sediment load	НТ	4hrs/day
12	2.9	Nypa & Rhizophora & Nypa	scanty sediment load	HT	6hrs/day

Table 2: Phyto-geomorphological Characteristics of Studied Permanent Plots

* Scanty sediment load - 1-10kg/day; Moderate sediment load - 10.1-20kg/day and Rich sediment load ->20kg/day; LT - Low Tide; MT-Mid Tide and HT-High Tide

sticks, logs, empty cans, plant parts and animal carcasses constitute significant part of the waste streams deposited onshore. The tidal regime oscillates every six hours between flooding and ebbing sequences with the concomitant impact on the water holding capacity of the mangrove forests. As described in Table 1, it is either the studied plots were completely inundated with flooded water all day round giving rise to permanently flooded forests or do so periodically leading to partially flooded forests corresponding to High and Mid tidal patterns. In others, the forest becomes flooded only during peak period of flooding.

Plots Design

> Barricaded study plots measuring $100 \times 100m^2$ each were split into groups of two (0 -10 m for group 1 and >10m for group 2) using altitude as the discriminatory index. Plots 1,2,3,4, 5and 6 were categorized as Group 1 while plots 7, 8,9,10,11 and 12 were categorized as Group 2. Table 3 showed plots

belonging to sub groups 1A and 2A were cleared fortnightly of siltation materials as against plots belonging to sub group 1B and 2B that were left un cleared for the first twelve calendar months of the research. In the subsequent twelve calendar months of the research work, plots belonging to sub groups 1B and 2B were cleared fortnightly of siltation materials while plots belonging to sub groups 1A and 2A were left un cleared.

Group	Sub	Plots	Experimental Variables
-	Group		
Experim	nental Desigr	n for First Year	
1	1A	1,4 & 6	Cleared of siltation materials
	1B	2,3 & 5	Left un cleared of siltation materials and hence
			served as control sites
2	2A	8,10 &12	Cleared of siltation materials
	2B	7,9&11	Left un cleared of siltation materials and hence
			served as control sites
Experimental Design for Second Yea		n for Second Ye	ar
1	1A	1,4 & 6	Left un cleared of siltation materials
	1B	2,3 &5	Cleared of siltation materials and hence served as
			control sites
2	2A	7,9&11	Left un cleared of siltation materials
	2B	8,10 &12	Cleared of siltation materials and hence served as
			control sites

Table 3 : Experimental Design

As a quality assurance measure, all plots were cleared of propagules and any standing biomass. During the study, parameters studied and manually enumerated were number of propagules deposited and numbers germinated. The experiment was conducted between April 2016 and March 2018. Correlation analysis was **used** to determine degree of siltation influence on propagule *stranding*.

Results and Discussion on number of propagules deposited

A total of 4,810 and 3,832 propagules were deposited across all the plots during the first and second year respectively. Propagules of *Nypa fructicans* contributed about 30% to the deposit record, as against those of *Rhizophora, Avincinnia* and *Laguncularia,* which contributed 24%, 23% and 22% respectively (Table 4).

Table 4 : Species and Propagule depositional r	record
--	--------

Sub	Plot	Total Number of	Propagule	Propagule
Group		propagules	Туре	Abundance
		deposited 1st year		First year
		(2nd year in		(2nd year in
		bracket)		bracket)
1A	1	654 (224)	Nypa	163 (54)
			Rhizophora	287 (91)
			Avincinnia	109 (42)

			Laguncularia	95 (37)
	4	1038 (308)	Rhizophora	369 (99)
			, Nypa	363 (76)
			Laguncularia	255 (68)
			Avincinnia	51 (65)
	6	756 (297)	Rhizophora	247 (74)
	· ·		Лура	198 (88)
			Laguncularia	157 (46)
			Avincinnia	154 (89)
1B	2	456 (599)	Laguncularia	177 (201)
10	-	100 (000)	Avincinnia	134 ((141)
			Rhizophora	75 (76)
			Лура	70 (82)
	3	348 (763)	Laguncularia	164 (290)
	5	310(703)	Avincinnia	89 (211)
			Rhizophora	56 (205)
			Nypa	39 (147)
	5	401 (658)	Avincinnia	194 (241)
			Laguncularia	107 (166)
			Rhizophora	69 (145)
			Nypa	31 (116)
2A	8	323 (104)	Rhizophora	128 (34)
			Nypa	106 (43)
			Avincinnia	89 (27)
	10	208 (78)	Nypa	176 (51)
			Laguncularia	28 (14)
			Rhizophora	4 (13)
	12	315 (109)	Rhizophora	97 (32)
			Avincinnia	84 (28)
			Nypa	68 (30)
			Laguncularia	66 (20)
2B	7	53 ((145)	Nypa	53 (98)
			Laguncularia	0 (47)
	9	189 (346)	Nypa	143 (238)
			Avincinnia	46 108)
	11	69 (201)	Nypa	48 (124)
			Avincinnia	21 (77)

The preponderance of Nypa propagules in the depositional record could have been influenced by a plurality of factors. First, it attest to its abundant population, as about two-fifth of the area was observed to be covered with *Nypa fructicans*, a position that found support in Asuk et al 2018 and Osabor et al 2008. Second, altitudinal regime above 10m seems an unfavourable element for *Rhizophora* and *Avincinnia* propagule emplacement. The propagules of red and white mangroves were observed deposited in two of the six plots with altitude above 10m as against that of *Nypa* and *Laguncularia* propagules that were observed in all and five plots respectively. On the contrary, while all four mangrove genera propagules were observed in all plots with altitude less than 10m, *Rhizophora*

and Avincinnia recorded the highest propagule deposition. The relationship between elevation and vegetation dynamics in mangrove ecosystems was shown by Krausss et al 2014 while Stocken et al 2019 ascribed density, size and shape of propagule as dispersal properties influencing extent, Petterson and Bell 2015 on the other hand correlated the influence of differential tidal actions to propagule establishment and stranding. Satyanarayana et al 2010 related distribution of Sonneratia caseolaris, Nypa fruticans, Avicennia alba, Rhizophora mucronata, and Bruquiera gymnorrhiza in part to elevation. Morpho-anatomical features of each mangrove propagule are probably critical barrier factors in overcoming elevation gradients for efficient establishment. Weight (Rabinowit 1978a), shape (Dennis et al 2012) and size (Dennis et al 2012). Propagules floating period, floating organ, obligate dispersal period, rooting period and capacity of sinking and re floating are other hydro dynamic features suggested by Rabinowit 1978b governing mangrove deposition. The relative light weight of Nypa and Laguncularia (0.62 and 0.41gm respectively) propagules coupled with excellent buoyancy features could explain their ability to overcome elevation barriers and establish dominance on higher elevations. On the other hand, ranges of 1.12-1.14gm and 34.37-29.01gm measured for the propagule weights of 100 samples each of Avincinnia and Rhizophora could explain in part the tidal regime's inability to efficiently overcome elevation gradients beyond 2m for their deposition.

Result and Discussion on Number of established and rooted Propagules

Table 5 revealed that about 34.51% of propagules established stranding in sub plots 1A and 2A (plots that were cleared of siltation as against 23.48% in plots 1B and 2B (control plots) in the first year. In the second year, 29.76% of the deposited propagules established stranding in plots 1B and 2B (plots cleared of siltation materials) as against 23.13% in plots 1A and 2A that were left un cleared.

Group	Sub	Plots	Experimental Variables
	Group		
	Resul	ts for First Year	
1	1A	1,4 & 6	245, 159, 188
	1B	2,3 & 5	49, 79, 52
2	2A	8, 10 & 12	216, 202, 127
	2B	7,9&11	44, 73, 59
Result for Second Year			r
1	1A	2,3 & 5	43, 51, 58
	1B	1,4 & 6	190, 146, 125
2	2A	7,9&11	49, 36, 22
	2B	8, 10 & 12	118, 107, 121

Table 5: Results on rooted and established propagules

The results clearly indicate two findings. First, the inability of about 70% of propagules to establish rooting in both growing seasons is due to factors exogenous to siltation. Second, siltation in the plots hindered propagules stranding.

First, the number of un-rooted and rooted propagules in all the plots does not add up. The loss could be attributed to predation and upsurge in tidal energy regime. Similar studies in Ibianga 1985 and Brown 1984. Factors inhibiting stranding and rendering about half of the deposited propagules non viable is unknown as there exists no morphological aberration or deformities. The suggestion of edge effects espoused by Peterson 2012 often created by mangrove-saltmarsh boundaries could be a critical factor. Edge effects had been shown to have induced habitat fragmentation (Lawrence et al 2007), species fragmentation (Essen and Renhorn 1998) and promoted fertile loci points for invasive and alien species proliferation (Holway 2005). The clustering of un-rooted propagules at several land ward gradients across the plots gives further credit to this suggestion. These areas would expectedly be exposed to salinity and nutrient levels outside the optimum ranges required for stranding establishment. It is highly probable also that all deposited propagules do not exhibit same maturation levels and hence hinders stranding. Success of seedling establishment has been shown as dependent on the maturation state of the seed (Locascio et al 2014). Stress-induced phenomenon such as tidal and wave actions, wind and biotic interactions often result in the shedding of immature propagules (personal field observation). Some of the biotic interplays include mammal- avian interactions with the propagules, microbial infestation, insect pest damages and physiologic disorders.

Second, the high energy environment of the Calabar coastline is well documented (Emeke et al 2010) resulting in huge continuous stream of sediment deposit. Removals of massive silt build up in the plots fortnightly encouraged mangrove stranding by about 9%. The importance of siltation in preventing propagule establishment is aptly demonstrated in the results obtained when plots without silt removal were reversed with those with silt removal. Siltation in the form of overburden hinders mangrove rooting by exerting huge un surmountable compressive stress on the propagule (Niklas 1992) thereby preventing propagule imbibitions to activate growth enzymes and in some instances where the latter process is achieved, chokes the developing epicotyls due to non availability of radiant energy. Preventing siltation by opening up blocked channels and regulated sand mining would likely improve natural regeneration. This remedial approach would undoubtedly address the intrinsic native challenges experienced in plot 4 where a statistically significant difference was observed between it and other plots exposed to same ecological challenge.

When data on siltation influence was subjected to correlation analysis, a 0.72 coefficient was obtained, implying siltation as an influencing factor for stranding success.

Conclusion

Altitude was observed as a determining factor in influencing propagule deposition whiles silt removal was found to contribute significantly to mangrove stranding just as other intrinsic factors such as alteration of normal hydrology could be other over arching factor hindering propagule establishment in the Calabar Estuary.

Recommendation

A detailed study on the influence of hydrology alteration to mangrove stranding should be undertaken before embarking on the planned assisted regeneration program.



Acknowledgement

Our appreciation goes to our post graduate students and Adiabo community.

References

Akanni, Adeniran & Onwuteaka, John & Uwagbae, Michael & Mulwa, Richard & Elegbede, Isa. (2018). The Values of Mangrove Ecosystem Services in the Niger Delta Region of Nigeria. 10.1016/B978-0-12-809399-3.00025-2.

Asuk, Sijeh & Nchor, Atim. (2018). Challenges of Community-based Ecotourism Development in Southern Eastern Nigeria: Case Study of Iko Esai Community. Journal of Scientific Research and Reports. 20. 1-10. 10.9734/JSRR/2018/42603.

Brown, B., Fadillah, R., Nurdin, Y., Soulsby I. and Ahmad, R (2014). CASE STUDY: Community Based Ecological Mangrove Rehabilitation (CBEsMR) in Indonesia, 7(2). Brown, M. S. Mangrove litter production and dynamics. 1984. The mangrove ecosystem. Research methods monograph on oceanographic methodology, (231-238).

Denis. J. R., E. 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

Emeka, Chimezie & Emeka, Victoria & J. Ukpong, A & A. Amah, E & , Ntekim & E. U., E. (2010). A Study on the Sedimentology of Tidal Rivers: Calabar and Great Kwa, S. E. Nigeria. European Journal of Scientific Research. 47. 370-386.

Esseen, Per-Anders & Renhorn, Karl-Erik. (1998). Edge Effects on an Epiphytic Lichen in Fragmented Forests. Conservation Biology. 12. 1307 - 1317. 10.1111/j.1523-1739.1998.97346.x.

Holway, D. A. (2005). Edge effects of an invasive species across a natural ecological boundary. Biological Conservation. 121. 561-567. 10.1016/j.biocon.2004.06.005.

Ibianga, M. S. (1985). Management objective for mangrove forest in Nigeria, pp. 88-93. In: The mangrove ecosystem of the Niger-Delta. B.H.R. Wilcox and C.B. Powell (editors). University of Port Harcourt Press, 357 p.

Krauss, K., K. McKee, C. Lovelock, D. Cahoon, N. Saintilan, R.Reef, and L. Chen. 2014. How mangrove forests adjust torising sea level. New Phytologist 202:19–34.

Laurance WF, Nascimento HEM, Laurance SG, Andrade A, Ewers RM, Harms KE, et al. (2007) Habitat Fragmentation, Variable Edge Effects, and the Landscape-Divergence Hypothesis. PLoS ONE 2(10): e1017. https://doi.org/10.1371/journal.pone.0001017.

Locascio, A. Roig-Villanova, I. Bernardi, J. and Varotto S. (2014). Current perspectives on the hormonal

control of seed development in Arabidopsis and maize: a focus on auxin. Front Plant Science, 5(1).

López-Portillo, Jorge & Lewis, Roy & Saenger, Peter & Rovai, A & Koedam, Nico & Dahdouh-Guebas, Farid & Agraz, Maricusa & Rivera-Monroy, Victor. (2017). Mangrove Forest Restoration and Rehabilitation. 10.1007/978-3-319-62206-4_10.



Niklas KJ (1992) Plant biomechanics: an engineering approach to plant form and function. The University of Chicago Press, Chicago protection: experience of the recent Indian Ocean tsunami. Landscape Ecol Eng 3:33–45

Niklas, K.J. (1992) Plant Biomechanics. An Engineering Approach to Plant Form and Function. University of Chicago Press, Chicago.

Osabor, V.N. & Egbung, Eneji & Okafor, Peter. (2008). Chemical Profile of Nypa fruiticans from *Cross River Estuary, South Eastern Nigeria*. Pakistan Journal of Nutrition. 7. 10.3923/pjn.2008.146.150.

Peterson JM, Bell SS (2015) Saltmarsh boundary modulates dispersal of mangrove propagules: Implications for mangrove migration with sea-level rise. Plos One, 10, 15.

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

Primavera, H. J & M. A. Esteban, J. (2008). A review of mangrove rehabilitation in the Philippines: Successes, failures and future prospects. Wetlands Ecology and Management. 16. 345-358. 10.1007/s11273-008-9101-y.

Primavera, J. H. and Esteban, J. M. A (2008). A review of mangrove rehabilitation in the Philippines: successes, failures and future prospects.

Rabinowitz, D., 1978a. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. J. Biogeogr. 5, 113–133

Rabinowitz, D., 1978b. Dispersal properties mangrove propagules. Biotropica 10, 45–57

Robert D., Schmitz, N.; Van der Stocken, T.; Nitto, D.D.; Dahdouh-Guebas, F.; Koedam, N. (2012) Size does matter, but not only size: Two alternative dispersal strategies for viviparous mangrove propagules. Aquat. Bot., 103, 66–73.

Satyanarayana B, Idris IF, Mohamad KA, Husain ML, Shazili NA & Dahdouh-Guebas F (2010) Mangrove species distribution and abundance in relation to local environmental settings: a case-study at Tumpat, Kelantan Delta, East coast of peninsular Malaysia. Botanica Marina 53(1): 79–88.

Suding, K. N., (2011). Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. Annu. Rev. Ecol. Evol. Syst. 42:465–87.

Van der Stocken, Tom & Carroll, Dustin & Menemenlis, Dimitris & Simard, Marc & Koedam, Nico. (2019). Global-scale dispersal and connectivity in mangroves. Proceedings of the National Academy of Sciences. 116. 201812470. 10.1073/pnas.1812470116.

Van der Stocken, Tom & De Ryck, Dennis & Balke, Thorsten & Bouma, Tjeerd & Dahdouh-Guebas, Farid & Koedam, Nico. (2013). The role of wind in hydrochorous mangrove propagule dispersal. Biogeosciences. 10. 3635-3647. 10.5194/bg-10-3635-2013.