Sains Malaysiana 51(8)(2022): 2351-2364
*http://doi.org/10.17576/jsm-2022-5108-02*

# Spatiotemporal Dispersal Study of Mangrove *Avicennia marina* and *Rhizophora apiculata* Propagules

(Kajian Penyebaran Spatiotemporal Propagul Pokok Bakau *Avicennia marina* dan *Rhizophora apiculata*)

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*Received: 30 August 2021/Accepted: 9 February 2022*

## ABSTRACT

The propagule dispersal pattern of the two common mangrove species, *Avicennia marina* (Forsk.) Vierh. and *Rhizophora apiculata* Blume at a mangrove fringed coast, in the southwest tip of Penang Island was examined. Propagule dispersal study of both species were carried out by release and recapture method, while early developments of propagule were observed by an on-site tethering system. *A. marina* propagules recorded higher dispersal rate as compared to *R. apiculata*. After 60 tidal cycles, almost all propagules had moved away from the initial release site under the influence of strong wave current. The *A. marina* propagules were observed to grow better and faster than the *R. apiculata* propagules. However, the propagules of both species eventually failed to establish at the study site due to strong wave effect as well as unfavourable soil condition. *A. marina* and *R. apiculata* were found to adopt different strategies in propagule dispersal and early growth. *A. marina* was notably better adapted to thrive in the coastal environment. In a similar open coastal area, wave current and soil condition are suggested to be the most critical factors affecting the mangrove propagule dispersal and early establishment.

Keywords: *Avicennia marina*; dispersal; mangrove; propagule; *Rhizophora apiculata*

## ABSTRAK

Corak penyebaran propagul dua spesies bakau yang biasa dijumpai iaitu *Avicennia marina* (Forsk.) Vierh. dan *Rhizophora apiculata* Blume di pinggir pantai bakau pada hujung barat daya Pulau Pinang telah diteliti. Kajian penyebaran propagul kedua-dua spesies ini dilakukan dengan kaedah tangkap, lepas dan tangkap semula. Sementara itu, perkembangan awal corak penyebaran diperhatikan dengan menggunakan sistem pengikatan di tapak. Propagul *A. marina* mencatatkan kadar penyebaran yang lebih tinggi berbanding dengan *R. apiculata*. Setelah 60 kitaran pasang surut, hampir semua propagul telah disebarkan dari tempat pelepasan awal di bawah pengaruh gelombang yang kuat. Propagul *A. marina* diperhatikan tumbuh lebih baik dan cepat daripada *R. apiculata*. Walau bagaimanapun, kedua-dua spesies tersebut akhirnya gagal bertapak di lokasi kajian disebabkan oleh kesan gelombang yang kuat dan juga keadaan tanah yang kurang sesuai. *A. marina* dan *R. apiculata* didapati menggunakan strategi yang berbeza untuk menyebarkan propagul dan pertumbuhan awal. *A. marina* beradaptasi dengan lebih baik untuk bercambah di tepi pantai. Di kawasan pantai yang terbuka, arus gelombang dan keadaan tanah disarankan menjadi faktor paling kritikal dalam mempengaruhi penyebaran propagul bakau dan percambahan awal.

Kata kunci: *Avicennia marina*; bakau; penyebaran; propagul; *Rhizophora apiculata*

## INTRODUCTION

Malaysia is endowed with rich diversity of mangroves. There are around 41 true mangrove species found, which ranked Malaysia second after Indonesia (FAO 2007). In Penang Island, mangrove vegetation was mainly distributed along the intertidal zone on the west coast, providing important ecological, physical and economical services (Penang State Government & DANCED 1998). However, the mangrove forests were undervalued and regarded as wasteland in the early days and largely reclaimed for agriculture, aquaculture and urbanisation developments (Ismail et al. 2001; UPEN & DANCED 1999). A report of year 1999 estimated that Penang state has lost 60% of its mangrove area since 1950s, with a decreasing rate of 1.2% per annum (UPEN & DANCED 1999). Macintosh and Ashton (2002) reviewed the worldwide mangrove conservation and management effort and concluded that there was still lack of information in many aspects. One of the areas that needs improvement is on the mangrove autecology (individual species ecology), which primarily involves the studies of species establishment and distribution (Lewis 2009; Lewis et al. 2006). As an effort to better understand the distribution and abundance of a species, it is vital to first examine its dispersal and early growth in a defined environmental setting (Aguiar & Sala 1997; Bolker & Pacala 1999; Bullock et al. 2006; Ehrlén & Eriksson 2003). Plant dispersal is referring to a stage where the propagating organs (fruit or seed) abscised from the parent trees, then moved by the dispersal agent (wind, water or animal) until they reach a suitable location for further establishment (Kellman 1975). In mangrove ecosystem, dispersal determines the distribution and abundance of a particular species from the perspective of propagule supply (Clarke 1993; Delgado et al. 2001; Duke et al. 1998; McGuinness 1997; Minchinton 2001; Rand 2000; Rabinowitz 1978b; Sengupta et al. 2005). Colonisation of a new environment is basically dependent on the availability and successful dispersal of propagules to the site (Ball 1980; Panapitukkul et al. 1998). The relation of propagule dispersal and zoning phenomenon of mangrove distribution is well explained by the Rabitnowitz's tidal sorting hypothesis (Rabinowitz 1978b). However, the hypothesis has been challenged by the subsequent observations (Clarke et al. 2001; Sousa et al. 2007), and more were agreed on the suggestion that tidal was one of the many factors that influence the spatial variation of species (Allen et al. 2003; De Ryck et al. 2012; McKee 1995; Rand 2000; Van der Stocken et al. 2019).

Mangrove trees produce water-dispersed propagules which are prematurely germinated under a phenomenon called vivipary or crytovivipary (Rabinowitz 1978a; Tomlinson 1986). Early growth of a propagule is indicated by the development of root system and production of shoot, and these can occur in the dispersal stage (Clarke et al. 2001). Initiation of root and shoot facilitates the establishment of a propagule at the stranding site (De Ryck et al. 2012; Rabinowitz 1978a). According to Saenger (2002), the propagules that have firmly rooted and possessed at least one leaf are considered fully established. Before the propagules can successfully establish, their survival is threatened by various factors, including pre- and post-dispersal predations (Farnsworth & Ellison 1997; Robertson et al.1990; Smith III 1987; Smith III et al. 1989), environmental stresses such as wave current (Clarke & Myerscough 1993; McKee 1995; McMillan 1971), soil condition (Clarke & Myerscough 1993; De Ryck et al. 2012; McGuinness 1997) and sedimentation (Delgado et al. 2001; Jurik et al. 1994; Terrados et al. 1997).

The study of propagule dispersal and early growth of mangrove plant species emphasises on the environmental influences particularly water quality, substrate condition, tidal position and wind effect (Clarke 1993; Duke et al. 1998). *In situ* study of mangrove propagule dispersal is sparse due to difficulty in tracing the movement of propagules in the intertidal zones (Van der Stocken et al. 2019). Only a handful of studies managed to cover several mangrove species, including *Rhizophora mangle* (Davis 1940; Sengupta et al. 2005; Sousa et al. 2007), *Kandelia candel* (Yamashiro 1961), *Rhizohpora mucronata* (Chan & Husin 1985; De Ryck et al. 2012; Komiyama et al. 1992), *Avicennia marina* (Clarke 1993), *Ceriops tagal* (De Ryck et al. 2012; McGuinness 1997), *Avicennia germinans* and *Laguncularia racemosa* (Sousa et al. 2007). Similarly, field investigation of propagule post-dispersal early growth was also limited, mostly confined to the New World species (Delgado et al. 2001; McMillan 1971; Rabinowitz 1978c; Sousa et al. 2007) and Australia (Clarke 1995; Clarke & Allaway 1993; Clarke & Myerscough 1993; McGuinness 1997; Minchinton 2001).

More research should be carried out in the Old World mangrove forests to heighten efforts for conservation in this area. One of the widely found species in Malaysia is *Rhizophora apiculata*, and it is also the preferred species used in restoration project for conservation and economical purposes (Chan et al. 1993). Their viviparous propagules are about 30 cm long and rod-like in shape with one end being the plumule and another end the radical (Drexler 2001; Kathiresan & Rajendran 2002). Another species is *Avicennia marina*, a pioneer that is widely distributed in the coast of tsunami affected countries. They bear greyish-green propagules that are almond size and slightly furry with short pointed apex. These propagules are cryptoviviparous which consist of a germinating embryo encased in pericarp upon maturity (Tomlinson 1986). In Malaysia, *R. apiculata* is mainly found in low energy estuaries, while *A. marina* grows in sea facing area (Chapman 1976). In the present study, we examine the *in situ* propagule dispersal and early growth properties for these two common yet important species.

## MATERIALS AND METHODS

A coastal mangrove fringe situated in the Southwest coast of Penang Island, Malaysia was selected as the study site (5° 18' N, 100° 11' E) (Figure 1). This area is located at the southern tip of a long stretch of mangrove forest that grows on the western coast facing the Straits of Malacca. The place is adjacent to the river mouth of Sungai Pulau Betong (Kuala Pulau Betong). At this site, soil type changes from sandy (sandy shore) to muddy (mud flat) with decreasing elevation. The surface soil from sandy zone contained 97% of sand, while for the muddy zone contained 96% of silt (Wong et al. 2020). Such topography is subjected to wave action (Chapman 1976), and it is common along the coast of Penang Island (personal observation). There are semidiurnal tides with the mud flat being flooded almost every day, but the upper sandy shore is only inundated during spring tide. For the local mangrove species, the season of propagule dispersal was roughly from May to September with a peak around July (personal observation). The field experiment was conducted coincide with the propagule dispersal season. Our study area covered a distance of approximately 500 m parallel to the intertidal shoreline.

Collection of propagules was carried out three days earlier before the experiment. Matured *A. marina* propagules were collected from the mangrove forest in Pantai Acheh, Penang Island (5° 24' N, 100° 11' E). However, insufficient number of ripe *R. apiculata* propagule were found at the same collection site. Therefore, *R. apiculata* propagules were collected in the Matang Mangrove Forest Reserve, Perak (4° 50' N, 100° 38' E). Matured propagules were picked directly from the trees to prevent osmotic effect from exposure to tidal water. These propagules were randomly harvested from different fruiting mangrove trees. The selected propagules of *A. marina* had a mean weight 1.37±0.02 g, mean length 2.05±0.01 cm and mean width 1.33±0.01 cm. As for the propagules of *R. apiculata*, the mean weight and size (length and diameter) were 24.32±0.31 g, 25.68±0.23 cm and 1.42±0.01 cm, respectively. A total of 160 propagules were selected for each species. *R. apiculata* propagules were marked with a thin coat of aerosol spray paint (ANCHOR, DPI Malaysia) on the exterior of hypocotyls, whereas the tiny *A. marina* propagules were sewed through their cotyledons without damaging the embryo with fishing lines of 0.25 mm diameter (speziline, OANYL). These markings were confirmed in a separate test earlier of not imposing significant effect on the propagules' buoyancy and development.

Release and recapture experiment was conducted during the spring low tide. A total of 80 marked propagules for each species were released at each of the two selected points: One within the sandy area and another within the muddy area. Tracing for the marked propagules was carried out during the daytime low tide after 1, 2, 4, 12, and 60 tidal cycles. The position of the recovered propagules was determined and recorded with a handheld GPS (GPSmap 60Cx, Garmin). The five censuses were coded as PS1(Day 1), PS2 (Day 2), PS3 (Day 3), PS4 (Day 7) and PS5 (Day 31). Propagule recovery rates of *A. marina* and *R. apiculata* were calculated for all the censuses from PS1 to PS5. The effects of both species and release location on the frequency of propagule recovery were then analysed by the Pearson Chi-square test. Based on the Haversine formula (Sinnott 1984), propagule dispersal distances were obtained from the recorded longitude and latitude coordinates. The mean dispersal distances were compared between species and release locations by employing non-parametric Mann-Whitney U test (SPSS 16.0). Distribution of propagule over the dispersal range was also examined. The direction of each dispersing propagule was calculated in angular degree based on the four main directions from the release point, which were 0 ° (north), 90 ° (east), 180 ° (south) and 270 ° (west). The seaward direction was about 310 ° from the release point, while the land is at the opposite direction with the intertidal shoreline extended to the northeast and southwest directions. From the calculated dispersal directions, the mean direction and circular variance were determined. The data were analysed with the Rayleigh's uniformity test and Watson-Williams F test (Fisher 1995). These circular statistics were run by the Oriana software (Kovach 2009). Dispersal speed was calculated through dividing the dispersal distance of a propagule by the number of tidal cycle. Mean dispersal speed of both species in the sandy and muddy zones was compared over the censuses. Other than that, propagule stranding location was also investigated. This experiment utilized tethering system to examine the post-dispersal processes of mangrove propagules (Allen et al. 2003; Clarke & Kerrigan 2002; Delgado et al. 2001; McGuinness 1997; Smith III 1987; Smith III et al. 1989). Tethering system was set up during the spring low tide on Day 29. A total of 32 propagules of each species were tethered randomly in each of the sandy and muddy zones. The propagules were tied to sets of tethering units which made up of wire string (each 0.3 cm diameter and 3 m long) and PVC pipes (each 2.5 cm diameter and 1 m long). For each unit, the wire string was held between two standing PVC pipes for allowing tethers of propagules. Fishing lines of 0.25 mm diameter and 30 cm long were carefully sewed through the cotyledons of *A. marina* propagule, and for *R. apiculata* the upper part of hypocotyls. The lines were used to fix the propagules to the wire string with a space interval of 30 cm between them. In each zone, there were a total of eight tethering units and each was loaded with eight propagules (four *A. marina* and four *R. apiculata*) which were placed prone on the ground and arranged in alternate species. The tethering units were randomly positioned with at least 20 m to each other. Physical condition, early development and mortality of each propagule were observed and recorded for a period of four months, with a total of ten field surveys. The censuses were coded as DC1 to DC10, respectively in the subsequent text. Only the propagules that were exposed could be investigated for their early growth and survival. The proportions of propagule that reached different stages of development as well as the mortality rates were calculated over time. The causes of mortality were identified and compared. The early growth of both species in the sandy and muddy zones was summarised in the form of total percentage, which was obtained by dividing the total number of propagules that achieved a particular developmental stage by the total number of tested propagules. These total percentages were converted into presence-absence data and then analysed by Pearson Chi-square test to compare the species and release location in each phase of early growth.

## RESULTS

The frequencies of propagule recovery were significantly different between *A. marina* and *R. apiculata* over the censuses except PS5 (Table 1). Conversely, no difference in propagule recovery was discovered between the two release locations. Figure 2 shows the species-specific rates of propagule recovery for the five censuses. The recovery rates of both species were found decreasing with time; and the recovery rates of *R. apiculata* propagule were always higher than the *A. marina* propagule. The highest propagule recovery rates were recorded in the first census (PS1) after experiencing one high tide (56% for *R. apiculata*; 13% for *A. marina*). Nonetheless, there were up to 69% of *R. apiculata* propagule and 97% of *A. marina* propagule lost within the first two days or after four spring high tides. In the last census (PS5), only a few *R. apiculata* propagules were found and none of the *A. marina* propagule was able to remain within the study area.

According to the results of Mann–Whitney U test (Table 2), the propagule dispersal distances differed between species for both release locations (except the sand area in PS2). Meanwhile, the dispersal distances of *R. apiculata* propagule varied between the release locations in PS1 and PS2, but no difference was detected in the following censuses. Apparently, the effect of release location on the dispersal distance of *R. apiculata* propagule was reduced over time. As for the *A. marina* propagules, no significant difference was found between the release locations from the two observations.

Figure 3 shows the frequency distribution of recovered *R. apiculata* and *A. marina* propagules in three categories of dispersal distances (0-10 m, 10-100 m and above 100 m) from their release points at sandy and muddy zones. Most of the recovered *R. apiculata* propagules traveled less than 10 m from both the release points (Figure 3(a) to (d)). Only until the last census (Figure 3(e)), the few remaining *R. apiculata* propagules were stranded within 10-100 m. In earlier observations (PS1 and PS2), the *R. apiculata* propagules from sandy area were more outspreading than those from muddy area. Compared to *R. apiculata*, the limited amount of recovered *A. marina* propagule showed a more widely spread pattern (Figure 3(f) to 3(i)). From PS2 to PS4, the *A. marina* propagules could only be traced at a distance of more than 10 m away from their origins. For both species, the changes of distance distribution through time were presenting a propensity of losing propagules from shorter to longer distance, which may lead to the dispersal out of study area.

Rayleigh's uniformity test showed that the directional movement of dispersing propagules was significant over the species, release locations and censuses (Table 3). The results indicated that the propagule dispersal direction was not uniformly distributed around the release point. Moreover, all the tested samples had variance (V) less than 0.60 and mostly (75%) less than 0.40 (Table 3). This reflected that the tested samples had small variations in dispersal direction. Accordingly, the dispersing propagules of both species moved in a particular direction and thus the mean angle of propagule dispersal could be determined.

Watson-Williams F test showed that the mean dispersal direction differed between the two species for both release locations ($P<0.05$). The mean direction of *A. marina* propagules was similar across the censuses and release locations (Table 3; Watson-Williams F test, $P>0.05$). Their mean angled correspond with the northeast direction, which runs parallel with the shoreline. As for the *R. apiculata* propagule, the pattern of dispersal direction was relatively complicated. The *R. apiculata* propagules from sandy source were distributed around north and northwest directions (seaward) while those from muddy source were distributed in the southeast direction (landward) for all censuses (Watson-Williams F test significant at $P<0.05$), except the observation in PS2 ($P=0.126$). However, after one-month period, all the remaining *R. apiculata* propagules were found in the northeast direction, like those of *A. marina*.

*Avicennia marina* propagules dispersed rapidly with average speed of exceeding 40 m per high tide. In PS2, the mean dispersal speed of *A. marina* propagules originated from muddy zone even reached 137 m per high tide. Comparatively, *R. apiculata* propagules had much slower movement with average dispersal speed of less than 40 m per high tide. The highest mean speed was recorded at 39 m per high tide by the *R. apiculata* propagules from sandy zone in PS2.

At this study site, mangrove propagules might have landed in strandline, dense roots and exposed area during low tide. From the analysis, most of the propagules of *A. marina* (minimum 48%) and *R. apiculata* (minimum 40%) were found within the strandline. A small number of released propagules were also found trapped within the aerial roots of mangrove trees (pneumatophores) and they were mainly of *A. marina*.

In the subsequent experiment to follow the development of propagule using the tethering method, the propagules of both species appeared in different physical conditions due to the unstable condition of the intertidal environment. In the sandy zone, *A. marina* propagules were frequently found exposed on the substrate (Figure 4(1a)). However, after the first three surveys, the number of exposed propagule gradually decreased, which chiefly caused by the continuous missing of *A. marina* propagules. There was no *A. marina* propagule left in the sandy zone since DC8 (60 days after release). Besides, it was very rare to find totally or partially buried *A. marina* propagule in this area. *R. apiculata* propagule had similar pattern of physical condition as shown by the *A. marina* propagules (Figure 4(2a)). These *R. apiculata* propagules were last found in DC8.

As in the muddy zone, most *A. marina* propagules were found to be exposed, and only small proportion of propagules were totally or partially buried in the substrate (Figure 4(1b)). After about one month, there was a drastic rise of missing propagules, in which DC7 (29 days after release) recorded the highest missing number (13 propagules). Similar to the sandy zone, the number of exposed propagules was dropped to zero in DC8. The remaining were only the buried propagules. In the last survey, none of the released *A. marina* propagules could be detected. For *R. apiculata*, after DC6 (21 days after release), the number of exposed propagules was decreasing while the missing propagules were increasing (Figure 4(2b)). In contrast to those in the sandy zone, the totally and partially buried *R. apiculata* propagules appeared in small proportion throughout the experiment. For both sandy and muddy areas, a series of propagule disappearance and mortality was accounted for the decrement in sample size over the experimental period (Figure 4).

*Avicennia marina* propagules were readily peeled off their pericarps within the first two days of exposure irrespective of their location. After experiencing the first high water (DC1), more than 45% of the *A. marina* propagules had shed off its pericarps. All *A. marina* propagules appeared without pericarps in DC3 (2 days after release). Soon after the shedding of the pericarp, these *A. marina* propagules entered the stage of root initiation. Almost all of the *A. marina* propagules had generated roots after one week of establishment in both the sandy and muddy zones. In the sandy zone, although the *A. marina* propagules had successfully initiated roots, many of them failed to further establish their roots. They were mostly found to have withering problem after root initiation. These propagules had their roots shrivel up since DC5 (14 days after release). Contrarily, in the muddy zone, *A. marina* propagules rarely showed any root developmental problem. Subsequent to root initiation, propagules normally anchor at the point where they were stranded. However, in this study site, only the *A. marina* propagules that were located at the muddy zone managed to anchor. The first observation of the propagule anchoring was during the second week (DC5), in which 15 anchoring out of the 26 observed *A. marina* propagules. However, there was only 1 anchoring *A. marina* propagule left in each of the next two censuses (DC6 and DC7). The rest were missing and believed to be swept away by tides.

*Rhizophora apiculata* propagules started to produce roots in both zones after one week of release (DC4). In the muddy zone, all *R. apiculata* propagules had generated roots by the third months (DC9), whereas only 20% root generation recorded in the sandy zone. Similar to *A. marina*, the *R. apiculata* propagules in the sandy zone showed higher number of root withering than the muddy zone. By third week, all *R. apiculata* propagules had their roots shrivel up. As in the muddy zone, 30% *R. apiculata* propagules failed to establish healthy roots throughout the censuses. Observation on the root establishment of *A. marina* and *R. apiculata* was restricted by propagule burial, disappearance and mortality, particularly after one month of exposure in the field.

*Avicennia marina* propagules had produced shoots intensively between the first and second weeks (between DC4 and DC5). Nearly 100% *A. marina* propagules in both zones had produced the first pair of leaves during that period. These *A. marina* propagules rapidly expanded their leaves after initiation of shoots. There were always higher rates of leaf expansion in the muddy zone than in the sandy zone. However, in DC7, 33% *A. marina* propagules in the sandy zone and 42% in muddy zone area were shown to have withering shoots. After DC7, there was no record of shoot initiation for *A. marina* propagules due to large number of missing propagules. On the other hand, *R. apiculata* propagules were comparatively very weak in shooting. Only two *R. apiculata* propagules found to initiate shoots in DC6 and DC7, and later in DC10, one was missing and another was dead of desiccation.

There were several factors accounted for the mortality of propagule, which are desiccation, physical damage, herbivory (predation) and burial in sediment. Mortality rate was high for *R. apiculata* propagules as well as the *A. marina* propagules in the sandy zone. For *A. marina*, no propagule was found dead until DC5. The highest mortality rate of 73% was recorded in DC7 by the *A. marina* propagules located in sandy zone. *A. marina* propagules primarily died of desiccation, and only a few were related to physical damage. None of them was found to be eaten. Compared to *A. marina, R. apiculata* propagules had relatively higher mortality rates. All the *R. apiculata* propagules of both zones were dead in DC8 and DC10 (121 days after release). There was a record of mortality for *R. apiculata* propagule in the sandy zone since DC4, but in the muddy zone, it was late until DC8. Most of the perished *R. apiculata* propagules were desiccated or physically damaged. Only two *R. apiculata* propagules that positioned in the sandy zone were found to have signs of herbivory and several were found to lose viability due to long period of burial.

There was higher proportion of *A. marina* propagules than *R. apiculata* propagules to reach each growing stage (except pericarp shedding) (Table 4). The difference was significant for both zones (Table 5(a)). Moreover, the propagules in the muddy zone developed better than those in the sandy zone (Table 4). *R. apiculata* propagules showed significant higher rate of root initiation in the muddy zone than in the sandy zone while *A. marina* propagules showed significant higher rates of anchoring, lifting and leaf expansion in the muddy zone (Table 5(b)). Meanwhile, the mortality rates were always higher in the sandy zone (Tables 4 and 5(b)). As a result, the *A. marina* propagules that fixed in the muddy zone were able to develop fully from pericarp shedding to leaf expansion. Over the four months period, these *A. marina* propagules performed the best early growth and the lowest mortality rate among all types of tested propagules. However, at the end of the experiment, all propagules of both species were either dead or missing.

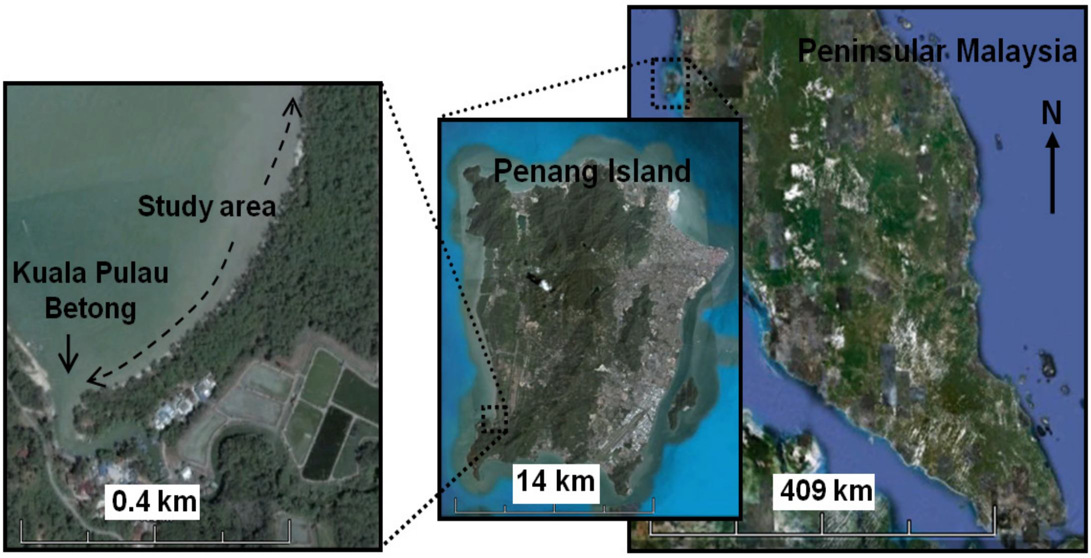


FIGURE 1. Location of the study site in the south-west coast of Penang Island, Peninsular Malaysia (adopted from: Google Earth 2021)

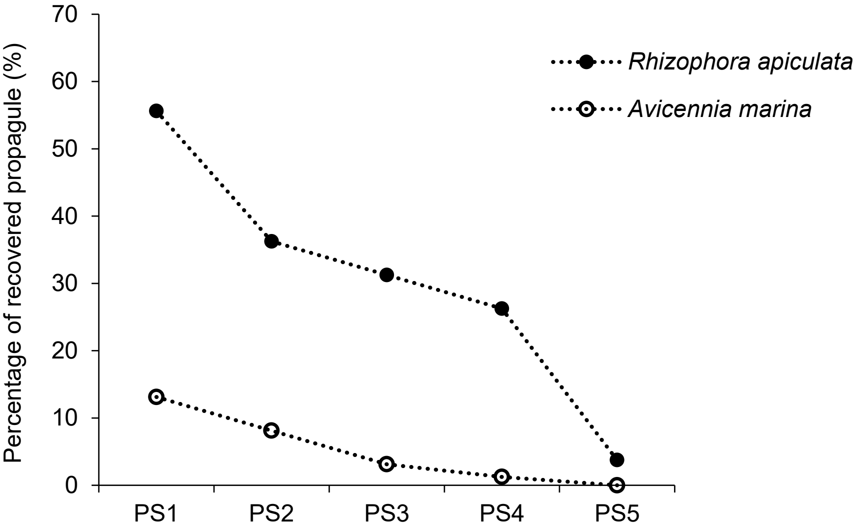


FIGURE 2. Propagule recovery rates for *Rhizophora apiculata* (solid circles) and *Avicennia marina* (open circles) in the five censuses (PS1 to PS5). The results are species-specific rates which combined the data of both release points at sandy and muddy areas

TABLE 1. Pearson Chi-square test on the effects of (a) species (*Avicennia marina* and *Rhizophora apiculata*) originated from different zones (1 and 2), and effects of (b) release location (sandy and muddy zones) for both species (3 and 4) on frequency of propagule recovery

| census | (a) Species | | | | | | (b) Release location | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | (1) Sand | | | (2) Mud | | | (3) *A. marina* | | | (4) *R. apiculata* | | |
| | df | $\chi^2$ | *P* | df | $\chi^2$ | *P* | df | $\chi^2$ | *P* | df | $\chi^2$ | *P* |
| PS1 | 1 | 17.634 | <0.001 | 1 | 50.390 | <0.001 | 1 | 2.686 | $0.101^{ns}$ | 1 | 3.064 | $0.080^{ns}$ |
| PS2 | 1 | 14.952 | <0.001 | 1 | 22.500 | <0.001 | 1 | 2.093 | $0.148^{ns}$ | 1 | 0.108 | $0.742^{ns}$ |
| PS3 | 1 | 13.701 | <0.001 | 1 | 32.164 | <0.001 | 1 | 1.858 | $0.173^{ns}$ | 1 | 1.862 | $0.172^{ns}$ |
| PS4 | 1 | 18.331 | <0.001 | 1 | 24.173 | <0.001 | 1 | 2.025 | $0.155^{ns}$ | 1 | 0.000 | $1.000^{ns}$ |
| PS5 | 1 | 3.057 | $0.080^{ns}$ | 1 | 3.057 | $0.080^{ns}$ | - | - | - | 1 | 0.000 | $1.000^{ns}$ |

$^{ns}$ = not significant

TABLE 2. Results of Mann-Whitney U test comparing propagule dispersal distances between (a) species (*Avicennia marina* and *Rhizophora apiculata*) at two different zones (1 and 2) and between (b) release location (sandy and muddy zones) for both species (3 and 4)

| | (a) Species | | | | (b) Release location | | | |
|---|---|---|---|---|---|---|---|---|
| census | (1) Sand | | (2) Mud | | (3) *A. marina* | | (4) *R. apiculata* | |
| | Z | *P* | Z | *P* | Z | *P* | Z | *P* |
| PS1 | -2.643 | <0.01 | -2.179 | <0.05 | -0.898 | $0.369^{ns}$ | -2.573 | <0.05 |
| PS2 | -1.093 | $0.274^{ns}$ | -3.938 | <0.001 | -1.400 | $0.161^{ns}$ | -5.713 | <0.001 |
| PS3 | -3.119 | <0.01 | NT | NT | NT | NT | -0.242 | $0.809^{ns}$ |
| PS4 | -2.372 | <0.05 | NT | NT | NT | NT | -0.777 | $0.437^{ns}$ |
| PS5 | NT | NT | NT | NT | NT | NT | -0.674 | $0.500^{ns}$ |

NT = not tested due to insufficient sample size for *Avicennia marina*

$^{ns}$ = not significant

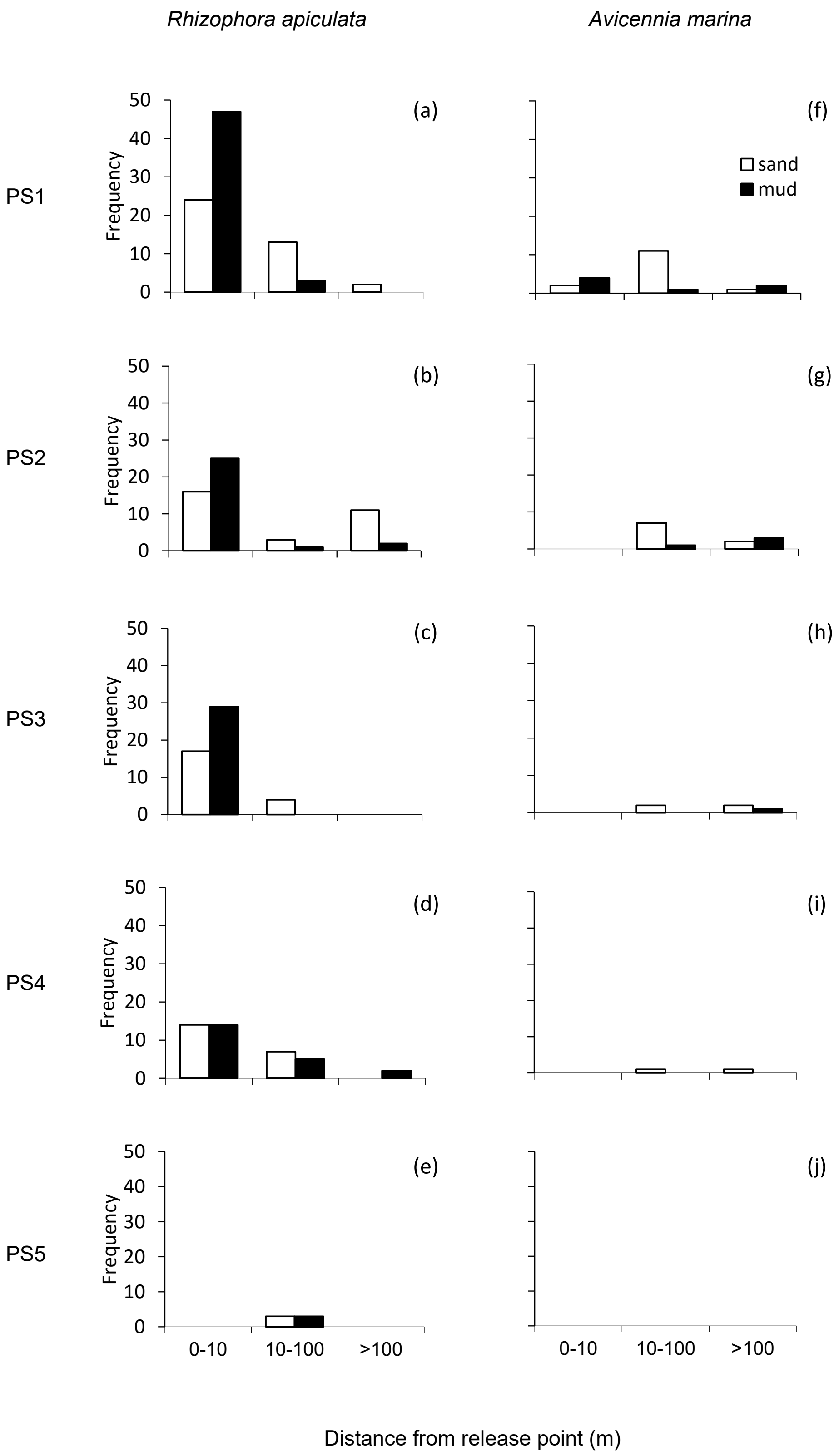


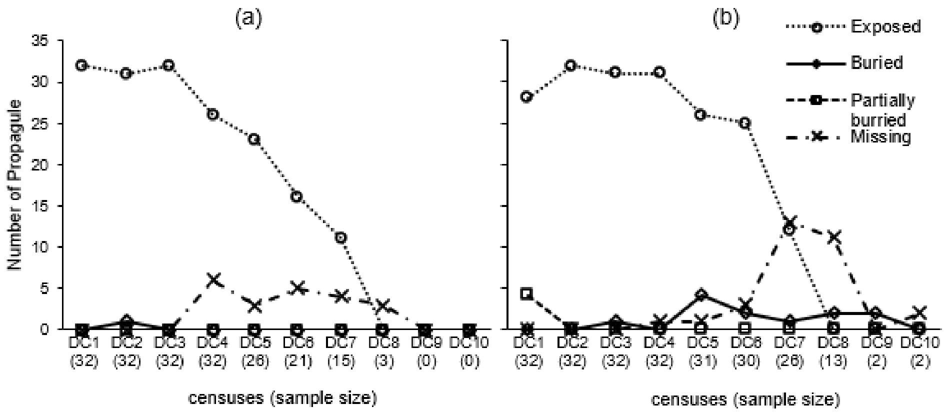
FIGURE 3. Frequency of recovered propagules of *Rhizophora apiculata* (left column) and *Avicennia marina* (right column) found at different distances (0-10 m, 10-100 m and above 100 m) from the release points at sandy (open bar) and muddy (solid bar) areas

TABLE 3. Descriptive parameters of the propagule dispersal directions of *Rhizophora apiculata* and *Avicennia marina*, which were released in the sandy and muddy areas of the study site. The mean direction, circular variance (measure of dispersion for directions) and result of Rayleigh's test (analysis of uniformity of directional distributions) are listed for the five censuses (PS1 to PS5)

| Species | | Mean | Circular | Rayleigh's test | |
|---|---|---|---|---|---|
| Census | Source | direction (°) | variance, V | Z | *P* |
| *Rhizophora apiculata* | | | | | |
| PS1 | sand | 12.1 | 0.32 | 16.109 | <0.001 |
| | mud | 115.4 | 0.14 | 35.489 | <0.001 |
| PS2 | sand | 337.1 | 0.48 | 8.187 | <0.001 |
| | mud | 358.3 | 0.13 | 21.137 | <0.001 |
| PS3 | sand | 297.6 | 0.43 | 6.904 | <0.001 |
| | mud | 124.8 | 0.57 | 3.761 | <0.10 |
| PS4 | sand | 347.8 | 0.23 | 12.599 | <0.001 |
| | mud | 122.7 | 0.31 | 9.893 | <0.001 |
| PS5 | sand | 45.2 | 0.01 | NT | NT |
| | mud | 64.2 | 0.00 | NT | NT |
| *Avicennia marina* | | | | | |
| PS1 | sand | 43.4 | 0.02 | 13.557 | <0.001 |
| | mud | 45.2 | 0.41 | 2.409 | <0.10 |
| PS2 | sand | 45.0 | 0.01 | 8.909 | <0.001 |
| | mud | 56.1 | 0.06 | 3.547 | <0.05 |
| PS3 | sand | 41.2 | 0.01 | 3.947 | <0.01 |
| | mud | - | - | NT | NT |
| PS4 | sand | 40.7 | 0.00 | NT | NT |
| | mud | - | - | NT | NT |
| PS5 | sand | - | - | NT | NT |
| | mud | - | - | NT | NT |

NT = not tested due to sample size less than 4

(1) *Avicennia marina*



(2) *Rhizophora apiculata*

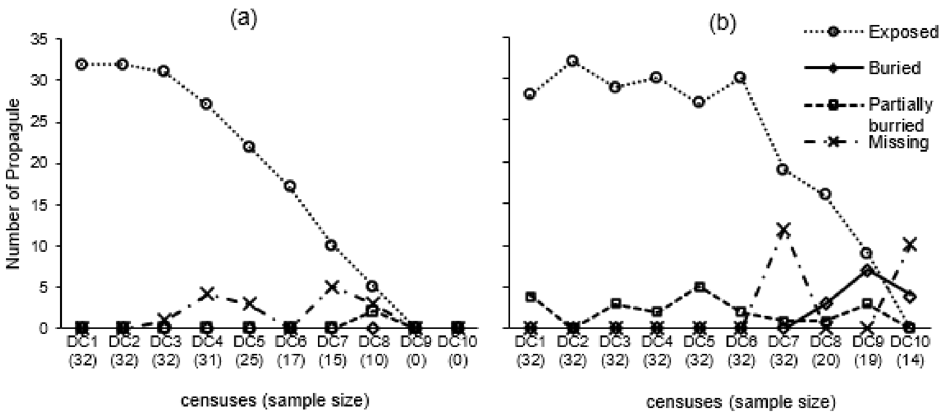


FIGURE 4. Physical conditions of the propagules of (1) *Avicennia marina* and (2) *Rhizophora apiculata* which fixed in (a) sandy and (b) muddy zones over the experimental period of four months (10 censuses). The number in bracket along the horizontal axis is the total number of propagules that being investigated (sample size) in that particular census

TABLE 4. Mean percentage (%±standard error) of the propagules in each stage of early growth for *Avicennia marina* and *Rhizophora apiculata* in the sandy and muddy zones over the four-month experimental period

| Propagule development | *Avicennia marina* | | *Rhizophora apiculata* | |
|---|---|---|---|---|
| | Sand | Mud | Sand | Mud |
| pericarp shedding | 100.0±0.0 | 100±0 | - | - |
| root initiation | 96.9±3.1 | 93.8±4.1 | 12.5±4.7 | 71.9±13.7 |
| anchoring | 0±0.0 | 25.0±10.6 | 0.0±0.0 | 0.0±0.0 |
| lifting | 0±0.0 | 28.1±14.5 | 0.0±0.0 | 0.0±0.0 |
| shoot initiation | 65.6±13.3 | 84.4±8.1 | 0.0±0.0 | 6.3±4.1 |
| leaf expansion | 12.5±6.7 | 75.0±11.6 | 0.0±0.0 | 0.0±0.0 |
| mortality | 34.4±13.3 | 3.1±3.1 | 65.6±4.6 | 31.3±11.3 |

TABLE 5. Influence of (a) species and (b) release location on the total percentages of propagules that achieved the growing phases (1 to 6) and those failed to survive (7) after four months of field exposure (Pearson Chi-square). No result for the data that is constant across the two tested samples

| Growing phase | (a) Species | | | | | (b) Release location | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Sand | | Mud | | | *Avicennia* | | *Rhizophora* | |
| | df. | $\chi^2$ | *P* | $\chi^2$ | *P* | df. | $\chi^2$ | *P* | $\chi^2$ | *P* |
| 1) Pericarp shedding | - | - | - | - | - | - | - | - | - | - |
| 2) root initiation | 1 | 45.967 | <0.001 | 5.379 | <0.05 | 1 | 0.350 | 1.000 | 23.127 | <0.001 |
| 3) anchoring | 1 | - | - | 9.143 | <0.01 | 1 | 9.143 | <0.01 | - | - |
| 4) lifting | 1 | - | - | 10.473 | <0.01 | 1 | 10.473 | <0.01 | - | - |
| 5) shoot initiation | 1 | 31.256 | <0.001 | 39.409 | <0.001 | 1 | 3.000 | 0.083 | 2.065 | 0.492 |
| 6) leaf expansion | 1 | 4.267 | <0.05 | 38.400 | <0.001 | 1 | 25.397 | <0.001 | - | - |
| 7) mortality | 1 | 6.250 | <0.05 | 8.892 | <0.01 | 1 | 10.256 | <0.01 | 7.570 | <0.01 |

## DISCUSSION

There was a substantial number of released propagules that could not be traced in the study area, particularly those of *A. marina*. Predation by herbivores (Komiyama et al. 1992; McGuinness 1997; Smith III 1987; Sousa et al. 2007), lost in standing water or bushes (Komiyama et al. 1992; Sousa et al. 2007) and dispersal out of the monitored area (Yamashiro 1961) are among the factors that responsible for the propagule disappearance over time. Predation of herbivorous crabs is always regarded as an important cause to the propagule loss. However, based on a trial experiment at the study site, it was shown that crab predation rates were insignificant for both mangrove species. There were possibilities that the dispersing propagules were trapped in the nearby bushes or sank to the bottom of standing water and thus difficult to be found. *R. apiculata* propagules are large and easily spotted even though when trapped within bushes or half submerged in standing water. On the other hand, *A. marina* propagules are smaller in size but improbable to sink in standing water since they can float constantly over a wide range of salinities for at least two months (Wong et al. 2020). However, the *A. marina* propagules were difficult to be detected when trapped within the dense mangrove roots and bushes. Irrespective of these factors, the chosen study site was an exposed wetland with fewer bushes, and hence we ruled out the chances of these propagules to be missed out due to difficulty in tracing. On the other hand, these propagules were probably dispersed out of the searching range during the course of study due to high wave energy at the site. Past records showed that the propagules of *R. apiculata* and *A. marina* were able to travel up to 1 and 50 km, respectively (Clarke 1993; Komiyama et al. 1992). We postulated that high wave energy coupled with less physical barriers has facilitated the export of propagules of both species from the study area.

Under the same environmental setting, *A. marina* propagules dispersed farther than *R. apiculata* propagules. This may be related to size and buoyancy of propagule. Smaller size propagules have less restriction in the dispersal process (Duke et al. 1998; Kellman 1975; Rabinowitz 1978c). As predicted by the tidal sorting hypothesis (Rabinowitz 1978b), the larger *R. apiculata* propagules appeared to be more resistance to the buffering of tidal water and became less efficient in dispersion compared to the smaller *A. marina* propagules. Apart from propagule size, *A. marina* propagules appeared to be more buoyant than *R. apiculata* propagules (Wong et al. 2020). The effect of release location on propagule dispersal distance was only significant for *R. apiculata* during the early stage of dispersal. The difference was linked to the surface soil condition rather than the tidal elevation which was associated with water influence (flooding frequency and inundation time). The *R. apiculata* propagules released onto the wet and sticky mud were more difficult to be moved by the tidal water as compared to the sandy site. However, the soil surface type seemed to have less impact on the *A. marina* propagules. This could be due to their smaller size that caused less contact with the substrate.

It is suggested that propagules of both species had similar travelling route but *R. apiculata* dispersed in a much slower rate. The north-eastward flowing of propagules highly corresponded with the direction of wave current (Wong et al. 2020). Propagule dispersal direction does not only relate to the tidal current (Huiskes et al. 1995; Rabinowitz 1978b), but also direction of wind (Clarke 1993; Harwell & Orth 2002; Huiskes et al. 1995;) and rainfall runoff (Sousa et al. 2007). However, in this case, the latter two factors were less impactful after referring to the meteorological data (Malaysian Meteorological Department) that showed wind predominantly blew to the opposite direction (south-westward) during the study period. Rainfall runoff was also less likely to be the main reason as well since it was a rather dry period. Consequently, wave current is among the most critical factors that influenced the propagule dispersal direction in this coastal area.

*Avicennia marina* propagules showed rapid development of root and shoot in the open coast environment as compared to *R. apiculata*. The growth of both species was always greater in the muddy zone than the sandy zone. The propagules of both species in the sandy area suffered from withering root and shoot. These affected propagules, if not missing, and the propagules were later found losing viability due to desiccation. Failure in developing roots among these propagules may relate to the soil moisture stress. Some of the fast rooting *A. marina* propagules were able to anchor in the muddy area. Difficulty in anchoring among the *A. marina* propagules, especially in the sandy area, was supposedly due to the wave effect. McKee (1995) observed that the mangrove propagules were difficult to establish at a lower intertidal zone, where tidal action recurrently moved them away from the soil surface. Delgado et al. (2001) also found that the developing mangrove propagules had to take more time and energy to reorient their anchoring roots each time they were washed away from original position. An earlier laboratory experiment by McMillan (1971) presented a negative relationship between water turbulence and root development of Avicennia germinans propagules. In some cases, even the artificially planted propagules were facing anchoring problem caused by wave attack, as described in a post-planting assessment by Awang et al. (2004).

In this study, inundation stress was of less importance since the frequently flooded muddy area showed better propagule establishment and survival. *R. apiculata* propagules seemed to be more sensitive to the coastal environment and more difficult to tolerate the associated stresses as compared to *A. marina*. This may be one of the limiting factors that controls the natural distribution of *R. apiculata* at the coastal area.

The study site was unfavourable for the establishment of both *A. marina* and *R. apiculata* and such condition was predominantly attributed to the environmental influences such as tidal waves and currents, soil condition and sedimentation. Meanwhile, for any mangrove restoration in such habitat, *A. marina* is a more appropriate species to be planted since they showed greater adaptation in the high tidal influenced environment. The obtained information is useful in the management of local mangroves especially the planning of restoration in the aspect of species selection and evaluation of planting site.

## CONCLUSION

*Avicennia marina* and *R. apiculata* have different strategies in propagule dispersal and early growth under the same environmental setting. *A. marina* propagules were found to be rapidly dispersed and able to establish at stranding site. As compared to *R. apiculata, A. marina* is recognised as a species that has better adaptation in the unstable seaward environment. This may also explain why this species is always found as a pioneer at the forefront of many shores, not only in Penang Island but elsewhere in Malaysia. Furthermore, environmental variables play a vital role in the dispersal and early establishment of mangrove propagules. For our study site, tidal wave energy and soil condition were the main controlling factors. Our study stresses that the knowledge of propagule dispersal and early development as well as local environmental factors are crucial in understanding and managing a mangrove forest, particularly in habitat restoration. Further investigation for each type of major species under different environmental conditions is strongly proposed to enhance knowledge to support mangrove conservation in Malaysia.

## ACKNOWLEDGEMENTS

We are grateful with the help from the District Forest Office Larut-Matang, Malaysian Meteorological Department, Fisheries Research Institute and School of Biological Science, USM. This study is financially supported by South China Sea Institute of Oceanology (SCSIO), Chinese Academy of Sciences (CAS) (International Partnership Program of Chinese Academy of Sciences, grant number 133244KYSB20180012) and USM fellowship.

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