MANGROVE PROPAGULE DISPERSAL AND EARLY GROWTH STUDIES OF *AVICENNIA MARINA* AND *RHIZOPHORA APICULATA*

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by

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LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
GPS	Global Positioning System
PCA	Principal component analysis
E	East
N	North
cm	Centimetre
g	Gram
ha	Hectare
l	Litre
m	Metre
ml	Millilitre
^{o}C	Degree Celsius
d.f.	Degree of freedom in the statistical hypothesis testing
MS	Mean square in the statistical hypothesis testing
F	F-value in the statistical hypothesis testing
t	t-value in the statistical hypothesis testing
Z	Z-value in the statistical hypothesis testing
χ^2	Chi-square value in the statistical hypothesis testing
p	p-value in the statistical hypothesis testing
HF	Horizontal float
HS	Horizontal sink
VF	Vertical float
VS	Vertical sink

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KAJIAN PENYEBARAN DAN PERTUMBUHAN AWAL PROPAGUL POKOK BAKAU *AVICENNIA MARINA* DAN *RHIZOPHORA APICULATA*

ABSTRAK

Penyelidikan telah dijalankan untuk mengkaji penyebaran propagul dan pertumbuhan awal bagi dua spesies umum di Malaysia, iaitu *Avicennia marina* dan *Rhizophora apiculata.* Kajian lapangan telah dijalankan di Kuala Pulau Betong, sebuah kawasan bakau persisiran pantai yang terletak di pantai barat Pulau Pinang. Pergerakan propagul pokok bakau dipantau dengan kaedah “release and recapture” sementara pertumbuhan awal propagul diperiksa di kawasan kajian dengan “tethering system”. Satu lagi ujikaji penyebaran terkawal telah dijalankan di makmal. Sifat penyebaran dan perkembangan propagul dari kedua-dua spesies telah diperhatikan di dalam air yang mengandungi tahap saliniti berlainan (0, 10, 20 dan 30). Keputusan kajian lapangan menunjukkan bahawa arah dan jarak penyebaran berbeza secara signifikan antara dua spesies untuk kedua-dua lokasi perlepasan propagul, iaitu zon pasang surut atas dan tengah ($P < 0.05$). Setelah satu bulan, 98 % propagul yang dilepaskan tersebar ke luar kawasan kajian kerana arus gelombang yang kuat. Selain itu, *A. marina* menunjukkan pertumbuhan yang lebih baik berbanding dengan *R. apiculata* di kawasan kajian ini. Walau bagaimanapun, tiada propagul yang berjaya berkembang secara kekal selepas tempoh empat bulan. Untuk kajian makmal, *A. marina* berkembang lebih cepat daripada *R. apiculata* dan berjaya menjadi bibit muda dalam air masin yang tahap salinitinya 10, 20 dan 30. Kebanyakan sifat penyebaran propagul didapati berbeza secara signifikan antara spesies ($P < 0.05$) dan antara air tawar dan air masin ($P < 0.05$). Kesimpulannya, propagul *A. marina* adalah

lebih cepat menyebar ke habitat yang sesuai dibandingkan dengan *R. apiculata*; dan ia memiliki sifat penyebaran termasuk kadar hidup yang tinggi, selalu terapung dan pertumbuhan yang pantas dalam persekitaran air masin. Dengan sedemikian, *A. marina* mempunyai kelebihan untuk menyesuaikan diri dalam keadaan penyebaran air di kawasan persisiran pantai yang dipengaruhi pasang surut dan gelombang air yang kuat. Di kawasan kajian ini, regenerasi pokok bakau secara semula jadi sukar berlaku kerana kesan gelombang dan keadaan tanah yang kurang sesuai. Untuk projek penanaman bakau di kawasan terbuka seperti ini, *A. marina* merupakan spesies yang lebih sesuai ditanam di bahagian dataran lumpur di bawah pengawalan gelombang air yang baik.

MANGROVE PROPAGULE DISPERSAL AND EARLY GROWTH STUDIES OF *AVICENNIA MARINA* AND *RHIZOPHORA APICULATA*

ABSTRACT

A study was conducted to investigate the propagule dispersal and early growth of two common species in Malaysia, *Avicennia marina* and *Rhizophora apiculata*. Field studies were carried out at Kuala Pulau Betong, a coastal mangrove area in the west coast of Penang Island. Movements of the mangrove propagules were monitored by the release and recapture method while their early growth were examined at the site by tethering system. Another "enforced dispersal" experiment was conducted under laboratory condition. Dispersal attributes and propagule developments of both species were observed in the water of a range of salinities (0, 10, 20 and 30). The field results showed that the dispersal direction and distance were significantly different between the two species for both of the release points at upper and middle intertidal zones ($P < 0.05$). After one month, 98 % of the released propagules were found dispersed away from the study area mainly due to strong wave current. Furthermore, *A. marina* performed a better growth than *R. apiculata* in the study area but none of them was able to permanently establish after four months period. In the laboratory experiment, *A. marina* developed more rapidly than *R. apiculata* and they were successfully developed into young seedlings in the saltwater with salinities of 10, 20 and 30. Most of the propagule dispersal properties were found significantly different between species ($P < 0.05$) and between fresh and saltwater ($P < 0.05$). In conclusion, *A. marina* propagules were more readily spread out for a preferable habitat compared to *R. apiculata*; and they have dispersal

properties of high survival rate, always buoyant and rapid growth in saltwater environments. Therefore, *A. marina* is better adapting to the water dispersal in the high wave and tidal influenced coastal areas. In this study area, natural regeneration is hard to take place due to wave effect and soil condition. For the mangrove planting project at similar exposed sites, *A. marina* should be a more appropriate species to plant in the mudflat area under proper control of wave effect.

1.0 INTRODUCTION

Mangroves are forests of salt-tolerant trees and shrubs that occupy the area between land and sea primarily the river banks, sheltered estuaries, shallow-water lagoons and low energy coastlines in the tropical and subtropical regions. The mangroves have developed specialized adaptations to live in this saline and frequently flooded environment. There are approximately 16 families and 40 to 50 species of mangrove depending on the classification (McKee, 1996a). In Malaysia, there are 41 mangrove species recorded by FAO (2007), representing the second highest number of mangrove species composition in the world.

According to Tomlinson (1986), mangrove species can be generally categorized into three groups: major elements (strict or true mangrove which occur only in the intertidal zone), minor elements (occupy peripheral habitat and rarely form pure communities) and associates (not restricted in the mangrove communities and may occur only in transitional vegetation). The major elements are comprised of families of Avicenniaceae, Combretaceae, Palmae, Rhizophoraceae and Sonneratiaceae. The other two mangrove groups are comparatively more extensive, especially those of associates.

Biogeographically, mangrove vegetation can be divided into two hemispheres, namely, the eastern group and the western group. The eastern group or the ‘Old World’ including East Africa, India, Southeast Asia, Australia and the Western Pacific, while the western group or the ‘New World’ including West Africa, South and Central America, Florida and the Caribbean (Chapman, 1976; Tomlinson, 1986). Both regions have very different floristic inventories in size and composition, where the mangroves in eastern group are more diverse than the western group.

Mangrove forests were once recognized as unproductive wasteland or transitional systems (Macintosh and Ashton, 2002). However, in the past few decades, studies have shown that the mangrove ecosystem is highly productive which directly or indirectly contributes to the ecological, physical and economical aspects. Ecologically, mangrove forest greatly supports the conservation of biological diversity in the tidal zones. The mangrove inhabitants include several endangered species, which range from reptiles (e.g. crocodiles, iguanas) and amphibians to mammals (e.g. tigers, manatees and dolphins) and birds (e.g. herons, egrets and eagles) (FAO, 2007). The system also serves as fish nursery which is exceptionally important in sustaining the near shore fishing industry (Harrison and Pearce, 2002). These fishery resources contain many commercial species that are economically valuable to the local communities (Husain and Ibrahim, 2001). Moreover, mangroves are crucial in supplying high quality timber as building materials and for making charcoal, firewood and tools. In Malaysia, the Matang Mangrove Forest Reserve is well known in sustainable production of fuel wood and poles began in year 1902-1904 (FAO and Wetlands International, 2006). In physical functions, mangrove plays a vital role in shorelines stabilization as well as prevention of coastal erosion and salt water intrusion. The vegetation also helps to absorb strong wind and reduce wave energy. They are functional in minimizing the impact of coastal hazards such as flood, monsoonal wind, storm surges, cyclones and hurricanes.

Considering the benefits provided, the mangrove should be regarded as a natural treasure which deserves conservation and well management. But in fact, the survivals of mangroves are under grave threat globally. The rising population and urbanisation in the coastal zones are continuously affecting the world's mangrove coverage. The urban development led to the conversion of mangrove areas into settlements, trading ports, recreational spots and other economical uses (Harrison and Pearce, 2002). In many countries, the governments encouraged the establishment of aquaculture and agriculture in the mangrove areas in order to boost the national economies (FAO, 2007). The high profit timber trade had also driven the over exploitation of mangrove forests (Macintosh and Ashton, 2002). Besides, some mangrove forests are degraded due to human-induced pollution such as oil spill, mismanagement of solid waste and discharge of untreated sewage (Ellison and Farnsworth, 1996). For these reasons, mangroves were destroyed and cleared in large scale. According to FAO (2007), about 3.6 million ha of mangroves have been lost from year 1980 to 2005. At regional level, Asia suffered the largest net loss with more than 1.9 million ha disappeared since 1980. Malaysia as one of the countries with large area and rich diversity of mangroves, has lost approximately 110, 000 ha of mangroves in that 25 years, chiefly due to land reclamation. This was absolutely a big loss, not only to the nation but to the world.

Unquestionably, mangrove losses bring negative impacts. When the mangrove ecosystems were severely threatened, the biodiversity in that particular area will be disrupted and the natural resources will no longer be sustainable. MacKinnon and MacKinnon (1986) have suggested that some 480 kg of fish lost in coastal fisheries per year for every hectare of mangroves cleared. Other than that, the mangrove loss can sometimes be disastrous. It has been claimed that the serious loss of life (300,000 to 500,000 lives) in Bangladesh during the 1970 typhoon was partly due to the fact that many of the mangrove swamps which provided coastal protection had been converted into paddy fields (McKee, 1996a).

Restoration is one of the essential ways to save mangrove forest (Macintosh and Ashton, 2002). Basically, mangroves can be restored in a specific site through natural regeneration or artificial regeneration (Field, 1998b). It is preferable to apply natural regeneration by means of low cost (Kairo et al., 2001) and self recovery (Lewis and Streever, 2000), which allows natural processes to select the most appropriate species and area for mangrove re-colonisation. However, low propagule supply may result in taking a very long time to reach climax state in an impacted area, which also refers as “propagule limitation” by Lewis (2005). Consequently, natural regeneration sometimes failed to meet human needs especially in the highly damaged region. In such circumstances, artificial regeneration is a better strategy to accelerate recovery by manually planting of propagules or seedlings.

In recent years, there is growing awareness among the policy makers and general public towards the importance of mangroves. This positive tendency has led to the development of large-scale mangrove restoration projects in many countries including the Southeast Asian countries (Ong, 1995; Field, 1996; Field, 1998a; Bosire et al., 2008). More significantly, after experiencing the Indian Ocean Tsunami of December 2004, the protective function of mangrove is vastly acknowledged (Kathiresan and Rajendran, 2005; Danielsen et al., 2005; Vermaat and Thampanya, 2006). Thereafter, mangrove planting programmes had mushroomed over the tsunami-affected countries including India (Gattenlöhner et al., 2007), Sri Lanka (IUCN, 2009) and Indonesia (Wibisono and Suryadiputra, 2006). In Malaysia, the Forestry Department has worked with NGOs to replant mangrove and more than five million saplings were planted nationwide over the five years after tsunami (Khalid, 2008; Yeoh, 2009).

There were cases reported that the restoration efforts had successfully improved the mangrove coverage as in the estuaries of Godavari and Krishna located in Andhra Pradesh, India (Ravishankar and Ramasubramanian, 2004). But regrettably, in other places, many of these well intended restoration projects ended up in failure as most planted seedlings were unable to establish and re-colonize the planting sites. One obvious example is Acheh, a highly tsunami-impacted region, where the post-planting assessment showed that only a small fraction of the restorations was successful (Wibisono and Suryadiputra, 2006; Onrizal and Mansor, 2010). Also, in Malaysia, substantial numbers of mangrove planting failed, such as the case in Kuala Sala (Awang et al., 2004), Pulau Sayap in Kedah and Sungai Burong in Penang Island (Tan and Ong, 2008). Under such circumstance, not only the restoration efforts were in vain, but both money and time were wasted.

A well planned restoration is always an effective way to overcome reduction in mangrove coverage. However, lack of essential knowledge and technical skills easily lead to restoration failure, as frequently happened in the Southeast Asian countries (Awang et al., 2004; Clough, 2008; Lewis et al., 2006; Onrizal and Mansor, 2010). Therefore, planting of mangrove should be carefully planned with good knowledge to increase the success rate. One of the most crucial steps in the planning is to put emphasis on the study of mangrove species ecology particularly the distribution pattern and seedling establishment (Elster, 2000; Ellison and Farnsworth, 2001; Lewis et al., 2006; Lewis, 2009). For this purpose, it is vital to examine the propagating dispersal of individual mangrove species as an effort to understand their distribution and early establishment.

As the scientific information of mangrove dispersal is scanty for many of the species and region, a study of mangrove propagule dispersal was initiated with the objectives of:

- To investigate the dispersal pattern and early growth of the propagules of two mangrove species, *Avicennia marina* and *Rhizophora apiculata* in a natural habitat of coastal mangroves.
- To figure out the propagule dispersal properties of two mangrove species, *A. marina* and *R. apiculata* in a range of water salinities.

2.0 LITERATURE REVIEW

2.1 Plant Dispersal

Generally, plant dispersal is a process of movement or transport of seeds away from the parent plant or an existing population. In detail, Kellman (1975) referred plant dispersal to a stage where the propagating organs (fruit or seed) abscised from the parent trees then move by dispersal agent (wind, water or animal) until they reach a suitable location for further establishment. Each type of the dispersal mechanisms associates the anatomical, physical and chemical specializations of the propagating organs; for instance, general adaptations of the water-dispersed fruit and seed are resistance to sinking (buoyancy), low specific gravity and uses surface tension (Howe and Smallwood, 1982).

Dispersal process is always being emphasized in the plant study since it is considered as one of the most important determinants of species distribution and abundance (Bullock et al., 2006). In plant ecology, dispersal is known to influence the spatial arrangement of individuals within a population (Bolker and Pacala, 1999); while in larger scale, it controls the regional dynamics of a plant species (Ehrlén and Eriksson, 2003). In order to study the plant dispersal, a better understanding of their reproductive method is essential to be the background knowledge. From this point of view, the mangrove reproduction will be discussed before entering the topic of mangrove dispersal.

2.2 Mangrove Reproduction

Mangroves reproduce sexually and have little or no capacity in vegetative regeneration. They exhibit two very unique reproductive strategies which are different from most terrestrial vegetation: hydrochory and vivipary (Rabinowitz, 1978a; Tomlinson, 1986). Hydrochory or the plant dispersal by water is a major mean in spreading of mangrove species. There are several kinds of dispersal unit including capsule (*Aegiceras*, *Avicennia* and *Sonneratia*), viviparous hypocotyl (*Bruguiera*, *Ceriops*, *Rhizophora* and *Kandelia*), aggregated head (*Nypa*) and seed (*Excoecaria*, *Pelliciera* and *Xylocarpus*) (Saenger, 2002).

Another character, vivipary, is refers to a phenomenon whereby the embryo has no dormancy and germinates while still attached to the parent tree (Rabinowitz, 1978b). *Rhizophora*, *Bruguiera*, *Kandelia* and *Ceriops* are those that characterized by viviparous propagation. Nonetheless, there is a more advanced condition existed in which the embryo emerges from the seed coat but not the fruit before it detach from the parent tree and this is named as cryptovivipary (Carey, 1934). This is a common feature found in *Aegiceras*, *Avicennia* and *Pelliciera*. Since there is no dormancy in the embryo, then it is consider no true seed for these mangroves (Tomlinson, 1986). In general, the propagating organs that germinated prematurely are conveniently called “propagule”. The propagule characteristics and germination type of the major components of mangroves are shown in Table 2.1.

Table 2.1: Propagule characteristics and germination type for the major mangroves (compiled from Tomlinson, 1986).

Family	Genus	Vivipary	Propagule type	Germination
Avicenniaceae	*Avicennia*	Cryptoviviparous	One–seeded fruit	Epigeal
Combretaceae	*Laguncularia*	None	One–seeded fruit	Epigeal
	Lumnitzera	None	One–seeded fruit	Epigeal
Palmae	*Nypa*	Cryptoviviparous	One–seeded fruit	Hypogeal
Rhizophoraceae	*Bruguiera*	Viviparous	Seedling	Epigeal
	Ceriops	Viviparous	Seedling	Epigeal
	Kandelia	Viviparous	Seedling	Epigeal
	Rhizophora	Viviparous	Seedling	Epigeal
Sonneratiaceae	*Sonneratia*	None	Seed	Epigeal

2.3 Mangrove Distribution

Mangroves are frequently observed to be distributed into clear zonation and the dominant species changes from landward to seaward area. It means that the mangroves are growing in monospecific bands parallel to the shoreline. The zonation differs among the forest types which can be modified by local topography, and also varied with the geographical changes. Generally, for many eastern regions including Malaysia, the species that dominate seafront are the *Avicennia* and *Sonneratia*, then taken over by the *Bruguiera* and *Rhizophora* while moving landward; in contrast, the *Rhizophora* species are regularly the seaward dominant in the western regions such as Florida, Caribbean and Atlantic South America (Chapman, 1976).

This interesting phenomenon has attracted many scientists and researchers for decades. Many of them have tried experimentally to figure out the reason behind and came out with different ideas. There were several famous hypotheses explaining the mangrove species zonation: (1) land building and plant succession over time (Davis, 1940) (2) geomorphological processes (Thom, 1967) (3) tidal sorting of propagule (Rabinowitz, 1978c) (4) interspecies competition (Ball, 1980) (5) predation of propagule (Smith, 1987a; Smith et al., 1989) and (6) physiological limitation over the gradient with different physicochemical conditions (Ball, 1988a, b; McKee, 1995a). For recent decades, the hypotheses (3), (4), (5) and (6) are frequently discussed and debated in explaining mangrove zonation.

One of the hypotheses, the Rabitnowitz's tidal sorting of propagule is based on the size and buoyancy of the propagules during the dispersal stage. The hypothesis proposed that the smaller propagules are brought further inland by flood tides, therefore they stranding and establishing around the upper tidal zone. Conversely, the larger propagules afford greater access to the soil surface and resistance to buffeting by moving water, resulted in better establishment in more seaward areas. This tidal sorting hypothesis was later supported by Jimenez and Sauter (1991) in a research on the zonation patterns of *Avicennia bicolor* and *Rhizophora racemosa* in the Pacific Coast of Costa Rica. However, it was also found ineffectively explain the mangrove distribution from the subsequent observations by Clarke et al. (2001), Stieglitz and Ridd (2001) and Sousa et al. (2007).

The subsequent hypothesis of propagule predation is basically relating the dominance of a mangrove species to frequency of propagule predation. Smith (1987a) found an inverse correlation between predation of propagule and canopy dominance in four out of the five studied species. He suggested the "dominance-predation" model which states that rates of predation are significantly higher in mangrove forests where conspecifics are rare or absent and lower where conspecifics are dominant. Some studies were found to fit the model (Robertson, 1991; Farnsworth and Ellison, 1997; Delgado, 2001) but some were not (McKee, 1995b; McGuinness, 1997b; Sousa and Mitchell, 1999; Clarke and Kerrigan, 2002). In this view, the model does not interpret the cause of mangrove zonation in the first place but more specifically providing idea on the maintenance of species composition of various zones (Saenger, 2002).

Hypotheses (4) and (6) highlight the biological processes of species interactions and responses to environmental factors in the stage of establishment and recruitment. Differences in physiological responses to the environmental setting such as salinity regime (Ball, 1988a, b) may result in zoning distribution of mangroves. Similar to the other hypotheses, they also failed to fully interpret the occurrence of mangrove zonation and only found to be true in certain locations and species. So far it is still a hot debate in explaining the unique patterns of mangrove distribution (Krauss et al., 2008).

In more recent studies, it showed that the spatial variation of species may be a multifactorial consequence. Rand (2000) proposed that the interactions of seed dispersal and post-dispersal factors may determine the species distribution and abundance patterns in salt marsh plant communities. McKee (1995a) and Allen et al. (2003) have also suggested that the pattern of mangrove distribution will be more effectively explained by considering the interactions of the biotic (e.g. competition, predation) and abiotic factors (e.g. light, oxygen and nutrient). Moreover, the rich experimental history in this topic has given a clue that the mangrove distribution is linked to the condition of tidal flooding and evolutionary tolerance of seedlings, saplings and trees to the environmental effects such as salinity and soil nutrient (Krauss et al., 2008). The dispersal of mangrove propagules, which is highly related to these environmental influences, is considered an important contributor to the mangrove distribution.

2.3.1 Propagule Dispersal and Mangrove Distribution

Fundamentally, dispersal is an early stage of plant life history that determines the distribution and abundance of a species (Rabinowitz, 1978c; Aguiar and Sala, 1997; Bullock et al., 2006). It is commonly recognized as a critical life stage which is crucial to the future establishment and survival of a plant. Therefore, dispersal is often demonstrated to limit the extent of plant populations (Primack and Miao, 1992; Scherff et al., 1994; Rand, 2000).

In mangrove ecosystem, dispersal is measured as one of the important factors that affect species' distribution in space and time from the perspective of propagule supply (Delgado et al., 2001; Minchinton, 2001; Sengupta et al., 2005). The colonisation of new environment is basically dependent on the availability and successful dispersal of propagules to the sites (Ball, 1980; Clarke, 1993; Duke et al., 1998a). In Pak Phanang Bay of Thailand, *Avicennia alba* rapidly colonized the accreting mud flats due to high propagule availability and successful dispersal to the sites of colonization (Panapitukkul et al., 1998). Seed availability may also control the plant abundance within tidal zone (Rand, 2000). Many studies have agreed that the propagule dispersal form the initial pattern of mangrove distribution (Rabinowitz, 1978c; Clarke, 1993; McGuiness, 1997a; Rand, 2000).!!!!

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Propagule dispersal, as an initial factor to shape the present and future mangrove distribution, is especially important in the unstable, highly saline and tidal affected habitat. Hence, the knowledge of propagule dispersal is no doubt essential to understand and predict the range expansion of a particular mangrove species. The dispersal process of a mangrove species can be examined by looking into the dispersal related characteristics as described in the subsequent sections.

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2.4 Propagule Dispersal Properties

2.4.1 Dispersal Parameter

Physical and physiological attributes (e.g. propagule size, viability and tolerance to predator's damage) of the mangrove propagules, couple with the influence of surrounding environment (e.g. water quality, substrate condition and tidal position), may lead to differences in dispersal pattern among species and sites (Duke et al, 1998a). The dispersal pattern of each species may directly determine the propagule supply and thus affecting the mangrove distribution and expansion. With some peculiar dispersal abilities, the mangrove propagules may travel great distances (Tomlinson, 1986; Saenger, 2002). According to Rabinowitz (1978a), the dispersal parameters are longevity, period of floating, period of "obligate dispersal" and period for establishment. These properties may have direct impact on the fate of dispersing propagules.

2.4.1.1 Longevity

Longevity means how long the propagule floats while remaining viable in the water. Previous studies showed that longevity of mangrove propagules varied for different species. *Rhizophora mangle* propagules can remain viable for more than 12 months in laboratory vessels (Davis, 1940). *Pelliciera rhizophorae* propagules are capable to float in salt water and survived for 3 months (Rabinowitz, 1978a). From a field experiment, Clarke (1993) found that the *Avicennia marina* propagules which were exposed to tides or totally submerged could remain viable up to 5 months. Drexler (2001) conducted an experiment to determine the maximum longevities of propagules of *Rhizophora mucronata* and *Rhizophora apiculata* and the final result was 150 and 89 days respectively. Overall, the estimated value for longevity is from 35 days to more than a year (Rabinowitz, 1978a).

2.4.1.2 Period of Floating

Mangrove propagules possess the ability to float in the water (buoyancy), even though for a limited time (Tomlinson, 1986). This enables the drifted propagule to reach a place where it has a chance of establishing and growing. The floating period shows how long the propagule can float in the water during the dispersal stage. Previous studies have found that the flotation time varied among species, populations of the same species in some cases and also with water condition (Rabinowitz, 1978a; Clarke and Myerscough, 1991; Clarke et al., 2001). According to the observation of Rabinowitz (1978a), the floating period can be as little as 1 day (*P. rhizophorae*) or a long period of 82 days (*Avicennia germinans*).

2.4.1.3 Period of “Obligate Dispersal”

Period of “obligate dispersal” is how long a propagule floats before it can establish the root system that helps in anchoring. This “obligate dispersal” phase is considered as a minimum period for propagule dispersal (Tomlinson, 1986). For example, in *Avicennia* propagules, the time between the pericarp loss (pericarp is a thin layer covers the propagule) and the development of radial roots is indicating the “obligate dispersal” period (Clarke, 1993). Rabitnowitz (1978a) estimated the “obligate dispersal” period for the propagules of various mangrove species and found that it ranged from 8 to 40 days. In her studies, the “obligate dispersal” period of *R. mangle* is approximately 40 days; while for *A. germinans*, it was estimated at 14 days; and it is about 8 days in *Laguncularia racemosa*.

2.4.1.4 Period for Establishment

Period for establishment is determined by the time length for permanent rooting of a dispersed propagule on stranding ground. The dispersing propagules would need to develop root system to trap sediment in the process of anchoring or permanent rooting. The study of Rabinowitz (1978a) showed that the establishment of propagule on soil surface cannot occur during a single low tide. She gave an estimation of 5 to 15 days for the six mangrove species in Panama (*L. racemosa*, *A. germinans*, *A. bicolor*, *R. mangle*, *P. rhizophorae* and *Rhizophora harrisonii*) to develop anchoring root system.

2.4.2 Dispersal Potential

The mangrove propagules have some exclusive characteristics which enhance their dispersal in the water. Primarily, these propagules are viviparous where germination instantly takes place after fertilization without any dormancy period (Das and Ghose, 2003). The lack of dormancy in mangrove propagules is always linked to their efficient spatial dispersal. In the unstable habitat, reduction in dormancy for the released propagules would raise the chance of survival and successful early growth by rapid development after stranding at a favourable place (Clarke et al. 2001). Furthermore, propagules of different species vary in weight, shape, ability to float (buoyancy) and initiation of root and shoot as their dispersal potentials (Clarke et al. 2001).

2.4.2.1 Size and Weight

Size and weight is an effective indicator of the propagule morphology. Propagule length, as a crude measure of size, has no close correlation with the weight. For instance, *R. mangle* has seedlings with 20 to 25 cm length that weigh 14 g while *P. rhizophorae* has seeds of about 8 cm length but are heavier with weight of 86 g (Rabinowitz, 1978b). Moreover, the propagule size shows a simple relation with the two germination types, epigeal (cotyledons expanded and exposed) and hypogeal (cotyledons not expanded and not exposed). Normally, the propagules with epigeal germination are small such as *Avicennia* and *Sonneratia*, and those with hypogeal germination (*Xylocarpus* and *Nypa*) are large (Tomlinson, 1986).

In fact, there is a great variation in propagule weight and size among the mangrove species worldwide. It is due to the fact that there are various types of mangrove fruits and seeds available, such as those of viviparous and non-viviparous (Saenger, 2002). Generally, the viviparous propagules can grow to a length that is relatively longer than the crytoviviparous propagules and non-viviparous seeds. For instance, the viviparous propagules of *R. mucronata* are growing very long while attached to the mother plant; their mean length at maturity is about 57 cm (Drexler, 2001). While for the crytoviviparous *Avicennia officinalis*, their average length is only 2.3 cm (Das and Ghose, 2003).

According to Tomlinson (1986), the propagule length varies from 0.1 cm to 70 cm for 16 genera of mangrove. Das and Ghose (2003) studied the seed morphology and germination patterns of 17 mangrove species in Sundarbans, India and their result showed that the fruit or seed weight ranged from as little as 0.09 g (*Sonneratia apetala*) up to 77.06 g (*Xylocarpus granatum*) in average. The differences in propagule size and weight very likely influence the performance in dispersal phase individually. This point has been highlighted in several research studies including the famous tidal sorting hypothesis (Rabinowitz, 1978c).

From the observations, the larger mangrove propagules are always advantageous in their dispersal process with greater resistance to predation, adequate food reserves and rapid establishment as well as less probable to be damaged by water movements (Saenger, 2002). Nevertheless, the larger propagule is believed to be more restricted in dispersal range and has lower possibility in finding a favourable habitat than the smaller one (Kellman, 1975). As for those smaller size propagules, they are being produced by mother trees at large quantity (Tomlinson, 1986) and are found to be more efficient in water travelling (Rabinowitz, 1978c; Delgado, 2001).

2.4.2.2 Buoyancy

Mature mangrove propagules are buoyant right after they are released from the mother plant. The floating ability of the mangrove propagules is recognized as the most important feature that aid in their movement in the water and could be a decisive factor in their dispersal pattern (Rabinowitz, 1978a; Clarke, 1993). A buoyant propagule is always known to be an efficient means of wide spread in the water based dispersal (Saenger, 2002). Buoyancy is also an adaptation to protect the propagules themselves from inauspicious effects of water stagnation (Abdel-Razik, 1991). In a bigger picture, propagule buoyancy may enhance dispersal and can be of great significance in both vegetation dynamics and restoration (Van Den Broek et al., 2005).

Differential buoyancy capacity is found among the mangrove species; the propagules of some species can float for a relatively long time in the water and they can be classified as “floater”, whiles those with limited floating period are “sinker”. For the floater type propagules, there is an increase chance of long distance dispersal and deposition in the higher elevation zones (Rabinowitz, 1978c), but also may be carried out of the system by tidal action (Duke et al., 1998a). Therefore, propagules that remain buoyant and viable for a longer period are recognized to have wider range of dispersal. As for the rapidly sink propagules, their dispersal may be restricted and ended up with a limited spreading from the parent trees. However, the characteristic of a sinker appears to be an advantage for those pioneer species which colonized the frequently flooded environments such as mudflat along the seafront area (Delgado et al., 2001). *L. racemosa*, as a successful seaward dominant in the Costa Rican estuary, their propagules spontaneously lost buoyancy after a short period. The propagules were observed to sink within the first week of "enforced dispersal" in a mesocosm study by Delgado et al. (2001). Apparently, the propagule of *L. racemasa* performed as a sinker.

There is another condition in which the propagules sink and then refloat, as shown in *A. marina*. In a field observation by Clarke and Myerscough (1991), the propagules of *A. marina* sank earlier at the brackish site and then began to refloat after two days of release. Apart from that, buoyancy capacity may not be identical for all propagules of the same species. McKee (1995a) found that about 92 % of *A. germinans* propagules were categorized as floaters while the rest sank in the sea water (sinkers). As for *R. mangle*, there were approximately 87 % floaters and 13 % sinkers.

A number of studies have been conducted to investigate the buoyancy capacities of the interested mangrove species to measure their dispersal. In a study by Rabinowitz (1978a), the propagules of *A. germinans* were found to be always buoyant, whereas those of *L. racemosa* and *R. harrisonii* only remain buoyant for a couple of weeks. From the dispersal potential study by Clarke et al. (2001), the investigated species which tended to float over a wide range of salinities within 15 days of observation including *A. marina*, *Cynometra iripa*, *Xylocarpus mekongensis, Heritiera littoralis, Rhizophora stylosa*, and *Ceriops tagal*. The species that sank over all salinity solutions are *Bruguiera parvifloara*, *Aegialitis annulata* and *Aegiceras corniculatum*. They suggested that the species more abundant in downstream were less buoyant than species that more abundant in upstream. Contrarily, Van Den Broek et al. (2005) reported that seed buoyancy was highest for wetland species that grow in almost permanently inundated area and lowest for species of rarely inundated wet meadows. With these research findings, it is clear that the community occurrence along the hydrologic gradient was somewhat reflected by the propagule buoyancy.

Some researchers attempted to figure out the floating period for certain mangrove species in fresh water as well as in salt water. Rabinowitz (1978a) reported that *Laguncularia* in Panama has an average floating period of 23 days in freshwater and 31 days in saltwater. It showed greater buoyancy in seawater than in freshwater for the same species, in which the result was later supported by the study of Clarke et al. (2001). Furthermore, the propagule buoyancy and weight have been investigated for their correlation. From the observations of 14 tropical mangroves, the weight and buoyancy are positively correlated, with the small propagules being less buoyant than the large ones (Clarke et al., 2001). In a study of pre-dispersal herbivory, Minchinton (2006) found that the intact propagules of *A. marina* were initially less buoyant than those that damaged by larval insects. However, the enhancement in buoyancy did not increase the dispersal distance of these insect-damaged propagules because their viability decline over time due to continuing destruction by the insects.

Buoyancy is associated with several different features of the propagule such as the radicle (as in *Rhizophora*), the pericarp and cotyledons (*Avicennia*), the endoderm (*Xylocarpus*), the seed testa (*Nypa* and *Sonneratia*) or the cotyledon (*Pelliciera*) (Saenger, 2002). Any changes in these features are supposed to affect the buoyancy. For instance, the *A. marina* propagules that shed their pericarps sank in the sea water while those that retained their pericarps floated (Clarke and Myerscough, 1991). Other specific adaptations, like aerial tissues and hairs that may trap air bubbles are found to enhance buoyancy for most of the halophytes (Huiskes et al., 1995). Noted that mangroves are kind of halophytes, but they can grow either in salt or fresh water environment, so called “facultative halophyte” (Ball, 1988a).

2.4.2.3 Initiation of Root and Shoot

Initiation of root and shoot indicate the germination and early growth of a plant seed. Mangrove propagules are capable to develop root and shoot during the water dispersal process. Referring to Clarke et al. (2001), the propagules of 14 tropical mangrove species showed a wide range of times taken to develop roots during “enforced dispersal”. For those studied propagules, the timing of root initiation was observed to range from 4 days to more than 3 weeks. It shows a very different strategy in dispersal and early establishment and it may be used to interpret the spatial distribution of a species. In addition, patterns of root initiation among the mangrove species appeared to be unrelated to buoyancy and propagule orientation (Clarke et al., 2001).

Clarke et al. (2001) also found that the abundance of mangrove species in upstream and downstream can be interpreted by the ability of shoot initiation and development over a range of water salinities. Their result showed that the species which grow abundant in upstream were positively correlated with species that slower in shoot initiation and grew taller in fresh and brackish water. Whereas, the species that dominant in downstream were positively correlated with species that have faster shoot initiation, grew well in higher salinities and could initiate shoots over a wide range of salinities.

Observation of root and shoot initiation can tell how good a propagule develop in an environmental setting for early establishment. The root growth can be reflected by several parameters including length of the longest root, number of root and root dry weight (Van Noordwijk and De Willigen, 1991). As for the shoot, the development is indicated by time for leaf expansion (Delgado et al., 2001), leaf count and leaf dry weight (Allen et al., 2003).

2.5 Propagule Dispersal Studies

Dispersal (movement of individuals between locations) and demography (dynamics of individuals at a location) are equally important in studying the distribution and abundance of a plant species (Bullock et al., 2006). However, the dispersal study lacks development and receives far less attention than the demography due to the inherent difficulties to trace movement of individuals. Similarly, the mangrove dispersal is not widely investigated even though this topic has been repeatedly emphasised and discussed for explaining mangrove distribution, zonation and colonisation. Available literatures on the field studies of mangrove dispersal are limited to several species, including *R. mangle* (Davis, 1940; Sengupta et al., 2005; Sousa et al., 2007), *Kandelia candel* (Yamashiro, 1961), *R. mucronata*

(Chan and Husin, 1985; Komiyama et al., 1992), *A. marina* (Clarke, 1993), *C. tagal* (McGuinness, 1997), *A. germinans* and *L. racemosa* (Sousa et al., 2007).

Davis (1940) tried to evaluate the dispersal ability of *R. mangle* propagules by applying the release and recapture method. He discovered that regular dispersal occurred over several kilometers. After twenty years, Yamashiro (1961) conducted the release and recapture experiment on *K. candel* in southern Japan. He followed the painted seedlings of *K. candel* over a period of 30 days. As a result, most propagules were carried more than 50 m away from the source and also not more than 2 % retrieved under the maternal tree. In Malaysia, Chan and Husin (1985) found that majority of *R. mucronata* propagules dispersed less than 20 m from the parent plant, and only a few propagules dispersed more than 65 m. After that, Komiyama et al. (1992) carried out a dispersal study in a mangrove forest of Ranong, southern Thailand. They concluded that most propagules of *R. mucronata* were stranded within 300 m from the release point within one month period. Clarke (1993) concluded that the dispersal of *A. marina* propagules was restricted to local range after he conducted a field experiment in south eastern Australia and found that approximately 78 % of propagules stranded within 1 km from their origin. For *C. tagal* in northern Australia, McGuinness (1997a) found that 76 % of the fallen propagules were remained within 1 m from the parent trees and 15 % of them were within an area between 1 m to 3 m and the rest (9 %) were dispersed more than 3m.

In a more recent study, Sengupta et al. (2005) examined the potential dispersal distance of *R. mangle* propagules in southwestern Florida by comparing deposition density with landscape characteristics of mangrove forests. The technology of remote sensing and Geographic Information Systems (GIS) were utilized to identify the landscape characteristics. The results indicated that increasing density of propagules stranded on beaches was related negatively to the distance of the deposition sites from the nearest stands of *R. mangle*. Besides, area size of those forests was found related to the propagule deposition but only effective in low-energy environments. Sousa et al. (2007) examined the dispersal patterns of three new world species (*R. mangle*, *A. germinans* and *L. racemosa*) in Punta Galeta, Panama. The propagules of all three species showed limited dispersal (mostly within 40 m from origin) and all moved seaward rather than travelled to inland areas.

In short, from these field dispersal studies, it can be summarized that the mangrove propagule dispersal is often localized, as previously mentioned by Clarke and Myerscough (1993), Minchinton (2001) and Saenger (2002). Moreover, some genetic analyses have shown that the mangrove gen flow is limited by distance, which further proven the dispersal may be localized (Duke et al., 1998b, Melville and Burchett, 2002). Similar dispersal pattern may happen to other halophytes as well. Rand (2000) have studied on the seed dispersal of five halophytic forbs and a shrub across a New England salt marsh tidal gradient. The findings indicated that those species have localized dispersal or limited movement out of parental environment. Therefore, long distance dispersal is always considered as a rare success and it may be governed by chance events (Ehrlén and Eriksson, 2003).

The field dispersal studies were mostly restricted at local scale and thus the outcomes may not comprehensively describe the dispersal nature for particular species. Nevertheless, the works have benefited the subsequent researches as important guidelines and background knowledge. One of the key points from these studies is that the mangrove dispersal is somehow related to the attributes of dispersal units (size, buoyancy, period of “obligate dispersal”) and their responses to the environmental conditions (tidal action, water current and wind effect) (Rabinowitz, 1978a, c; Clarke and Myerscough, 199l; Clarke and Myerscough, 1993; Clarke, 1993).

2.6 Early Growth of Propagule

Mangrove propagules lack dormancy and continuously develop while on the maternal trees and during dispersal (Rabinowitz, 1978c). The early growth of a propagule is indicated by the development of root system and production of shoot. Initiation of both young roots and shoot can occur during the propagule dispersal stage (see subtopic 2.4.2.3; Clarke et al., 2001). Development of root and shoot facilitates the anchoring of a dispersing propagule as well as establishment at stranding site (Rabinowitz, 1978a). The process of early growth is different according to type of propagule. But, essentially, the propagule grows with initiation of root and shoot and then permanent rooting, leaf expansion and finally erected from the ground.

Referring to Howe and Smallwood (1982), early establishment of a plant is the process during which a germinating seed takes root, finish up parental provisioning and consider independent as a seedling. In mangrove system, generally, the propagules that have firmly rooted and possessed at least one leaf are assumed fully established (Saenger, 2002). However, before the propagules can successfully