

**INFLUENCE OF ENVIRONMENTAL
STRESSORS ON PLANT GROWTH PLASTICITY
OF *Mimosa pigra* TOWARDS CHANGES OF SOIL
CHEMICAL PROPERTIES**

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UNIVERSITI SAINS MALAYSIA

2020

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CHEMICAL PROPERTIES**

by

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Thesis submitted in fulfilment of the requirements

for the degree of

Doctor of Philosophy

February 2020

ACKNOWLEDGEMENT

All praises to Allah s.w.t because of his blessed I can complete my field work and writing successfully. I am deeply indebted and would like to give big appreciation to my main supervisor, Associate Professor Dr. Asyraf bin Mansor and my co-supervisor, Dr. Hasnuri binti Mat Hassan for their endless knowledgeable guidance in academic and non-academic matters throughout my journey.

I would like to thank Ministry of Education Malaysia (KPM) under scheme MyBrain15 (MyPhD) for providing financial support to assist this research program. Big appreciation to Malaysian Agricultural Research and Developmental Institute (MARDI), Serdang for assisting and conducting several intricate analyses for this project.

Thanks to all academic and non-academic staff of School of Biological Sciences, Universiti Sains Malaysia that helps me to get through all the fieldwork and lab work studies. Deep thanks also to all my fellow friends from Lab Botany (Fasihah, Norahizah, Syafiq, Diana and Azila) and Lab 321 (Izzuddin, Azira and Fariza), as well as my dearest Dr Wan Norhaniza W. Hassan (USM) and Dr Suziana Mat Yassin (USM) for their support, time and idea.

Special thanks to my beloved parents, Mr. Ali Sulaiman and Mrs. Salsiah Mohd Arsad, my lovely siblings (Al-Wafi, Farahiyah and Saiful) and other family members for their endless prayer, support and great encouragement. Deep thanks to everyone who has helped me directly or indirectly and prayed for my success during my entire study.

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LIST OF SYMBOLS AND ABBREVIATIONS

cm	centimetre
mm	millimetre
mg	milligram
ml	millilitre
min	minute
M	molarity
psi	pounds per square inch
rpm	revolutions per minute
g	gram
kg	kilogram
i.e.	in essence (in other words)
e.g.	exempli gratia (for example)
°C	degree Celsius
n	number of replication / observations
N	total of sample size
p	statistical significance value
r	correlation coefficient

**KESAN TEKanan PERSEKITARAN KEATAS KELENTURAN
PERTUMBUHAN POKOK *Mimosa pigra* TERHADAP PERUBAHAN SIFAT
KIMIA TANAH**

ABSTRAK

Kejayaan penaklukan spesies tumbuhan invasif kebanyakannya dibantu oleh sesetengah ciri-ciri penyesuaian morfologi dan fisiologi. Penubuhan anak benih *Mimosa pigra* pada awal waktu pertumbuhan khususnya dalam persekitaran yang tertekan adalah sangat penting untuk proses naturalisasi spesies ini. Spesies ini dianggap sama ada mampu untuk mengekalkan kecergasan yang tinggi dibawah kondisi yang tidak selesa atau mempunyai kelebihan ke atas persekitaran yang aman, atau kedua-duanya sekali. Sebagai tumbuhan kekacang, spesies ini berpotensi sebagai penggalak tanah selain menjadi tumbuhan pengambil nutrisi tanah yang agresif atau “exhaustive”. Untuk menilai perkara tersebut, tiga keadaan sumber tekanan manipulatif telah dikenakan kepada *M. pigra* untuk mengenal pasti ciri-ciri berkait yang membolehkan *M. pigra* bersifat invasif di bawah kondisi tertekan dan sama ada *M. pigra* menunjukkan mekanisme adaptasi yang kuat sebagai tindak balas kepada keadaan pertumbuhan yang manipulatif. Selain itu, perubahan nutrisi tanah yang disebabkan oleh perubahan pertumbuhan *M. pigra* juga telah dinilai. Biji-biji benih *M. pigra* telah ditanam dan berkembang sehingga menghasilkan pod matang di bawah tiga keadaan pertumbuhan yang berbeza; 1) Persaingan intraspesies (empat subplot bersaiz sama telah ditanam dengan 25 g, 50 g, 75 g dan 100 g biji benih *M. pigra*), 2) Teduhan cahaya awal (biji benih telah berkembang di bawah empat kecerunan cahaya ambien antara 25 % hingga 75 %) dan 3) Tekanan air jangka pendek (pengairan telah dihentikan pada peringkat pertumbuhan pokok yang berbeza

dan telah dipulihkan selepas 12 hari). Prestasi pertumbuhan *M. pigra* dari kesemua keadaan telah dianalisa dari segi; morfologi, fisiologi (pengambilan dan peruntukan nutrisi pokok), prestasi fenologi dan kelenturan pokok terhadap sifat-sifat kimia tanah. Kajian ini mendapati bahawa ciri-ciri kelenturan morfo-fisio dan fenologi *M. pigra* adalah tinggi terhadap perubahan kepadatan spesies dan sumber cahaya disebabkan kebanyakan ciri-ciri terkesan dengan perubahan persekitaran pertumbuhan, $p < 0.05$. Manakala berdasarkan nisbah N: P tumbuhan, *M. pigra* yang tumbuh di bawah semua keadaan pertumbuhan dan tahap-tahap tekanan tidak menghadapi kekurangan N mahupun P (nisbah di antara 10 hingga 22 N g⁻¹ P g⁻¹). Kajian ini juga mendapati kelenturan ciri-ciri pertumbuhan morfologi (pertumbuhan dan biomas), pengambilan N dan peruntukan P di dalam akar dan kecergasan pokok (perubahan dalam permulaan kematangan reproduktif) adalah tindak balas perkembangan evolusi yang signifikan yang dianggap bertanggungjawab terhadap penubuhan *M. pigra* dalam persekitaran yang diberikan. Manakala, penubuhan spesies dalam keadaan manipulatif yang diberikan telah merubah sifat kimia tanah dan kesannya bergantung kepada persekitaran. Penubuhan spesies ini telah meningkatkan ketersediaan N (pada keadaan persaingan yang tinggi, 522 % dan tekanan air, 75 % hingga 98.4 %), P (pada keadaan teduhan, 2355- kali ganda hingga 3927- kali ganda) dan K (pada keadaan persaingan yang tinggi, 83 % hingga 425 %). Manakala, pertumbuhan *M. pigra* menurunkan jumlah N, P dan K dan bahan organik tanah. Sebagai kesimpulan, *M. pigra* bukan tumbuhan pemulihan nutrisi tanah mahupun “exhaustive” disebabkan kesan tumbuhan ini adalah berbeza antara keadaan-keadaan pertumbuhan manipulatif dan tahap-tahap tekanan. Walaupun spesies ini dikategorikan sebagai invasif, peranan *M. pigra* dalam memperbaiki status nutrisi tanah dalam jangka masa panjang boleh dinilai dengan lebih lanjut.

INFLUENCE OF ENVIRONMENTAL STRESSORS ON PLANT GROWTH
PLASTICITY OF *Mimosa pigra* TOWARDS CHANGES OF SOIL
CHEMICAL PROPERTIES

ABSTRACT

The succession of invasive plants species is mostly facilitated by certain adaptive morphological and physiological traits. The establishment of *Mimosa pigra* seedling at early growth period, particularly in stressful environment is most crucial for the naturalization of this species. This species is assumed as either being able to maintain high fitness under unfavourable condition or has advantage over favourable environments, or both. As a legume plant, this species might has potential as soil enhancer despite of become exhaustive. To assess this, three manipulative stress growth conditions were imposed on *M. pigra* to specifically identify related traits enabling *M. pigra* invasiveness under stressful conditions and whether *M. pigra* expresses high adaptability mechanism in response to manipulative growth conditions. Furthermore, the soil nutrient changes relative to the effects of *M. pigra* growth was also evaluated. The seeds of *M. pigra* were seeded and grown until the plant successfully produced mature pod under three different growth conditions; 1) Intraspecific competition (four similar size subplots were seeded with 25 g, 50 g, 75 g and 100 g of *M. pigra* seeds), 2) Initial light shading (seeds were grown under four different light gradient ranging from 25 to 75 % of ambient light) and 3) Short-term water stress (water withdrawal at different plant growth stages and restored after 12 days). The growth performances of *M. pigra* from those 3 different conditions were analysed in term of; morphological, physiological (plant nutrient uptake and allocation), phenological performance, and the plasticity of the plant towards soil

chemical properties. This study found the morpho-physio and phenological plasticity of *M. pigra* were high towards changes in species density and light resources as most of the traits were affected with the changes of growth conditions, $p < 0.05$. Meanwhile based on plant N:P ratio, *M. pigra* grew under different growth conditions and level of stresses had neither N nor P limitation (ratio ranged between 10 to 22 N g⁻¹ P g⁻¹). This study also found that the plasticity traits of morphological growth (growth and biomass), N uptake and P allocation in roots and plant fitness (changes in onset of reproductive maturity) are the significant evolutionary growth respond that are deemed responsible for *M. pigra* establishment under given environments. Meanwhile, the species establishment in the manipulated conditions had changed the soil chemical properties in which the effect was environmental-dependent. The species-establishment had increased the availability of N (high competition, 522 % and water stress, 75 % to 98.4 %), P (shade condition, 2355-fold to 3927-fold) and K (high competition, 83 % to 425 %). Meanwhile, the growth of *M. pigra* had a significant decrease of total N, P and K, and SOM. As a conclusion, *M. pigra* is neither restorative nor exhaustive, which the effect was dissimilar among the manipulative growth conditions and stress levels. Although the species can be classified as invasive, the role of *M. pigra* in improving soil status for a long run can be further assessed.

CHAPTER 1

INTRODUCTION

1.1 Background of study

Mimosa pigra L. is a woody legume plant native to tropical America is reported as an invasive noxious weed (Global Invasive Species Database, 1998). The population of this species has expanded from its native (to South and Central America) throughout others tropical countries, including in Malaysia (Napompeth, 1983). In Malaysia, this species was gazetted in as an A2 pest in the 4th Schedule of the Agriculture Pest and Noxious Plants (Import/Export) Regulation (Anwar & Sivapragasam, 2001). This species is highly competence and thus can easily colonized and established in wide range of ecological habitats (Marambe *et al.*, 2004; Asyraf *et al.*, 2007; Beilfuss, 2007). The invasiveness of *M. pigra* causes it difficult to be restrained from spread to the other area. Therefore, *M. pigra* becomes the target of a large biological control program as chemical and mechanical methods are seemingly providing only short-term solutions. The classical biological control appears to be more effective option for the long-term management of this weed.

The invasiveness trait of this invasive weed species may be enhanced based on the habitat dynamic, the characteristics of the invaded habitats (Casper & Jackson, 1997; Funk, 2013) and the adaptive plasticity of the invasive species (Richards *et al.*, 2006; Hulme, 2008; Skalova *et al.*, 2013). In the field condition, *M. pigra* is not as invasive as in its native habitat, compared when it invade a new habitat (Lonsdale, 1992). However, series of this species intrusion in new regions in which the species might undergo adaptive evolutionary changes had adversely affected the ecological systems as well as the native plant and animal diversity of the particular area. As the issue is continuously happened, that will give daunting challenge for environmental

managers, researchers and farmers to encounter with the problems arise (Waterhouse, 1993; Walden *et al.*, 2004; Mohd-Shariff & Abu-Bakar, 2006).

1.2 Research significance

Mimosa pigra has ability to shift environmental balance and thus performed distinct dominant character in field. The plant has high rate of establishment and rapid growth regardless of environment once it has been introduced or invaded (Lonsdale, 1992; Walden *et al.*, 2004). The invasion become worst as this species form monospecific stand (Braithwaite *et al.*, 1989) causing impenetrable dense thicket which slowly displacing native or/and coexist species in the invaded area (Lonsdale, 1992; Paynter, 2004; Walden *et al.*, 2004; Beilfuss, 2007).

The adaptive mechanism shown by the invasive species in certain locality maybe govern by the response patterns of morphological and physiological traits of the plant (Richards *et al.*, 2006; Hulme, 2008; Davis, 2009; Skalova *et al.*, 2013). Based on Funk (2013) the succession and naturalization of a specific invasive species may govern by the ability of the species to acquire the available resources successfully compared with the native species. Besides, Crisóstomo *et al.* (2007) had highlighted that an observation and a study of physiology, development and characteristic of a specific species may give a certain advantages in the establishment and colonization of new areas. On top of that, Van Kleunen *et al.* (2011) also acknowledged that the responses are alternatively driven by an intrinsic higher tolerance to the stressor due to constitutive trait differences.

The disparate interest of those opinions might give an insight in conducting a research on factors explaining *M. pigra* invasiveness as little study has been conducted specifically on this species. Besides Hulme (2008) has long suggested

that, an array of experiment should be made to analyse and discern the plant different fitness response scenarios that in multiple growth conditions. In order to gather the comprehensive data, a practical approach has been designed to obtain all the information on the plant responses within the study period. Hence, this study has been designed to monitor the *M. pigra* functional traits (i.e., morphological, phenological and physiological) under variable growth conditions to give an insight explaining and identifying a suite of general traits elucidate its invasiveness.

The impact of invasive species invasion can be variable as it may alter the norm of the invasive plants' beneficiary or/and the indigenous of the ecological system (particularly, soil environment and impact to neighbouring plant) (Leicht-young *et al.*, 2009; Weidenhamer & Callaway, 2010). Despite the severity impacts of *M. pigra* on the global ecological biodiversity, information on the effect of this species to the soil chemical is lacking. However, Miller *et al.* (2004) had reported that high colonization of *M. pigra* had increased and improved soil fertility in surface soil, which was not experimentally being proven by the study. This might highly related as *M. pigra* is categorized as legume plant with the ability to fix nitrogen and associate with beneficial microorganism (mycorrhiza) (Lonsdale, 1992; Loik, 2007).

1.3 Problem statements

Capability of invasive species particularly *M. pigra* to invade and establish in wide range of habitat type, in which the invasion is not ecosystem-specific has been long known. However, there is a scarcity of experimental research that confined on how manipulative environments might influence the entire functional structure of *M. pigra* and biogeochemistry of the growth environment especially in Malaysia. Thus, in this study, the *M. pigra* was screened for the ability to acquire the available soil nutrient and its impact on the soil chemical properties.

1.4 Research objectives

- (i) To quantify the best morpho-physiological adaptive mechanism of *M. pigra* in response to manipulative growth conditions.
- (ii) To determine the nutrient status in *M. pigra* under manipulative resources conditions.
- (iii) To identify related plant functional traits which enable *M. pigra* establishment under different stress conditions.
- (iv) To determine the soil chemical properties changes relative to the *M. pigra* manipulative growth conditions.

CHAPTER 2

LITERATURE REVIEW

2.1 Introduction

Mimosa pigra L. or known as semalu gajah in Malaysia (Heard, 2004) is listed as invasive woody weed (Global Invasive Species Database, 1998). The presence of *M. pigra* was firstly recorded in Malaysia in 1980 by Department of Agriculture (DOA). This species has created massive ecological and economical problem in ecosystems functioning regardless of habitat invaded by the species (Baki *et al.*, 1996). Numerous studies have been reported on the habitat alteration which the species become a problematic to the aboveground living organism which include the habitat competition with the native plant species and the alteration of animal nest (Lonsdale, 1993; Walden *et al.*, 2004; Charles & Dukes, 2007). The issue may linked from aboveground to the belowground habitat encompass of competition with soil resources (water and nutrient) or the alteration of the soil mechanical and chemical characteristics.

Mimosa pigra (Fabaceae) is a woody legume plant categorized under sub-family Mimosaceae. It is characterized as a semi-aquatic weedy shrub plant that is native to South and Central America as well as Mexico (Wilson & Pitkethley, 1992; Marko, 1999; Paynter, 2004). Legume plants are known to have an ability to fix nitrogen and this was also demonstrated by *M. pigra* as it also produced nodule for atmospheric nitrogen fixation process (Napompeth, 1983). Several previous studies revealed interesting facts whereby habitat that having invasive species has increase in aboveground biomass and soil nutrient concentration (Vitousek *et al.*, 1987; Levine *et al.*, 2003; Dassonville *et al.*, 2008). A study on *Lupinus perinnis* by Lee *et al.*

(2003) revealed that this weedy legume plant was able to enhance the N concentration of non-legume adjacent plant.

Theoretically, the invasion of *M. pigra* might have a relationship to the soil fertility which may contribute on soil nutrient increment. However, as an invasive legume species there is a possibility for *M. pigra* to perform; which either contribute to the nitrogen in soil or as invasive character that eliminate or impede native species by competition of nutrient (acquire more nutrient than neighbouring species) or growth spaces which no study has been made to prove these factors. The impact of *M. pigra* invasion on soil properties status and the capacity for this plant to acquire soil nutrient are not well understood. To date, only Suwignyo and Wiroatmodjo (1983) had covered strive mechanism of *M. pigra* in wide environment. However, there is an ambiguity whether the ability of the nutrient acquisition by *M. pigra* is the principal factor for plant species and habitat alteration caused by this species.

The aim of this review is to provide an overview of the basic information on the biology of *M. pigra* and its growth in wild environment. This review also provides a previous and current issue on the effect of *M. pigra* invasion on species and habitat alteration. An intense overview also being made on the invasion impact of *M. pigra* and several legume plants on soil nutrient status.

2.2 The exotic *Mimosa* species in Malaysia

The genus *Mimosa* comprises of 300 to 500 species worldwide (Nielsen, 1992). In Malesia floristic region, there are three introduced and naturalised species (i.e., *Mimosa pudica*, *Mimosa invisa* and *Mimosa pigra*) that also are assigned as one of major important weeds in Southeast Asia (Waterhouse, 1993). In Malaysia, the genus

Mimosa (particularly *M. pigra*, *M. pudica* and *M. invisa*) is known for its weedy elements, however, *M. pigra* is better known for its invasive trait and is recorded in 100 world's most exceedingly invasive alien species (Baki *et al.*, 1996; Global Invasive Species Database, 1998; Lowe *et al.*, 2000).

Invasive traits can be defined differently within certain range of growth conditions particularly in competitive environment. The traits can be found as early as juvenile stage as the most competitive plant species able to survive and confer greater survivorship at low growth conditions (Craine & Dybzinski, 2013). It is very complex to identify 100 invasive species from around the world that truly invasive than any others. Hence, the invasive species were chosen for the list according to two profound criteria; 1) the serious impact on biological diversity and/or human activities and 2) the illustration of critical issues encompassing biological invasion (Global Invasive Species Database, 1998). Thus, every species that meet these criteria will be considered into the invasive species.

2.3 The phenology of *M. pigra*

Mimosa pigra is a sexually propagated species in which reproduction and dissemination agent is mainly by seed. It flowers every month but abundant flowering and seed production occur mostly during the rainy season all year round (Lonsdale, 1992). Seeds are produced in individual seed pods segments that are covered with bristles to help the pods float and spread via water. The average number of pods produced by a healthy *M. pigra* are 58 pods per branch which made 1144 seeds (with 19 seeds per pod) (Wara-Aswapati, 1983) and in Malaysia it can produces seed all year round (Asyraf, 2007). Under normal conditions, an individual of *M. pigra* can produce an average of 95, 000 seeds per year

(Suwunnamek, 1983; Lonsdale, 1992). Meanwhile, in large infestation areas, annual seed production may reach up to 220, 000 (Walden *et al.*, 1999; Thorp, 2001). High productivity of the seeds therefore become one of significant traits of an invasive species contributing to the high species abundance in invaded area and contributing to the highly species spread throughout different geographical areas and ecosystems (Radosevich *et al.*, 2007).

From seeds, the plant starts to flower around the age of 6 to 8 months following germination under ideal growing conditions (Lonsdale & Abrecht, 1989; Lonsdale, 1992; Marko, 1999). However, the flowering process varies in different climatic conditions. The development of its flowers takes approximately 7 to 9 days and the production of mature seed pods occurs within 25 days or more. The whole process from flower buds to ripe seeds takes about 5 weeks (Wara - Aswapati, 1983). Precedent study had reported that the earliest first flowering usually occurs in 2 to 4 months after germination (Binggeli, 2005) with the average plant height of 77 cm. The trees can only produce at least two flowers per plant at the beginning of seedling growth and none of these flowers could produce seeds after the first flowering. The first pods may be obtained only from flowers that are produced within 18 weeks (Marambe *et al.*, 2004).

2.4 The morphological and growth performance of *M. pigra*

The plant is medium in size with a height of 3 to 3.6 m and can grow up to 6 m tall (Suwunnamek, 1983; Walden *et al.*, 1999). Stems are greenish in young plants with a diameter of 2.5 to 7.5 cm that are armed with scattered large prickles, while older stems become woody when matured (Paynter, 2004). The fernlike compound leaves are green in colour up to 20 to 25 cm long and bipinnate, consisting of sharp

spines that fold together when touched or injured, and at nightfall. The root is a branching taproot, reaching between 1 to 2 m depth. In its native region, *Mimosa pigra* tends to grow in smaller sizes than when it grows in an invaded area with low productivity of pods and seeds (Lonsdale, 1992).

Mimosa pigra favours a wet-dry tropical climate and grows in open moist sites such as floodplains, coastal plains, and river banks (Marambe *et al.*, 2004; Beilfuss, 2007). The humidity in such places encourages seed germination especially as flood waters recede, allowing the seeds to undergo different stages of environmental triggering factors (Sheded & Hassan, 1999). This species is able to establish in wide range of environments in Malaysia, which had been reported inhabited in open, disturbed and derelict area by Baki *et al.* (1996) and Asyraf and Crawley (2011). In addition, Paynter (2004) also reported that the wet-dry season as such in Malaysia is the best time for the invasion process and promote the establishment of *M. pigra*. The rapid establishment and vigorous growth of *M. pigra* in wide range of environments gave higher chances for this plant to become more invasive when introduced into new locality (Theoharides & Dukes, 2007; Hulme, 2008). Thus, its population has been extended from its origin country which is tropical parts of central and south America throughout others tropical country.

2.5 The factors govern the invasive species establishment under wide range of environments

Invasive species are known with the higher traits of biodiversity threatening, by locally displacing ecosystem balancing and functioning in many ways. The traits are governed by multiple functional traits (i.e., morphological, physiological and phenological features) which depend on species- and site-specific. These traits are

measurable at plant individual level which regulates the plant performance and individual fitness by means of their impact on growth, survival and reproductive output (Theoharides & Dukes, 2007; Violle *et al.*, 2007). The rapid spread and establishment of invasive plant species depend on particular traits of both the invasive plant and the condition of the invaded habitats (Traveset & Richardson, 2006).

Referring to Funk (2013), invasive species are tend to invade a high-resource and disturbed environments. The ability to invade such high-resource environment may govern by the ability of the species to fully acquire the resource availability compared to the native plant species. However, the existence and the succession of some invasive species in low-resource environment may occur through resource conservation. It is well explained as the plant allocating the available resource efficiency by display a slow growth hence, retained high tissue longevity. Invasive species are more generalist in high competition area owing to the high value of performance-related traits (i.e., physiology, leaf-area allocation, shoot allocation, growth rate, size and fitness) hence, survived and successfully compete with native non-invasive species. Beside those factors had briefly clarified and explained the succession of the first stage of invasion (Crisóstomo *et al.*, 2007; Van Kleunen *et al.*, 2010).

Non-invasive (e.g., *Mucuna bracteate*) and invasive legume plant (e.g., *M. pigra*) is known to have nodules that help the plant to fix nitrogen throughout entire growing season if conditions are ideal (Brewin, 2010). Many nitrogen fixers are correlated with weedy species as well as invasive legume plant and, as faster-growing species it can utilize nutrient richness more quickly than non-legume slow-growing species (Haubensak & Parker, 2004). Therefore, nodule had play

marginal factors for the species establishment and confers the plant the ability to grow and establish even in the low soil fertility (Rodríguez-Echeverría, 2009). However, any stressor factors (e.g., nutrient status, relative humidity, and varying temperature and soil water) that reduce plant activity (i.e., leaf performance or photosynthesis) will reduce nitrogen fixation process and nodule functioning that could contribute to early nodule senescence (Sanz-Sáez *et al.*, 2010; Aranjuelo *et al.*, 2014).

The efficiency of nutrient uptake also one of the key traits of invasive plant species, by displaying high aboveground plant biomass and nutrient concentration (Dassonville *et al.*, 2008). The invasive plant also has an ability to outcompete for nutrient with adjacent plant by resources pre-emption (Asner & Vitousek, 2005) that further deemed of the plant survivability through the economically use of nutrient acquisition prior to death. These functional traits are important mechanisms that govern the species successional in most of invasion series.

The invasion of invasive species always come in a form of dense colonization particularly *M. pigra* is partly attributed from the strong fitness traits; large number of seed production, long dormancy, high germination rate, rapid growth and establishment (Lonsdale, 1992). High seed production of the plant is not only ensure the successful rate of species establishment and spreads (Parciak, 2002), but also a good strategy in ensuring the sustainability of future offspring which contributed from the the accumulation of seed bank and long seed dormancy. The magnitude and frequency of human intervention and history of plant invasion also promote series of invasion to the area (Radosevich *et al.*, 2007; Laube *et al.*, 2015) as the situation has created feasible condition to for plant growth. The climatic status and dynamic activities happened in such places encourages seed germination

which allow the seeds to undergo different stages of environmental triggering factors (Sheded & Hassan, 1999).

2.6 The impact of invasive species (including *M. pigra*) invasion on the ecosystem's dynamic

2.6.1 Aboveground environment

This alien species profoundly altering many communities and ecosystems balance by suppress and outcompete with other native plant species. This impact had declined native species richness and cover, which converting the area into unproductive ecosystems which are only able to sustain lower levels of biodiversity (Global Invasive Species Database, 1998; Gurevitch & Padilla, 2004). The ability of plants to impede and displacing coexistence species may govern by several factors such as resources pre-emption, plant exudation and soil microbial effect on soil (Haubensak & Parker, 2004). Rapid changes of plant community (i.e., grassland to woodland) are closely associated with rapid substantial changes of soil fertility. The shifting of community composition related to the exotic species invasion may potentially from the nutrient enhancement and the negative effects found in the invaded soils (Haubensak & Parker, 2004).

Some species like *M. pigra* is resistance to adverse environmental conditions, whereby the plant can withstand anaerobic conditions (as an emergent plant), and eventually becomes a serious threat to the various species of flora and fauna in both terrestrial and aquatic area (Lonsdale, 1993; Walden *et al.*, 2004). The extensiveness of *M. pigra* infestation, whilst covers huge areas of standing waters and the bank of waterbodies (Binggeli, 2005) has become major concerned for the sustainability function of the aquatic ecosystems. In Thailand, the infestation of *M.*

pigra in reservoirs had increased the build-up of sediment in reservoirs which limit the useful life of the reservoirs (Robert, 1983) and affect alteration of hydrological systems in Australia dam (Walden *et al.*, 2004). Several national and international wetlands gazetted as Ramsar sites were potentially are at risk owing to the *M. pigra* infestation (Walden *et al.*, 2004).

2.6.2 Belowground (soil chemical properties)

Shrub encroachment in grassland or any plain area can cause significant rapid changes not only in species habitat alteration, but seemingly to the soil nutrient levels and distribution. There are three possible situation in invaded area that lead to the changing of the soil environment (particularly soil microbial community); the ability of the invaded plant to acquire and outcompete for the nutrient with neighbouring non legume plant (i.e., exhaustive mechanism), the ability of the plant to self-fertilizing and promoting the mutualism interaction with soil microbes (i.e., restorative mechanism) and differences sites of invasion may significantly determine the magnitude of the invasion and the status of the invaded soil properties (Asner & Vitousek, 2005; Dassonville *et al.*, 2008; Kao-Kniffin & Balsler, 2008). These possible factors may determine the augmentation of soil nutrient concentration and providing substantial nutrient to fulfil others plant needed relative with the invasion series.

The invasions alter the major components of soil chemical properties such as carbon (C), nitrogen (N), phosphorus (P) and potassium (K) and, quality and quantity of resource available to soil microorganism. This occurrence, in turn shift the composition and abundance of microbial members and lead to the alteration of nutrient pools and cycles in soil (Ehrenfeld, 2003). Changes in soil fertility with

invasion might be distinctive with N₂-fixing plants and non-fixing plants, and the effect can vary even between congeneric species. Certain plants have different advantages over nutrient requirements such as N (as legume plants able to do N fixation) and P (root clusters by legume and non-legume plants) (Koerselman & Meuleman, 1996). However, the changes on the soil will be huge if the invaded plant has an ability to fix nitrogen (Haubensak & Parker, 2004).

Miller *et al.*, (2004) had reported that high colonization of *M. pigra* increased soil fertility (organic carbon, total N, available P and available zinc) and improved nutrient redistribution from the lower soil profile to the surface. Legume invasive species had been reported to increase the soil nitrogen availability via nitrogen fixation in invaded areas (Levine *et al.*, 2003). However, most of the fixed nitrogen went directly into the plant and little amount leaked into the soil. The fixed nitrogen would directly go into the soil when vegetation (i.e., roots, leaves and fruit) of the legume die and decomposed (Berg *et al.*, 1995; Haubensak & Parker, 2004). As the plant grows older and produces greater N-rich litterfall, the N availability in soil may increase. Thus, uptake of available N becomes more important than nitrogen fixation as the invasion proceeds (Haubensak & Parker, 2004; Troeh & Thompson, 2005). Besides N fixation process, the increasing nutrient status through mineralization and nitrification processes was also common in legume invaded soils (Ehrenfeld, 2003), which the area may have potential for establishing native or introduced vegetation.

The impacts of invasive species invasion on soil nutrients are depending on the species invaded and the locality conditions (species- and site-specific) (Meyerson *et al.*, 2000; Belnap & Philips, 2001; Dassonville *et al.*, 2008). Plant composition of the invasion area, the ecosystem traits or the invasion site properties will enhance

or negating the impact of plant invasion on the magnitude activities of soil microorganism and nutrient status (Ehrenfeld, 2003; Kao-Kniffin & Balser, 2008). Studies by Duda *et al.* (2003), Chapuis-Lardy *et al.* (2006) and Liao *et al.* (2008) reported an increase of soil nutrient status under invasive plant species as compared to uninvaded ecosystems or/and before being invade, while some reported vice versa (Christian & Wilson, 1999; Leary *et al.*, 2006). Meanwhile, the invaded plots have higher topsoil nutrients compared to uninvaded area, when the plot is initially had low in nutrient concentration, and vice versa (Dassonville *et al.*, 2008). Regardless of the type of species invade, soil nutrient (such as, available nitrate) concentration and N mineralization and nitrification rates were greater under the exotic than the native species (Ehrenfeld *et al.*, 2001). However, Alpert *et al.* (2000) had different findings as in many cases that the disturbance from invasive plant species gave a subsequent impact in increasing soil resource availability by removing other competitor plants.

2.7 The impact of environmental stressors on plant growth and nutrient acquisition

Resource competition has long been regarded as a major mechanism responsible for successful plant invasions. Plants in general acquire three main classes of essential resources for development which are nutrients, water and light for the individual plants to compete for growth. However, the plant growth can be limited by the excessing or/and limiting of those resources (Funk, 2013). The plasticity of plants in response to resources changes had play significant roles in sustaining the plant growth and survivability (Gratani, 2014; Quinet *et al.*, 2015). Individual plants acquire different amount and type of resources from common

pool of potential resources depending on the plant growth stages (Ashman & Puri, 2002; Troeh & Thompson, 2005). The complexity of resource competition is caused not only from the variability of resource limitation in space and time and between species, but also derived from the complexity of the resources themselves. The disparate properties of nutrients, water and light generates unique means for plants to compete for these resources (Craine & Dybzinski, 2013), in which the mechanism involve in the resources acquired in the context of several invasive plant species will be briefly explained by previous studies in further sub-section.

2.7.1 Resources competition in above- and belowground soil

Aboveground and belowground resources competitions are often involved within the process of plant competition. Plant competitions occur in three criteria which are; intra-specific (competition between the plant with same species), inter-specific (competition between different species of plants) and size-asymmetric competition (competition of the contested resources between larger and smaller individuals) (Schwinning & Weiner, 1998).

In these situations, the plants are involved with aboveground competition at early growth stage which solely competes for single resource, light. However, greater competition among plants takes place belowground. In contrast to aboveground competition, belowground competition is far more complex as the plants have to compete for space and broad range of soil resources, including water and at least 16 essential mineral nutrients. Resources competition in plant is physiologically described on the process happening at belowground environment as such mechanisms involved directly with nutrient competition and water by the plants (Casper & Jackson, 1997) .

Competition for resources has long been considered tolerably impartial in structuring species communities and generates stress to plant. The mechanisms of nutrient competition have influenced the species distribution and evolution of plant morphologically especially in structuring root growth (i.e., higher root length or/and dense root) (Craine & Dybzinski, 2013). The mechanism may involve a trade-off number of biomass to specific plant parts for resources uptake (i.e., via photosynthesis or/and nutrient uptake) (Bazzaz, 1996; Radosevich *et al.*, 2007).

The successful establishment and distribution of invasive species in newly invaded area, and its persistence are most likely through resources pre-emption in which the species is known to have superior ability to acquire more nutrient than the native co-occurring species (Matzek, 2011; Gioria & Osborne, 2014). Plants compete for nutrient by pre-empting the nutrients from coming into contact with adjacent plants, which require the plant to maximize root length (Craine & Dybzinski, 2013; Gioria & Osborne, 2014). Competition for resources are very crucial at the beginning of plant invasion where, the invaded plant had an advantages over with the co-occurring species through superior competitive ability (Gioria & Osborne, 2014). Most of the impact of nutrient competition and species establishment evolved the phenotypic plasticity that shaping the plants growth and allow the plant to strive in breadth environment (Richards *et al.*, 2006; Hulme, 2008; Skalova *et al.*, 2013).

The invasion and colonization of *M. pigra* are often formed dense thicket whereby the resources competition is an inevitable factor to deal during the plant establishment. As being reviewed by the previous studies, the plasticity of plant had govern the species establishment along range of environmental gradients. However, there has been an argument as the mechanism might differ depends on

the existing factors (i.e., heterogenous vegetative composition, stage of invasion, plant phenotypic traits) circulating the growth environment (Gioria & Osborne, 2014). Given that under intense intraspecific competition, invasive populations may have lower fitness (Van Kleunen *et al.*, 2001) and a reduced competitive ability (Bossdorf *et al.*, 2004). As addressed by Gioria and Osborne (2014), future studies should focus to fulfil this research gap, given the importance that intraspecific competition may play, especially at the early stage of invasion. Therefore, the establishment of *M. pigra* in high density of conspecific colonization might be influenced by different factors, which is important to be studied to enlighten the species survivability in field.

2.7.2 Light limitation

Light resource is one of the factors that influences the susceptibility of the environment to permit establishment and colonization of invasive species (Davis, 2009). In 2015, Warren *et al.* had reported a negative correlation between canopy cover and species existences, by further explained that low light penetration reduce the presence of invasive species which also supported by others previous literatures (Dommanget *et al.*, 2013; Marlor *et al.*, 2014). In reviewing literatures, highly shaded plants are often performed low phenotypic plasticity as compared with plants growing in open area (Stuefer & Huber, 1998; Valladares & Niinemets, 2008; Offord *et al.*, 2014). High requirement of light resources by invasive plant and weedy species make most of this species are often found invading and colonizing an open area (Nielsen, 1992).

Different eco-physiological of invasive plant species might either displayed shade-tolerant or shade-intolerant (Martin *et al.*, 2009; Gommers *et al.*, 2013; Dlugos

et al., 2015) or possess the combination of these two strategies. Under different light limiting condition, certain species display high plasticity as a mechanism to acquire ample light resources, maximize light foraging and to escape from the shade (Hopkins & Huner, 2009; Gommers *et al.*, 2013), and employ a “shade-intolerant” mechanism. The plant may perform height increment, branching reduction, low biomass and RGR, and low fecundity (Valladares & Niinemets, 2008; Gommers *et al.*, 2013; Dlugos *et al.*, 2015) under light reduction. Whilst, shade-tolerance plant had less plasticity in morphological growth, long lived (Gommers *et al.*, 2013), but able to maintain growth rate even in low light (Valladares & Niinemets, 2008).

The individual plants either in similar or different species will acquire different quantum of light. In fact, different intensities of light penetration had various impact on plant morphological and physiological adaptation as well as modification structures of leaf tissue (Shrestha & Cole, 2013; Fan *et al.*, 2018). In low light environment, plants may either strive by morphologically adapting by plasticity changes (i.e., formation of large biomass) and/or by performing nutrient conservation or/and nutrient pre-empting (Güsewell, 2004; Funk, 2013). The formation of a large biomass by many invasive species is often associated with their superior capacity to compete for light. However, in some cases, such as shrub or understory plants that had lower exposure to light, the plants may either acquire more resources from soil nutrients and water or performed nutrient-use efficiency as compensation to the light sources for growth. Plants had superior capacity to compete for belowground resources rather than light. The plants adapted to low light might possess a suit of related traits to operate such efficiency function within the plant parts to survive (Godoy *et al.*, 2011; Funk, 2013). Interestingly it was supported by research conducted by Shrestha and Cole (2013) with the findings

stated that viburnum species (shrub plant) that was grown in shade had greater plant growth, quality and water use efficiency.

Generally, invasive species is shade-intolerant (Dommanget *et al.*, 2013; Marlor *et al.*, 2014; Warren *et al.*, 2015). To date, only 133 of invasive species (exception for *M. pigra*) are categorized as shade-tolerance species as being reviewed by Martin *et al.* (2009). High dependence of this species on light resources suggesting that low possibility of *M. pigra* to be found in highly shaded environment as in plantation and no existence reported in Malaysia forested area (Asyraf & Crawley, 2011). Given that the distribution of *M. pigra* invasion are covered mostly in the open sites area, this species might be assumed as shade intolerant plant. Certain shade intolerant juvenile's plant or newly emerged seedlings may strive from shade grow vigorously until exposed to ample light source (Funk, 2013). Plant rapidly responded to accelerated light levels simulating canopy gap morphologically and physiologically (Yamashita *et al.*, 2000). This was similar from research conducted by Martin *et al.* (2010) on exotic shade-intolerant species (*Ailanthus altissima*). The study found that, this exotic tree species only requires small gap of light penetration to initiate its growth and succeed naturalizing even in low light forest condition (Knapp & Canham, 2000).

Therefore, based on the previous literatures, as successful invasive species establishment is often associated with the superior capacity of the plant to compete for light, assessments of competition for this single factor should thus be examined to thoroughly monitor the impact of the stress to the associated functional traits during the species establishment.

2.7.3 Water restrain environment

In field conditions, water stress can occur in many ways either prolonged or short-term stress in which the effects are varies to the plants which are geographical-, climatic- and species-dependent (Rud *et al.*, 2014; Laube *et al.*, 2015). Several reports have mentioned that the limitation of water had limited the growth performances of plant by impeding the physiological and morphological performances of the plant (Vurayai *et al.*, 2011; Osakabe *et al.*, 2014). Besides, the effect of different level of water stress may also impaired plant productivity such as in crop legume plants (Moore, 2015). This happened owing to the declining effect of drought tolerance efficiency by the plant. Several species had showed imparity different effects relative to the water limitation (e.g. growth impairment, reduction of nodulation functional and production) as plasticity mechanism in order to acquire nutrient for continuing their growth (Talukdar, 2013).

A meta-analysis reviewed by Cavaleri and Sack (2010) and Gioria and Osborne (2014) had reported that invasive plant may also show adaptive mechanism relative to the water limitation, as there was a similarity in an adaptive mechanism of the invasive and native plants in low water precipitation. Both species exhibited similar value of leaf level water use efficiency, and invasive species had lower pre-dawn water potential as compared to native species. Generally, water acquisition by plant is strongly influenced by the root depth, root to shoot ratio and mycorrhizal association (Loik, 2007). A number of studies reported that the invasive species had higher water acquisition demonstrated through higher root to shoot biomass than less invasive woody species (Grotkopp & Rejmanek, 2007) and native species (DeFalco *et al.*, 2003). The species allocated more biomass to root for efficient water uptake which gives an advantage for N

acquisition. Thus invasive plant should maintain high N content to have greater water use efficiency which helps to survive in drought (DeFalco *et al.*, 2003; Grotkopp & Rejmánek, 2007).

Manipulation of soil moisture changes (extreme drought, inundate and/or repetition of wet-dry conditions) may probably influenced the absorption of plant nutrients (Troeh & Thompson, 2005). Restrained or reduced water supply physically not just makes water less accessible to the plant but additionally diminish the accessibility of certain plant essential elements. Phosphorus is a good example; the solubility of phosphorus is low in the soil. However, if a higher amount of water was supplied, it helps in increasing the rate of dissolved phosphorus and the rate of phosphorus uptake (Troeh & Thompson, 2005). Other nutrients are likewise affected by soil water in their own particular ways. For example, nitrogen, sulphur and certain micronutrients were released by the microbial action in soil. However, the activity is roughly proportional with soil water in controlling the rate of nutrients release. If the water was restrained, it will directly slow down decomposition of the organic matter by microbial activity, thus reducing the rate of nutrients release (He & Dijkstra, 2014; Sharma & Gobi, 2016).

Based on those previous studies, it was anticipated that native species can survive and compete well in low water availability condition owing to the presumed adaptation to the water stress condition prior to the invasion of invasive species. However, there were several invasive species able to survive and compete under water stress which may govern by multiple associated plant functional traits. Therefore, future studies should address this research gap given that *M. pigra* can survive in wide ecological water environment (i.e., dry to semi wet land).

2.8 Nutrients in soil and plant

2.8.1 Macro- and micronutrient

Seventeen elements are recognized as being essential for plant growth as the absence will intrude the plants to complete a normal life cycle. Three of them are oxygen, carbon and hydrogen that are supplied through water and air. The remaining, 14 elements are considered to be plant nutrients which further divided into two main groups based on the quantity normally required in which both groups distinct in the concentrations found in tissue or required in nutrient solutions: 1) macronutrient (elements need in large amounts) and 2) micronutrient (required in small quantities) (Munson, 1998; Troeh & Thompson, 2005; Hopkins & Huner, 2009).

Macronutrients constitute of nitrogen (N), sulfur (S) and phosphorus (P), where the elements are obtained mostly from organic matter, while calcium (Ca), magnesium (Mg) and potassium (K) are obtain mostly from mineral solids. These are essential elements involved in the structure of molecules. Micronutrients constitute of eight elements; boron (B), chlorine (Cl), copper (Cu), iron (Fe), manganese (Mn), molybdenum (Mo), nickel (Ni) and zinc (Zn). These elements serve in catalytic and regulatory roles such as enzyme activators (Bohn *et al.*, 2001; Troeh & Thompson, 2005; Hopkins & Huner, 2009).

Each nutrient element is varies in properties and rate of diffusion in soil as the properties of the soil influence the behaviour of the nutrients by altering the rate of diffusion. Despite of the plants acquiring nutrient from the soil, nutrients supply depends on several factors such as soil microbial activity (organic matter decomposition), plant activity (senescence, microbial association), soil pH and climates (Brady & Weil, 2014). The plant activities may determine the decreases

and increases the nutrient availability in soil (Craine & Dybzinski, 2013). The freshly fallen leaves, dying roots and animal residues decomposed by the soil microbial and become part of soil organic matter. The decomposition of the organic matter produces acids and other substances that help soil minerals to decompose and release plant nutrients. Supplying plant nutrients is one of the significant functions of organic matter in soil as they provide some of elements (i.e., N, P, and S) needed for plant growth (Bohn *et al.*, 2001). Amount and the quality of soil organic matter and the presence of adequate soil fauna and microorganisms are the parameters determining the soil fertility status (Juo & Franzluebbers, 2003; Troeh & Thompson, 2005).

Soil pH has great impacts on the availability of plant nutrients as its influences the; rate of plant nutrient release by weathering, amounts of nutrient ion stored in cation-exchange site and the nutrients solubility in soil. The soil pH in tropical country is slightly acidic (ranging between 3.3 – 7, based on Turner & Engelbrecht, 2011), owing to the wet and dry climates that encourage weathering process occur where leaching is intense (remove bases and lower the pH in time) (Troeh & Thompson, 2005). Soil pH has little or indirect effect on plant growth, however it is a good guide in predicting which element is deficient in the plant as the availability of soil nutrients is depending on the soil pH level. The optimum pH for maximum nutrient available is between 6.0 and 7.5 in which the mineralization rate of organic matter is more favourable within that range (Troeh & Thompson, 2005; Brady & Weil, 2014)