ECOLOGICAL DEGRADATION AND RECOVERY IN THE FORMER MEGA RICE PROJECT TROPICAL PEATLAND ECOSYSTEM, CENTRAL KALIMANTAN, INDONESIA

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Declaration

I hereby declare that this thesis is my original work and it has been written by me in its entirety. I have duly acknowledged all the sources of information which have been used the thesis.

This thesis has also not been submitted for any degree in any university previously.

Grace V. Blackham

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Summary

Forested tropical peatlands in Southeast Asia are important as global carbon stores and for biodiversity conservation yet are being rapidly converted to agriculture or degraded into fire-prone non-forest vegetation. Although large areas have been abandoned, there is little evidence for the subsequent recovery of forest. This study investigates forest degradation and recovery in the former Mega Rice Project area: an abandoned attempt to convert one million hectares of tropical peatland for rice production in Central Kalimantan, Indonesia. The thesis is divided into seven chapters.

Chapter 1 presents an overview of tropical forest degradation and tropical peatlands. Chapter 2 outlines the study site, including details on the development of the Mega Rice Project.

Chapter 3 investigates the composition and abundance of woody plant species regenerating in an area of forest regrowth (FR). The results show that the natural regeneration of woody plants in the FR is dominated by a few abundant species (*Combretocarpus rotundatus*, *Melastoma malabathricum*, *Cratoxylum arborescens/glaucum*, *Ploarium alternifolium* and *Syzygium myrtifolium*) but also contains a diverse array of tropical peat swamp forest species, albeit in low abundances.

Chapter 4 investigates how the impacts of land conversion in the former Mega Rice Project area, specifically the fire history and changes to the natural hydrology, influence the composition and species richness of woody plants. The results of generalised linear models and constrained correspondence analysis show that the number of years since the last fire, the number of times an area has burnt, the number of drought months and the number of flooding months are important determinants of species richness.

Chapter 5 investigates the composition and abundance of seed rain over the period of one year in the FR. The results show that for tree and shrub species the seed rain largely reflects the composition of woody plants that already exist in the area. The majority of seeds are wind-dispersed or dispersed by bulbuls (Pycnonotidae) and other small- and medium-sized birds and this reflects the composition of dispersal agents found in the degraded area. The results also show that established trees are important as nuclei for regeneration, especially for animal-dispersed woody plant species.

In Chapter 6 experimental trials are used to examine and compare the level of post-dispersal seed removal in FR and in an area of continuous logged peat swamp forest (CLF). The trials show that post-dispersal seed removal is higher for animal-dispersed seeds than for wind-dispersed seeds in both FR and CLF and is likely to be post-dispersal seed predation by ground-feeding rodents.

Chapter 7 provides an overview of the results and discusses their implications in regard to the natural regeneration potential of degraded tropical peatlands. The combined results of this thesis suggest that some human intervention will be required to assist forest recovery in degraded tropical peatland.

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List of Abbreviations

IAFCP = Indonesia-Australia Forest Carbon Partnership

CLF = continuous logged peat swamp forest

FR = forest regrowth

1. Introduction

1.1 The tropical forest degradation crisis

It is estimated that humans have converted 26% of the land area worldwide to agriculture (World Resources Institute, 2000) and in the tropics land conversion has mainly occurred in previously forested areas. Between 2001 and 2004 over 540000 hectares of the Southern Brazilian Amazon was converted from forest to cropland (Morton et al., 2006) and between 1990 and 2005 over 1 million hectares of forest in Malaysia was converted to oil palm plantation (Koh and Wilcove, 2008). At present the estimated annual area of humid tropics being deforested stands at 5.8 million hectares (Achard et al., 2002). However, much of this conversion is unsustainable, with half of the forest cleared each year becoming degraded after only a short period (Houghton, 1994). It has been estimated that 2.3 million hectares of the humid tropics experiences degradation every year (Achard et al., 2002).

It is important to clarify what is meant by degradation in tropical forested areas and to distinguish it from deforestation. While deforestation is the act of clearing forest it does not necessarily lead to a long-term loss of forest cover if regeneration takes place. Ecological degradation, in contrast, does not necessarily involve a loss of overall forest area but rather is the loss of ecosystem components (vegetation, soil, fauna) or the deterioration of function of ecosystem components (Lanly, 2003). Of course, this deterioration can occur because of the processes used to clear an area of forest or because of events that occur post-clearance but it is important to note that deforestation does not automatically equate to degradation.

The main ecological questions that underpin research on degraded lands in tropical regions are what successional processes occur after degradation has occurred, are these lands capable of regenerating naturally and will these areas return to what they once were or become something else entirely.

1.2 Tropical peatlands

Tropical peatlands are found in Central America, South America, Africa, mainland and south Asia, Southeast Asia and in the Pacific region (Andriesse, 1988, Rieley et al., 1996a, Page et al., 2011). Forty-seven per cent of the world's tropical peatland is found in Indonesia, primarily on Sumatra, West Papua and Kalimantan (Rieley et al., 1996a), covering a land area of 206 950km^2 (Page et al., 2011).

Most of the peatlands in Indonesia are ombrogenous (Rieley et al., 1996a, Page et al., 1999), in that they are ecosystems where precipitation is the only source of water and nutrient supply to the peat surface (Clymo, 1983, Page et al., 2004). Tropical peatlands are characterised by their consistently high water-tables with wet season flooding (or near-surface levels of water) and water drawing down to just below the peat surface during the dry season (Page et al., 2009b). These water-holding characteristics make tropical peatland ecosystems important in water level regulation, acting as important water catchment and control systems (Rieley et al., 1996a) by moderating water levels and preventing or reducing flooding and drought in the areas surrounding the peat swamp (Phillips, 1998, Wosten et al., 2006).

The flora of tropical peatlands was first described in detail for the peat swamps of Sarawak (Malaysian Borneo) and Brunei (Anderson, 1963). Floral descriptions of other areas of tropical peatland have since been compiled, including for Central Kalimantan , Peninsula Malaysia (Faridah-Hanum et al., 2005) and Thailand (Phengklai and Niyomdham, 1991). Tropical peatlands typically consist of a series of vegetation types that transition from high forest at the wetter edges of the dome to denser, lower canopied forest in the interior (Rieley et al., 1996b). Anderson (1963) recognised six phasic communities in Brunei: mixed swamp forest, a transitional zone, alan bunga forest, phasic community 4, transitional forest and open stunted forest. Page et al. (1999) looked at vegetative patterns on the Sabangau peat dome in Central Kalimantan, Indonesia, and found four main forest types; riverine, mixed-swamp, low pole and tall pole. Many of the same plant species were found to be present in each forest type, only changing in relative abundance and height (Page et al., 1999). At present it is not understood if these vegetation patterns are found on all peat domes or show variation dependent on other characteristics of that peat dome.

Looking specifically at the woody plant species found in tropical peatlands, most families of lowland dipterocarp rain forest plants are represented and common peatland species include *Alstonia pneumatophore, Lophopetalum multinervum, Campnosperma coriacea, Gonystylus bancanus, Palaquium burckii, Tetramerista glabra, Durio carinatus, Koompassia malaccensis, Parastemon urophyllum, Dyera lowii, Mezzettia leptopoda, Shorea platycarpa, Shorea teysmannnia* and *Shorea uliginosa* (Rieley et al., 1996b). However, tropical peat swamp forests in Southeast Asia are typically less diverse than other tropical forests in the region. For example, a survey of peat swamp forests in Central Kalimantan found 168 tree species (total survey area = 0.96 ha) (Poesie et al., 2011) which is less than that recorded for most rain forests in the same region (100 – 290 species per 1 ha plot) (Corlett, 2009).

While no mammals, birds, reptiles or amphibians have been recorded exclusively in tropical peatlands (Posa et al., 2010) Southeast Asian tropical peatlands have been found to be important habitats for a number of threatened and endangered species including the orang-utan (*Pongo pygmaeus*) (Morrogh-Bernard et al., 2003, Wich et al., 2008) and Southern Bornean gibbon (*Hylobates albibarbis*) (Buckley et al., 2006, Cheyne et al., 2008).

1.3 Land conversion in tropical peatlands

In the last few decades much of this naturally forested tropical peatland has begun to be exploited and developed, with large areas undergoing land conversion for agriculture, or being subjected to logging (Rieley et al., 1996a, Yule, 2010). Recent studies using remote-sensing techniques and geographic information systems (GIS) to quantify and classify land-cover change suggest that between 1990 and 2008 almost 2 million hectares of tropical peatlands in Peninsula Malaysia and on the islands of Borneo and Sumatra were converted into industrial plantations, with a further 1.2 million hectares becoming agricultural small-holdings (Miettinen and Liew, 2010). Agricultural conversion has mainly been for large-scale oil palm plantations and *Acacia* plantations to produce paper pulp (Miettinen et al., 2012a), but also includes the cultivation of rice, rubber, coconut and pineapple (Yule, 2010, Miettinen et al., 2012a).

Land conversion in tropical peatlands typically involves forest clearance and changes to the natural hydrology through the implementation of drainage systems (Rieley et al., 1996a, Yule, 2010). However, even with these major modifications to the peatland ecosystem, not all tropical peatland land conversion actually reaches the plantation or agricultural stage. This can be for many reasons, but often it is because the techniques and methods used in land conversion were not suitable for use in tropical peatlands and so the projects failed, with the areas left as degraded wastelands (Page et al., 2009b). Recent estimates suggest that 1.8 million hectares of the 16 million hectares of tropical peatlands found in Peninsula Malaysia and on the islands of Borneo and Sumatra now exists as degraded land (Miettinen and Liew, 2010), with extensive areas of degraded peatland in the provinces of Riau and Jambi in Sumatra and in Central, East and South Kalimantan in Indonesian Borneo (Hooijer et al., 2006).

Peatland degradation releases carbon (Page et al., 2002), impacts biodiversity, causes downstream hydrological deterioration and can negatively impact local communities (Page et al., 2009b). Interestingly, recent land-cover change studies have also found that areas of tropical peatlands classed as secondary regrowth twenty years ago remain in the same state today (Miettinen and Liew, 2010), that is, fern- and sedge-dominated landscapes with very few or no trees (Page et al., 2009b).

1.4 Succession

Ecological succession is generally divided into primary succession and secondary succession; primary succession being the colonisation of vegetation on newly formed or exposed substrate and secondary succession being the replacement of pre-existing vegetation following a major disturbance (Finegan, 1984, Glenn-Lewin and van der Maarel, 1992). It is secondary succession that occurs on degraded lands.

Tropical forest succession has been described by many authors (Uhl et al., 1981, Finegan, 1992, Corlett, 1995) and generally involves the following processes: Through disturbance the original vegetation of an area is removed. Following abandonment this area is then colonised by herbs and shrubs, followed by pioneer tree species which are gradually replaced by climax forest species.

It was originally thought that secondary succession always followed a trajectory towards a stable climax vegetation (Clements, 1916, Horn, 1974) but general consensus now suggests that there are multiple pathways of secondary succession and no single final vegetation type (Connell and Slatyer, 1977, Whittaker, 1953, Pickett et al., 2009). Indeed, an area may have a number of alternative states, all of which are considered stable (i.e. persist for a relatively long period of time) and resilient to change (Holling, 1973, Holing et al., 1995). This means that post-disturbance, an area may persist in a different state to that of the area pre-disturbance, but which itself is stable and resilient to change unless major alterations to the current system functions are made.

The actual course that secondary succession takes post disturbance, and the composition and abundance of the resulting natural regeneration of woody plant species, is contingent upon the characteristics of the original forest, the biophysical conditions of the area and the type and level of disturbance that took place (Corlett, 1995, Hobbs and Norton, 2004, Chazdon, 2003). These characteristics and conditions can be seen as ‘filters’ which limit the rate of succession that occurs and control the composition and abundance of the emerging secondary vegetation (Corlett and Hau, 2000). It may be that the current state of the filters in an area holds the ecosystem in a state that, while different to the forest that previously covered the area, is stable and resilient to change, unless major alterations to the current filters are made.

Much of the literature on natural regeneration calls these filters ‘barriers’ (Nepstad et al., 1990, Zimmerman et al., 2000, Hooper et al., 2005). However, the term barrier suggests that a process is being entirely blocked and prevented whereas often the process is still occurring but is limited or reduced in some way. Therefore, a more appropriate term is ‘filters’ to natural regeneration and this is the term that will be used for the purposes of this dissertation.

Much of the work on the natural regeneration of vegetation in degraded tropical regions has focussed on abandoned pastures and old fields (Cramer et al., 2008), primarily in the Neo-Tropics (e.g. Uhl et al., 1988a, Aide et al., 2000, Galindo-Gonzalez et al., 2000, Rivera et al., 2000, Zimmerman et al., 2000, Hooper et al., 2004) and has involved study areas several hectares in size (Chazdon, 2003). More recent work has looked at various aspects of natural regeneration on degraded land in Southeast Asia, for example in Hong Kong (Hang Hau, 1997, Au et al., 2006, Chung and Corlett, 2006), Singapore (Corlett, 1991, Shono et al., 2006), China (Wang et al., 2010) and Indonesia (Cleary and Priadjati, 2005, Slik et al., 2008).

For abandoned tropical old fields the most important filters to the natural regeneration of tree species have been identified as dispersal, competition from herbaceous vegetation, predation and poor soil conditions (Holl, 1999, Zimmerman et al., 2000, Cubina and Aide, 2001, Nepstad et al., 1996).

1.5. Filters to tropical secondary succession in degraded tropical peatlands

It is beyond the scope of this work to investigate all potential filters acting on the natural regeneration in degraded tropical peatlands and therefore this work focusses on the filters directly connected to the land conversion practices used in tropical peatland conversion, namely, the use of fire in land clearance activities; the implementation of a drainage system to alter the natural hydrology; and, the changes to the processes of seed dispersal caused by the large-scale removal of the natural forest-cover and its associated faunal assemblage.

Table 1.1 gives a brief overview of what is currently known about each of these filters for tropical forests in general and for tropical peatlands. A more detailed examination of each filter is provided in the introduction section of the relevant chapter.

Table 1.1. Overview of filters potentially limiting natural regeneration on degraded tropical peatlands, including current knowledge for other tropical forest types.

Filter	Effect on successional trajectories in other tropical forests	References	Current knowledge in degraded tropical peatlands	References	Thesis Chapter
Fire	• Changes woody plant species composition and dominance patterns.	• Nykvist (1996), Cochrane and Schulze (1999), Cleary et al. (2006), Slik et al. (2008), Yassir et al. (2010)	• Reduces species richness.	• van Eijk et al. (2009), Page et al. (2009b)	Chapter 4
Hydrology	• Flooding leads to low tree density and low species richness, with the composition limited to species that can grow and persist under flooded conditions.	• Martínez and Lugo (2008)	• Long and deep flooding events lead to low woody plant species diversity.	• Wosten et al. (2006)	Chapter 4
Seed dispersal	• Seed rain decreases with increasing distance from the nearest seed source. • Seed rain in degraded tropical areas primarily made up of wind-dispersed species and small-fruited, small-seeded species. • Remnant trees can act as nuclei for natural regeneration.	• Cubina and Aide (2001), Ingle (2003), de Melo et al. (2006), Dosch et al. (2007) • Au et al. (2006), Barbosa and Pizo (2006) • Guevara et al. (1986), Nepstad et al. (1991), Guevara and Laborde (1993), Galindo-Gonzalez et al. (2000), Carriere et al. (2002), Hooper et al. (2005)	• No studies have investigated seed dispersal in intact or degraded tropical peatlands.	N/A	Chapter 5
Post-dispersal seed predation	• No obvious trend when comparing rates of post-dispersal seed removal to that in intact forest ecosystems. • Disturbance can change the composition and abundance of secondary dispersers and post-dispersal seed predators.	• Hau (1997), Holl and Lulow (1997), Notman and Gorchov (2001) • Nepstad et al. (1991), Cole (2009)	• Some scatter-hoarding by rodents in intact tropical peatland • No studies have investigated the processes of post-dispersal seed predation in degraded tropical peatland.	• Van der Meer et al. (2008)	Chapter 6

1.6 Research aims

To truly understand the natural regeneration ability of degraded tropical peatland information is required on what vegetation is regenerating in the area, how this vegetation compares with the vegetation growing in non-impacted areas and which filters are limiting successional processes in the area. With this in mind, my thesis aims to explore the natural regeneration potential of woody vegetation in an area of degraded tropical peatland, to establish how the current vegetation relates to the impacts that caused the degradation, and to examine other potential filters to recovery: seed dispersal and post-dispersal seed predation. This work was carried out in the former Mega Rice Project Area in Central Kalimantan, Indonesia.

Specifically, this thesis aims to answer the following research questions:

1) What woody plant flora is present in the degraded area of Block A NW of the former Mega Rice Project area and where?
2) Is the current woody plant flora related to specific impacts of land conversion and degradation in the area, namely the fire history and changes to the hydrology of the area?
3) What is the composition and abundance of seed rain in the degraded area?
4) What is the level of post-dispersal seed removal occurring in the degraded area and how does this compare to levels in relatively intact tropical peatland? How does this relate to the composition and abundance of ground-feeding small mammals in both areas?

I hope that my research will provide new insights into the processes of natural regeneration in this important ecosystem.

2. Study Area

This work took place in the former Mega Rice Project Area in Central Kalimantan, Indonesia.

2.1 History of the Mega Rice Project

A Presidential Decree in 1995 began the development of one million hectares of tropical peatlands in Central Kalimantan, Indonesia, into land for rice cultivation (Aldhous, 2004). The development was known as ‘Proyek Pengembangan Lahan Gambut Satu Juta Hektar’ or the Mega Rice Project. The development covered an area of 1 462 000 hectares of mostly forested tropical peatlands (61% of the area), encompassing a region bound by the Sabangau River to the west, the Barito River to the east, the Java Sea to the south and a northern border which roughly follows the Palangka Raya – Buntok road ((Mott-MacDonald and Deltares, 2008). This area was divided into five blocks: A, B, C, D and E (Figure 2.1).

Implementation of this project involved the removal of forest by clear-felling (Muhamad, 2001), the use of fire to clear the remaining timber debris (Boehm and Siegert, 2001) and the excavation of a system of 4600 km of canals (Aldhous, 2004) to drain excess water from the area whilst also providing irrigation for the rice fields (Muhamad, 2001). In 1999, four years after implementation, a Presidential Decree was issued cancelling the project (Muhamad, 2001, Page et al., 2009c). This was due in part to the peat-soils of the area not being suitable for rice production and in part because the canal system had led to the over-drainage of the area and unsuccessful irrigation (Page et al., 2009b, Page et al., 2009c). By the time the project was cancelled most of the area had already been logged and cleared (McCarthy, 2001).

The Mega Rice Project area has also been subjected to a number of fire events, with parts of Block C having burnt up to four times in the last twenty years (Page et al., 2009b). The most extreme fire event occurred during the 1997-1998 ENSO event where many managed fires got out of control and 51.3% of the Mega Rice Project area burnt (Page et al., 2002).

Today the former Mega Rice Project area is an abandoned, degraded, treeless landscape, with malfunctioning drainage canals and with regular outbreaks of large-scale fires (Page et al, 2008).

2.2 Climate and elevation.

Central Kalimantan experiences a wet tropical climate which comprises of a wet season from November to April and a dry season from June to August (Page et al., 2004). The mean annual temperatures are between 25 – 27 ^{0}C (Page et al., 2004) and the average annual rainfall in Palangka Raya, the provincial capital, is 2700 mmyr^{-1} (Hooijer et al., 2008). The former Mega Rice Project area has an elevation that begins at sea level at the coast and increases to up to 30 m above sea level inland (Mott-MacDonald and Deltares, 2008, Wosten et al., 2008). The majority of the area lies in the range of 1 – 12 m above sea level (Mott-MacDonald and Deltares, 2008, Mawdsley et al., 2009).

2.3 Study sites

In order to understand the level of ecological degradation and recovery in the former Mega Rice Project area I chose two areas, Block A North West and Block E (Figure 2.2), which encompass two habitats with different levels of disturbance: forest regrowth and continuous logged peat swamp forest (see section 3.2.1 and section 6.2.1). These sites were chosen based on their disturbance history and accessibility.

Figure 2.1. Location Map of the former Mega Rice Project area in Central Kalimantan, Indonesia, showing how the area was divided into five blocks (adapted from Mawdsley et al. (2009)).

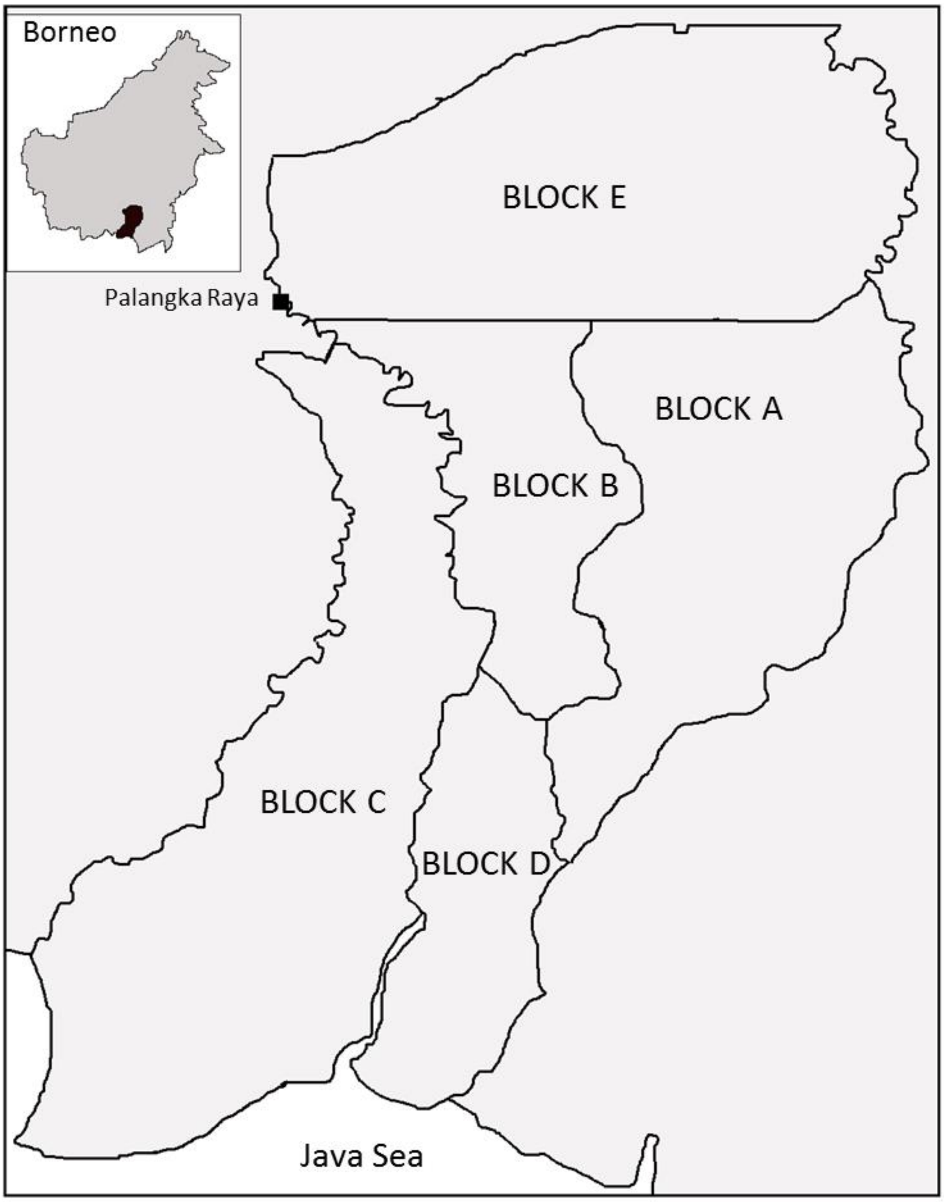
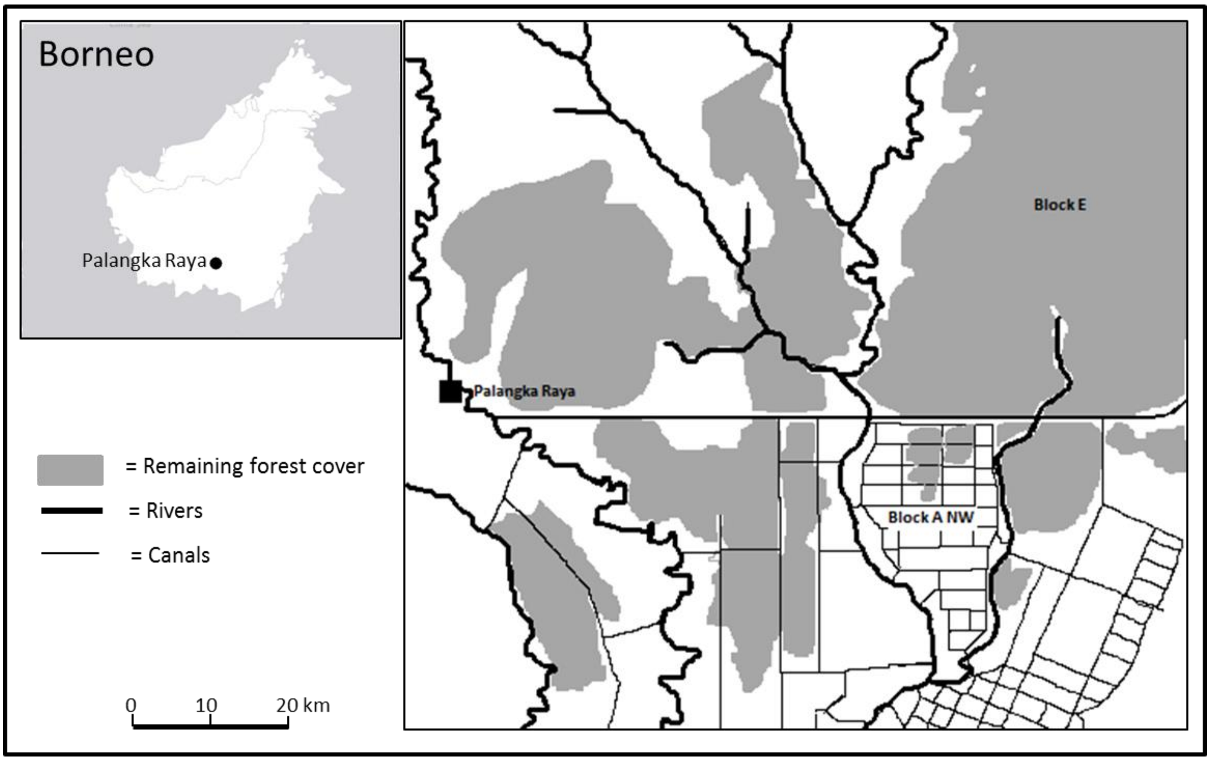


Figure 2.2. Map of north region of the former Mega Rice Project, Central Kalimantan, Indonesia (adapted from Mawdsley et al. (2009)), showing Block E and Block A NW.



3. What has persisted in the present-day landscape and where?

3.1 Introduction

Tropical peatlands are naturally forest-covered ecosystems (Rieley et al., 1996b, Bruenig, 1990) that once covered an estimated area of 247 778 km^2 of Southeast Asia (Page et al., 2011). However, in the last few decades much of this naturally forested land has begun to be exploited and developed, with areas undergoing large-scale drainage and land clearance for agriculture, or being subjected to logging (Rieley et al., 1996a, Yule, 2010). The use of remote-sensing techniques and geographic information systems (GIS) to quantify and classify areas of peatland degradation and regeneration over different timeframes has found that 1.8 Mha of the 16 Mha of tropical peatlands found in Peninsula Malaysia and on the islands of Borneo and Sumatra now exists as degraded land (Miettinen and Liew, 2010), with extensive degraded peatlands located in the provinces of Riau and Jambi in Sumatra and Central, East and South Kalimantan in Indonesian Borneo (Hooijer et al., 2006). Degraded peatlands are defined as areas previously consisting of tropical peat swamp forest that have subsequently been deforested and usually drained, and now exist as shrubland or limited forest regrowth. In the majority of cases, while GIS can be used to classify successional stages such as early and late secondary forest, a lack of ground-truthing of these different vegetation types means that this type of study lacks qualitative insight into the abundance and composition of the plant species that inhabit these areas. Meta-analysis exploring the effect of human-driven land-use change in the tropics has found that forest conversion and degradation greatly reduces biodiversity, with abandoned agricultural land having the highest impact and selective logging the lowest impact (Gibson et al., 2011). This suggests that the large-scale land conversion that has occurred in Southeast Asian tropical peatlands is likely to be having a highly detrimental effect on its biodiversity. In order to better understand the long-term effects of this land conversion, we need to investigate the composition and abundance of the woody plant species that recolonise deforested and drained peatlands and compare it to the vegetation of intact tropical peat swamp forests. Through this we can begin to understand the successional processes at play in deforested and drained tropical peatlands, establish the potential for their recovery and posit whether the likely recovery trajectory is towards that of the previous vegetation or some novel forest type.

The composition and abundance of secondary woody vegetation regrowth after disturbance has been explored in other Southeast Asian tropical forest ecosystems (e.g. Sovu et al., 2009, Goldsmith et al., 2011, Do et al., 2011, Corlett, 1991, Brearley et al., 2004, Slik et al., 2008). Looking specifically at tropical rain forests on the island of Borneo, studies have found that secondary regrowth differs from primary forest in terms of species richness, species composition and dominance patterns. Brearley et al. (2004), found that the species richness of old secondary forest growth in areas of abandoned cultivation was lower than that of primary forest with a compositional similarity of only 24%, while Slik et al. (2008) found that species composition and dominance patterns of tree species changed dramatically after fire, with the recruitment of tree species that were never, or rarely, found in unburnt forest.

Some work has already begun to explore natural regeneration in deforested and drained tropical peatland. Results have found that the number of woody plant species present in deforested and drained tropical peatland is less than that of intact peat swamp forest ecosystems (Gunawan et al., 2007, van Eijk et al., 2009, Page et al., 2009b). It has also been shown that fern, climber, sedge and grass species establish in deforested and drained peatlands after disturbance (Page et al., 2009b, van Eijk et al., 2009) and that *Combretocarpus rotundatus* is one of the dominant recolonizing tree species (Chokkalingam et al., 2009, Page et al., 2009b, Hoscilo et al., 2013).

A potential reason for the differences seen in woody plant composition and abundance is a change in the assemblage of seed dispersal agents present in the area after disturbance. In severely degraded areas where successional processes require plants to establish in an otherwise deforested area, the species composition will consist of plant species that still have dispersal agents present in the area or that are dispersed by other means e.g. wind or water (Corlett, 2007). A summary of seed dispersers in degraded areas of tropical Asia suggests assemblages are likely to include: birds, mainly consisting of frugivorous but partly insectivorous passerine birds, dominated by bulbul species, but potentially also non-passerines including Megalaimidae (barbets) and Columbidae (fruit-pigeons) and some tolerant Bucerotidae (hornbills); bats (Pteropodidae), although most studies come from the degraded Neotropics; macaques (*Macaca* sp.); civets (Vivernidae); rats (Muridae); and squirrels (Sciuridae) (Corlett and Hau, 2000). The majority of these birds and mammals consume small-seeded fruits and this will lead to a plant species composition skewed towards small-seeded and wind dispersed plants. Indeed, studies of vegetation in degraded tropical areas generally report a plant composition less diverse than that of intact forest, primarily made up of wind-dispersed species and small-fruited, small-seeded species (Au et al., 2006, Weir and Corlett, 2007).

In order to explore the patterns of natural regeneration of vegetation occurring on degraded tropical peatland I investigated the woody plant species composition and abundance of an area of deforested and drained tropical peatland in Block A North West of the former Mega Rice Project. I also looked at how the main dispersal agents for the woody plant species could explain differences in the composition and abundance of woody plants. This work also forms the baseline data for the rest of my thesis.

Specifically, this chapter aims to:

1) Determine the woody plant species composition and abundance in deforested and drained tropical peatland in Block A NW, Central Kalimantan, Indonesia;
2) Investigate the composition and abundance of woody plant species in relation to their respective dispersal agents and presence in intact tropical peatlands in Central Kalimantan.

3.2 Methods

3.2.1 Study site

This work took place in the former Mega Rice Project Area in Central Kalimantan, Indonesia (see Chapter 2). Based on disturbance history and accessibility, the north-western part of Block A (02°17’77”S; 114°31’23”E) (Figure 3.2) was chosen as the field site for this study.

The location for the vegetation surveys was a region of forest regrowth (FR) in Block NW. This area is approximately 45 000 ha in size and forms part of the Mantangai peat dome. Most of the peat in this area reaches depths of greater than 3m (Mawdsley et al., 2009). The boundaries of Block A NW are the Kapuas River in the west, the Mantangai River in the east and the two primary Mega Rice Project canals to the north. It is roughly 60 km by 20 km in size, divided into compartments by 300 km of canals, with each compartment roughly 2.5 by 2.5km in size (Mawdsley et al., 2009).

Figure 3.1. Map of north region of the former Mega Rice Project, Central Kalimantan, Indonesia (adapted from (Mawdsley et al. 2009), showing the location of transects used for vegetation surveys in the forest regrowth (FR).

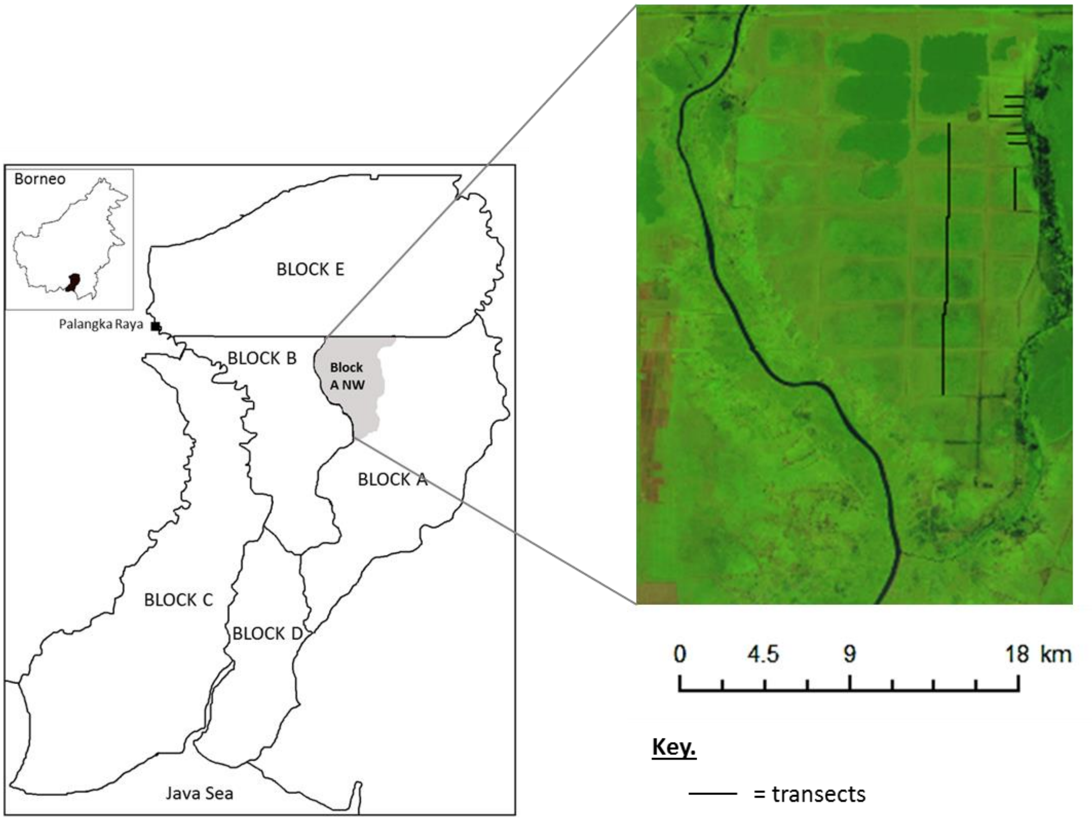


Figure 3.2. Forest regrowth (FR) in Block A NW of the former Mega Rice Project. This photo shows FR in compartment d-3, which was cleared of forest in 1996-1997 and has burnt twice. The last fire occurred four years prior to this photo being taken.

3.2.2 Vegetation surveys

3.2.2.1 Choice of survey method

Studies on undisturbed tropical peatlands have used plot methods to investigate plant composition (e.g. Page et al., 1999, Simbolon and Mirmanto, 1999, Purwaningsih and Yusuf, 1999, Mogea and Mansur, 1999, Siregar and Sambas, 1999, Jusoff et al., 2007). In degraded peatland plots have also been used to compare vegetation in areas with different fire histories (Page et al., 2009b). Methods range from a single plot design (e.g. Siregar and Sambas, 1999, used a single 70 m x 150 m plot), multiple plots spread throughout an area (e.g. Jusoff et al., 2007) and transect plots that reach lengths of up to 3000 m (e.g. Mogea and Mansur, 1999).

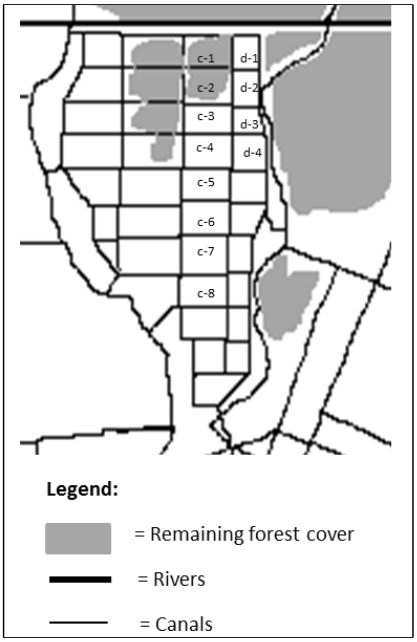
Block A NW of the former Mega Rice Project has two characteristics that lend themselves to a survey design of many small plots made at intervals along a transect. Firstly, the excavation of drainage canals in the area has caused the compartments to form ‘mini-domes’ because subsidence from oxidation is greatest closer to the canals (Mawdsley et al., 2009). This increase in elevation towards the centre of each block may provide an environmental gradient which affects vegetation composition. If a single large plot was made on each compartment any changes along this gradient would not be recorded. Secondly, a GIS land-cover analysis for the area, using Landsat images, ASTER satellite data and PALSAR L-band radar data (see Mott-MacDonald and Deltares, 2008, for details), divides Block A NW into ten different habitat types (Mawdsley et al., 2009). While a method with few large plots could be designed so that a plot is placed in each of the habitat types, a survey design with many small plots laid out along a transect has the benefit of being able to describe the maximum variation over the shortest distance (Kent and Coker, 1992). Preliminary observations made during a reconnaissance trip in June 2009 also suggested that the habitat types in the area were not as uniform as the land-cover images suggested. Basing a distribution of plots on those habitat types would have the potential of missing the levels of heterogeneity suggested by these preliminary observations. For all of these reasons a survey method of many small plots laid out along a transect was chosen as the survey method for this study.

There are issues with accessibility for some of the compartments in Block A NW, where low water levels in the dry season prevent the use of canals to get to areas in the interior. Since seasonality, growth and other time-related measurements were not recorded, areas were surveyed when they were most accessible.

3.2.2.2 Transect and plot lay-out

The inventory of natural regeneration in the FR was carried out in 2009 and 2010. A pre-existing transect set up by the Indonesia-Australia Forest Carbon Partnership (IAFCP) for hydrological surveys runs down the centre of the compartments c-1, c-2, c-3, c-4, c-5, c-6, c-7 and c-8. The transect met the requirements of the vegetation survey method discussed in section 3.2.2.1 and so was utilised and became the primary survey transect (Figure 3.6). The numbering of compartments follows the system set up by IAFCP by (Figure 3.7). I conducted vegetation surveys in the FR portion of this transect which covered compartments c-3 to c-8. I made additional transects on the compartments d-2, d-3 and d-4 to increase the size of the area surveyed. These additional transects were of a minimum length of 1 km and a maximum length of the length of the compartment (between 2 km and 2.5 km), at least 500 m away from any other transects or perpendicular canals. In all cases, surveys began at the canal-edge of a compartment and I established temporary plots of 20 m x 20 m (0.04 ha) at 100 m intervals along each transect. A GPS reading was taken for each plot. A total of 223 plots (total plot area = 8.92 ha) were constructed in the FR.

Figure 3.3. Map of Block A NW region of the former Mega Rice Project area, Central Kalimantan, Indonesia, showing compartments.



3.2.2.3 Inventory of woody plant species and environmental variable measurements

In each plot, all individual woody plants ≥ 0.5 m in height, excluding climbers, were identified to local name in the field and the height was estimated by trained observers who had been previously tested on woody plants of known height. Plant heights were separated into five classes: ≤3 m; 3.1 – 10 m; 10.1 – 20 m; 20.1 – 30 m; and >30.1 m. Diameter at breast height (DBH) was not measured because although all individual woody plants in plots were visible and their heights could be estimated, the extensive fern cover meant that it was not always possible to physically reach an individual to measure DBH. Percentage ground cover was estimated for ferns, woody plants and exposed ground. Individual woody plants were identified to local name. Voucher specimens, including ferns, were collected, labelled, dried and sent to Herbarium Bogoriense, Botany Division, Research centre for Biology, Cibinong Science Centre, Indonesia, for identification to scientific name. When no scientific name was available plants were placed into morphospecies, retaining their local name to distinguish them in analysis. Nomenclature was based on the most recently accepted plant names (The Plant List, 2010).

The dispersal agent for each species was established based on Corlett (1998 and personal communication). The woody plant species list was compared with species lists for relatively intact peat swamp forests in Central Kalimantan to identify which species are also present in mature forests in the area. The species lists used were: A 2 ha phenology plot also located at Tuanan Research Station (Bastian, 2008); Sungai Lading located just outside of, but bordering, the Mawas area (Bastian, 2008); the Natural Laboratory of Peat Swamp Forest in the Sabangau Forest (Harrison et al., 2010); and a checklist of plant species in the peat swamp forests of Central Kalimantan comprised from surveys of the Lahei area, the Sabangau Forest and Tanjung Puting National Park (Simbolon and Mirmanto, 1999).

3.2.3 Data analysis

All stem-based analyses were split into two size classes: a) 0.5 – 3 m in height, hereafter referred to as sapling and shrubs, and b) >3.1 m in height, hereafter referred to as trees. Classic rarefaction curves were generated for each size class to assess the completeness of the vegetation surveys using EstimateS version 8.2 (Colwell, 2006). To estimate true species richness non-parametric estimators (bias-corrected Chao 1 and 2, jackknife 1, jackknife 2) were calculated by resampling the data 1000 times. These analyses were carried out using EstimateS version 8.2 (Colwell, 2006).

Species rank abundance curves were constructed to visualise relative species abundance for both size classes. Species comprising <1% of the total number of individual woody plants recorded for each size class were classified as rare species.

3.3 Results

3.3.1 Inventory of woody plant species

A total of 8805 individual woody plants were recorded in the surveys, comprising of 6085 saplings and shrubs and 2720 trees. This was made up of 79 morpho-species, of which 78 could be identified to at least genus level (Table 3.1). Smoothed rarefaction curves, scaled to individuals, showed that the vegetation surveys were a good representation of the species richness in the forest regrowth area for both sapling and shrub and tree classes (Figure 3.4). The non-parametric estimators calculated and the proportion of observed relative to estimated 'true' species richness also suggest that the majority of species in the forest regrowth were observed in the vegetation surveys (Table 3.2).

In FR 69.11% of all individual woody plants were between 0.5 - 3 m in height, 30.41% were between 3.1 m and 5 m and the remaining 0.48% was composed of the remaining height classes combined (10.1 – 20 m, 20.1 – 30 m, >30.1 m) (Figure 3.5). This 0.48% is made up of individuals of *Campnosperma coriaceum,* Co*mbretocarpus rotundatus, Mezzettia havilandii, Dyera polyphylla, Ploiarium alternifolium, Shorea beccariana, Diospyros areolata, Diospyros curranii, Diospyros evena, Blumeodendron tokbrai, Dialium platysepalum, Litsea grandis* var. *rufofusca*, *Aglaia* sp., *Gymnacranthera farquhariana, Horsfieldia* sp., *Syzygium myrtifolium, Syzygium* sp., *Ardisia copelandii,, Prunus grisea, Timonius* sp., *Palaquium ridleyi* and *Stemonurus scorpioides.* Full details of each species by height class are in Appendix A.

Species rank abundance curves (Figure 3.6) show that for both saplings & shrubs and trees, the area was dominated by a few abundant species, and the steep slope of both curves indicates low species evenness. The woody plant *Combretocarpus rotundatus* accounted for 44.3% of all trees and 23% of all saplings & shrubs recorded (Table 3.3). The two size classes also shared six of the same most abundant species (Table 3.3). The sapling & shrub species composition contained 53 (70.7%) rare species while the tree composition contained 52 (72.2%) rare species. *Combretocarpus rotundatus* was also the most widespread woody plant, with saplings and trees of the species found in 66.5% and 49.6% of all plots respectively

(Table 3.4). Of the 79 morpho-species recorded in the vegetation surveys 57% have been recorded in at least one other peat swamp forest in Central Kalimantan (Table 3.2).

3.3.2 Ground cover

The ground cover comprised of four species of fern (Pteridophyta), with *Stenochlaena palustris* (42.1% ± 30.2) dominating the mean percentage ground cover, followed by *Blechnum indicum* (22.5% ± 29.4), *Nephrolepis hirsutula* (14.9% ± 25.1) and *Pteridium esculentum* (7.7% ± 19.9), as well as tree cover (6.3% ± 16.1), bare ground (5.2% ± 10.6) and standing or fallen dead wood 1.3% ± 8.1) (Table 3.5).

3.3.3 Dispersal agents

The woody plant species composition showed an array of dispersal agents, with the largest number of species dispersed by bulbuls and other small- to medium-sized birds (25.3% of sapling & shrub species; 22.2% of tree species), followed by wind-dispersed species (18.7% and 19.4% respectively) but with a number of species dispersed by mammals (excluding rodents and bats) (14.7% and 16.7%), larger birds (13.3% and 13.9%) or a combination of both (10.7% and 11.1%) (Figure 3.7). Wind-dispersed individuals (42.9%) and bulbul-dispersed individuals (38.9%) equally dominated the sapling & shrub composition, while wind-dispersed individuals (61.5%) dominated the tree composition (Figure 3.7).

Table 3.1. Woody plant species found forest regrowth (FR) in vegetation surveys carried out in Block A NW in the former Mega Rice Project area in Central Kalimantan, Indonesia, including dispersal agent (based on Corlett (1998) and pers. comm). Where the dispersal agent is classified as mammals, this is mammals excluding bats and rodents unless otherwise stated. Records of each species in relatively intact peat swamp forest in Central Kalimantan are indicated as follows: TU = Tuanan phenology plot (Bastian, 2008); SL = Sungai Lading (Bastian, 2008); SA = Sabangau Forest (Harrison et al., 2010); CKPSF = Central Kalimantan peat swamp forest check-list (Simbolon and Mirmanto, 1999).

Family	Species	Saplings & shrubs	Trees	Dispersal Agents	Checklist
Anacardiaceae					
	Campnosperma coriaceum (Jack) Hallier f.	✓	✓	Bulbuls, larger birds	TU SL SA CKPSF
	Campnosperma squamatum Ridl.	✓	✓	Larger birds, mammals	SA
Anisophylleaceae					
	Co*mbretocarpus rotundatus* (Miq.) Danser	✓	✓		SA CKPSF
Annonaceae					
	Goniothalamus malayanus Hook.f. & Thomson	✓	✓	Larger birds, mammals	
	Mezzettia havilandii Ridl.	✓	✓	Larger birds, mammals	CKPSF
	Polyalthia hypoleuca Hook.f. & Thomson	✓	✓	Larger birds, mammals	TU SA CKPSF
	Xylopia caudata Hook.f. & Thomson	✓	✓	Larger birds, mammals	CKPSF
Apocynaceae					
	Alstonia pavonina	✓	✓		
	Dyera polyphylla (Miq.) Steenis	✓	✓		TU SL SA CKPSF
Aquifoliaceae					
	Ilex cymosa Blume	✓	✓	Bulbuls	TU SA CKPSF
Bonnetiaceae					
	Ploiarium alternifolium (Vahl) Melch.	✓	✓		TU SA CKPSF

Table 3.1 (continued)

Family	Species	Saplings & shrubs	Trees	Dispersal Agents	Checklist
Burseraceae					
	Santiria griffithii Engl.	✓	✓	Larger birds	CKPSF
	Santiria laevigata Blume	✓	✓	Larger birds	TU SL CKPSF
Calophyllaceae					
	Calophyllum soualattri Burm.f.	✓	✓	Mammals	SL SA CKPSF
Cannabaceae					
	Trema orientalis (L.) Blume	✓	✓	Bulbuls	CKPSF
Chrysobalanaceae					
	Licania splendens (Korth.) Prance		✓	Bulbuls	TU SL SA
Clusiaceae					
	Garcinia nigrolineata Planch. ex T.Anderson	✓	✓	Mammals	
	Garcinia sp. 1	✓	✓	Mammals	SA
Crypteroniaceae					
	Dactylocladus stenostachys Oliv.	✓	✓		TU SA CKPSF
Dipterocarpaceae					
	Cotylelobium lanceolatum Craib	✓	✓		SA
	Shorea balangeran Burck	✓	✓		SA CKPSF
	Shorea beccariana Burck	✓	✓		
	Shorea smithiana Symington	✓	✓		
	Shorea sp.	✓	✓		
Ebenaceae					
	Diospyros areolata King & Gamble	✓	✓	Mammals	SA
	Diospyros confertiflora (Hiern) Bakh.	✓	✓	Mammals	TU SL SA
	Diospyros curranii Merr.	✓	✓	Mammals	
	Diospyros evena Bakh.	✓	✓	Mammals	SA CKPSF

Table 3.1 (continued)

Family	Species	Saplings & shrubs	Trees	Dispersal Agents	Checklist
Elaeocarpaceae					
	Elaeocarpus sp.	✓	✓	Bulbuls, larger birds, mammals	
Euphorbiaceae					
	Blumeodendron tokbrai (Blume) Kurz	✓	✓	Mammals	SA
	Macaranga diepenhorstii (Miq.) Müll.Arg.	✓	✓	Bulbuls	
Fabaceae					
	Archidendron borneense (Benth.) I.C.Nielsen	✓	✓		SA
	Caesalpinia sp.	✓	✓		
	Dialium platysepalum Baker	✓	✓		
Fagaceae					
	Lithocarpus sp.	✓	✓	Rodents	SA CKPSF
Hypericaceae					
	Cratoxylum arborescens (Vahl) Blume AND *Cratoxylum glaucum* Korth.	✓	✓		TU SL SA CKPSF
Lauraceae					
	Alseodaphne coriacea Kosterm.	✓	✓	Larger birds	TU SL SA CKPSF
	Cryptocarya enervis Hook.f.	✓	✓	Bulbuls	
	Litsea grandis var. rufofusca (Kosterm.) Ng	✓	✓	Bulbuls	TU CKPSF
	Phoebe grandis (Nees) Merr.	✓	✓	Larger birds	SA
Lecythidaceae					
	Barringtonia longisepala Payens	✓			
	Barringtonia reticulata (Blume) Miq.	✓	✓		CKPSF
Melastomataceae					
	Melastoma malabathricum L.	✓	✓	Bulbuls	

Table 3.1 (continued)

Family	**Species**	**Saplings & shrubs**	**Trees**	**Dispersal Agents**	**Checklist**
Meliaceae					
	Aglaia sp.	✓	✓	Larger birds	
	Chisocheton patens Blume	✓	✓	Larger birds	
	Sandoricum beccarianum		✓	Mammals	SA
Myristicaceae					
	Gymnacranthera farquhariana (Hook.f. & Thomson) Warb.	✓	✓	Larger birds	TU SL SA CKPSF
	Horsfieldia crassifolia (Hook.f. & Thomson) Warb.	✓	✓	Larger birds	TU SL SA CKPSF
	Horsfieldia sp.	✓	✓	Larger birds	
	Knema stenophylla (Warb.) J.Sinclair	✓	✓	Larger birds	
Myrtaceae					
	Melaleuca cajuputi Powell	✓	✓		
	Rhodamnia cinerea Jack	✓	✓	Bulbuls	TU SL CKPSF
	Syzygium myrtifolium Walp.	✓	✓	Bulbuls	
	Syzygium oligomyrum Diels	✓	✓	Larger birds, mammals	CKPSF
	Syzygium palembanicum Miq.	✓	✓	Larger birds, mammals	CKPSF
	Syzygium sp.	✓	✓	Bulbuls	
	Syzygium sp.3	✓	✓	Bulbuls	
	Syzygium sp.4	✓		Bulbuls	
	Syzygium zeylanicum (L.) DC.		✓	Bulbuls	SA
	Tristaniopsis whiteana (Griff.) Peter G.Wilson & J.T.Waterh.	✓	✓		TU CKPSF
Phyllanthaceae					
	Antidesma coriaceum Tul.	✓		Bulbuls	CKPSF
	Antidesma montanum Blume	✓		Bulbuls	CKPSF

Table 3.1 (continued)

Family	Species	Saplings & shrubs	Trees	Dispersal Agents	Checklist
Polygalaceae					
	Xanthophyllum discolor Chodat	✓	✓	Larger birds, mammals	
Primulaceae					
	Ardisia copelandii Mez	✓	✓	Bulbuls	
Rhizophoraceae					
	Pellacalyx axillaris Korth.	✓		Bats	
Rosaceae					
	Prunus grisea Kalkman	✓	✓	Bulbuls, larger birds	
Rubiaceae					
	Ixora havilandii Ridl.	✓	✓	Bulbuls	
	Pavetta sp.	✓		Bulbuls	
	Rothmannia grandis	✓	✓	Mammals	
	Timonius sp.	✓	✓	Bulbuls	CKPSF
Rutaceae					
	Melicope lunu-ankenda (Gaertn.) T.G. Hartley	✓	✓	Bulbuls	
Sapindaceae					
	Nephelium lappaceum L.	✓	✓	Mammals	SA
Sapotaceae					
	Palaquium ridleyi King & Gamble	✓	✓	Mammals including bats	TU SL SA CKPSF
	Pouteria malaccensis (C.B.Clarke) Baehni	✓	✓	Mammals including bats	TU
Stemonuraceae					
	Stemonorus scorpiodes	✓	✓	Mammals	TU SL SA CKPSF
	Stemonurus secundiflorus	✓	✓	Animal - unknown	

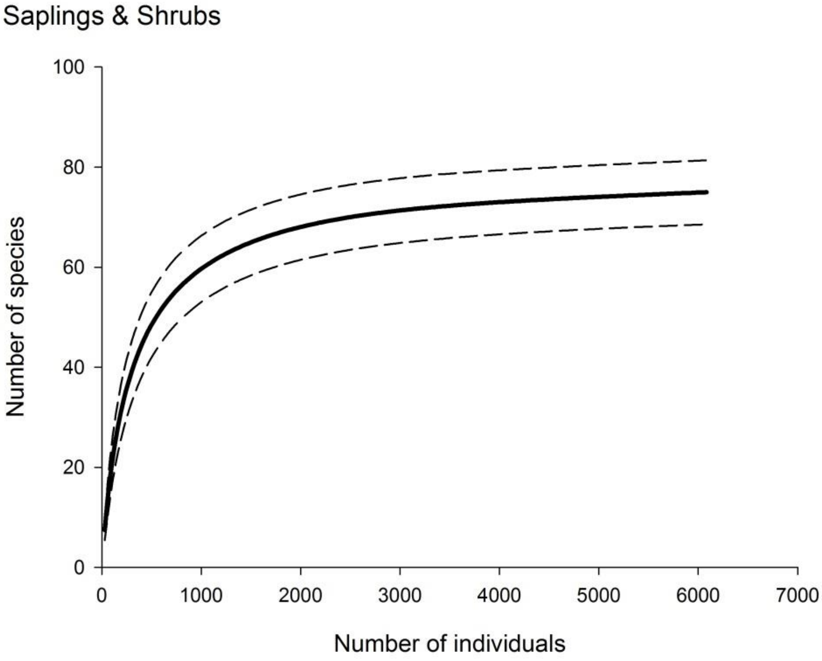
Table 3.1 (continued)

Family	Species	Saplings & shrubs	Trees	Dispersal Agents	Checklist
Thymelaeaceae					
	Gonystylus bancanus (Miq.) Kurz AND *Gonystylus brunnescens* Airy Shaw	✓	✓	Larger birds, rodents	SL SA CKPSF
Verbenaceae					
	Clerodendrum sp.	✓		Bulbuls	
Unknown					
	Unknown - Ketapi hutan		✓	Unknown	
	Total	75	72		

Table 3.2. Results and nonparametric species richness estimators for woody plant species from vegetation plots in forest regrowth (FR) in the former Mega Rice Project Area, Central Kalimantan, Indonesia. Proportion of observed species richness to each of the computed estimates is shown in parenthesis.

	Saplings and Shrubs	Trees
Individual woody plants	6085	2720
Species observed	75	72
Mean no. species per plot	7.5 ± 4.7	3.4 ± 5.0
Species richness estimators:		
Chao 1 mean	87.5 (85.7)	73.79 (97.57)
Chao 2 mean	87.5 (85.7)	74.23 (97.00)
Jack 1 mean	79.98 (93.77)	78.96 (91.19)
Jack 2 mean (trees)	83.96 (89.33)	75.07 (95.91)

Figure 3.4. Smoothed rarefaction curves showing woody plant species richness, scaled to individuals, with 95% confidence intervals shown (dotted lines), in the forest regrowth of Block A NW in the former Mega Rice Project area, Central Kalimantan, Indonesia.



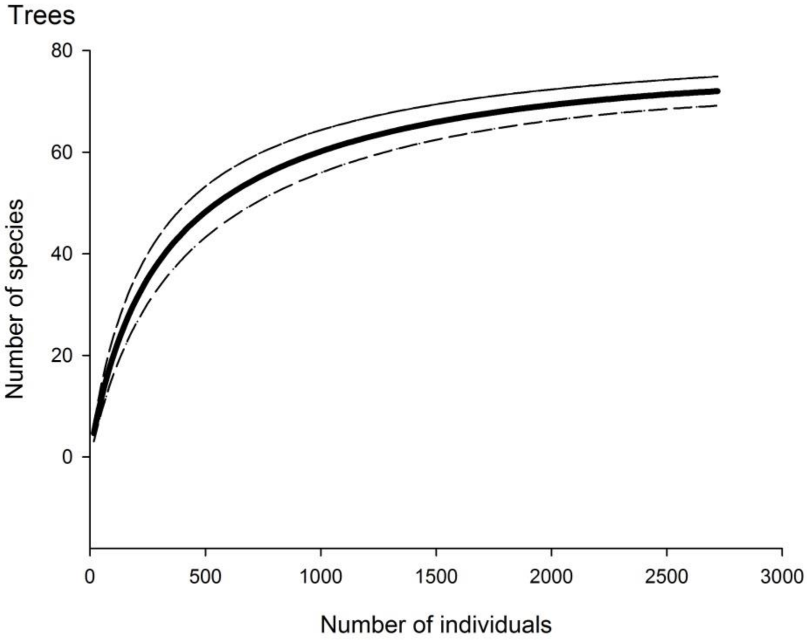


Figure 3.5. Estimated heights of woody plants recorded in vegetation surveys in forest regrowth of Block A NW in the former Mega Rice Project area, Central Kalimantan, Indonesia.

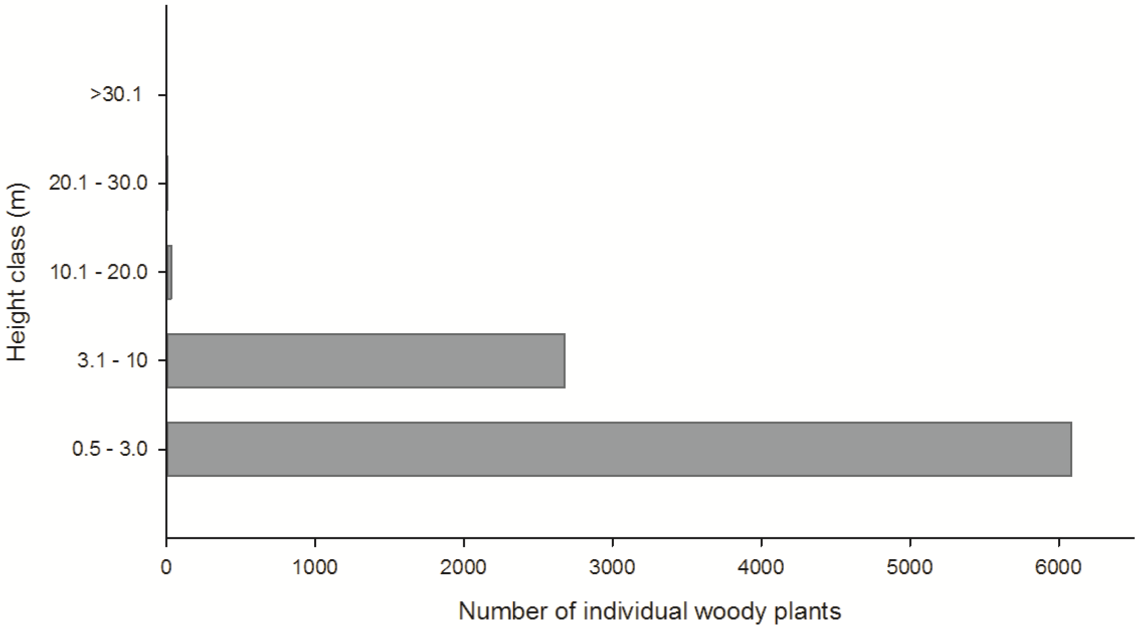


Figure 3.6. Rank abundance curves of species for saplings and shrubs and trees recorded in vegetation plots in forest regrowth in Block A NW of the former Mega Rice Project, Central Kalimantan, Indonesia.

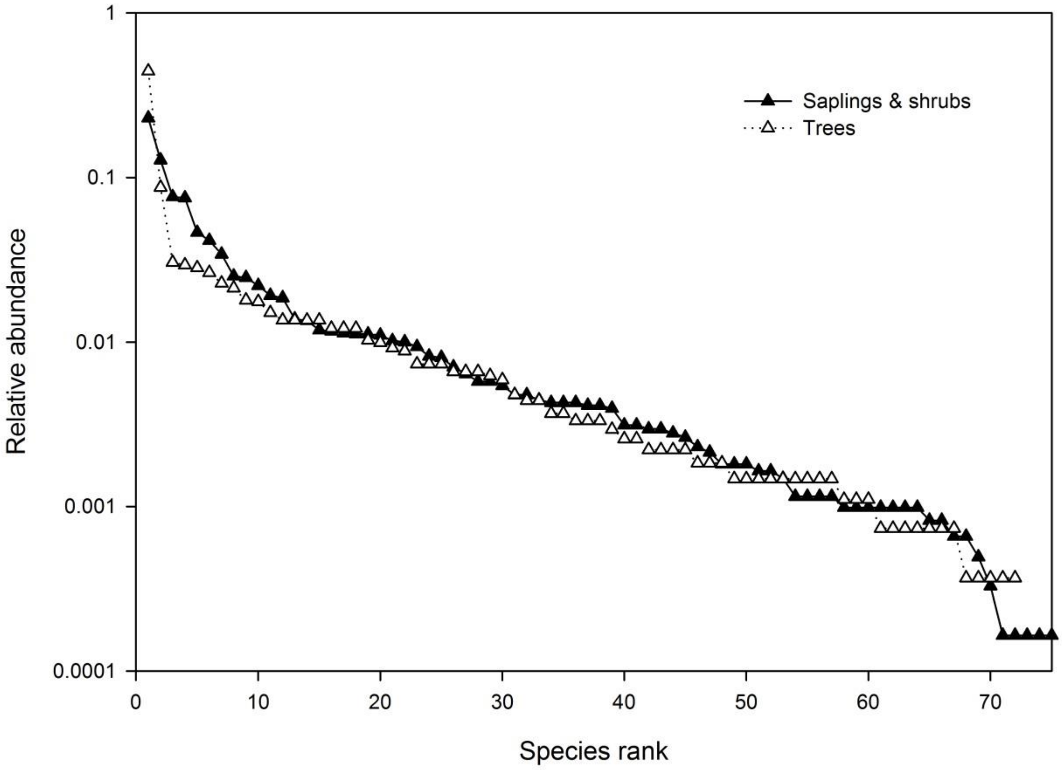


Table 3.3. Ten most abundant species of woody plants for forest regrowth in the former Mega Rice Project area in Central Kalimantan, Indonesia, with dispersal agent (based on Corlett (1998) and pers. comm). Where the dispersal agent is classified as mammals, this is mammals excluding bats and rodents unless otherwise stated.

Size class	Family	Species	Percentage abundance	Dispersal agent
Saplings and shrubs	Anisophylleaceae	*Combretocarpus rotundatus*	23	Wind
	Melastomataceae	Melastoma malabathricum	12.8	Bulbuls
	Hypericaceae	*Cratoxylum glaucum* and *Cratoxylum arborescens*	7.6	Wind
	Bonnetiaceae	*Ploiarium alternifolium*	7.5	Wind
	Rutaceae	*Melicope lunu-ankenda*	4.6	Bulbuls
	Lauraceae	*Cryptocarya enervis*	4.1	Bulbuls
	Myrtaceae	*Syzygium* sp.3	3.4	Bulbuls
	Myrtaceae	*Syzygium myrtifolium*	2.5	Bulbuls
	Elaeocarpaceae	*Elaeocarpus* sp.	2.5	Bulbuls, larger birds, mammals
	Myrtaceae	*Melaleuca cajuputi*	2.2	Wind
Trees	Anisophylleaceae	*Combretocarpus rotundatus*	44.3	Wind
	Hypericaceae	*Cratoxylum glaucum* and *Cratoxylum arborescens*	8.7	Wind
	Myrtaceae	*Syzygium myrtifolium*	3.1	Bulbuls
	Sapindaceae	*Nephelium lappaceum*	2.9	Mammals
	Fagaceae	*Lithocarpus* sp.	2.8	Rodents
	Elaeocarpaceae	*Elaeocarpus* sp.	2.6	Bulbuls, larger birds, mammals
	Dipterocarpaceae	*Shorea beccariana*	2.3	Wind
	Bonnetiaceae	*Ploiarium alternifolium*	2.1	Wind
	Myrtaceae	*Syzygium palembanicum*	1.8	Larger birds, mammals
	Rutaceae	*Melicope lunu-ankenda*	1.8	Bulbuls

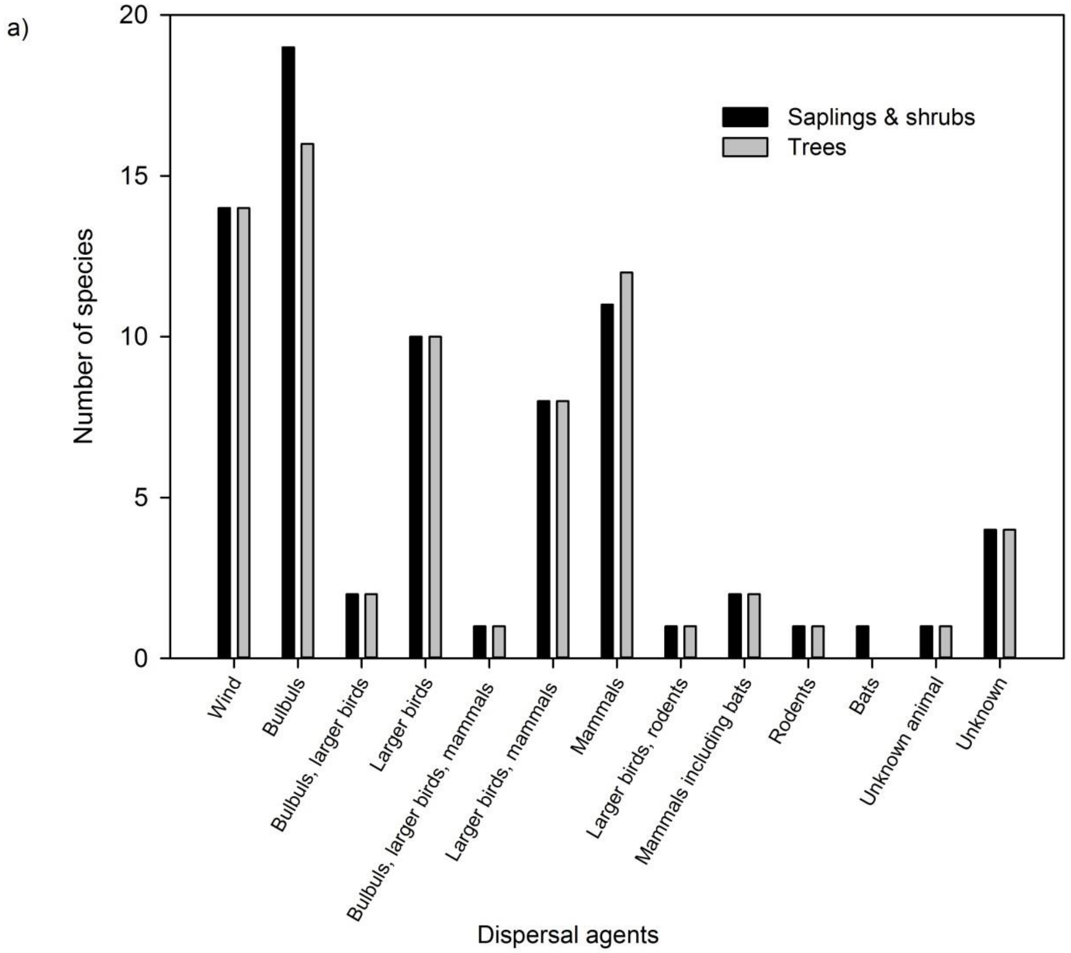
Table 3.4. Ten most widespread species of woody plants for forest regrowth in the former Mega Rice Project area in Central Kalimantan, Indonesia, with dispersal agent (based on Corlett (1998) and pers. comm).

Size class	Family	Species	Number of plots	% of plots	Dispersal agent
Saplings and shrubs	Anisophylleaceae	*Combretocarpus rotundatus*	149	66.5	Wind
	Melastomataceae	*Melastoma malabathricum*	104	46.4	Bulbuls
	Hypericaceae	*Cratoxylum arborescens* and *Cratoxylum glaucum*	95	42.4	Wind
	Elaeocarpaceae	*Elaeocarpus* sp.	73	32.6	Bulbuls, larger birds, mammals
	Rutaceae	*Melicope lunu-ankenda*	67	29.9	Bulbuls
	Aquifoliaceae	*Ilex cymosa*	65	29.0	Bulbuls
	Theaceae	*Ploiarium alternifolium*	59	26.3	Wind
	Myrtaceae	*Syzygium* sp. 3	54	24.1	Bulbuls
	Myrtaceae	*Syzygium myrtifolium*	44	19.6	Bulbuls
	Clusiaceae	*Garcinia nigrolineata*	41	18.3	Mammals
Trees	Anisophylleaceae	*Combretocarpus rotundatus*	111	49.6	Wind
	Hypericaceae	*Cratoxylum arborescens* and *Cratoxylum glaucum*	59	26.3	Wind
	Elaeocarpaceae	*Elaeocarpus* sp.	34	15.2	Bulbuls, larger birds, mammals
	Myrtaceae	*Syzygium myrtifolium*	29	12.9	Bulbuls
	Sapindaceae	*Nephelium lappaceum*	27	12.1	Mammals
	Clusiaceae	*Garcinia nigrolineata*	23	10.3	Mammals
	Fagaceae	*Lithocarpus* sp.	22	9.8	Bats
	Theaceae	*Ploiarium alternifolium*	21	9.4	Wind
	Lauraceae	*Litsea grandis* var. rufofusca	20	8.9	Bulbuls
	Aquifoliaceae	*Ilex cymosa*	19	8.5	Bulbuls

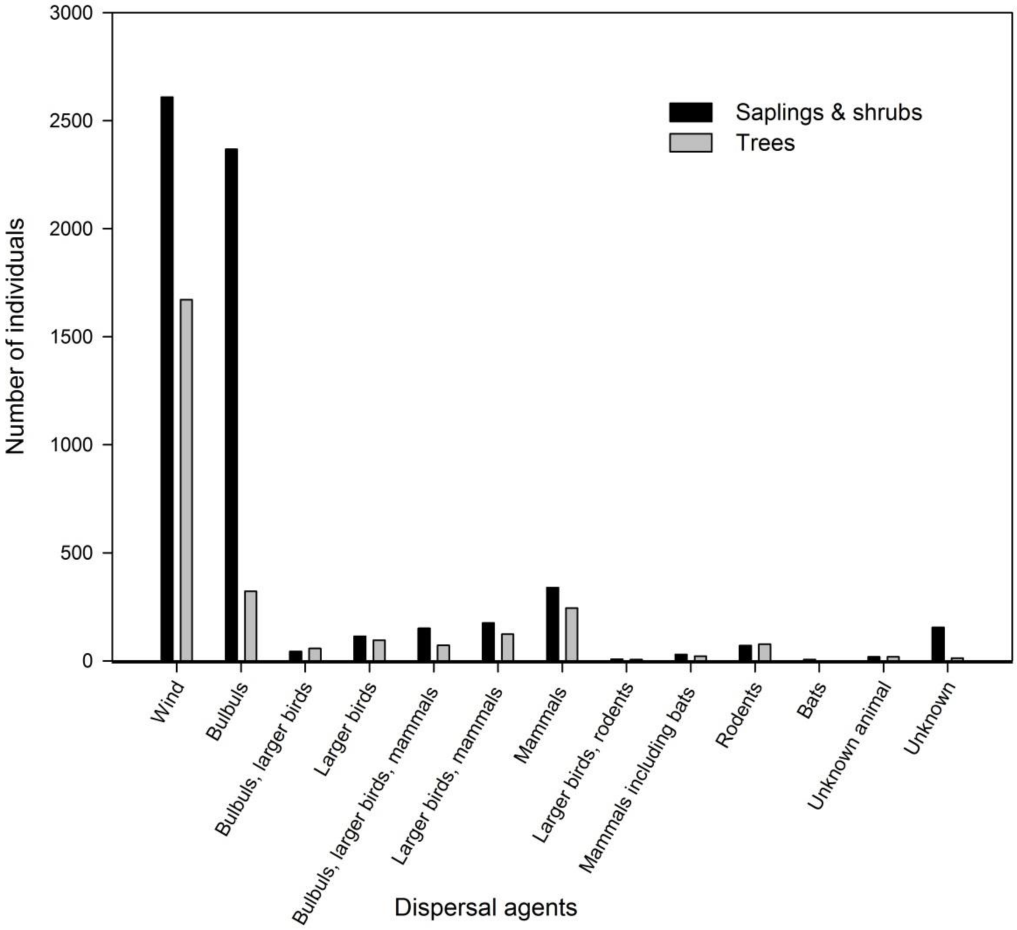
Table 3.5. Mean estimated percentage of ground cover, with standard deviation, per 20 m x 20 m vegetation plot for the forest regrowth in Block A NW, former Mega Rice Project area, Central Kalimantan, Indonesia.

Ground cover type	Ferns				Other		
	Stenochlaena palustris (Burm.) Bedd.	*Pteridium esculentum* (Forst.) Nakai	*Blechnum indicum* Burm.f.	*Nephrolepis hirsutula* (G.Forst.) C.Presl	Trees	Bare ground	Standing or fallen dead wood
Mean estimated percentage of plot area	42.1 ± 30.2	7.7 ± 19.9	22.5 ± 29.4	14.9 ± 25.1	6.3 ± 16.1	5.2 ± 10.6	1.3 ± 8.1

Figure 3.7. Abundance of saplings & shrubs and trees by dispersal agent showing a) number of species and b) number of individual woody plants, for an area of forest regrowth (FR) in Block A NW of the former Mega Rice Project. Where the dispersal agent is classified as mammals, this is mammals excluding bats and rodents unless otherwise stated.



b)


Saplings & shrubs
Trees
Number of individuals
0
500
1000
1500
2000
2500
3000
Wind
Bulbuls
Bulbuls, larger birds
Larger birds
Bulbuls, larger birds, mammals
Larger birds, mammals
Mammals
Larger birds, rodents
Mammals including bats
Rodents
Bats
Unknown animal
Unknown
Dispersal agents

3.4 Discussion

The woody plant composition consisted largely of species that also grow in mature peat forest (Bastian, 2008, Harrison et al., 2010, Morrogh-Bernard, 2009, Simbolon and Mirmanto, 1999), although it also contained some typical woody pioneer species of non-peatland open sites in SE Asia, such as *Melastoma malabathricum* and *Macaranga diepenhorstii* (Nykvist, 1996, Slik et al., 2008). The area was dominated by a few abundant species but also contained a high diversity of woody plant species, albeit in low abundances. This is a very different finding to that of studies on natural regeneration of woody plant species on degraded lands in other forest types in Southeast Asia, which typically finds that areas are recolonized by a relatively small number of genera (Corlett, 1991, Corlett, 1995, Do et al., 2011, Slik et al., 2008). Possible explanations for the patterns of woody plant composition and abundance see in the forest regrowth of Block A NW are the composition of dispersal agents present in the area, the survival of individuals through fire and forest clearance events, and the resprouting ability of some species.

While both the saplings & shrubs and tree class woody plant composition show a wide-range of dispersal agents, in terms of numbers, both classes were dominated by wind-dispersed species or those dispersed by bulbuls and other small- and medium-sized birds, and this likely reflects the composition of dispersal agents in the area. Less than 20 years ago the study area formed part of a near-intact peat dome ecosystem that included apes (Bornean orang-utan, *Pongo pygmaeus*; Bornean agile gibbon, *Hylobates albibarbis*), monkeys (macaques, *Macaca* spp.), deer (sambar, *Rusa unicolor*; mousedeer, *Tragulus* sp.), fruit-eating carnivores (sun bear, *Helarctos malayanus*; civets, Viverridae), flying foxes (*Pteropus* *vampyrus*) and smaller fruit bats (Harrison et al., 2011) as well as a diversity of forest birds, including hornbills, fruit pigeons and other large-gaped species (Posa, 2011 and pers.comm.). Camera traps and direct observations confirm that most of these taxa, including orangutans, gibbons, macaques, sambar deer, sun bears and hornbills, still survive in the degraded forest fragments of Block A NW (Posa pers. comm.) and while some of these may leave the forest to cross open habitats, their movement will be limited by the canal system. Surveys in the forest regrowth showed that the yellow-vented bulbul (*Pycnonotus goiavier*) dominated an avian community made up of small passerines, with no larger-gaped species present (Posa, 2011). This dominance of bulbuls and lack of large bird and mammal dispersal agents likely explains the high number of bulbul-dispersed individuals found in the surveys.

However, the species composition for both saplings and shrubs and trees shows an array of dispersal agents, many of which are unlikely to be found in the area. The presence of woody plant species without their complementary dispersal agents may be due to individual woody plants surviving through fire events. Block A NW was cleared and burnt in 1997 (Aldhous, 2004) and I carried out my surveys in 2009 and 2010. This means that any natural regeneration of woody plants was a maximum of thirteen years old at the time of my surveys. Looking at the estimated height data, and working on the assumption that all woody plants ≤ 3m are natural regeneration and all woody plants ≥ 10.1 m are remnant vegetation (with the origin of woody plants of intermediary heights uncertain), the survival of individuals through fire events may explain the presence of 21 of the woody plant species found in FR.

It is also possible that the presence of woody plant species without their complementary dispersal agents may be due to natural regeneration through resprouting. The resprouting of woody plant species after disturbance has been seen in studies of areas of abandoned cultivation in the Neotropics. For example, Uhl et al. (1988a) found that 94 of 171 tree species identified in abandoned pastures in Eastern Amazonia demonstrated sprouting ability and Guimaraes and Proctor (2007) found that while pioneer species dominated among secondary forest seedlings in natural regeneration on areas of abandoned slash and burn cultivation in lowland evergreen rain forest in Eastern Amazonia, some primary forest species were present in the area in the form of resprouts. Resprouting ability has also been seen after disturbance in the forests of Southeast Asia. In burnt areas of dipterocarp forest in East Kalimantan 17% of above-ground-killed seedlings and saplings of primary forest species showed sprouting ability, and these sprouts appeared to play an important role in the persistence of primary forest species post-fire (Van Nieuwstadt et al., 2001). For tropical peatlands, van Eijk et al. (2009) found that a number of woody plant species demonstrated the ability to resprout after fire events in Berbak National Park, Sumatra, and seed bank assessments in the Sabangau region of Central Kalimantan found that severed roots in the peat samples were able to resprout, although species could not be identified (Laura Graham, pers. comm.). While it was unfeasible to examine all the individual woody plants found in the vegetation surveys for resprouts, future research should investigate resprouting ability in forest species of peat swamp forests to establish if and how this method of natural regeneration influences the composition and abundance of woody plant species in degraded tropical peatland.

The composition of dispersal agents and the ability to resprout also explains the dominance of certain woody plant species in the forest regrowth. Overall, the vegetation plots were dominated by *Combretocarpus rotundatus*, which is found in relatively undisturbed tropical peatlands and is one of the dominant species in various phasic communities on peat domes in Central Kalimantan (Harrison et al., 2010, Simbolon and Mirmanto, 1999, Mirmanto, 2010, Poesie et al., 2011, Page et al., 1999) and Brunei (Anderson, 1963). As well as dominating parts of relatively undisturbed tropical peatlands, *C. rotundatus* also shows a number of traits that explain why it dominates forest regrowth. Firstly, it is a wind-dispersed species that produces seed all year round (chapter 5) which suggests it can be dispersed from far away seed sources and potentially in large numbers. Secondly, *C. rotundatus* has the ability to resprout after fire events and while the extensive fern coverage made it unfeasible to check woody plants for evidence of resprouting, my vegetation surveys in compartment c-8 were carried out after a recent fire and I found evidence of individuals of *C. rotundatus* resprouting (Figure 3.8). This means that *C. rotundatus* has two means of colonising a degraded peatland area, presuming it was part of the original species composition, and explains the dominance of this species in FR.

Of the other most abundant woody plant species in FR, the shrub species *M. malabathricum* and tree species *S. myrtifolium* are small-seeded and animal-dispersed and these traits likely explain their dominance in the FR. *M. malabathricum* has also been found in degraded tropical peatlands in Sumatra (Chokkalingam et al., 2009, van Eijk et al., 2009) as well as on degraded lands of other forest types in Kalimantan (Brearley et al., 2004, Slik et al., 2008, Yassir et al.,

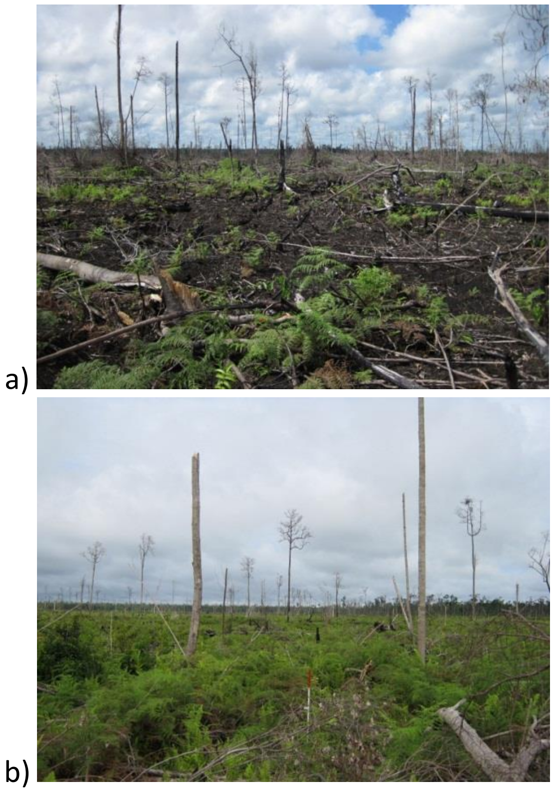
2010) and in other parts of Southeast Asia (e.g. Singapore, Corlett, 1991). Similarly, *Cratoxylum arborescens/glaucum* and *Ploiarium alternifolium* have both been recorded on degraded peatlands in Sumatra (Chokkalingam et al., 2009) with *C. arborescens* also found to dominate old secondary rain forest in Barito Ulu, Central Kalimantan (Brearley et al., 2004) and *P. alternifolium* also found on degraded land in Singapore (Corlett, 1991). Both are wind-dispersed species and this trait likely explains their abundance in the area.

Looking at the herbaceous ground cover in the forest regrowth, fern species dominated throughout the area. Ferns are not found naturally in tropical peat swamp forests and have probably colonised the area via long-distance wind-dispersed spores (Cleary and Priadjati, 2005). This domination of ferns after disturbance has also been seen on degraded lands and after disturbance in other parts of the tropics (Cleary and Priadjati, 2005, Cohen et al., 1995, Slocum et al., 2004, Shono et al., 2006, Walker, 1994, Walker et al., 2010). Fast-growing fern stands may inhibit the colonisation of woody plant species by out-growing seedlings and resprouts and excluding other plants (Aide et al., 1995, Cleary and Priadjati, 2005, Shono et al., 2006, Walker, 1994). The ferns in Block A NW are indeed fast-growing; a fire incident on compartment D1 in November 2009 cleared the area of its vegetation, six months later the area had sparse fern coverage and fifteen months after the fire the area had widespread fern coverage (personal observation) (Figure 3.9). The speed with which ferns were able to colonise D1, and in doing so inhibit the colonisation of other plant species, may partly explain the sparseness of woody plant individuals in the study area.

Overall, the forest regrowth was found to have a high diversity of woody plant species and although dominated by just a few species, the composition was also made up of a large number of mature forest species, albeit in low abundances. While this initially suggests a successional trajectory towards forest recovery, the speed at which this takes place will be dependent on a number of factors including levels of seed dispersal in the area. At present, the most abundant woody plant species are either wind-dispersed or dispersed by the dominant avian seed disperser in the area, the yellow-vented bulbul (*Pycnonotus goiavier*). This suggests that these species will continue to be dispersed within the area. In contrast, a lack of large bird and mammal dispersal agents in forest regrowth may limit the further dispersal of the larger-seeded forest species currently found within the degraded area. If this is the case then the woody plant species composition and abundance in FR of Block A NW will continue to be dominated by wind-dispersed and bulbul-dispersed species in the future. Potential seed dispersal limitations will be explored further in chapter 5 where I investigate seed rain in an area of FR in Block A NW.

Figure 3.8. Example of *Combretocarpus rotundatus* resprout after a fire event (compartment c-8) in forest regrowth of Block A NW, former Mega Rice Project Area, Central Kalimantan, Indonesia.

Figure 3.9. Photos of an area in compartment d-1 of Block A NW in a) May 2010, six months after fire affected the area and b) Feb 2011, fifteen months after fire affected the area, showing the growth of ferns during this time.



4. Impacts of the implementation of the Mega Rice Project and their relationship to the natural regeneration of woody plants in Block A NW

4.1 Introduction

Tropical peatlands are water-logged, naturally forested ecosystems and it is these very characteristics that mean some kind of modification to the natural forest cover and natural hydrology of the area is necessary if any form of economic land use is to take place (Page et al., 2009c). Since 1990 nearly half of the tropical peatlands on the islands of Sumatra and Borneo and in Peninsula Malaysia have been converted into other land-cover types, although interestingly, for Peninsula Malaysia and Sumatra, this land-cover change has been into industrial plantations such as oil palm and pulp wood, whereas on Borneo, previously forested land has mainly become degraded, deforested areas (Miettinen and Liew, 2010). In part, this increase in degraded peatland area on Borneo is because much of the land conversion of tropical peatland is done without proper assessment of the area or because of a lack of knowledge of the functioning of tropical peatlands (Page et al., 2009b). The successional pathways that occur in a degraded area are entirely dependent upon the specific disturbances that have taken place and the conditions of that area prior to those disturbances (Hobbs and Norton, 2004). In chapter 3 I investigated the composition and abundance of woody plant species in the forest regrowth of Block A NW of the former Mega Rice Project Area. In this chapter I examine if and how this composition and abundance is related to the environmental impacts of the land conversion implemented during and after the instigation of the

Mega Rice Project, specifically the fire history, hydrology and distance to the nearest canal.

4.1.1 Fire

Undisturbed tropical forests are resistant to fire but disturbances such as logging may make these forests susceptible to fire (Uhl et al., 1988b, Field et al., 2009, but see Cochrane, 2003 for a review). Indeed, tropical peatlands specifically are naturally water-logged ecosystems not prone to fire, but the drainage systems implemented in land conversion increase susceptibility (Page et al., 2002) because dry peat burns more easily (Usup et al., 2004). Low groundwater levels have been connected to areas of fire damage; for the 1997 El Nino year a 74% correspondence was found between groundwater levels below 0.4 m and fire damage in the Sabangau catchment and Block C of the former Mega Rice project (Wosten et al., 2008).

All fires occurring in tropical peatlands are started by people. This can be for various reasons, including as a tool to clear land, to aid resource extraction or as a weapon in land disputes (Dennis et al., 2005). Once lit, these fires can run out of control. For example, large-scale commercial companies have used fire to open up land for oil palm and timber plantations and some of these fires have escaped into other areas (Page et al., 2009c). In other situations such as during conflicts between smallholders and large companies, unmanaged fires are purposefully lit (Suyanto, 2007). See Page (2009b) for an in-depth review of the causes of fire in tropical peatlands in Southeast Asia.

While we have a good understanding of when, where and why fires have occurred on Borneo and in the peatlands of Kalimantan over the last twenty years (Siegert and Hoffmann, 2000, Dennis and Colfer, 2006, Tansey et al., 2008, Langner and Siegert, 2009, Segah et al., 2010, Miettinen et al., 2012b), work is only now beginning to link the impact of fire to the natural regeneration in these areas. Fire has been found to have a great effect on natural regeneration in other parts of the tropics, where fire events have been found to alter woody plant species composition and dominance patterns in tropical forests (Nykvist, 1996, Cochrane and Schulze, 1999, Cleary et al., 2006, Slik et al., 2008, Yassir et al., 2010). Similarly, work on tropical peatlands looking at the regeneration of woody plants in areas impacted by fire found a decrease in species richness when compared with intact peat swamp forest ecosystems (van Eijk et al., 2009, Page et al., 2009b). The number of fires has also been found to influence woody plant species composition in degraded tropical peatland. Work in Block C of the former Mega Rice Project area showed that an increasing number of fires leads to retrogressive succession to fern communities (Page et al., 2009b, Page et al., 2009c). This suggests that fire can have a large impact on the natural regeneration in degraded tropical peatlands.

4.1.2 Hydrology

The conversion of tropical peatlands to other land-uses requires changes to the natural hydrology (Page et al., 2009c) and typically involves the excavation of a drainage system. The draining of the land is carried out because plantation crops (e.g. oil palm [*Elaeis guineensis*] and *Acacia* spp.) grow best if water levels are maintained more than 0.5 m below the peat surface (Page et al., 2009c). Drainage systems have been based on the need to remove excess rainwater to prevent flooding and use the assumption that excess rainwater in the system is removed by surface runoff (Ritzema, 2007), but this uncontrolled drainage often leads to extreme changes in water levels, including drought and flooding. Modelling of groundwater levels in relatively intact and in drained tropical peatlands found that groundwater levels in all areas showed year-to-year and month-to-month variation (Wosten et al., 2006). However, groundwater levels in drained tropical peatland were lower overall than in relatively intact peatland and in ‘drought’ years the intact peatland returned to its original hydrological state quicker than drained areas in the same region (Wosten et al., 2006).

In the Mega Rice Project area a system of 4600 km of canals was established (Aldhous, 2004) with the aim of providing both drainage and a water supply to the area (Mawdsley et al., 2009). The drainage system for Block A was planned so that water from the main rivers on either side of Block A (intended to be managed by gates that were never built) would pass through primary canals to secondary and tertiary canals, with a separate supply and drainage system (Mawdsley et al., 2009). However, this plan did not take into account the peat domes that make up much of the area and was never fully completed (Mawdsley et al., 2009). At present we know very little about how changes in hydrology through the implementation of a drainage system affect the natural regeneration of woody plants in areas of degraded tropical peatland such as the former Mega Rice Project area.

The findings of other studies investigating the connection between hydrology and vegetation in tropical peatlands suggest that alterations to the natural hydrology are likely to impact the composition of woody plants in the area. For example, it has been found that tree species in undisturbed tropical peatlands show adaptations to the year-round high water table by having lateral roots or horizontal root architecture (Nishimura and Suzuki, 2001). This type of root system allows for more effective absorption of nutrients from the relatively rich upper stratum of waterlogged peat (Nishimura and Suzuki, 2001) but makes them susceptible to drought if the groundwater level drops below the level of the root system (Nishimura et al., 2007). This suggests that any changes to the natural hydrology of a tropical peatland, particularly the implementation of drainage systems, are likely to have an impact on the natural regeneration of woody plants in that area.

Conversely, it has also been found that flooding can occur in degraded tropical peatlands, because subsidence through peat oxidation and combustion lowers the peat surface (Wosten et al., 2006). Investigation into the effect of flooding depth and duration on natural regeneration of peat-swamp vegetation distinguished seven distinct vegetation types based on flooding patterns (Wosten et al., 2006). At one extreme, year-round deep flooding areas were dominated by sedges with low plant species diversity, while at the other extreme, areas with low level and short duration flooding were able to form a closed-canopy of pioneer tree species along with the establishment of some climax tree species, within seven years of a fire event. This suggests that changes to the natural hydrology of tropical peatlands that lead to water inundation are also likely to impact the composition of woody plants able to grow in the area.

The implementation of a drainage system may also impact tropical peatland ecosystems by increasing human access to the area. The low load-bearing capacity and high water table of peat make road transportation unfeasible and so access is mainly by waterways and therefore a canal system increases accessibility (Jaenicke et al., 2010). Indeed, canals are often cut to facilitate timber transportation in logging operations (Jaenicke et al., 2010, Posa et al., 2011). In the Tropics increased human access into forests, typically through road construction, has been linked to increased forest degradation (Laurance et al., 2009), for example, around 95% of all deforestation and fires in the Brazilian Amazon occur with 50 km of roads (Laurance et al., 2001). Similarly, most of the damage from the 1997 fires in the Mega Rice Project area was found to occur adjacent to drainage canals (Page et al., 2002). This suggests that the construction of a drainage system may have detrimental effects on tropical peatlands beyond altering the natural hydrology of the area.

4.1.4 Combinations of impacts

The impacts of fire and hydrology in tropical peatlands are not independent. As mentioned in section 4.1.1, dry peat, and specifically peat with groundwater levels below 0.4 m, has a high risk of catching fire (Wosten et al., 2008). Conversely, fire can also contribute to flooding in degraded tropical peatlands. Firstly, fire causes a reduction in the vegetation cover which in turn lowers the transpiration rate and leads to deeper surface water for longer times in the wet season; secondly, peat oxidation and combustion lead to subsidence (the lowering of the peat surface); and thirdly, burnt peat has a reduced capacity to store water (Wosten et al., 2006).

Fire and hydrology can also have a direct impact on the woody plants established in an area. Van Nieuwstadt and Sheil (2005) looked at the separate and combined effects of drought and fire in dipterocarp forest in East Kalimantan and found that drought mainly killed larger diameter woody plants while fire killed small diameter woody plants. This suggests that the combination of both drought and fire has more detrimental effects to the composition and abundance of woody plant species than either impact has separately.

4.1.5 Study aims

The aim of this study is to establish how fire and hydrology have impacted the natural regeneration of woody vegetation in Block A NW of the former Mega Rice Project area, Central Kalimantan, Indonesia.

4.2 Methods

4.2.1 Study site

The Block A NW region of the Mega Rice Project area is an area of forest regrowth (FR) in the north-western part of Block A (02°17’77”S; 114°31’23”E). The area is part of the Mantangai peat dome and is approximately 45 000 ha in size. The boundaries are the Kapuas River in the west, the Mantangai River in the east and the two primary Mega Rice Project canals to the north. The canal system divides the area into compartments, each roughly 2.5 x 2.5 km (Mawdsley et al., 2009). Most of the peat in this area reaches depths >3 m.

4.2.2 Inventory of woody vegetation

As described in Chapter 3, an inventory of natural regeneration in FR was carried out in 2009 and 2010 utilising a pre-existing transect set up by the Indonesia-

Australia Forest Carbon Partnership (IAFCP) as the primary survey transect as well as temporary complimentary transects on the compartments d-2, d-3 and d-4. In total, 223 vegetation plots were measured. The data on woody plants was separated into two size classes based on height with a) all individual woody plants 0.5 – 3 m in height classed as sapling-shrubs, and b) all individual woody plants >3.1 m in height classed as trees.

4.2.3 Environmental variables

Data on the fire history and current hydrological state of Block A NW was provided by IAFCP, but was not available at the start of my research. Every attempt was made to design the vegetation surveys in such a way that IAFCP data would cover the same locations. In total, IAFCP environmental data corresponded with 86 of the 223 vegetation plots.

4.2.3.1 Fire

A set of unpublished fire history maps for Block A NW was kindly provided by IAFCP. These maps were constructed using Landsat imagery covering the Block A NW region for the period 1990–2010. The dataset encompasses the time period from before the implementation of the Mega Rice Project up until the vegetation surveys described in Chapter 3 were carried out. For each year, a selection of Landsat images were used to establish the location of burn scars from fires that occurred that year. These locations were then combined into a single shapefile of the total area burnt for that year. All the shapefiles were combined to produce a single multipart polygon map showing how many times different parts of Block A NW have burnt between 1990–2010. I used ArcMap Version 10.0 (ESRI, 2011) to plot the GPS coordinate of each vegetation plot onto this map and recorded the number of times each plot had been burnt. My vegetation surveys in 2009 were carried out before fires occurred that year and this was factored in when calculating the fire history of plots.

I also used ArcMap Version 10.0 to overlay the individual shapefiles chronologically and then plotted the GPS coordinate of each vegetation plot onto this and recorded the year each vegetation plot last burnt. This was then used to calculate the number of years since the last fire (present time = 2010) for each vegetation plot. Vegetation plots that were found to have never burnt during the time period examined were removed from further analysis.

4.2.3.2 Hydrology

Hydrology data was kindly provided by the IAFCP. Monthly measurements of groundwater levels were taken using dipwells installed along the same primary transect I used to carry out my vegetation surveys. Each vegetation plot was paired with its nearest dipwell i.e. a dipwell located within 50 m of the plot; 86 vegetation plots had a paired dipwell. Groundwater level measurements were taken at each dipwell on a monthly basis between March 2011 and January 2013 (excluding January 2012, March 2012 and May 2012). This time period encompassed 2 wet seasons and 2 dry seasons. In total, 31 measurements were taken at each dipwell. The mean groundwater level in metres was calculated for each dipwell where 0 m was the peat surface; negative numbers showed depths below the peat surface and positive numbers showed inundation above the peat surface. For each dipwell the number of months where the groundwater level was ≤ -0.5 m was calculated as a measure of drought conditions (hereafter known as number of drought months).

Tropical peatlands have a natural groundwater level just below or just above the peat surface (Page et al., 2009b), sinking during the dry season to between -0.2 and -0.4 m (Takahashi et al., 2002), so a groundwater level of ≤ -0.5 m is viewed as below 'normal' tropical peatland water fluctuations. The number of months where the groundwater level was >0 m was calculated as a measure of flooding conditions (hereafter known as number of flooding months).

The distance from each plot to the nearest canal was measured using the measure tool in ArcMap Version 10.0 to measure the shortest straight-line distance from the GPS coordinate of each plot to the nearest canal edge using an unpublished vector map of all Block A NW canals provided by IAFCP.

4.2.4 Data analysis

Patterns in the species composition of the 223 individual vegetation plots using total counts for each species were visualised by non-metric multi-dimensional scaling (NMDS) using the vegan library (Oksanen et al., 2011) in R 2.14 ((R Development Core Team, 2011). The similarity measure used was the Chao-Jaccard similarity index, which is more robust to variations in sample size, especially for species-rich sites with many rare species, than traditional similarity metrics (Chao et al., 2005). Data for a number of the environmental variables was not normally distributed therefore Spearman's rank order correlations were used to test associations between pairs of environmental variables (Dytham, 2011) using the software SPSS version 16.0 (SPSS, 2007).

To test for spatial autocorrelation in the woody plant community composition I conducted separate partial Mantel Tests for sapling-shrubs and trees using the package vegan in R (Oksanen et al., 2011). The sapling-shrub matrix contained 86 plots where data for all the measured environmental variables was available. Not all vegetation plots contained tree class individuals so the tree matrix included only the 55 plots which did and for which data for all the measured environmental variables was available. Three distance matrices were used for each test: the respective woody plant community dissimilarity matrix, the environmental dissimilarity matrix and the geographical distance matrix. The environmental variables used were the mean groundwater level (m), the number of drought months, the number of flooding months, the number of times burnt, the number of years since the last fire and the distance to the nearest canal (m). Standardised Mantel statistics were calculated using Pearson's product moment correlation using 999 permutations to test for significance.

I investigated the relationship between the woody plant species composition (species abundance matrices) and the environmental variables associated with fire, hydrology and distance using constrained correspondence analysis (CCA) (Terbraak, 1986). CCA was chosen because the purpose of the analysis was to describe community variation with respect to a particular set of environmental variables (see McCune, 1997). Sapling-shrub and tree composition matrices were analysed separately (86 plots and 55 plots respectively). The environmental variables used were number of times burnt, number of years since last fire, distance to the nearest canal, number of drought months and number of flooding months. Mean groundwater depth was not used in the analysis because it had a strong correlation with the number of drought months and the number of flooding months. I used the vegan package in R (Oksanen et al., 2011) to run the analyses. An analysis of variance

(ANOVA) permutation test within the vegan package was used to determine the significance of the resulting models.

Using the package glmulti (Calcagno and de Mazancourt, 2010) I used generalised linear models to investigate the factors that best predicted woody plant species richness. The two tree classes were analysed separately (86 plots and 55 plots respectively). A set of 32 *a priori* models were assembled using all combinations of candidate environmental variable predictors: number of times burnt, number of years since last fire, number of drought months, number of flooding months and distance to nearest canal. Mean groundwater depth was not used in the analysis because it had a strong correlation with the number of drought months and the number of flooding months. Analysis did not include pairwise interactions. The number of woody plant species per plot was used as the response variable and all models had a Poisson error structure. The models were then compared and ranked using Akaike's information criterion corrected for small sample size (AICc). The measure ΔAICc is the difference between the AICc of the top-ranked model and the current model and models with ΔAICc <2 are viewed as having substantial support while the measure *w*AICc provided relative weight to any particular model relative to the entire model set, where 0 equals no support and 1 equals complete support (Burnham and Anderson, 2002). The Nagelkerke R^2 was also calculated for each model using the package rms (Harrell Jr, 2013) and ranges from 0 – 1, where higher values indicate a better model fit (Nagelkerke, 1991).

4.3 Results

All results are for the 86 vegetation plots with complete environmental variable data unless otherwise stated.

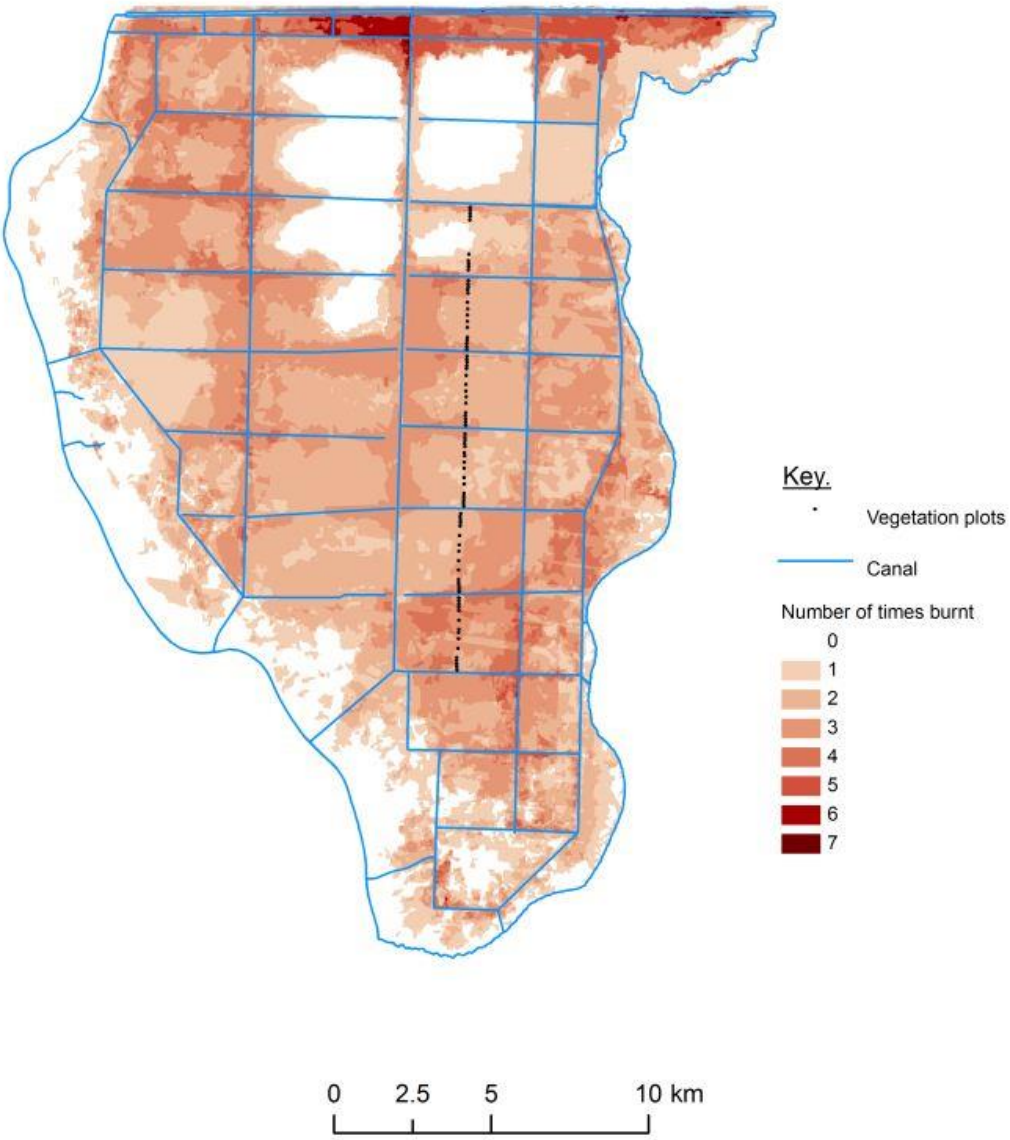
4.3.1 Environmental variables

4.3.1.1 Fire history

No fire events were recorded for the years 1991 - 1996 and 2010. Areas of Block A NW have been affected by fire up to seven times between 1990 - 2010. In total, 21.19% of Block A NW has never burnt, 17.94% burnt once, 29.70% burnt twice, 22.13% burnt 3 times, 6.66% burnt 4 times, 1.91% burnt 5 times, 0.42% burnt 6 times and 0.04% burnt 7 times (Figure 4.1). The most widespread fires occurred in 1997, 2002 and 2009 when 60.04%, 40.47% and 30.91% of Block A NW burnt, respectively. Looking specifically at the fire history of the vegetation plots used in the analysis, the majority of plots have burnt two or three times (Figure 4.1). The number of years since the last fire in a plot ranged from 1 - 13 years (Figure 4.1). Vegetation plots closer to canals have generally burnt more times than plots further away from canals (Figure 4.1).

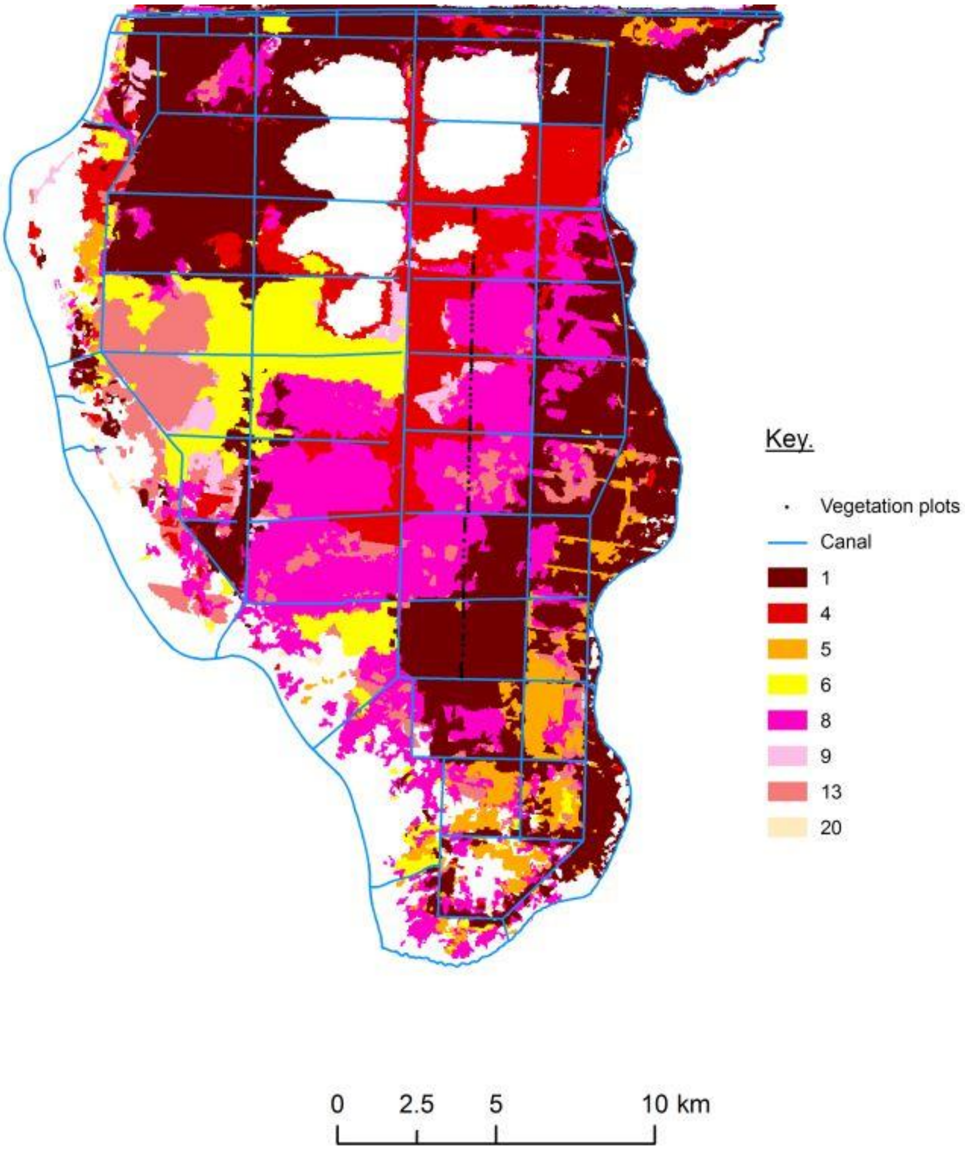
Figure 4.1. Fire History of Block A NW of the former Mega Rice Project area, Central Kalimantan, Indonesia, based on burn scar analysis, showing the location of vegetation plots and a) the number of times the area has burnt between 1990 - 2010; and b) the number of years since the last fire.

a)



No. of times burnt.	No. of vegetation plots.
1	7
2	56
3	21
4	2

b)



No. years since last fire.	No. of vegetation plots.
1	17
4	18
5	1
8	46
9	11
13	15

4.3.1.2. Hydrology

For the time period examined, mean groundwater level across the study area fluctuated slightly around the ground surface (0 m) except for two distinct dips, with groundwater level lowest in September 2011 and October 2012 (Figure 4.2). No dip in mean groundwater level occurred in 2010. The highest mean groundwater level was +0.06 m ± 0.10 in December 2010, while the lowest was -0.64 m ± 0.15 in September 2011. Almost all of the vegetation plots (83 plots, 97.6%) had a mean groundwater level <0 m. All plots had <10 drought months, 18 had ≥16 flooding months, 19 had 10-15 flooding months, 32 had 1–9 flooding months and 17 had no flooding months. Plots closer to a canal generally had a higher percentage of drought months while plots further away from a canal generally had a higher percentage of flooding months (Figure 4.3).

Figure 4.2. Mean groundwater level (m) for all dipwells connected to vegetation plots in Block A NW of the former Mega Rice Project area. S.D. shown as error bars.

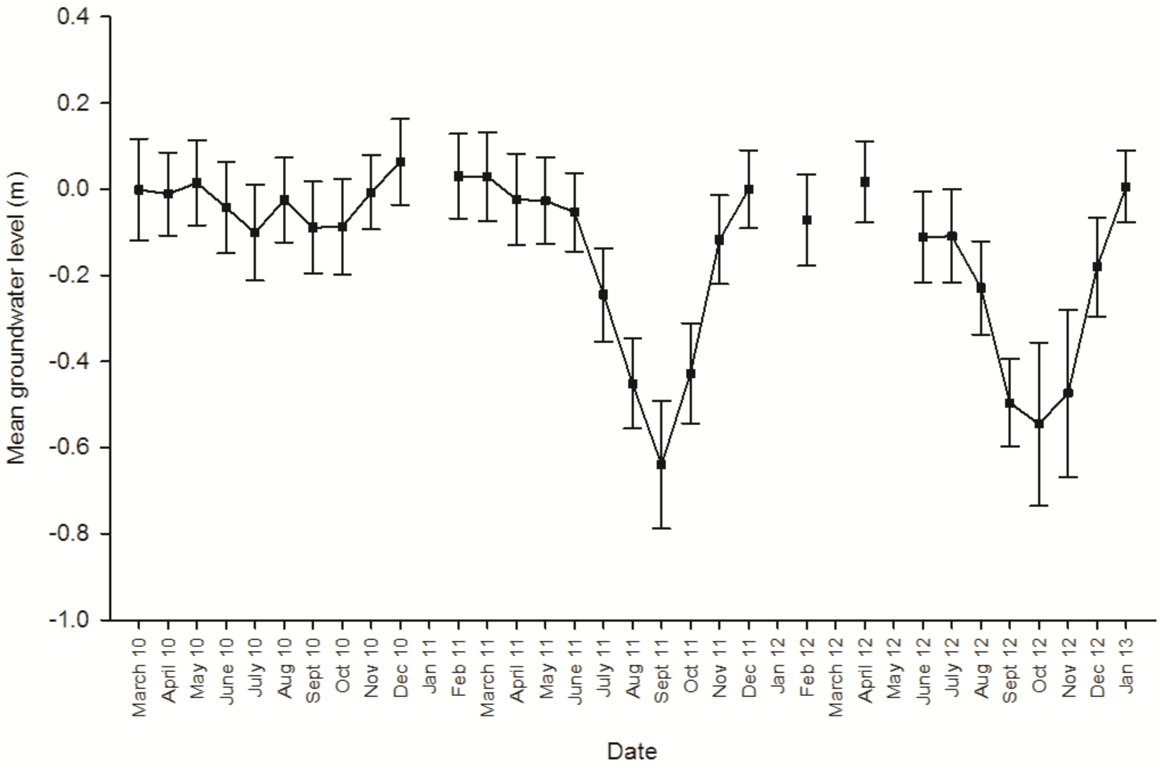
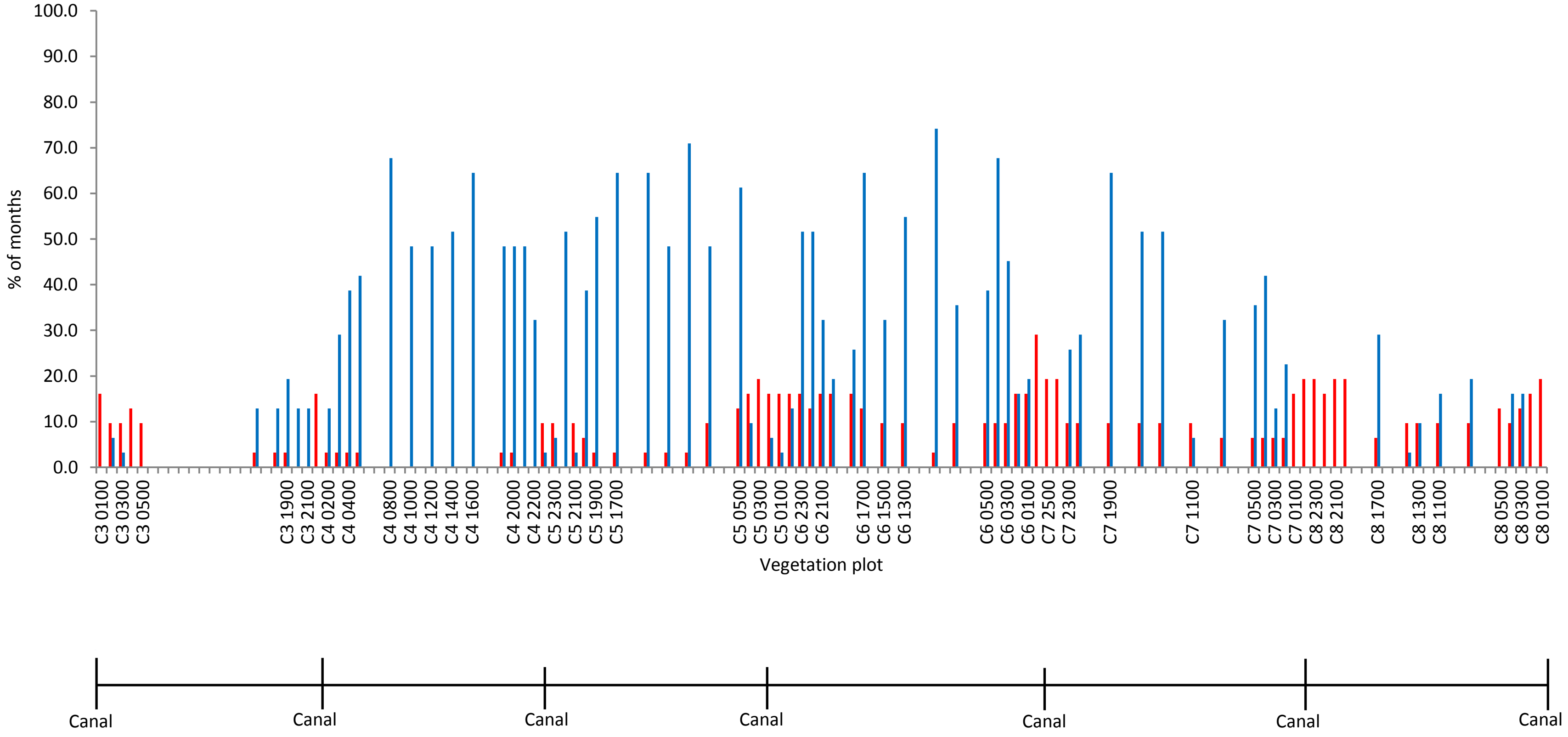


Figure 4.3. Bar graph showing the percentage of flooding months (in blue) and drought months (in red) for vegetation plots in Block A NW of the former Mega Rice Project area, Central Kalimantan, Indonesia for the period March 2010 – Jan 2013. The tick-marks below the graph denote the location of canals in relation to the vegetation plots.



4.3.2 Relationships between environmental variables

Spearman’s rank order correlations found that several environmental variables were strongly correlated (Table 4.1). The two fire-related variables, number of times burnt and number of years since the last fire, showed a strong negative correlation. The number of times burnt also showed a negative correlation with the mean groundwater level, the number of flooding months and the distance to the nearest canal. The number of years since the last fire showed the opposite, with a positive relationship with the mean groundwater level and the number of flooding months.

The hydrology-related variables were also strongly correlated; mean groundwater level had a significant negative relationship with the number of drought months and a significant positive relationship with the number of flooding months, while the number of flooding months and the number of drought months were negatively correlated. Distance to the nearest canal showed a negative correlation with the number of drought months and a positive correlation with the number of flooding months.

Table 4.1. Correlations between environmental variables in forest regrowth in Block A NW. Values indicate Spearman’s rank correlation coefficient. Values in bold indicate significant correlations (P <0.05).

	Number of years since last fire	Mean water depth (m)	Number of drought months	Number of flooding months	Distance from nearest canal (m)
Number of times burnt	**-0.511**	**-0.226**	0.164	**-0.250**	**-0.292**
Number of years since last fire		**0.387**	-0.128	**0.51**	0.201
Mean water depth (m)			**-0.759**	**0.934**	**0.563**
Number of drought months				**-0.602**	**-0.345**
Number of flooding months					**0.526**

4.3.3 Woody plant community composition, species richness and environmental variables

NMDS produced a three-dimensional ordination as the best graphical representation of the community composition of woody plants in Block A NW (Figure 4.4). The ordination shows a general continuum among the vegetation plots with some clustering but with no obvious groups. The partial Mantel tests showed no significant spatial autocorrelation in woody plant community composition among sites for sapling-shrubs (r = -0.08079, P = 0.97) or trees (r = -0.08467, P = 0.93) after accounting for the environmental variables.

The CCA for sapling-shrubs produced 5 axes that together accounted for 19.6% of the total variance in sapling-shrub species abundance among plots (Figure 4.5). Eigenvalues, which range between 0 and 1, measure the importance of each axis. The first ordination axis accounted for 40.3% of this variance, the second axis accounted for 27.9% and the third axis for 10.1%; the fourth and fifth axes were not interpreted. The entire ordination accounted for more variation than expected by chance (ANOVA permutation tests, N = 200, P = 0.005), indicating a significant relationship between the sapling-shrub species abundance and the environmental variables examined. Figure 4.5 indicates that the majority of sapling-shrub species are located near the centre of the ordination and show positive relationships with years since the last fire and the number of flooding months and distance to the nearest canal, and negative relationships with the number of times burnt and the number of drought months. Species that don't follow these trends include *Melastoma malabathricum*, *Nephelium lappaceum*, *Pavetta* sp., and *Melicope lunu-*

ankenda, which have positive relationships with the number of times burnt, and *Melaleuca cajuputi* and *Cryptocarya enervis* which have positive relationships with the number of drought months.

The CCA for trees produced 5 axes that together accounted for 17.2% of the total variance in tree species abundance among plots (Figure 4.6). The first ordination axis accounted for 44.1% of this variance, the second axis accounted for 32.2% and the third axis for 20.3%; the fourth and fifth axes were not interpreted. The entire ordination accounted for more variation than expected by chance (ANOVA permutation tests, N = 200, P = 0.005), indicating a significant relationship between the tree species abundance and the environmental variables. Figure 4.6 indicates that the majority of tree species are located near the centre of the ordination and show a positive relationship with the number of flooding months and a negative relationship with the number of drought months.

For sapling-shrubs the best ranked GLM contained the variables number of times burnt, number of drought months and number of flooding months as predictors, with the model weight showing reasonable support (*w*AICc =0.26) (Table 4.2). However the Nagelkerke R^2 value suggested poor model fit ($R^2 = 0.283$). Examination of the coefficients of variables in the best ranking model showed that the number of times burnt and the number of drought months exerted a negative effect on the number of species, while the number of flooding months exerted a positive effect (Table 4.3). When the coefficients were exponentiated they showed that each additional burning event decreased species richness by 22%, each additional month of drought decreased species richness by 10% and each additional month of flooding increased species richness by 2%.

For trees the best ranked GLM contained the variables number of years since the last fire and number of drought months, although the model weight showed limited support (*w*AICc =0.18) (Table 4.4). Similarly, the Nagelkerke R^2 value suggested poor model fit ($R^2 = 0.056$). Examination of the coefficients of variables in the best ranking model showed that the number of years since the last fire exerted a positive effect on the number of species while the number of drought months exerted a negative effect (Table 4.5). When the coefficients were exponentiated they showed that for each additional year since the last fire species richness increased by 8% while each additional month of drought decreased species richness by 12%.

Figure 4.4. Non-metric multidimensional scaling (NMDS) plot of the woody plant species composition for vegetation plots in forest regrowth (FR) in Block A NW, showing the first 2 axes. The plot has a stress value of 0.14 which suggests that it is a fair representation of the similarities between plots.

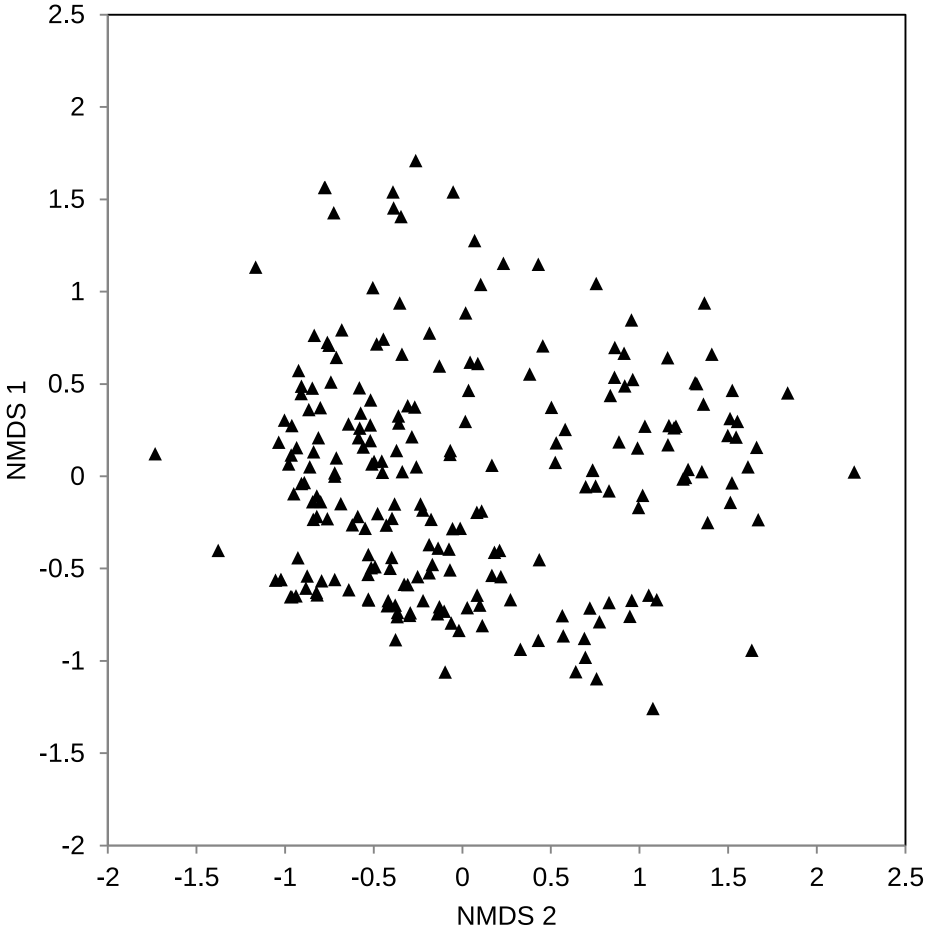


Figure 4.5. CCA ordination of sapling-shrub species composition and environmental variables for vegetation plots in forest regrowth (FR) in Block A NW showing the first 2 axes. The model explains 19.6% of the constrained variance. Vegetation plot scores are represented by blue circles, species scores are labelled by abbreviated species names (see Appendix B for a complete list of species names and their abbreviations). Vectors represent the environmental variables and the length of the vector indicates the variation.

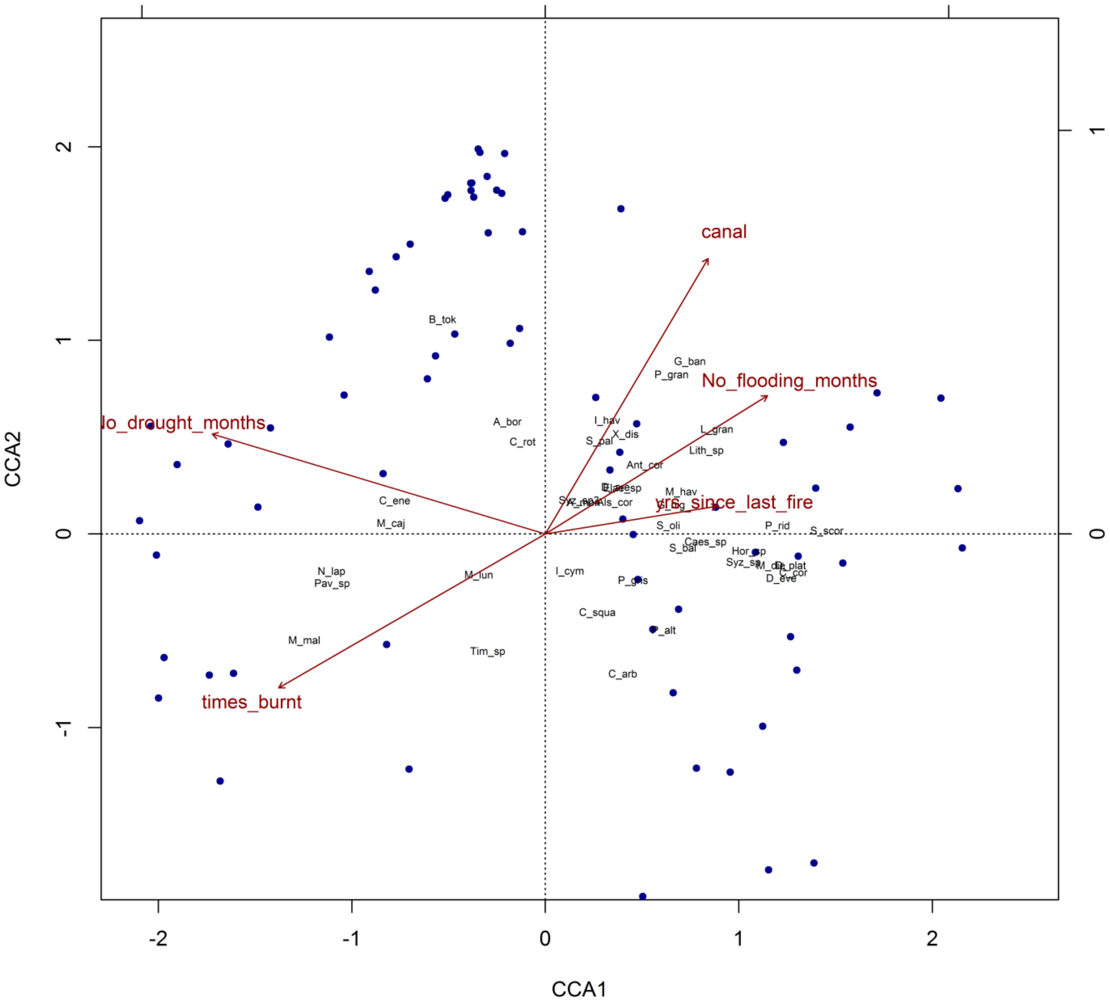


Figure 4.6. CCA ordination of tree species composition and environmental variables for vegetation plots in forest regrowth (FR) in Block A NW showing the first 2 axes. The model explains 17.2% of the constrained variance. Vegetation plot scores are represented by blue circles, species scores are labelled by abbreviated species names (see Appendix B for a complete list of species names and their abbreviations). Vectors represent the environmental variables and the length of the vector indicates the variation. The unlabelled vector represents distance to the nearest canal.

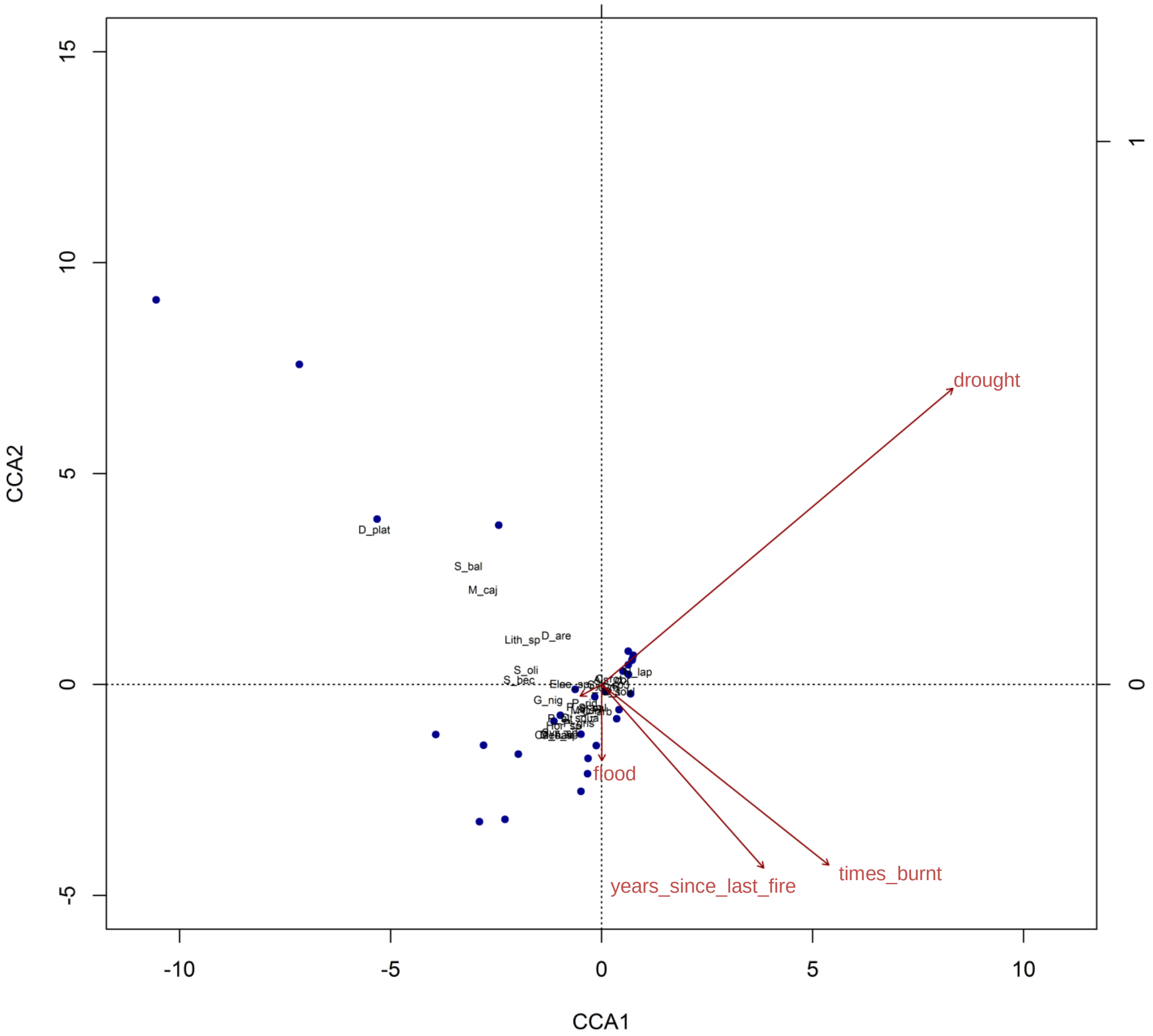


Table 4.2. Best ranking generalised linear models for the effect of the environmental variables number of times burnt, number of years since last fire, number of drought months, number of flooding months and distance to nearest canal on sapling-shrub species richness. k = number of model parameters, Log-L = log-likelihood, AICc = Akaike's information criterion corrected for small sample size, ΔAICc = difference between AICc of the top-ranked and current model, wAICc = AICc weight. R^2 = Nagelkerke R^2.

Model Description	k	Log-L	AICc	*w*AICc	ΔAICc	R^2
~ times_burnt + drought + flood	4	-210.68	429.85	0.26	0	0.283
~ times_burnt + drought + flood + canal	5	-210.11	430.97	0.15	1.11	0.283
~ times_burnt + drought + canal	4	-211.35	431.20	0.13	1.35	0.278
~ times_burnt + last_fire + drought + canal	5	-210.47	431.68	0.10	1.83	0.281
~ times_burnt + last_fire + drought + flood	5	-210.67	432.08	0.08	2.23	0.283

Table 4.3. Coefficient estimates, standard errors (Std.Error) and 95% confidence intervals (95% CI) for the best ranking generalised linear model for sapling-shrub species richness.

Model term	Coefficient	Std. Error	95% CI
Intercept	2.379	0.226	1.927 – 2.814
times_burnt	-0.253	0.083	-0.416 – - 0.089
drought	-0.109	0.029	-0.167 – -0.052
flood	0.017	0.008	0.002 – 0.032

Table 4.4. Best ranking generalised linear models for the effect of the environmental variables number of times burnt, number of years since last fire, number of drought months, number of flooding months and distance to nearest canal on tree species richness. k = number of model parameters, Log-L = log-likelihood, AICc = Akaike's information criterion corrected for small sample size, ΔAICc = difference between AICc of the top-ranked and current model, wAICc = AICc weight. R^2 = Nagelkerke R^2.

Model Description	k	Log-L	AICc	*w*AICc	ΔAICc	R^2
~ last_fire + drought	3	-127.9	262.21	0.18	0	0.056
~ last_fire + drought + canal	4	-126.9	262.54	0.16	0.3	0.063
~ drought + canal	3	-128.8	264.15	0.07	1.9	0.037
~ last_fire + drought + flood + canal	5	-126.6	264.38	0.06	2.2	0.075
~ times_burnt + last_fire + drought	4	-127.8	264.46	0.06	2.2	0.073

Table 4.5. Coefficient estimates, standard errors (Std.Error) and 95% confidence intervals (95% CI) for the best ranking generalised linear model for tree species richness.

Model term	Coefficient	Std. Error	95% CI
Intercept	0.811	0.293	0.213 – 1.362
last_fire	0.078	0.04	0.011 – 0.149
drought	-0.132	0.05	-0.226 – -0.041

4.4 Discussion

4.4.1 Environmental variable patterns

Investigation into the environmental impacts of the land conversion implemented during and after the instigation of the Mega Rice Project show interesting patterns in the physical nature of the environment of Block A NW. The hydrological data for Block A NW shows a general trend for flooding during the wet season while groundwater levels drop during the dry season. The lowest groundwater levels recorded, in September 2011 and October 2012, occurred mid to late in the dry season of Kalimantan and so are likely the results of low rainfall. These two drops in mean groundwater level were more than 0.4 m below the peat surface, which is the depth at which peat starts to become susceptible to fire (Wosten et al., 2008). Interestingly, there was no large drop in groundwater level for 2010, which was unusually wet, with no distinct rainy or dry season (Tuanan Research Station, unpublished rainfall data). Longer-term studies of the hydrology of Block A NW will show if the groundwater levels in 2010 were atypical or if a lack of a drop in groundwater level during typical dry season months is a regular occurrence. The results for 2011–2012 in Block A NW show similar general patterns to hydrological studies of degraded peatland in Sumatra, where widespread flooding during the wet season and groundwater levels as low as -1.5 m during the dry season were also seen (Wosten et al., 2006). They also suggest that groundwater levels follow the rainfall periodicity (Wosten et al., 2006). However, the highest mean groundwater levels recorded in the FR (0.06 m ± 0.10) were considerably lower than the levels found in other areas of degraded tropical peatland. For example, groundwater levels in Sumatra can reach up to 2 m (Wosten et al., 2006, van Eijk et al., 2009).

At the plot level, mean groundwater level was negatively correlated with number of drought months and positively correlated with number of flooding months, and drought is negatively correlated with flooding. This suggests that individual plots either flood more or suffer drought more, but not both. Adding to this, the distance to the nearest canal showed a negative correlation with the number of drought months and a positive correlation with the number of flooding months, which means that areas closer to a canal experience more drought months while those further away experience more flooding months. This suggests that the drainage system is causing diverging hydrological trajectories based on distance from the nearest canal. Indeed, it has been found that the drainage impact in degraded peatlands is strongest close to canals (Hooijer et al., 2008) and this likely explains the drought and flooding patterns seen for the vegetation plots.

The distance to the nearest canal also showed a negative relationship with the number of times a plot has burnt. As mentioned above, the number of flooding and drought months a plot experiences is likely due, at least in part, to its proximity to a canal, with plots closer to the canal experiencing greater drainage and thus less flooding. Since dry peat is more susceptible to fire (Usup et al., 2004, Wosten et al., 2008) this may explain the patterns in burning seen for the vegetation plots. Also, fires in tropical peatland are started by people (Dennis et al., 2005) and since the areas closest to the canal are the most accessible this may also help explain why areas closer to the canal have burnt more often. Likewise, it may be that fires are unable to spread further away from the canals because the peat is wetter and so does not catch fire.

The number of times a plot burnt is also negatively correlated with the number of years since the last fire. This suggests there may be positive feedbacks occurring which make areas that have burnt more likely to burn again, and so there are fewer years since the last fire for these areas. Indeed, fire has been found to create positive feedbacks in future fire susceptibility in other tropical forest types (Siegert et al., 2001, Cochrane et al., 1999, Goldammer et al., 1996) and has been suggested for tropical peatlands as well. Natural regeneration in forest regrowth in degraded tropical peatlands that have experienced fire often includes widespread groundcover of ferns or sedge. This type of vegetation dries out quickly and burns more easily than undisturbed forest vegetation and so this increased flammability creates a positive feedback loop for fire in degraded tropical peatlands (Page et al., 2009b, Page et al., 2009c).

In summary, it seems that the distance to the nearest canal influences the hydrology, with areas closer to the canal experiencing more drought months and areas further away from the canal experiencing more flooding month. This hydrological gradient in turn affects which areas can catch fire, with only dry peat able to burn. Areas closer to the canal are not only drier but also more easily accessible to people, who start the fires in the first place. Additionally, positive feedbacks make burnt areas more susceptible to fire in the future.

4.4.2 Effect of environmental variables on woody plant regrowth

The results of the CCA exploration and GLM analysis show that a combination of fire-related and hydrology-related variables influence species composition and species richness in the forest regrowth of Block A NW. Other studies have found similar results, for example, work on degraded peatlands in Berbak National Park also suggested that the combination of the number of fires, flooding depth and flooding duration best explain the woody plant species richness (van Eijk et al., 2009).

Fire was found to have a negative effect on species richness for both saplings and shrubs and trees, although the specific variables differed for the different size classes. The GLM result shows that an increase in the number of years since the last fire has a positive effect on tree species richness. Correspondingly, the CCA plot shows that most of the species have a positive relationship with the number of years since the last fire. Studies in other tropical forest types have shown that most pre-existing seedlings and saplings and many trees are killed by fire (Cleary et al., 2006, Cochrane and Schulze, 1999, Woods, 1989) which reduces the woody plant diversity of an area. Similarly, an increase in species richness with increasing length of time since the last fire has been found in other forest types, for example, in burnt areas of dipterocarp forests in East Kalimantan, Indonesia (Yassir et al., 2010). The number of years since the last fire likely influences species richness because a fire event kills woody plants thus reducing the species diversity of an area. Therefore, a longer length of time since the last fire gives more time for seeds of different species to arrive in an area, germinate and establish, and thus increase the diversity of the species composition. This effect is probably more pronounced for the tree class because of the length of time required for a plant to grow to tree height.

Interestingly, the fire variable found in the highest ranking GLM model for saplings and shrubs was not the number of years since the last fire but rather the number of times an area has burnt. Correspondingly, the CCA plot shows the majority of species cluster away from vector for the number of times burnt. These results are similar to work carried out in the degraded peatland of Block C of the former Mega Rice Project which also found that the more times an area has burnt the lower the woody plant species richness (for all tree classes) (Page et al., 2009a, Page et al., 2009b). There is currently little information on why this effect is seen. Studies on temperate peat have shown that fire alters some of the physical and chemical properties of peat (Dikici and Yilmaz, 2006). If this is also the case for tropical peat then it may be that these changes make the peat substrate less hospitable for some plant species to germinate and grow. This will reduce the number of species able to recolonize a burnt area, and if this effect increases the more times an area is burnt this could explain the negative relationship with species richness. Of course, research in tropical peatlands is required to establish if this is the case.

Looking at the hydrology variables, for the best ranking GLM models for both saplings and shrubs and trees an increase in the number of drought months was found to have a negative effect on species richness. Correspondingly, the majority of species show a negative relationship with this variable in the CCA plots for both size classes. As mentioned in Section 4.2.1, many tropical peatland tree species have horizontal roots (Nishimura and Suzuki, 2001) therefore if groundwater drops below the level of the roots it will likely have an adverse effect on survival. Indeed, drought in intact tropical peatlands has been found to kill trees. Nishimura et al. (2007) found forest-wide tree mortality at 6.13% yr $^{-1}$ in tropical peat swamp forest in Central Kalimantan during a two-year period after drought. Species-specific differences in mortality were also found (Nishimura et al., 2007), a result that has also been observed in logged and unlogged dipterocarp forest on Borneo after extreme drought (Slik, 2004, Nakagawa et al., 2000). This suggests that drought can affect species richness through disproportionate mortality of species with less tolerance to drought conditions. Since my results suggest that the majority of species in the FR seem to have a low tolerance to drought this likely limits the diversity of species able to persist in areas of the forest regrowth that experience longer periods of drought.

Interestingly, the GLM results show that an increase in the number of flooding months has a positive effect on the species richness of saplings and shrubs. Similarly, the majority of species show a positive relationship with the number of flooding months in the CCA plot. Flooding itself is not an unusual occurrence in undisturbed tropical peatlands in the region, but rather this ecosystem is characterised by its consistently high water-tables which lie just below the peat surface during the dry season and have wet season near-surface water levels or flooding (Page et al., 2009b). Indeed, many tropical peatland woody plant species show adaptations to these high water levels including lateral root growth (Nishimura and Suzuki, 2001), knee roots and pneumatophores (Yule, 2010, Jackson et al., 2009). Similarly, planting trials have shown that a number of tropical peatland woody plant species show tolerance of low level flooding (groundwater levels up to +0.5 m) as seedlings and saplings (van Eijk et al., 2009). However, this apparent tolerance of low level flooding does not explain why my results suggest a positive relationship between the number of flooding months and species richness in the forest regrowth i.e. that species richness increases with an increase in the number of flooding months. It may be that the low level flooding seen in this study is the optimal condition for peat swamp species that are adapted to water-logged environments and so areas with longer flooding periods will have higher species richness than areas with shorter flooding periods. Indeed, studies in other degraded tropical peatlands have found that the highest levels of woody plant species recolonisation occur in areas with low levels of flooding (Wosten et al., 2006, van Eijk et al., 2009). However, these studies also suggest that if flooding depth and duration increases beyond the levels currently seen in Block A NW it will have a negative effect on species richness (Wosten et al., 2006). Therefore it is possible that the positive relationship currently seen is only applicable for the current data range of this study and that any increase in flooding duration beyond this may not follow this positive pattern.

There are a number of limitations of the analysis used in this study. Firstly, while CCA describes community variation with respect to a particular set of environmental variables (Terbraak, 1986, McCune, 1997) and GLM assess the relationship between a response variable and predictor variables (Nelder and Wedderburn, 1972) it is important to remember that correlation is not necessarily causation and so the results do not necessarily identify causal mechanisms.

Secondly, species richness was used as the response variable in the GLM analysis. This is a coarse measure of the variation in diversity of the vegetation plots because it only provides information on the number of species, not which species occur in a plot. That said, my results provide a basic understanding of the ways in which fire and changes to the hydrology influence woody plants in the forest regrowth. Future research can build on this by using experiments to establish species-specific effects (and this will be discussed further in Chapter 7).

Thirdly, the CCA models only accounted for 19.6% and 17.2% of the variance in composition of sapling-shrubs and trees respectively, while the highest ranking GLM models for both size classes only have limited support based on the data. This suggests that factors other than those examined in this study are also likely to be influencing the woody plant composition and species richness in the forest regrowth. These may include fire intensity (Page et al., 2009b, Hoscilo et al., 2013), peat depth and the nutrient composition of the peat. Future research that includes other environmental variables will help build on my results. It is also important to note that the hydrology data covers a relatively short period of time and changes in vegetation related to hydrology in the long-term need to be explored.

In conclusion, this study found that the impacts of fire and changes to the hydrology are influencing the woody plant regrowth in Block A NW and suggested that if the current scenario of high levels of drought, multiple fires and short intervals between fires continues then the species richness will remain limited. Therefore restoration measures that address these factors will be required to overcome the limitations that they cause. I will discuss this further in the General Discussion in Chapter 7.

5. Seed rain into the forest regrowth of Block A NW

5.1 Introduction

For plants to be able to recolonize a degraded area, seeds must either be able to persist in the seed bank or disperse into the area. Burned tropical peatlands are unlikely to have seeds persisting in the seed bank because fires burn the seed-containing surface layers of peat as well as the vegetation. This suggests that forest regeneration on burned peatland will be highly dependent on seed dispersal. However, in degraded habitats, where both the plant and animal assemblages have been disturbed, seeds may not reach potentially suitable sites due to a loss of nearby seed sources, dispersal agents, or both (Wunderle, 1997).

In deforested habitats in the tropics, seed dispersal, measured as seed rain, has been found to decrease with increasing distance from the forest edge (Holl, 1999, Cubina and Aide, 2001, Ingle, 2003, de Melo et al., 2006, Dosch et al., 2007). However, most research has only looked at seed dispersal distances of < 100 m from the nearest seed source (Ingle, 2003, Cubina and Aide, 2001, de Melo et al., 2006, Dosch et al., 2007). Yet degraded tropical peatlands are often expansive (Hooijer et al., 2006) and can extend several kilometres (and across physical barriers) from the nearest seed source. This suggests that seeds can only be dispersed into the degraded area by dispersal agents that are able to cover large distances. In natural tropical forest environments up to 75% of plant species are animal-dispersed (Howe and Smallwood, 1982, Wunderle, 1997) so the availability of suitable animal vectors is likely to have a large impact on the plants that are able to recolonize a degraded area (Holbrook and Loiselle, 2009). A review of seed dispersers in degraded areas of tropical Asia recognized several groups, including partly frugivorous passerine birds, a few non-passerines, fruit bats (Pteropodidae), macaques (*Macaca* sp.), civets (Viverridae), rats (Muridae), and squirrels (Sciuridae), the majority of which consume only relatively small-fruited, small-seeded fruits (Corlett, 2002). As a result, seeds dispersed into a degraded area would be expected to be skewed towards small-seeded and wind-dispersed plants. Indeed, studies of seed rain in degraded tropical areas generally report a composition much less diverse than that of intact forest, primarily made up of wind-dispersed species and small-fruited, small-seeded plant species (Au et al., 2006, Barbosa and Pizo, 2006).

Seeds may be dispersed into a degraded area by dispersers coming out of nearby forest, although many forest animals are reluctant to venture into open areas (Silva et al., 1996). Many studies in other degraded forest areas have found that remnant trees act as nuclei for regeneration (Guevara et al., 1986, Nepstad et al., 1991, Guevara and Laborde, 1993, Galindo-Gonzalez et al., 2000, Carriere et al., 2002, Hooper et al., 2005) by bringing dispersers, particularly birds, into degraded areas and thereby increasing the seed dispersal. In the Neotropics, trees retained during tropical forest clearance to provide shade for cattle showed increased levels of seed rain in their immediate vicinity (Guevara et al., 2004). Similarly, abandoned pastures with patches of woody vegetation showed greater levels of tree seedling establishment than pastures without woody vegetation (Nepstad et al., 1990). The nature of tropical peatland fires means that not all of the surface fuel material burns (Usup et al., 2004), so areas of vegetation, including remnant trees, may survive through a fire. These could potentially act as nuclei for forest regeneration, as could early-successional tree species that have already recolonized the degraded area.

Seeds may also be dispersed from within the degraded area itself. Martini and dos Santos (2007) suggested that the high number of small-sized seeds and wind-dispersed seeds found in the seed rain on previously burnt areas in the Atlantic Forest, Brazil, were from pioneer plants that had already recolonized the area. Similarly, vegetation surveys of forest regrowth on degraded tropical peatlands (Chapter 3) have found that some woody plant species have already recolonized the area, although the distribution of individual woody plants is sparse. In expansive degraded areas such as Block A NW it is likely that vegetation that has already recolonized the area may also act as seed sources.

The aim of this chapter was to investigate seed dispersal in the forest regrowth of Block A NW in the former Mega Rice Project area, Central Kalimantan, Indonesia. Three specific questions were addressed:

(1) What is the composition and abundance of the seed rain?

(2) To what extent are established trees acting as nuclei for forest regeneration?

(3) What is the contribution of endogenous (contributed by the local community) versus exogenous (dispersed from outside sources) seed rain?

5.2 Materials and methods

5.2.1 Study site

This study was carried out in Block A North-West (Block A NW) (2°17’00”S and 114°31’33E) of the former Mega Rice Project area in Central Kalimantan, Indonesia (described in section 3.2.1). Block A NW is divided into compartments by 300 km of canals, each compartment being roughly 2.5 by 2.5 km (Mawdsley et al., 2009). The compartment d-3 was chosen as the location of the seed traps due to its year-round accessibility. The main habitat of this compartment is forest regrowth (FR) with dense fern coverage and a sparse distribution of woody plants. At its closest point d-3 lies 1.17 km away from the nearest forest edge, with a drainage canal and the Mantangai River lying in between.

5.2.2 Seed trap design and lay-out

The 1 m² seed traps were made locally from PVC piping and 1 mm mesh netting, and were suspended 1 m above the ground by four PVC supports. Due to flooding in the study area it was not possible to place seed traps directly on the ground; this meant that while traps captured fruits and seeds falling directly from trees, and those spat or defecated from above, the traps could not capture seeds dispersed by terrestrial animals (Du et al., 2012, Muller-Landau et al., 2008). The seed traps were open from February 2011 to February 2012, encompassing both the wet and dry seasons of Kalimantan. Dense fern coverage made it logistically impossible to place traps randomly. Instead, a 1 km long main transect was established, with five 400 m transects laid out perpendicular to and crossing this transect at 200 m intervals. I placed ten traps on each perpendicular transect out in the open and a further ten traps under established trees or patches of established trees (Figure 2). Due to the sparse woody cover, trees a minimum of 2 m in height were chosen based on their proximity to the transect and included individuals of *Alstonia* sp., *Antidesma coriaceum*, *Combretocarpus rotundatus*, *Cratoxylum arborescens/glaucum* (not consistently distinguished in the field), *Elaeocarpus acmocarpus*, *Melicope lunu-ankenda*, *Ilex cymosa, Litsea* sp*., Palaquium* sp*., Ploiarium alternifolium*, *Syzygium* sp., and *Timonius* sp.. Each trap was placed at least 5 m from any other trap. In total I placed fifty traps under trees and fifty in the open. Ground vegetation was cleared underneath the immediate area where a trap was placed, but overhanging vegetation was not removed. Traps were checked at 15 ± 3 day intervals for one year.

5.2.3 Seed identification

Seed identification was carried out by Andri Thomas, an expert on the flora of the local peatlands. Seeds were identified to species where possible. Morphological characteristics (shape, colour etc.) were also recorded and where species identification was not possible these features were used to differentiate morphological groups. Twenty seeds of each species (or as many as were captured when this was < 20) were measured for length, width and breadth. The dispersal mode and dispersal agents for each species were established based on appearance and information from Corlett (1998). Woody plant vegetation surveys carried out in Block A NW included the construction of twenty 20 m x 20 m temporary plots in compartment d-3 and a further 204 plots across the wider forest regrowth area (see section 3.2.2). The resulting woody plant species list was used to establish which seed rain species were also present as established woody plants in compartment d-3 or the wider forest regrowth area.

5.2.4 Data analysis

Seed counts were standardised to numbers of seeds m^{-2} y^{-1}. For the traps placed under trees, seeds of the same species as the tree were excluded from the counts in order to distinguish ‘foreign’ (not conspecific) from total (including conspecific) seed rain (Carriere et al., 2002). For both total and foreign seeds, seed species richness and seed numbers in traps under trees and in the open were compared using Mann Whitney U tests (SPSS 16.0). Patterns in the species composition of the total seed rain for individual traps were analysed by non-metric multi-dimensional scaling (NMDS) using the package R (R Development Core Team, 2011). Data were square-root transformed and then submitted to Wisconsin double standardization to down-weight the effect of the most abundant seed species. The similarity measure used was the Bray-Curtis coefficient. Species rank abundance curves were constructed to visualise relative species abundance for seeds captured in traps in the open and under trees. A Spearman’s rank-order correlation was also used to investigate the relationship between mean seed width and number of seeds captured for foreign animal-dispersed seeds.

5.3 Results

Over the one-year period, a total of 61 149 mature seeds were collected (Table 5.1). The mean number of seeds captured was significantly higher under trees (1127.8 ± 1241.2 m^{-2} y^{-1}) than in the open (95.2 ± 172.9 m^{-2} y^{-1}) (Mann Whitney U, P <0.001). A total of 38 morphospecies were collected, of which 28 could be identified to genus or species (Table 5.1). The mean number of species captured per trap was also significantly higher under trees (6.8 ± 2.6) than in the open (2.4 ± 0.9) (Mann Whitney U, P <0.001), and the two-dimensional NMDS plot (Fig. 5.1) shows a clear distinction in species composition between them. Species rank abundance curves (Fig. 5.2) show that the seed rain under trees and in the open was dominated by a few abundant species, and the steep slope of both curves indicates low species evenness. The woody liana, *Uncaria elliptica,* accounted for 40.2% of the total number of seeds captured, 69.7% of those captured in the open and 37.7% of those captured under trees. The tree, *Combretocarpus rotundatus*, ranked second, with 34.4% of the total number of seeds captured, 15.4% of those captured in the open, and 36.1% of those under trees. Combined, these two species accounted for 74.6% of the total number of seeds captured.

Of all the seeds trapped, 28 010 (38%) were foreign. As with total seeds, the mean number of foreign seeds captured was also significantly higher under trees (465.0 ± 846.5 m^{-2} y^{-1}) than in the open (95.2 ± 172.9 m^{-2} y^{-1}) (Mann Whitney U, P = 0.03), as was the mean number of species (5.4 ± 2.6 and 2.4 ± 0.9 m^{-2} y^{-1}, respectively) (Mann Whitney U, P < 0.001). Foreign seed rain was made up of 36 morphospecies, 28 of which could be identified to genus or species (Table 5.1) and the two-dimensional NMDS plot (Fig. 5.1) shows a clear distinction in species composition between the two trap locations. Species rank abundance curves (Fig. 5.2) show a similar pattern to that obtained with all seeds. *U. elliptica* was the most abundant foreign seed under trees and in the open, accounting for 91.0% and 69.7%

of seeds respectively. *C. rotundatus* ranked second, accounting for 1.7% and 15.4% of seeds respectively (Table 5.1).

Most individual foreign seeds were wind-dispersed: 94.2% under trees and 99.8% in the open. Wind-dispersed species included 9 species: 6 trees, 2 climbers and 1 grass. Both of the commonest seed species, *U. elliptica* and *C. rotundatus*, are wind-dispersed. All foreign seeds of wind-dispersed trees were captured in the open, except for a single seed of *Shorea balangeran*, while most foreign seeds of climbers (>80%) were captured under trees. Most species of foreign seeds were animal-dispersed (21 species), while 6 species had an unknown dispersal mode. No significant correlation was found between mean seed width and number of seeds captured for foreign animal-dispersed seeds (Spearman's rank-order correlation, rs = -0.214, P = 0.35). The majority (81.8%) of foreign animal-dispersed seeds had a mean width < 4 mm (Fig. 5.3). Most were from trees known or inferred to be dispersed by bulbuls (Pycnonotidae) and other small- and medium-sized birds, although a few species were probably dispersed by larger birds and/or mammals (including bats, but excluding rodents) (Table 5.1). Regardless of plant habit, > 90% of the foreign seeds of each animal-dispersed species were found under trees and only 8 individual animal-dispersed seeds were found in the open: seven of *Melicope lunu-ankenda* and one of *Syzygium* sp. 3. The tree and shrub species found in the foreign seed rain accounted for 3112 (11%) of all foreign seeds caught and generally consisted of species also recorded in the vegetation surveys (Table 5.1). Only four species were not recorded in the vegetation surveys (Table 5.1).

Table 5.1. Seed species collected in 100 1m² seed traps from February 2011 to February 2012 in degraded tropical peatland, Central Kalimantan, Indonesia. ¹ = tree species recorded in vegetation surveys in compartment d-3; ² = tree species recorded in vegetation surveys of forest regrowth of Block A NW. For animal-dispersed tree and shrub species the major dispersal agents are indicated where known (based on Corlett, 1998).

				Traps in the open		**Traps under trees**		**Traps under trees foreign seeds only**	
Family	**Species**	**Plant habit**	**Dispersal mode**	**Total seeds**	**Seeds m^{-2} yr^{-1}**	**Total seeds**	**Seeds m^{-2} yr^{-1}**	**Total foreign seeds**	**Seeds m^{-2} yr^{-1}**
Anacardiaceae	*Campnosperma coriaceum*	Tree ¹ ²	Bulbuls, large birds	0	0	1	0.02	1	0.02
Anisophylleaceae	*Combretocarpus rotundatus*	Tree ¹ ²	Wind	735	14.7	20326	406.52	393	7.86
Annonaceae	*Xylopia fusca*	Tree	Large birds, bats	0	0	1	0.02	1	0.02
Apocynaceae	*Alstonia* sp.	Tree ¹	Wind	8	0.16	1857	37.14	1	0.02
Apocynaceae	*Urceola brachysepala*	Climber	Wind	3	0.06	12	0.24	12	0.24
Aquifoliaceae	*Ilex cymosa*	Tree ¹ ²	Bulbuls	0	0	7	0.14	3	0.06
Bonnetiaceae	*Ploiarium alternifolium*	Tree ¹ ²	Wind	263	5.26	6672	133.44	0	0
Dipterocarpaceae	*Shorea balangeran*	Tree ¹ ²	Wind	0	0	1	0.02	1	0.02
Elaeocarpaceae	*Elaeocarpus acmocarpus*	Tree ¹ ²	Large birds, bats	0	0	2	0.04	0	0
Elaeocarpaceae	*Elaeocarpus* sp.	Tree ²	Bulbuls, Large birds, bats	0	0	48	0.96	48	0.96
Fabaceae	*Archidendron borneense*	Tree ²	Unknown	0	0	1	0.02	1	0.02
Flagellariaceae	*Flagellaria* sp.	Climber	Animal	0	0	21	0.42	21	0.42
Hypericaceae	*Cratoxylum arborescens* and *Cratoxylum glaucum*	Tree ¹ ²	Wind	407	8.14	2704	54.08	233	4.66

Table 5.1. (continued)

				Traps in the open		Traps under trees		Traps under trees foreign seeds only	
Family	**Species**	**Plant habit**	**Dispersal mode**	**Total seeds**	**Seeds m^{-2} yr^{-1}**	**Total seeds**	**Seeds m^{-2} yr^{-1}**	**Total foreign seeds**	**Seeds m^{-2} yr^{-1}**
Lauraceae	*Litsea* sp.	Tree [1,2]	Bulbuls, Large birds	0	0	51	1.02	41	0.82
Loranthaceae	*Lepidaria* sp.1	Parasite	Animal	0	0	4	0.08	4	0.08
Melastomataceae	*Melastoma malabathricum*	Shrub [1,2]	Bulbuls	0	0	52	1.04	0	0
Myrtaceae	*Syzygium* sp.	Tree [1,2]	Bulbuls	0	0	485	9.7	144	2.88
Myrtaceae	*Syzygium* sp. 3	Tree [1,2]	Bulbuls	1	0.02	2097	41.94	371	7.42
Myrtaceae	*Syzygium* sp. 4	Tree [1,2]	Bulbuls	0	0	108	2.16	60	1.2
Phyllanthaceae	*Antidesma coriaceum*	Tree [2]	Bulbuls	0	0	29	0.58	29	0.58
Phyllanthaceae	*Antidesma montanum*	Tree [2]	Bulbuls	0	0	1	0.02	1	0.02
Rubiaceae	*Gardenia tubifera*	Tree	Animal	0	0	60	1.2	60	1.2
Rubiaceae	*Gynochthodes coriacea*	Climber	Animal	0	0	228	4.56	228	4.56
Rubiaceae	*Timonius* sp.	Tree [2]	Bulbuls	1	0.02	17	0.34	17	0.34
Rubiaceae	*Uncaria elliptica*	Climber	Wind	3317	66.34	21262	425.24	21262	425.24
Rutaceae	*Melicope lunu-ankenda*	Tree [1,2]	Animal	7	0.14	284	5.68	260	5.2
Rutaceae	*Tetractomia obovatum*	Tree	Wind	16	0.32	1	0.02	1	0.02
Sapotaceae	*Palaquium* sp.1	Tree	Bats, other mammals	0	0	8	0.16	8	0.16
Unknown	Sample A 08	Unknown	Animal	0	0	18	0.36	18	0.36
Unknown	Sample A 09	Unknown	Unknown	0	0	1	0.02	1	0.02
Unknown	Sample A 10	Unknown	Unknown	0	0	2	0.04	2	0.04

Table 5.1. (continued)

				Traps in the open		**Traps under trees**		**Traps under trees foreign seeds only**	
Family	**Species**	**Plant habit**	**Dispersal mode**	**Total seeds**	**Seeds m^{-2} yr^{-1}**	**Total seeds**	**Seeds m^{-2} yr^{-1}**	**Total foreign seeds**	**Seeds m^{-2} yr^{-1}**
Unknown	Sample A 11	Unknown	Animal	0	0	4	0.08	4	0.08
Unknown	Sample A 13	Unknown	Unknown	0	0	1	0.02	1	0.02
Unknown	Sample A 14	Unknown	Unknown	0	0	3	0.06	3	0.06
Unknown	Sample A 15	Unknown	Unknown	0	0	2	0.04	2	0.04
Unknown	Sample A 16	Unknown	Animal	0	0	1	0.02	1	0.02
Unknown	Sample Liana bajakah balayan	Climber	Animal	0	0	17	0.34	17	0.34
Unknown	Sample Parei ampit	Grass	Wind	1	0.02	1	0.02	1	0.02
				4759		56390		23251	
				95.18		1127.8		465.02	

Figure 5.1. Two-dimensional non-metric multidimensional scaling (NMDS) plots of 100 individual seed traps in degraded peatland, Central Kalimantan, Indonesia, for a) total seed species composition and b) foreign seed species composition. The total seed species plot has a stress value of 0.21 which suggests it is a fair representation of the similarities between traps. The outlying point is a trap in the open which only captured *Cratoxylum arborescens/glaucum* seeds over the course of the year. The foreign species plot has a stress value of 0.21 which suggests it is a fair representation of the similarities between traps.

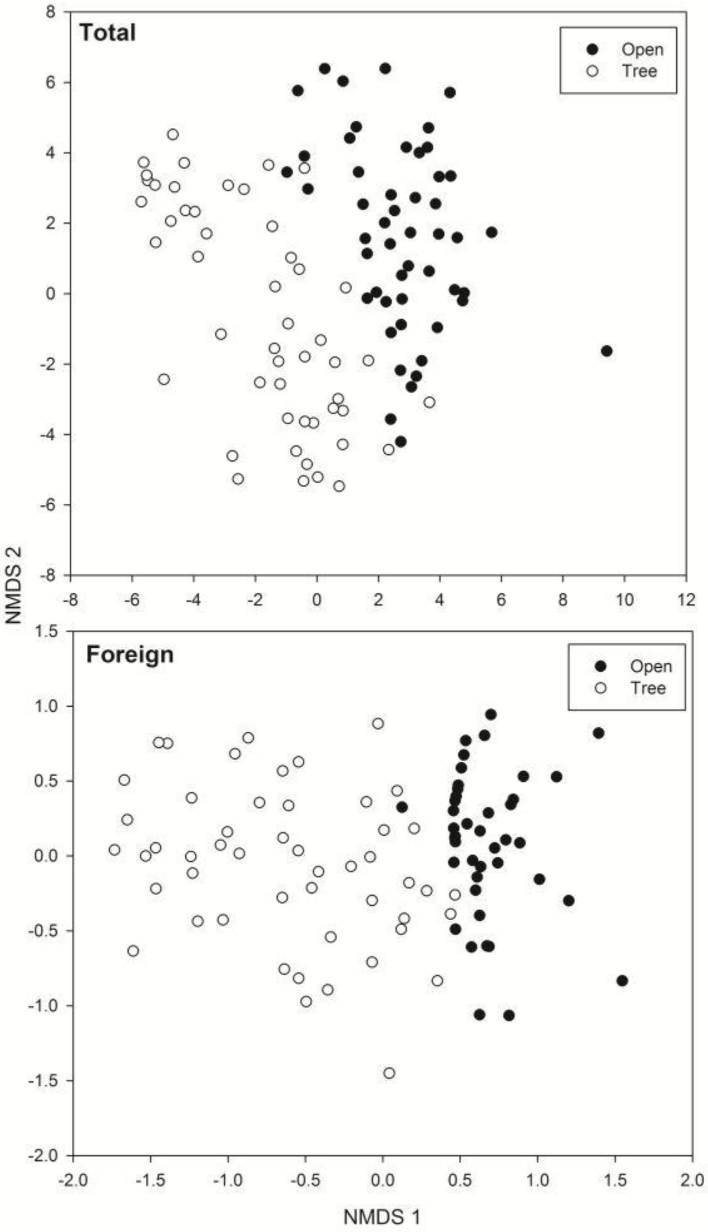


Figure 5.2. Rank abundance curves of seed species for a) total seed rain and b) foreign seed rain, captured in traps in the open and traps under trees in degraded peatland, Central Kalimantan, Indonesia. Blue data points indicate wind-dispersed species, red data points indicate animal-dispersed species, yellow data points indicate unknown dispersal agents.

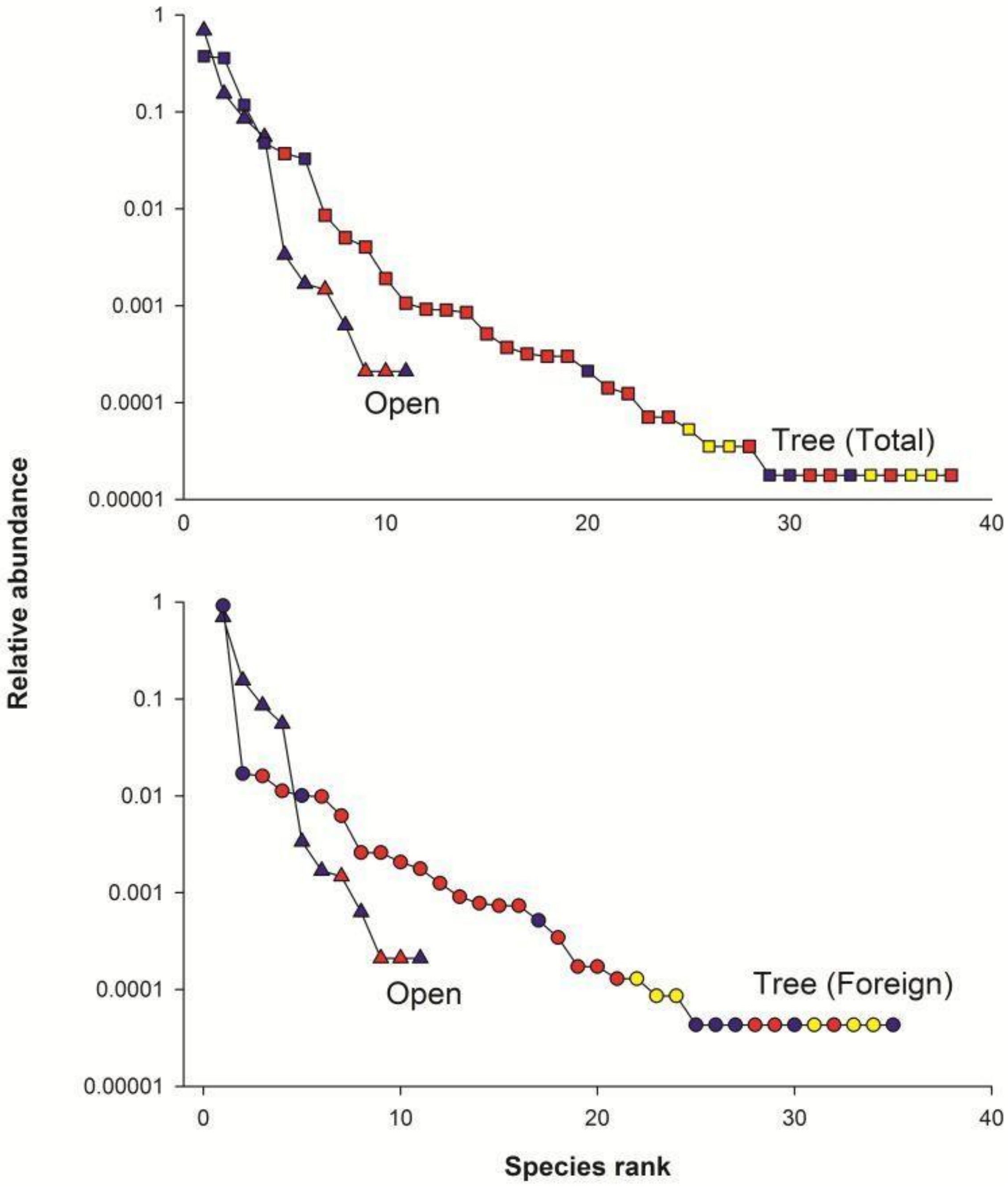
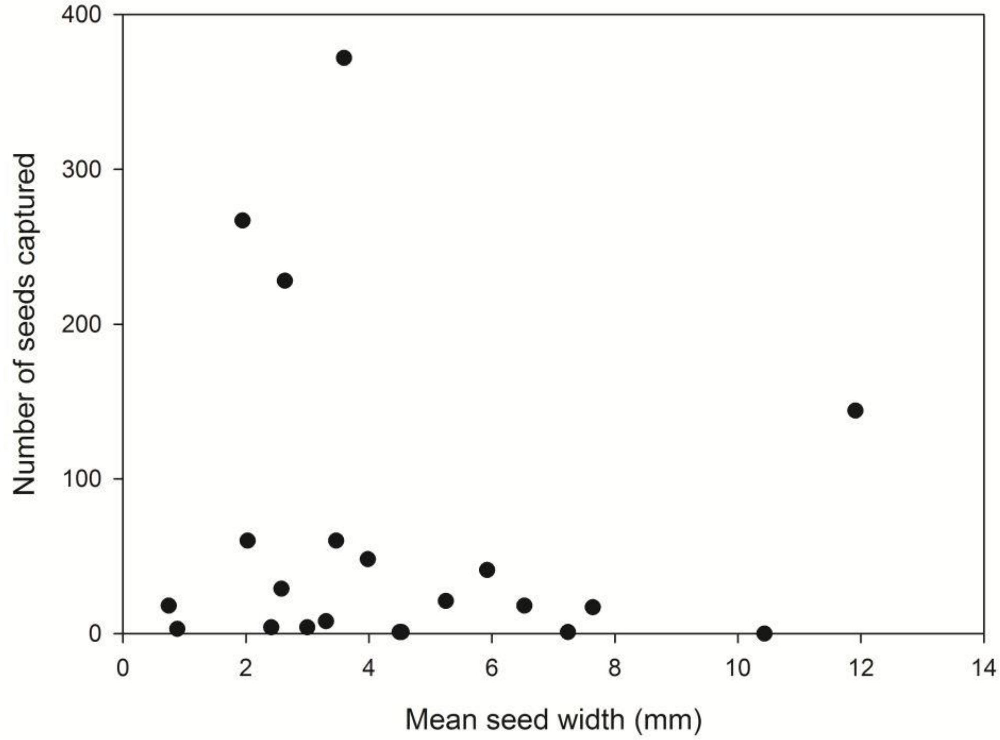


Figure 5.3. Animal-dispersed foreign seed size compared with number of seeds caught. The outlier, with a large seed size and high abundance, is *Syzygium* sp..



5.4 Discussion

This study found that wind-dispersed seeds highly dominated both the total seed rain and foreign seed rain in an area of forest regrowth on degraded tropical peatland. Wind-dispersed seeds have also been found to dominate abandoned pastures and areas of natural regeneration in other parts of the tropics (Dosch et al., 2007, Zamora and Montagnini, 2007, Gonzales et al., 2009). This dominance of wind-dispersed seeds in the study area is due to the seeds of a single species; *U. eliptica. U. eliptica* is a wind-dispersed climber that is present throughout the study area, fruits year round (Blackham, personal observation), and produces many tiny seeds, which are on average just 4.3 mm in length. This high seed production probably explains why seeds of this species dominated the seed rain. Seeds of this species also dominated the foreign seed rain for traps under trees and this is probably due to the climbing habit of this species. *U. eliptica* is a climber that uses hooks to cling to other vegetation for support (Putz and Holbrook, 1991) and with the widespread fern cover of Block A NW the only suitable supports would be the established trees in the area. This association between the *U. eliptica* and trees means that there are more likely to be climbers by the traps under trees than by traps in the open and this explains why so many seeds of this species were found in these traps (no hanging vegetation was removed from above traps). The fact that a large number of these seeds were also found in traps in the open indicates that this species can also successfully disperse into open areas. The second most abundant species for both total and foreign seed rain and for both traps in the open and under trees was another wind-dispersed species *C. rotundatus. C. rotundatus* is the dominant tree species found in the forest regrowth area (Chapter 3) and 30% of the traps under trees were placed under *C. rotundatus* trees so it seems logical that its seeds would be one of the most abundant seeds to be captured. Interestingly, when seeds of the focal tree were excluded to calculate foreign seed rain *C. rotundatus* was still the second most abundant foreign seed in traps under trees. Like *U. eliptica, C. rotundatus* also produces seeds year round (Blackham, personal observation) and this, along with the dominance of this tree species in the area likely explains the high abundance of *C. rotundatus* seeds captured in this study.

Overall, the foreign seed rain showed a higher diversity of animal-dispersed species than wind-dispersed species. This pattern has also been found in a lowland Philippine forest successional area (Gonzales et al., 2009) and shows that the forest regrowth area still contains animal-dispersers that are capable of dispersing a wide array of plant species. Since natural tropical forest environments are dominated by animal-dispersed plant species (Howe and Smallwood, 1982, Wunderle, 1997) the presence in the seed rain of animal-dispersed species with an array of dispersal agents is a positive sign for the recovery of forest plant species in the degraded area because it points to the establishment of a diverse composition of woody plants that will themselves attract frugivores to the area in the future and so further enhance the diversity of woody plants recolonizing the area (Carriere et al., 2002).

Indeed, of the seeds of tree species with known dispersal agents captured in the traps, dispersers comprise of bulbuls (Pycnonotidae) and other small- and medium-sized birds, larger birds and mammals, including bats but excluding rodents. This composition likely reflects the faunal composition of the area. Half of the animal-dispersed tree species are dispersed by bulbuls and other small- and medium-sized birds and this predominance is likely due to the high abundance of bulbuls in the area. Bulbuls, and in particular the yellow-vented bulbul (*Pycnonotus goiavier*) were the dominant species recorded in bird surveys in the area (Posa, 2011). Interestingly, while seeds dispersed by larger birds were found in the seed rain no hornbills (Bucerotidae) or fruit pigeons (a clade of Columbidae) have been recorded in Block A NW (Posa, 2011) and so how these seeds were dispersed remains unclear. For the mammal-dispersed species, while there have been no surveys of bats (Pteropodidae) in the area, work on bats in other parts of Southeast Asia has found that their role in seed dispersal in degraded landscapes is limited, especially in comparison to bird dispersal (Corlett, 2002, Gonzales et al., 2009, Ingle, 2003), and this likely explains why only a single species found in the seed rain in this study is bat-dispersed, and not exclusively. No surveys of other mammal species in the forest regrowth of Block A NW have taken place either and while potential mammal dispersers such as long-tailed macaques (*Macaca fascicularis*) were seen near the Mantangai River they were not seen in the immediate study area (Blackham, personal observation) and therefore the absence of mammal-dispersers may explain why few mammal-dispersed species were found. Also, the raised trap design necessitated by periods of flooding in the study area meant that seeds dispersed by terrestrial mammals that may be present in the area, such as civets (Viverridae) and rats (Muridae), were unlikely to be captured in the traps and this may also explain why fewer mammal-dispersed species were found in the seed rain.

Looking specifically at the foreign seed rain under established trees, the foreign seed rain was dominated by wind-dispersed seeds, even when seeds of the species of the focal tree were excluded. This is an unusual finding since other studies carried out in the tropics have found foreign seed rain under focal trees to be dominated by animal-dispersed seeds (Guevara et al., 1986, Nepstad et al., 1991, Galindo-Gonzalez et al., 2000, Carriere et al., 2002, Hooper et al., 2005). However, when the most abundant seed species, *U. eliptica*, is excluded there are over twice as many animal-dispersed foreign seeds in traps under trees than foreign wind-dispersed seeds, a result more similar to that found in other studies (Guevara et al., 1986, Nepstad et al., 1991, Galindo-Gonzalez et al., 2000, Carriere et al., 2002, Hooper et al., 2005).

Importantly, the foreign seed rain in traps under trees was more diverse than that of traps in the open and contained almost all of the animal-dispersed seeds captured in this study. Since a large number of the animal-dispersed tree species found in the foreign seed rain are dispersed by bird dispersal agents this suggests that birds are using established trees in the degraded area as perching sites to rest on and defecate as they have also been shown to do in degraded areas in the Neotropics (Guevara and Laborde, 1993). This suggests that established trees are acting as focal sites for the dispersal of bird-dispersed seeds and this makes them important nuclei for the natural regeneration in the forest regrowth area.

Looking at the species found in the foreign seed rain, the majority of the tree and shrub species recorded in the seed rain are species also recorded in vegetation surveys carried out on the same compartment (d-3) or in wider vegetation surveys of the forest regrowth of Block A NW (see chapter 3). This suggests that the tree and shrub species that are being dispersed in the forest regrowth area are primarily coming from sources within the degraded area rather than from outside sources. These results are similar to that of a study that used artificial bird perches to encourage frugivorous birds into degraded peatland in Central Kalimantan. They observed that the majority of seeds found in seed traps beneath the artificial perches were of species already known to occur in the degraded zone (Graham and Page, 2012). Similarly, a study of seed rain in a burnt area in the Atlantic forest in Brazil suggested that the species composition of the seed rain was due to the local abundance of those plants in the area rather than dispersal from outside areas (Martini and dos Santos, 2007). Other studies have found that seed rain is greatly reduced at distances of less than a hundred metres from the nearest seed source (Holl, 1999, Cubina and Aide, 2001, Ingle, 2003, de Melo et al., 2006, Dosch et al., 2007) and in this study the nearest seed source was over a kilometre away and across physical barriers of canals and rivers.

Only four tree and shrub species recorded in the seed rain are not accounted for in the vegetation surveys of the forest regrowth of Block A NW. One species is wind-dispersed (*Tetractomia obovatum*), while the majority are animal-dispersed (*Xylopia fusca, Palaquium sp.1.* and *Gardenia tubifera*). While the vegetation surveys were not exhaustive, and so these species may exist somewhere in the degraded area, it is feasible that these seeds are being dispersed from the nearest forest sites over a kilometre away. The maximum displacements for two bulbul species (*Pycnonotus* sp.) during maximum measured gut passage times in degraded habitat in Hong Kong were found to be over 1 km (Weir and Corlett, 2007) which is a similar distance to the nearest forest edge in this study and the fruits of the three unaccounted for animal-dispersed tree and shrub species fit within the gape width of the yellow-vented bulbul (*P. goiavier*). Therefore, while the majority of the seed rain seems to be coming from seed sources within the degraded area some dispersal from the forest seed source is possible.

It is important to note that seed rain does not equate to plant establishment and so while seeds may be being dispersed in the forest regrowth area they might not germinate and grow. Plant establishment is affected by the other filters to natural regeneration which include nutrient availability, the hydrology of the area (duration of drought or flooding), post-dispersal seed predation and competition from herbaceous vegetation (Holl, 1999, Zimmerman et al., 2000, Cubina and Aide, 2001, Nepstad et al., 1996). Future studies should investigate how these filters affect establishment from seed for different woody plant species in degraded tropical peatland areas.

The results show that the seed rain both in the open and under trees is sufficient for the development of a woody plant cover but that plant diversity will be limited, consisting of woody plant species already inhabiting the degraded area rather than the recruitment of species from outside seed sources. In particular, there is a dominance of the climber *U. eliptica* and the tree *C. rotundatus.* This suggests that without the implementation of restoration measures, such as the planting of large-fruited animal-dispersed tree species not currently found in the degraded area, the forest regrowth in Block A NW will remain as an area with limited woody plant diversity dominated by wind-dispersed and small-seeded species for the foreseeable future.

6. Post-dispersal seed removal in the former Mega Rice Project Area

6.1 Introduction

After primary dispersal of a seed has taken place, any further movement of the seed is classed as post-dispersal seed removal (Janzen, 1971, Vander Wall et al., 2005). Work in tropical ecosystems has found that post-dispersal seed removal can vary dramatically both between and within communities (Janzen, 1971) and that rates of seed removal may also differ for seeds of different species within a single habitat (Notman and Gorchov, 2001, Holl and Lulow, 1997). Currently, very little is known about the processes of post-dispersal seed removal in natural tropical peatland ecosystems (except Van der Meer et al., 2008) and nothing is known about the rates of post-dispersal seed removal in degraded peatland areas. Tropical peatlands in their natural state are water-logged, forest-covered, acidic and nutrient-limited (Rieley et al., 1996a). These traits may lead to different patterns of post-dispersal seed removal than those found in other types of tropical forest. Furthermore, high rates of tropical peatland conversion over the last twenty years have led to an increase in the area of degraded peatlands in Indonesia (Miettinen and Liew, 2010) and this may have an effect on patterns of post-dispersal seed removal which in turn will impact natural regeneration occurring in the degraded areas.

6.1.1 Post-dispersal seed predation or secondary dispersal?

Post-dispersal seed removal does not always equate to post-dispersal seed predation and may in fact be secondary seed dispersal (Vander Wall et al., 2005). Whether an animal is a seed predator or seed disperser depends on how the seed is processed; seeds can be consumed and destroyed, consumed but pass through the gut unharmed, or hoarded (Janzen, 1971), and if seeds that are hoarded germinate before the individual returns to consume them this can be seen as a form of secondary dispersal (Hulme, 2002, Vander Wall et al., 2005). In general, unless seeds have been tracked to their fate it is inappropriate to label post-dispersal seed removal as post-dispersal seed predation (Vander Wall et al., 2005).

6.1.2 Post-dispersal seed removal in Southeast Asia

Post-dispersal seed removal agents in Southeast Asia include rodents (Wells and Bagchi, 2005, Wells et al., 2009), bearded pigs (*Sus barbatus*) (Curran and Leighton, 2000), wild boar (*Sus scrofa*), pig-tailed macaques (*Macaca nemestrina*), ground squirrels, porcupines, ants and other insects (Corlett, 2009). Rodent species in Southeast Asia vary in how they process seeds and this variation distinguishes them as post-dispersal seed predators or secondary dispersers. For example some *Maxomys* species are scatter-hoarders (Yasuda et al., 2000) which makes them secondary dispersers. In contrast *Rattus* species are seed predators because they directly consume seeds or are larder hoarders. Larder hoarders concentrate food items at one site (Vander Wall, 1990), often the individual’s nest, which not only makes seeds unlikely to be forgotten but are also poor sites for germination and establishment (Corlett, 2009). This means that the composition and abundance of rodents in an area will impact the level of secondary seed dispersal and post-dispersal seed predation. Both scatter- and larder-hoarding rodents may also disperse seeds that they swallow and defecate intact, but this is only likely with seeds small enough to escape destruction in the mouth (Wells et al. 2009).

Our current knowledge of post-dispersal seed removal in the Southeast Asian tropics comes from limited work carried out in dipterocarp forests and shows variation in post-dispersal seed removal across sites and seed species. In a seed removal experiment involving seeds of forty different species in Gunung Palung National Park, West Kalimantan, on average around half of the seeds of each species tested were removed after thirty days (Blate et al., 1998). In contrast, a longer study in Danum Valley, Sabah, Malaysia found lower rates of seed removal with only 16% of *Parashorea malaanonan* seeds and 20% of *Lithocarpus gracilis* seeds exploited (Wells and Bagchi, 2005). Other researchers have used camera traps to establish the fate of removed seeds (Yasuda et al., 2000).

More general studies of small mammal composition and abundance, including rodents, in the forests of Southeast Asia have also been carried out, in different habitats and following various types of disturbance, including forest fragmentation (Charles and Ang, 2010, Lynam and Billick, 1999), logging (Wells et al., 2007, Liat et al., 2003), conversion to tree plantations (Stuebing and Gasis, 1989) and landscape degradation (Chung and Corlett, 2006). Varied effects of disturbance have been found, including a complete loss of forest species in disturbed areas (Charles and Ang, 2010), a loss of rare species but the persistence of common species (Wells et al., 2007) and the invasion of exotic species (Lynam, 1997). Since small mammal species handle and exploit seeds differently any change in species composition and abundance is likely to affect the level of post-dispersal seed removal in these habitats.

6.1.3 Post-dispersal seed removal in tropical degraded areas

Current knowledge of post-dispersal seed removal in degraded habitats shows no obvious trend when comparing rates of post-dispersal seed removal to that in intact forest ecosystems. Experiments comparing seed removal within the forest, in open pasture and under isolated remnant trees in Costa Rica found the proportion of seeds remaining under isolated trees was significantly higher than in the forest or pasture (Holl and Lulow, 1997) while studies comparing Peruvian lowland tropical forest and fallow agricultural sites found seed predation was not significantly different between sites (Notman and Gorchov, 2001). Neither is there an obvious trend in post-dispersal seed removal between differing degraded habitats: on degraded hillside sites in Hong Kong seeds of eleven of the twelve species tested were completely removed from a shrubland site while only one species was completely removed from a grassland site (Hau, 1997).

Disturbance can change the composition and abundance of secondary dispersers and post-dispersal seed predators and this change can impact the level of post-dispersal seed predation and secondary dispersal in a degraded area. For example, large hard-coated seeds dispersed into Amazonian old fields persist longer than small-seeded species because the ants and rodents that inhabit the degraded area are unable to penetrate the large seeds' hard shells and consume them (Nepstad et al., 1991). Similarly, experiments in tropical forests found that unprotected seeds experienced higher levels of seed predation than those in exclosures that excluded vertebrate predators (Notman and Gorchov, 2001, Hautier et al., 2010) therefore if vertebrate seed predators, including rodents, are missing in degraded habitats this will impact the overall level of seed predation. Indeed, a comparison of post-dispersal seed predation in abandoned pasture, secondary forest and primary forest fragments in montane rain forest in Costa Rica found that insects or fungi were responsible for a higher proportion of seed mortality than rodents in pasture, while rodents were responsible for more of the predation in forest fragments, and suggested that this could be because mammalian seed predators may be less abundant in the successional habitats examined (Cole, 2009).

6.1.4 Research aims

I used seed removal experiments to pursue the following research objectives:

1) Compare the level of post-dispersal seed removal in an area of forest regrowth in Block A NW and an area of continuous logged peat swamp forest in Block E;

2) Establish whether levels of post-dispersal seed removal varied between seeds of different species;

3) Establish whether levels of post-dispersal seed removal were connected to the abundance of ground-feeding rodents in the area;

4) Establish whether post-dispersal seed removal was secondary seed dispersal or post-dispersal seed predation;

5) Establish whether post-dispersal seed predation is acting as a filter limiting natural regeneration in degraded tropical peatlands.

6.2 Methods

6.2.1 Study site

This work took place in the former Mega Rice Project area located in Central Kalimantan, Indonesia. Two habitat types were used: 1) continuous logged peat swamp forest (CLF) and 2) forest regrowth (FR). A description of the FR habitat type can be found in section 3.2.1. The continuous logged peat swamp forest (CLF) habitat used in this study was located at Tuanan Field Research Station. This research station is situated in the 300 000 ha Mawas conservation area in Block E of the former Mega Rice Project (02°09’06”S; 114°26’26”E). It is part of the same peat dome as the study site of Block A NW, although now separated from Block A by the two primary Mega Rice Project canals. The forest at Tuanan was selectively-logged in the 1990s and has been further subjected to illegal logging (van Schaik et al., 2005). All logging stopped in 2002 (Vogel et al., 2009).

I used two pre-existing transects in CLF and two purposely cut transects in FR for seed removal trials (Figure 6.1). Each transect was used for a single seed removal experimental trial lasting 14 days. One set of trials (one CLF transect and one FR transect) was carried out in May 2011 while the other set of trials took place in

November 2011. They were not run concurrently due to logistical issues but all trials were conducted in the wet season when water levels were similar.

6.2.2 Seed removal trials

For the seed removal trials I used seeds of one native animal-dispersed peat swamp species fruiting at the time of study, *Nephelium lappaceum* or *Syzygium muelleri*, seeds of the dominant species found in FR *Combretocarpus rotundatus* (wind-dispersed) and seeds of locally bought *Artocarpus heterophyllus* (jackfruit). Mean seed sizes are shown in Table 6.1. *A. heterophyllus* was chosen because tropical peatland tree species have complex fruiting patterns (Harrison et al., 2010) and seeds of native species are not always available. *A. heterophyllus* has been used in other studies on seed predation (e.g. Sodhi et al., 2003, Van der Meer et al., 2008) since it seems to be a reasonable model for large seeds (Sodhi et al., 2003) and also has the benefit of allowing for cross-site comparisons. Fruits of the native peat swamp species were collected from CLF and FR by climbing trees to retrieve ripe fruits. Seeds were removed from fruit and cleaned to remove all fleshy parts, except for *C. rotundatus*, which is a winged seed with no fleshy parts. The removal of fleshy parts ensured that any removal by dispersal agents was due to the attractiveness of the seed only. None of the species used have lipid-rich arils or elaiosomes so cleaning the seeds did not remove any specific adaptations to attract dispersal agents such as ants. One metre of cotton thread ending in numbered flagging tape was attached to each seed with non-toxic glue. Marking allows for the tracking of removed seeds (Forget, 1990). Other seed removal studies have found no difference between the removal of marked and unmarked seeds (Brewer and Rejmánek, 1999, Wenny, 2000, Kitamura et al., 2008). A caveat of this technique is that the marking itself could affect the distance a seed is moved in comparison to an unmarked seed. However, it is not possible to evaluate the effect of marking on the distance a seed is moved because there is no way to track unmarked seeds and so while this is a recognised issue, marking is the only way to gain reliable knowledge on the fate of removed seeds (Vander Wall et al., 2005).

Figure 6.1. Location of transects used for seed removal trials and ground-feeding rodent surveys.

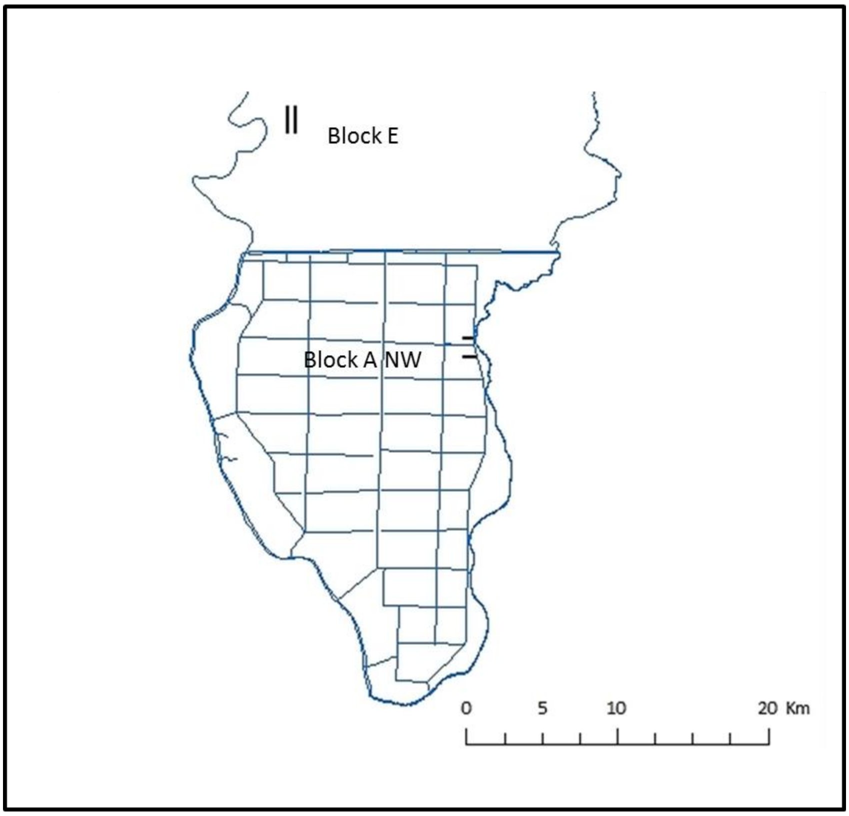


Table 6.1. Mean seed sizes (with standard deviation) in mm. Number of seeds measured in parentheses.

Species	Length	Width	Breadth
Combretocarpus rotundatus (including wings) (20)	20 ± 2.1	25.9 ± 3.6	0.04 ± 0.02
Nephelium lappaceum (6)	16.7 ± 2.7	10.0 ± 2.1	10.5 ± 1.9
Syzygium muelleri (10)	11.6 ± 1.8	11.8 ± 0.4	11.8 ± 0.6
Artocarpus heterophyllus (10)	29.2 ± 1.4	20.8 ± 2.8	13 ± 3.9

6.2.2.1 Seed placement

A set of nine seeds made up of three seeds of each species (always *C. rotundatus* and *A. heterophyllus*, with the third species either *N. lappaceum* or *S. muelleri*) was laid out in a grid, with a 50 cm gap between seeds. Each grid will be referred to from this point on as a ‘seed station’. A total of twenty seed stations were laid out at 50 m intervals along each of the transects, giving a total of 360 seeds (9 x 20 x 2) in each habitat type. Seed stations were at least 1 m from the main transect line and not directly under the crown of a single tree. Where necessary, a 2 m² area was cleared of above-ground vegetation to provide a substrate to place seeds on. Leaf litter and over-hanging vegetation were left intact.

6.2.2.2 Monitoring

Seed stations were checked every day for fourteen days, with seeds classed as handled or not handled. Handled seeds were further classed as eaten at the seed station or removed. Where seeds were removed a search of the surrounding area (a radius of 20 m) was carried out for the removed seeds and their threads. This search radius assumes rodents do not usually carry seeds further than 20 m (Van der Meer et al, 2008). Removed seeds were further classed as eaten if seed fragments were found, removed (fate unknown) if no seed fragments were found, cached if seeds were found below the soil surface or below leaf litter, or missing if the thread could not be relocated. Cached seeds were checked for every day until the end of the trial (day 14). Seeds with evidence of seed coat damage (by insects or rodents) were also classed as preyed upon (Holl and Lulow, 1997) and not counted as surviving, except in *C. rotundatus* where damage to the wings was not counted as long as the seed remained intact.

6.2.3 Ground-feeding rodent surveys

I conducted a mark and recapture trapping session along each of the transects to assess the composition and abundance of ground-feeding rodents weighing less than 1 kg. Surveys were carried out within a month of the seed removal trial on each transect.

6.2.3.1 Animal capture and handling

Animals were caught using Tomahawk collapsible live traps model 201 (Tomahawk Live Traps IIC). Traps were covered with locally available materials (fallen leaves, ferns, dead wood etc.) for camouflage and rain protection. At each transect ninety traps were used, with single traps set at 10 m intervals on the forest floor but away from the transect line. A seven day trapping session (630 trap nights) was conducted along each transect. Traps were baited with a mixture of banana and peanut butter, opened at 16.30 and checked the following morning at 07.00. Animals were marked with Monel ear tags (National Band and Tag Co., USA), measured and then released. Species were identified using *A Field Guide to the Mammals of Borneo* (Payne and Francis, 2005) with body, tail, ear and foot measurements taken. All captured animals were also photographed.

6.2.4 Evidence of post-dispersal seed removal

Ten camera traps (Bushnell Trophy camera, 5 megapixel model, Bushnell, Inc.) were used for one experimental trial in CLF and one experimental trial in FR. A camera trap was placed at every second seed station, between 10 and 20 cm from the ground and with a view of the seeds. Cameras were set to take a 20 second video when the sensor was triggered.

6.2.5 Data analysis

6.2.5.1 Seed removal trials

In order to establish the levels of post-dispersal seed removal in CLF and FR data were analysed as the proportion of seeds remaining at each seed station. This was because the survival of individual seeds at each seed station could not be considered as independent of one another. Data were pooled for each habitat, giving 40 seed stations for CLF and 40 seed stations for FR. A Mann-Whitney U test was used to test for a significant difference in the number of seeds surviving with an intact seed coat after 14 days in CLF and FR (SPSS. V16). In order to look at variation in levels of post-dispersal seed removal amongst species the cumulative percentage removal of seeds over time was calculated for each species for CLF and FR. In order to establish the overall fate of seeds in the removal trials, percentages of each of the seed fates (described in 6.2.2.2) were calculated for FR and CLF. A Mann Whitney U test was used to test for a significant difference in the distance seeds were moved in CLF and FR.

6.2.5.2 Ground-feeding rodent surveys

I calculated captures per unit effort (CPUE), corrected for sprung traps and total captures (Nelson and Clark, 1973). I used a Spearman's rank-order correlation to establish whether there was a relationship between CPUE per transect and the percentage of seeds removed per transect (SPSS. V16).

6.3 Results

6.3.1 Seed removal trials

6.3.1.1 Levels of post-dispersal seed removal in CLF and FR

The mean number of seeds remaining with an intact seed coat at a seed station (out of a possible 9) after 14 days was 5.6 (±2.8) in FR and 1.6 (±1.1) in CLF. A significant difference was found between seed stations in FR and CLF ($P < 0.05$). In total, 82.8% of seeds were removed in CLF and 38.1% in FR. No seeds were removed from 15% of the seed stations in FR while ≥6 seeds were removed from every seed station in CLF.

6.3.1.2 Variation in levels of post-dispersal seed removal amongst species (Figure 6.2)

C. rotundatus seeds had the lowest and slowest levels of removal in both CLF and FR, with almost half of the seeds removed by day fourteen in CLF and almost a quarter of the seeds removed in FR. *N. lappaceum* seeds had a higher overall percentage of removal in CLF than FR. In FR 46.7% of seeds had been removed by the sixth day and no more seeds were removed after this point. In comparison, in CLF 91.7% of seeds had been removed by the sixth day and seeds continued to be removed until 100% of the seeds had been removed by the last day of the trial. *S. muelleri* seeds had the most variation between sites. 95% of *S. muelleri* seeds were removed in CLF after one day, whereas only 5% of seeds of this species were removed in FR for the same time period. By the third day of the trial all seeds of this species had been removed from CLF whereas by the last day of the trial only 31.7% of had been removed in FR. *A. heterophyllus* seeds also had a higher overall percentage of removal in CLF than FR. No more seeds were removed in CLF after the tenth day, although 99% of seeds had already been removed. Seeds continued to be removed in FR until the last day of the trial when 50% of seeds had been removed.

6.3.1.3 Seed fate

I was able to locate and establish the fates of all the seeds (Table 6.2). In CLF more seeds were handled than not handled while in FR more seeds were not handled than handled. In both CLF and FR the largest number of seeds was eaten at the seed station (191 and 118 respectively). More seeds were eaten away from the seed station in CLF than in FR (99 and 17 seeds respectively) and more seeds were cached in CLF than in FR (8 and 2 respectively). Of the cached seeds only 1 seed remained cached and intact at the end of the study. This was a seed of *A. heterophyllus* in CLF.

The smallest distance a thread was found moved from its original position at a seed station was 0.2 m in CLF and 0.31 m in FR, the largest 5.5 m in CLF and 2.5 m in FR. The mean distance a thread was found from its original position was 1.15 m (±0.89) in CLF and 0.99 m (±0.61) in FR (P=0.5). The single *A. heterophyllus* seed that remained cached and intact at the end of the experiment was cached at a distance of 0.5 m from its original position. In both habitats a number of the moved threads converged at the same spot.

6.3.2 Ground-feeding rodent surveys

I trapped a total of 363 individuals (trapped on a total of 690 occasions) from 10 species, with a sampling effort of 2520 trap-nights (Table 6.3). In the CLF I found more individuals and more species (8 species, 214 individuals) than in FR (7 species, 149 individuals). The most abundantly trapped species by habitat were *Rattus tiomanicus* in FR, which accounted for 73.8% of all individuals captured, and *Maxomys whiteheadi* in CLF, which accounted for 45.8% of all individuals captured. No significant correlation was found between percentage of seeds removed and the CPUE of ground-feeding rodents for each transect (Spearman's rank-order correlation, rs = -0.2, P = 0.8).

6.3.3 Evidence of post-dispersal seed removal

Videos obtained by camera traps revealed 4 instances of rats consuming seeds at seed stations in FR. From the size of the rats it is likely they were individuals of *R. tiomanicus.* In CLF 12 instances of seeds being consumed at seed stations were recorded: 1 instance was by an individual of either *T. minor* or *T. splendidula* while the other 11 instances were by rats. From their size and tail colouration the rats were all from the *Maxomys* genus, but it was not possible to identify them to species. In CLF there were also 3 instances of rats removing seeds from seed stations. Again, from their size and tail colouration the rats were all from the *Maxomys* genus, but it was not possible to identify them to species.

Figure 6.2. Cumulative percentage seed removal over time for a) *Combretocarpus rotundatus*, b) *Nephelium lappaceum*, c) *Syzygium muelleri* and d) *Artocarpus heterophyllus*. ▲ = CLF, ■ = FR.

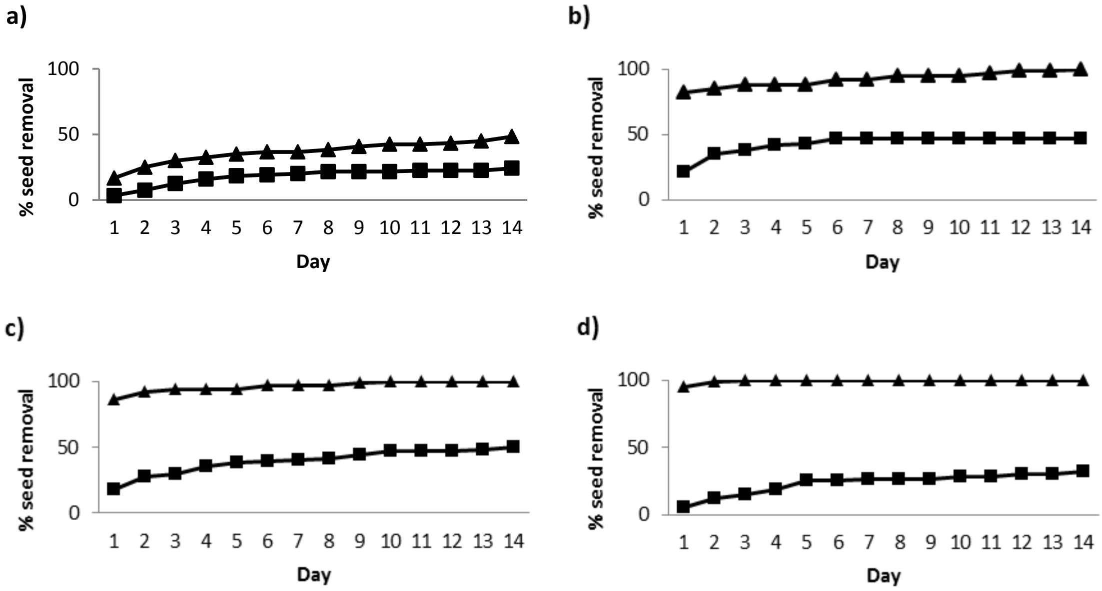


Table 6.2. Fate of thread-marked seeds in two tropical peatland habitats, Central Kalimantan, Indonesia.

		Seed fate					
		Not handled	Handled				Total
			Not removed	Removed			
					Cached		
			Eaten at seed station	Eaten away from seed station	Eaten by end of study.	Not eaten by end of study.	
Continuous logged peat swamp forest	Total count	62	191	99	7	1	360
	% of total	17.2	53.1	27.5	1.9	0.3	100
Forest regrowth	Total count	223	118	17	2	0	360
	% of total	61.9	32.8	4.7	0.6	0	100

Table 6.3. Number of individuals of all ground-feeding rodent species trapped. Total trap effort for each transect in parentheses.

			Continuous logged Peat Swamp Forest		Forest regrowth	
Species		Total no. of individuals	CLF1 (630)	CLF2 (630)	FR1 (630)	FR2 (630)
Rodentia						
Muridae						
Lenothrix canus	Grey Tree Rat	**2**	2	-	-	-
Maxomys rajah	Brown Spiny Rat	**83**	36	30	7	10
Maxomys surifer	Red Spiny Rat	**14**	4	9	1	-
Maxomys whiteheadi	Whitehead's Rat	**113**	32	66	2	13
Niviventer cremoriventer	Dark-tailed Tree Rat	**22**	12	10	-	-
Rattus tiomanicus	Malaysian Field Rat	**110**	-	-	40	70
Sundamys muelleri	Muller's Rat	**6**	4	2	-	-
Sciuridae						
Callosciurus notatus	Plantain Squirrel	**4**	-	-	4	-
Scandentia						
Tupaiidae						
Tupaia minor	Lesser Treeshrew	**6**	1	4	-	1
Tupaia splendidula	Ruddy Treeshrew	**3**	-	2	-	1
Grand Total		**363**	**91**	**123**	**54**	**95**
Number of species			7	7	5	5

6.4 Discussion

Results of this study showed a significantly higher level of post-dispersal seed removal in CLF compared with FR. It is important to note that this result only looks at post-dispersal seed removal at one study site and with a small sample size and this limits how widely the findings can be generalised to other forested and other degraded tropical peatlands. That said, the results of this study are comparable with those of other studies comparing rates of post-dispersal seed removal in degraded habitats with that in intact forest ecosystems (e.g. Aide and Cavelier, 1994, Osunkoya, 1994, Hammond, 1995). The level of seed removal found for CLF is higher than that found in dipterocarp forests in Southeast Asia (Blate et al., 1998, Wells and Bagchi, 2005) but not unusual for seed removal experiments in other forest types. In other parts of the Tropics studies in intact forest have found over 50% of seeds removed in seed removal experiments (Holl and Lulow, 1997, Wenny, 2000). The lower level of seed removal found for FR is lower than that found in degraded landscapes in other parts of the Tropics (Myster, 2003, Holl and Lulow, 1997, Osunkoya, 1994).

The results of the ground-feeding rodent surveys showed that the two habitat types shared five of the same species. However, the abundance of each species differed between habitats. The most abundant species in CLF was *M. whiteheadi,* while this species was only the third most abundant in FR. It is interesting that *M. whiteheadi* was found in high abundance in CLF and also found in FR since it has been found to show a significant preference for primary dipterocarp forest over logged forest in Peninsula Malaysia (Yasuda et al., 2003). This suggests that while the species may prefer primary forest it can persist in disturbed habitats.

In FR, *R. tiomanicus* dominated the rodent community, but was not recorded in CLF. *R. tiomanicus* is typically found in scrubland, grassland, rubber plantations and oil palm plantations but rarely in undisturbed forest (Harrison, 1957, Buckle et al., 1997, Wood, 1984, Payne and Francis, 2005). A study of *R. tiomanicus* in an oil palm (*Elaeis guineensis*) plantation in Johore, Malaysia, found that while the overwhelming majority of small mammals captured were *R. tiomanicus*, a very small number of *Maxomys rajah, M. whiteheadi, Rattus exulans* and *Callosciurus notatus* (plantain squirrel) individuals were also present (Wood, 1984). This is a very similar species composition to that found in this study for the FR area (although no *R. exulans* were encountered and two *Tupaia sp*. individuals and a single *M. surifer* individual were captured). The vegetation structure of the FR is in many ways similar to that of palm oil plantations, for example, FR is dominated by ferns and ferns are abundant in the ground-cover of older (twenty years plus) oil palm plantations, accounting for up to 70% of the undergrowth (Dahlan et al., 1993). These similarities in vegetation composition and structure could explain why the same species are found in both habitats. The lack of trees in the FR explains the lack of arboreal rats (*Lenothrix canus* and *Niviventer cremoriventer*) captured.

In other forest types it has been shown that disturbance causes a loss of native species and the invasion of generalists (in Kerangas forest) (e.g. Charles and Ang, 2010) or the loss of rare species and the perseverance of common species (in dipterocarp forest) (Wells et al., 2007). For the forest regrowth the high abundance of the generalist *R. tiomanicus* and the lack of the arboreal rat species suggests that the extreme degradation caused by the implementation of the Mega Rice Project has led to the loss of native species and the invasion of generalists and so is more similar to the pattern seen in the fragmentation of Kerangas forest (Charles and Ang, 2010).

Other studies carried out in Southeast Asia have also attributed seed removal to rodents. Van der Meer et al. (2008) used video cameras to record seed removal agents in seed removal trials in peat swamp forest in Sarawak, Malaysia and identified rodents, either *Maxomys whiteheadi* or *Sundamys muelleri* and *Callosciurus notatus*, as the primary seed removal agents, all of which were also found in my ground-feeding rodent surveys. Yasuda et al. (2000) investigated the removal of oil palm fruit (*Elaeis guineensis*), rather than seeds, and found most removal was by the long-tailed giant rat, *Leopoldamys sabanus*, a species not found in my surveys, with some removal by rodent *Maxomys* spp.

While the camera traps did not record seed removal events by any of the other species captured in the ground-feeding rodent surveys, all of the species captured do consume seeds to some degree (Yasuma and Andau, 2000 in, Meijaard et al., 2005, Wells and Bagchi, 2005, Van der Meer et al., 2008). Since the cameras were not placed at all seed stations and therefore did not record every seed removal event during the experiment it is possible individuals of these species were also responsible for seed removal.

Overall, the results of my study suggest that rodents are important seed removal agents in both FR and CLF of tropical peatlands. However, it is important to note that the seeds used in this study were too large for removal by most ants (>20 mg) (Corlett, 2009). Studies in degraded environments in the Neotropics have found that found that ants, insects or fungi were responsible for the majority of post-dispersal seed removal (Myster, 2004, Fornara and Dalling, 2005, Cole, 2009), therefore future studies should include seeds capable of removal by ants and other insects.

Looking at seed fate, in both CLF and FR habitats only a tiny proportion of seeds were cached initially and only a single seed of *A. heterophyllus* in CLF remained cached and intact by the end of the study. *Rattus* species are seed predators rather than scatter-hoarders (Cheng et al., 2005, Hau, 1997, Chang and Zhang, 2011) and so the high abundance of *R. tiomanicus* in FR may explain the absence of caching in this habitat. Interestingly, *Maxomys* species are known hoarders, although reports are mixed as to whether they are scatter-hoarders (Yasuda et al., 2000), larder hoarders (Wells and Bagchi, 2005, Medway, 1983) or both (Kitamura et al., 2004), and accounted for 82.7% of all the individuals captured in CLF yet almost no caching behaviour was seen in this habitat.

The almost complete lack of caching of seeds in both habitats is comparable to the findings of Van der Meer et al. (2008) who reported that only 3% of experimental jackfruit seeds were cached in a peat swamp forest in Sarawak, Malaysia. In comparison, seed removal experiments in dipterocarp rainforest in Peninsula Malaysia found that 29.4% of seeds were cached, although caching was only short-term and no caches remained intact for more than one week (Yasuda et al., 2000).

The lack of caching seen in my study may be due to the physical characteristics of tropical peatlands. Tropical peatlands are typically water-logged environments (Rieley et al., 1996a) and degraded areas often experience extensive periods of flooding (Wosten et al., 2006). This high water-table removes potential underground caching sites and so makes caching impractical in tropical peatlands. Also, tropical peat swamp forest does not have masting events as in dipterocarp forests (Cannon et al., 2007a, Cannon et al., 2007b). It has been suggested that caching occurs during masting events because the surplus of food allows for food storage after animals have satiated themselves (Janzen, 1971). The absence of a food surplus in tropical peat swamp forests could thus explain the lack of caching behaviour in this environment. Overall, this suggests that the physical characteristics of tropical peatlands may play a bigger part in whether seeds are cached than the composition of ground-feeding rodents. The lack of caching behaviour shows that it is likely that post-dispersal seed predation rather than secondary dispersal is occurring in both habitats. This has implications for plant recruitment in both habitats because it reduces the number of seeds available.

Although seeds were not cached in my study, the seed fate results show that seeds were not always consumed at the seed station. For the CLF site, a total of 29.7% of threads were found moved from their original position and videos from camera traps showed three instances of seeds being carried away from seed stations by rats. However, the mean distance a thread was found from its original position was small and in many instances threads moved over the same time period (e.g. the twenty-four hours between checks) converged at the same spot which suggests that seeds were moved to a spot to be consumed rather than cached. Wells and Bagchi (2005) found similar displacement behaviour by rodent seed predators in dipterocarp forest in Malaysia and suggested that the movement of seeds is a strategy to consume the seed in a protected place. Since the seed stations used were cleared of ground vegetation and therefore exposed to predators this likely explains the movement of seeds in this study as well.

In the FR site only a small percentage (5.3%) of threads were found moved from their original position and there were no occurrences of seeds being carried away from a seed station recorded by the camera traps. As with seed removal in CLF, this may have been the individual moving to a preferred spot to consume the seed rather than the caching of a food item.

The lack of a correlation between CPUE of ground-feeding rodents and the percentage of overall seed removal may be a consequence of single individuals having a large influence on the rate of seed removal by consuming all the seeds at a seed station. Indeed, camera traps show repeat recordings of what appears to be the same individual returning to a seed station and consuming multiple seeds within a single evening. Similar repeat visits within a short space of time were also seen in peat swamp forest in Sarawak, Malaysia (Van der Meer et al., 2008). However even if high rates of seed removal are being caused by just a few individuals, this does not reduce the impact of that seed removal on plant recruitment.

In a similar fashion, 15% of seed stations in FR had no seeds removed while seeds were removed from all seed stations in CLF. Work investigating variables that can affect the behaviour of seed removal agents has found that microhabitat effects such as the presence of shrubs, liana density, proximity to tree trunks and overall vegetation cover can influence levels of seed removal (Schupp, 1988, Bowers and Dooley, 1993, Hulme, 1994, Manson and Stiles, 1998, Meiners and LoGiudice, 2003, Pena-Claros and De Boo, 2002). Microhabitat effects in FR may explain why some seed stations experienced no seed removal and future studies should investigate this. The untouched seed stations accounted for 37.5% of the total number of seeds tested in FR habitat, suggesting that microhabitat effects could have a large influence on the overall level of seed removal in the area and this may explain the lower level of seed removal in FR compared with CLF. Seeds were removed from all seed stations in CLF which suggests less of a microhabitat effect in this habitat.

My results found that there were differences in the rates of post-dispersal seed removal between the four species tested. Closer examination of the animal-dispersed seeds tested in the seed removal trials shows that *A. heterophyllus*, *S. muelleri* and *N. lappaceum* all had extremely high levels of seed removal in CLF with 99 – 100% of seeds removed by the end of the study. In FR lower levels of seed removal were found for each animal-dispersed species, with 30 - 50% of seeds removed by the end of the study and this reflects the overall pattern of fewer seeds being removed in FR than in CLF. In contrast, *C. rotundatus* had the lowest percentage of seed removal after fourteen days in both CLF and FR. This is unsurprising since it was the only wind-dispersed species used in the experiments and low levels of removal have been reported for wind-dispersed species in other studies (Fornara and Dalling, 2005). It has been suggested that seed size (Doust, 2010, Blate et al., 1998, Osunkoya, 1994, Dirzo et al., 2007), nutritional content, the thickness of the seed coat and the presence of chemical defences can have an affect on seed removal rate (Janzen, 1971, Osunkoya, 1994). In this study the level of seed removal was comparable for the animal-dispersed seeds *A. heterophyllus*, *S. muelleri* and *N. lappaceum* in both FR and CLF, even though *A. heterophyllus* is a much larger seed and this suggests that size does not affect the likelihood of seed being removed, a result also found by Hau (1997) and Holl and Lulow (1997). Although I did not measure the nutrient content of the seeds, it is likely that the animal-dispersed species had a higher nutritional value than the wind-dispersed *C. rotundatus* seeds and this probably explains the higher levels of seed removal of the animal-dispersed species in this study.

The difference in the level of seed removal between the animal-dispersed seeds and wind-dispersed seeds has implications for the natural regeneration of woody plants in the forest regrowth of Block A NW. The results of Chapter 5 show that *C. rotundatus* is the second most abundant seed found in both the total seed rain and foreign seed rain in the forest regrowth of Block A NW. This high abundance combined with the observed lower level of seed removal of the species in comparison to that of animal-dispersed seeds has the potential to affect tree recruitment in the area. Not only are there more seeds of *C. rotundatus* in the area but they are removed less and, excluding other filters to plant establishment, this suggests a higher level of recruitment of *C. rotundatus* in the area in comparison to other woody plant species.

While FR shows a significantly lower level of seed removal than CLF this does not necessarily translate to a lesser effect of seed removal on plant recruitment.

Post-dispersal seed removal has a different level of impact on plant recruitment dependent on the input of seeds. Areas with low seed densities or located far away from parent plants experience greater effects from seed predation and thus a reduction in plant recruitment in comparison to areas with high seed densities where availability of suitable sites for growth are more likely to limit plant recruitment than post-dispersal seed predation (Crawley, 1992). This means that the removal of 38.1% of seeds in an area likely to have a low level of seed input such as the FR site could have a greater effect on overall plant recruitment than the removal of 82.8% of seeds in an area of higher seed input such as the CLF site.

The impact of differential removal of different seed species will also depend on their relative abundance in the seed rain. In the FR there is an abundance of wind-dispersed seeds and fewer animal-dispersed seeds in the seed rain (Chapter 5) and therefore a higher level of removal of animal-dispersed seeds than wind-dispersed seeds could reduce the overall number of animal-dispersed seeds present in the area and skew the woody plant recruitment even further towards wind-dispersed species.

7. General Discussion

This thesis investigated the natural regeneration ability of degraded tropical peatland by surveying the composition and abundance of woody plant species regenerating in an area of forest regrowth (FR) in Block A NW of the former Mega Rice Project area. The specific impacts of land conversion and degradation in the FR were explored and their relationship with the current woody plant flora was investigated. Seed dispersal and post-dispersal seed removal were examined as filters potentially limiting successional processes in the FR.

My results showed that the current state of the natural regeneration of woody plants in the FR of Block A NW was dominated by a few abundant species (*Combretocarpus rotundatus, Melastoma malabathricum, Cratoxylum arborescens/glaucum, Ploarium alternifolium* and *Syzygium myrtifolium*) but also contained a diverse array of tropical peat swamp forest species, albeit in low abundances (Chapter 3). I also found that the most abundant sapling-shrub species were either wind-dispersed or dispersed by bulbuls (Pycnonotidae) and other small- to medium-sized birds and this matched the likely composition of dispersal agents in the area. The most abundant tree species had a range of dispersal agents, however many of these dispersal agents are unlikely to be found in the FR. Therefore, it was suggested that the tree composition is due to natural regeneration through resprouting behaviour.

Further investigation found that this composition of woody plants was connected to the impacts of land conversion and to filters limiting the successional processes in the area. Of the filters examined, the hydrology of the area, fire history, seed dispersal and post-dispersal seed predation were found to be limiting the natural regeneration potential of the forest regrowth in Block A NW.

In Chapter 4 I investigated the specific impacts of the Mega Rice Project land conversion. I found that the implementation of a drainage system has led to a general trend for flooding during the wet season while groundwater levels drop during the dry season. I also found that the drainage system is causing diverging hydrological trajectories based on distance from the nearest canal with areas closer to a canal generally have a higher percentage of drought months while areas further away from a canal generally have a higher percentage of flooding months. Exploration of the fire history of Block A NW found that the occurrence of fire is widespread and the majority of the area has burnt more than once. I also explored how the species richness woody plants related to these impacts. My results showed that the number of years since the last fire, the number of times an area has burnt, the number of drought months and the number of flooding months were important determinants of species richness.

In Chapter 5 I investigated potential seed dispersal limitations in the FR through a study of seed rain. My results showed that for tree and shrub species the seed rain largely reflected the composition of woody plants that already exist in the area rather than coming from outside sources. The majority of seeds were wind-dispersed or dispersed by bulbuls (Pycnonotidae) and other small- and medium-sized birds and this reflected the composition of dispersal agents found in the degraded area. I also found that established trees were important as nuclei for regeneration, especially for animal-dispersed woody plant species. The main conclusions that could be drawn from this were that while the seed rain in the open and under trees was sufficient in number for the development of woody plant cover the low diversity of seeds meant that the resulting woody plant composition would be limited.

In Chapter 6 I investigated whether the removal of seeds post-dispersal but pre-germination could also be limiting the diversity of woody plant species recolonizing the FR of Block A NW. Seed removal trials found that post-dispersal seed removal was higher for animal-dispersed seeds than for wind-dispersed seeds in both FR and in an area of continuous logged peat swamp forest (CLF) and was likely to be post-dispersal seed predation by ground-feeding rodents, with no caching behaviour seen (Chapter 6). Since there was an abundance of wind-dispersed seeds and fewer animal-dispersed seeds in the seed rain (Chapter 5) the higher level of removal of animal-dispersed seeds than wind-dispersed seeds found in the experimental trials could potentially reduce the overall number of animal-dispersed seeds present in the area and skew the woody plant recruitment even further towards wind-dispersed species. Therefore the findings of the experimental trials suggested that post-dispersal seed predation was potentially a filter limiting the processes of natural regeneration.

Looking at all of the results combined, it seems that each of the filters acts at a specific point along the regeneration timeline. My results suggest that the initial potential woody plant species composition in the FR is determined by seed dispersal, with this potential composition reduced by the limiting influence of each subsequent filter. Seed rain in the FR comes from plants within the degraded area and thus the initial potential composition is limited to those woody plant species already established in the forest regrowth (possibly from resprouts or remnant vegetation). Some of these seeds, likely more animal-dispersed seeds than wind-dispersed seeds, are consumed post-dispersal, which further limits the woody plant composition. Seeds that are not consumed and germinate are then limited by the hydrological state of the area they were dispersed into and their species-specific flood and drought tolerance. Plants that are able to establish in these conditions then grow and produce seeds that make up the seed rain. The occurrence of fire at any point in the regeneration timeline returns the process back to zero.

Indeed, the combined results of this thesis suggest that without intervention, the forest regrowth of Block A NW will persist as an area dominated by a limited number of wind-dispersed and bulbul-dispersed woody plant species that are able to tolerate the hydrological state of the area. The extent of the natural regeneration will also be dependent on the number of years since the last fire occurred in the area. Therefore, if the aim is to restore a more diverse forest cover some human intervention will be required. Human intervention should be considered as a three-phase restoration process which first stops the occurrence of fire in the area, second restores the hydrology; and third enriches the woody plant species composition.

My results showed that number of years since the last fire is an important determinant in woody plant species richness with the majority of species showing a positive relationship with an increasing time interval since the last occurrence of fire.

This suggests that fire prevention is an important first step in the restoration of degraded tropical peatlands. As discussed in section 4.1.1, all fires in tropical peatlands are started by people for various reasons including as a tool to clear land, to aid resource extraction or as a weapon in land disputes (Dennis et al., 2005). Therefore fire prevention will require site-specific investigation into the underlying reasons behind why fires are started and mediation at regional and local levels to stop or reduce these activities (Tomich and Lewis, 2002). Current fire mitigation activities in tropical peatlands generally focus on fire suppression rather than fire prevention (Adinugroho et al., 2005) which is not ideal for restoration because areas still burn. Fire prevention programmes have been implemented in some parts of Indonesia, for example in Jambi, Sumatra, and in West Kalimantan, involving land management and crop protection strategies that both reduce the requirement for fire in land-clearing activities and reduce the ability of fire to spread (Otsuka et al., 2002). However, the success of these programmes was limited because many farmers did not have the financial resources to implement the necessary strategies or were reluctant to employ the laborious tasks the strategies required (Otsuka et al., 2002). This suggests that fire prevention schemes may require some form of financial incentive if they are to be successful. Fire prevention in degraded tropical peatlands may also be achieved through the implementation of measures which raise groundwater levels. Research has found that tropical peatlands with groundwater levels ≤ -0.4 m are highly susceptible to fire (Wosten et al., 2008) and therefore if groundwater is maintained above this level fires will be harder to ignite.

Restoring the hydrological integrity of the area is also important for other reasons. My results suggest that the current hydrological state of the FR influences the woody plant species richness of the area, with species richness decreasing with an increasing number of drought months and increasing with an increasing number of flooding months. The current hydrological state of the FR in Block A NW shows a general trend for flooding during the wet season with groundwater levels dropping to as low as -0.6 m during the dry season. Therefore, to aid natural regeneration processes and increase species richness in the area, hydrological restoration should aim to retain groundwater levels in the wet season and reduce drops in groundwater level in the dry season, thereby reducing the number of drought months the area experiences. This will also return the hydrology of the area to something closer to its natural state, that is, a consistently high water-table which lies just below the peat surface during the dry season and near or above the surface during the wet season (Page et al., 2009b).

Hydrological restoration attempts in degraded tropical peatlands generally involve blocking drainage canals through dam construction (Suryadiputra et al., 2005, Jauhiainen et al., 2008, Jaenicke et al., 2010). It has been suggested that a series of dams built close together is required to successfully raise groundwater depth levels (Wosten and Ritzema, 2001, Suryadiputra et al., 2005, Hooijer et al., 2008, Mawdsley et al., 2009). Limited results show that damming drainage systems does raise groundwater levels. For example, annual minimum groundwater depth was 0.68 m higher after dam construction in a deforested area of Block C of the former Mega Rice Project (Jauhiainen et al., 2008) and construction of dams to block illegal logging ditches in peat swamp forest in South Barito, Kalimantan, raised groundwater levels by up to 0.4 m (Suryadiputra et al., 2005).

Hydrological restoration in degraded tropical peatlands through dam building has mainly focussed on raising groundwater levels to mitigate carbon dioxide emissions (Jauhiainen et al., 2008, Jaenicke et al., 2010, Jaenicke et al., 2011) rather than with a view to aiding forest recovery. This means that there is currently no information on whether raising groundwater levels positively impacts woody plant composition and abundance as my results suggest it might. Therefore, future research specifically investigating the woody plant composition before and after groundwater levels are raised is required to better inform hydrological restoration plans and ensure that they are beneficial for both preventing carbon release and the natural regeneration of woody plants.

Finally, my results also suggest that human intervention will be required to overcome the seed dispersal limitations found in Chapter 5. The seeds currently dispersed in the FR are limited to species already found within the degraded area. Therefore, enrichment planting, focussing on tropical peatland species not currently found in, or only found in low numbers in the FR should be implemented to increase species diversity. It should also aim to include large-seeded animal-dispersed species to encourage a wider composition of dispersal agents into the area. Seedling planting has been carried out in other areas of degraded tropical peatland with varying levels of success. Experimental trials in degraded tropical peatland in Thailand had positive results, with survival rates of over 50% of individuals for 19 of the 28 woody plant species tested after a minimum of 9 years (Nuyim, 2005). In contrast, replanting efforts in Block A NW, mainly close to the primary Mega Rice Project canals (Suryadiputra et al., 2005) were decimated by fires in 2009 (personal observation). This shows the importance of a long-term commitment to restoration projects if they are to be successful. Indeed, a realistic time frame for the reestablishment of a closed canopy forest on tropical peatland is between 10 – 20 years (Page et al., 2009b) therefore if replanting schemes are to be successful they will require long-term monitoring, maintenance and funding.

Overall, the successful restoration of a diverse forest cover in Block A NW will require human intervention that overcomes the filters currently limiting natural regeneration processes. The restoration activities undertaken should factor in the timescale required for a closed canopy forest cover to be achieved and the necessary monitoring and maintenance procedures to ensure that this goal is reached.

The forest regrowth in Block A NW is one example of the expansive degraded tropical peatlands that now exist in Indonesia. My research showed that the natural regeneration of woody plants in degraded tropical peatland is complex and somewhat site-specific, because the filters limiting natural regeneration are so linked to the initial land conversion and resulting degradation. For example, land conversion in Block A NW involved changes to the hydrology of the area and widespread removal of natural forest cover and its accompanying fauna and it is these very things that are now limiting successional processes. This agrees with the idea that the course secondary succession takes is contingent upon the characteristics of the original forest, the biophysical conditions of the area and the type and level of disturbance that took place (Corlett, 1995, Chazdon, 2003, Hobbs and Norton, 2004). Similar land conversion techniques have been used on tropical peatlands across Southeast Asia and so it is likely that my results reflect general trends in the composition and abundance of woody plants and the filters limiting the natural regeneration.

My study provides a starting point for further research investigating these filters at multiple sites and over longer-time periods, which will help to establish a wider picture of succession in degraded tropical peatlands. Recommendations for further research that will build on and compliment the results of this study include:

- Surveys of other tropical peatland areas (both intact and degraded) to gain a better understanding of how vegetation differs under different land-uses.

- The establishment of long-term vegetation plots to enable monitoring of woody plants in the forest regrowth and investigate longer-term trends and changes in patterns of species composition and abundance. This will allow for better understanding of the trajectory of vegetation regrowth in degraded tropical peatlands. The results of monitoring activities can also act as a "control" to establish what affect any restoration efforts may have in comparison to a non-intervention baseline.

- Mechanistic experiments to further explore the functional traits of the tropical peatland woody plants for both species currently found and currently not found in the forest regrowth. This should include germination and planting experiments for tropical peatland woody plant species not currently found in the forest regrowth to confirm whether species are currently dispersal-limited, establishment-limited or both. This research will aid in the identification of key woody plant species that could be used for replanting restoration activities.

- Investigation of other filters which may be limiting successional processes in degraded tropical peatlands, including competition from ferns and other herbaceous vegetation and peat nutrient composition.

In conclusion, with 1.8 million hectares of tropical peatland in Indonesia and Malaysia now existing in a degraded state (Miettinen and Liew, 2010), my research provides an important and valuable contribution to the understanding of why these areas are not undergoing forest recovery and can be used as a basis to inform restoration efforts to improve their chances of success.

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Appendix A.

Estimated heights of woody plants recorded in vegetation surveys in forest regrowth of Block A NW in the former Mega Rice Project area, Central Kalimantan, Indonesia.

Family	Species	0.5 - 3.0	3.1 - 10.0	10.1 - 20.0	20.1 - 30.0	>30.1
Anacardiaceae						
	Campnosperma coriaceum (Jack) Hallier f.	14	36	1	0	0
	Campnosperma squamatum Ridl.	7	4	0	0	0
Anisophylleaceae						
	Combretocarpus rotundatus (Miq.) Danser	1399	1199	1	5	1
Annonaceae						
	Goniothalamus malayanus Hook.f. & Thomson	17	1	0	0	0
	Mezzettia havilandii Ridl.	43	23	2	0	0
	Polyalthia hypoleuca Hook.f. & Thomson	6	4	0	0	0
	Xylopia caudata Hook.f. & Thomson	5	24	0	0	0
Apocynaceae						
	Alstonia pavonina	19	4	0	0	0
	Dyera polyphylla (Miq.) Steenis	4	7	1	2	0
Aquifoliaceae						
	Ilex cymosa Blume	117	33	0	0	0
Bonnetiaceae						
	Ploiarium alternifolium (Vahl) Melch.	458	56	2	0	0
Burseraceae						
	Santiria griffithii Engl.	6	6	0	0	0
	Santiria laevigata Blume	1	1	0	0	0
Calophyllaceae						
	Calophyllum soualattri Burm.f.	6	4	0	0	0

Appendix A. (continued)

Family	**Species**	**0.5 - 3.0**	**3.1 - 10.0**	**10.1 - 20.0**	**20.1 - 30.0**	**>30.1**
Cannabaceae						
	Trema orientalis (L.) Blume	39	5	0	0	0
Chrysobalanaceae						
	Licania splendens (Korth.) Prance	0	4	0	0	0
Clusiaceae						
	Garcinia nigrolineata Planch. ex T.Anderson	68	41	0	0	0
	Garcinia sp. 1	3	2	0	0	0
Crypteroniaceae						
	Dactylocladus stenostachys Oliv.	2	3	0	0	0
Dipterocarpaceae						
	Cotylelobium lanceolatum Craib	26	3	0	0	0
	Shorea balangeran Burck	61	37	0	0	0
	Shorea beccariana Burck	13	60	1	1	0
	Shorea smithiana Symington	11	7	0	0	0
	Shorea sp.	1	2	0	0	0
Ebenaceae						
	Diospyros areolata King & Gamble	24	23	4	0	0
	Diospyros confertiflora (Hiern) Bakh.	7	2	0	0	0
	Diospyros curranii Merr.	6	2	2	0	0
	Diospyros evena Bakh.	10	4	1	0	0
Elaeocarpaceae						
	Elaeocarpus sp.	150	72	0	0	0
Euphorbiaceae						
	Blumeodendron tokbrai (Blume) Kurz	7	19	1	0	0
	Macaranga diepenhorstii (Miq.) Müll.Arg.	26	1	0	0	0
Fabaceae						
	Archidendron borneense (Benth.) I.C.Nielsen	49	5	0	0	0
	Caesalpinia sp.	33	2	0	0	0
	Dialium platysepalum Baker	6	15	3	0	0
	Lithocarpus sp.	71	77	0	0	0

Appendix A. (continued)

Family	Species	0.5 - 3.0	3.1 - 10.0	10.1 - 20.0	20.1 - 30.0	>30.1
Hypericaceae						
	Cratoxylum arborescens (Vahl) Blume and *Cratoxylum glaucum* Korth.	465	237	0	0	0
Lauraceae						
	Alseodaphne coriacea Kosterm.	26	6	0	0	0
	Cryptocarya enervis Hook.f.	252	4	0	0	0
	Litsea grandis var. rufofusca (Kosterm.) Ng	67	32	1	0	0
	Phoebe grandis (Nees) Merr.	19	20	0	0	0
Lecythidaceae						
	Barringtonia longisepala Payens	1	0	0	0	0
	Barringtonia reticulata (Blume) Miq.	72	4	0	0	0
Melastomataceae						
	Melastoma malabathricum L.	778	1	0	0	0
Meliaceae						
	Aglaia sp.	6	6	2	0	0
	Chisocheton patens Blume	10	2	0	0	0
	Sandoricum beccarianum	0	6	0	0	0
Myristicaceae						
	Gymnacranthera farquhariana (Hook.f. & Thomson) Warb.	1	9	1	0	0
	Horsfieldia crassifolia (Hook.f. & Thomson) Warb.	16	12	0	0	0
	Horsfieldia sp.	25	26	2	0	0
	Knema stenophylla (Warb.) J.Sinclair	4	2	0	0	0
Myrtaceae						
	Melaleuca cajuputi Powell	134	7	0	0	0
	Rhodamnia cinerea Jack	50	9	0	0	0
	Syzygium myrtifolium Walp.	153	82	1	0	0
	Syzygium oligomyrum Diels	57	13	0	0	0
	Syzygium palembanicum Miq.	35	49	0	0	0
	Syzygium zeylanicum (L.) DC.	0	1	0	0	0
	Syzygium sp.	82	36	1	0	0
	Syzygium sp. 3	208	33	0	0	0

Appendix A. (continued)

Family	**Species**	**0.5 - 3.0**	**3.1 - 10.0**	**10.1 - 20.0**	**20.1 - 30.0**	**>30.1**
	Syzygium sp. 4	84	0	0	0	0
	Tristaniopsis whiteana (Griff.) Peter G.Wilson & J.T.Waterh.	11	18	0	0	0
Phyllanthaceae						
	Antidesma coriaceum Tul.	62	0	0	0	0
	Antidesma montanum Blume	35	0	0	0	0
Polygalaceae						
	Xanthophyllum discolor Chodat	5	3	0	0	0
Primulaceae						
	Ardisia copelandii Mez	29	16	1	0	0
Rhizophoraceae						
	Pellacalyx axillaris Korth.	6	0	0	0	0
Rosaceae						
	Prunus grisea Kalkman	29	18	2	0	0
Rubiaceae						
	Ixora havilandii Ridl.	25	4	0	0	0
	Pavetta sp.	9	0	0	0	0
	Rothmannia grandis	68	16	0	0	0
	Timonius sp.	69	8	1	0	0
Rutaceae						
	Melicope lunu-ankenda (Gaertn.) T.G. Hartley	282	48	0	0	0
Sapindaceae						
	Nephelium lappaceum L.	113	80	0	0	0
Sapotaceae						
	Palaquium ridleyi King & Gamble	18	11	0	1	0
	Pouteria malaccensis (C.B.Clarke) Baehni	11	9	0	0	0
Stemonuraceae						
	Stemonorus scorpiodes	27	36	0	0	1
	Stemonurus secundiflorus	18	18	0	0	0
Thymelaeaceae						
	Gonystylus bancanus (Miq.) Kurz and *Gonystylus brunnescens* Airy Shaw	7	6	0	0	0

Appendix A. (continued)

Family	Species	0.5 - 3.0	3.1 - 10.0	10.1 - 20.0	20.1 - 30.0	>30.1
Verbenaceae						
	Clerodendrum sp.	1	0	0	0	0
Unknown						
	Unknown - Ketapi hutan	0	2	0	0	0
	Total	6085	2678	31	9	2

Appendix B.

List of woody plant species and their associated abbreviations used in the CCA ordinations shown in Figure 4.5 and Figure 4.6 (Chapter 4), in alphabetical order.

Species	**Abbreviation**
Aglaia sp.	Agl_sp
Alseodaphne coriacea	Als_cor
Antidesma coriaceum	Ant_cor
Antidesma montanum	A_mon
Archidendron borneense	A_bor
Blumeodendron tokbrai	B_tok
Caesalpinia sp.	Caes_sp
Calophyllum soulattri	C_soul
Campnosperma coriaceum	C_cor
Campnosperma squamatum	C_squa
Combretocarpus rotundatus	C_rot
Cratoxylum arborescens / glaucum	C_arb
Crptocarya enervis	C_ene
Dactylocladus stenostachys	D_sten
Dialium platysepalum	D_plat
Diospyros areolata	D_are
Diospyros cf. *curranii*	D_cur
Diospyros evena	D_eve
Elaeocarpus sp.	Elae_sp
Garcinia nigro-lineata	G_nig
Gonystylus bancanus / brunescens	G_ban
Horsfieldia sp.	Hor_sp
Ilex cymosa	I_cym
Ixora havilandii	I_hav
Lithocarpus sp.	Lith_sp
Litsea grandis var. *rufofusca*	L_gran
Macaranga diepenhorstii	M_die
Melaleuca cajuputi	M_caj
Melastoma malabathricum	M_mal
Melicope lunu-ankenda	M_lun
Mezzettia havilandii	M_hav
Nephelium lappaceum	N_lap
Palaquium ridleyi	P_rid
Pavetta sp.	Pav_sp
Pheobe grandis	P_gran
Ploiarium alternifolium	P_alt

Appendix B. (continued)

Species	**Abbreviation**
Prunus grisea	P_gris
Shorea balangeran	S_bal
Shorea beccariana	S_bec
Stemonorus scorpiodes	S_scor
Syzygium oligomyrum	S_oli
Syzygium palembanicum	S_pal
Syzygium sp.	Syz_sp
Syzygium sp.3	Syz_sp3
Timonius sp.	Tim_sp
Tristaniopsis whiteana	T_whit
Xanthophyllum discolor	X_dis
Xylopia caudata	X_cau