IMPACTS OF SILVICULTURAL SYSTEM ON GENETIC DIVERSITY OF *Shorea parvifolia* IN THE TROPICAL SECONDARY FOREST, CENTRAL KALIMANTAN, INDONESIA

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2016

TOKYO METROPOLITAN UNIVERSITY
DISSERTATION FOR A DEGREE OF DOCTOR OF TOURISM SCIENCE

TITLE:

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ACKNOWLEDGMENTS

First, I would like to express sincere appreciation and gratitude to my supervisors, Prof. Dr. Shinya Numata (Tokyo Metropolitan University) and Prof. Dr. Yoshihiko Tsumura (Tsukuba University) for their helpful advice, invaluable discussion, and continuous encouragement during my studies at Tokyo Metropolitan University. I also thank Prof Dr. Toshio Kikuchi (Tokyo Metropolitan University) for serving as my dissertation's reviewer, and for his comments and suggestions to improve this document.

I would like to acknowledge Dr. Asako Matsumoto, Dr. Naoki Tani, Dr. Saneyoshi Ueno, Dr. Kentaro Uchiyama, and Dr. Tetsuro Hosaka, who helped to ensure the success of my studies, including teaching me how to conduct research in the laboratory and to analyze and interpret data. I would also like to thank the members of the Tree Genetic Laboratory in the FFPRI, Tsukuba who were a great help in laboratory work.

I am grateful to PT Sari Bumi Kusuma in Central Kalimantan, Indonesia, in particular Mr. Adlin, for the permission to conduct research in the PT Sari Bumi Kusuma site. I also extend thanks to Mr. Yudhi Hendo, Mr. Susilo Purnomo, Mr. Jatmoko, Mr. Yasir, Mr. Ragil Kasianto, Mr. Taufik, Mr. Saminto, and the research and development staff of PT Sari Bumi Kusuma who helped me to collect and manage data during sampling in Central Kalimantan, Indonesia.

I am also grateful to the Tokyo Metropolitan Government for financial support of my studies through the Asian Human Resource Fund. Furthermore, I thank the Ministry of Culture and Education of Indonesia and Universitas Gadjah Mada (UGM), which gave permission for me to study at Tokyo Metropolitan University, Japan.

Finally, I would like to express my deepest gratitude to my family, especially my parents, my lovely wife, and my sons in Indonesia for their endless encouragement, spiritual support, and prayer for me during my studies in Japan.

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SUMMARY

Chapter I

Lowland dipterocarp forest in Southeast Asia is one of the most diverse terrestrial ecosystems, both in terms of species richness and number of endemics. This type of forest is dominated by dipterocarp species, and dipterocarp wood plays a vital role in the tropical timber markets of Southeast Asian countries. Forest management by silvicultural treatment (selective logging) is used to maintain growing stock and a new regenerating, or remnant, tree population for the next cutting cycle. Silvicultural practices influence the genetic diversity and mating system of remnant trees.

Maintaining the genetic diversity of tree populations in logged forests is important for the long-term health and survival of tree populations, because genetic diversity is critical for both short-term evolutionary adaptation and the long-term health of species and communities (Templeton, 1995; Schaberg et al. 2003; White et al. 2007; Frankham et al. 2009). For instance, inbreeding depression has a negative effect on seed development in *Neobalanocarpus heimii* and *S. acuminate*, reducing the germination, growth and survival rates of seedlings (Naito et al. 2005, 2008). Moreover, reducing the number of reproductive trees by selective logging alters the genetic composition of reproductive trees, and likely has a negative effect on the genetic diversity of progeny. Understanding the effects of selective logging on genetic diversity and mating systems is very important for maintaining forest productivity, avoiding regeneration failure, and sustainable management of lowland dipterocarp forests.

Chapter II

This study was conducted in lowland of dipterocarp forests in the Sei Seruans block of the PT Sari Bumi Kusuma (PT SBK) concession, Central Kalimantan (00° 38'– 01° 07' S and 111° 54'–112° 26' E). This forest is managed under a selective logging system with a cutting cycle of 30 years. Commercial trees with minimum dbhs > 50 cm (TPTI) and > 40 cm (TPTJ) are harvested and small trees (± 25 individual/ha; dbh ≥ 20 cm) of commercial species are left for the next logging rotation. This study focused on *Shorea parvifolia*, an emergent dipterocarp species which lives on clay soil in lowland dipterocarp forests. This species is found on lower hill slopes and valleys at elevations of less than 800 m a.s.l. in Indonesia (Sumatra), Malaysia (Peninsular Malaysia), Singapore, and Thailand. The flowering and fruiting periods of *S. parvifolia* are irregular and it is pollinated by small insects such as thrips and small beetles. Samples were collected from four silvicultural systems: 1) primary forest (PF), 2) the first rotation of selective logging of trees > 50 cm in dbh (R1), 3) the second rotation of selective logging of trees > 50cm in dbh (R2), and 4) the second rotation of selective logging of trees > 40cm in dbh (R3). Samples were also collected from an enrichment planting area, where artificial regeneration is promoted by addition of commercial tree species in the logged forest.

Chapter III

Selective logging systems have been used to manage lowland dipterocarp forests and prevent the rapid decline of forest resources in Southeast Asia, but little is known about the impacts of selective logging on the genetic diversity of Southeast Asian rainforests. My research evaluated the effects of silvicultural systems with different cutting rotations and enrichment planting regimes on the genetic diversity of *Shorea parvifolia*, an abundant and ecologically important tree in Southeast Asian rainforests. My results showed that genetic diversity was not significantly different between primary forest and the other silvicultural systems in most respects; however, the proportion of private alleles is significantly different between them. Intensive second-rotation (R3) harvesting of individuals > 40 cm dbh resulted in a sizable

reduction in the number of reproductive trees and a dramatic decrease in the numbers of rare and private alleles, suggesting a negative impact on the genetic diversity of the remaining tree population. Enrichment planting with *S. parvifolia* in the logged forest improved some genetic parameters, significantly increasing the number of rare alleles in treatment R3 in particular. I conclude that the genetic diversity of logged tropical forests gradually decreases depending on the logging rotation time, especially with respect to sensitive genetic parameters such as the numbers of rare and private alleles, and that enrichment planting with native dipterocarps can maintain or even increase the genetic diversity of logged tropical forests in Southeast Asia.

Chapter IV

The main silvicultural management system used to maintain the lowland dipterocarp forest in Indonesia is selective logging. In brief, the cutting cycle of selective logging is 30 years, and mature commercial species, mainly dipterocarps, are removed solely based on the diameter at breast height (DBH) without consideration of their ecological characteristics, such as species composition and the reproductive ability of the remnant trees. Selective cutting reduces the density of reproductive trees, which may affect pollen dispersal and the mating system of remnant trees in the lowland dipterocarp forest. I evaluated the effect of the cutting rotation on the mating system, gene flow and genetic diversity of populations of *S. parvifiolia*. I compared three population types: primary forest (PF), first rotation (R1) and second rotation (R2) of selective cutting (the minimum size for selective cutting in R1 and R2 was > 50 cm dbh). Our result revealed that the selective logging with multi-rotation significantly impacted the differentiation (Φ_{ft}) of genetic diversity between pollen clouds ($P < 0.05$), although the estimate of average pollen dispersal distance (δ) was not statistically significantly different among silvicultural treatments. Multi-rotation selective cutting also reduced the outcrossing rate (t_m) ($P > 0.05$) and the effective of pollen donor in the logged forest. Moreover, the number of pollen donor in the plot was affected by the basal area of reproductive tree. These results suggest that reducing the number of reproductive trees by multi-rotation

cutting might increase biparental inbreeding by reducing the density of reproductive trees in selectively logged forests. I conclude that multiple rotations of selective cutting (dbh > 50 cm) as currently practiced may reduce high-quality timber reproduction and is not sustainable management of tropical forests of Southeast Asia.

Chapter V

Selective logging reduces the number of large trees and the basal area of the forest, with more than 50% total reduction in the basal area of trees in the LOA. Selective logging will also change the distribution and composition of certain species in logged lowland dipterocarp forests by reduction of the density of reproductive trees and the genetic diversity of remnant trees. Furthermore, the outcrossing rate after selective logging of trees > 50 cm dbh was still high, because the reproductive density of conspecific flowering trees was sufficient to maintain the mating system in the logged forest. This result suggested that selective logging of trees > 50 cm dbh had a slight impact on the genetic diversity and mating system of *S. parvifolia*. Finally, I considered the implications of my findings in light of published works about the impact of selective cutting on genetic diversity for the purpose of dipterocarp conservation. I found that enrichment planting with native species could improve environmental quality of logged areas from a genetic diversity perspective and that a combination of selective logging with a minimum diameter of 50 cm and enrichment planting could maintain diversity in logged forests to achieve sustainable forest management in the future.

CHAPTER 1
GENERAL INTRODUCTION

1.1 Tropical rainforests

The tropical rainforest of Southeast Asia is one of the world's most species-rich terrestrial ecosystems. It is high in endemic species and supports 18.7% of the world's plant biodiversity (Fig. 1-2) (Whitmore1998; Myers et al. 2000; Sodhi et al. 2004). The number of plant, mammal, bird, reptile, and amphibian species in Southeast Asia is 25,000 (endemics: 15,000), 328 (endemics: 115), 815 (endemics: 139), 431 (endemics: 268), and 226 (endemics: 179), respectively (Mittermeier et al. 2004; Sodhi et al. 2004). The high diversity of plant species in the tropical rainforest (especially in Borneo) results in above-ground biomass 60% higher (457.1 Mg ha^{-1}) than that of the Amazon rainforest (Slik et al. 2010), with 128 ± 13.4 Mg ha^{-1} of its the total above ground carbon in the primary forest (Saner et al. 2012).

High biodiversity is essential to ecosystem function and can contribute to ecosystem services, especially those related to human habitability and quality of life (MAE 2005; Diaz et al. 2006; Elmqvist et al. 2011). Ecosystem services include: 1) provisioning (e.g., food, water, fibers, and fuel), 2) regulation (e.g., of climate, water, and disease), 3) support (e.g., primary production and soil formation), and 4) cultural services (e.g., spiritual, aesthetic, recreational, scientific, and educational) (MAE 2005). For example, in terms of eco-tourism, the high biodiversity of the tropical rainforest offers excellent opportunities to attract conservation-minded tourists to see wild plants and animals, such as orangutans, in their natural habitats (Evans 2000, Wich et al. 2008 and 2011) (Figs. 1-2 and 1-3). Ecotourism has proven successful in

many tropical regions, such as Taman Negara and Endau-Rompin in Malaysia (Stecker 1996) and Ulu Temburong National Park in Brunei Darussalam (Ahmad 2014).

One of the tropical rainforest types in Southeast Asia is lowland dipterocarp forest, which is dominated by the family Dipterocarpaceae as the dominant climax tree types. Dipterocarpaceae includes 16 genera, of which 81.3 % are found in Asia, as are 470 of the 510 total species (Asthon 1982). In Indonesia, the highest numbers of dipterocarp species are found on Kalimantan and Sumatra Islands, which have 269 (58% endemicity) and 113 species (10% endemicity), respectively (Symington 2004).

Dipterocarp species account for 50–80% of emergent individuals and 40% of understory trees (Ashton 1982; Appanah1998), occupying 41.7% of the basal area and accounting for 15.6–21.9% of all trees in the lowland dipterocarp forest (Slik et al. 2003; Davies et al. 2005). In primary forests, the total wood volume was estimated at 212 m^3 ha^{-1}, of which dipterocarps account for 86.9% (Bischoff et al. 2005). Dipterocarps are primarily harvested to produce high-quality wood, while some dipterocarps, called tengkawang species, produce non-timber forest products (NTFP), such as kernels and fat, which are used in cosmetics (Blicher-Mathiesen 1994). Dipterocarp wood dominated the total global consumption of tropical hardwood species exported to some countries (ITTO 2012). As such, dipterocarps play a vital role in the tropical timber market in Southeast Asia (Appanah 1998).

Based on the level of disturbance, lowland dipterocarp forest is divided into two types: primary and secondary. Primary forest refers to untouched, pristine forest subjected to limited human intervention, which has retained high species diversity of both trees and animals (DeWalt et al. 2003). Secondary forests are forests regenerating through natural processes after significant removal or disturbance of the original vegetation by human or natural causes at a single point in time or over an extended period. Secondary forest displays major differences in forest structure and/or canopy species composition compared with pristine primary forest. Forest areas can also be categorized based on purpose and function; in Indonesia the three types are 1) protection forest, 2) conservation forest, and 3) production forest

(Forestry Law, article 6 UU-41, 1999), of which only the production forest is used for the production of timber and non-wood forest products.

The degradation of forests in Southeast Asia has been higher than in any major tropical region due to conversion to alternative land use, forest fires, and the over exploitation of wildlife (Sodhi et al. 2004). In Indonesia, the annual forest cover loss between 1990 and 2000 was 1.78 Mha $year^{-1}$ (Hansen et al. 2009). From 2000 to 2012, forest cover loss in Indonesia decreased to 1.21 Mha $year^{-1}$, with 38 % of the forest cover loss occurring within primary forest, especially on Kalimantan and Sumatra Islands, which are the main sites of lowland dipterocarp forests (Margono et al. 2014). This has the direct effect of decreasing plant biodiversity, and also increases the risk of extinction of dipterocarp species, which are essential to the tropical forests of Southeast Asia (Maycock et al.2012; IUCN 2015).

Forest ecosystems provide several services, including timber production, and wood is one of main products of lowland dipterocarp forests. Dipterocarp wood products dominate the overall global consumption of tropical hardwood species, and these woods are the main materials exported from Indonesia and Malaysia (ITTO 2012). Thus, dipterocarps play a vital role in the Southeast Asian tropical timber market (Appanah 1998). Despite being an important ecosystem service, timber production has a negative impact on biodiversity. Over the last 21 years (1990–2011), wood production in dipterocarp forests decreased by 80% (MoF 2012). In 2013, the total timber production from natural forest concessions in Indonesia was 3.67 M m^3, dominated by wood from lowland dipterocarp forests (MoF 2014). This indicates that dipterocarp species are still a major target for timber harvesting from forest concessions under the selective-logging silvicultural system, despite some dipterocarps being categorized as endangered species (Asthon 2004; Maycock et al. 2012; IUCN 2015). Therefore, management of lowland dipterocarp forests using selective logging is very important for the sustainability and conservation of dipterocarp species in the logged forests.

1.2 Managing tropical rainforests

The sustainable management of tropical rainforests is an important issue for conservation of biodiversity globally. Tropical rainforests in Southeast Asia have high species richness, a particularly complex multi-layered vertical structure, diverse age and species compositions, and the emergent forest canopy is dominated by commercially valuable dipterocarp species (Whitmore 1998; Slik et al. 2003). However, these forests have been degraded by large-scale commercial logging and other human activities. To prevent a rapid decline in ecologically and economically valuable forest resources, selective logging systems are used for timber extraction (Appanah 1998; Dawkins and Philip 1998; Putz et al. 2012) based on a polycyclic (multi-aged) approach in which the annual net forest productivity is equal to the annual harvesting (Appanah 1998). Logging regulations in dipterocarp forests generally allow the cutting of all trees of commercial species that exceed the minimum diameter. Extraction rates vary between 8 and 15 stems or 50 and 100 m^3 ha^{-1} (Sist et al. 2003a) when the goal is to maintain the proportion of dipterocarps in emergent canopy layers over time (Forestry Department of Peninsular Malaysia 1997; Shaharuddin 2011)

Each Southeast Asian country uses a selective logging system for sustainable forestry, such as the Malayan Uniform System (MUS) and Selective Management System (SMS) in Malaysia, and the Philippine Selective Logging System (PSLS) (Wyatt-Smith 1963). The goal of selective logging is to ensure a sufficient number of trees remain and regenerate after logging to achieve sustainable forest management (Appanah 1998). Selective logging is also a part of the maintenance and preservation plans for indigenous species in forest concessions (Sist et al. 2003a).

The MUS is used in lowland dipterocarp forest for the harvest of mature trees (diameter at breast height [dbh] $\geq$ 45 cm), and entails poisoning and girdling all defective relic and non-commercial species down to 5 cm dbh with a cutting cycle of 60–80 years (Wyatt-Smith 1963). The MUS was practiced during 1948 and late 1970 (Okuda et al. 2003), and the keys to its success are having an adequate number of seedlings and suitable maintenance (Wyatt-Smith 1963). The SMS is used on hillier terrain, where harvest is limited to commercial tree species above a certain size (45

cm dbh for non-dipterocarps and 50 cm for dipterocarp species) with a cutting cycle of 25–35 years (Okuda et al. 2003). This system retains a sufficient number of residual trees to be harvested in the next rotation 30 years later (Thang 1987).

In Indonesia, the tropical rainforest is primarily managed by two silviculture systems: the selective cutting system (Tebang Pilih Tanam Indonesia; TPTI) and a system combining selective cutting with strip planting (Tebang Pilih Tanam Jalur; TPTJ) (MoF 2009). In these systems, the minimum diameters of commercial trees allowed to be harvested are 50 cm and 40 cm, respectively, and the logging cycle is 30 years (MoF 2009). The annual cutting allowance is determined based on a forest inventory one year prior to cutting (Sist et al. 2003a). In principle, mature trees with commercial value are felled and extracted, and small trees are left to mature for the next harvest. This method is based on the assumption that the majority of small and medium trees remain after selective logging, allowing for regeneration (Fatawi and Mori 2000). TPTI leaves behind a small number of commercial trees (> 25 individuals ha^{-1}) with DBH > 20 cm after selective logging. If the number of remaining trees is insufficient, enrichment planting is conducted within three years of logging (Sist et al. 2003b). Similarly, in TPTJ, enrichment planting is conducted to promote regeneration after selective logging.

Several studies have been conducted to measure the impact of selective logging on basal area, finding a reduction from 51 to 57.5 % (Lee et al. 2002 and 2007). Meanwhile, the timber stock recovery for the same tree species or new species harvested in the second and third cuts were only 35% and 54%, respectively, of the timber volume extracted during the first harvest from primary forest (Putz et al. 2012). This suggests that timber stocks in the second and third rotations of selective logging are lower than those in the first rotation.

Selective logging removes mature commercial trees and at the same time may destroy non-commercial stems during cutting and wood extraction (Jenning et al. 2001). It can damage more than 50% of trees in the stand and affect the structure, species composition, and production of the logged-over area (LOA) (Pinard and Putz 1996; Hut and Ditzer 2001; Kartawinata et al. 2001; Sist et al. 2003a). On the other hand, the impacts of selective logging on the genetic diversity of forests are less

understood, such as whether high genetic diversity of important tree species can be maintained in logged forests. Decreasing the density of adult trees can result in inbreeding depression by increasing the chances of mating with genetically similar individuals. Therefore, it is important to maintain genetic diversity within a forest to avoid inbreeding, which may lead to decline of the forest ecosystem (Tsumura 2011).

Moreover, the increasing intensity of harvesting and shortening of harvest rotations may lead to large openings in the canopy, increase the distance among conspecific trees and reduce genetic diversity, especially in terms of allele loss (Lacerda et al. 2008). This suggests that tropical forest management must consider not only wood production, but also genetic diversity to maintain long-term productivity and sustainability of forests.

1.3 The importance of genetic diversity to sustainable forest management

Genetic diversity is defined as variation in the genetic composition of individuals within or among species, and it contributes to ecosystem diversity and function. Genetic diversity can be quantified at three levels: (1) among trees of a single species in individual populations or stands; (2) among geographical areas or sites within a single species; and (3) among species (Frankham et al. 2002; White et al. 2007). Genetic diversity is very important for the long-term survival of species, as species with low genetic diversity may not adapt to environmental changes and are more susceptible to extinction from disease and environmental change (Hawley et al. 2005; Ledig 1986; White et al. 2007; Schaberg et al. 2008) (Fig. 1-4).

Forest disturbances such as selective logging can cause a decrease in genetic diversity, which is associated with increased inbreeding and thus inbreeding depression. Such disturbance can result in reduced reproduction and decreased species diversity (Lowe et al. 2005; Frankham et al. 2009; Tsumura 2011) through genetic isolation of related individuals and consequently consanguineous mating. Inbreeding reduces the proportion of heterozygotes and increases the proportion of homozygotes due to inbreeding depression (Keller and Waller 2002). Inbreeding depression can reduce the fitness and viability of a population, which can contribute

to the extinction of that population (Keller and Waller 2002; Frankham et al. 2009; Angeloni et al.2011).

Thus, maintaining the genetic diversity of tree populations in forest ecosystems is an important aspect of sustainable forest management (Jennings et al. 2001). It is also vital to the long-term health and survival of populations because genetic diversity is critical for both short-term evolutionary adaptation and the long-term health of species and communities (Templeton 1995; Schaberg et al. 2003; White et al. 2007; Frankham et al. 2009). Today, genetic diversity is used as a forest certification indicator to gauge the effects of forest management practices (Prabhu et al. 1998; FSC 2010; ITTO 2005) because once lost, rich diversity is impossible to re-create in the short term (White et al. 2007).

Previous studies of the impacts of selective logging on some dipterocarp species focused on only the first logging rotation and found that responses varied among species. Selective logging caused loss of genetic diversity in some diptercarp species, such as *Shorea megistophylla* (Murawski et al. 1994), *S. curtisii* (Obayashi et al. 2002), *S. leprosula* (Ng et al. 2009), and *S. platyclados* (Javed et al. 2014). However, other studies reported that selective logging did not affect the mating system of *Dryobalanops aromatica* (Kitamura et al., 1994) or the genetic diversity of *S. ovalis* (Ng et al. 2009). Thus, the impacts of selective logging on genetic diversity among dipterocarps in LOA of forest may be species-specific.

Furthermore, small population size following selective logging leads to random genetic drift, which erodes the genetic diversity of remnant trees and their progeny and increases inbreeding (White et al. 2007). When inbreeding depression occurs, it has strong negative effects on seed development and germination, as well as seedling growth and survival (Naito et al. 2005, 2008), and these effects lead to decreasing forest productivity and promote failure of forest regeneration.

1.4 Overall aims of thesis

To evaluate the effects of different forest management practices and the number of logging rotations on the genetic diversity of *S. parvifolia*, I compared the genetic diversity of four forest types under different silvicultural systems: primary

forest (PF) as a reference population, the first rotation of selective logging (dbh > 50 cm) (R1), the second rotation of selective logging (dbh > 50 cm) (R2), and the second rotation of selective logging (dbh > 40 cm) (R3). The effect of enrichment planting on genetic diversity in the logged forest was investigated, as were the mating systems and gene flow in *S. parvifolia* populations among different silvicultural systems to better understand the effects of logging. Based on the results of this study, I discuss the impact of different silviculture systems on the genetic diversity and mating system of remnant populations of *S. parvifolia*.

In Chapter 2, I describe the study site in the Sari Bumi Kusuma concession, the silvicultural system used to manage lowland dipterocarp forests, and the target species (*Shorea parvifolia*). In Chapter 3, I discuss how different silvicultural systems and the number of logging rotations affect the genetic diversity of *S. parvifolia*. Chapter 4 includes discussion of how mating system patterns, gene flow, and biparental inbreeding in *S. parvifolia* are influenced by the number of logging rotations. Finally, in Chapter 5, I discuss the implications of selective logging on reducing genetic diversity and the importance of enrichment planting to improve both genetic diversity and timber stock in tropical secondary forests, and offer suggestions for genetic conservation of dipterocarps.

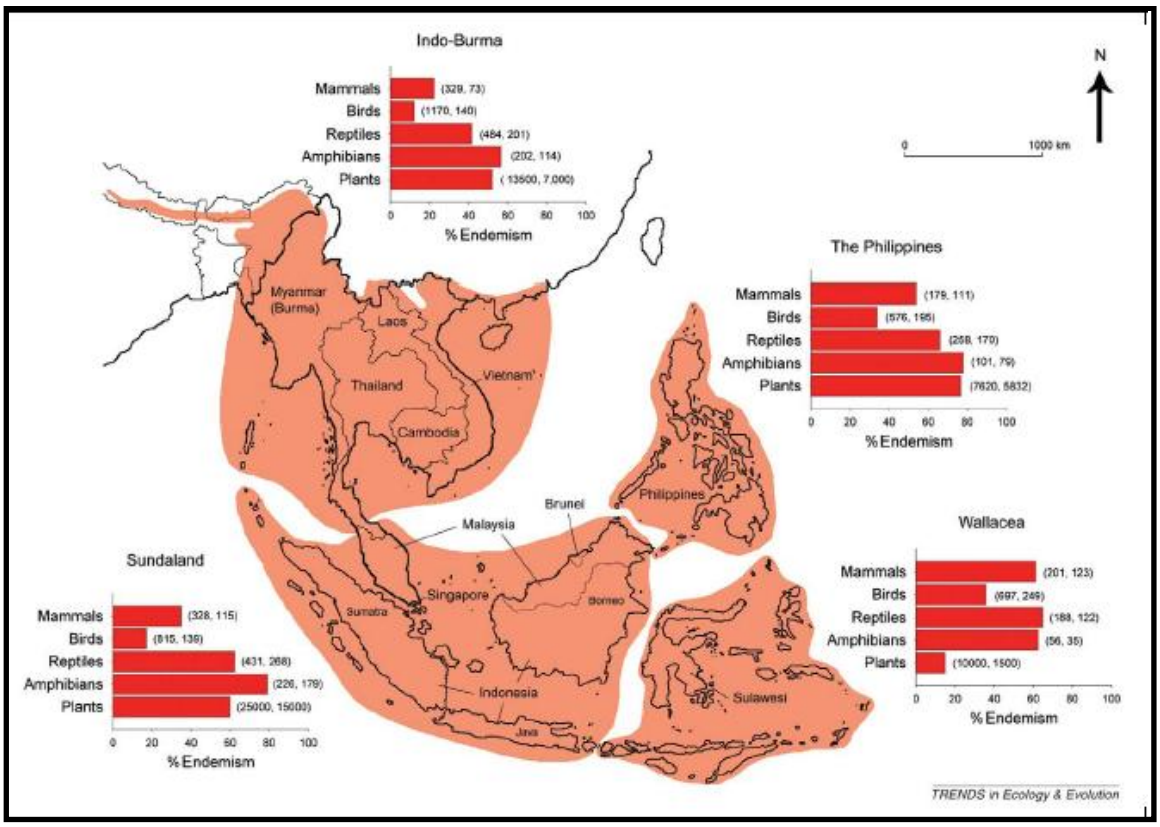
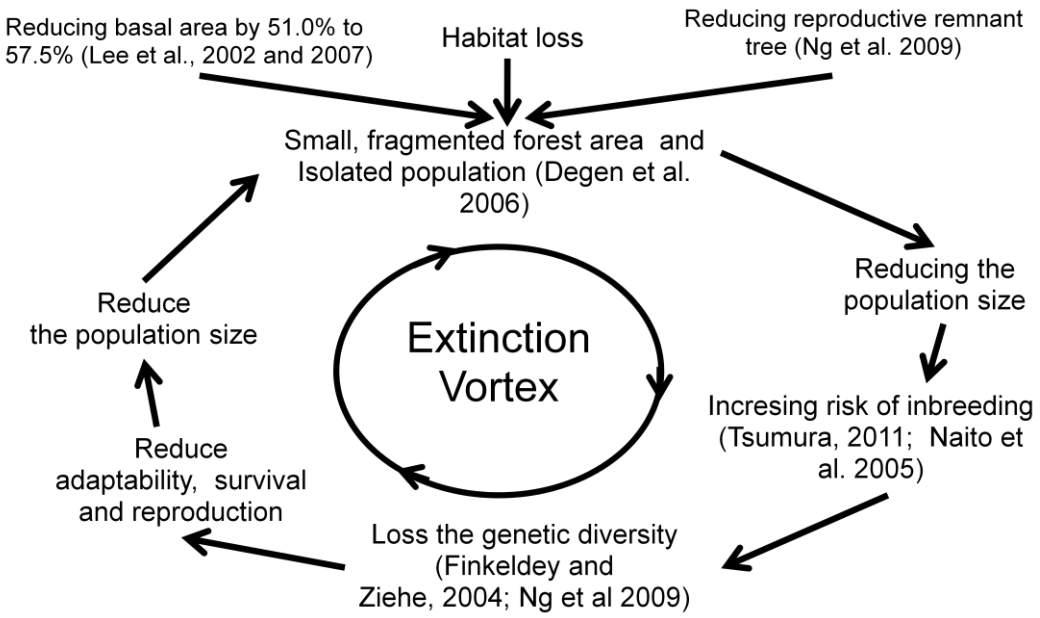


Fig 1-1 Species richness and endemism in Southeast Asia. The four biodiversity hotspots overlapping Southeast Asia are highlighted in red. Bars represent the percentage of species endemic to the respective hotspot. Numbers in parentheses represent total and endemic species known to science, respectively. The island of Borneo includes the political divisions of Brunei, Malaysia and Indonesia. The Indo-Burma hotspot includes part of Bhutan, Nepal, eastern India, southern China, as well as islands such as Hainan and the Andamans. Details of biodiversity hotspot boundaries, and numbers of total and endemic species within each hotspot were taken from Conservation International (Source: Sodhi et al. 2004; Conservation International 2004)

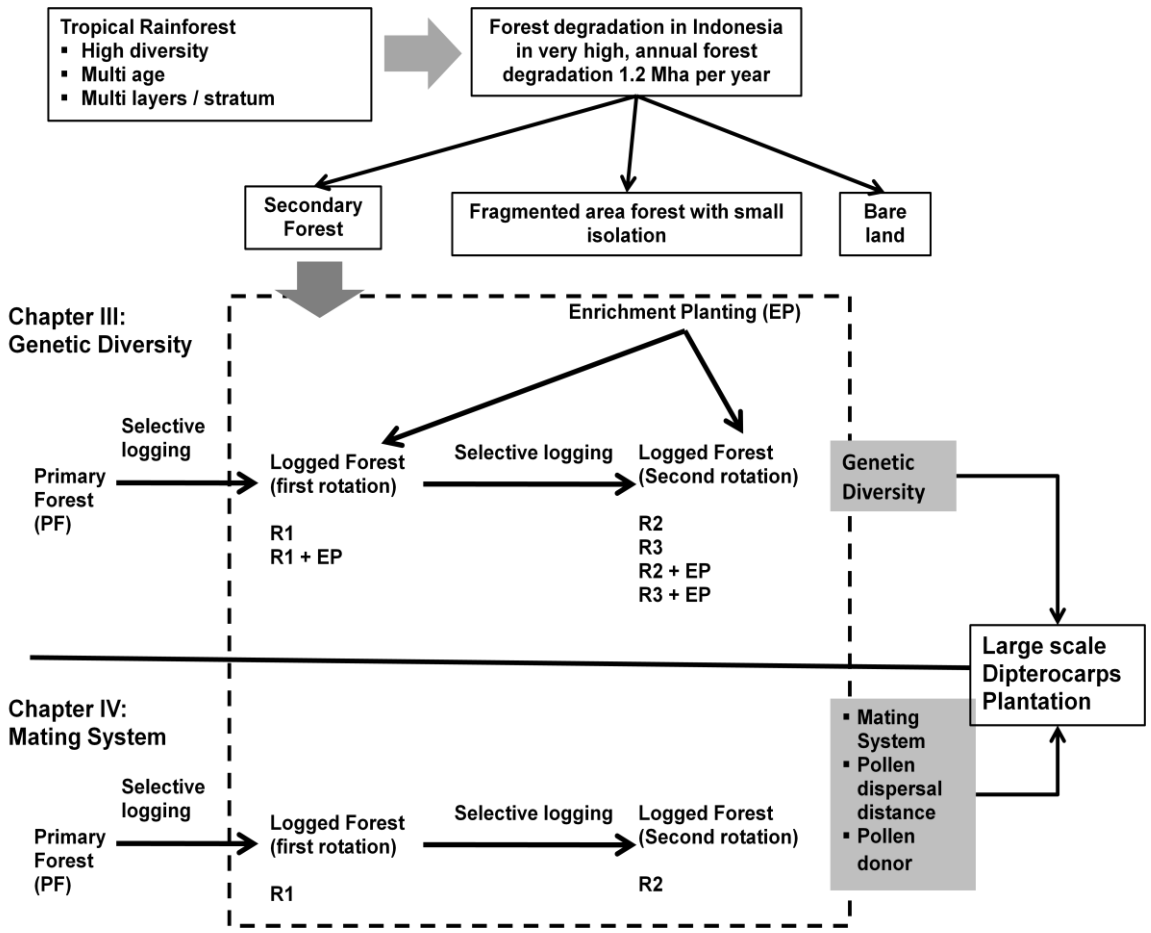
Fig 1-2. Illustration of lowland dipterocarp forest in Central Kalimantan, Indonesia

Fig 1-3. An intangible value of high biodiversity of tropical rain forest



Source: Source: Frankham et al. 2009, modified

Fig. 1-4. The extinction vortex. This describes the possible interactions between human impacts, inbreeding, loss of genetic diversity and demographic instability in a downward spiral towards extinction



Note:
PF : Primary forest
R1 : First Rotation with limit dbh > 50 cm
R2: Second Rotation with limit dbh for cutting > 50 cm
R3: Second Rotation with limit dbh for cutting > 40 cm

Fig. 1-5 The research framework

CHAPTER II
STUDY SITE AND PLANT MATERIAL

2.1 Study site description

This study was conducted in the natural forest at Sei Seruan block of PT Sari Bumi Kusuma (PT SBK) concession, Central Borneo (00° 38'– 01° 07' S and 111° 54'–112° 26' E) (Fig. 2-1). PT SBK is one of the lowland dipterocarp forests in Indonesia, because 90% elevation of area is under 400 m a.s.l (above sea level) (Anonymous 2010). PT SBK received the first concession in 1978 located in sites that are the Sei Seruyan (Central Kalimantan) and Sei Jelai-Sei Delang (West Kalimantan) (Forestry Agreement (FA) No:FA/N/016/III/1978 and Decree No 599/Kpts/Um/11/1978). Thought Decree of the Minister of Forestry No: 201/Kpts-II/1998, the total area of PT SBK in Sei-Seruyan is 147,600 ha, managed under two silviculture systems, namely, selective cutting (Tebang Pilih Tanam Indonesia ;TPTI) and selective cutting and strip planting (Tebang Pilih Tanam Jalur;TPTJ).

The climate in PT SBK is categorized as type A, very wet region with the number of wets month more than 10.5 months (Scmidt and Ferguson 1951). The mean annual rainfall is 3,882 mm $year^{-1}$ and the number of rainy days varies from 94 to 189 days (Anonymous 2010). Therefore, the soil type is Ultisol, which is strongly weathered and acidic due to leaching (Chesworth 2008). Ultisol is a mineral soil with a B_2 horizon that contains 20% more clay than the upper B_1 layer.

2.2 Selective logging system in Indonesia

The main silvicultural system adopted to manage tropical rain forest is selective logging systems, which are usually based on limit diameters and phenotypic assessments of trees and the large tree with favorable traits are preferable harvested (Finkeldey 2011). In Indonesia, the main silvicultural management systems developed on the lowland dipterocarps forest include selective logging (Tebang Pilih Tanam Indonesia; TPTI) and selective logging with strip planting (Tebang Pilih Tanam Jalur; TPTJ) (Ministry of Forestry 2009). In brief, the logging cycle of these systems is 30 years, and mature commercial species, mainly dipterocarps, are logged based on the diameter at breast height (dbh) without consideration of their abundance (Lee et al. 2002) or any potential effects on the genetic diversity of the remaining trees to the next generation (Ng et al. 2009; Finkelday 2011).

TPTI is applied on the polycyclic (multi aged) forest and can harvest the commercial tree with dbh more than 50 cm. To maintain the forest productivity in the next rotation, this system relies on leaving the commercial and potential trees (± 25 individual/ha) with dbh is 20 cm and above after selective logging. It is assumed that diameter and volume increment of remnant commercial trees are 1 cm $years^{-1}$ and 1 m^3 ha^{-1} per year, so the remnant tree could be as target harvested on the next cutting cycle (van Gardingen et al. 2003). The productivity by TPTI is relys on natural regeneration, while enrichment planting will be conducted if the number of regeneration is not sufficient on TPTI area (Fig. 2-2). Forest maintenance is also conducted to increase the productivity of the remnant commercial trees thought the liberation cutting including clearing the understory vegetation (all woody climber and non-commercial sapling) every two years until six years after selective logging (Sist et al 2003; MoF 2009). However, an annual increment of the diameter of commercial tree in the logged over forest (LOA) is less than 1 cm $year^{-1}$ (Pelissier et al. 1998; Sist and Nguyen-The 2002; Bischoff et al. 2005; Yamada et al. 2013). It suggested that 30 years for cutting rotation is not enough to recover on wood production before logging. TPTJ is also applied on the polycyclic (multi-aged) forest and can harvest the commercial trees with dbh more than 40 cm. The regeneration in

TPTJ is conducted by artificial enrichment plating using strip-planting technique (Fig. 2-3) to maintain the high productivity of the forests.

2.3 Enrichment planting

Enrichment planting is artificial regeneration by adding trees of usuful species in the logged forest that is inadequate on the number of offspring to increase the density commercial tree and to timber productivity (Kettle 2010; Lamb 2014). In the secondary lowland dipterocarp forest under TPTI, an enrichment planting will be conducted if the number the wood stock of commercial species, especially dipterocarp species, is insufficient because the survival rate of commercial species is very poor due to destructive logging methods (Appanah 1998). The advantage of enrichment planting using native species in the logged forest using strip planting is to increase biodiversity secondary (Ashton et al. 2001; Kettle 2010) and also to maintain productivity and ecological services (Millet et al. 2013). On the other hand, enrichment planting has also possibility to change the genetic structures in the later generations of remnant trees due to gene flow from planted trees, if it is used an unknown anda limit number of genetic variation for planting (Finkeldey and Ziehe 2004).

To maintain the genetic diversity of logged forest, the material for enrichment planting, both seeds and wildlings should be collected from high number of non-related parent trees to ensure the availability of quality of germplasm of dipterocarps (Kettle 2010; Riina et al. 2014). The enrichment planting on TPTJ silvicultural system is conducted using dipterocarps species such as *S. parvifolia, S. leprosula, S. johorensis* and others, which might increase the standing stock of logged forests and conserve dipterocarp species and also have a role of *ex-situ* conservation. Likewise, dipterocarp species for enrichment planting will be well adapted to the local environment and therefore effective tomaintain the genetic diversity and forest productivity in the dipterocarp species.

The space of enrichment planting is applied (2.5 x 20 m) at 200 individual/ha using the native species, especially dipterocarps species (Fig. 2-4) (Na'iem and Faridah 2006; Soekotjo 2009). The strip planting is 3.0 m width and thus the

undisturbed area is existing 17 m width, or 85% of total space is remained to maintain and even increase the ecosystem biodiversity, while the gap opening of 3 m line (15% of total space) is implemented to allow light entering planting lines optimally (Na'iem and Faridah 2006; Soekotjo 2009). The material for enrichment planting is collected from seeds and wildlings from neighbor areas. The maintenance of material for enrichment planting is 9-12 months in the nursery.

2.4 Plant material

Family Dipterocarpaceae is distributed in the tropical region of Africa, South America and Asia (Fig. 2-5). The Dipterocarpaceae comprises 510 species in 17 genera (Ashton, 1982), with the five largest genera are *Shorea* (196 species), *Hopea* (104 species), *Dipterocarpus* (70 species), and *Vatica* (65 species) (Ashton 2004). In Asia, dipterocarps have could be found in the lowland and hill land, ranging elevation from 0 to 1,200 meters in elevation, where the large tree will mainly occupy the emergent stratum, while seedling, sapling and small tree could survive in the understory (Ashton 1988; Zipperlen and Press 1996, Kobayashi et al. 2001, Phillips et al. 2002).

The number of dipterocarp species in Asia region is the largest than that of the other regions, 13 genera and 470 species (Aston 1982; Maury-Lechon and Curtet 1998; Symington 2004), where the Borneo Island is the most species abundant region in Asia, with 13 genera and 269 species (Symington 2004). Peninsular Malaysia has 14 genera with 160 species, Sumatra Island has 12 genera with 113 species and fewer genera are found in the Philippine, Thailand, Myanmar and India (Symington 2004). Meanwhile, in Java Island the number is only recorded 5 genera and 10 species, although the location is very close with Sumatra and Borneo Island (Asthon 1982; Symington 2004).On the other hand, dipterocarp species is also found in the Sulawesi, Maluku and New Guinea (Symington 2004).

Shorea parvifolia is one of the member family Dipterocarpaceaeand the most common canopy-emergent tree species in the lowland tropical rainforest with short and sharp buttresses and well-shaped tall bole (Appanah and Weinland 1996) (Fig. 2-6a). Stipules is broadly ovate, obtuse and caduceus, while leaves are thinly

coriaceous, veins glabrous or sparsely scabrids-pubescent below (Soepadmo et al. 2004) (Fig. 2-6b). *Shorea parvifolia* is widely distributed species occurring in southern Thailand (Pattani), Malay Peninsula, Sumatra and Borneo (Ashton, 1982; Appanah and Weinland, 1993; Newman et al. 1996; Moury-Lechon and Curtet1998; Symington 2004). It can be found on clay soil in lowland dipterocarp forests, lower hill slopes and valleys below 800 m a.s.l. (Ashton 1982; Appanah and Weinland 1993;Newman et al. 1996). The species is shade-tolerant (Phillips et al. 2002) and one of the more economically important timber tree species in the Dipterocarpaceae which is a member of the red meranti group (Symington 1943). The timber of *S. parvifolia* is used to make furniture, veneers, plywood and other products.This species is categorized as endangered in Southeast Asia (Ashton 1998; Phillips et al. 2002).

2.4.2 Reproductive biology of *S. parvifolia*

Because *S. parvifolia* is a member of Dipterocarpaceae, the flowering and fruiting is irregular, 1–6 yr, and only extends over a short time (Ashton et al. 1988; Appanah and Weinland, 1993; Numata et al. 2003). The usual time of mass flowering varied among location, where the general flowering season in Borneo starts from September to January (Brearley et al. 2007), whereas in Peninsular Malaysia starts both spring and autumn flowerings of *S. parvifolia* can be seen (Ashton et al. 1988; Numata et al. 2012). In the genus *Shorea*, the first species to flower sequence is *S. bracteolata* followed by *S. macroptera* and the last species to flower were *S. kunstlerii*. Meanwhilethe flowering of *S. parvifolia* is in the middle of flowering sequence within the period of 2-3 weeks flowering (Asthon et al. 1988; Brearley et al. 2007).

The fruit of *S. parvifolia* is pollinated by small insects such as thrips and small beetles (Appanah and Chan 1981; Bawa 1998; Sakai et al. 1999). Only the adult tree of *S. parvifolia*, diameter exceed 30 cm could contribute as pollen donor on the flowering season (Tani et al. 2009). The fruit is become mature about 16 weeks after first flowering and come down at the same time with other red meranti species, i.e. *S. acuminata* and *S. leprosula* (Asthon et al. 1988; Appanah and Weinland 1996). and will be dispersed by wind (Ashton 1982; Bawa 1998).

The seed is categorized as recalcitrant seeds and could not storable for long time (Otsamo et al. 1998; Sasaki 1980; Symingthon 2004), so the seed is lack as soil seed bank (Aston 1982). The seed of *S. parvifolia* is winged and dispersed by wind or gravity (fruits with wing-like sepals, see Fig. 2-6c; Asthon 1982; Bawa 1998; Curran and Leighton 2000; Seidler and Plotkin 2006; Turner et al. 1997), but it was dispersed by the sort distance (Takeuchi et al. 2004) (Fig. 2-6c). The seedling of *S. parvifolia* is generally shade-tolerant and can persist in the forest floor and under canopy for several years, though the increasing opening/light is favorable for satisfactory years and growth (Asthon 1998). The average annual diameter increment of *S.parvifolia* is range 1.17 - 1.2 cm, so the rotation of 30 years for commercial sawlogs is attainable in the good sites (Appanah and Weinland, 1993).

Table 2-1 Comparison between TPTI and TPTJ silvicultural systems in Indonesia

	Selective Logging (TPTI)	**Selective Logging with Strip Planting (TPTJ)**
Harvest Method	Selective Logging	Selective Logging
Limit Diameter	> 50 cm	> 40 cm
Regeneration/ enrichment planting	If the area is lack of regeneration number	Strip planting with native species (100-200 individual/ha)
Maintenance	less	Intensive
Growth of Residual Stand Diameter		
- Residual trees*****	0.2-0.3 cm per year	0.2-0.3 cm per year
- Planted trees	-	> 1.7 cm per years
Rotation / cutting cycling	30 years	30 years
First Rotation (N/ha)	10-15 trees (natural stand)	-
Second Rotation	8-12 trees (natural stand)	10-12 trees (natural stand) 80 -120 trees (planted stand)

Source: Ministry of Forestry (2009) Decree no: 11/Menhut-II/2009: Silvicultural System in The Natural Forest productions. Ministry od Forestry. Jakarta Indonesia

***** = Pelissier et al. (1998); Sist and Nguyen-The (2002) and Bischoff et al. (2005)

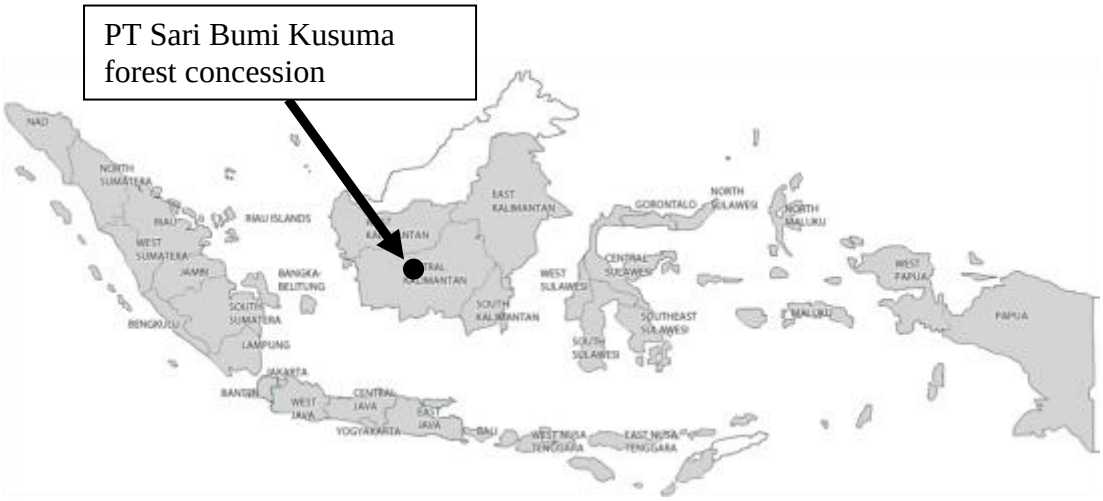


Fig. 2-1 Studied forest site, PT Sari Bumi Kusuma forest concession, Central Kalimantan in Indonesia

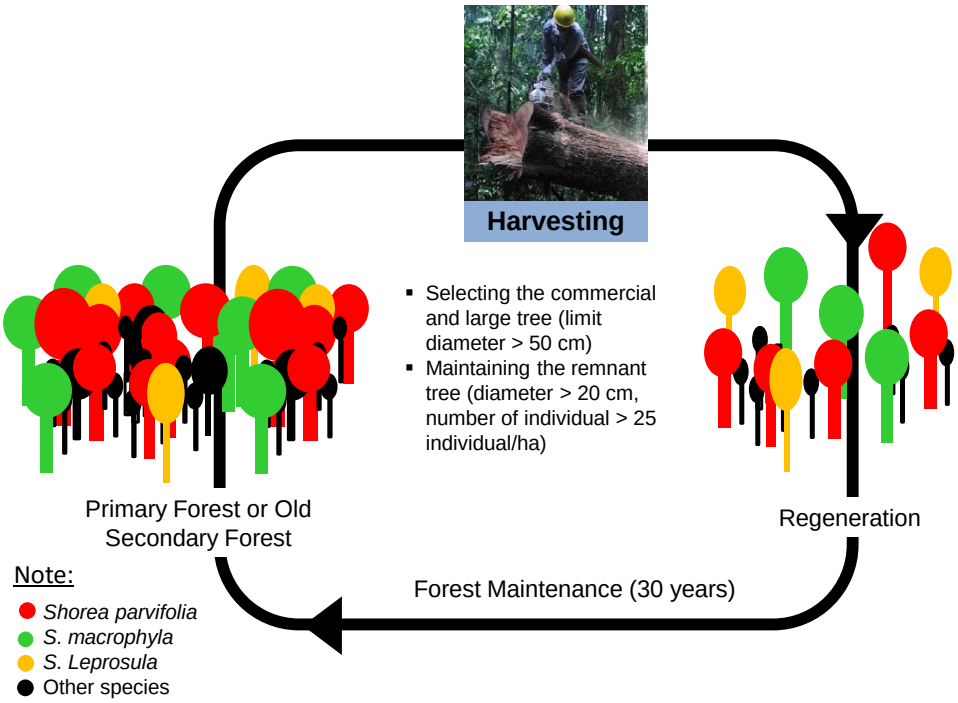


Fig. 2-2. Selective logging system, in local terms known as Tebang PilihTanam Indonesia, TPTI

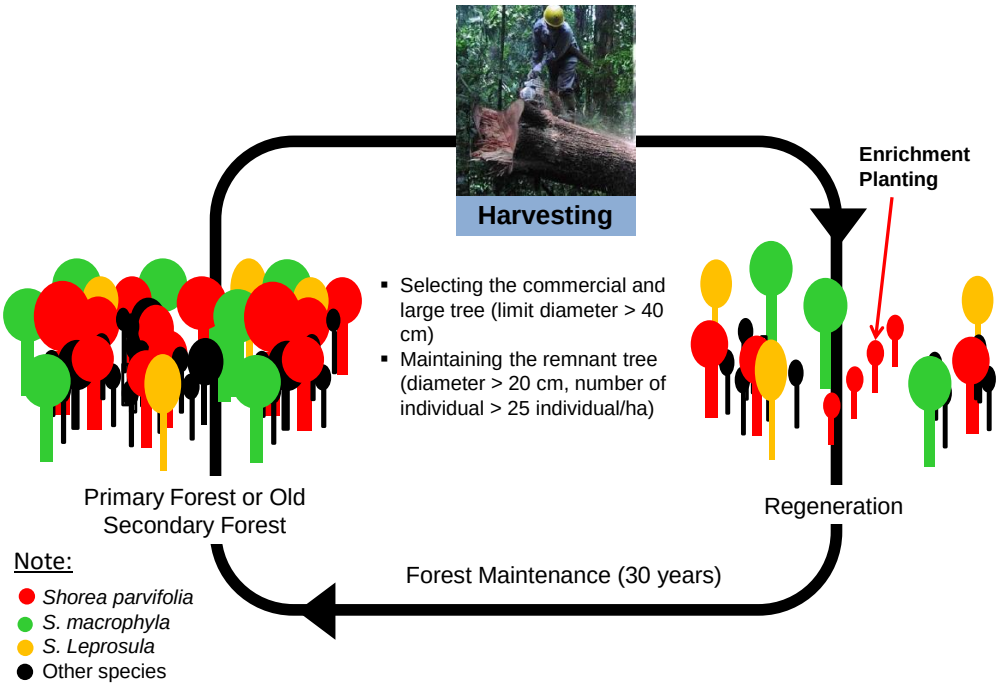
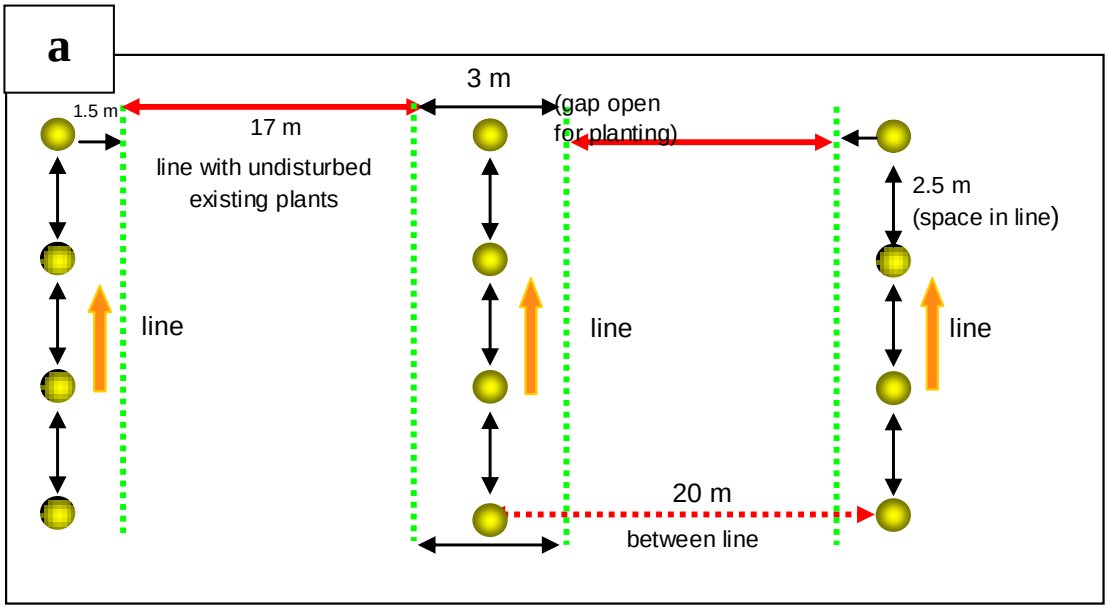


Fig. 2-3. Selective logging and strip planting system, in local terms known as Tebang Pilih Tanam Jalur, TPTJ



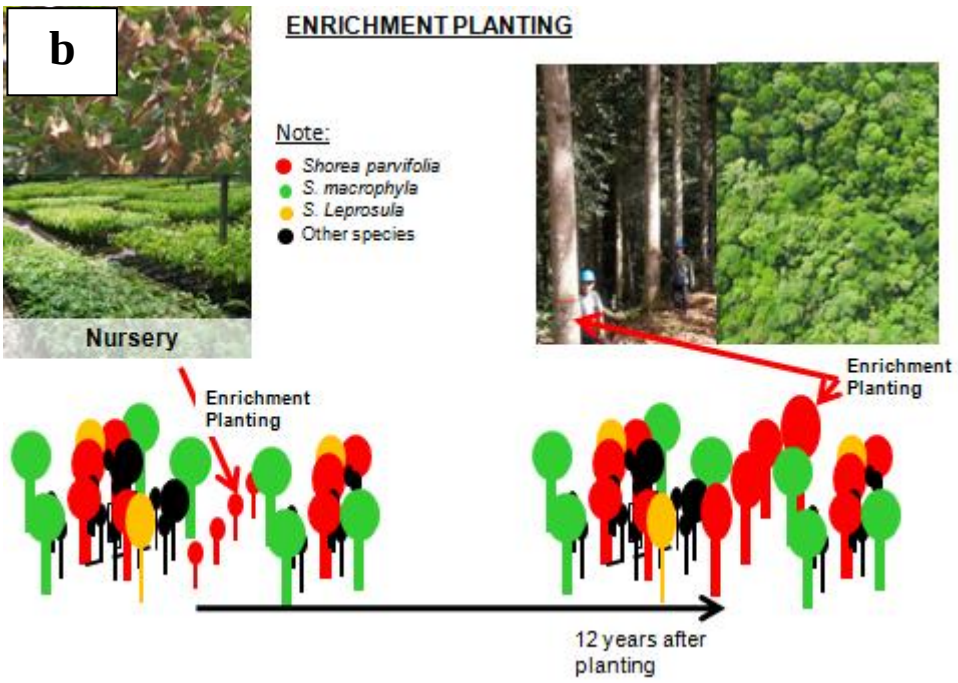


Fig. 2-4 The design and establishment process of enrichment planting

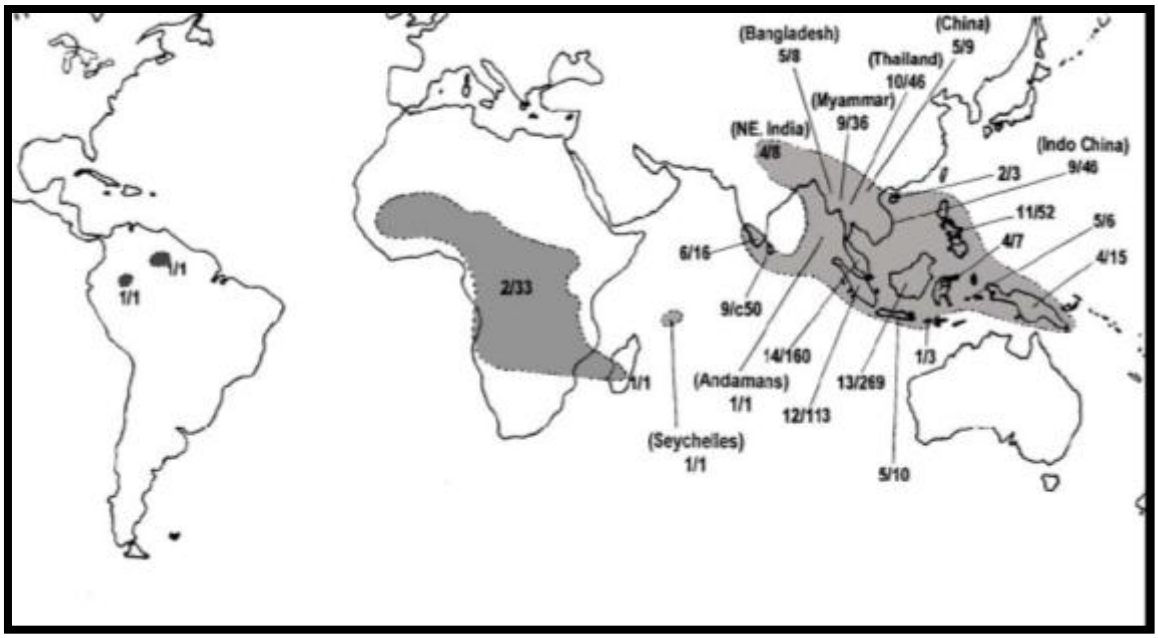


Fig. 2-5 Distribution of species in Dipterocarpaceae (Symington 2004)

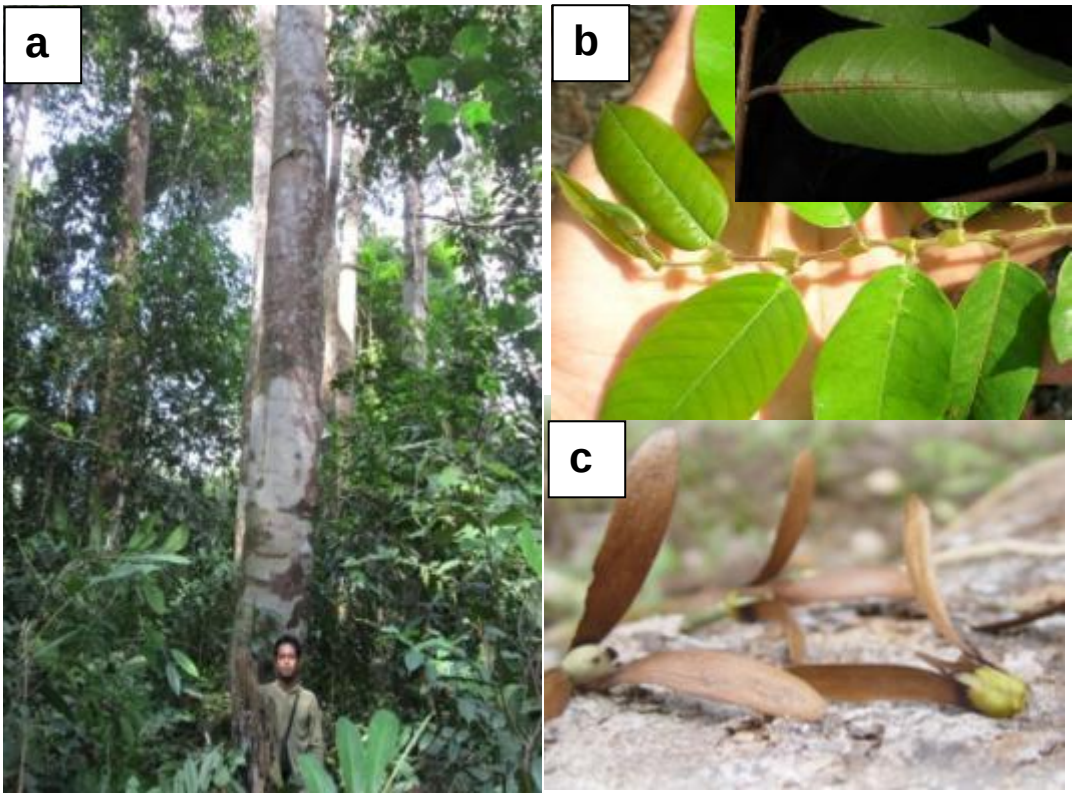


Fig. 2-6 Morphological characteristics of *S. parvifolia*: (a) mature tree, (b) leaf characteristic, and (c) mature fruit

CHAPTER III.

EFFECTS OF DIFFERENT SILVICULTURAL SYSTEMS ON THE GENETIC DIVERSITY OF *Shorea parvifolia* POPULATIONS IN THE TROPICAL RAINFOREST, CENTRAL KALIMANTAN, INDONESIA

Keywords: *Shorea parvifolia*, genetic diversity, selective logging, rotation, enrichment planting

3.1 Introduction

Tropical forests in Kalimantan contain a high diversity of tree species and dominated by dipterocarp as commercial and valuable tree species. The commercial tree in the tropical rainforest is managed using selective logging which will harvest the large and commercial trees (limit diameter for cutting > 40 cm or 50 cm) without taking into account their abundance (Lee et al. 2002) or any potential effects on the genetic diversity of the remaining trees (Ng et al. 2009). Selective logging will make fragmentation of forest area and reduce the large tree / reproductive tree where the forest fragmentation forest due to selective logging was dependent on the felling intensity where the high intensity of logging is more fragmented area than medium or low of logging intensity (Sist et al. 1998). High intensity of logging was high probability loss genetic diversity of remnant tree in the secondary forest. However,

silvicultural management practices entailing logging rotations of several decades may affect the genetic diversity of logged forests (Finkeldey and Ziehe 2004).

The impacts of selective cutting on forest genetic diversity are not well understood. For example, it is largely unknown whether the genetic diversity of important tree species is maintained in logged forests (Obayashi et al. 2002). Generally, large commercial trees are removed by selective logging, and this could alter the genetic diversity of the species harvested through genetic drift and bottleneck effects. Furthermore, decreasing the density of flowering conspecific trees would be expected to increase the rate of selfing. Thus, after selective logging, mating between related individuals in the logged forest can cause inbreeding depression due to increased homozygosity and/or frequencies of recessive deleterious alleles (Charlesworth and Charlesworth 1987). It is therefore important to maintain the genetic diversity of forests in order to avoid inbreeding and its consequences (Tsumura 2011). Inbreeding depression can result in regeneration failure in the early stages of life (Wang et al. 1999; Naito et al. 2005; White et al. 2007) because inbreeding can cause reduced embryo viability and seedling survival (Charlesworth and Charlesworth 1987; Naito et al. 2005).

Maintaining the genetic diversity of tree populations in forest ecosystems is important for the long-term health and survival of these populations because genetic diversity is critical both for short-term evolutionary adaptation to environmental change and for the long-term health of species and communities (Templeton 1995; Schaberg et al. 2003). Genetic diversity is used as a forest certification indicator with which to gauge the effects of forest management practices (Prabhu et al. 1998; ITTO 2005; FSC 2010) as a way of achieving sustainable forest management. However, there has been very little research on the effect of genetic diversity on forest management in second-rotation selective cutting and enrichment planting systems in dipterocarp forests. Previous studies on the impacts of selective dipterocarp logging on genetic diversity focused only on the first logging rotation, and results varied among species. Selective logging is known to reduce genetic diversity in some dipterocarp species, such as *Shorea megistophylla* (Murawski et al. 1994), *S. curtisii* (Obayashi et al. 2002), *S. leprosula* (Ng et al. 2009), and *S. platyclados* (Javed et al.

2014). On the other hand, selective logging showed no effect on the mating system of *Dryobalanops aromatica* (Kitamura et al. 1994) or on genetic diversity in *S. ovalis* (Ng et al. 2009). The impacts of selective logging on dipterocarp genetic diversity thus probably depend on unique species characteristics, such as the mating system, main pollinator, seed dispersal system, and whether or not the species is apomictic.

To monitor genetic diversity in the short term, e.g. to look at the impacts of forest management practices and fragmentation, it is best to use genetic markers such as microsatellites because they are highly polymorphic and informative. They are also very useful in assessing certain genetic parameters that are highly sensitive to human disturbance, e.g. the allelic diversity of rare, private alleles, or allelic richness (Petit et al. 1998). Estimation of allelic diversity using microsatellite markers can allow us to understand changes in, and the dynamics of genetic diversity in populations.

Shorea parvifolia is one of the most common tree species in lowland tropical rainforests. This fast-growing species is endangered in Southeast Asia (Ashton 1998; Phillips et al. 2002). It can be found on clay soil in lowland dipterocarp forests on lower hill slopes and valleys below 800 m a.s.l. (Ashton 1982; Appanah and Weinland 1993; Newman et al. 1996). The species is shade-tolerant (Phillips et al. 2002) and is one of the more economically important timber tree species in the Dipterocarpaceae. A member of the red meranti group (Symington 1943), its wood is used to make furniture, veneers, plywood, and other products. Its flowering and fruiting are irregular (Appanah and Weinland 1993, Numata et al. 2003), and it is pollinated by small insects such as thrips and small beetles (Sakai et al. 1999). The average annual diameter increment in *S. parvifolia* is in the range 1.17–1.20 cm, and therefore a rotation of 30 years for the production of commercial sawlogs is considered to be feasible at good sites (Appanah and Weinland 1993). Understanding the effects of selective logging on the genetic diversity of *S. parvifolia* is important for both the maintenance of genetic diversity and the sustainable management of tropical rainforests.

Here, the objectives of research were to evaluate the effects of different silvicultural systems and the number of logging rotations on the genetic diversity of *S. parvifolia*. I compared four forests managed under different silvicultural systems: 1) primary forest, as a reference population, 2) the first rotation of selective logging (dbh > 50 cm), 3) the second rotation of selective logging (dbh > 50 cm), and 4) the second rotation of selective logging, in which smaller trees (dbh > 40 cm) were also harvested. The effect of enrichment planting, an artificial regeneration system in which dipterocarp species are planted in the logged forest, on genetic diversity in this forest was also investigated.

3.2 Materials and methods

3.2.1 Study sites and sample collection

I established study plots (populations) in four silvicultural systems: 1) primary forest (PF), 2) the first rotation of selective logging of trees > 50 cm in dbh (R1), 3) the second rotation of selective logging of trees > 50cm in dbh (R2), and 4) the second rotation of selective logging of trees > 40 cm in dbh (R3) at Sari Bumi Kusuma forest concession in Central Kalimantan, Indonesia. Sample collection at R1, R2 and R3 plots was conducted during July-September, 2013, two years after the last cutting. Mass flowering had occurred in this area in 2012 after selective logging. Each silvicultural system treatment was assessed at five plots, and each enrichment planting treatment was assessed at three plots; a random sampling method design was used and the average number of samples per plot was 19.4 individuals (Table 3-1). I collected fresh leaf tissue from a total of 427 small *S. parvifolia* seedlings derived from the flowering of 2012, from 23 plots. Primary forest comprised undisturbed lowland tropical rainforest with high species diversity, dominated by Dipterocarpaceae. R1 and R2 forests had been managed by selective logging (TPTI) of trees > 50 cm in dbh, which had occurred, respectively, once and twice before. R3 was in the second rotation of selective logging of trees > 40 cm in dbh by selective logging and strip planting (TPTJ). I also collected fresh leaf tissue from artificially enrichment-planted individuals (EP) to assess the resulting changes in the genetic diversity of the logged forest. Enrichment planting is an artificial regeneration

system entailing the strip planting of dipterocarp seedlings at densities of 100 to 200 seedlings ha^{-1} (Ministry of Forestry 2009); the seeds and seedlings used for enrichment planting were collected randomly from primary forest and logged forest within the forest concession area. EP was carried out in the logged forest, where the main objective of EP was to add to the stock of commercial trees available for the next rotation. EP can also include the introduction of dipterocarp species that have high growth rates, and/or produce useful materials such as timber and illipe nut, into a logged forest where those species did not previously grow, in order to increase the productivity of the logged forest for the next rotation. In this logged forest, *S. parvifolia* was the species planted.

Distances between sampled individuals within the plots ranged from 5 to 30 m, and distances between plots exceeded 2.5 km. The distribution of all samples was mapped using a Garmin 76 CSx handheld GPS (Fig. 3-1). The reference natural populations used to evaluate the genetic structure within and among the study populations have been used in a previous study (Ohtani et al. unpublished data); they include two populations each from Central Borneo, East Borneo and Peninsular Malaysia and three populations from Sumatra, and the number of individuals in each population ranged from 12 to 57.

3.2.2 DNA extraction and genotyping

Total DNA was extracted from all samples using a DNeasy Plant Mini Kit (Qiagen). After initially screening 33 loci, I determined the genotype of each sample using 12 expressed sequence tags (EST) and 5 genomic microsatellite loci developed in *S. leprosula*: *Tum0303D01*, *Tum0305A11*, *Tum0308A08*, *Tum0309D20*, *Tum1402P02*, *Tum1405J22*, *Tum1407K20*, *Tum1601J23*, *Tum1602F14*, *Tum1602G19*, *Tum1602R17*, *Tum1610H08* (Ohtani et al. 2012), *SleE14f*, *Sle079*, *Sle111a*, *Sle216*, and *Sle267* (Lee et al. 2004).

I carried out polymerase chain reaction (PCR) amplifications in 8-μL reaction solutions containing 1 μL of DNA (5 $ng\mu L^{-1}$), 4 μL of multiplex kit (QIAGEN) (Table 3-S1), 0.2 μM of each primer, and 2 μL of sterile distilled water, using a GeneAmp 9700 (Applied Biosystems). PCR amplification was performed with an

initial denaturation at 95ºC for 15 min, followed by 32 cycles of 30 s at 94ºC, annealing at 50ºC or 56ºC (depending on primer pair; Table 3-S1) for 90 and 72ºC for 60 s, and a final extension step at 60ºC for 30 min. The PCR products were genotyped using a 3130 Genetic Analyzer (Applied Biosystems) with a mixture containing 0.2 μL of calibrated internal size standard (GeneScan 400HDROX; Applied Biosystems) and 9 μL of Hi-Di for each sample. The genotypes of individuals were then determined using Geneious 7.1 software (Biomatters Ltd., Auckland). Finally, I used Micro-Checker (Ver. 2.2.3) to test for null alleles and to assess the conformance of loci to Hardy–Weinberg equilibrium expectations (Van Oosterhout et al. 2004). Loci with large numbers of null alleles were removed from further analysis.

3.2.3 Statistical analysis

Genetic diversity

I estimated several population genetic parameters to compare genetic diversity in the four silvicultural systems: the number of alleles per locus (N_a), the effective number of alleles (N_e) (Kimura and Crow 1964), Shannon's index (I), and the observed and expected heterozygosity (H_e), using GenAlEx 6.5 (Peakall and Smouse 2012). Allelic richness (R_s) and private allele richness were estimated using the HP-Rare 1.1 software package (Kalinowski 2005), correcting for sample size (n) in each population using the rarefaction method, which fixes n as the smallest number of individuals among all loci analyzed. I used pooled data from five plots in each silvicultural system because the numbers of individuals in some plots were small, especially in R3. I calculated the coefficient of inbreeding (F_{IS}) for each silvicultural system (Nei 1977), and the statistical significance of the F_{IS} value was assessed by randomized tests using GenAlEx 6.5. Significant differences in genetic parameters among silvicultural systems were analyzed using one-way analysis of variance (ANOVA), then multiple comparisons among the means of each silvicultural system were analyzed at $P < 0.05$ by Tukey's HSD test using SPSS for Windows version 16.0 (SPSS, Inc., Chicago, IL).

I also calculated gene diversity partitioning at each level using coefficients of gene differentiation based on Hedrick's standardization (G'_{ST}) among populations (Hedrick 2005). I conducted a bottleneck test for each of the four populations to understand changes in past population size. This analysis was performed under the infinite allele model and the two-phase model using two different tests: the sign test and the Wilcoxon signed-ranks test, each with 1000 runs in BOTTLENECK 1.2.02 (Cornuet and Luikart 1996; Piry et al. 1999). I calculated the *M*-ratio using Arlequin3.5.2 (Excoffier and Lischer 2010), which examines the ratio of the number of alleles and the allele range to detect reductions in population size (Garza and Williamson 2001).

Genetic structure

I calculated Nei's unbiased genetic distance between populations from the four silvicultural systems and reference *S. parvifolia* populations from Sumatra, Malaysia, and Central Borneo (Ohtani et al. unpublished data) to evaluate the genetic relationships among our four subject populations. I then constructed a network tree using a NeighborNet network in SplitsTree 4.0 (Huson and Bryant 2006). To detect population structure and infer the most appropriate cluster size (*K*), I used the Bayesian clustering method in STRUCTURE V.2.3.4 (Pritchard et al. 2000; Hubisz et al. 2009). The most likely value of *K* was determined in STRUCTURE HARVESTER v.0.9.62 (Earl and vonHolt 2012) using the Evanno method (Evanno et al. 2005) to predict the most probable number of subgroups in the population. I used default parameters, varying *K* from 1 to 10 in STRUCTURE; each run comprised 50,000 burn-in iterations and 100,000 recorded iterations and was replicated 5 times. I also conducted STRUCTURE analysis of only the populations from the four silvicultural systems to compare genetic structure among treatments. I used the CLUMPP 1.1.2 software to find the optimal alignments of *R* replicate cluster analyses of the same data (Jakobsson and Rosenberg 2007). For analysis of molecular variance (AMOVA), I used only data from the four experimental

populations to test whether genetic variance was partitioned among treatments using Arlequin3.5.2.

3.3 Results

3.3.1 Available polymorphic loci

Of the 33 loci tested, 17 loci showed clear genotypes and were therefore considered suitable for evaluating the genetic diversity of each population and comparing genetic structure among populations (Table 3-2). The remaining 16 loci showed some evidence of null alleles, were monomorphic, or did not yield PCR amplification products (Table 3-S1). Among the 17 suitable loci, *Sle216* showed the highest polymorphism in terms of the number of alleles, and *Tum1405J22* showed the lowest number of alleles (Table 3-2). Expected heterozygosity (H_e) ranged from 0.232 to 0.946, and the average *H*e values for genomic SSRs and EST-SSRs were 0.773 and 0.597, respectively. The F_{IS} values suggested that all but two loci conformed to Hardy–Weinberg proportions (Table 3-2).

3.3.2 Genetic structure of *S. parvifolia* populations

The overall genetic differentiation among experimental populations was low (G'_{ST}=0.11). The G'_{ST} values varied among loci, ranging from 0.002 at *Tum1405J22* to 0.39 at *Sle079*, while the average G'_{ST} values for genomic SSRs and EST-SSRs were 0.197 and 0.111, respectively (Table 3-2). Similarly, hierarchical AMOVA analysis revealed that genetic differentiation among plots within a given silvicultural system was higher than that among silvicultural systems, with values of 6.03% and 1.59%, respectively; both differences were statistically significant (Table 3-3). The proportion of variance among individuals within a plot was 6.62% and the variation within individuals was 85.77% ($P < 0.05$).

Bayesian clustering analysis in STRUCTURE for the 17 loci using the four experimental populations and the reference populations revealed that *S. parvifolia* populations could be divided into two main clusters: Sumatra-Malaysia and Borneo (highest ΔK at $K = 2$) (Figs. 3-2a and 3-3). At the second highest ΔK, $K = 3$, the Borneo population was divided into two groups (Fig. 3-2a), with three populations

from PF differentiated from the other experimental populations (Fig. 3-2a, gray shading). Cluster 3 (Fig. 3-2a, black) at the second highest ΔK of $K = 3$ was common in the logged forests (R1, R2, and R3), in two populations from PF and in natural populations from Central and East Borneo. Within the experimental populations (silvicultural systems), *S. parvifolia* populations were divided into two main clusters (highest ΔK at $K = 2$) (Fig. 3-2b). There was some genetic structure: three PF populations and one R2 population formed one cluster (gray) while all other populations were assigned to the other cluster (black) (Fig. 3-2b).

3.3.3 Genetic diversity in four kinds of silvicultural system

The number of private alleles was not significantly different among silvicultural systems, but it was significantly different between PF and the other silvicultural systems ($P < 0.05$) (Table 3-4). The other genetic diversity parameters were not significantly different between PF and the other silvicultural systems. The EP population had moderate genetic diversity in terms of *N*e, *R*s, and the number of rare alleles. The genetic diversity of logged forests was increased by EP, especially with respect to *Rs* and the number of rare alleles (Table 3-4).

No significant deviation from Hardy–Weinberg equilibrium was found in 73% of the plots in the four silvicultural systems. F_{IS} values were positive and significant in 20% (1 of the 5 plots) of plots in PF and 60% (3 of the 5 plots) of plots in R1 ($P < 0.05$) (Table 3-5). The F_{IS} values for R2 and R3 plots conformed to Hardy–Weinberg expectations. We could not calculate F_{IS} for four R3 plots because they contained insufficient numbers of seedlings.

The bottleneck test detected significant excess heterozygosity in one plot of PF and one plot of R1 under the infinite allele model (IAM), and in two plots of PF, one plot of R1, and one plot of R2 under the two-phase model (TPM) (Table 3-6). I could not run the bottleneck test in four of the R3 plots because of an insufficient number of seedlings. The mean *M*-ratio values of the plots ranged from 0.42 to 0.56; these values were not statistically different among silvicultural systems. All of the *M*-ratio values were lower than the critical value, *M*-ratio < 0.68, indicating that there

had been past reductions in population size based on the Garza–Williamsons index (2001).

3.4 Discussion

DNA markers for evaluating genetic diversity

Both types of microsatellite marker showed sufficient polymorphism to make it possible to study the genetic diversity within and among the experimental populations. The genetic diversity of genomic SSRs was higher than that of EST-SSRs in all silvicultural systems. These results confirmed previous studies reporting that genomic SSRs were more polymorphic and informative than EST-based markers (see review by Ellis and Burke 2007). Nevertheless, our results confirm the applicability of all our microsatellite markers to closely related dipterocarps (Abasolo et al. 2009; Pandey and Geburek 2009; Tani et al. 2009; Tinio et al. 2014). Twelve EST-SSR markers (Table 3-2) that were originally developed in *S. leprosula* (Ohtani et al. 2012) were transferred to *S. parvifolia*. Thus, the results suggest that the transferability of genomic SSRs and EST-SSRs to closely related taxa is high due to the conservation of DNA sequences between closely related species, especially in transcribed regions of the genome such as those represented by EST-SSRs.

3.4.1 Genetic structure of silvicultural systems

When comparing genetic diversity among silvicultural systems, underlying genetic structure must be considered. If the genetic structure is weak and genetic differentiation among populations is low, it is possible to make direct comparisons of genetic diversity among silvicultural systems. In this study, I used pooled data from five plots in each silvicultural system to evaluate the genetic diversity of these systems. The genetic differentiation between the plots from the four silvicultural systems was very low. Nevertheless, I detected some variation in genetic structure within the experimental forests; three plots in PF could be differentiated from the other two PF plots and also from most other experimental forests. These three PF plots are near a high mountain (697 to 1,670 m) and somewhat separated from other populations (Fig. 3-1); thus, their genetic differentiation from the other PF plots may

be explained by the mountain's functioning as a barrier. Because *S. parvifolia* is generally found in lowlands and on hills below 800 m a.s.l. (Appanah and Weinland 1993; Newman et al. 1996), *S. parvifolia* forests in the study area may be structured by both distance and local geography, resulting in limited gene flow. The different in the number of private alleles between PF and the other systems may therefore be related to the geographic separation between them (Fig. 3-2b).

3.4.2 Genetic diversity among silvicultural systems

Generally, selective logging would be expected to decrease the density of reproductive trees and the genetic diversity in logged forests. Our results reveal that private alleles differed significantly between PF and the other silvicultural systems. The other genetic diversity parameters, including *R*s, *I*, *H*e and the number of rare alleles, in the PF were also slightly higher than those in the other silvicultural systems. The genetic diversity of future generations in logged forests depends on the diversity of remnant mother trees after logging and on gene flow from neighboring stands.

As a measure with which to observe short-term decreases in genetic diversity, such as those occurring during a logging event, the number of private alleles was found to be a very sensitive parameter in this study, while other studies have suggested that *R*s, and the numbers of rare alleles, are also appropriate (Obayashi et al. 2002; Ng et al. 2009). The expected heterozygosity (*H*e) was less sensitive, because more common alleles are retained within remnant tree populations after selective logging, maintaining a high level of heterozygosity regardless of the logging rotation used (Cloutier et al. 2006; Ng et al. 2009). In contrast, removing large trees by selective logging would quickly reduce the number of rare and private alleles because of their very low frequencies in the population. These parameters are also useful and important in conservation genetic applications, for example as indicators of the effects of logging on genetic diversity (Petit et al. 1998). In this study, most of the genetic diversity was not significantly different between primary forest and logged forest, suggesting that the impacts of selective logging on genetic diversity are small. However, in R3, the allelic diversity indices *I* and *R*s decreased

by 12.98% and 19.53%, respectively, vs. PF, and they were much lower than the values in R1 and R2. R1 and R2 showed similar results, probably because some gene flow via seed and pollen from outside and from within the logged forest may contribute to the maintenance of genetic diversity even in a second logging rotation forest such as R2. The main difference between R3 and the other logging systems (R1 and R2) is the size of harvested trees, > 50 cm dbh for R1 and R2, and > 40 cm dbh for R3 (Anonymous 2014). Thus, a lower dbh at harvest had a more strongly negative impact on the genetic diversity of the species because remnant trees are relatively small and immature, offering reduced chances for seed reproduction (Tani et al. 2012; Riina et al. 2014). Moreover, although allogamous trees such as *S. parvifolia* may be more resistant to the impact of harvesting (Sakai et al. 1999; Ng et al. 2009), successful regeneration for the next rotation depends on the density and genetic diversity of remnant *S. parvifolia* trees.

The results show that selective logging decreased the numbers of both rare and private alleles. Relative to PF, the decreases in the proportions of rare alleles were 4.38, 9.98 and 39.90 %, for R1, R2 and R3 respectively. Meanwhile, the decreases in the proportions of private alleles relative to PF was 49.14, 66.38 and 80.17% for R1, R2 and R3, respectively. This implies that increasing the number of logging cycles and harvesting trees of smaller dbh will decrease the number of reproductive individuals in logged forests, with negative impacts on genetic diversity. Generally, loss of genetic diversity, especially of rare and private alleles, can decrease a species genetic potential to adapt to and survive environmental change (Ledig 1986; Hawley et al. 2005; Schaberg et al. 2008). Rare and private alleles are vital, in terms of genetic diversity, in promoting conservation and sustainable forest management. In the future, rare and private alleles collected from seeds or seedlings of *S. parvifolia* in surrounding primary forests should be delivered to logged forests through enrichment planting and established conservation genetic programs.

Current selective logging criteria are based solely on the dbh of commercial trees, without taking into consideration the number of trees harvested or their genetic diversity. Consequently, the genetic diversity of remnant trees in logged forests is

likely to be affected and this will have an impact on future generations, particularly in sites like R3. Fewer remnant trees in logged forests would result in increased mating with close relatives and subsequent inbreeding depression (Murawski et al. 1994; Lee et al. 2000; Obayashi et al. 2002; Fukue et al. 2007; Naito et al. 2008). The density of adult reproductive trees is an important factor affecting the mating patterns of tropical canopy tree species (Naito et al. 2005). For example, inbreeding depression in seedlings and saplings of *Neobalanocarpus heimii* (Dipterocarpaceae) resulted in smaller seed sizes, and much lower germination and survival rates, than those in plants from outcrossed seeds (Konuma et al. 2000; Naito et al. 2005). Increasing inbreeding depression in dipterocarp populations might have additional negative consequences, such as severe seed abortion and/or regeneration failure.

Decreasing the size of a population through activities such as selective logging may decrease the effective population size, reduce the number of alleles, and limit mating opportunities (André et al. 2008). The results are consistent with simulation studies which show that decreasing dbh at harvesting and increasing the rotation cycle will lead to the loss of genetic diversity in neotropical tree species (Degen et al. 2006; Sebbenn et al. 2008) and also in tropical tree species such as *S. leposula* (Ng et al. 2009). According to the simulation model, the short-term effect of selective logging would be to reduce the number of alleles (Ng et al. 2009) and rare alleles (Sebbenn et al. 2008). On the other hand, the observed (H_o) and expected (H_e) heterozygosity would not be affected by selective logging because the rate of reduction in *He* per regeneration by genetic drift is very low (Savolainen and Kärkkäinen 1992).

F_{IS} values among silvicultural systems varied among plots in each silvicultural system (Table 3-5); in particular, the F_{IS} values for three populations in R1 deviated from Hardy–Weinberg equilibrium expectations. This result may suggest that a certain number of reproductive trees is necessary to avoid inbreeding in a logged forest. Thus, to maintain high genetic diversity in such forests, at least one reproductive individual per ha should be maintained (Jenning et al. 2001), although the required density of reproductive trees may differ among dipterocarp species because the main pollinator can vary (Nason et al. 1998). The F_{IS} values for

three plots in R1 and one plot in PF were significant and positive, indicating an excess of homozygotes within these plots (White et al. 2007); this may be due to inbreeding resulting from selfing or biparental mating (Lee et al. 2000). Similar results were reported in *S. curtisii* (Obayashi et al. 2002), *S. ovalis* ssp. *Sericea* (Ng et al. 2004), and *S. leprosula* (Lee et al. 2000), wherein F_{IS} values were significantly above zero. The result of a bottleneck test suggests that one plot of R2 shows evidence of a recent bottleneck brought about by logging.

3.5 Conclusions

I evaluated the effects of different silvicultural systems on genetic diversity in *S. parvifolia*. My results showed that two of the harvesting rotations (R1 and R2; dbh > 50 cm) slightly reduced genetic diversity, but that an intensive second rotation (R3; dbh > 40 cm) greatly decreased the number of rare and private alleles and allelic richness. Consequently, the genetic diversity of logged tropical forests could be preserved by maintaining some individuals with a dbh of > 50 cm. Moreover, I suggest that the genetic diversity of logged forests can be maintained or even increased by conserving primary forests as seed sources to provide genetic material for enrichment strip planting of native dipterocarps in logged forests

Figure legends

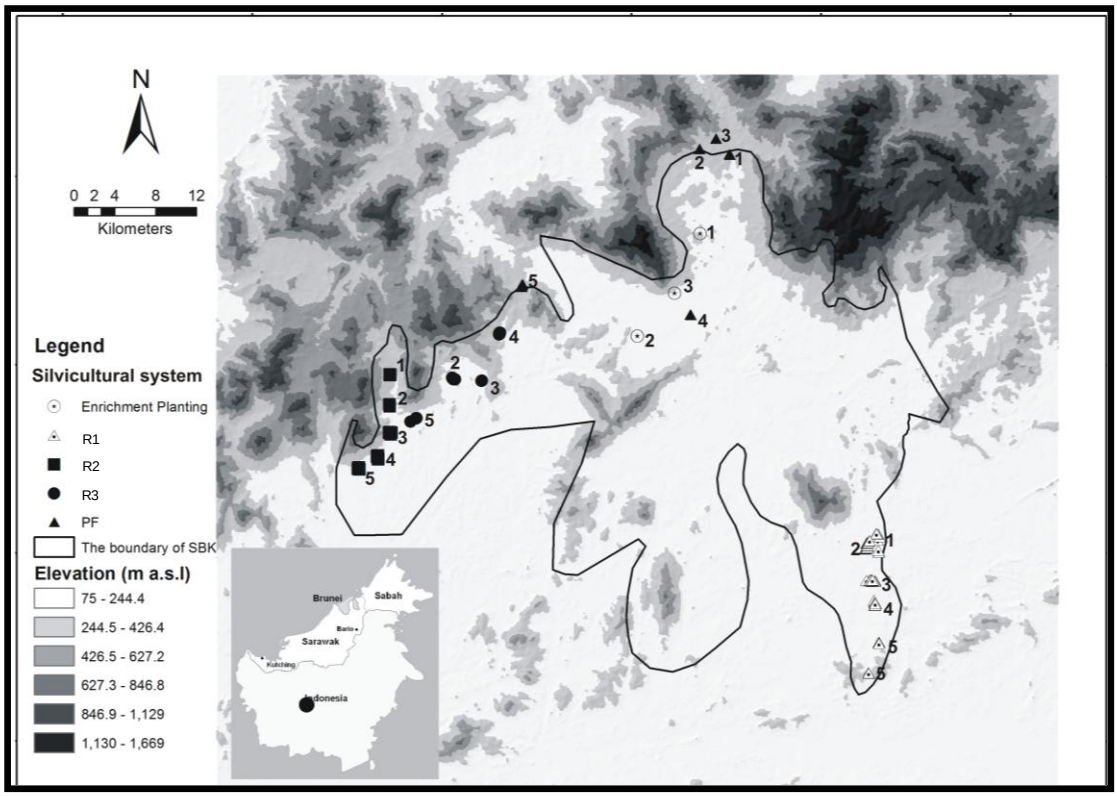


Fig. 3-1. Field sites used for *S. parvifolia* sample collection.

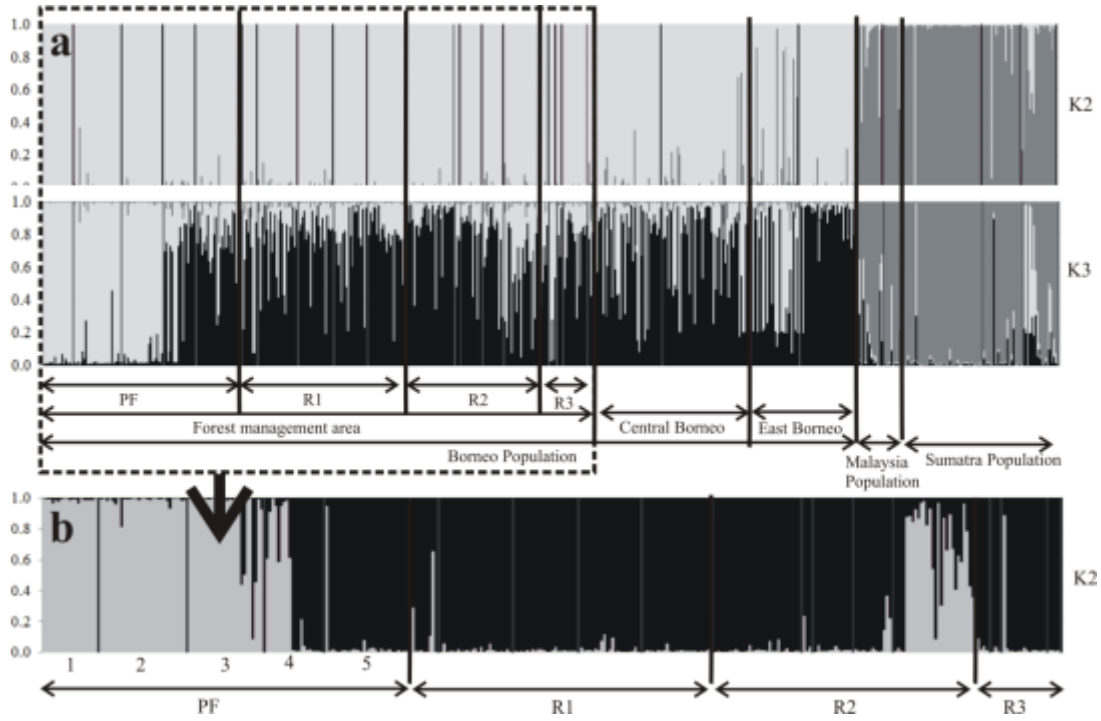


Fig. 3-2. a) Genetic relationships among the 20 plots from four silvicultural systems and reference populations surveyedusing STRUCTURE (Pritchard et al. 2000) based on 17 SSRs. The models with K = 2 and K = 3 were optimal on the basis of the delta K valueand the highest log-likelihood value, respectively; b) STRUCTURE results for 20 plots from four silvicultural systems (no reference populations) with K = 2.

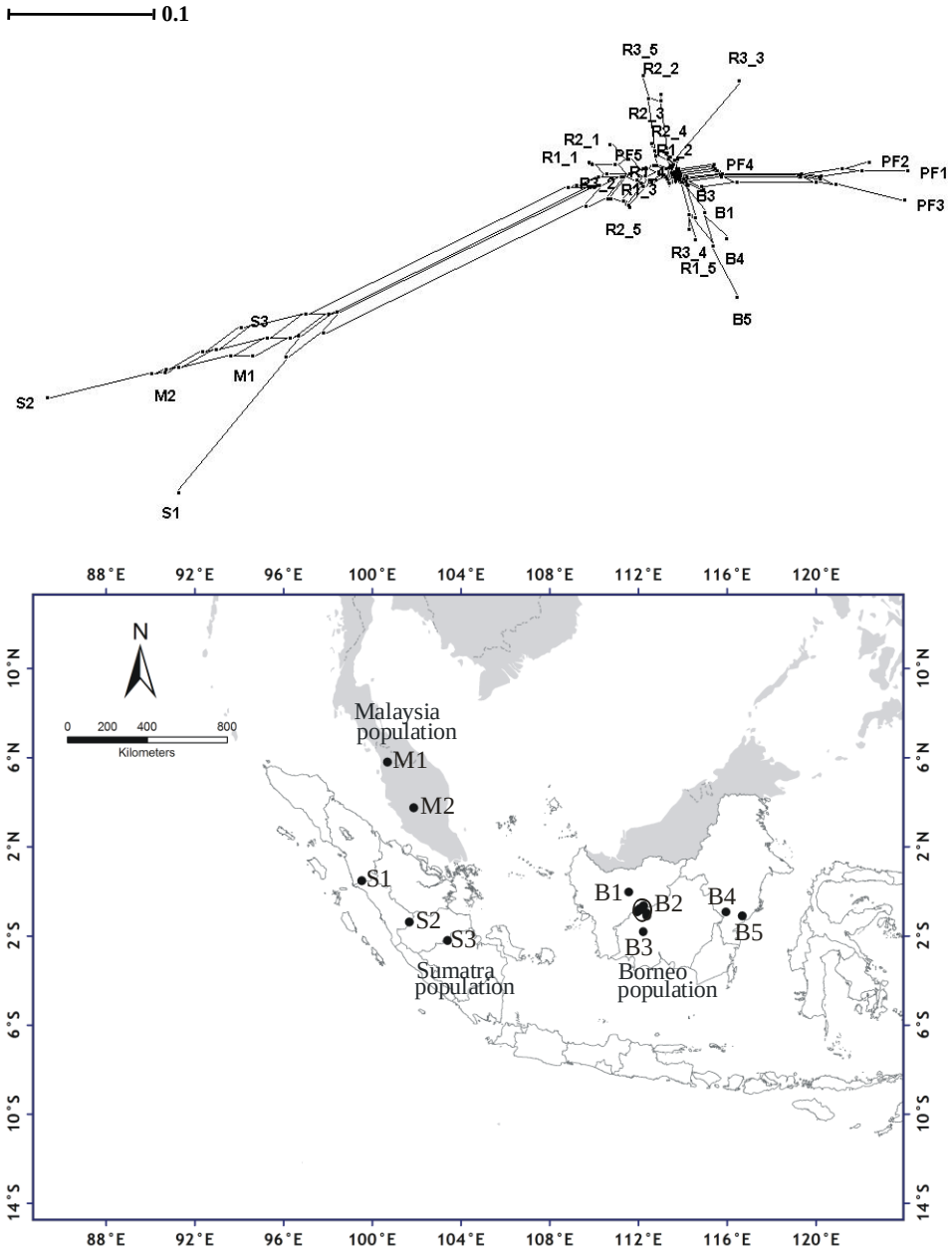


Fig. 3-3. NetworkTree showing the genetic relationships among reference and silvicultural system populations using genetic distances from Reynolds et al. (1983). Malaysia populations are M1 (Bukit Enggang) and M2 (Klau); Sumatra populations are S1 (Singtang), S2 (Nanjak Makmur), and S3 (Asialog); Borneo populations are B1 (Bukit Baka population), B2 (silvicultural system, consisting of PF, R1, R2, and R3), B3 (Sarpatim population), B4 (Sumalindo population), and B5 (ITCIKU population)

Table 3-1. Locations of studied sites in *S. parvifolia* including four silvicultural systems (PF, R1, R2, and R3) and enrichment planting (EP).

Silvicultural System	Plot	Latitude	Longitude	Elevation (m)	Number of Samples
PF	1	0.647S	112.253E	236	19
	2	0.641S	112.226E	310	30
	3	0.632S	112.241E	350	26
	4	0.789S	112.219E	193	20
	5	0.765S	112.071E	272	29
R1	1	0.924S	111.927E	177	9
	2	0.996S	112.373E	200	25
	3	1.024S	112.384E	170	22
	4	1.041S	112.380E	150	21
	5	1.079S	112.385E	166	24
R2	1	1.001S	112.223E	138	30
	2	0.867S	111.953E	287	3
	3	0.893S	111.954E	206	13
	4	0.925S	111.927E	207	13
	5	0.914S	111.944E	195	28
R3	1	0.717S	112.228E	221	-
	2	0.845S	112.010E	157	4
	3	0.864S	111.994E	203	3
	4	0.804S	112.052S	248	15
	5	0.883S	111.973E	198	4
EP	1	0.717S	112.227E	235	30
	2	0.807S	112.172E	200	30
	3	0.770S	112.205E	225	29
Total					427

Table 3-2. Genetic diversities at17microsatellite loci over all analyzed populations of *S. parvifolia.*

Locus	N_a	N_e	H_o	H_e	G'_{st}	F_{IS}
Genomic SSR						
Sle079	17.25	7.66	0.785	0.897	0.390	-0.021
Sle111a	20.00	10.60	0.772	0.925	0.195	0.066
Sle216	22.50	13.37	0.767	0.946	0.310	0.090*
Sle267	5.50	1.45	0.264	0.306	0.020	0.046
SleE14	12.00	4.63	0.653	0.793	0.069	0.07
Average	15.45	7.54	0.648	0.773	0.197	
EST SSR						
Tum0303D01	6.00	2.32	0.521	0.573	0.023	0.042
Tum0305A11	7.00	3.46	0.659	0.719	0.053	-0.077
Tum0308A08	12.50	3.36	0.600	0.714	0.051	0.018
Tum0309D20	6.25	3.89	0.677	0.758	0.087	0.013
Tum1402P02	9.00	1.99	0.397	0.503	0.022	0.086
Tum1405J22	2.00	1.30	0.251	0.232	0.002	-0.065
Tum1407K20	5.00	1.74	0.236	0.400	0.113	0.233*
Tum1601J23	8.50	1.70	0.434	0.410	0.032	-0.114
Tum1602F14	7.00	3.32	0.646	0.706	0.009	-0.008
Tum1602G19	17.00	9.48	0.895	0.911	0.158	-0.051
Tum1602R17	4.75	2.13	0.529	0.535	0.032	-0.135
Tum1610H08	7.25	2.78	0.566	0.697	0.325	-0.034
Average	7.69	3.12	0.534	0.597	0.076	

*Significantly different from zero ($P < 0.05$)

Table 3-3. Analysis of molecular variance (AMOVA) partitioning of total genetic diversity within and among plots in various silvicultural systems.

Source of variation	d.f.	Sum of square	Variance components	Percentage of variation	*P* -value
Among silvicultural systems	3	97.184	0.08800	1.59	0.0176
Among plot within silvicultural systems	15	253.410	0.33329	6.03	<0.001
Among individuals within plot	319	1746.806	0.36590	6.62	<0.001
Within individuals	338	1603.500	4.74408	85.77	<0.001
Total	675	3700.901	5.53127		

Table 3-4. Comparison of genetic diversity among four silvicultural systems and effect of enrichment planting on genetic diversity. The standard error of each parameter is shown in parentheses.

Silvicultural System	**N**	N_e	I	R_s	H_e	**No. Common alleles[a]**	**No. Rare alleles[b]**	**No. Private Alleles[c]**
PF	124	4.56(0.90)	1.54(0.18)	8.19(1.21)	0.65(0.05)	4.41(0.41)	4.11(0.83)	1.16(0.24)a
R1	101	4.67(1.07)	1.47(0.18)	7.72(1.19)	0.63(0.06)	4.35(0.56)	3.93(0.88)	0.59(0.09)b
R2	87	4.62(0.98)	1.46(0.20)	7.92(1.21)	0.61(0.06)	4.24(0.53)	3.70(0.78)	0.39(0.09)b
R3	26	3.84(0.65)	1.34(0.15)	6.59(0.89)	0.62(0.05)	4.47(0.52)	2.47(0.51)	0.23(0.08) b
R1+EP*	190	4.92(1.12)	1.53(0.20)	8.29(1.27)	0.63(0.06)	4.35(0.57)	4.54(0.95)	0.44(0.05)b
R2+EP*	176	5.02(1.15)	1.51(0.20)	8.23(1.27)	0.62(0.06)	4.18(0.53)	4.00(0.82)	0.35(0.06)b
R3+EP*	115	4.72(1.01)	1.49(0.20)	8.09(1.23)	0.62(0.06)	3.94(0.52)	4.50(0.89)	0.35(0.06)b

Effective number of alleles per locus (*N*e); Shannon index diversity (*I*); Allelic richness (*R*s); Expected heterozygosity (*H*e). [a]Allele frequency ≥ 0.05; [b] Allele frequency < 0.05; [c] alleles that are found only in a single population among a collection of populations. Different letters after values indicate significant differences at α 95%.

*: Genetic diversity parameters were estimated using the pooled data from R1 and EP, R2 and EP, and R3 and EP, respectively.

Table 3-5. Fixation indices (F_{IS}) for each plot in four silvicultural systems.

Plot	PF	R1	R2	R3
1	0.044	0.103*	0.016	N/A
2	0.076*	0.093*	N/A	N/A
3	-0.015	0.048	-0.021	N/A
4	0.082	0.161*	0.036	0.054
5	0.016	-0.011	0.019	N/A

*Significantly different from zero ($P < 0.05$); NA= not available; the number of seedlings was less than 5 samples

Table 3-6. The results of bottleneck tests on *S. parvifolia* populations in four silvicultural systems under two models of mutation: the infinite allele model (IAM) and the two-phase model **(**TPM**)** (with variance = 30 and probability = 70 percent); *M*-ratio= mean Garza–Williamson statistic (Garza and Williamson 2001).

Silvicultural System	**Sub population**	**IAM**	**TPM**	***M*-ratio**
PF	1	0.032*	0.406	0.48
	2	0.549	0.046*	0.42
	3	0.550	0.047*	0.46
	4	0.185	0.583	0.56
	5	0.347	0.265	0.50
R1	1	NA	NA	NA
	2	0.539	0.595	0.49
	3	0.130	0.049*	0.49
	4	0.033*	0.409	0.48
	5	0.190	0.415	0.51
R2	1	0.355	0.249	0.51
	2	NA	NA	NA
	3	0.567	0.08	0.52
	4	0.569	0.001*	0.46
	5	0.182	0.433	0.48
R3	1	NA	NA	NA
	2	NA	NA	NA
	3	NA	NA	NA
	4	0.318	0.255	0.55
	5	NA	NA	NA

*P < 0.05;NA= not available; the number of seedlings is less than the minimum required for the bottleneck test

Supplementary material

Table 3-S1. Primer combinations used for PCR processing, amplification, polymorphisms, and possibility of null alleles.

No	Primer Combinations 1	Allele range (bp)	Amplification	Polymorphism	Possibility of null allele
1	*Tum1407K20*	366-394	+	+	-
2	*Tum0307P09*	296-331	+	+	+
3	*Tum1602R21*	247-268	+	+	+
4	*Tum1610H08*	181-197	+	+	+
5	*SleE14*	212-237	+	+	-
No	Primer Combinations 2				
1	*Tum0305A11*	90-122	+	+	-
2	*Sle303a*	145-169	+	+	+
3	*Tum1601J23*	152-177	+	+	-
4	*Shc11*	180-200	-	-	+
5	*Tum1602F14*	337-366	+	+	-
6	*Shc09*	180-250	-	-	+

[1] : "+ "= amplified; "-" = no amplified

[2] : "+ "= polymorphism; "-" = no amplified and / or monomorphism

[3]: I estimated the null allele frequency by Micro-Checker, where "+ "= null allele exist ; "-" = no null allele

Table 3-S1. continued

No	Primer Combinations 3	Allele range (bp)	Amplification	Polymorphism	Possibility of null allele
1	*Sle105*	132-146	-	-	+
2	*Sle118*	145-176	+	+	-
3	*Sle267*	106-128	+	+	-
4	*Tum1405013*	194-211	+	+	+
5	*Tum0303D01*	300-308	+	+	-
6	*Tum1602R17*	324-342	+	+	-
No	Primer Combinations 4				
1	*Tum1402P02*	362-390	+	+	-
2	*Tum0308A08*	319-349	+	+	-
3	*Shc07*	200-230	-	-	+
4	*Tum1405J22*	225-244	+	+	-
5	*Sle271a*	122-132	+	-	+
6	*Sle392*	161-231	-	-	+

[1] : "+ "= amplified; "-" = no amplified

[2] : "+ "= polymorphism; "-" = no amplified and / or monomorphism

[3]: I estimated the null allele frequency by Micro-Checker, where "+ "= null allele exist ; "-" = no null allele

Table 3-S1. continued

No	Primer Combinations 5	Allele range (bp)	Amplification	Polymorphism	Possibility of null allele
1	*Tum0309D20*	319-350	+	+	-
2	*Tum1602G19*	161-184	+	+	-
3	*Sle079*	155-198	+	+	-
4	*Shc03*	150-220	+	+	+
5	*Sle111a*	138-154	+	+	-

No	Primer Combinations 6				
1	*Sle074a*	110-130	-	-	+
2	*Shc07*	200-230	+	+	+
3	*Sle216*	93-112	+	+	-
4	*Sle392*	161-231	+	+	+
5	*Sle384*	191-219	-	-	+

[1] : "+ "= amplified; "-" = no amplified

[2] : "+ "= polymorphism; "-" = no amplified and / or monomorphism

[3]: I estimated the null allele frequency by Micro-Checker, where "+ "= null allele exist ; "-" = no null allele

Table 3-S2. Genetic diversity in each plot in various silvicultural systems. The standard error of each parameter is shown in parentheses.

Silvicultural System	**Sub pop**	***N*e**	***I***	***R*s**	***H*e**	**No. Common alleles[a]**	**No. Rare alleles[b]**	**No. Private Alleles[c]**
PF	1	3.52(0.50)	1.30(0.14)	3.07(0.23)	0.62(0.05)	4.71(0.49)	0.99(0.22)	0.18(0.05)
	2	3.49(0.58)	1.31(0.15)	3.00(0.23)	0.61(0.05)	4.29(0.50)	1.04(0.21)	0.23(0.05)
	3	3.23(0.54)	1.20(0.15)	2.84(0.25)	0.57(0.05)	3.41(0.44)	0.64(0.15)	0.16(0.05)
	4	3.97(0.79)	1.27(0.17)	3.02(0.29)	0.59(0.06)	4.71(0.69)	0.60(0.16)	0.12(0.03)
	5	3.94(0.70)	1.35(0.17)	3.10(0.27)	0.61(0.06)	4.59(0.51)	0.82(0.20)	0.14(0.05)
R1	1	3.71(0.56)	1.28(0.16)	3.23(0.3)	0.60(0.06)	5.53(0.75)	1.22(0.36)	0.15(0.06)
	2	3.67(0.61)	1.32(0.17)	3.05(0.27)	0.59(0.06)	4.18(0.52)	0.74(0.20)	0.11(0.02)
	3	3.95(0.82)	1.33(0.17)	3.09(0.27)	0.60(0.06)	3.94(0.44)	0.99(0.23)	0.10(0.03)
	4	4.30(0.88)	1.39(0.17)	3.19(0.27)	0.63(0.05)	4.24(0.53)	1.16(0.28)	0.13(0.04)
	5	4.11(0.84)	1.32(0.17)	3.09(0.28)	0.61(0.06)	4.24(0.55)	0.79(0.23)	0.11(0.04)

Effective number of alleles per locus (*N*e); Shannon index diversity (*I*); Allelic richness (*R*s); Expected heterozygosity (*H*e). [a]Allele frequency ≥ 0.05; [b] Allele frequency < 0.05; [c] alleles that are found only in a single population among a collection of populations. Different letters after values indicate significant differences at α 95%.

Table 3-S2. Continued

Silvicultural System	Sub pop	*Ne*	*I*	*Rs*	*He*	No. Common alleles[a]	No. Rare alleles[b]	No. Private Alleles[c]
R2	1	3.13(0.48)	1.17(0.16)	2.79(0.26)	0.54(0.06)	3.59(0.44)	0.79(0.19)	0.09(0.03)
	2	2.27(0.23)	0.83(0.11)	2.82(0.26)	0.48(0.06)	2.82(0.26)	0.59(0.26)	0.04(0.04)
	3	3.31(0.47)	1.21(0.15)	3.00(0.27)	0.58(0.06)	3.53(0.35)	0.73(0.18)	0.10(0.03)
	4	3.87(0.70)	1.31(0.17)	3.16(0.3)	0.60(0.06)	4.00(0.50)	0.84(0.19)	0.11(0.04)
	5	3.64(0.59)	1.30(0.16)	3.02(0.26)	0.60(0.06)	3.94(0.45)	0.71(0.17)	0.10(0.03)
R3	1	NA	NA	NA	NA	NA	NA	NA
	2	3.24(0.39)	1.17(0.11)	3.45(0.27)	0.61(0.05)	4.00(0.36)	0.78(0.20)	0.07(0.04)
	3	2.22(0.32)	0.72(0.13)	2.59(0.34)	0.41(0.07)	2.59(0.34)	0.65(0.23)	0.07(0.04)
	4	3.12(0.40)	1.17(0.14)	2.91(0.24)	0.58(0.05)	3.76(0.39)	0.41(0.10)	0.03(0.01)
	5	2.70(0.27)	1.03(0.10)	3.07(0.24)	0.57(0.04)	3.53(0.32)	0.73(0.23)	0.13(0.06)

Effective number of alleles per locus (*N*e); Shannon index diversity (*I*); Allelic richness (*R*s); Expected heterozygosity (*H*e). [a]Allele frequency ≥ 0.05; [b] Allele frequency < 0.05; [c] alleles that are found only in a single population among a collection of populations. Different letters after values indicate significant differences at α 95%.

Table 3-S2. Continued

Silvicultural System	Sub pop	*Ne*	*I*	*Rs*	*He*	No. Common alleles[a]	No. Rare alleles[b]	No. Private Alleles[c]
R1 + EP	1	4.14(0.78)	1.37(0.18)	3.10(0.28)	0.61(0.06)	4.12(0.56)	0.78(0.22)	0.09(0.02)
	2	4.23(0.87)	1.40(0.18)	3.09(0.28)	0.61(0.06)	4.06(0.54)	0.69(0.15)	0.09(0.02)
	3	4.49(0.96)	1.46(0.19)	3.17(0.29)	0.61(0.06)	4.24(0.45)	0.97(0.20)	0.13(0.03)
R2 + EP	1	3.97(0.76)	1.34(0.18)	3.00(0.29)	0.58(0.07)	4.12(0.51)	0.77(0.18)	0.08(0.02)
	2	4.24(0.85)	1.39(0.18)	3.10(0.29)	0.60(0.06)	4.06(0.55)	0.87(0.18)	0.09(0.02)
	3	4.21(0.79)	1.44(0.19)	3.16(0.29)	0.61(0.06)	4.18(0.45)	0.95(0.21)	0.14(0.04)
R3 + EP	1	4.02(0.74)	1.34(0.18)	3.07(0.28)	0.60(0.06)	4.06(0.59)	0.93(0.23)	0.07(0.02)
	2	3.88(0.73)	1.34(0.17)	3.02(0.27)	0.60(0.06)	4.12(0.53)	0.56(0.12)	0.07(0.02)
	3	4.07(0.73)	1.41(0.18)	3.15(0.28)	0.61(0.06)	4.35(0.48)	0.95(0.23)	0.15(0.04)

Effective number of alleles per locus (*Ne*); Shannon index diversity (*I*); Allelic richness (*Rs*); Expected heterozygosity (*He*). [a]Allele frequency ≥ 0.05; [b] Allele frequency < 0.05; [c] alleles that are found only in a single population among a collection of populations. Different letters after values indicate significant differences at α 95%

CHAPTER IV

EFFECT OF LOGGING ROTATION ON MATING SYSTEM AND GENE FLOW OF *Shorea parvifolia* IN THE LOWLAND DIPTEROCARPS FOREST

Keywords: *Shorea parvifolia*, selective logging, rotation, genetic diversity, outcrossing

4.1 Introduction

Selective logging is the principal silvicultural system to manage the lowland dipterocarp forest with the objective conserving the wood for future use to achieve sustainable forest management (Ratnam et al. 2014). In brief, the mature commercial valuable trees less than 50 cm diameter of breast height (dbh) will cut by the selective logging. The selective logging is conducted of a 30 years cutting cycle as basis for the determination of Annual Allowable Cut (AAC) for forest concessionaire. Thus, some trees less than 50 cm dbh will be remained in the logging site for the future regeneration. The selective logging is also conducted to keep forest connectivity between the logged forests, old secondary forest and conservation forest in the forest concessionaire area (Sist et al. 1998; Meijaard and Sheil 2008).

The reduction of basal area caused by selective cutting was ranged from 51 to 57.5 % (Lee et al. 2002 and 2007). It implied that selective cutting will change the distribution and composition of certain species in the logged forest of lowland dipterocarp forest due to reduction of density of reproductive tree. Furthermore, the selective logging may change the frequency of genotypes and promote to change the genetic constitution of remnant trees (Jenning et al. 2001; Hawley et al. 2005).

Increasing distance between the reproductive trees by selective cutting may effects on the movement of the pollinator of dipterocarp because the pollinator of dipterocarps is mainly animal such as trips, small beetle and the other insects (Sakai et al. 1999; Lee et al. 2000; Tani et al., 2012). Thus, selective cutting may also influence the mating system of particular species due to increasing distance between conspesifics (Hawley et al. 2005; Lowe et al. 2005; Cloutier et al. 2007). There is some risk of inbreeding due to mating among reproductive trees with genetically related individuals. Furthermore, inbreeding has negative effects for particular species, such as reducing the germination rate, growth, survival rates, and also reducing the resistance against pest and disease (Huges at al. 2008; Naito et al. 2005 and 2008).

In previous studies, selective logging was negative impact on mating system in lowland dipterocarp species. The outcrossing rate of the logged forest was lower than that of the primary forest in *Dryobalanops aromatica*, *Shorea megistophylla* and *S. curtisii* (Lee 2000, Murawski et al.1994; Obayashi et al. 2002 but the difference of them between the forests was fluctuated between the species. This suggests that the sensitivity against logging was different for each dipterocarp species probably because of the differences of main pollinators, population density and species' turnover rate (Kettle et al. 2011, Masuda et al. 2013, Tani et al 2016).

Furthermore, selective logging with cutting cycle of 30 years would decrease the population size, the genetic diversity and timber production (Degen et al. 2006; van Gardingen et al. 2006; Sebbenn et al. 2008; Ng et al. 2009). It also created higher genetic distances between the original population and the population at the end of the logging cycles (Degen et al 2006). It indicated that selective logging could not recover secondary forest well, which probably caused lower density population and was still dominated by non-reproductive tree during forest recovery. In the context *S. parvifolia*

in the secondary lowland dipterocarps forest, selective logging would directly influence mating system of the remaining individual after logging. Hence, understanding the effects of selective logging on mating system, gene flow, and genetic diversity in *S. parvifolia* is important for both the maintenance of genetic diversity and the sustainable management of lowland dipterocarps forest.

The objectives of this study were to assess mating system, gene flow and genetic diversity of *S. parvifolia* in the different the number of logging rotations. Three kinds of forest populations with different the number of logging rotation were chosen to compare mating system, gene flow and the genetic diversity to see the impact of selective logging,which were 1) primary forest as a reference population, 2) the first rotation of selective logging, and 3) the second rotation of selective logging, where the limit diameter for logging dbh of both rotation was > 50 cm.

4.2 Materials and methods

Study site and sample collection

The study was conducted at Sari Bumi Kusuma forest concession, Central Kalimantan (00° 36'– 01° 10' S and 111° 39'–112° 25' E). The samples were collected from 1) primary forest (PF), 2) the first selective logging rotation with more than 50 cm dbh trees being harvested (R1), and 3) the second selective logging rotation with the same method of selective logging (R2). Selective logging of R1 was conducted in 2012, while selective logging of R2 was conducted in 1983 and 2012, as the first and second of selective logging, respectively. The PF and R2 consisted of 5 circular subplots, while R2 consisted of 4 circular subplots. Each subplot was established in radius 50 m from each seed collection tree (mother tree). The dbh size of all trees more than 20 cm in dbh in the subplots was measured and the distribution of all trees was mapped using a Garmin 76 CSx handheld GPS (Fig. 4-1). These mapped *S. parvifolia* trees were considered to be candidates for reproductive trees. In each subplot, I collected inner bark tissues of all *S. parvifolia* trees (dbh > 20 cm). I also collected fallen fresh seeds under the crown of 5, 4 and 5 mother trees in PR, R1 and R2 plots, respectively. I used 125 seeds of each mother tree for the germination test in the nursery. The 40-50 seeds

for each mother tree were used for microsatellite genotyping. After germination, I also collected the leaf tissues from the seedlings for microsatellite genotyping.

DNA extraction and genotyping

Total DNA was extracted from all samples using a DNeasyPlant Mini Kit (QIAGEN). The genotype of each sample was determined using 10 microsatellite loci on expressed sequence tags (EST-SSR), namely, *Tum0305A11*, *Tum0309D20*, *Tum1405D13*, *Tum1405J22*, *Tum1407K20*, *Tum1601J23*, *Tum1602F14*, *Tum1602L17*, *Tum1602L21*, *Tum1610H08* (Ohtani et al. 2012) and 6 genomic microsatellite loci, namely, *SleE14f*, *Sle*105, *Sle267*, *Sle303a*, *Shc03* and *Shc09* (Lee et al. 2004). The polymerase chain reaction (PCR) amplification was performed in 8-μL reaction solution containing 1 μL of DNA (5 ngμL^{-1}), 4 μL of multiplex kit (QIAGEN), 0.2 μM of each primer, and 2 μL of sterile distilled water using GeneAmp 9700 (Applied Biosystems). For initial denaturing, I set the PCR amplification temperature as follows: 15 min at 95ºC, followed by 32 cycles of 30 s at 94ºC, and 90 s at 50ºC or 56ºC (depending on primer pairs) and 72ºC for 1 min. A final extension step was conducted at 60ºC for 30 min after the 32 cycles. The PCR products were genotyped using a 3130 Genetic Analyzer (Applied Biosystems) with a mixture containing 0.2 μL of calibrated internal size standard (GeneScan ROX 400HD; Applied Biosystems) and 9 μL of Hi-Di for each sample. The electrophoretogram of each individual were then visualized using Geneious 7.1 software (Biomatters Ltd., Auckland) to conduct genotyping.

Statistical analysis

Pollen dispersal kernel

To estimate the distance of pollen dispersal, I performed the analysis using a TWOGENER (Smouse et al. 2001), approach with POLDISP (Robledo-Arnuncio et al. 2007). The principle of TWOGENER was based on the calculation of the differentiation parameter (Φ_{ft}), the differentiation of allelic frequencies among the pollen pools sampled by several mother trees that are spatially distributed in the landscape and computed to estimate pollen dispersal parameters. Furthermore, the estimate of pollen dispersal curve was determined from relationship between Φ_{FT} and dispersal distance

(Austerlitz and Smouse, 2001) that can be justified by the several estimates of pollen dispersal formula (Austerlitz and Smouse 2002). I tested the normal and exponential dispersal functions and used the observed adult density for each population. The densities of adult trees were calculated using the average spatial distribution of adult trees in PF, R1 and R2 plots.

Furthermore, exponential power dispersal function (or kernel) was also used to calculate the probability of pollen travel from its origin (0,0) to be present in the pollen cloud at position (x, y) (Wright 1943; Clark 1998). The exponential power dispersal kernel has been frequently used to model pollen dispersal pattern (Austerlitz et al. 2004; Klein et al. 2008; Tani et al. 2012), which is written as:

$$p(a,b,r) = \frac{b}{2\pi a^2 \Gamma(2/b)} exp\left(-\left(\frac{r}{a}\right)^b\right)$$

where Γ was the classically defined gamma function (Abramowitz and Stegun 1964), and "r" is $\sqrt{x^2+y^2}$ as the distance of pollination computed from the female / mother tree, located at the origin, to the pollinating male, in any direction (Austerlitz and Smouse 2002). The parameter "b" was the shape parameter affecting the tail of the dispersal function and "a" was a scale parameter homogeneous to a distance (see details in Clark et al. 1999; Austerlitz et al. 2004). The shape parameter b also describes the shape of the dispersal kernel tail, with $b<1$ indicating fat-tailed dispersal (that is, the long-range decay of probability is slow) and $b>1$ indicates dispersal is thin-tailed, with a rapid decrease of the dispersal function, implying few long-distance dispersal events (Austerlitz et al. 2004). Meanwhile, the estimate of the pollen dispersal distance (δ), travelled by a pollen grain was calculated under the kernel *p(a,b,r),* (Clark et al. 1998), assuming a dispersal curve and a density of reproducing adults (d) in the landscape, is given by:

$$\delta = a\frac{\Gamma(3/b)}{\Gamma(2/b)} \text{ and } d = \frac{n}{S}$$

where "n" was the number of reproductive adult tree in the subplot and "S" was the size of subplot in squared meter (Robledo-Arnuncio et al. 2007).

Mating system

Mating system of each silvicultural system was assessed based on the mixed-mating model using the software Multilocus MLTR version 3.1 (Ritland 2004). The parameter of mating system included the followings, multi-locus outcrossing rate (*tm*), single-locus outcrossing rate (*ts*), mating among relatives rate (the biparental inbreeding (*tm -ts*), and multi-locus paternity correlation (the proportion of full ships among outcrossed offspring; $r_{p(m)}$). The number of pollen donors contributing to each mother tree (N_{ep}) was also estimated using the formula of $1/r_{p(m)}$ (Ritland, 1989).

Paternity assignment, effects of population density and selective logging rotation

The paternity of each seed was assigned by comparison between multi locus genotypes of the seed, mother trees and candidate pollen donors in each subplot and its statistical significance was tested by maximum likelihood assignment using CERVUS 3.07 software (Marshall et al. 1998). For likelihood test in the CERVUS, I set the mistyping rate to 1%, 264 of candidate parents for the 10,000 simulated genotypes based on allele frequency to calculate 80% (relaxed) and 95% (strict) confidence level. The adult tree of 81, 61 and 122 in PF, R1 and R2 were assumed as potential paternal candidates, because dipterocarp trees more than 20 cm dbh were considered to start reproductive growth (Appanah 1993). The most likely parent and pair parent were determined by Δ statistic (Marshall et al. 1998) using the alleles frequency of the adult tree as the candidate of pollen donor with positive LOD score (logarithm of likelihood ratio). However, if the paternal candidates identified by the likelihood procedure had more than two mismatches in the simple exclusion procedure, I assumed that the paternal tree of the offspring was located outside the plot.

The cross-pollinated seed of each mother tree was determined by paternity assignment (CERVUS, Marshall et al. 1998). The outcrossing rate was directly calculated as rate of cross-pollinated offsprings to the total sample of each mother trees. To investigate effects of population density and selective logging rotation on outcrossing rate and number of pollen donors of each mother tree, generalized linear mixed model (glmmML) was applied using the paternity results of seed and seedling by R3.2.3 (The R Development Core Team, glmmML package). Here, I used binomial and

Poisson distributions for outcrossing rate and number of pollen donors as responsible variables, and as explanatory variables. I also used basal area in each subplot and mother trees' attribution to the plots (PF, R1 and R2) by using dummy variable. AIC was used to evaluate the model fitting (Akaike 1987).

4.3 Result

Pollen dispersal kernel estimates

The correlated paternity within maternal correlated paternity and sibships ($r_{p(m)}$) increased with increasing the rotation of cutting cycle, in which R2 showed the highest value among treatments both in POLDISP and MLTR software (Table 4-1 and 4-3). The global estimate Φ_{FT} in PF is lowest among treatments that were 0.259, while the Φ_{FT} in R1 and R2 was 0.310 and 0.334, respectively (Table 4-1). Based on the tree density of adult tree (dbh > 20 m), the estimate mean distance of pollen dispersal distance (δ) was very short that was 13.08 m, 12.35 m and 9.10 m for PF, R1 and R2, respectively (Table 4-2, Fig 4-2). The shape of dispersal kernel (indirect estimate) was nearly exponential shape because the shape parameter *b* for all treatments was closed to 1 (Table 4-2). Thus, it revealed that pollen dispersal in all treatments was very short distance on indirect estimations.

Mating system

The multi-rotation of selective logging reduced in outcrossing rate (t_m), although it was not significantly different among population ($P > 0.05$) (Table 4-3). The outcrossing rate (t_m) in each population was still high more than 89.4% (Table 4-3). Meanwhile, the values of biparental inbreeding in both seed and seedling stages were still high ($t_m - t_s > 0.26$) (Table 4-3). The paternity correlation ($r_{p(m)}$) was significantly different among populations ($P < 0.05$), in which the paternity correlation of R2 was highest of all the populations. Increasing of paternity correlation ($r_{p(m)}$) reduced the number of pollen donor in the logged forest, which were evidently from lowest value of the number of pollen donor in R2 among the treatments. Furthermore the pollen donor in the PF dominated by large size (dbh > 50 cm), while in the logged forest was

dominated by medium size of dbh (35-49 cm) (Table 4-S1). On the other hand, the selective logging would significantly reduce the germination rate of seed ($P < 0.05$), where the average germination rate of each population were 96.3% (PF), 86.5% (R1) and 89.1% (R2) (Fig 4-S2).

Paternity assignment, effects of population density and selective logging rotation

The total exclusion probability for identifying the second parent of offspring in the paternity analysis in PF, R1 and R2 was 0.999977, 0.999838, and 0.999971, respectively. The proportion of allogamous seed sired by pollen donors inside the plot in PF, R1 and R2 was 24.06%, 19.55% and 16.10%, respectively (Table 4-1). An outcrossing rates were explained by population density (basal area of surrounding conspecific trees in the subplot), more than 99% and 90%. Wald confidence interval of the explanatory variable did not include zero in seed and seedling analyses, respectively. The reduction of the basal area due to selective logging significantly reduced the number of pollen donor ($P < 0.05$) (Table 4 and 5). The effect of basal area on number of pollen donors was relatively stronger in seed samples than in seedling samples. On the other hand, rotation cycle of selective logging didn't significantly affect ($P > 0.05$), however R2 has more effect on number of pollen donor than only 1 rotation cycle (R1) in seedling according to AIC. A simplest model_P1 for both seed and seedling samples was the best model to speculate the number of pollen donor by AIC (Table 5). On the other hand, all parameters' coefficient for outcrossing rate didn't show significance among populations.

4.4 Discussion

Pollen dispersal and mating system

Reduction of the density of reproductive tree by selective logging, in theory, would influence on mating system and pollen dispersal of certain species in the logged forest, and especially the pollen dispersal distance is negatively correlated with the density of reproductive tree (Stacy et al. 1996). In this study of mating system of *S. parvifolia* in the lowland dipterocarp species, Indonesia, I found that the global pollen differentiation (Φ_{FT}) among silvicultural treatments was significantly different ($P <$

0.05). However, the estimate of average pollen dispersal distance (δ) was very short (Table 4-2) and not statistically significant different among the treatments ($P > 0.05$). It was suggested that the logging activity is not affected on the pollen dispersal distance of the remnant trees of *S. parvifolia* in this forest. The average pollen dispersal distance (δ) in our plot was shorter than in Pasoh forest reserve, Malaysia, which ranged from 250 to 450 m (Tani et al. 2009). It could be explained that the density of pollen donor contributing on mating system of *S. parvifolia* in our plot was higher (the flowering tree density was > 3 trees ha^{-1}) than that in Pasoh (the flowering tree density was 0.23 tree ha^{-1}). The short pollination distance in our plot was also probably due to the clumped distribution of this species in this forest and also still maintain relatively high density of mature tree of this species after logging. The pollen dispersal distance (δ) of dipterocarp was also different by species and their main pollinator. For instance, the average pollen dispersal distance (δ) on *S. leprosula* and *Neobalanocarpus heimii* was longer, 700 to1,000 m and 524 m (Fukue et al. 2007; Tani et al 2009, Konuma et al. 2000), respectively. On the other hand, the average pollen dispersal distance of *S. curtisii* was much shorter, 65.03 to 81.55 m in 1998 and 2005 with different flowering intensity, respectively (Table 6). In terms of pollinator of dipterocarp, thrips with weak flyer was observed visiting flowers as the main pollinator for *Shorea spp.* (Appanah and Chan 1981; Sakai et al. 1999). Although some beetles (Chrysomelidae and Curculionidae, Coleoptera) contributed to pollination of *S. parvifolia* in Sarawak (Sakai et al. 1999). These studies suggested that this short pollen dispersal distance was due to the relatively high density of reproductive trees in the vicinity of the respective mother trees.

The estimated multi-locus outcrossing rate (t_m) of *S. parvifolia* in the logged forest was lower than PF. Although the outcrossing rate (t_m) of *S. parvifolia* in the logged forest was still higher than those of others dipterocarp species, i.e. *Dryobalanops aromatica* (Lee 2000), *S. curtisii* (Obayashi et al. 2002), *Dipterocarpus tempehes* (Kenta et al. 2004), and *S. leprosula* (Fukue et al. 2007). Because the reproductive tree density of this species is maintained to be high even after logging. The different outcrossing rate in dipterocarps species is closely related to the reproductive tree density of neighborhood and their pollinators (Murawski et al. 1990). The genetic diversity of remnant trees and a degree flowering synchrony of conspecific flowering tree in logged

forest are also important to maintain high outcrossing rate and produce healthy seeds (Tsumura et al. 2003).

Decreasing of outcrossing rate in logged forest, it was probably caused by decreasing the number of reproductive tree an effective pollen donor in R2 compare to those of PF and R1. It was affected by decreasing of basal area in the logged forest due to selective logging. Therefore, the proportion of allogamous seed sired by pollen donors inside the plot is decreasing by the rotation of logging, 24.06% in PF, 19.55% in R1, 16.10% in R2. Furthermore, the correlated paternity estimate ($r_{p(m)}$) in PF was lower than in logged fores indicating that the pollen donor to each offspring in PF are more unrelated compare to that of the logged forests. It suggested that PF maintains an effective network of gene flow among reproductive trees on flowering than that of the logged forests.

Non-significant of outcrossing rate among population in our estimation because the logged forest still remained the reproductive trees with the medium class diameter (dbh 35-50 cm) and small class diameter (dbh < 35 cm) which have positive impact on mating system (Tabel 4-S1). Even in such medium and small size trees sometimes can produce pollen to participate on the mating system (Tani et al. 2012). It suggested that the mating between *S. parvifolia* trees with different age classes as overlapped generations efficiently maintained genetic diversity because the remnant trees after selective logging still have high genetic diversity.

Effect of inbreeding and biparental inbreeding

I detected high biparental inbreeding both in seed and seedling stages. This phenomenon were supported by high value of correlated paternity, Φ_{FT} and bi-parental value (Table 4-1, 4-3 and 4-5) in all populations. It indicates that mating with closely relatives occur frequently and selective logging increase the consanguineous mating among the remnant trees. Furthermore, the high correlated paternity in the PF and logged forests due to the aggregated natural distribution of *S. parvifolia* trees, rather than random distribution (Suzuki et al. 2009; Tito de Morais et al. 2015). Furthermore, an aggregate distribution of this species would affect pollinator behavior, which may lead to cause the nearest-neighbor pollination (Levin 1984; Takeuchi et al. 2004;

González-Varo et al. 2010). On the other hand, the seeds of *Shorea spp.* disperse by wind and gravity for several ten meters, which is still closed to the mother tree (Takeuchi et al. 2004; Seidler and Plotkin 2006). Thus, selective logging would enhance both the possibility of mating with relatives and the inbreeding (Lee et al. 2000; Murawski et al. 1994).

I also found that the biparental inbreeding value in the seed stage is higher than that in the seedling stage, except in R2. This suggested that inbreeding depression occur at the germination stage in this species. The inbreeding depression occurs in many different stages of plants, such as germination, plant growth and yield (Charlesworth and Charlesworth 1987; Frankham et al. 2002). Our result confirms the previous results in other dipterocarp species, *Neobalacarpus heimii* (Naito et al. 2005; 2008) and *Dryobalanops aromatica* (Lee 2000). The high values of biparental inbreeding in all plots suggest the neighbor trees were more closely related, therefore maintaining the distance of reproductive trees was one of option to reduce consanguineous mating, but I carefully consider to keep the high outcrossing rate and genetic diversity in this option.

Implication for selective logging in lowland dipterocarps forest

Selective logging would reduce the basal of *S. parvifolia* area due significantly affect on the number of pollen donor ($P < 0.05$) (Table 4-4 and 4-5). The effect of basal area on number of pollen donors was relatively stronger in seed samples than in seedling samples. Moreover, selective logging will influence to the mating system of *S. parvifolia*, which resulted reducing pollen dispersal distance and increasing mating among genetically related individual (bi-parental inbreeding). However, the outcrossing rate slightly reduced by selective logging ($P > 0.05$) because the remnant trees (dbh < 50 cm) after logging could keep some alleles in the logged forest (Jenning et al. 2001; Sebbenn et al. 2008) and also can contribute on pollination. It suggested that even in the small size trees with different age classes could some work for mating and maintain the genetic diversity within logged forest. Therefore, the long-term sustainable timber production in managed forest depends on the healthy seed production and regeneration of important forestry tree species. If the seed production and regeneration were not

sufficient, the artificial regeneration (enrichment planting) of timber species in the logged forest is necessary (Arruda et al. 2015).

In our study, selective logging showed the less effective of pollen donor (especially in the R2). This means less genetic diversity, if I repeat selective logging. To recover genetic diversity in the logged forest, some scenario for tropical and neotropical species have been developed (Sebbenn et al. 2008; Ng et al. 2009). For instance, allelic diversity of *S. leprosula* could not recover until 51 years after logging, while tolerable for dbh cutting limit was > 80 cm to preserve 100% allelic diversity (Ng et al. 2009). In Amazon forest, for *Bagassa guianensis* and *Manilkara huberi*, the changing genetic diversity by decreasing limit diameter cutting is higher than the length of the cutting cycle. Thus, both species could maintain 90% or more of its genotypic diversity under 65 year cycles for cutting rotation (Sebbenn et al. 2008). This result indicated to rethink how the genetic diversity of logged forest could be improved through enrichment planting using native species with high genetic diversity of seedling collected from primary forests (Widiyatno et al. 2016), although the main objective of enrichment planting are to improve the value and standing wood stock of secondary tropical forest (Ashton et al. 2001; Schulze 2008; Kettle 2010). Seeds or wildlings for enrichment planting should be collected from a large population size and at least 30 randomly selected mother trees with genetically unrelated (Dvorak et al. 1999, Brown and Hardner 2000; Rogers and Montalvo 2004; Alfaro et al. 2014). Furthermore, the study of mating system of enrichment planting tree should be conducted to measure the effectiveness of pollen flow and mating system to contribute on improving genetic diversity of the next generation in the logged forest.

4.5 Conclusions

I concluded that the selective logging (dbh > 50 cm) with multi rotation maintained the genetic diversity and had a small effect on the mating system of *S. parvifolia* in logged lowland dipterocarp forest. It suggests that selective logging with multi rotation, dbh more than 50 cm, could preserve the density of reproductive tree and maintain outcrossing of *S. parvifolia* rate in the logged forest. Consequently, the genetic diversity and mating system of *S. parvifolia* in the R1 and R2 could support the fitness of offspring to achieve sustainable forest management in the tropical rainforest.

Figure legends

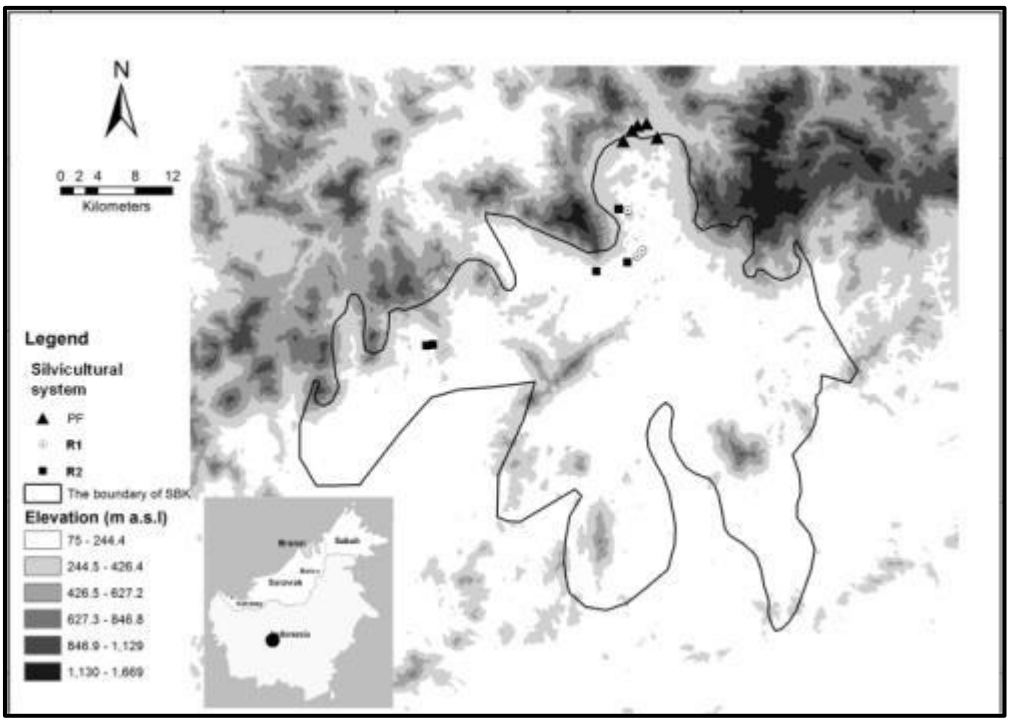


Fig. 4-1. The field site of *S. parvifolia* sample collection

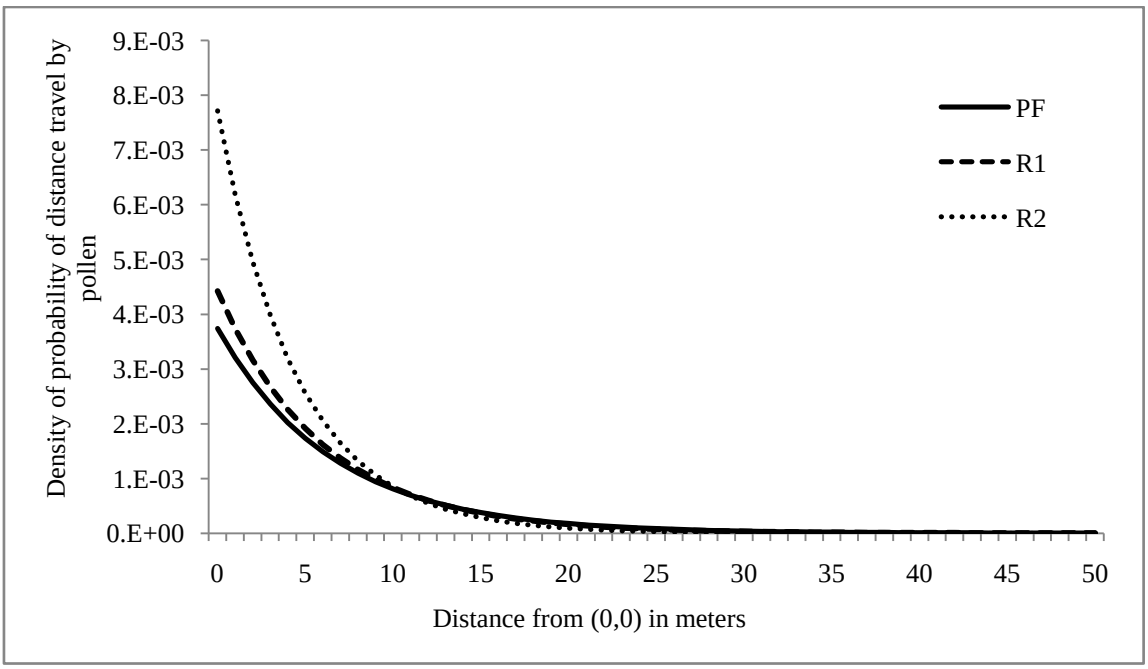


Fig 4-2. Estimated normalized pollen dispersal kernels from model 1. Grey, black and dotted lines indicate dispersal kernels (derived from the posterior means of a and b) for the PF, R1 and R2, respectively

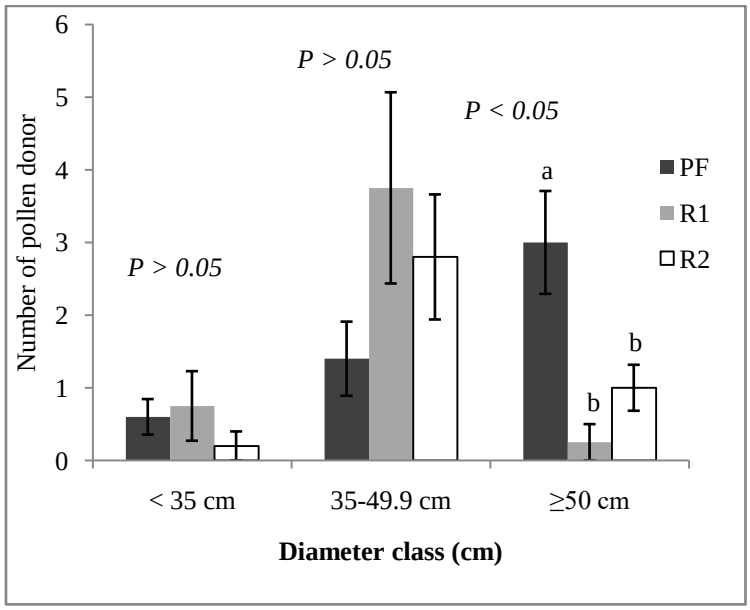


Fig 4-S1. Distribution of pollen donor in various diameter class in various rotation of selective logging (PF: primary forest, R1: first rotation; R2: second rotation of selective logging)

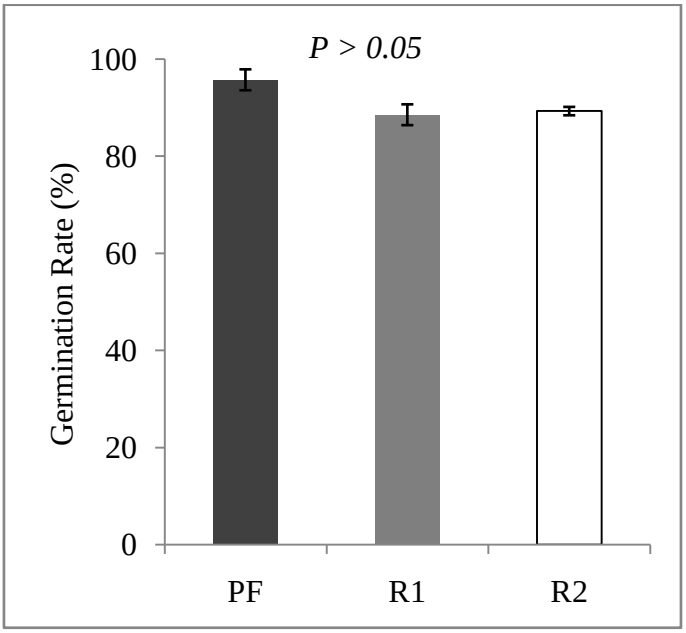


Fig 4-S2. Germination rate of mother trees in various selective logging

Table 4-1. Adjustment of pollen dispersal kernel using pairwise pollen pool differentiation estimates for *S. parvifolia* in various selective logging

Selective logging	Mother Tree	Correlated Paternity	ΦFT	The proportion of allogamous seed sired by pollen donors inside the plot (%)
PF	1	0.43		21.05
PF	2	0.12		12.50
PF	3	0.68		36.00
PF	4	0.35		18.18
PF	5	0.51		32.56
Average		0.42	0.259	24.06
R1	1	0.62		0.00
R1	2	0.55		16.13
R1	3	0.39		34.78
R1	4	0.32		27.27
Average		0.47	0.31	19.55
R2	1	0.41		24.24
R2	2	0.24		2.50
R2	3	0.99		25.00
R2	4	0.34		17.65
R2	5	0.97		11.11
Average		0.59	0.334	16.10

Table 4-2 . Parameter estimate for tree dispersal distance by TWOGENER

		de (tree/ha)	Scale (a)	Shape (b)	Average distance, δ (m)
Normal	PF	0.0018589	9.24	2	11.58
	R1	0.0018220	8.19	2	10.67
	R2	0.0029539	6.43	2	8.06
Exponential	PF	0.0018589	6.54	1	13.07
	R1	0.0018220	6.16	1	12.33
	R2	0.0029539	4.55	1	9.09
Exponential power	PF	0.0018589	6.51	0.998	13.08
	R1	0.0018220	6.11	0.994	12.35
	R2	0.0029539	4.53	0.998	9.10

Table 4-3. Estimate of mating system by MLTR in various rotation of selective logging system

		N	t_m	t_s	$t_m - t_s$	$r_{p(m)}$	Nep
Seed	PF	193	0.959(0.053)	0.602(0.081)	0.357(0.124)	0.330(0.101) a	3.03
	R1	123	0.943(0.044)	0.563(0.057)	0.379(0.055)	0.563(0.055) b	1.78
	R2	170	0.894(0.064)	0.548(0.058)	0.346(0.052)	0.685(0.152) b	1.46
Seedling (after germination)	PF	145	0.973(0.033)	0.633(0.067)	0.269(0.055)	0.318(0.115)	3.14
	R1	145	0.970(0.072)	0.702(0.081)	0.268(0.081)	0.456(0.130)	2.19
	R2	129	0.966(0.035)	0.593(0.064)	0.373(0.073)	0.515(0.137)	1.94

Note: t_m = estimated multi locus outcrossing rate; t_s= estimated single locus outcrossing rate ; $t_m - t_s$ = Biparental inbreeding, mating among relatives ; $r_{p(m)}$ = the correlation of paternity (fraction of siblings that share the same father); Nep = the effective pollen donor

Table 4-4. The estimation of outcrossing rate, a number of tree and pollen donor in each plot by CERVUS

Selecti-ve logging	Mother Tree	No. of samples		Percentage of outcross seed (%)		No. of pollen donor		Density of reproductive tree in plot	Basal area (m2)
		Seed	Seedling	seed	Seedling	seed	Seedling		
PF	1	41	29	78.0	79.3	4	2	16.0	2.8
PF	2	35	32	77.1	87.5	2	1	12.0	3.1
PF	3	27	33	70.4	48.5	6	5	24.0	3.5
PF	4	44	32	88.6	96.9	3	2	14.0	3.3
PF	5	46	31	82.6	83.9	6	4	16.0	3.7
	Average			79.4	79.2	4.2	2.8	16.4	3.3
R1	1	38	32	92.1	100.0	0	0	9.0	0.8
R1	2	44	32	77.3	84.4	3	4	8.0	0.7
R1	3	34	29	100.0	103.4	6	1	12.0	1.2
R1	4	23	33	95.7	97.0	6	5	33.0	3.9
	Average			88.9	92.8	3.84	2.6	15.7	2.0
R2	1	37	25	94.6	100.0	8	4	34.0	4.9
R2	2	46	30	100.0	100.0	2	1	18.0	2.2
R2	3	32	21	71.9	66.7	2	2	6.0	1.4
R2	4	37	23	100.0	100.0	8	7	33.0	4.6
R2	5	18	18	33.3	33.3	3	0	31.0	3.3
	Average			80.0	80.0	4.6	2.8	24.4	3.3

Table 4-5. GlmmML model of outcross rate and the number of pollen donor on basal area of remnant tree *S. parvifolia* in various selective logging

	Intercept			basal			PF vs R1 and R2			PF and R1 vs R2			Random effect		df	R deviance	AIC
	coef	se	p-value	coef	se	p-value	coef	se	p-value	coef	se	p-value	ave	se			
Outcross rate estimated from seed samples																	
Model_O1	-0.187	0.15	0.21	0.009	0.05	0.85							3.50E-12	0.08	11	7.76	13.76
Model_O2	-0.289	0.20	0.15	0.021	0.05	0.68	0.110	0.14	0.44				4.51E-09	0.08	10	7.17	15.17
Model_O3	-0.188	0.15	0.21	0.007	0.01	0.89				0.019	0.15	0.897	3.93E-10	0.08	10	7.74	15.74
Outcross rate estimated from seedling samples																	
Model_O1	-0.119	0.17	0.48	-0.012	0.06	0.82							4.21E-12	0.11	11	11.15	17.15
Model_O2	-0.244	0.23	0.28	0.002	0.06	0.97	0.134	0.16	0.40				1.58E-10	0.11	10	10.45	18.45
Model_O3	-0.118	0.17	0.49	-0.010	0.06	0.86				-0.025	0.17	0.883	5.25E-09	0.11	10	11.13	19.13
Number of pollen donors estimated from seed samples																	
Model _P1	0.443	0.39	0.25	0.323	0.11	0.0031**							3.56E-08	0.20	11	12.5	18.50
Model _P2	0.367	0.42	0.38	0.323	0.11	0.0025**	0.121	0.27	0.66				1.78E-10	0.20	10	12.3	20.30
Model _P3	0.432	0.40	0.27	0.341	0.11	0.0039**				-0.127	0.28	0.657	5.82E-08	0.20	10	12.3	20.30
Number of pollen donors estimated from seedling samples																	
Model _P1	-0.107	0.49	0.83	0.355	0.14	0.0098**							2.42E-06	0.66	11	17.84	23.84
Model _P2	-0.145	0.53	0.78	0.354	0.14	0.0092**	0.066	0.34	0.84				1.23E-05	0.65	10	17.8	25.80
Model _P3	-0.140	0.51	0.78	0.396	0.15	0.0096**				-0.265	0.36	0.464	1.26E-07	0.51	10	17.29	25.29

** : significance levels at 0.0

Table 4-6. Outcrossing rate and gene flow of dipterocarps species

Species	Forest Type	Main Pollinator	Outcrossing rate (%)	Reproductive tree density per Ha	Average gene flow distance (m)	Reference
Dipterocarpus tempheses	Primary forest	Apis	93.0; 96.0	3.95	192; 222	Kenta et al. 2004
Neobalanopcarpus heimii	Primary forest	Apis, Trigona	93.07	0.71	191.2	Konuma et al. 2000
Shorea trapezifolia	Logged forest	Small insect	54.4;61.7	24		Murawski et al. 1994
Shorea leprosula	Primary Forest	Small bettles, thrip	86.85	0.55	369	Fukue et al. 2007
Shorea leprosula	Primary forest	Small bettles, thrip	72.1; 74.5	1.52	60; 154	Tani et al. 2009
Shorea curtisii	Primary forest	Apis	91.7	24	65; 81; 67	Tani et al. 2012
Shorea maxwelliana	Primary forest	Small beetles and weevils	-	3.6	273; 283.	Masuda et al. 2013

CHAPTER 5
GENERAL DISCUSSION

Shorea parvifolia is a commercially important emergent tree of the lowland dipterocarp forest that is widespread in Indonesia (Sumatra and Kalimantan Islands) and other Southeast Asian regions, such as Peninsular Malaysia (Malaysia and Singapore), Sarawak (Malaysia), and Thailand (Newman et al. 1996, Symington et al 2004). STRUCTURE analysis revealed that *S. parvifolia* was clearly divided into two main genetic clusters representing Borneo and Sumatra-Malaysia, with two admixed populations in the Borneo population and one admixed population in the Sumatra-Malaysia population (Chapter 3). A genetic difference between Borneo and Sumatra-Malaysia populations was also reported for others dipterocarp species, i.e., *S. curtisii* (Kamiya et al. 2012) and *S. leprosula* (Ohtani et al. 2013). The separation of these populations was caused by scarcely-forested land connecting Sumatra and Borneo and a predominance of tropical lowland rainforest during glacial periods in the Pleistocene (Iwanaga et al. 2012) along with long-term population persistence and limited seed dispersal (Kamiya et al., 2012). This suggests that the Borneo population of *S. parvifolia* is separate from Sumatra and Malaysian populations.

5.1 Impact of selective logging on genetic diversity of *S. parvifolia*

Selective logging is one of the principal silvicultural systems for management of lowland dipterocarp forests, with the objectives of conserving timber for future use and sustainable forest management (Ratnam et al. 2014). Removing large trees by selective logging changes forest structure and composition as well as the regeneration dynamics of residual trees. Selective logging reduces the number of large trees and the basal area of the forest, where the total reduction in basal area for trees 1 cm DBH within the LOA was more than 50% (Johns 1988; Seng et al. 2004; Lee et al. 2002 and 2007), and damage was spread across all taxa and diameter classes (Johns 1988; Saiful and Latiff 2014). For instance, selective logging removes 24.1% of the total tree species, including rare species and commercial timber trees (Saiful and Latiff 2014). This implies that selective logging will change the distribution and species composition of logged lowland dipterocarp forest due to the reduced density of reproductive trees.

Removing large trees by selective logging alters the density and age class structure of the remaining trees in the logged forest. This change leads to direct losses of genetic diversity, connectivity, and effective population size due to the bottleneck effect, genetic drift, and an insufficient number of seedlings for regeneration (Ledig 1992; Jennings et al. 2001; Finkeldey and Ziehe 2004; Wernsdorfer et al. 2011). In *S. parvifolia*, selective logging also affects the number of private alleles; the difference was not significant among all silvicultural systems but PF was significantly different from other silvicultural systems ($P < 0.05$), while other measures of genetic diversity (*Ne, He, I, Rs*, common and rare alleles) exhibited no significant differences among treatments ($P < 0.05$) (Chapter 3). Especially in R3 (the second rotation with dbh > 40 cm), the allelic diversity indices *R*s and *I* decreased and were much lower than the values for R1 and R2.

The main difference among logging systems is the size of harvested trees: > 50 cm dbh for R1 and R2, and > 40 cm dbh for R3. In R1 and R2, 8 to 12 individuals per ha were harvested, while in R3 harvests were 12 to 16 individuals per ha (Anonymous 2014). Thus, the lower dbh at harvest has a strong negative impact on genetic diversity because remnant trees are relatively small and immature, and thus

reproduction may decline (Tani et al. 2012; Riina et al. 2014). Selective logging is also known to cause negative impacts on genetic diversity in other diperocarps, e.g., *Shorea megistophylla* (Murawski et al. 1994), *S. curtisii* (Obayashi et al. 2002), *S. leprosula* (Ng et al. 2009), and *S. platyclados* (Javed et al. 2014). However, selective logging had no significant effect on genetic diversity in the dipterocarp species *Dryobalanops aromatica* (Kitamura et al. 1994) and *S. ovalis* (Ng et al. 2009). This result suggests that the genetic response of each dipterocarp species to a silvicultural system might differ due to differences in spatial distribution and density, shade tolerance, growth rate, and type of mating system (Ratnam et al. 2014).

S. parvifolia exhibits a clumped, rather than random, distribution of trees under natural conditions (Suzuki et al. 2009; Tito de Morais et al. 2015), and individuals within each clump have a high probability of being genetically similar compared with individuals in other clumps (Takeuchi et al. 2004; Ng et al. 2009). This is because the clumped distribution affects pollinator behavior, resulting in nearest-neighbor pollination and inbreeding (Takeuchi et al. 2004). On the other hand, the fruits of one mother tree can be dispersed a short distance by wind or gravity, reaching surrounding mother trees (Chan 1980; Turner et al. 1997; Curran and Leighton 2000; Takeuchiet al. 2004; Seidler and Plotkin 2006). Therefore, it has been suggested that removal of trees by selective logging should be random, with the purpose of leaving a few individuals behind in each clump. This will ensure the maintenance of stand-scale genetic diversity and, at the same time, reduce the chances of mating among relatives, thus minimizing the effect of inbreeding depression due to biparental mating (Ng et al. 2009)

5.2 Impact of selective logging on the mating system of *S. parvifolia*

The mating system plays a fundamental role in determining the pattern of genetic diversity within and among populations (Hamrick 1982; Barrett 2003) through pollen and seed dispersal (Levin and Kerster 1974). Furthermore, characteristics of the mating system, such as the proportion of outcrossing, influence the genetic makeup of offspring (Robledo-Arnuncio et al. 2004)

Dipterocarps are predominantly outcrossing species (Bawa, 1998; Tsumura et al. 2003) pollinated by insects (Appanah 1979; Appanah and Chan 1981; Bawa 1998; Momose et al. 1998). For outcrossing species, the movement of pollen and seeds plays an important role in increasing genetic variation within a population while reducing the genetic differentiation among populations (Bawa 1998). It is important to understand the reproductive processes of outcrossing plants, as well as to develop methods for conservation of plant populations (Tsumura et al. 2003). Meanwhile, inbreeding, and especially selfing, can result in large reductions in genetic diversity within a population (Bawa 1998; Ingvarsson 2002), increases in the expression of deleterious recessive alleles (Lee et al. 200) and reductions in the survival and growth rates of the next generation (Wang et al. 1999). This suggests that the maintenance of high outcrossing rates is crucial to avoid inbreeding depression in future generations, especially in logged dipterocarp forests (Bawa 1998).

Selective logging reduces the diameter class distribution of reproductive trees in the logged forest, where the remnant forest will be dominated by medium-size trees, while PF is dominated by large trees (Chapter 4). However, reproductive trees in the medium (35–50-cm DBH) and small (DBH < 35 cm) size classes are still present in the LOA. The minimum number of mother trees necessary to maintain genetic diversity for next generation is more than 1 individual that can contribute to the mating system per ha (Jenning et al. 2001; Tani et al 2009).

The observed outcrossing rate of *S. parvifolia* in logged forest is lower than in primary forest, especially in treatment R2 ($P > 0.05$). This difference among populations was due to the genetic pool and number of pollen donors in each plot. The outcrossing rate of dipterocarp species such as *S. parvifolia* depends on the density of reproductive and flowering trees in the forest (Murawski et al. 1990; Murawski and Hamrick 1992; Fukue et al. 2007). Moreover, the flowering period of each dipterocarp species is very short, less than 3 weeks (Ashton et al. 1988; Brearley et al. 2007), and synchronized flowering among individuals of the same species in a certain area can increase the probability of outcrossing.

On the other hand, type and behavior of pollinator are important factors due to their role bringing pollen to conspecific trees in the LOA (Ghazoul et al. 1998). For instance, thrips cannot carry pollen over long distances because these insects are very small and weak fliers (Appanah and Chan 1981; Bawa 1998; Momose et al. 1998; Sakai et al. 1999). On the other hand, bees including honeybees are pollinators capable of carrying pollen long distances (Appanah 1985; Dayanandan et al. 1990). Maintenance of high diversity among *S. parvifolia* offspring depends not only on the number of reproductive and flowering trees, but also on the movement of pollinators.

The outcrossing of *S. parvifolia*, both in the first and second rotation of the logging cycle, was higher than for other dipterocarp species, e.g., *S. megistophylla* (Murawski et al.1994), *Dryobalanops aromatica* (Lee 2000), and *S. curtisii* (Obayashi et al. 2002). This may be due to the clumped distribution of this species at the sampling site and the differences among pollinators of dipterocarp species.

To maintain high genetic diversity of *S. parvifolia* in a logged forest, it is very important to increase mating between unrelated reproductive trees. This will avoid inbreeding and promote high genetic diversity in offspring by maintaining the number of potential pollen donors after logging. The medium size class (35–50-cm DBH) of *S. parvifolia* remained in the forest after logging and could produce pollen for mating (Tani et al. 2012). This suggests that the mating of *S. parvifolia* trees in different age classes might be an efficient way to maintain genetic diversity.

5.3 The importance of enrichment planting using native species to improve genetic diversity and forest productivity

Enrichment strip planting after selective logging adds native species through an artificial regeneration system in logged forests, and thus could increase dipterocarp tree density and productivity. Enrichment planting using native species is advantageous for conservation of both the species themselves and their genetic diversity (Thomas et al. 2014), and can be adapted to the local environment to support biodiversity and ecosystem functions (Tang et al. 2007). Furthermore, enrichment planting will ensure high productivity in the logged forest with very

limited disturbance to the existing LOA ecosystem (Soekotjo 2009; Na'iem and Faridah 2006).

The genetic diversity parameters *N*e and *R*s and the number of rare alleles in enrichment-planted forests were always higher than those in the primary forest. This suggests that enrichment planting may help to preserve genetic diversity in logged forests. If seedling stock (in the form of seeds and seedlings) for enrichment planting is collected from primary forests or buffer zones surrounding large forest concessions, the resulting genetic diversity would ensure successful regeneration and increase productivity in logged forests. On the other hand, if enrichment planting uses material collected from a small number of mother trees and closely related individuals, the fitness of offspring in the next generation might be reduced (Stacy 2001; McKay et al. 2005; Thomas et al. 2014)

Enrichment planting of dipterocarp species, including *S. parvifolia*, increases the standing stock of logged forests and helps to conserve dipterocarps, much like *ex situ* conservation. Moreover, dipterocarp species used for enrichment planting are well adapted to their local environment because the seeds for enrichment planting are collected from forests surrounding the logged forests. This approach is therefore effective at maintaining not only the genetic diversity of dipterocarps but also the tropical rainforest ecosystem in general.

Although enrichment planting is a promising approach, its main constraints when using native species such as dipterocarps are irregular flowering (Appanah 1993; Numata et al. 2003) and recalcitrant seeds (Otsamo et al. 1998). Therefore, the effects of enrichment planting on genetic diversity will depend on both the planting stock and sampling site. The high genetic diversity of *S. parvifolia* found in primary forest sites is useful for developing tree breeding programs to increase the productivity of logged forests. However, breeding activity can reduce overall genetic diversity (Skreppa, 1994); thus, sufficiently diverse breeding stock must be used to maintain genetic diversity.

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