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Photo: Malin Gustafsson

Sebastian Backlund

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Sebastian Backlund

FOREWORD

This is a master thesis about tropical tree ecology in Sabah, Borneo. The opportunity was offered to me by Ulrik Ilstedt (Associate Professor) and Jan Falck (Assistant Professor) from the Department of Forest Ecology and Management, SLU. They are both involved in the INIKEA Forest Rehabilitation Project in Sabah, Borneo, which had an opportunity for a student to perform a master thesis. I thought the idea sounded very interesting for several reasons, first I wanted to go abroad to widen my senses and step outside of my "safe zone". As well, the subject of tropical forest ecology appeals to me and I believe it is an important topic.

Because of and for Göran, Marie, Jonathan, Daniela, Erica, Åsa, Elsa and others who feel met, dedicated to Bengt. I believe in progress, I believe in making better, I believe in the future… Do you and I share the same vision?

ABSTRACT

In the tropics, logging and wild fire can result in degraded secondary forests with lower biodiversity than in the natural forest. One way to limit forest degradation is to rehabilitate the present large areas of secondary forests. However, there is a lack of knowledge concerning the ecology of tropical tree species and further studies would be advantageous for future rehabilitation efforts of degraded rainforest. The objective of this study was to investigate how mother trees in secondary forest and different site factors affect the abundance and spatial distribution of natural regeneration of non-pioneer tree species in a tropical rainforest in Sabah, Malaysia.

The study took place in the INIKEA Forest Rehabilitation Project area, which suffered from wild fire in 1983 and has been selectively logged over both before and after the fire. Natural regeneration and site variables were inventoried in plots, while mother trees were inventoried in the whole survey area. Species were divided into groups used in the INIKEA enrichment planting; *Dipterocarps*, *Non-Dipterocarps* and *Fruit trees* while remaining species were set as *Other timber*. *ArcGIS* was used for positioning natural regeneration and mother trees while the *Spearman Rank Correlation Coefficient* was used for the statistical analysis.

All groups analyzed had a positive correlation between the number of naturally regenerated plants per hectare and the number of mother trees per hectare. The species group *Dipterocarps* had a generally lower regeneration capability than *Other timber*. *Shorea* generally had a lower regeneration capability compared to other *Dipterocarp* genera analyzed in the study. *Dryobalanops spp.* and *Dryobalanops keithii* Sym had fewer naturally regenerated plants on sites which had a lot of natural regeneration from other species. *D. keithii* also had more natural regeneration located to creeks or areas were water flow during heavy rains than on dryer locations, indicating adaptation for more open areas or disturbed locations. *Parashorea tomentella* (Sym) Meijer on the other hand had more natural regeneration located to sites which had a lot of natural regeneration from other species. This may indicate that *P. tomentella* has more shade tolerant properties. *Dryobalanops* indicated longer dispersal ability for natural regeneration than earlier studies have shown. *Parashorea spp.* and *Shorea spp.* showed short dispersal abilities for natural regeneration, a pattern in conformity with earlier studies. An exception was *P. tomentella,* showing dispersal ability up to 75 m. Comparing seed weights and dispersal abilities indicated that shorter dispersal capability is not due to heavier seeds. An indication that the regeneration process in Sabah´s rainforests are worthy of further studies is that in an area of nearly 20 ha 119 species were recorded, which had various regeneration success. Of these, 47 species were found only as mother trees which probably had not regenerated after the wild fire of 1983 and 21 species that had established without any mother trees found within the area of inventory. The result of the present study has contributed to better understanding of the regeneration dynamics of tropical tree species and this new knowledge can be used for improvement of rehabilitation methods.

Keywords: Dipterocarpaceae, Dipterocarps, dispersal, mother trees, natural regeneration, site factors, tropical rainforest.

SAMMANFATTNING

I tropikerna kan skogsavverkning och skogsbrand resultera i degraderade sekundära skogar med lägre biologisk mångfald än i naturskogen. Ett sätt att begränsa skogsdegradering är att skydda och rehabilitera de idag vanligt förekommande stora områdena av sekundära skogar. Det finns dock en brist på kunskap gällande tropiska trädslags ekologi och ytterligare studier skulle förbättra framtida rehabiliteringar av skadad regnskog. Syftet med denna studie var att undersöka hur moderträd i sekundär skog och olika ståndortsfaktorer påverkar förekomst och spridning av naturlig föryngring av icke pionjärträdslag i en tropisk regnskog i Sabah, Malaysia.

Studien utfördes i ett område som tillhör INIKEA Forest Rehabilitation Project. Detta område drabbades av skogsbrand 1983 och har skogsavverkats selektivt både före och efter branden. Naturlig föryngring och ståndortsfaktorer inventerades i provytor, medan moderträd inventerades i hela experimentområdet. Arter delades in i grupper som används i INIKEA:s rehabiliterings-plantering; *Dipterocarps*, *Non-Dipterocarps* och *Fruit trees* medan övriga arter placerades i gruppen *Other timber*. *ArcGIS* användes för att positionera naturlig föryngring och moderträd medan *Spearman Rank Correlation Coefficient* användes för den statistiska analysen.

Alla grupper som analyserats hade en positiv korrelation mellan antalet naturligt föryngrade plantor och mindre träd per hektar och antalet moderträd per hektar. Artgruppen *Dipterocarps* hade en generellt lägre föryngringskapacitet än *Other timber*. *Shorea* hade en lägre föryngringskapacitet jämfört med andra *Dipterokarp*-släkten som analyserats i studien. *Dryobalanops spp.* och *Dryobalanops keithii* Sym hade färre naturligt föryngrade plantor på platser där naturlig föryngring från andra arter förekom i större utsträckning. *D. keithii* hade också mer naturlig föryngring vid bäckar eller områden där vatten flödar vid kraftigt regn än på torrare platser, vilket indikerar en anpassning till mer öppna områden eller störda platser. *Parashorea tomentella* (Sym) Meijer däremot hade mer naturlig föryngring på platser som har mycket naturlig föryngring från andra arter. Detta kan tyda på att *P. tomentella* har mer skuggtoleranta egenskaper. *Dryobalanops* indikerade en längre spridningsförmåga för föryngring än tidigare studier har visat. *Parashorea spp.* och *Shorea spp.* visade sig ha en kort spridningsförmåga för föryngring, mer i likhet med tidigare studier. Ett undantag var *P. tomentella* som hade en spridningsförmåga på upp till 75 meter. En jämförelse mellan frövikt och spridningsförmåga visade att kortare spridningskapacitet inte beror på tyngre frön. En indikation på att föryngringsprocessen i Sabahs regnskogar är värd fördjupade studier är att det på en yta av nästan 20 ha registrerades 119 arter, som hade varierande föryngringsframgång. Av dessa fanns 47 arter bestående av endast moderträd som troligtvis inte hade föryngrat sig efter skogsbranden 1983 och 21 arter som etablerat sig utan att några moderträd hittades inom området. Resultatet från denna studie har bidragit till bättre förståelse av föryngringsdynamik för tropiska trädslag och denna nya kunskap kan användas för att förbättra rehabiliteringsmetoder.

Nyckelord: Dipterocarpaceae, Dipterocarper, moderträd, naturlig föryngring, spridning, ståndortsfaktorer, tropisk regnskog.

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INTRODUCTION

The current rate of biodiversity loss is higher than the assumed natural frequency and it is increasing (Purvis & Hector, 2000). The main causes for biodiversity decline are e.g. climate change, habitat loss and fragmentation, invasive species and land-use change (Thomas, et al., 2004). Biological diversity is valued for several reasons. For example it supplies free ecosystem services like drinkable water, clean air, fertile soils, providing for human civilization and life overall (Ehrlich & Ehrlich, 1992). Human activities as deforestation, one reason for habitat loss, contribute to threaten this diversity (Grainger, 1993). Except the direct threat to species, deforestation cause soil degradation, changes in water flows and increased sedimentation of rivers (Grainger, 1993). This in itself can obstruct regeneration of forests (Grainger, 1993).

In the tropics, instead of clear-cutting, other logging methods are often used like selective logging, but these still have an impact on the ecosystem (Buschbacher, 1990); soils are damaged and there are changes in biomass and species composition (Grainger, 1993). The amount of non-pioneers (long-lived and slow-growing) species decreases (Ashton, et al., 2001). Instead of deforestation, we use the terms degraded or secondary forests for a forest with a lower biodiversity (Chokkalingam & De Jong, 2001). After logging, a forest is in a stage of regeneration, largely through natural processes (Chokkalingam & De Jong, 2001). When performing selective logging the stems most valuable as timber are cut down while others are not harvested. For the tropical forests of Southeast Asia it generally means that it is only allowed cutting down trees with a diameter breast height (dbh) of 60 cm or more, usually trees with a dbh of 120 or more are also forbidden to logging (FAO Forestry Papers, 1989). If the intervals between selective logging are too short, this kind of forestry is unsustainable leading to accumulative disturbances with insufficient time for regeneration (Whitmore, 1998; Meijaard, et al., 2005). Also disturbed forests are more prone to suffer from wild fire (Beaman, et al., 1985), which can severely degenerate the pool of seedlings at the forest floor (Woods, 1989). One way to limit forest degradation and deforestation is to protect and rehabilitate the present large areas of secondary or regrowth forests (Lamb, et al., 2005). Factors that have negative impact on recovery are among others soil compaction, low density of and long distance to non-pioneer mother trees (Whitmore, 1998).

Dipterocarpaceae (Dipterocarps) are evergreen non-pioneer trees dominating the biomass of Southeast Asian tropical rainforests (Appanah & Turnbull, 1998). The family contains of 15 to 19 genera and 470 to 580 species (Appanah & Turnbull, 1998), and the *Dipterocarp* forests are among the richest globally when it comes to flora and fauna (Whitmore, 1975). Luc (2010) recently showed that enrichment planting together with maintenance significantly increase the number of *Dipterocarp* species in degraded areas. This indicates that enrichment planting is a good way to rehabilitate secondary *Dipterocarp* forests and increase tree diversity. She also found that in some areas there might already be enough natural *Dipterocarp* regeneration for the forest to recover. Soil properties and topography have shown to be of importance for the spatial distribution of tropical forest trees (Itoh, et al., 2003a; Baldeck, et al., 2012) and specific site conditions are more favorable to some tropical tree species than others (Ashton, et al., 1995; Palmiotto, et al., 2004).

Studies have shown that spatial variation in water availability in tropical forests results in different seedling mortality across habitats (Ashton, et al., 1995; Comita & Engelbrecht, 2009). According to the studies, location in the topography has an impact on how much moisture the soil holds. Ridges for example tend to be drier than other parts of the topography, especially during droughts (Ashton, et al., 1995). In one study some *Dipterocarp*

species showed soil-related habitat specializations (Palmiotto, et al., 2004). It was suggested that the different responses were not related to nutrient status but rather to water-holding capacity. One possible theory is that nutrient poor soils often contain more sand, also giving the soil lesser water-holding properties (Palmiotto, et al., 2004). A contrasting view is that nutrient availability is a major factor limiting the establishment of tropical tree seedlings on soils degraded by heavy machinery (Nussbaum, et al., 1995). It has also been shown that soil compaction of logging machines disturbs the soil adversely. Tree growth, soil pore distribution (important for water properties), soil nutrient contents and microbial properties are negatively affected by heavy machinery used for skidding (Ilstedt, 2002).

There is support that higher light intensities can increase tree seedling growth and survival of tropical tree species (Romell, 2011). Itoh, et al. (1997) showed results supporting the importance of canopy gaps for survival of two natural regenerated *Dipterocarp* species as both saplings ($1 \leq dbh < 5$ centimeters (cm)) and as poles ($5 \leq dbh < 30$ cm). Apparently increased shading had no negative effect on seedling survival in this study but light may be important for seedlings to evolve into saplings. Another study found that lateral light available in all directions is favorable for *Dipterocarp* seedlings (Bebber, et al., 2002), further emphasizing the importance of light. An earlier study (Itoh, et al., 1997) showed that for the *Dipterocarp* species *Dryobalanops lanceolata* Burck and *Dryobalanops aromatica* Gaertn. F the relationship between seedling density and mother trees were constant within the closest 10 meters (m). After a distance of 10 m the seedling density decreased rapidly and at 30 to 40 m from mother trees it was basically zero. The mean density of saplings and poles peaked at 15 to 20 m from closest mother tree (Itoh, et al., 1997). For *D. aromatica* it has also been shown that the size of trees up to a dbh of 60 cm are positively related to fruiting, while a larger dbh has no further effect on fruiting (Itoh, et al., 2003b). In addition to dbh, fruiting was also correlated to site conditions, such as elevation, slope inclination and soil texture (Itoh, et al., 2003b). More knowledge about tropical tree species is needed, and further studies investigating the relationship between natural regeneration, mother trees and site factors would be advantageous for rehabilitation.

One biodiversity "hotspot" is the Island of Borneo (Figure 1), located in Southeast Asia (Myers, et al., 2000). Previously the whole Island was covered with a rich and diverse tropical rain forest, where the tree layer was dominated by *Dipterocarps* (Falck & Wai, 2010). Today a majority of the forests have been selectively logged over or converted into other uses like oil-palm plantations, also almost a million hectares (ha) were affected by wild fires in 1982 and 1983 (Alloysius, et al., 2010). In 1998 the INIKEA Forest Rehabilitation Project started in Sabah, a Malaysian state located in the northern tip of Borneo Island (Figure 1). The project is a collaboration between the Yayasan Sabah Group (YSG) and the Swedish furniture company IKEA. YSG is a state-owned organization that manages a million ha of forest in Sabah. IKEA, through the Sow-A-Seed Foundation, is together with YSG funding this project with objectives to rehabilitate the forest and improve biodiversity through enrichment planting and liberation treatment using indigenous species in parts of the degraded forest of eastern Sabah (Alloysius, et al., 2010). The Swedish University of Agricultural Sciences (SLU) has been involved from the start providing scientific consultation and performing scientific experiments.

In the INIKEA Forest Rehabilitation Project, two enrichment planting methods have been used; line planting and gap-cluster planting (Alloysius, et al., 2010). The gap-cluster method dominates the rehabilitation and has been used in about two thirds of the replanted area (Alloysius, et al., 2010). Line planting is used in the most degraded forests (Alloysius, 2012). For the enrichment planting a number of different species are used with the aim to enhance

biodiversity (Alloysius, et al., 2010). A random mixture of 70 % *Dipterocarps*, 25 % *Non-Dipterocarps* and 5 % *Fruit tree* seedlings is being planted. In areas where the natural regeneration is still rich a treatment called liberation is used; here enrichment planting is expected to be redundant and to aid the natural regeneration it is cut free from competing vegetation (Alloysius, et al., 2010). These are usually areas that are very steep, located around ridges and near riparian zones (Alloysius, et al., 2010). Ten years into the project an inventory was implemented, it was recognized that the growth of some species varied between different planting spots (Alloysius, et al., 2010), this indicates that site factors may have important influence on growth. The ecological and biological requirements for many of the species used for planting have never been studied (Alloysius, et al., 2010). Others as well have tried to emphasize the importance of further studies, especially for *Dipterocarp* species (Blakesley, et al., 2002). The knowledge gap prevents species from being matched against different site conditions, not maximizing survival and growth increment in enrichment planting.
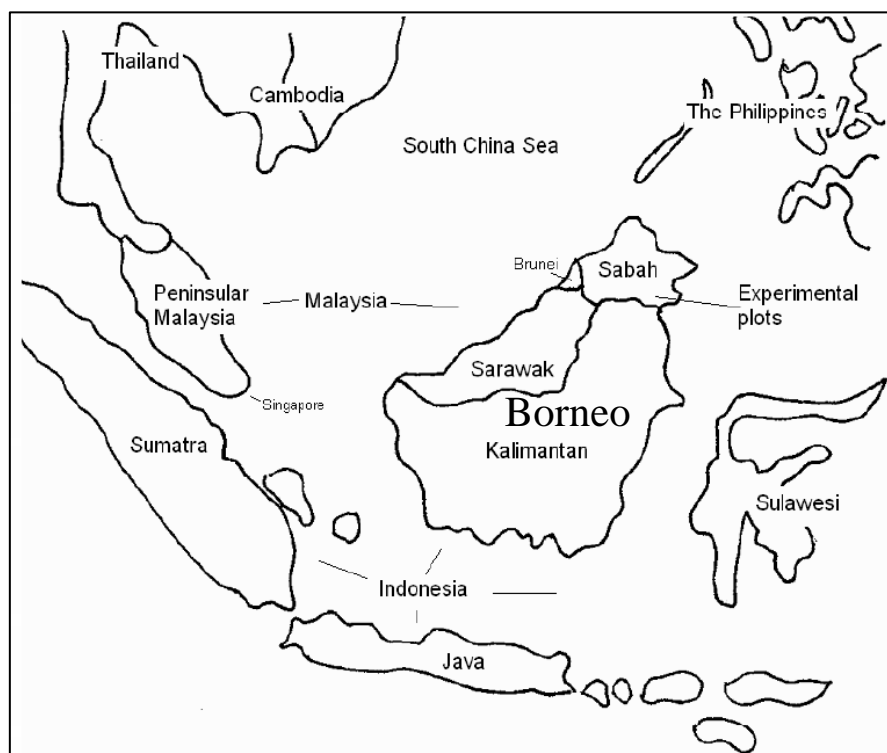
Figure 1. Map over Southeast Asia, location of the island of Borneo with the state boundaries for Malaysia (Sabah and Sarawak), Indonesia (Kalimantan), Brunei and position of experimental plots in eastern Sabah (Forshed, 2006).

Objectives

The objective of this study was to investigate how mother trees and site factors may contribute to the abundance and spatial distribution of natural regeneration of non-pioneer tree species in a tropical rainforest in Sabah, Malaysia. Specifically, I tested the hypotheses that the number of natural regenerated tree plants at a specific location is associated with the number of nearby mother trees, and that the effect decreases at some unknown distance. Furthermore I wanted to see if such relationships differed between species and groups of species present.

MATERIAL AND METHODS

Study area

This study took place in the INIKEA Forest Rehabilitation Project area; located approximately 100 kilometers northwest of the city of Tawau and is one contiguous area of 18.500 ha (Alloysius, et al., 2010). Sabah suffered from severe droughts followed by wild fires in 1983 that affected parts of the area with different intensity (Alloysius, et al., 2010). The project area has been logged over, using selective logging, both before and after the fires (Alloysius, et al., 2010). This has resulted in a degraded tropical forest. Greater parts of the affected area were after the disturbances dominated by pioneer species, like *Macaranga spp.*, with high amount of climbers, lianas and vines (Alloysius, et al., 2010).

Data collection

A survey of possible areas was done before deciding for the actual one. The decisive reason for the chosen area (Figure 2) was that it had a dominating slope that was thought to contain a disturbance gradient from the ridge and downwards, neither enrichment planting nor liberation had been performed in the area. At the ridge the normal treatment would had been liberation, followed down slope by gap-cluster planting and finally line planting (Alloysius, 2012). The survey area was in general less affected by wildfire than the majority of the INIKEA Forest Rehabilitation Project area (Alloysius, 2012).
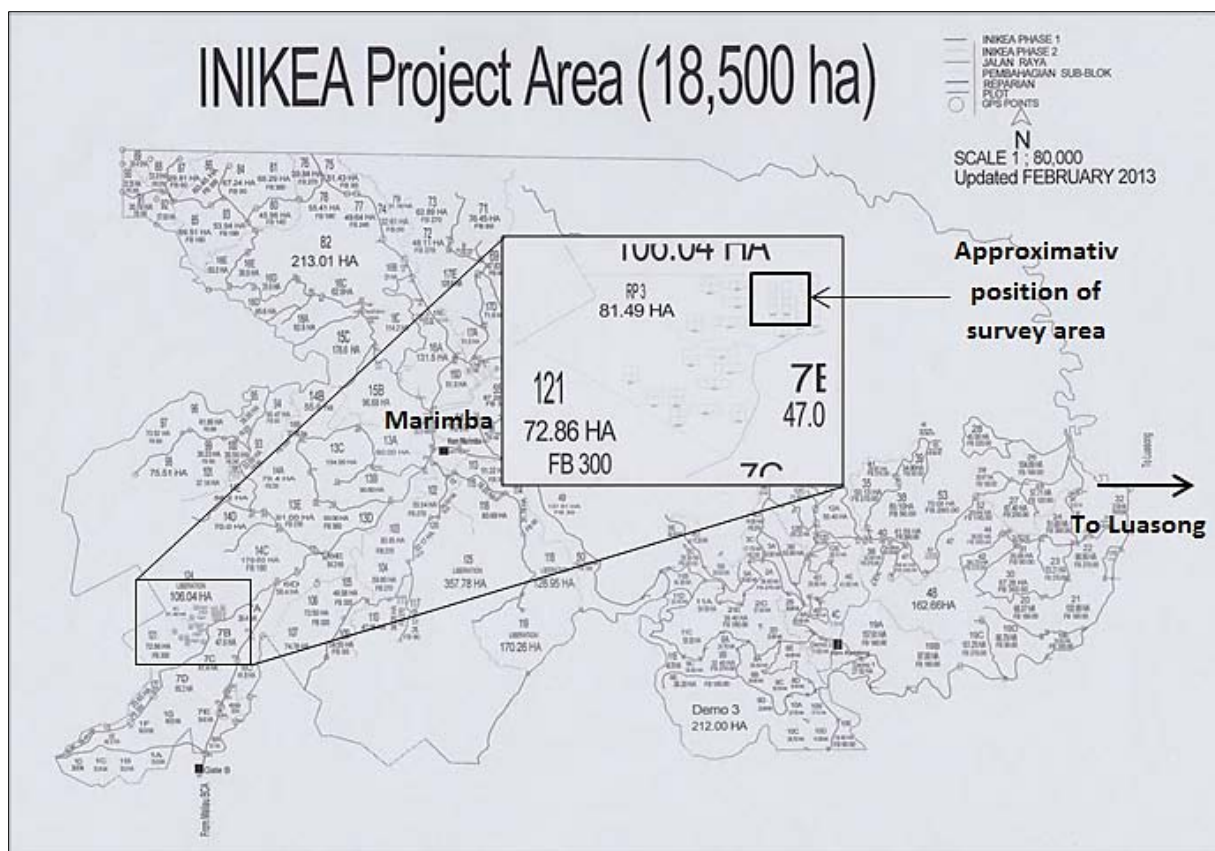
Figure 2. Map of INIKEA Forest Rehabilitation Project area, pointing out location of survey area for master thesis (David Alloysius, Manager of INIKEA Forest Rehabilitation Project).

After positioning my survey area the coordinates of the area was determined. This was done by first locating the closest reference point (M11; explained in experimental design) of my survey area in relation to a point at the road used for access, and thereafter measuring the distance (128.5 m) between these positions in a 180° bearing. The position on the road was marked with a colored wooden stick (approximately 0.5 m in height and made out of the durable Belian wood). At this position an average of four GPS-coordinate positioning's gave a latitude of 4 35 36.0225, longitude of 117 09 34.9680 (global geodetic reference system WGS 84) and an altitude of 319.5 m. Each morning before starting the field work the altimeter was calibrated at this position. The use of GPS inside the forest was too inaccurate, therefore the necessity of reaching the road to be able to measure from the reference position.

Experimental design for natural regeneration and site variables

For the inventory of natural regeneration and site variables a cluster grid was arranged. The plots were arranged four and four (Figure 3) around a grid center point (also called cluster-plot center point), one plot in each cardinal direction. In total 25 clusters, giving 100 plots were deployed in a quadratic grid. Using clusters is more effective than systematically deploy plots in formation (Schreuder, et al., 1993). Smaller sized plots are faster to inventory because they are easier to overview. Also a small plot area made the spatial analysis of natural regeneration towards mother trees more precise, because the positions of the natural regeneration were considered to be in the plot center. A distance of 51 m between each grid
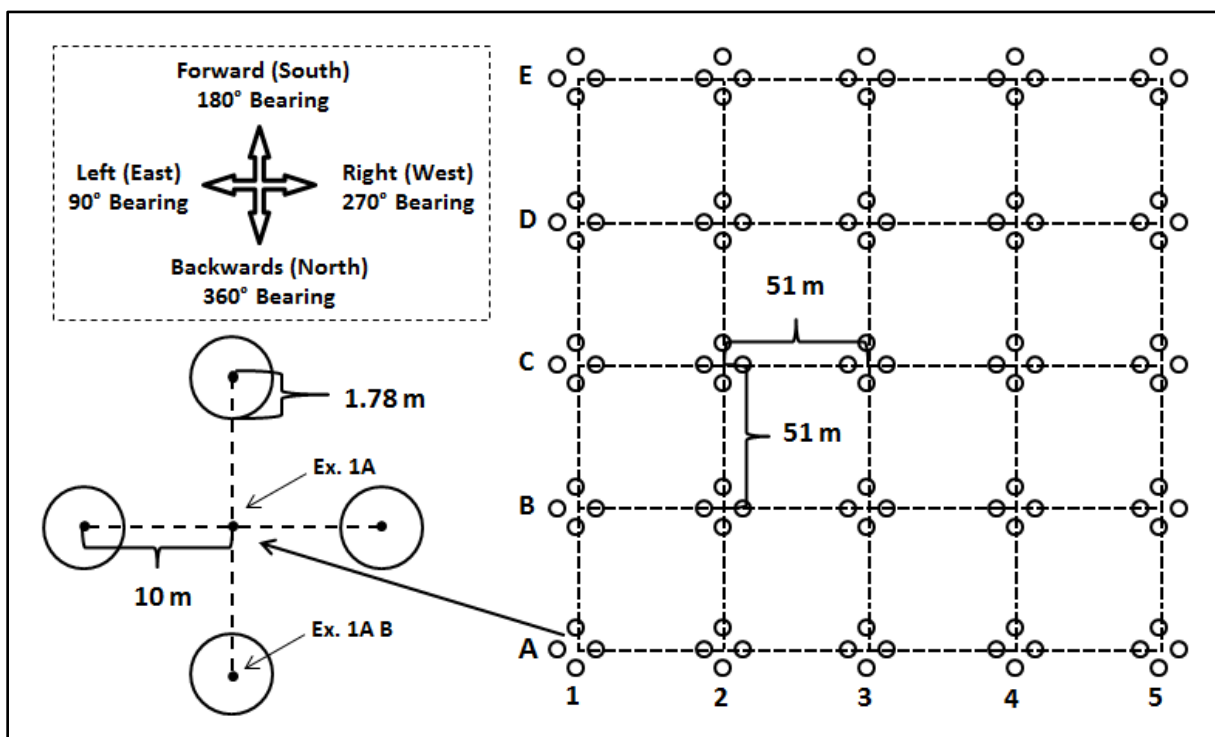
Figure 3. Schematic figure showing spatial deployment of the cluster-plot grid and system of naming the plots in the INIKEA Forest Rehabilitation Project area. The cluster-plots consist of four grouped plots which had its center points positioned 10 m outside the cluster-plot center point in each cardinal direction. The plots had a radius of 1.78 m and thereby an area of 10 m^2. Each cluster-plot was named by a number from to the x-axis and a letter from the y-axis. Each plot was named according to the name of the cluster-plot followed by a letter corresponding to the first letter in its direction (F=Forward, R=Right, B=Backwards and L=Left). The 1A cluster-plot was the first cluster-plot established and the area of interest was located south of this point, therefore Forward came to have the same direction as south.

center point (Figure 3) was chosen to eliminate future statistical faults in terms of a re-inventory after prospective rehabilitation; rehabilitation treatments are made with 10 m intervals. The radius of the plot was 1.78 m (Figure 3) giving a plot area of 10 m^2.

While considering the gradient of interest, deployment of the grid was chosen from the ridge and downwards. A tree on the ridge was chosen as starting point (Figure 4) and from there a randomized distance (between 0-10 m) of 5 m in a 275° bearing (following the ridge) gave the first grid center point 1A.

The distance from grid center point to plot center point was 10 m (Figure 3). The grid center points and plot center points were marked by a colored Belian stick with the center point or plot number written on it. This was done by the INIKEA research team, using a tape measure; trying to measure with consideration of the horizontal distance. Inside the plots the natural regeneration and site variables (Table 1) were noted.

Table 1. Implemented in the INIKEA Forest Rehabilitation Project. Description of site variables and explanation of measurement methods used in the data collection. The variables were chosen to identify environmental descriptors influencing the establishment of natural regeneration. Site variables were measured on each specific plot but because of the cluster-plot method (grouping of plots in four) the data for the plots in a cluster were summed up. Therefore only continuous variables were used making an average for each cluster, with exception of the variable Rehabilitation method which was measured on cluster level in the field

Variable	Unit	Description of variable	Description of measure
Depth organic soil	cm	Continuous variable. Depth of coarse organic litter on top of soil.	Measured close to plot center point with a ruler.
Leaves	%	Continuous variable. Percent leaves covering the plot surface.	Estimated on each plot.
Waterway	%	Continuous variable. Percent of plot area consisting of waterway (creek) or recently heavily affected by running water, e.g. traces of flowing water after heavy rains.	Estimated on each plot.
On road	%	Continuous variable. Percent of plot area consisting of old service roads used at the former logging.	Estimated on each plot.
Close to road	%	Continuous variable. Percent of plot area ≤ 5 m from old service road.	Estimated on each plot.
Undisturbed	%	Continuous variable. Percent of plot area undisturbed by the variables Waterway, Road or Close to road.	Estimated on each plot.
Slope degree	Degrees (°)	Continuous variable. Degree of slope.	Measured on each plot using a slope measurement instrument.
Altitude	m	Continuous variable. Meter above calibration point (319.5 m above sea level).	Measured on each plot using an altimeter (air pressure).
Rehabilitation method	1-3	Class variable. Estimated the most likely rehabilitation method (used in INIKEA Forest Rehabilitation Project).	Estimated for each cluster by INIKEA research team leader.

Because of its decrease in secondary forests this study focused on non-pioneer tree species, only non-pioneer tree species were asked to be noted. Naturally regenerated tree plants that were ≥ 30 cm in height to < 25 cm in dbh were noted (dbh is defined as the diameter of the tree 130 cm above germination point). Species name and size was noted, when the size of the plants was ≥ 30 cm to ≤ 130 cm only height was noted, plants higher than 130 cm was noted by dbh in cm (with one decimal). A measuring rod was used to measure the height while a

tape measure and calipers were used to measure the dbh. The natural regeneration was inventoried by INIKEA research team leader and some of his crew. For both natural regeneration and mother trees a divided stem above breast height was counted as just one tree, if the stem was divided below breast height it was noted as several trees. Dead trees have not been noted.

Site variables

The site variables measured (Table 1) were chosen to identify environmental descriptors influencing the establishment of natural regeneration. The variables were measured or estimated inside each unique plot, or according to its precise proximity.

Experimental design for mother tree inventory

After completing the data collection for natural regeneration and site variables all mother trees were positioned. Earlier studies, including only a few species, suggest that dbh size for fruiting *Dipterocarps* are approximately 30 cm (Itoh, et al., 1997; Itoh, et al., 2003b). In this study the cut off measurement between natural regeneration and mother trees were set to a dbh of 25 cm, given mentioned studies, with a 5 cm margin to minimize the risk of missing any mother tree. Thus was mother trees defined as non-pioneer species ≥ 25 cm in dbh positioned inside the cluster-plot grid and outside with a buffer zone of 100 m.

The buffer of 100 m was chosen because of the possibility that natural regeneration could have its origin not only from mother trees inside the cluster-plot grid but also from outside. For each mother tree, species name (both Malay and scientific), dbh, altitude, slope, direction of slope, reference point, bearing to reference point, distance to reference point and annotator were noted.

The reference points used inside the cluster-plot grid to position mother trees were the wooden sticks marking cluster center points and plot center points. Outside the grid new reference points were deployed (Figure 4). These were named with the letter M (for mother trees) followed by an individual number. At the cluster-plot grid margin a plot would be positioned 10 m outside the cluster-plot center point, these 10 m plus the radius of the plot of 1.78 m gives a total of 11.78 m. This is the reason for the mother tree buffer zone to reach 112 m outside the cluster center points (Figure 4). In the corners the diagonal distance was longer than 112 m; this was not taken into consideration because of the complexity to measure which trees were inside the 112 m. Distances to the reference points differ on the left and right side (Figure 4). At first an extra column of cluster-plots was planned (column 6 in Figure 4) and wooden sticks were placed out for the cluster center points and plot center points. These positions were not used for inventory of natural regeneration or site variables but used as reference points for mother trees. The data collection was done in November and December 2012.
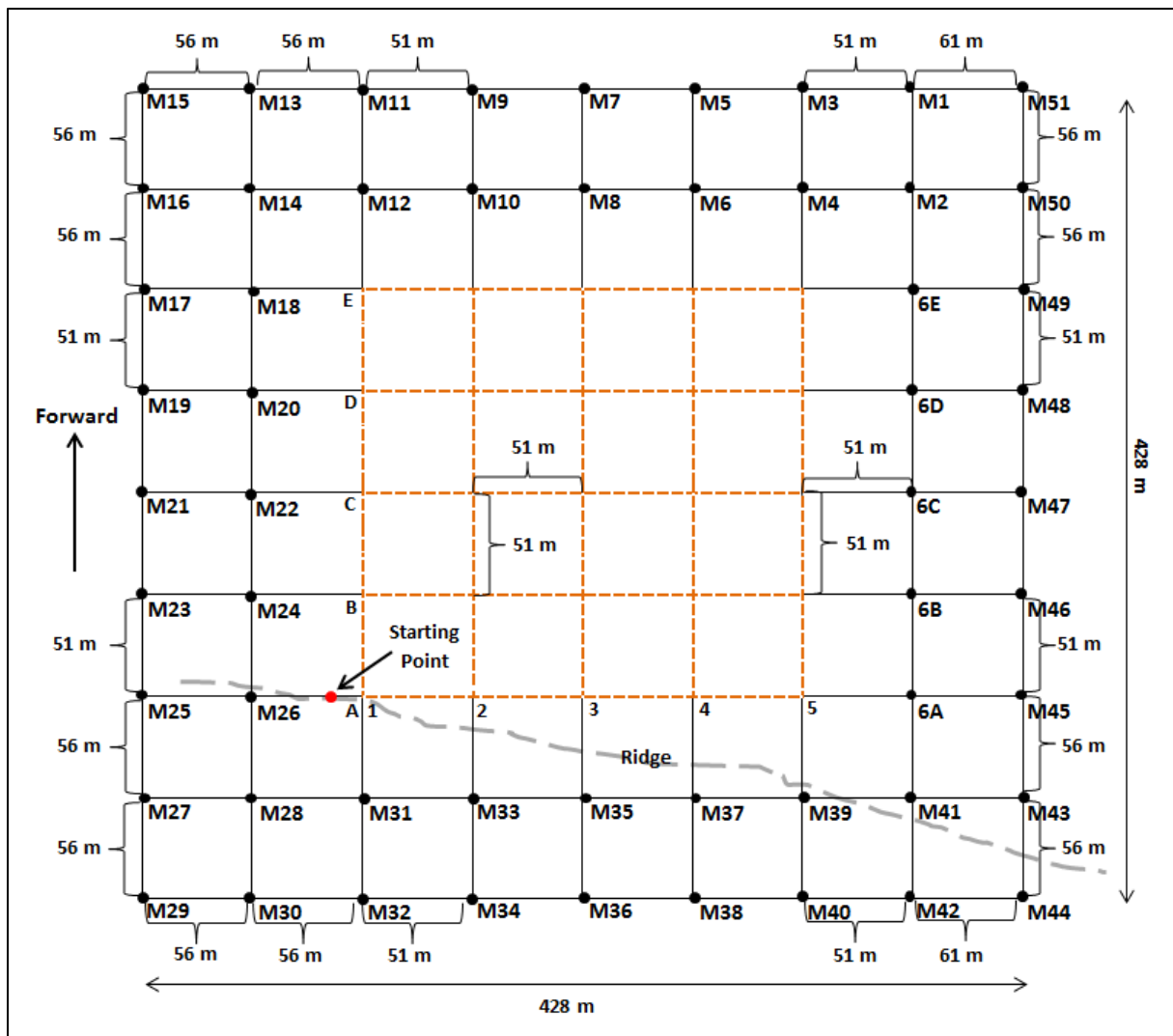
Figure 4. Schematic figure, INIKEA Forest Rehabilitation Project area, showing distances and deployment of reference points used for positioning of mother trees. The mother trees were positioned by measuring distance and bearing to a suitable reference point, which were earlier mutually positioned with known distance to each other. Orange area (dashed line making up a grid) is the cluster-plot grid (see Figure 3). The red dot indicates the approximate position of the grid starting point (a tree) from which a randomized distance gave the first cluster-plot center point (see Figure 3), from which the rest of the survey area was laid out. A dashed line represents the approximate position of one of the ridges in the area; it was the upper point of a slope determining the positioning of the survey area. Forward indicates in which direction the cluster-grid was positioned and inventoried, also indicating the direction of south.

Structuring of data

Each plot and mother tree was given its unique position in relation to the south west corner of the study area. Five mother trees had a suspected improper reference point but were still assessed to contribute to the analysis and were retained in the data set (Ilstedt, 2013). One mother tree had a dbh smaller than 25 cm; this was probably a clerical error because mother trees with a dbh smaller than 25 cm were not to be noted and was therefore retained in the data set. Five other mother trees were given an obviously incorrect position by ending up outside the survey area. It was assessed that mother trees with a not too inaccurate position would contribute more to the analysis retained in the data set than being removed (Ilstedt, 2013). Therefore, trees more than 5 m outside the survey area were decided to be excluded.

Due to this exclusion two mother trees were removed from the data set. For the descriptive statistics a selection of species was done. It was based on the following criteria: Species (1st) have mother trees, and (2nd) do not set seed before 25 cm in dbh. For the ratio of natural regeneration (NR) and mother trees (MT) per hectare, species included had both NR and MT and suited the second criteria. In the statistical analysis the species included could have only MT, only NR or both and the criteria that the species included do not set seed before 25 cm in dbh was still implemented. A grouping of the species was also done according to the enrichment planting species categories used in the INIKEA Forest Rehabilitation project (Alloysius, et al., 2010); this includes *Dipterocarps*, *Non-Dipterocarps* and *Fruit trees*. Species that do not fit these categories were set as *Other timber* (OT). *Non-Dipterocarps* are commercial species important for logging or as non-timber products; *Fruit trees* are species giving fruit for human consumption or as food for bigger mammals and birds.

From the raw data, the number of NR and MT for each scientific species was compiled. The accumulated values for NR ha^{-1} and MT ha^{-1} were done starting with the species with lowest MT ha^{-1} and then with ascending accumulation. All the coordinates of the NR and MT were positioned into the computer program *ArcGIS*; giving maps were spatial relations could visually be analyzed. Species were named both according to Malay and scientific names. For some trees a Malay species name could not be scientifically specified and could actually be an entire family, genus or two scientific species. These not scientifically specified species were still included in the analysis. The distinction of which species most possibly set seed before 25 cm in dbh was given to me by INIKEA research team leader (Lojingi, 2012).

Statistical analysis

Because of the cluster method the four plots in a cluster will be relatively strongly dependent of each other; having a shorter distance between them than to other plots. Observations that are strongly dependent of each other cause faults when implementing statistical analyses. Also, the amount of data when dividing into species or genus/groups were too low (Ranneby & Kuljus, 2013). Therefore, the regeneration for each cluster was summed up, giving 25 observations instead of 100. Given this, the continuous site variables could be used making an average for each cluster (Table 1). For class variables averages are difficult to implement correctly and hence were not included in the statistical analysis.

For the statistical analysis the species with the highest NR from three different *Dipterocarp* genera were compared with its specific whole genus (Table 2). *Dipterocarp* species were chosen because of their dominance and importance to biodiversity (Whitmore, 1975) and because of their use in the INIKEA enrichment planting (Alloysius, et al., 2010). *Dryobalanops spp.* and *Parashorea spp.* contained only two and three species respectively, whereas *Shorea spp.* included at least 20 species. *Dryobalanops keithii* Sym and *Parashorea tomentella* (Sym) Meijer was dominating their respective genus while *Shorea parvifolia* Dyer made up approximately a quarter of the genus NR. Also the group *Fruit trees* was included in the analysis because it is used in the INIKEA enrichment planting (Alloysius, et al., 2010) and possibly contains similar properties, although the species are not related.

The natural regeneration were divided into four classes; Seedlings (30-130 cm in height), Saplings (0.1-10 cm in dbh) and Poles (10.1-24.9 cm in dbh) and total number of natural regeneration (in consultation with Ilstedt (2013)). As a variable in the analysis, regeneration for all other species than the examined group/species in a specific cluster (Other regeneration (OR)) were divided into above classes. In *ArcGIS* a tool called *Point distance* was used to

calculate all distances from cluster center points (the center for the aggregated "cluster plot") to mother trees. This data was divided into classes of 25 m "concentric rings" and different "circular distances" starting from cluster center point, ex. 0-50 m or 0-75 m (Figure 5). To accomplish this, a function called *Frequency* in *Excel* was used, giving the count of mother trees in each "concentric ring" or "circular distance" from cluster center point.

Table 2. Metadata for species/groups used in the statistical analysis. The genus analyzed includes the specific species from the same genus that were also independently analyzed. Natural regeneration (NR) is the total number of naturally regenerated tree plants (≥30 cm in height to < 25 cm in diameter breast height (dbh; diameter 130 cm above germination point)), values in brackets are per hectare and values without brackets show registered values in whole experimental area (Mother trees) as well as in total plot area (Seedlings, Saplings, Poles and total NR). Species included in groups do not likely set seed before 25 cm in dbh (Lojingi, 2012). Seedlings were defined as non-pioneer tree species ≥30 cm in height to 130 cm in height, Saplings as 0.1 to 10 cm in dbh and Poles as 10.1 to 24.9 cm in dbh. Mother trees were defined as non-pioneer tree species ≥ 25 cm in dbh

Species/group	Number of					
	Species	Seedlings	Saplings	Poles	NR	Mother trees
Dryobalanops spp.	2	67 (670)	9 (90)	3 (30)	79 (790)	139 (7.59)
Dryobalanops keithii	1	55 (550)	5 (50)	1 (10)	61 (610)	82 (4.48)
Parashorea spp.	3	122 (1220)	13 (130)	3 (30)	138 (1380)	147 (8.02)
Parashorea tomentella	1	103 (1030)	8 (80)	0 (0)	111 (1110)	89 (4.86)
Shorea spp.	20[1]	30 (300)	24 (240)	6 (60)	60 (600)	283 (15.45)
Shorea parvifolia	1	7 (70)	6 (60)	2 (20)	15 (150)	69 (3.77)
Fruit trees	14	22 (220)	44 (440)	5 (50)	71 (710)	147 (8.02)

[1]*Shorea spp.* includes species with Malay names which does not correspond to one specifically scientific species and may therefore include more species than 20.
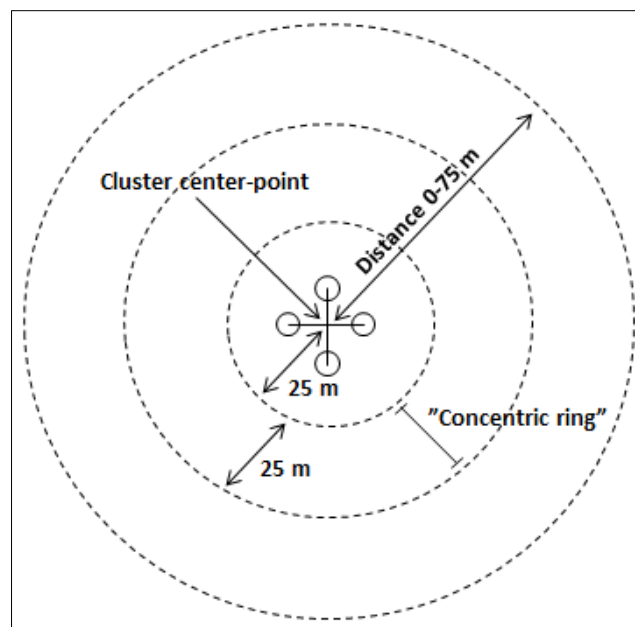
Figure 5. Schematic figure, INIKEA Forest Rehabilitation Project area, showing example of "concentric rings" and "circular distance" for statistical analysis, viewed from cluster-plot center point (see Figure 3). The "concentric rings" were 25 m wide with the first one starting from each cluster-plot center point. The "circular distance" always started from a cluster-plot center point with a distance of 25 to 125 m with 25 m intervals.

Data concerning natural regeneration, other regeneration, count of mother trees at different distances and averages for continuous site variables were transferred to the statistical software *Minitab* for analysis. *The Spearman Rank Correlation Coefficient* was used to analyze possible correlations, using total natural regeneration as response variable because of the few numbers of observations. *The Spearman Rank Correlation Coefficient* was used instead of *Pearson product moment correlation coefficient* since the data was not normally distributed (parametric) (Ranneby & Kuljus, 2013), and because of many null values (Bluman, 1997). The computations for the rank correlation coefficient involve ranking of each variables set of data (Bluman, 1997). This makes them more robust and accepting against outliers but more imprecise, therefore values given in the computation cannot be interpreted exactly (Hollander & Wolfe, 1999; Ranneby & Kuljus, 2013). The rank correlation is also adapted to non-linear relations (Ranneby & Kuljus, 2013), which intuitively is more likely in nature.

RESULTS

Natural regeneration and mother trees

A total of 119 Malay named species were found in the survey, whereof 92 were corresponding to a specific scientific species. Twenty one of the Malay named species was found to have only natural regeneration, 47 were only found as mother trees and 51 species had both natural regeneration and mother trees. According to the criteria specified in material and methods for the descriptive statistics *Dipterocarps* includes 29 Malay named species, *Non-Dipterocarps* 7 Malay named species, *Fruit trees* 14 Malay named species and *Other timber* 16 Malay named species (Appendix 1). For all species, including those that most likely set seed before 25 cm in dbh, a total number of 10 270 natural regenerations (NR) per hectare and 74.3 mother trees (MT) per hectare were found (Appendix 1). Excluding those that most likely set seed before 25 cm in dbh gave a total number of 7 800 NR ha^{-1} and 73.6 MT ha^{-1} (Appendix 1). Thirteen of the Malay named species found in the survey did most likely set seed before 25 cm in dbh (Lojingi, 2012).

Figure 6. Natural regeneration (NR) per hectare and mother trees (MT) per hectare for species divided into groups used in the enrichment planting in the INIKEA Forest Rehabilitation Project (Alloysius, et al., 2010). NR was defined as non-pioneer tree species ≥30 cm in height to < 25 cm in diameter breast height (dbh; diameter 130 cm above germination point) and MT as non-pioneer tree species ≥ 25 cm in dbh. Species included in groups do not likely set seed before 25 cm in dbh (Lojingi, 2012). *Non-Dipterocarps* are commercial species important for logging or as non-timber products, *Fruit trees* are species giving fruit for human consumption or as food for bigger mammals and birds and *Dipterocarps* are species belonging to the family of Dipterocarpaceae. Species that do not fit these categories are set as *Other timber*.

There were differences among the INIKEA enrichment planting species groups (Alloysius, et al., 2010) concerning NR ha^{-1} and MT ha^{-1} (Figure 6). All *Dipterocarp* species except two did not exceed 200 NR ha^{-1}, they ranged from 200 NR ha^{-1} down to almost 0 NR ha^{-1} (Figure 6).

These species ranged from 0.7-3.8 MT ha^{-1}. *Dipterocarps* had two species found as extreme values; *Parashorea tomentella* (Sym) Meijer had 1110 NR ha^{-1} and 4.86 MT ha^{-1} and *Dryobalanops keithii* Sym had 610 NR ha^{-1} and 4.48 MT ha^{-1} (Appendix 1). They had both far more NR ha^{-1} and MT ha^{-1} than the other *Dipterocarps*. The *Non-Dipterocarp* species were distributed between 60-140 NR ha^{-1}, and ranged between 0.2-5.7 MT ha^{-1} (Figure 6). The *Fruit trees* had a similar relation between NR and MT as the *Dipterocarps* (excluding the two extreme values), most of them had relatively low numbers in both NR ha^{-1} and MT ha^{-1} (Figure 6). Many species included in *Other timber* showed low values for both NR ha^{-1} and MT ha^{-1} (Figure 6), while some species in the group had higher NR ha^{-1} and MT ha^{-1} with a distribution in the range of 160-510 NR ha^{-1} and 0.3-1.9 MT ha^{-1}. *Other timber* had one extreme value of 560 NR ha^{-1} and 5.59 MT ha^{-1}.

The groups also showed differences for the accumulated NR and MT per ha (Figure 7). It was found that *Other timber* had a steeper curve for the number of accumulated NR ha^{-1} and MT ha^{-1} than any other group (Figure 7). For *Dipterocarps* to accumulate 2000 NR ha^{-1} they needed approximately 20 more MT than *Other timber* (Figure 7), almost a factor of three. *Fruit trees* and *Non-Dipterocarps* seemed to have a similar curve as *Dipterocarps* (Figure 7); however, these curves were shorter partially due to fewer species.
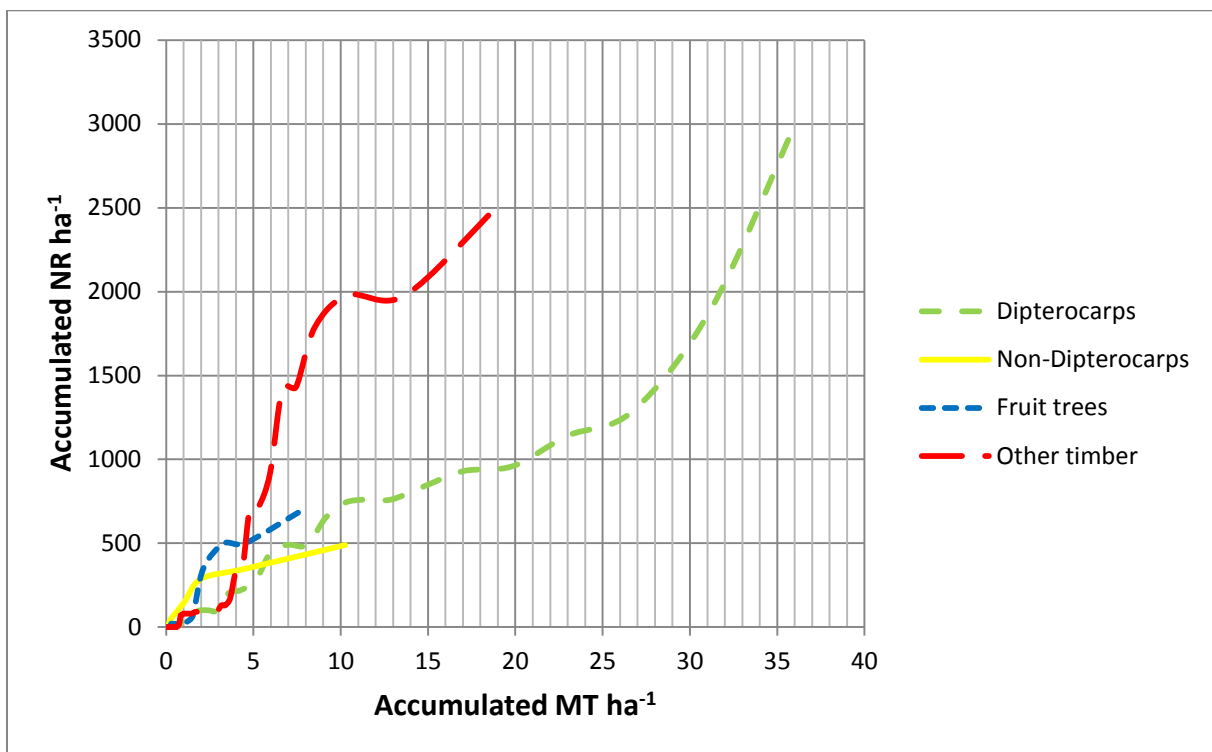
Figure 7. Accumulated natural regeneration (NR) and mother trees (MT) per hectare for species divided into groups used in the enrichment planting in the INIKEA Forest Rehabilitation Project (Alloysius, et al., 2010). Definitions as in Figure 6. Starting with the species which had lowest MT per ha. Species included in groups do not likely set seed before 25 cm in dbh (Lojingi, 2012).

The Spearman rank correlation showed that *Dipterocarps* and *Other timber* had a positive correlation between NR ha^{-1} and MT ha^{-1} at a P-value of 0.000 (Table 3). *Non-Dipterocarps* and *Fruit trees* also showed a positive correlation but at a P-value of 0.014 and 0.018 separately (Table 3), they also had fewer observations (number of species).

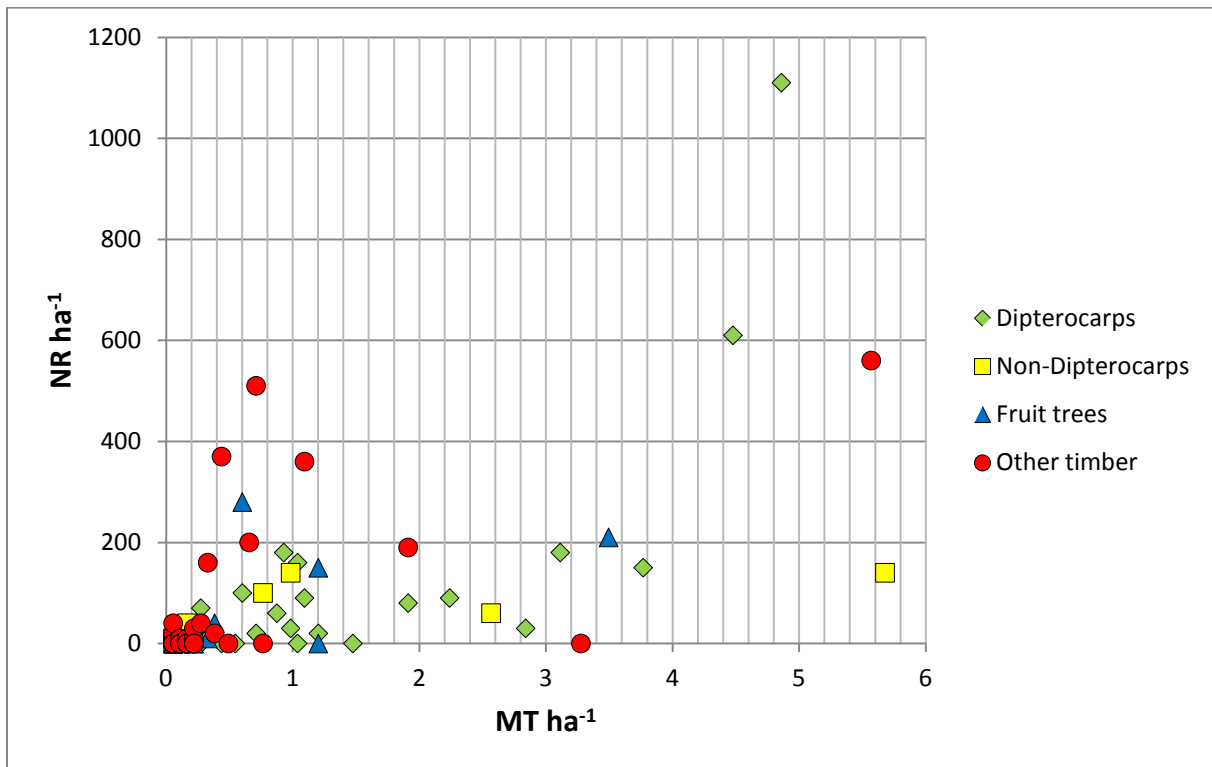Table 3. Spearman rank correlation coefficient for natural regeneration (NR) per ha and mother trees (MT) per ha for species divided into groups used in the enrichment planting in the INIKEA Forest Rehabilitation Project (Alloysius, et al., 2010). Definitions as in Figure 6. Species included had MT and do not likely set seed before 25 cm in dbh (Lojingi, 2012). Number of species infers to number of observations

Group	Number of species	Correlation	P-value
Dipterocarps	29	0.713	0.000
Non-Dipterocarps	7	0.855	0.014
Fruit trees	14	0.620	0.018
Other timber	16	0.514	0.000

Species that represent the above mentioned groups had a variety in the ratio of NR MT^{-1} ha^{-1} (Figure 8). The ratio showed *Mallotus sp.* at the top with approximately 847 NR MT^{-1} ha^{-1} and *Shorea johorensis* Foxw at the bottom with approximately 11 NR MT^{-1} ha^{-1}. The species having above 250 NR MT^{-1} ha^{-1} were dominated by *Other timber,* whilst no *Dipterocarp* species reached over 257 NR MT^{-1} ha^{-1} (*Shorea faguetoides* Ashton). The *Dipterocarps* were evenly distributed from *S. faguetoides* down to *S. johorensis* in the interval of 11-257 NR MT^{-1} ha^{-1} (Figure 8). Also in the similar range all the *Non-Dipterocarps* species encountered could be found, but they were somewhat divided into two groups in the range. *Lithocarpus, Quercus* and *Eusideroxylon zwageri* Teijsm. & Binn had around 24 NR MT^{-1} ha^{-1} at the lower end and the four other *Non-Dipterocarps* (*Koompassia excelsa* (Becc) Taub*, Pentace laxiflora* Merr*, Aquilaria malaccensis* Lamk and *Heritiera simplicifolia* (Mast.) Kost.) were somewhat grouped around 130-244 NR MT^{-1} ha^{-1} (Figure 8). Two *Fruit trees*, *Diospyros spp* and *Sindora beccariana* baker or *Sindora iripicina* de Wit, had relatively high (466 and 366) NR MT^{-1} ha^{-1} compared to the other *Fruit trees* which ranged from approximately 31-125 NR MT^{-1} ha^{-1} (Figure 8).

The number of NR was shown to be different among species found in the plots, the distribution also varied between seedlings, saplings and poles (Appendix 1). This includes species that do not likely set seed before 25 cm dbh. The numbers ranged from the highest value for the entire study for seedlings at 103 to no seedlings, saplings varied from 40 to no saplings and poles from 4 to no poles (Appendix 1). The amount of species having equal or more saplings than seedlings was approximately 60 percent (Appendix 1). From the species that do not likely set seed before 25 cm in dbh, 13 Malay named species had only NR and 47 had only MT.
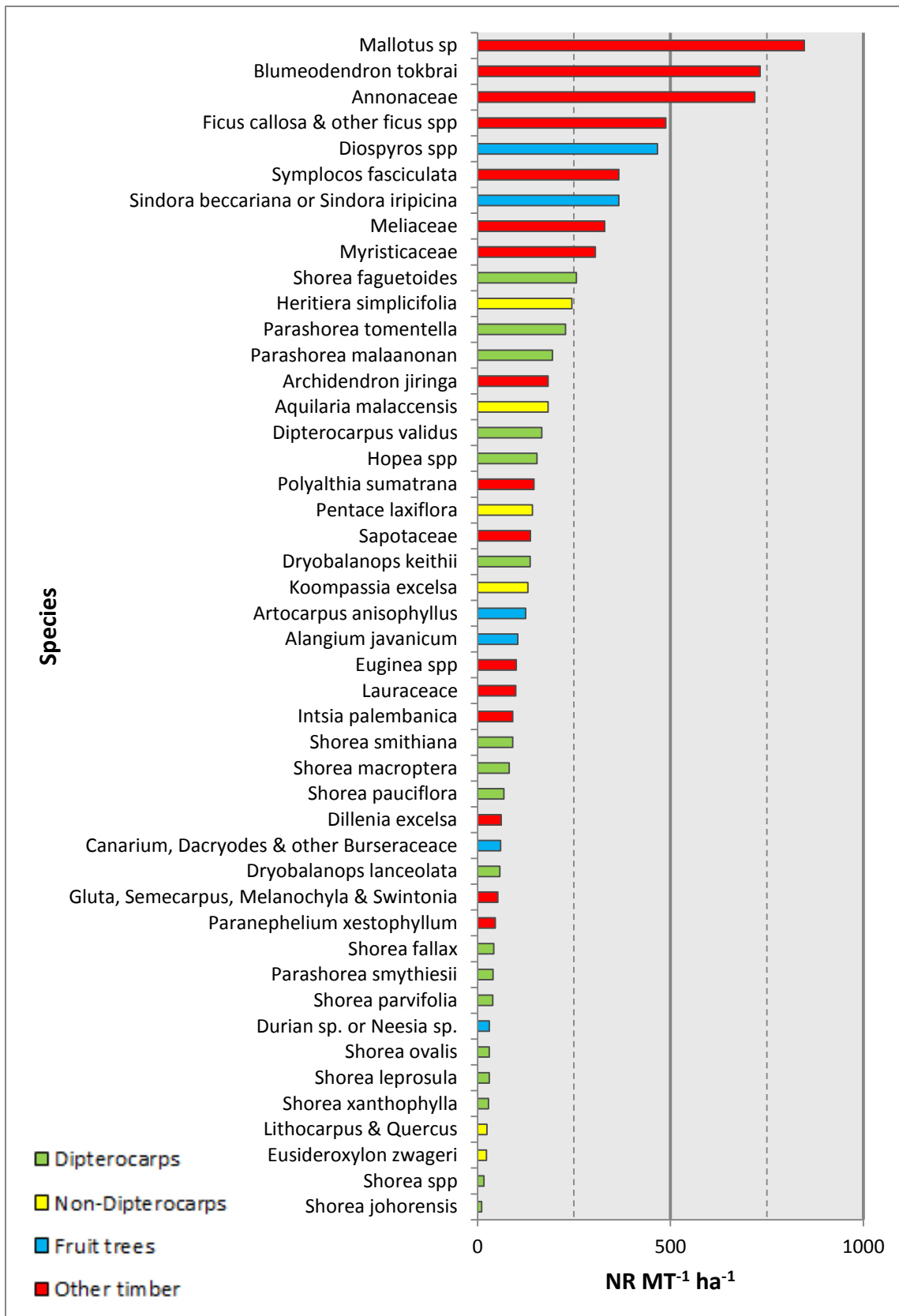
Figure 8. Ratio of natural regeneration (NR) and mother trees (MT) per hectare, color indicates division into species groups used in the enrichment planting in the INIKEA Forest Rehabilitation Project (Alloysius, et al., 2010). Definitions as in Figure 6. Species included has both NR and MT and do not likely set seed before 25 cm in dbh (Lojingi, 2012).

Spatial distribution of mother trees and regeneration

The spatial distribution of MT and NR varied between species and groups of species. Both MT and NR of *P. tomentella* was located mainly to the north-western side of the survey area (Figure 9). Another smaller grouping of MT could be seen at the eastern side with some NR around cluster 1C and 1D. In the middle of the cluster area (green dots are plots, a group of four make up a cluster) there was neither MT nor NR; the similar trend could be seen in the south of the cluster area. In the south, outside the cluster area there was some presence of MT (Figure 9). For the map showing *Parashorea spp.* (all *Parashorea* species found combined; in total three species (Table 2)) there were an even greater dominance of MT in the northwest corner (Appendix 2). The grouping added some NR in the north-eastern corner of the cluster area and some in the south. Still to a great extent MT and NR were missing in the central and southern parts of the cluster area (Appendix 2).
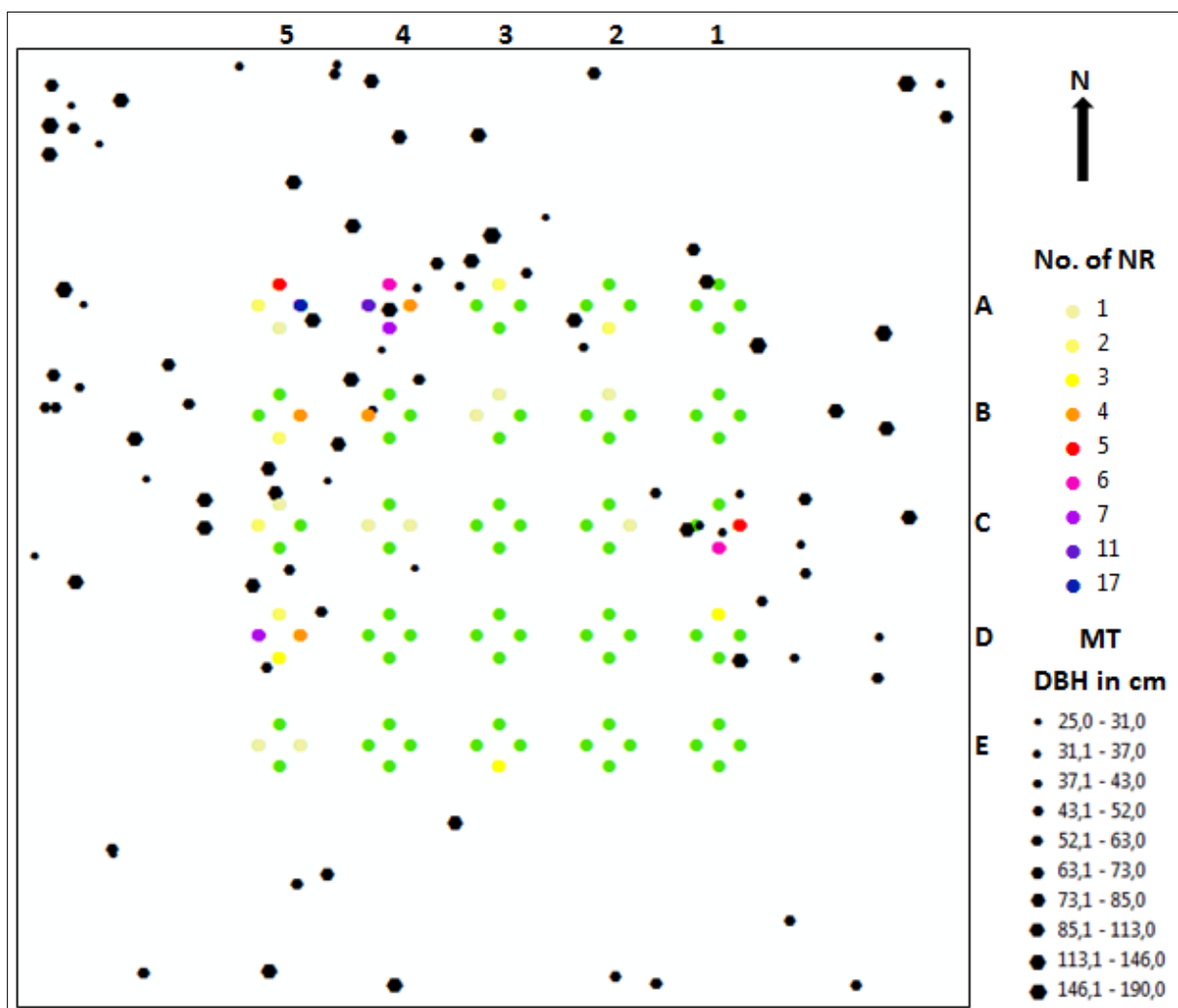
Figure 9. Map showing natural regeneration (NR) and mother trees (MT) for *Parashorea tomentella* (Sym) Meijer. Definitions as in Figure 6. Black dots are MT, green dots are sample plots without any NR and dots with other colors are sample plots with different numbers of NR. The sample plots are 10 m² circular plots which were inventoried for NR and site conditions. Numbers and letters in the margin show the system of naming a specific plot cluster, which is the grouping of four sample plots.

D. keithii showed an opposite pattern to *P. tomentella*, with NR and MT located to the central and southern parts of the cluster area (Figure 10). Only three plots containing NR from both species could be found. In the south and west, outside the cluster grid groupings of MT were found. *Dryobalanops spp.* (two species, (Table 2)) added some NR, but still the occurrence is very low in the western, north-western and north-eastern parts of the cluster grid (Appendix 3). Compared to other species and species groups, NR and MT for *Shorea spp.* seemed to have a relatively uniform distribution in the survey area except in the central and southern parts of the cluster grid (Appendix 4). In that area there was a reduction of NR and MT. In comparison, *Fruit trees* also seemed to have a relatively uniform distribution of NR and MT across the whole survey area (Appendix 5).
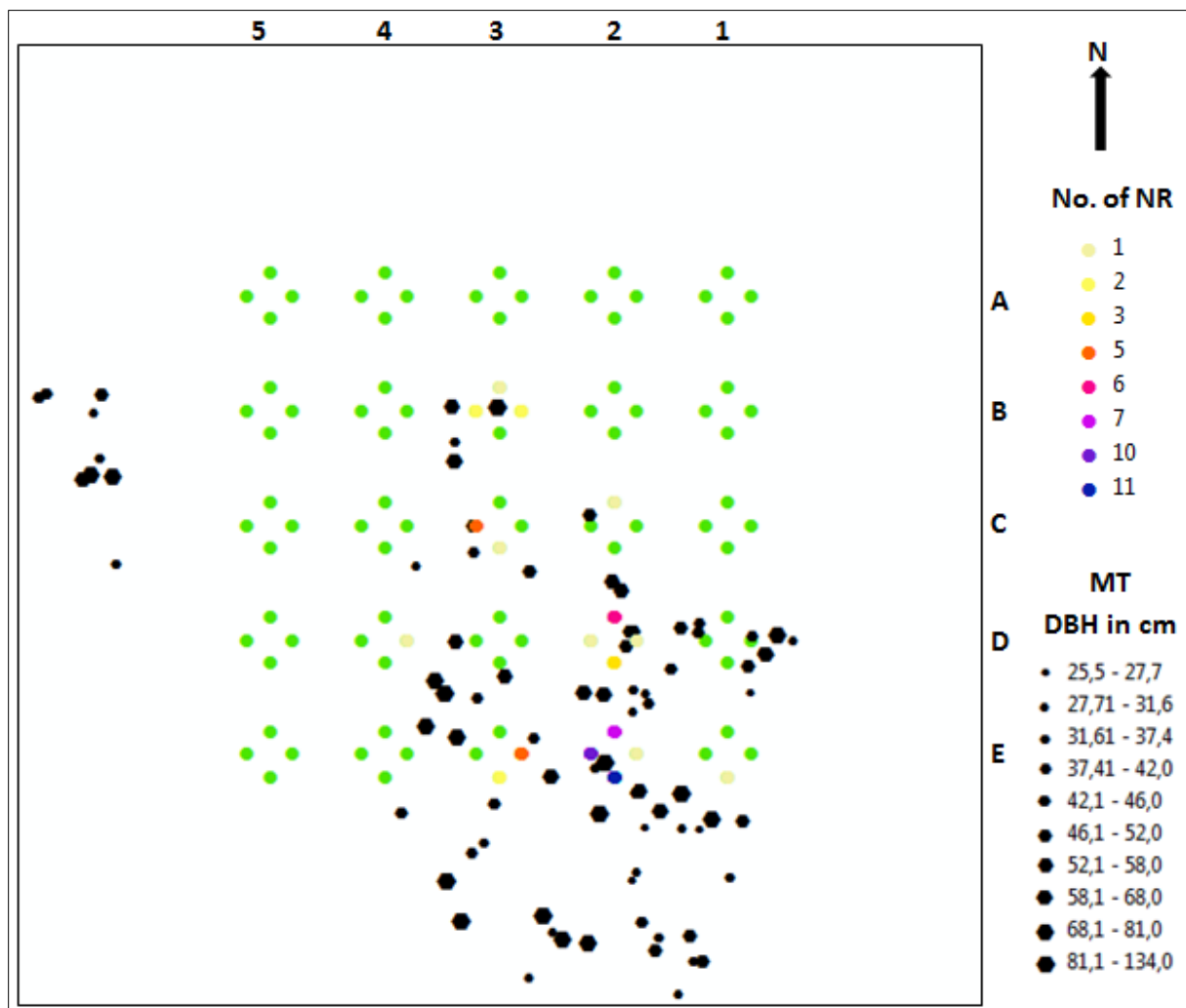
Figure 10. Map showing location of natural regeneration (NR) and mother trees (MT) for *Dryobalanops keithii* Sym. Definitions as in Figure 6. Black dots are MT, green dots are sample plots without any NR and dots with other colors are sample plots with different numbers of NR. The sample plots are 10 m² circular plots which were inventoried for NR and site conditions. Numbers and letters in the margin show the system of naming a specific plot cluster, which is the grouping of four sample plots.

The spearman rank correlation indicated different spatial distributions among the species. The "concentric rings" showed a positive correlation between NR and MT for *Dryobalanops spp.* up to 74.9 m; with a stronger correlation for the closest 24.9 m (Table 4, Figure 11). *D. keithii* showed a positive correlation between NR and MT up to 99.9 m with the weakest P-value of 0.004 between 75-99.9 m, after which there is clearly no correlation (Table 4). For *P.*

tomentella the "concentric rings" showed a positive correlation between NR and MT on a distance of 0-74.9 m, with a stronger significance the closest 49.9 m (Table 4). *Parashorea spp.* showed a much shorter distance with only a positive correlation the first 24.9 m (Table 4, Figure 11). *Shorea spp.* had a positive correlation between NR and MT in 0-24.9 m with a P-value of 0.002; it also showed a weaker correlation in 75-99.9 m with a P-value of 0.054 (Table 4, Figure 11). *Shorea parvifolia* Dyer only showed a positive correlation between NR and MT in 25-49.9 m with a P-value of 0.042 (Table 4). The scientifically heterogeneous group *Fruit trees* only had a positive correlation between NR and MT in 0-24.9 m with a P-value of 0.023 (Table 4). The "circular distances" showed the same pattern as the "concentric rings".
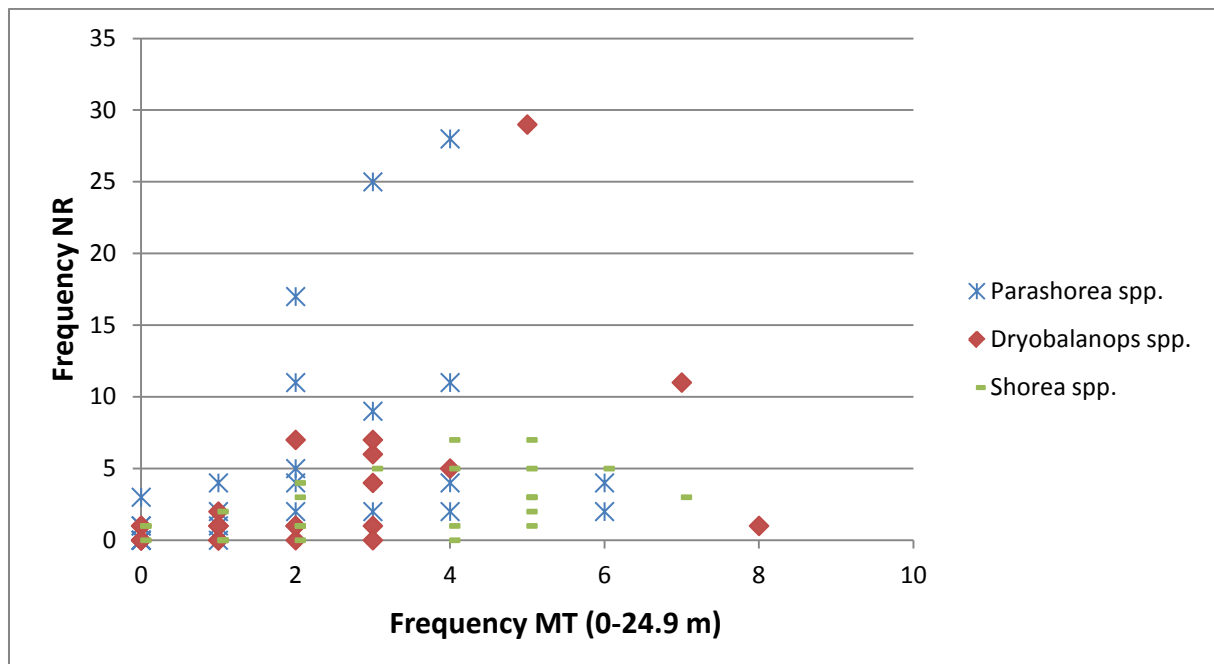
Figure 11. Diagram from study in the INIKEA Forest Rehabilitation Project showing plotted values (n=25) for natural regeneration (NR) and number of mother trees (MT) located within 24.9 m of the cluster plot center-point for *Parashorea spp.*, *Dryobalanops spp.* and *Shorea spp.* Definitions as in Figure 6. Cluster-plots are four grouped sample plots with aggregated data, the sample plots was 10 m^2 circular plots which were inventoried for NR data and site conditions. The cluster-plot center point is the center located between the four aggregated plots in a cluster, from this position the data for MT of the cluster-plot was divided into classes of 25 m "concentric rings" (see Figure 5).

Correlation between natural regeneration and site variables

Species groups in the spearman rank correlation analysis had a variety of species included; also differences in distribution between seedlings, saplings and poles could be noted between species, genera and *Fruit trees* (Table 2). Both *Dryobalanops spp.* and *D. keithii* showed a negative correlation, between NR and Other regeneration (OR) with a P-value of 0.026 and 0.000 separately (Table 4). This indicated that there was less *Dryobalanops* NR when there were more OR (Figure 12). For *D. keithii*, no cluster plot with a frequency of OR above 32 had any NR (Figure 12). *D. keithii* also showed a positive correlation between NR and Waterway with a P-value of 0.077 (Table 4). Both *Dryobalanops spp.* and *D. keithii* had a negative correlation between NR and Altitude with a P-value of 0.003 and 0.000 separately, indicating more *Dryobalanops* NR in the lower altitude (Table 4, Appendix 6).

Table 4. Spearman rank correlation coefficient and P-value for species/groups and analyzed variables (see Table 1) in the INIKEA Forest Rehabilitation Project (n=25). Total amount of natural regeneration (NR) on the cluster-plot was used as response variable for the specific species/group. Cluster-plots are four grouped sample plots with aggregated data, the sample plots were 10 m^2 circular plots which were inventoried for NR data and site conditions. The distance variables (see Figure 5) infers to the number of mother trees (MT) located within the distance interval from the specific cluster-plot center point. The cluster-plot center point is the center located between the four aggregated sample plots in a cluster. *Other regeneration* was NR located on cluster-plots which were not corresponding to the specific species/group analyzed, other definitions as in Figure 6. Bold numbers indicates a correlation with a P-value ≤ 0.090

Variable	Dryobalanops spp.		Dryobalanops keithii		Parashorea spp.		Parashorea tomentella		Shorea spp.		Shorea parvifolia		Fruit trees	
	NR	*P*	NR	*P*	NR	*P*	NR	*P*	NR	*P*	NR	*P*	NR	*P*
Other regeneration	**-0.445**	**0.026**	**-0.742**	**0.000**	0.320	0.119	**0.621**	**0.001**	0.318	0.121	0.166	0.429	0.170	0.417
Organic soil depth	0.034	0.871	-0.208	0.317	-0.058	0.783	-0.222	0.285	0.009	0.964	**0.375**	**0.065**	-0.064	0.760
Leaves	0.117	0.579	-0.178	0.393	0.214	0.304	0.038	0.857	0.081	0.700	**0.360**	**0.077**	0.115	0.583
Waterway	0.190	0.364	**0.360**	**0.077**	0.000	0.998	0.138	0.512	-0.148	0.479	-0.170	0.417	-0.117	0.577
Road	-0.078	0.710	-0.272	0.189	-0.037	0.861	0.105	0.617	0.124	0.555	0.106	0.614	0.238	0.252
Close to road	-0.107	0.611	-0.159	0.448	0.056	0.790	0.040	0.850	**0.346**	**0.090**	0.071	0.736	-0.214	0.305
Undisturbed	0.014	0.947	0.143	0.496	-0.024	0.911	-0.165	0.431	-0.241	0.245	-0.051	0.810	-0.117	0.577
Slope	-0.004	0.986	0.281	0.173	-0.108	0.608	0.026	0.904	-0.130	0.537	-0.293	0.154	0.035	0.867
Altitude	**-0.575**	**0.003**	**-0.764**	**0.000**	**0.480**	**0.015**	0.317	0.122	**0.379**	**0.061**	0.303	0.141	0.224	0.282
Rehab	0.090	0.668	0.051	0.808	-0.170	0.416	-0.069	0.745	0.015	0.942	-0.153	0.464	-0.204	0.328
0-24.9 m	**0.627**	**0.001**	**0.607**	**0.001**	**0.650**	**0.000**	**0.724**	**0.000**	**0.593**	**0.002**	0.276	0.181	**0.453**	**0.023**
25-49.9 m	**0.488**	**0.013**	**0.653**	**0.000**	0.305	0.139	**0.605**	**0.001**	0.174	0.406	**0.409**	**0.042**	-0.038	0.858
50-74.9 m	**0.421**	**0.036**	**0.644**	**0.001**	0.220	0.291	**0.404**	**0.045**	0.312	0.129	0.161	0.443	-0.180	0.389
75-99.9 m	0.320	0.118	**0.555**	**0.004**	0.043	0.840	0.107	0.612	**0.390**	**0.054**	0.018	0.932	0.237	0.255
100-124.9 m	0.258	0.213	0.193	0.355	0.191	0.360	0.099	0.636	0.163	0.436	0.065	0.758	0.092	0.663

The analysis showed a positive correlation between *P. tomentella* and OR with a P-value of 0.001 (Table 4), in contrast to *Dryobalanops spp.* and *D. keithii* this correlation indicated more NR with higher frequency of OR (Figure 12). For *Parashorea spp.* NR had a positive correlation with altitude with a P-value of 0.015 (Table 4). *Parashorea spp.* had in contrast to *Dryobalanops spp.* and *D. keithii* more NR on a higher altitude (Appendix 6).
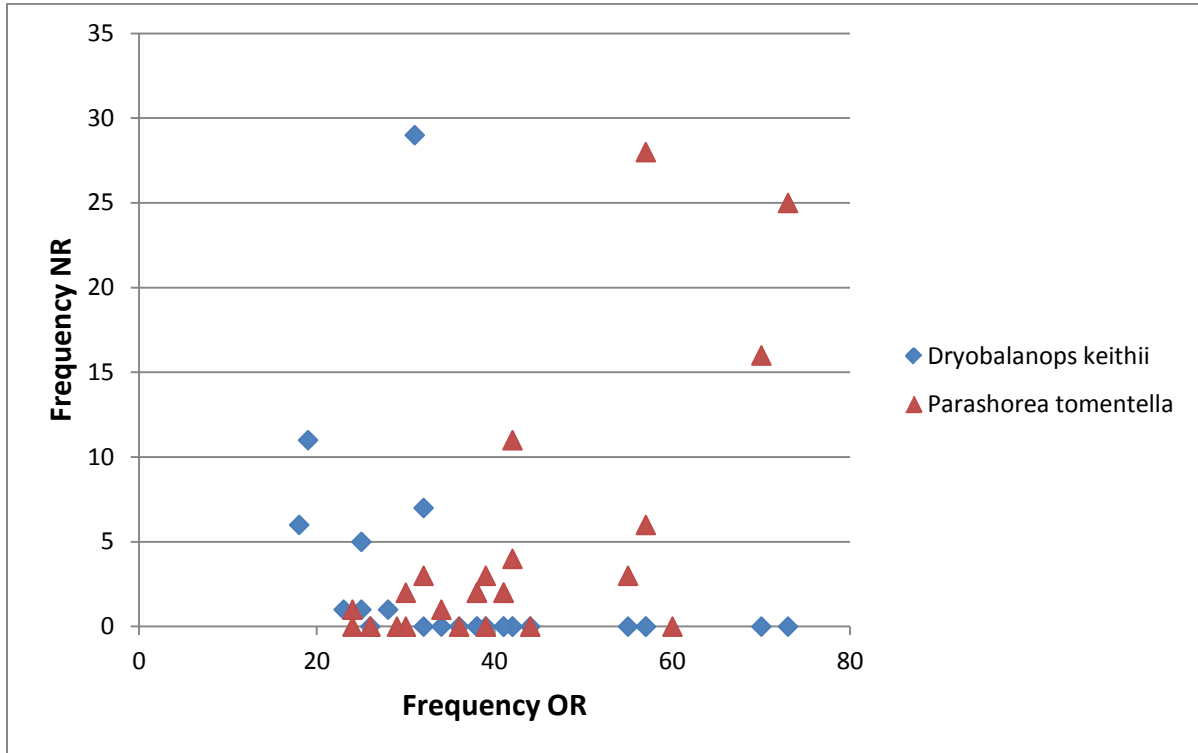
Figure 12. Diagram from study in INIKEA Forest Rehabilitation Project showing plotted values (n=25) for natural regeneration (NR) and other regeneration (OR) for *Dryobalanops keithii* Sym and *Parashorea tomentella* (Sym) Meijer located in the cluster-plots. Cluster-plots are four grouped sample plots with aggregated data, the sample plots was 10 m^2 circular plots which were inventoried for NR data and site conditions. *Other regeneration* were NR located on cluster-plots which is not the specific species/group analyzed. NR was defined as non-pioneer tree species ≥30 cm in height to < 25 cm in diameter breast height (dbh; diameter 130 cm above germination point).

Shorea spp. indicated a week positive correlations between NR and Close to road and between NR and Altitude with a P-value of 0.090 and 0.061 separately, a correlation similar to *P. tomentella* (Table 4). On the similar significance level *S. parvifolia* showed a weak positive correlation between NR and Organic soil depth and between NR and Leaves (Table 4).

DISCUSSION

The contribution of mother trees to abundance of natural regeneration

The INIKEA enrichment planting species groups were different concerning number of mother trees (MT) and natural regeneration (NR) per ha (Figure 6). The analyses showed a strong positive correlation between number of NR ha^{-1} and MT ha^{-1} for *Dipterocarps*, indicating more NR ha^{-1} with a higher number of MT ha^{-1}. However, a general limitation in regeneration capability was indicated and the majority of the *Dipterocarp* species did not exceed 200 NR ha^{-1} irrespective of the number of MT ha^{-1}, which varied from 0.06 MT ha^{-1} to 3.77 MT ha^{-1}. The two *Dipterocarp* species, *Parashorea tomentella* (Sym) Meijer and *Dryobalanops keithii* Sym, distinguished themselves by having higher number of NR ha^{-1} and MT ha^{-1} than other species in the group, a possible indication of the species being favored by disturbance. *Other timber* also showed a strong positive correlation between number of NR ha^{-1} and MT ha^{-1}, indicating more NR ha^{-1} if the number of MT ha^{-1} increased. The group with the largest number of species in the survey was *Other timber* followed by *Dipterocarps*, while *Fruit trees* and *Non-Dipterocarps* consisted of fewer species (Appendix 1). *Other timber* could possibly include species benefited from disturbance, explaining the large presence.

The groups also showed differences for the accumulated NR ha^{-1} and MT ha^{-1} (Figure 7), *Dipterocarps* and *Other timber* differed pronouncedly. As an example, for *Dipterocarps* to accumulate 2000 NR ha^{-1} they needed approximately three times as many MT ha^{-1} as *Other timber*, again indicating lower regeneration capability for *Dipterocarps*. When comparing the amount of planted seedlings per ha in the INIKEA Forest Rehabilitation Project and the results in this study, it appears that few MT is needed to achieve a similar regeneration. Performing line planting, the INIKEA project staff plant approximately 374 seedlings per ha, and when implementing gap-cluster planting approximately 400 seedlings per ha (Alloysius, et al., 2010). This study suggested that approximately 10 MT ha^{-1} is needed to accomplish similar results (Figure 7), possibly supporting the use of the liberation method in areas similar to the studied. This says nothing about the biodiversity, but only how to achieve a similar number of seedling establishment. There is an advantage in applying the multispecies approach in the enrichment planting methods. It provides a possibility to control the increase of tree diversity, an important factor considering the biodiversity aim of the INIKEA Forest Rehabilitation Project. Luc (2010) showed that enrichment planting under a 10 year period doubled the number of *Dipterocarp* species in the sample plots compared to not rehabilitated forests, and that the treated areas had a higher number of unique *Dipterocarp* species. Also, the seedlings might become more evenly distributed when implementing enrichment planting.

The ratio of NR MT^{-1} ha^{-1} among species varied in the study (Figure 8). The group of species with the highest NR MT^{-1} ha^{-1} ratio was *Other timber*, while *Dipterocarp* in general had a moderate to low regeneration capability per MT and ha. 10 out of 11 *Shorea* species were among the 12 *Dipterocarp* species that had a value lower than 100 NR MT^{-1} ha^{-1}. This is indicating that *Shorea* had many species present but a generally low regeneration capability. Giving the assumption that even if there are some *Shorea* MT present in a location, liberation treatment may not be suitable. Enrichment planting might be necessary to ensure *Shorea* regeneration.

The survey area was approximately 18.3 ha and from the 119 species encountered, 47 were only found as MT and 21 species only as NR. Giving the assumption that the 47 species which had only MT present may have a poor regeneration capability or lacking suitable

habitats in the area. Also, possible NR might have been smaller than 30 cm in height (only seedlings ≥30 cm were noted in survey) or the amount of regeneration were so low that even if present in the area by chance NR were located outside the plots. The 21 species having only NR, consisting of a majority of *Other timber* species, possibly had their dispersal sources outside the area, indicating several hundred of meters in dispersal capability. One option is dispersal by animals and birds (Ghazoul & Sheil, 2010); other possibilities are that they had their MT removed by former logging or wild fire and that the NR is of older age or that the MT just recently died of other causes. Flowering, seed production, seed germination and seed predation are other possible factors affecting the dispersion or establishment of tropical tree seeds, the importance of these aspects are not fully understood.

Spatial association between natural regeneration and mother trees

Dryobalanops spp. had a strong positive correlation between NR and MT up to a distance of 74.9 m and *D. keithii* a strong positive correlation as far away as 99.9 m (Table 4), indicating good dispersal ability. An earlier study performed in Sarawak, Borneo on *Dryobalanops lanceolata* Burck and *Dryobalanops aromatica* Gaertn. F showed no correlation with distance the first 10 m from MT for seedlings (Itoh, et al., 1997), where most of the seedlings were still under the canopy. The seedling density decreased quickly with increasing distance outside the closest 10 m from MT to almost no seedlings at 40 m (Itoh, et al., 1997). Others have been noting relatively short dispersal distances for *Dipterocarps* (Soerianegara & Lemmens, 1994), and it has been claimed that effective dispersal of seeds is limited to 20-40 m from MT (Kuusipalo, et al., 1996). The above mentioned studies points towards a shorter dispersal ability while my results indicated longer dispersal ability for *Dryobalanops* than earlier noticed. The same species as I analyzed are not included in those studies, but *D. lanceolata* is included in *Dryobalanops spp.* used in this study. *D. keithii* have a mean weight per seed of 10.00 grams (g) and *Dryobalanops spp.* a mean weight of 9.09 g per seed (Table 5). These are relatively heavy seeds for *Dipterocarps*, in Appanah & Turnbull's (1998) list over *Dipterocarp* species (not including all *Dipterocarp* species) the seed weights range from a mean value of 0.059 g per seed (*Vatica mangachapoi* Blanco) to a mean of 33.33 g per seed (*Shorea pinanga* Scheffer). This gives the assumption that seed weight may not be related to dispersal ability, at least not for *Dryobalanops*. Instead other factors might be of importance for seed dispersal distances, like the relationship between seed weight and seed wing surface area or shape of the seed wings.

Parashorea spp. had a short distribution pattern, showing a positive correlation between NR and MT only in 0-24.9 m (Table 4). On the other hand, *P. tomentella* did show a strong positive correlation all the way from 0-74.9 m (Table 4). *Parashorea spp.* and *P. tomentella* have lighter seeds than the *Dryobalanops* species analyzed (Table 5); again emphasizing that shorter dispersal ability had no relation with heavier seeds.

Shorea spp. showed a strong positive correlation between NR and MT at 0-24.9 m and a weak positive correlation between NR and MT at 75-99.9 m (Table 4). The correlation ended distinctively from 0-24.9 m to 25-49.9 m (Table 4), indicating relatively short dispersal ability compared to other species and genera analyzed, more similar to what others have noted (Soerianegara & Lemmens, 1994; Itoh, et al., 1997). Important to note is that *Shorea spp.* in this analysis consisted of at least 20 different species (Table 5), making it difficult to draw conclusions from the group for particular species because of differences among species in the genus (Ashton, et al., 1995). *Shorea parvifolia* Dyer only showed a positive correlation between NR and MT at 25-49.9 m (Table 4). The result should be read with caution,

Table 5. Seed information (Appanah & Turnbull, 1998) for species and groups analyzed, INIKEA Forest Rehabilitation Project area. For the statistical analysis the species with the highest amount of natural regeneration from three different *Dipterocarp* genera were compared with its specific whole genus (Table 2). *Dipterocarp* species were chosen because of their dominance and importance to biodiversity (Whitmore, 1975) and because of their use in the INIKEA enrichment planting (Alloysius, et al., 2010). Number of species refers to the number of species included in species groups in the analysis. Values for species groups are averages of the mean values taken from Appanah & Turnbull (1998) for specific species

Species/group	Number of species	Mean no. of seeds per kilogram	Mean weight per seed (grams)	Mean length (millimeter)	Mean width (millimeter)
Dryobalanops spp.	2	110[1]	9.09	26	23
Dryobalanops keithii	1	100	10.00	n/a	n/a
Parashorea spp.	3	553[2]	1.81	21	15
Parashorea tomentella	1	180	5.56	30	20
Shorea spp.[3]	20[4]	1031[5]	0.97	20	12
Shorea parvifolia	1	1300	0.77	17	10

[1]Mean values for individual species included in *Dryobalanops spp.* range between 100-120 seeds per kilo.
[2]Mean values for individual species included in *Parashorea spp.* range between 180-940 seeds per kilo.
[3]The average mean values are based on seed information found for 9 out of 20 species.
[4]*Shorea spp.* includes species not specifically identified and may include more than 20 species.
[5] Mean values for individual species included in *Shorea spp.* range between 160-1900 seeds per kilo.

S. parvifolia had less NR than other species analyzed and will therefore give a more uncertain result. Anyway, considering the results it is possible to assume that *Shorea* has relatively short dispersal ability but also very light seeds (Table 5); again this indicates that shorter dispersal ability had no relation with heavier seeds.

Fruit trees showed a strong positive correlation between NR and MT at 0-24.9 m (Table 4), indicating a short dispersal ability. This may be natural due to the size of their fruits and the fact that they lack wings, in comparison to the *Dipterocarps*. The group *Fruit trees* is a heterogeneous group, a potential common property is the one of giving fruit possibly appreciated for consumption by mammals and birds.

The contribution of site variables to abundance of natural regeneration

Site conditions can imply major constraints on seedling survival (Kettle, 2010) and it has been shown that tropical tree species do not aggregate at random (Ashton, et al., 1995). Different performances according to specific topographic or edaphic site habitat associations are normal for tropical trees (Ashton, et al., 1995; Ashton, et al., 2001; Palmiotto, et al., 2004; Nishimura, et al., 2008). Also species deriving from the same family can have different preferences for habitat associations (Ashton, et al., 1995).

Both *Dryobalanops spp.* and *D. keithii* had a strong negative correlation between NR and Other regeneration (OR). Demonstrating that *Dryobalanops* regeneration and *D. Keithii* performs worse when located together with regeneration from other species. *Dryobalanops* may be negatively affected by competition or have different site preferences compared to the majority of other species in the study. Another outcome was that *D. keithii* had a weak positive correlation between NR and Waterway, indicating that more *D. keithii* regeneration was located in Waterways. Waterways were defined as; percentage of plot located in creek or areas were water flow during heavy rains. A likely assumption would be that there are few number of tree plants in these areas due to the disturbances of flowing water, which probably

leads to less competition and more open habitats. Strengthening this theory is the fact that *D. keithii* has relatively heavy seeds, in average 10.00 g per seed (Table 5). These seeds are approximately 2 to 10 times heavier compared to other *Dipterocarp* species and genera analyzed (Table 5). It has been indicated by simulation that heavy tropical rains can remove seeds from planting sites (Pinard, et al., 1996); heavy seeds may contribute to resistance of such disturbances. However, it should be noted that the mentioned experiment only included pioneer tree species. *D. keithii* may be a weak competitor adapted to establish in more open areas, or it could be good at setting seeds and surviving at disturbed locations.

An interesting result is that *P. tomentella* had a strong positive correlation between NR and OR. Showing that *P. tomentella* regeneration performed better together with regeneration of other species or indicating that *P. tomentella* have similar site preferences as regeneration from other species. This positive correlation may indicate that *P. tomentella* have more shade tolerant properties. Under dense canopy increased light intensities generally benefit tropical tree species (Romell, 2011) and more open conditions are needed for *D. lanceolata* and *D. aromatica* seedlings to develop into saplings (Itoh, et al., 1997). Other *Dipterocarp* species have shown to perform differently in similar light conditions, benefiting from either partly shaded or more open areas of establishment (Ashton, et al., 1995).

Parashorea spp. (Appendix 2) and *P. tomentella* (Figure 9) demonstrated different spatial distributions compared with *Dryobalanops spp.* (Appendix 3) and *D. keithii* (Figure 10). Comparing the spatial distributions of *P. tomentella* and *D. Keithii* indicated a distinctive difference with almost opposite spatial distributions. The two species only shared NR in 3 of the 100 plots (10 m^2 per plot); still they were two of the most dominating species in the whole survey. One reason why *Dryobalanops* was a dominating genus and why *D. keithii* was a dominating species in the survey area may be related to the shorter fruiting intervals for *Dryobalanops* compared with other *Dipterocarp* species (Itoh, 1995). Also, both *Dryobalanops spp.* and *D. keithii* had a strong negative correlation between NR and Altitude, demonstrating more *D. keithii* NR in the lower altitude. In contrast, *Parashorea spp.* demonstrated a strong positive correlation between NR and Altitude, indicating more *Parashorea spp.* in the higher altitude. The difference is most likely connected to something other than the actual altitude; from the lowest located plot to the highest there was a difference of only 64 m. Several theories are plausible; *Dipterocarp* species have different soil-related habitat specialization, performing differently on nutrient rich or nutrient poor soil types (Palmiotto, et al., 2004). The differences are suggested not being related to nutrient availability, but instead an effect of different water-holding capacities between clay-rich and sand-rich soils, different mycorrhizal flora in the soil types or a toxic effect because of higher aluminum or ion concentrations in nutrient rich soil (Palmiotto, et al., 2004). There is also support for the idea that spatial variation in water availability shapes species habitat associations (Comita & Engelbrecht, 2009). Ridges for example tend to be drier than other parts of the topography, especially during droughts. There might be differences in the degree of disturbance, like logging, between areas located in lower and higher altitude, affecting the establishment of seedlings differently. However, this cannot explain the different distribution pattern for the older MT, likely established before modern logging activities started. Instead these MT might have been affected by other disturbances at the time of establishment.

S. parvifolia had a weak positive correlation between NR and Leaves, indicating more NR together with more leaves. Leaves were defined as percent of leaves covering the plot surface. Romell (2011) observed something similar; in a germination and survival experiment most of the seeds were lost due to predation. However, the seeds seemed to have established better in

plots covered with leaves (statistically insignificant), where the seeds probably were harder for predators to locate.

Results uncertainties and improvements

In the field, members from INIKEA research team assisted with the data collection. There were at least two persons identifying the species when implementing the inventory of MT and one person identifying the natural regeneration. Also, the data may include some pioneer species although these were specifically asked to be avoided. The data contained few observations of natural regeneration, therefore the need of summarizing into genera and other groups and merging plot values into cluster values for the analysis. Different site variables were collected; some were class variables which could not later be used as a result of merging the values.

This study showed longer dispersal distances for some species than indicated by earlier studies (Itoh, et al., 1997). However, the previous study was conducted in Lambir Hills National Park, Sarawak which is probably less disturbed than the area of current study. If dividing the "concentric rings" into smaller sizes more precise result may have been achieved. Still some species or species groups would have got longer dispersal distances than showed by earlier studies. However, in this study smaller "concentric rings" would not have been possible because of the summation of plot values into cluster values. The diameter of a cluster is 23.56 m which gives the smallest possible "concentric ring".

The study was only implemented in a single area; more general conclusions could be made by performing the study at other locations as well. Especially concerning the results for the amount of regeneration for different species groups. With a study of multiple areas more general conclusions could also be made about individual species. The whole survey area varied in terms of vegetation structure (S. Backlund, *pers. obs.*). Some parts of the area contained very few mother trees and had a lot of climbers while other parts were more similar to pristine tropical rainforest (Alloysius, 2012). Overall when comparing the experimental area to other degraded forests in the INIKEA project area there were many MT present (Alloysius, 2012). The study area had a relatively low degree of disturbance, comparing this study to similar studies performed in more degraded areas would be of high interest.

One possibility for developing the correlation analysis is to add the dbh size for MT as a factor in the relation between MT and amount of NR. This would investigate if bigger trees are more important than smaller tress for the amount of NR on a specific plot. Because of some uncertainty when the different tree species starts to set fruit, similar analyses as performed in this study could be done with different size definitions for MT. Another possible proceeding forward could be a multivariate analysis investigating how mother trees and site factors may contribute to the abundance and spatial distribution of natural regeneration of non-pioneer tree species. Also, future studies may further investigate why *D. keithii* had a negative correlation between NR and OR and *P. tomentella* a positive correlation between NR and OR.

CONCLUSIONS

All groups used in the enrichment planting in the INIKEA Forest Rehabilitation Project (*Dipterocarps*, *Non-Dipterocarps* and *Fruit trees*) and *Other timber* had a positive correlation between natural regeneration (NR) ha^{-1} and mother trees (MT) ha^{-1}. The species group *Dipterocarps* generally had lower regeneration capability than *Other timber*. For *Dipterocarps* to accumulate 2000 NR ha^{-1} they needed approximately three times more MT than *Other timber*. This study suggests that approximately 10 *Dipterocarp* MT ha^{-1} is needed at a location to achieve a similar number of NR ha^{-1} as the enrichment planting of the INIKEA project. *Shorea* generally had a lower regeneration capability compared to other *Dipterocarp* genera analyzed in the study. Indicating that for *Shorea,* enrichment planting is a more suitable treatment than liberation even if there is *Shorea* MT present.

Dryobalanops spp. and *Dryobalanops keithii* Sym had less NR on sites which had a lot of NR from other species. *D. keithii* had more NR located to creeks or areas where water flow during heavy rains, indicating adaptation for more open areas or disturbed locations. *Parashorea tomentella* (Sym) Meijer on the other hand had more NR located to sites which had a lot of NR from other species. This may indicate that *P. tomentella* have more shade tolerant properties. There were a distinctive difference in spatial distribution between the two species *P. tomentella* and *D. keithii*, possibly related to soil-related habitat specialization.

Dryobalanops indicated longer dispersal ability for NR than earlier studies have shown, up to 99.9 m from MT for *Dryobalanops spp.* and up to 74.9 m for *D. keithii*. *Parashorea spp.* and *Shorea spp.* showed shorter dispersal abilities with NR ending at 24.9 m from MT, more similar to earlier studies. An exception was *P. tomentella,* showing dispersal ability up to 74.9 m. Comparing seed weights and dispersal abilities indicated that shorter dispersal capability had no relation with heavier seeds. Also, *Fruit trees* showed short dispersal ability, ending at 24.9 m.

The INIKEA Forest Rehabilitation Project has added experience and knowledge for rehabilitation of secondary tropical forests in South East Asia (Alloysius, et al., 2010). The project objectives are to plant numerous species, mainly *Dipterocarps*, and to support natural regeneration, in order to improve biodiversity in these forests. Enrichment planting has shown to increase the number of *Dipterocarp* species in treated areas (Luc, 2010). For many of the species used in the INIKEA enrichment planting there is lack of knowledge concerning their ecological and biological adaptations (Alloysius, et al., 2010). The results of the present study have contributed to the understanding of regeneration dynamics of tropical tree species and improvement of rehabilitation methods. Primarily, contribution has been given to the understanding of regeneration capabilities for some of the INIKEA enrichment planting groups, specific species and species groups. Moreover, the study has contributed to the understanding of the distribution patterns of some tropical species and species groups. Specifically, by contributing with knowledge about seedling dispersal distances the liberation method is possibly improvable.

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APPENDICES

Appendix 1. Table showing all noted species, total number of Seedlings, Saplings and Poles. Also showing; total number of mother trees (MT), group association, number of natural regeneration (NR) per hectare and MT per hectare in survey area, INIKEA Forest Rehabilitation Project. Seedlings were defined as non-pioneer tree species 30-130 cm in height, Saplings 0.1-10 cm in diameter breast height (dbh; diameter 130 cm above germination point), Poles 10.1-24.9 cm in dbh, NR ≥30 cm in height to < 25 cm in dbh and MT ≥ 25 cm in dbh. Species marked with asterisk (*) do most likely set seed before 25 cm in dbh (Lojingi, 2012). The species are divided into groups (see Figure 6) that are used in the enrichment planting in the INIKEA Project (Alloysius, et al., 2010); Dipt. for *Dipterocarps*, FT for *Fruit trees*, ND for *Non-Dipterocarps*, while species that are not used in the enrichment planting were set as *Other timber* (OT)

| | **Number of** | | | | | | |
Species	Seedlings	Saplings	Poles	MT	Group	NR ha^{-1}	MT ha^{-1}
Adinandra spp.	0	0	0	3	OT	0	0.16
Aglaia elliptica	0	0	0	1	OT	0	0.05
Aporusa elmeri*	1	6	0	1	OT	70	0.05
Aporusa grandistipula*	31	7	0	0	OT	380	0.00
Aglaia squamulosa & other Aglaia spp.	0	0	0	1	OT	0	0.05
Alangium javanicum	1	3	0	7	FT	40	0.38
Alstonia spp.	0	0	0	1	OT	0	0.05
Annonaceae	22	29	0	13	OT	510	0.71
Baccaurea parviflora*	15	22	0	2	OT	370	0.11
Bhesa paniculata*	2	0	0	0	OT	20	0.00
Aquilaria malaccensis	0	1	0	1	ND	10	0.05
Archidendron jiringa	0	1	0	1	OT	10	0.05
Ardisia elliptica	4	10	0	0	OT	140	0.00
Artocarpus anisophyllus	5	10	0	22	FT	150	1.20
Dimorphocalyx murinus*	0	4	0	0	OT	40	0.00
Artocarpus elasticus	0	0	0	2	FT	0	0.11
Baccaurea latifolia	0	0	0	1	OT	0	0.05
Barringtonia macrostachya	0	0	0	1	OT	0	0.05
Blumeodendron tokbrai	0	3	1	1	OT	40	0.05
Calophyllum obliquinervium	0	0	0	9	OT	0	0.49
Canarium odontophyllum	0	0	0	1	FT	0	0.05
Canarium, Dacryodes & other Burseraceace	5	13	3	64	FT	210	3.49
Fagraea volubilis & several other Fagraea spp.*	1	1	0	0	OT	20	0.00
Cleistanthus megacarpus	0	0	0	1	OT	0	0.05
Cleistanthus paxii	8	19	2	0	OT	290	0.00
Dialium indum	0	0	0	4	FT	0	0.22
Dillenia excelsa	0	1	0	3	OT	10	0.16
Dillenia spp.	0	0	0	4	OT	0	0.22
Diospyros spp.	9	17	2	11	FT	280	0.60

Koilodepas longifolium*	14	40	0	0	OT	540	0.00
Dipterocarpus caudeferus	0	0	0	19	Dipt.	0	1.04
Dipterocarpus globosus	0	0	0	8	Dipt.	0	0.44
Leea indica*	0	1	0	0	OT	10	0.00
Dipterocarpus spp.	0	0	0	27	Dipt.	0	1.47
Dipterocarpus validus	2	8	0	11	Dipt.	100	0.60
Dryobalanops keithii	55	5	1	82	Dipt.	610	4.48
Mallotus wrayi*	13	35	0	1	OT	480	0.05
Dryobalanops lanceolata	12	4	2	57	Dipt.	180	3.11
Duabanga moluccana	0	0	0	14	OT	0	0.76
Durian sp. or Neesia sp.	0	1	0	6	FT	10	0.33
Durio kutejensis	0	0	0	1	FT	0	0.05
Endospermum diadenum	0	0	0	1	OT	0	0.05
Euginea spp.	14	40	2	102	OT	560	5.57
Eusideroxylon zwageri	4	2	0	47	ND	60	2.57
Ficus callosa & other ficus spp.	4	11	1	6	OT	160	0.33
Glochidion borneensis	2	1	0	0	OT	30	0.00
Gluta, Semecarpus, Melanochyla & Swintonia	0	2	0	7	OT	20	0.38
Heritiera simplicifolia	3	1	0	3	ND	40	0.16
Homalium foetidum or Homalium grandiflorum	0	0	0	4	OT	0	0.22
Homalnthus populneus	0	0	0	3	OT	0	0.16
Praravinia suberosa*	13	20	1	2	OT	340	0.11
Pternandra coerulescens*	0	1	0	0	OT	10	0.00
Ryparosa acuminata*	3	10	0	6	OT	130	0.33
Hopea nervosa	0	0	0	2	Dipt.	0	0.11
Saurauia ferox*	1	5	0	0	OT	60	0.00
Hopea spp.	15	1	0	19	Dipt.	160	1.04
Hydnocarpus borneensis	0	0	0	1	OT	0	0.05
Hydnocarpus spp.	0	0	0	3	OT	0	0.16
Intsia palembanica	0	1	0	2	OT	10	0.11
Koompassia excelsa	9	1	0	14	ND	100	0.76
Lauraceace	6	12	1	35	OT	190	1.91
Lithocarpus & Quercus	4	9	1	104	ND	140	5.68
Mallotus floribundus	7	15	0	0	OT	220	0.00
Mallotus sp	19	16	2	8	OT	370	0.44
Mangifera pajang	0	0	0	1	FT	0	0.05
Meliaceae	12	22	2	20	OT	360	1.09
Melicope luna- akenda	0	0	0	1	FT	0	0.05
Mesua macrantha	2	1	0	0	OT	30	0.00
Michelia montana	0	1	0	0	OT	10	0.00
Microcos crassifolia	0	0	0	1	OT	0	0.05
Myristicaceae	3	17	0	12	OT	200	0.66
Nauclea subdita	0	4	0	0	OT	40	0.00
Neolamarckia cadamba	0	0	0	60	OT	0	3.28
Nephelium lappaceum	0	0	0	3	OT	0	0.16

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Nephelium mutabile	0	0	0	3	OT	0	0.16
Octomeles sumtrana	0	0	0	2	OT	0	0.11
Oncosperma horridum	0	0	0	1	OT	0	0.05
Orophea myriantha	3	7	0	0	OT	100	0.00
Paranephelium xestophyllum	0	0	1	4	OT	10	0.22
Parartocarpus or artocarpus	0	0	0	4	FT	0	0.22
Parashorea malaanonan	15	2	1	17	Dipt.	180	0.93
Parashorea smythiesii	4	3	2	41	Dipt.	90	2.24
Parashorea tomentella	103	8	0	89	Dipt.	1110	4.86
Parinari oblongifolia	0	0	0	4	OT	0	0.22
Pentace adenophora	2	6	1	0	ND	90	0.00
Pentace laxiflora	5	9	0	18	ND	140	0.98
Polyalthia cauliflora	0	0	0	1	OT	0	0.05
Polyalthia sumatrana	1	3	0	5	OT	40	0.27
Pterospermum spp.	0	0	0	2	OT	0	0.11
Sapotaceae	2	1	0	4	OT	30	0.22
Scaphium longipetiolatum	0	0	0	1	OT	0	0.05
Schima walichii	1	5	0	0	OT	60	0.00
Scorodocarpus borneensis	0	0	0	1	ND	0	0.05
Shorea agamii	0	0	0	1	Dipt.	0	0.05
Shorea argentifolia	0	0	0	3	Dipt.	0	0.16
Shorea faguetoides	3	3	1	5	Dipt.	70	0.27
Shorea fallax	3	5	0	35	Dipt.	80	1.91
Shorea gibbosa	0	0	0	10	Dipt.	0	0.55
Shorea johorensis	2	1	0	52	Dipt.	30	2.84
Shorea leprosula	2	0	1	18	Dipt.	30	0.98
Shorea leptoderma	0	0	0	3	Dipt.	0	0.16
Shorea macroptera	5	3	1	20	Dipt.	90	1.09
Shorea ovalis	0	1	0	6	Dipt.	10	0.33
Shorea parvifolia	7	6	2	69	Dipt.	150	3.77
Shorea parvistipulata	0	1	0	0	Dipt.	10	0.00
Shorea pauciflora	5	1	0	16	Dipt.	60	0.87
Shorea platyclados	1	0	0	0	Dipt.	10	0.00
Shorea smithiana	1	1	0	4	Dipt.	20	0.22
Shorea spp.	1	1	0	22	Dipt.	20	1.20
Shorea superba	0	0	0	5	Dipt.	0	0.27
Shorea symingtonii	0	0	0	2	Dipt.	0	0.11
Shorea xanthophylla	0	1	1	13	Dipt.	20	0.71
Sindora beccariana or Sindora iripicina	2	0	0	1	FT	20	0.05
Symplocos fasciculata	1	1	0	1	OT	20	0.05
Teijsmanniodendron holophyllum	0	1	1	0	OT	20	0.00
Walsara pinnata	0	0	0	22	FT	0	1.20
Vatica spp. or Cotylelobium spp.	0	0	0	5	Dipt.	0	0.27
Wendlandia dasythyrsa	0	0	0	1	OT	0	0.05
Xylopia ferruginea	0	0	0	2	OT	0	0.11

Appendix 2. Map from study in INIKEA Forest Rehabilitation Project showing natural regeneration (NR) and mother trees (MT) for *Parashorea spp*. Definitions as in Figure 6. Black dots are MT, green dots are sample plots without any NR and dots with other colors are sample plots with different numbers of NR. The sample plots were 10 m^2 circular plots which were inventoried for NR and site conditions. Numbers and letters in the margin show the system of naming a specific plot cluster, which is the grouping of four sample plots.
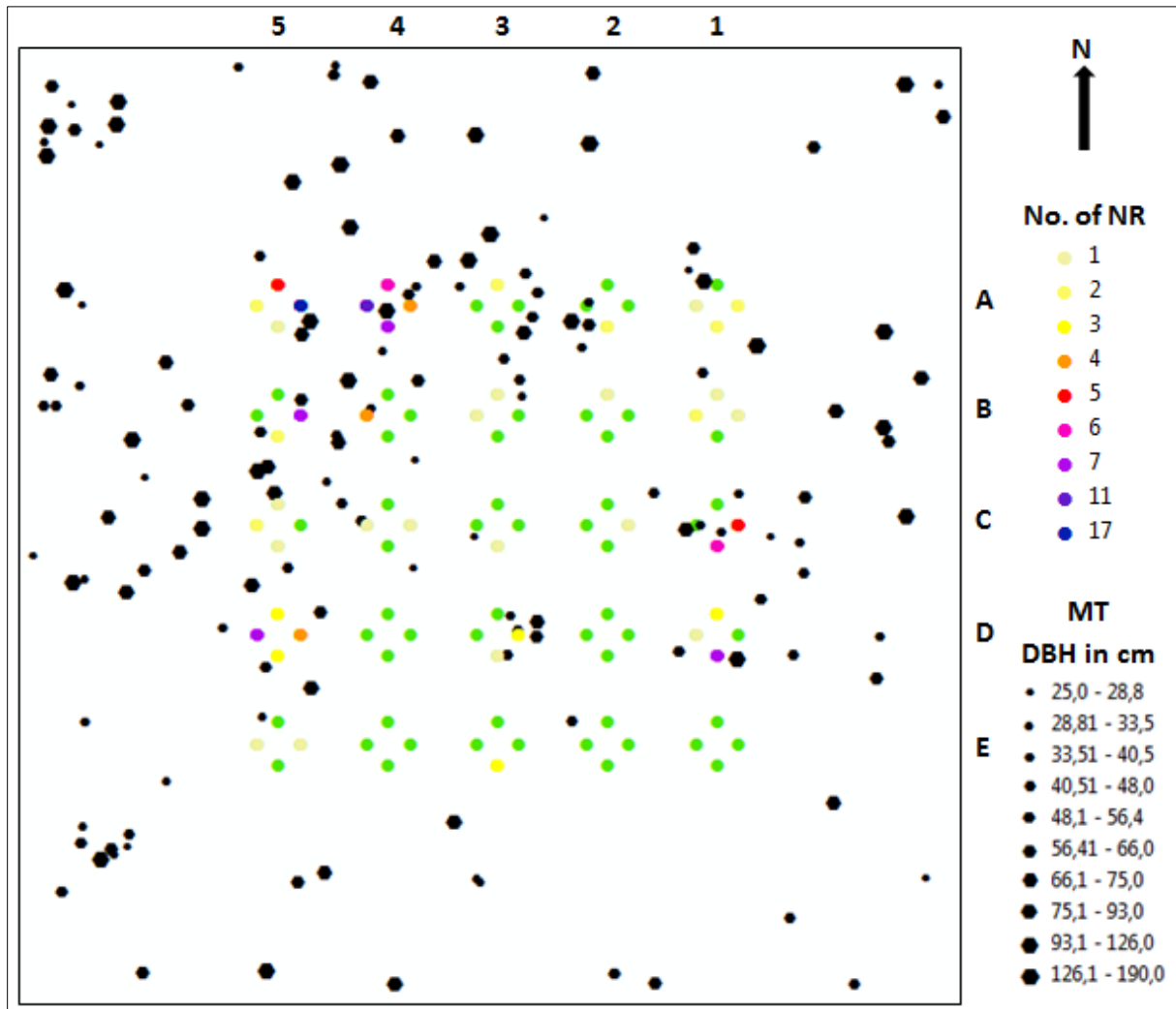
Appendix 3. Map from study in INIKEA Forest Rehabilitation Project showing natural regeneration (NR) and mother trees (MT) for *Dryobalanops spp*. Definitions as in Figure 6. Black dots are MT, green dots are sample plots without any NR and dots with other colors are sample plots with different numbers of NR. The sample plots were 10 m^2 circular plots which were inventoried for NR and site conditions. Numbers and letters in the margin show the system of naming a specific plot cluster, which is the grouping of four sample plots.
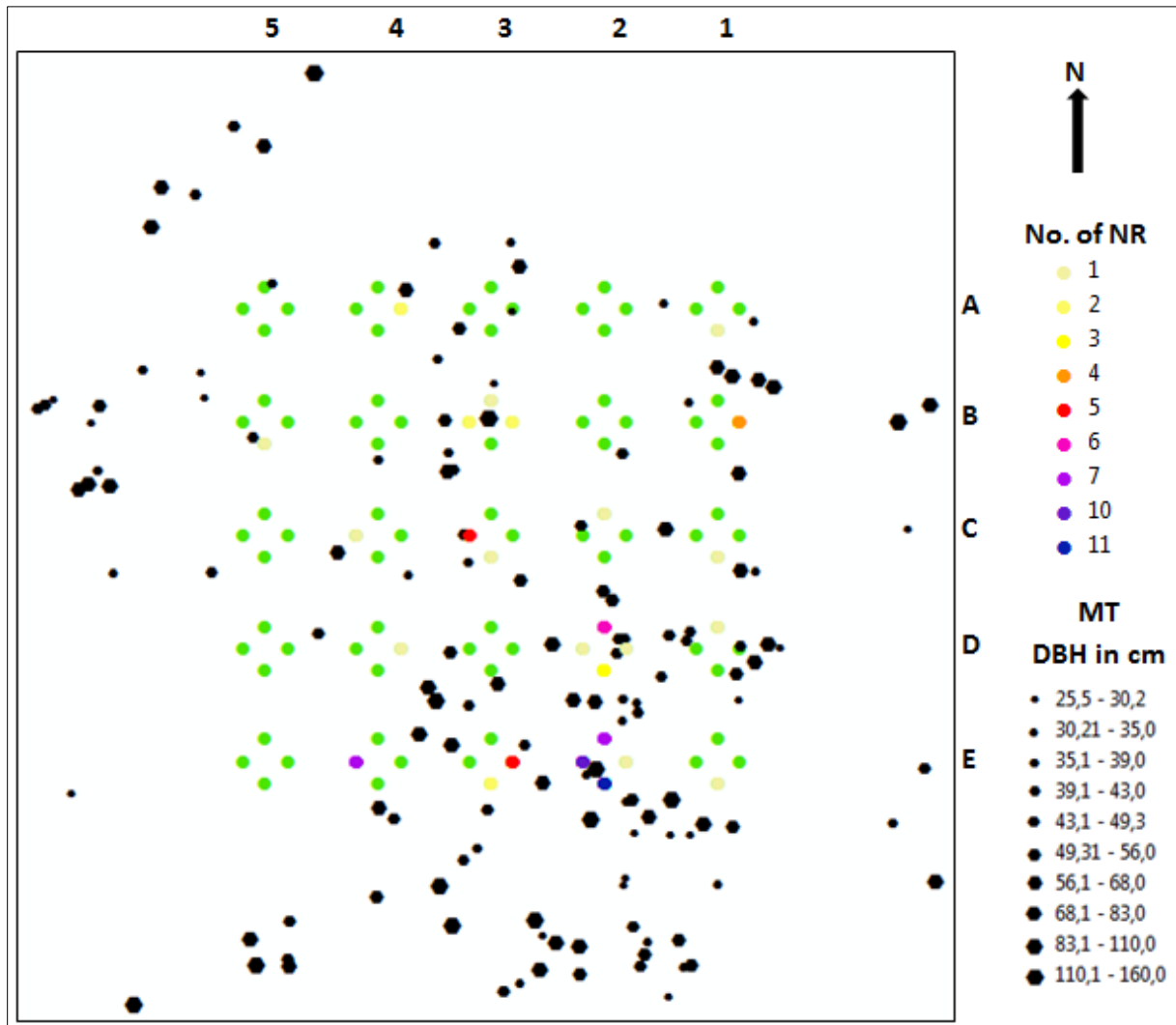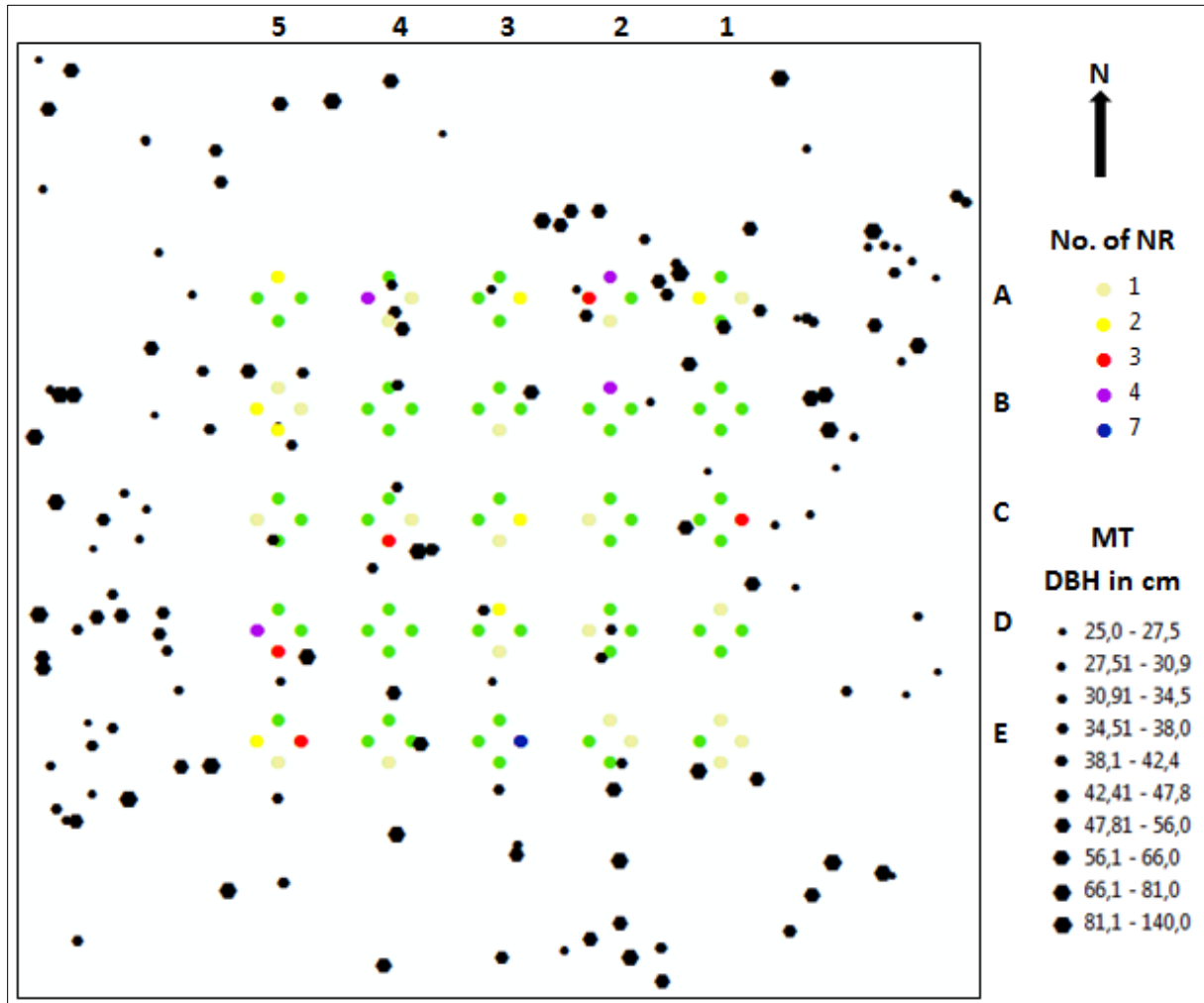
Appendix 4. Map from study in INIKEA Forest Rehabilitation Project showing natural regeneration (NR) and mother trees (MT) for *Shorea spp*. Definitions as in Figure 6. Black dots are MT, green dots are sample plots without any NR and dots with other colors are sample plots with different numbers of NR. The sample plots were 10 m^2 circular plots which were inventoried for NR and site conditions. Numbers and letters in the margin show the system of naming a specific plot cluster, which is the grouping of four sample plots.
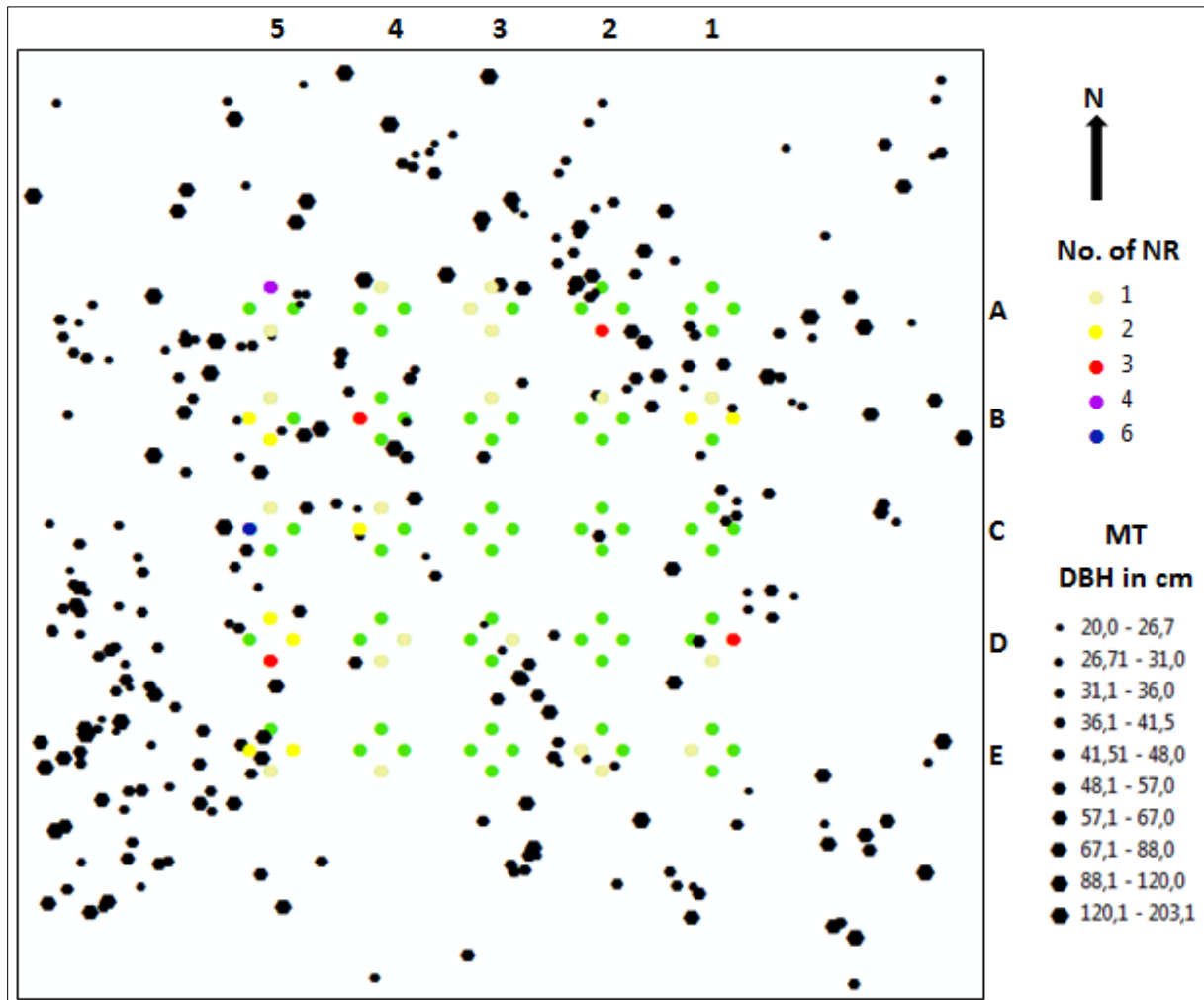
Appendix 5. Map from study in INIKEA Forest Rehabilitation Project showing natural regeneration (NR) and mother trees (MT) for *Fruit trees*. Definitions as in Figure 6. Black dots are MT, green dots are sample plots without any NR and dots with other colors are sample plots with different numbers of NR. The sample plots were 10 m^2 circular plots which were inventoried for NR and site conditions. Numbers and letters in the margin show the system of naming a specific plot cluster, which is the grouping of four sample plots. *Fruit trees* are a group of species used in the enrichment planting in the INIKEA Project (Alloysius, et al., 2010). Specifically, trees giving fruit for human consumption or as food for bigger mammals and birds.

Appendix 6. Diagram from study in INIKEA Forest Rehabilitation Project showing plotted values (n=25) for natural regeneration (NR) and altitude for *Dryobalanops keithii* Sym and *Parashorea spp* located in the cluster-plots. Cluster-plots were four grouped sample plots with aggregated data, the sample plots were 10 m^2 circular plots which were inventoried for NR and site conditions. NR was defined as non-pioneer tree species ≥30 cm in height to < 25 cm in diameter breast height (dbh; diameter 130 cm above germination point) and altitude as meter above a reference (calibration) point.
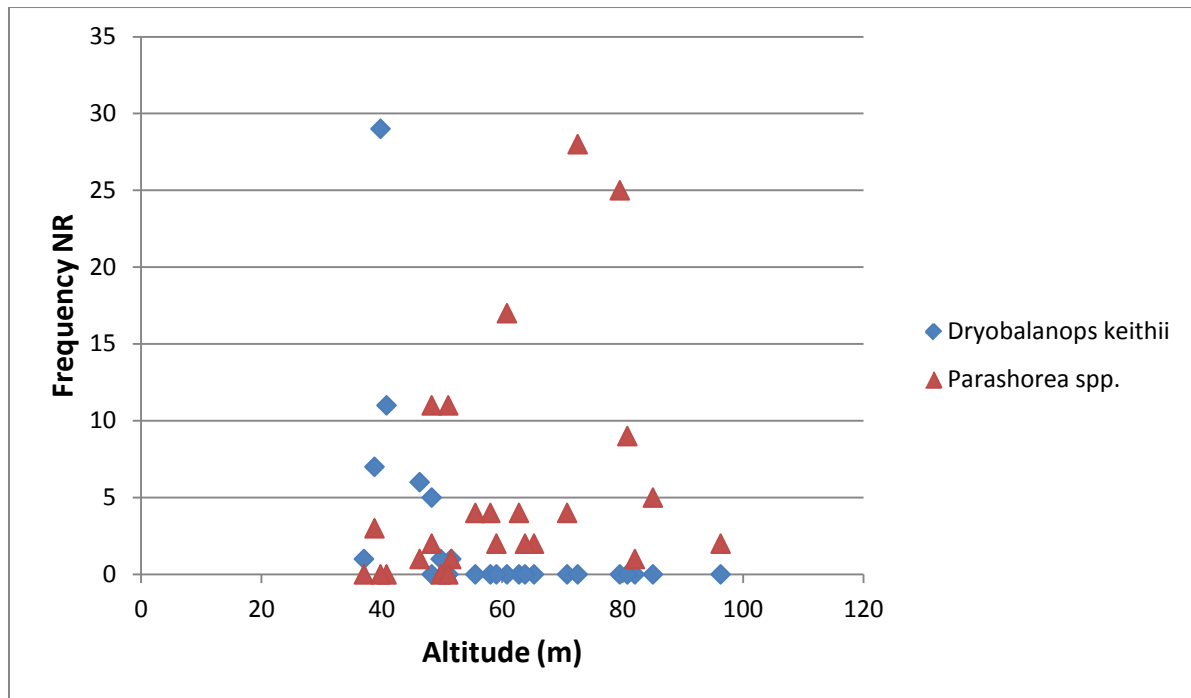
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