Examensarbeten 2014:2

Fakulteten för skogsvetenskap
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Tree species traits response to different canopy cover for 34 tree species in an enrichment planted tropical secondary rain forest in Sabah, Malaysia

Trädslagsegenskapers respons på olika krontäckning för 34 trädarter i en hjälpplanterad sekundär tropisk regnskog i Sabah, Malaysia

Photo: Li Videkull

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Sveriges Lantbruksuniversitet
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ABSTRACT

Tropical rain forests only cover around six percent of the world's land area and contain around 70 % of the world´s animals and plants. Tropical rainforests have been, and still are, negatively affected by human activities. These activities lead to forest degradation which has negative impacts on production and biodiversity.

Between 1970-1980 forests in Borneo, Sabah, Malaysia, was subjected to intense logging. In 1982 and 1983 Sabah was exposed to a prolonged drought followed by wildfires which further ruined the already damaged forests. In 1998 the Yayasan Sabah Group and IKEA started a forest rehabilitation project in the degraded forest in the Kalabakan region in Yayasan Sabah Concession Area in Malaysia. The main aim of the program is to improve the biodiversity status in the degraded tropical rain forest within the project area. To improve or accelerate the regeneration in the rehabilitation areas, enrichment plantings are used. Information about tropical tree species traits is limited, which complicate the rehabilitation work. Functional traits for plants are traits that affect growth, reproduction and survival and hence the plants fitness to the environment. Tree species used to be grouped after their demand for light and growth pattern. Light demanding pioneer species often have low wood densities and fast growth and shade tolerant climax species tend to have high wood densities and slow growth. However, the pioneer-climax classification is considered as a continuum.

The objectives of this study were to investigate how different canopy cover affected tree species traits for 34 tree species in an enrichment planted tropical secondary rain forest, and if tree species growth response to increased light after a shade adjustment was related to tree species specific wood densities. The results indicated that tree individuals with least available light generally had smaller dbh (diameter in breast height) and lower tree heights compared to tree individuals with higher light availability. The maximum measured dbh and heights for tree individuals decreased with increasing wood density. Increased dbh growth and horizontal crown growth for the investigated tree species were observed after the shade adjustment. The increased growth was correlated with wood density which showed to be negatively correlated both with dbh growth and horizontal crown growth. A negative trend between wood density and height growth after the shade adjustment was found, but this was not statistically proven. The investigated tree species in this study indicated different adaptations to light depending on wood density even though they all are classified as climax species. Information from this study, on how species with different wood density, respond to light, can be used to adapt the choice of tree species for the current lighting conditions in the forest. This information can improve the rehabilitation work in the INIKEA Forest Rehabilitation Project and elsewhere in Malaysia.

SAMMANFATTNING

Tropisk regnskog täcker cirka sex procent av jordens landyta och innehåller ungefär 70 procent av världens djur- och växtarter. Tropiska regnsskogar har påverkats negativt av mänsklig aktivitet genom tiderna och vilket än idag är en pågående process. Dessa mänskliga aktiviteter har lett till förstörelse av de tropiska regnskogarna vilket har negativa effekter på både produktion och biodiversitet.

Mellan 1970-1980 avverkades skogarna i Borneo, Sabah, Malaysia, intensivt. Under 1982 och 1983 utsattes Sabah för en långvarig torka följt av skogsbränder som ytterligare försämrade tillståndet för de redan skadade skogarna. 1998 startade Yayasan Sabah Group och IKEA ett skogsrehabiliteringsprojekt i de degraderade skogarna inom Yayasan Sabah skogsmarker i Malaysia. Syftet med projektet är att förbättra den biologiska mångfalden i de degraderade tropiska regnskogarna inom projektområdet. För att förbättra eller påskynda föryngringen i rehabiliteringsområdena används hjälpplantering. Informationen om tropiska trädarters egenskaper är begränsad, vilket försvårar rehabiliteringsarbetet. Funktionella egenskaper för växter är egenskaper som påverkar tillväxt, fortplantning och överlevnad och därmed växter anpassning till miljön. Trädarter brukar grupperas efter deras ljusbehov och tillväxtmönster. Ljuskrävande pionjärarter har ofta låg veddensitet och snabb tillväxt medan skuggtåliga klimaxarter ofta har hög veddensitet och långsam tillväxt. Det är viktigt att vara medveten om att pionjär-klimax klassificeringen betraktas som ett kontinuum.

Syftet med denna studie var att undersöka hur olika krontäckning påverkar trädslagsegenskaper hos 34 olika trädarter i en återplanterad sekundär tropisk regnskog. Om trädarters tillväxtrespons på ökat ljus efter en ljushuggning var relaterat till veddensitet undersöktes också. Resultaten visade att trädindivider med minst tillgängligt ljus generellt hade mindre dbh (diameter i brösthöjd) och lägre trädhöjder jämfört med trädindivider med mer tillgängligt ljus. De högsta uppmätta dbh och höjderna för trädindividerna minskade med ökad veddensitet. Ökad dbh-tillväxt och horisontell krontillväxt observerades efter ljushuggningen för de undersökta arterna. Den ökade tillväxten var negativt korrelerad med veddensitet. Efter ljushuggningen kunde en negativ trend mellan veddensitet och höjdtillväxt observeras, men detta kunde inte bevisas statistiskt. De undersökta trädarterna i denna studie visade sig ha olika anpassningar till ljus beroende på veddensitet, trots att de alla klassificeras som klimaxarter. Information från denna studie, om hur trädslag med olika veddensitet svarar på ljus, kan användas för att anpassa trädslagsval för rådande ljusförhållanden i skogen. Denna information kan förbättra rehabiliteringsarbetet i INIKEA Forest Rehabilitation Project och på andra håll i Malaysia.

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1. INTRODUCTION

1.1 Tropical rain forest

Tropical rain forests cover around six percent of the world's land area. They are characterized by containing a large number of deciduous trees forming tall and dense forests (Corlett & Primack 2011). Tropical forests are complex and diverse, containing 70 % of all animals and plants in the world (Sands 2005). Tropical forests are found close to the equator (Whitmore 1998; Sands 2005). There are different rain forest formations classified according to differences in climate, soil, soil water content and altitude (Whitmore 1998). The main factor that differ them from one another is the duration and severity of the dry periods (Sands 2005). The climate in tropical regions is warm, with a mean temperature of at least 18 centigrade for the coldest month (Walsh, 1996). Tropical rain forests are wet all year round with an average annual rainfall of at least 1700 mm, but can range to over 10 000 mm. Dry periods are absent or short, lasting less than four consecutive months. A dry period is characterized with a monthly rainfall less than 100 mm. Overall the temperature, day length, humidity and precipitation are rather constant during the year (Sands 2005).

The largest block of tropical rain forest is found in South America and consist of 4×10^6 km^2. The Eastern tropics are the second largest block of tropical rain forest. This area covers around 2.5 × 106 km^2. This area is centered on the Malaya archipelago and stretches to northeast Australia. This block also includes parts of India, Sri Lanka, Bangladesh, Laos, Thailand, Vietnam and Cambodia. The smallest blocks is located in Africa and consist of 1.8 × 106 km^2. Madagascar also consists of small parts of tropical rain forest (Whitmore 1998).

1.2 Dipterocarp forest

Tropical lowland evergreen rain forests are the main forest formations in the lowlands in the Eastern tropics (Whitmore 1998). In Asia most forest are called dipterocarp forests because the majority of the biomass comprises trees from the family *Dipterocarpaceae* (Corlett & Primack 2011). These forests occur at altitudes from sea level to 1200 m above sea level and the soils consist predominantly of oxisols and ultisols (Whitmore 1998). The forest area in Malaysia is approximately 20.5 million hectare (FAO & ITTO 2011) and 17.1 million hectare of it constitutes of dipterocarp forest (Blaser et al. 2011). Dipterocarp forests are the most common in many southeastern countries in Asia. These forests dominate the international tropical timber market because of their wide range of applications by the timber industry (Corlett & Primack 2011). The family contains 19 genera and more than 500 species (Maury-Lechon & Curtet 1978). Trees from this family often reach high heights of 40-60 meters (Becker 1996). The trunks are straight without side branches until the canopy is reached. The stem base is buttressed which make dipterocarp trees very stable and therefore they often die standing (Corlett & Primack 2011). Dipterocarp species flower and fruit together only once every 3-8 year, this phenomena is called mast flowering and fruiting (Montagnini & Jordan 2005). The mast flowering of dipterocarps is triggered by drought (Sakai et al. 2006). In Borneo the draughts are associated with the El Niño Southern Oscillation (ENSO). The events occur with 2-8 years intervals. A strong El Niño entails low rainfall with drought as a result (Corlett & Primack 2011). The seedlings of dipterocarps can survive under the canopy (Swaine & Whitmore 1988).

1.3 Forest degradation

Forest degradation is changes in the forest stand, where canopy cover stays above ten percent, which have negative impacts on production and biodiversity (FAO 2000). Primary forests are defined to be natural and untouched whereas secondary forests have developed after large-scale disturbances caused by humans or natural catastrophic events (ITTO 2002). The time it takes for forests to recover from disturbances depends on the severity of it (Whitmore 1998). After a disturbance several successional changes will occur which includes shifts in species composition, forest structure and dynamic (ITTO 2002). Factors like site fertility, forest age, earlier land use and seed access determines the structure and species composition of secondary forests (Montagnini & Jordan 2005). In the early succession of secondary forests the species composition tends to be dominated by light demanding species. But during the successional stages a shift in species composition towards a dominance of late successional species will occur (Whitmore 1998; ITTO 2002). Secondary forests are important in conservation purpose because they for many taxonomic groups can hold the same species richness as primary forests (Barlow et al. 2007). Many tropical rain forests have been affected negatively by human activities (Corlett & Primack 2011) and in Malaysia the forested area has decreased with 1.92 million hectares from 1990 to 2010 (FAO 2010). The human population in Malaysia is around 28.9 million (2011) and is predicted to increase to 46.9 million in 2100 (United Nations 2011). The growing population is one of the major causes of forest loss because forests are converted to other land uses to meet the increased human demand for resources (Sands, 2005). In Southeast Asia most deforestation is caused by tree crop plantations of oil palms (Corlett & Primack 2011). These plantations are holding much less species compared to primary and secondary forests (Fitzherbert et al. 2008). The demand for biofuel is increasing and since oil palms are very productive biofuels this is another big threat for the world's tropical rain forests (Corlett & Primack 2011). Deforestation and forest degradation leads to fragmentation which is a patchwork on remaining forests areas. Fragmentation leads to biodiversity loss. In which extent depends of the size of the fragments, distance between fragments and the quality of the habitat between the fragments (Laurance et al. 2002; Ewers & Didham 2006; Corlett & Primack 2011).

Malaysia is one of the world’s largest timber exporters. Especially dipterocarps are coveted by the timber industry. The loggings are selectively done, i.e. only a few trees per hectare are cut. The selective harvest system is based on removal of tree with dbh on 45 cm or more (Blaser et al. 2011). These operations often cause degradation because of damages on remaining trees, soil exposure and compaction (Corlett & Primack 2011). According to Verburg & van Eijk-Bos (2003) the changes in species compositions over time is greater in selectively logged forests compared to virgin forests. In their study logging operations results in reduction in tree stem density and logged forests contains large proportion of species with low wood density compared to virgin forest.

1.4 Forest restoration & rehabilitation

Degraded forests have undergone a decrease of biodiversity and productivity (Lamb & Gilmour 2003). Degraded forests often have low fertility, high fire frequency, bad conditions for seed germination and are exposed to competition from other plants (ITTO 2002). Forest restoration is a management system that refers to primary forests. The aim with restoration is to enhance natural processes of forest regeneration to regain its once productive and healthy ecosystem.

Forest restoration seeks to restore biodiversity, species composition, as well as forest structure and processes to their natural state. If restoration will succeed depends on the forest ecological status, structure, remaining species and disturbance history. The existing regeneration has to be managed carefully during the restoration work to ensure regrowth and if necessary enrichment planting can be done (ITTO 2002). The term rehabilitation refers to forest lands where the pristine productivity or structure is recovered and where some of the pristine biodiversity is regained (Lamb & Gilmour 2003). According to ITTO (2002) the aim with the rehabilitation is to reestablish the forest ecosystem so both its production- and protection functions are regained. The most important when starting to rehabilitate degraded forest lands is to understand the cause of degradation and determine if it is possible to affect or stop it. The rehabilitation work should promote natural regeneration at first and if it is needed enrichment planting can be done (ITTO 2002).

1.5 The forest cycle

The forest cycle is driven by gap dynamics. When gaps are created more light can reach the forest floor, but in which amount depends on gap size. Gaps are created when trees fall or die depending on different causes like wind, fire, ageing, volcanic eruption etc. (Whitmore 1989). The forest cycle can be divided in different phases; regeneration, building, mature, ageing and degrading phase (Whitmore 1989; Emborg et al. 2000). The gaps differ in size and allow species with different light requirements to establish which causes dissimilarities in species composition to the next growth cycle. The gap dynamic thus determines the species composition in the forests (Whitmore 1989). In general more shade tolerant species establish in small gaps while light demanding species occupies the larger gaps. After large disturbances, when large gaps are created the light demanding species dominate the early succession. The shade tolerant species can exist in the shade below the canopy of the pioneer species, and later in the growth cycle when the light demanding species starts to die off take over and dominate the next growth cycle. Due to the mosaic of gaps, all stages of the growth cycle exist in the forest which contributes to a variety of different canopy layers (Whitmore 1998). Tropical lowland forests contain trees of different sizes. Different species reach different heights in the canopy (Whitmore 1998). Gap dynamics differs between forests, for example in Borneo catastrophic events are rare resulting in dominance of shade tolerant species (Whitmore 1989).Tree species differs in their response to light for seed germination and are therefore used to be classified in two groups, pioneer species or climax species (Swaine & Whitmore 1988). It is important to be aware that the pioneer-climax classification may be considered as a continuum. No accurate and precise boundaries can be drawn between the two groups. Overlapping traits for both pioneer and climax species occur in reality (Turner 2001). Pioneer species need much solar radiation to germinate and will therefore establish after disturbances like landslides, gaps created by fallen trees, harvesting etc. (Swaine & Whitmore 1988). Pioneer species are characterized by having a wide ecological niche (Hall & Swaine 1980), fast growth, rapid seed production, small seeds, low wood density and often short lifespan (Swaine & Whitmore 1988). Climax species are characterized by having the ability to germinate in the shade, produce few and large seeds, slow height growth, sometimes having long life spans, wide range of wood densities and often narrower ecological niches (Whitmore 1998). Even though climax species often can germinate and grow in shade there are differences in required light (Swaine & Whitmore 1988). In Malaysia climax species are divided in two groups, Light Hardwoods (LHW) and Heavy Hardwood (HHW), depending on wood properties. LHW include the Light Red Meranti *Shorea* spp. (*Dipterocarpaceae*) and have low density wood with a pale color. HHW have high density wood with dark color. Climax species classified as LHW need more solar radiation to germinate and have faster growth. HHW include climax species that can germinate and grow in shade and they have a slower growth (Swaine & Whitmore 1988).

1.6 Tree species traits and trade-offs

Water, nutrients and light are essential for all green plants. Via photosynthesis green plants convert solar light to energy. There is a limitation in light and space in forests which affect tree growth and mortality (Ghazoul & Sheil 2010). To assimilate water, nutrients and light plants have developed special adaptations to assert themselves in the competition (Ghazoul & Sheil 2010). Functional traits for plants are traits that affect growth, reproduction and survival and hence the plants fitness (Violle et al. 2007). A trade-off is a situation when the investment in one trait that increases the fitness in return influences another trait negatively (Stearns 1989). Wright et al. (2010) states that a number of trade-offs exist in tropical trees. For example they report that growth rate is positively related to mortality rate and that growth rate and wood density is negatively correlated.

Growth rates for tropical trees are of practical reasons usually measured as diameter growth (Turner 2001). Diameter growth is positively correlated with light availability (King et al. 2005). Trees can use more energy for growth when light availability increases (Ghazoul & Sheil 2010). Tree crown architecture is the overall shape of the tree and determines the light catching capacity for trees (Valladares & Niinemets, 2007). A growing tree is using products from the photosynthesis to produce new leaves and roots to increase the carbon and nutrient uptake for future extension (King 1994). According to a study by Sterck & Bongers (2001) branch extension is positively correlated with increased light. A trade-off between branching and height growth exist, producing a wide crown will be at the expense of slower height growth (Valladares & Niinemets, 2007). Different branching patterns give rise to different traits. A wide and low crown can effectively capture light but will easily be overtopped. A narrow crown is on the opposite not that effective in capturing light (Valladares & Niinemets, 2007). Tree species with high wood densities have shown to be more efficient in widen their crowns compared to species with low wood densities (Anten & Schieving 2010; Iida et al. 2012). Species with a low wood density instead grow rapidly in height to reach the open canopy (Kohyama 1987).

Wood density is the weight per unit volume (Ghazoul & Sheil 2010). In the tropics there is a wide range of wood densities (van Gelder et al. 2006). Wood density is often associated with growth (Turner, 2001) and a trade-off between these two factors exists. Species with pioneer properties tend to have low wood densities and climax species high wood densities (van Gelder et al. 2006). According to Iida et al. (2012) stem diameter is positively correlated with tree height and negatively correlated with wood density. Species with low wood densities may therefore have a more rapid diameter growth than species with high wood densities (Iida et al. 2012). According to Anten & Schieving (2010) low density wood is associated with efficient height growth. In their study stem mass per unit height was positively correlated with wood density. Species with low wood densities can construct more stem volume than species with high wood densities with the same mass of wood (van Gelder et al. 2006). The low construction costs for species with low wood densities (van Gelder et al. 2006) is the reason to their rapid height and diameter growth (Anten & Schieving 2010; Iida et al. 2012). Since wood density is negatively correlated with growth (Anten & Schieving 2010; Iida et al. 2012) and positively correlated to mechanical stability, which may increase the resistance to damages (van Gelder et al. 2006) and increase the survival (Poorter et al. 2010) a trade-off between tree growth and mechanical stability may be expected.

Mortality among seedlings is size dependent. Seedlings in lower height classes have higher mortality than those in higher height classes (Turner 1990). The potential height growth determines if the tree will reach the canopy (Clark & Clark 2001). In a study by Clark & Clark (2001) height growth was measured from a juvenile to a mature state over a 16-year period for pioneer and nonpioneer species in a lowland Neotropical rain forest in Costa Rica. In their study pioneer species dated highest mean height growth in the smaller diameter classes (1-4 and 4-10 cm). All species showed a lower annual height growth than their potential growth. This is due to suppression caused by competition with neighboring plants and physical damages that inhibit height growth (Clark & Clark 2001).

1.7 Experimental design for the INIKEA Forest Rehabilitation Project

This study was situated in the INIKEA Forest Rehabilitation Project, Sabah, Borneo. Between 1970-1980 forests in Sabah was subjected to intense logging (Reynolds et al. 2011). In 1982 and 1983 Sabah was exposed to a prolonged drought. This caused forest fires which also destroyed and damaged the forests. Fires are not a common phenomenon in tropical rain forests so the forests are not adapted to fires and therefore the impact was devastating (Garcia & Falck 2003). Even though the fire was kept on the forest floor almost all forest species were perished, only some big trees survived. After the fire a succession of pioneer species started which changed the forest structure towards a less diverse forest with fewer species (Garcia & Falck 2003). In 1998 the Yayasan Sabah Group and IKEA started a forest rehabilitation project in the degraded forest in the Kalabakan region in Yayasan Sabah Concession Area in Malaysia. The state-owned organization, Yayasan Sabah Group, manages a million hectares of tropical rain forest in Sabah, Malaysia. The Swedish University of Agricultural Sciences is also involved in the projects by providing research and technical consultations. The main aim of the program is to improve the biodiversity status in the degraded tropical rain forest within the project area (Alloysius et al. 2010). The total project area is 18 500 ha and today approximately 12 000 ha of the area have been rehabilitated (Alloysius et al. 2010). Two different enrichment planting methods are used in the project, line planting and gap-cluster planting, the latter being the predominant method (Alloysius et al. 2010).

1.8 Objectives

Information about tropical tree species´ traits are limited and therefore more research is needed to get a better understanding how to manage the tropical rain forests and maintain a high biodiversity. The objectives of this study were to investigate how different canopy cover affected tree species traits for 34 tree species in an enrichment planted tropical secondary rain forest, and if tree species growth response to increased light after a shade adjustment was related to tree species specific wood densities. The purpose of my is to increase the knowledge of the traits of the different tree species to get a better understanding about the species growth rates and responses to available light. This information can hopefully be used to classify the species in functional groups which will facilitate management and planning in the INIKEA Forest Rehabilitation Project.

In this study I investigated the hypotheses that:

- Tree species have different growth rates in relation to surrounding light
- Light is a limiting factor for tree growth both within and among species in this lowland Dipterocarp rain forest
- Tree species growth response to increase light after a shade adjustment can be related to tree species specific wood densities

2. MATERIAL & METHODS

2.1 Study site

The study was performed in an experiment area called Species Demo Plot, located in the INIKEA Forest Rehabilitation Project area in the southeast of Sabah, Malaysia, west of the town Tawau in the Kalabakan Forest Reserve (Garcia & Falck 2003) lat 4°36'N, long 117°14'E (Romell 2007). The mean annual precipitation for the study site is around 2890 mm per year and the daily temperature is fluctuating between 22.0-32.7 °C (Romell 2007).

Figure 1. Map of Borneo (Wikimedia Commons 2012) and the location of the INIKEA Forest Rehabilitation Project.

2.2 Planting method in the study site

The study site was planted in 2008 according to the line planting method. For this method lines are created every tenth meter and lines are two meters wide. Trees are planted every third meter along the line. Large trees in and between the lines are selectively girdled to increase the light condition on the forest floor. Shrubs, undergrowth, non-commercial small trees and climbers are also removed to increase the light and decrease competition (Garcia & Falck 2003). The study site consists of 34 planting lines with twenty planting points along each line. 34 species were planted in the area with approximately 20 individuals of each species (Anon. 2008).

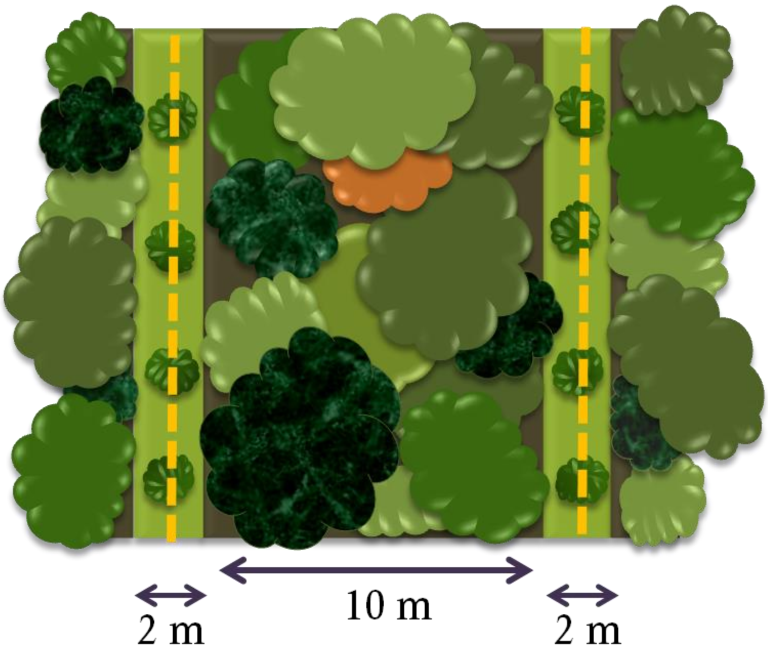

Figure 2. Illustration of the line planting method used in the INIKEA Forest Rehabilitation Project. Figure by Malin Gustafsson.

2.3 Planting material

The INIKEA Project has a nursery located in Luasong. The planting material consists of seedlings and wildings (Garcia & Falck 2003). Dipterocarp species flower and fruit together only once every 3-8 year (Montagnini & Jordan 2005) so seed collection takes place during these years. Seeds are picked directly from the forest floor and then germinated in the nursery (Alloysius et al. 2010). Wildlings are naturally regenerated seedlings from the last mast years that grow in the forest (Alloysius et al. 2010). After wildlings are picked in the field they are incubated in chambers with plastic cover 2-3 months in the nursery (Garcia & Falck 2003).

2.4 Maintenance of the enrichment planting

Maintenance of the enrichment planted areas is necessary to ensure good results. Measures that reduce competition and increase the amount of light is important for seedling survival and growth (Alloysius et al. 2010). To reduce competition weeding is done three times annually the two first years and after that with longer intervals (Garcia & Falck 2003). Fallen debris like branches and dead climbers that can harm the seedling is removed. Shade adjustments are also needed to open up both the lower and upper forest canopy and hence increase light availability for the planted trees. Shade adjustments are done by girdling unwanted large trees and removal of small trees and shrubs (Garcia & Falck 2003). Shade adjustments can be done up to four times during the maintenance period of ten years (Alloysius et al. 2010).

2.5 Measurements

In April 2012 an inventory was done in the Species Demo Plot before the shade adjustment that was performed in February 2013. My inventory was implemented four months after the shade adjustment, the 21th of June to the 4th of July 2013. For detailed working schedule for the Species Demo Plot see Appendix 1. All living planted trees in the 34 lines were measured. Tree height and stem height was measured to the nearest centimeter with a measurement stick. Stem height is the length from the stem base to the first living branch. The stem diameter was determined at 0.30, 1.30 (diameter at breast height, dbh) and 1.80 meter from the stem base to the nearest millimeter with a calliper. The crown width was taken perpendicular both along and across the planting line to get an average value on horizontal crown growth. This measurement was taken with a measuring tape and was determined to the nearest centimeter. Leaved stem length was also measured with a measuring tape to the nearest centimeter. This is the length from the first leaf on a branch to the end of it and this measurement was taken from three branches on a tree, one branch from the upper crown, one from the middle and one from the lower crown. The internode length is the distance between internodes on a branch. Four internodes on each branch selected for measurement were measured with a ruler and were determined to the nearest millimeter. Leaf length, width and thickness were measured on two leaves on each of the branches. Leaf length and width were measured to the nearest millimeter with a ruler. Leaf thickness was determined to the nearest nanometer with a thickness gauge. For each planting line fisheye photos were taken in between all the planted trees. From these photos ground cover was assessed. Estimation of the tree crown area that was exposed to direct sunlight for the individual tree crowns were done subjectively. These estimates were referred as crown illumination index (CII) and followed a classification system including five classes. Class one includes individuals with crowns not exposed to direct light, class two is only exposed to some side light, class three has some overhead light, class four has full overhead light and class five has a crown fully exposed to light both vertical and laterally (like a 90° inverted cone encompassing the crown) (Dawkins 1958 referenced in Jennings et al. 1999). Wood densities for the investigated tree species were taken from a wood density database and scientific papers (Köhler 1998; World Agroforestry Centre 2004). Wood density for some of the tree species could not be found. Some of the investigated tree species in this study were not able to be identified to species but only to genus. Wood density values for these species were therefore taken for the genus as a whole.

2.6 Calculations and data analysis

The statistical program MINITAB Statistical Software (2009) was used for the analysis. Linear regression is a simple model used to estimate relationships between variables (Wonnacott & Wonnacott 1990). The relation between crown illumination index (CII) and tree species traits dbh, height and wood density was illustrated in scatterplots. The difference in growth for the tree species traits, height, dbh, crown width, leaved stem length, internode length and leaf size index (leaf length × leaf width) and the difference in available light expressed as ground cover before and after the shade adjustment were calculated for all individuals. Regressions between the difference in growth for the tree species traits and the difference in ground cover before and after the shade adjustment were done for each tree species. The coefficients for growth from the regressions for each species estimated the change in mean response in growth per unit increase in ground cover. The coefficients for the tree species traits response in growth before and after the shade adjustment were used together with wood densities for the species in a new regression to determine the relation between the two parameters. If $P \leq 0.050$ the results of the statistical analyses were considered to be significant.

3. RESULTS

3.1 Tree species growth response to light

The highest and lowest measured values of dbh and the calculated median dbh for the 34 tree species in this study is summarized in Table 1. The greatest portion of the planted trees belonged to the tree family *Dipterocarpaceae*. There were substantial differences among tree species greatest measured dbh. *Shorea platyclados* had highest median dbh and also the highest measured dbh. Species from the tree family *Dipterocarpaceae* and genus *Shorea* showed highest median dbh. Generally species with higher wood densities had lower median dbh.

Table 1. Maximum and minimum diameter at breast height (dbh) measured in June/July 2013 and calculated median values on dbh for the 34 investigated tree species planted in the INIKEA Forest Rehabilitation Project. Values on median dbh calculated from the measured dbh:s. Severely damaged trees are not included in the table. Family names taken from World Agroforestry Centre (2004). Wood density (air dried) for *Pentace laxiflora* and *Parashorea tomentella* according to Köhler (1998) and wood density (moisture content 15 %) for the remaining species according to World Agroforestry Centre (2004). Authors to species names taken from Richards, 1996; Roskov et al. 2013.

Family	Species name	Wood density (kg/m^3)	Median dbh	Max dbh	Min dbh
Dipterocarpaceae	*Shorea platyclados* S.	600	3.2	10.2	0.7
Dipterocarpaceae	*Shorea leprosula* M.	520	2.9	9.1	1
Dipterocarpaceae	*Shorea beccariana* B.	510	2.8	5.8	0.5
Dipterocarpaceae	*Shorea macroptera* D.	490	2.7	6.7	0.6
Dipterocarpaceae	*Shorea fallax* M.	625	2.4	5	0.6
Dipterocarpaceae	*Shorea parvifolia* D.	450	2.4	4.3	0.8
Dipterocarpaceae	*Shorea ovalis* B.	510	2.2	7.1	0.5
Euphorbiaceae	*Baccaurea* sp	790	2.2	3.1	0.8
Dipterocarpaceae	*Shorea falciferoides* F.	893	2.1	2.9	0.2
Dipterocarpaceae	*Dryobalanops lanceolata* B.	665	2	4.6	0.7
Tiliaceae	*Pentace adenophora* K.	-	2	3.2	1
Bombacacea	*Canarium* sp	585	1.9	4.2	0.4
Euphorbiaceae	*Baccaurea angulate* M.	-	1.9	2.9	0.9
Tiliaceae	*Pentace laxiflora* M.	360	1.9	5.6	0.4
Dipterocarpaceae	*Parashorea malaanonan* M.	490	1.8	5.9	0.6
Dipterocarpaceae	*Parashorea tomentella* M.	506	1.7	4.5	0.7
Dipterocarpaceae	*Shorea macrophylla* A.	400	1.7	6.8	0.6
Dipterocarpaceae	*Dryobalanops keithii* S.	780	1.5	4.5	0.9
Dipterocarpaceae	*Shorea leptoderma* M.	-	1.5	3.8	0.7
Leguminosae	*Koompassia excelsa* T.	830	1.5	2.8	0.5
Dipterocarpaceae	*Shorea* sp	578	1.5	3.9	0.5
Dipterocarpaceae	*Dipterocarpus conformis* S.	950	1.4	4.6	0.4
Sterculiaceae	*Heritiera* sp	730	1.4	3.2	0.6
Anacardiaceae	*Mangifera pajang* K.	-	1.4	2.8	0.8
Leguminosae	*Sindora irpicina* de W.	600	1.4	1.7	0.6
Dipterocarpaceae	*Shorea pauciflora* K.	630	1.3	3.7	0.6
Bombacacea	*Durio* spp	750	1.2	4	0.4
Anacardiaceae	*Mangifera odorata* G.	610	1.2	1.7	0.7
Meliaceae	*Walsura pinnata* H.	-	1.1	1.9	0.7
Dipterocarpaceae	*Hopea ferruginea* P.	700	1	3.3	0.5
Dipterocarpaceae	*Shorea xanthophylla* S.	640	1	1.7	0.1
Dipterocarpaceae	*Parashorea smythiesii* W-S.	754	0.9	2.4	0.3

Leguminosae	*Intsia palembanica* M.	790	0.9	1.2	0.5
Ebenaceae	*Diospyros* sp	1030	0.7	1.2	0.4

Most tree individuals, representing all studied species, were exposed to light that had crown illumination index classified as two or three. The result when analyzing dbh, wood density and CII and tree height, wood density and CII showed the same pattern. CII was significantly correlated with dbh growth and height growth ($P < 0.0001$). Tree individuals with CII one, those with lowest available light, had both small dbh and low tree heights. Tree individuals exposed the highest levels of light, CII four and five, were not common in the study site. Trees with CII four or five generally showed to have had relatively high growth rates. Wood density and CII together was significantly correlated with dbh growth ($P = 0.005$; $R^2 = 25.9$ %) and height growth ($P = 0.002$; $R^2 = 21.6$ %). In the various wood density classes both dbh and tree height were generally higher for individuals with CII four or five in comparison with tree individuals with less light availability. Both the widest and highest individuals had rather low wood densities, between 300 and 600 kg/m^3. Also the narrowest and shortest individuals were found in the same wood density interval, between 700 and 1050 kg/m^3. The absolutely narrowest and shortest individuals had wood densities around 1050 kg/m^3. The maximum measured dbh and heights for tree individuals decreased with increasing wood density (Figure 3 and 4).

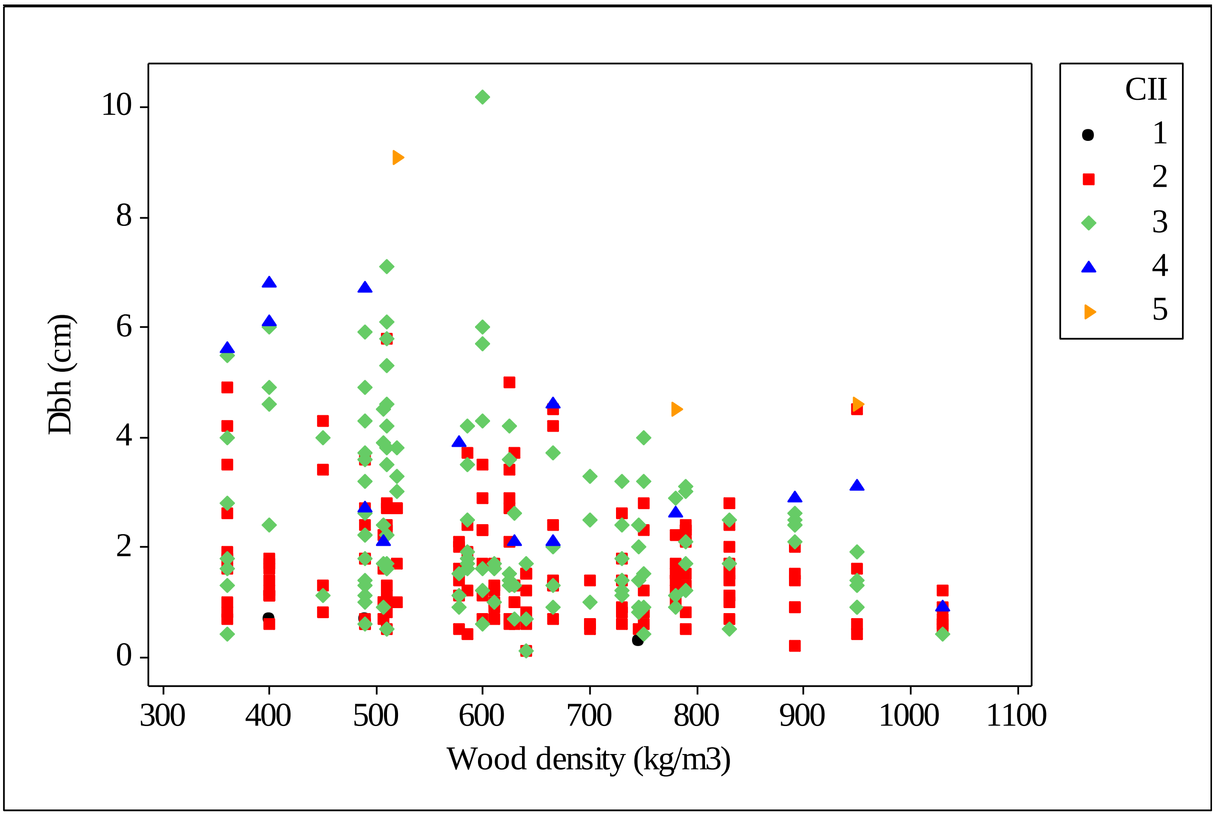

Figure 3. The relationship between tree diameter in breast height (dbh), wood density and light availability for individuals belonging to 34 different tree species used in the enrichment planting in the INIKEA Forest Rehabilitation Project. Light availability is referred as crown illumination index (CII) and was classified as: 1=not exposed to direct sunlight, 2=exposed to some side light, 3=exposed to some overhead light, 4=exposed to full overhead light and 5= crown fully exposed to light both vertical and laterally (like a 90° inverted cone encompassing the crown) (Dawkins 1958 referenced in Jennings et al. 1999).

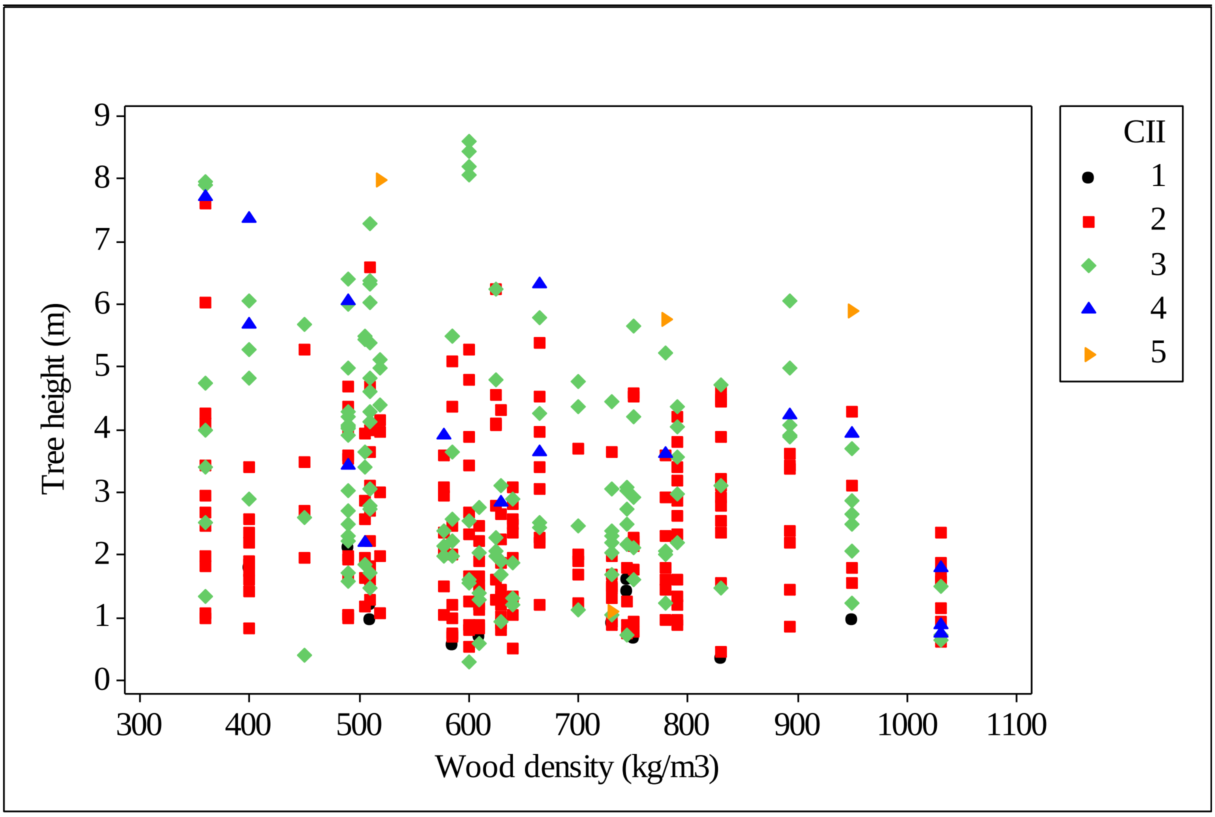

Figure 4. The relationship between tree height, wood density and light availability for individuals belonging to 34 different tree species used in the enrichment planting in the INIKEA Forest Rehabilitation Project. Light availability is referred as crown illumination index (CII) and was classified as: 1=not exposed to direct light, 2=exposed to some side light, 3=exposed to some overhead light, 4=exposed to full overhead light and 5= crown fully exposed to light both vertical and laterally (like a 90° inverted cone encompassing the crown) (Dawkins 1958 referenced in Jennings et al. 1999).

3.2 The relationship between tree species response to increased light after a shade adjustment and wood density

The regressions between difference in growth for the tree species traits and the difference in ground cover before and after the shade adjustment showed that most of the 34 investigated tree species had grown more after the shade adjustment. But it was not possible to relate the increased growth for the tree species traits to a changed ground cover. The tree species traits dbh, crown width and height were significantly correlated with increased growth after the shade adjustment, while the tree species traits leaved stem length, internode length and leaf size index was not significantly correlated. The coefficients for growth for the tree species traits, dbh, crown width and height, from the above mentioned regression, see Appendix 2, were then used in regression analyses together with wood density to examine if there was a change in growth rate after the shade adjustment. Dbh growth and horizontal crown growth after the shade adjustment were significantly correlated to wood density. Height growth after the shade adjustment was not significantly correlated to wood density.

The response in dbh growth after the shade adjustment showed a significant negative correlation with wood density (P = 0.026; R^2 = 17.1 %) for the 34 tree species. Tree species with lower wood densities generally showed higher dbh growth after the shade adjustment compared to species with higher wood densities. Dbh growth rates after the shade adjustment varied greatly among the investigated tree species (Figure 5).

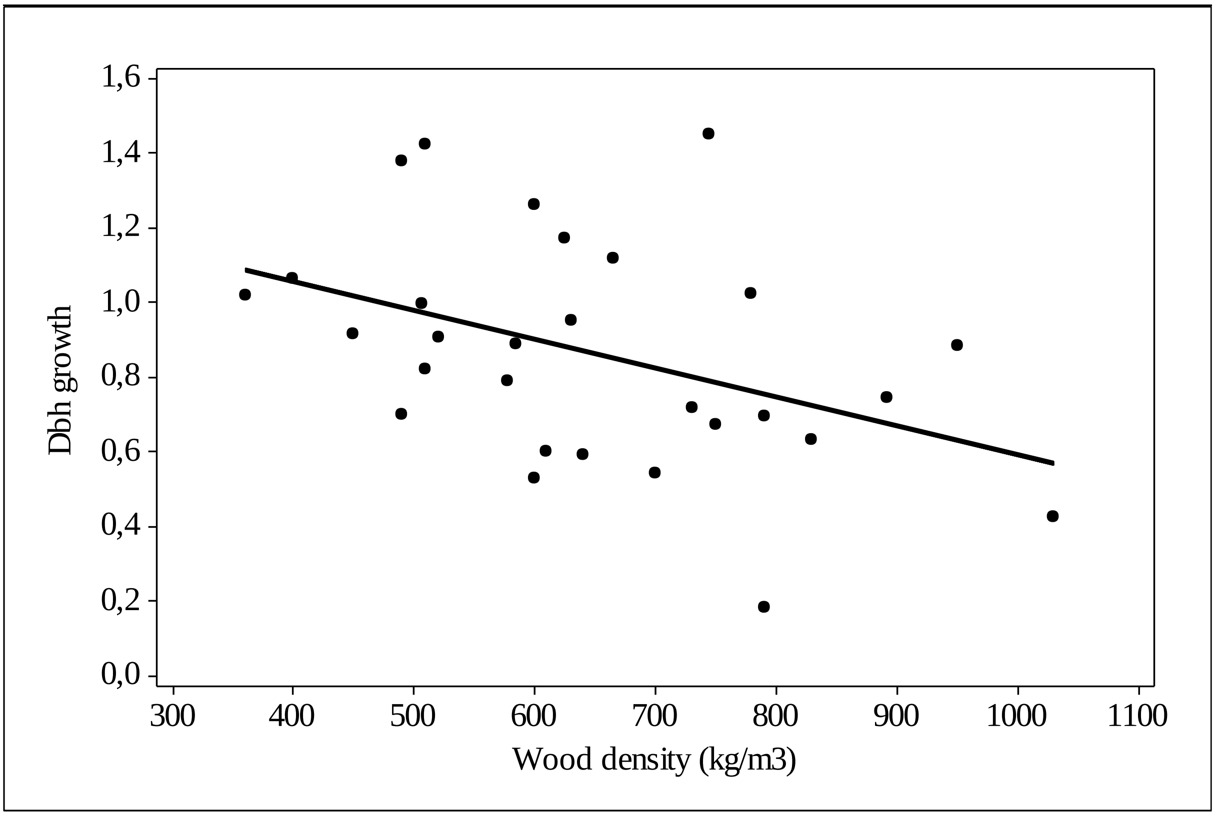

Figure 5. The relationship between dbh (diameter at breast height) growth and wood density for 34 tropical tree species used in the enrichment planting in the INIKEA Forest Rehabilitation Project. Diameter growth is expressed as coefficients for diameter growth against ground cover from regression analysis for the 34 tree species.

The response in horizontal crown growth after the shade adjustment was significantly negatively correlated to wood density for the 34 investigated tree species (P = 0.040; R^2 = 14.8 %). This indicated that species with higher wood densities had lower horizontal crown growths after the shade adjustment than species with lower wood densities. It seemed to be large response differences among tree species in horizontal crown growth after the shade adjustment between the 34 investigated species (Figure 6).

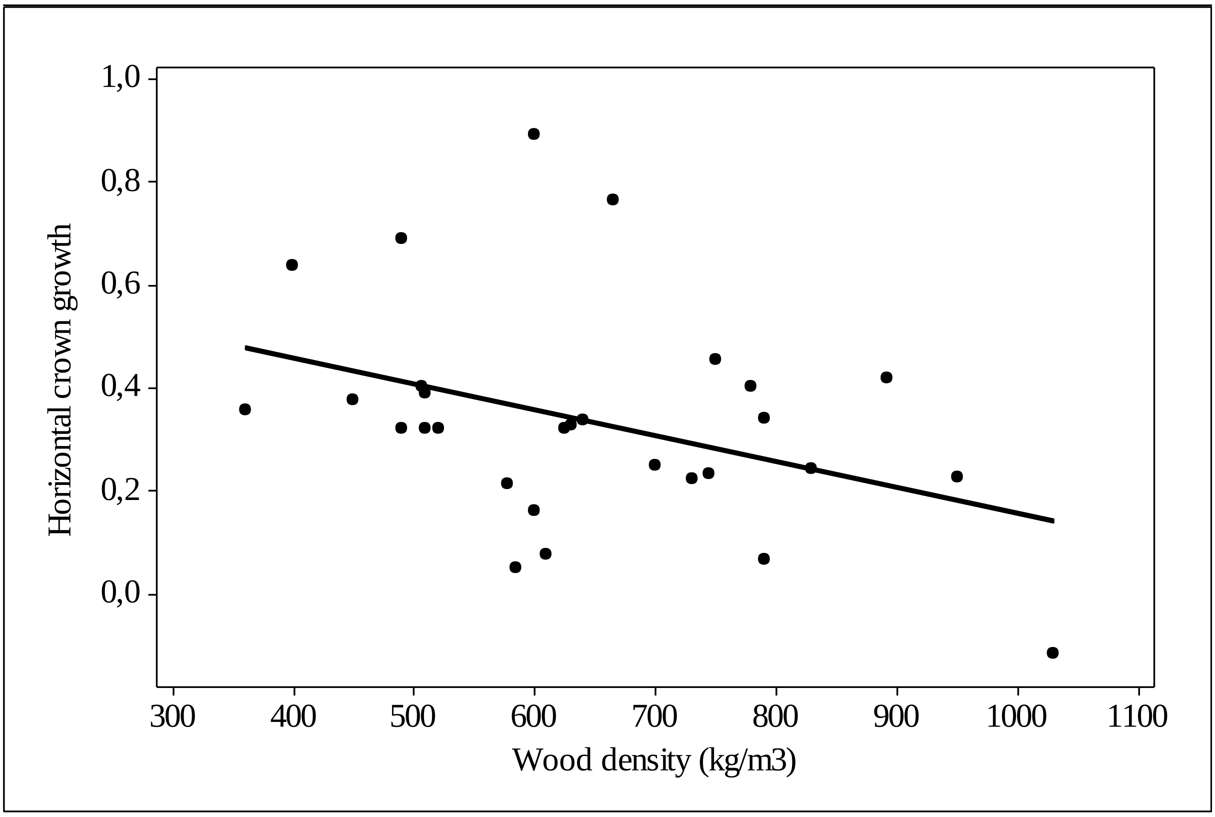

Figure 6. The relationship between horizontal crown growth and wood density for 34 tropical tree species used in the enrichment planting in the INIKEA Forest Rehabilitation Project. Horizontal crown growth is expressed as coefficients for diameter growth against ground cover from regression analysis for the 34 tree species.

There was a large variation in height growth after the shade adjustment between the 34 investigated tree species and hence the relation with wood density was not significant (P = 0.191; R^2 = 6.3 %). The spread in height growth after the shade adjustment was bigger for species with a density below 650 kg/m^3. This analysis indicated that species with lower densities had higher height growths after the shade adjustment, but this was not statistically proven (Figure 7).

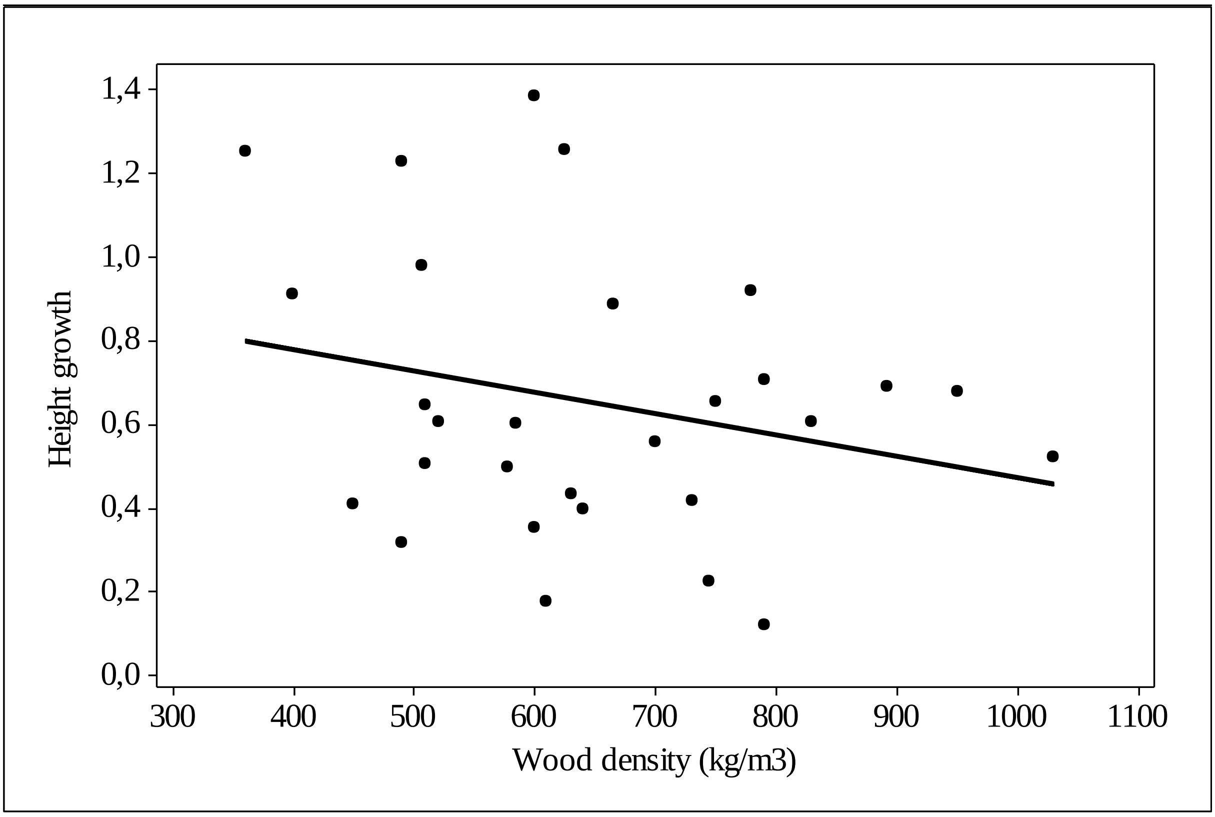

Figure 7. The relationship between height growth and wood density for 34 tropical tree species used in the enrichment planting in the INIKEA Forest Rehabilitation Project. Height growth is expressed as coefficients for diameter growth against ground cover from regression analysis for the 34 tree species.

4. DISCUSSION

4.1 Tree species traits response to different light environment

Dbh growth rates for the 34 planted tree species differed greatly (Table 1). King et al. (2005) reports similar results in their study performed in mixed dipterocarp forests of Malaysia. The observed variation in dbh growth between tree species in this study had probably many reasons. Likely reasons to the variations may be variations in light availability (King et al. 2005), microclimate (Whitmore, 1998), different growth rates for tree species (Clark & Clark 2001), variation in soil resources and damages by pathogens and pests (King et al. 2005).

Sunlight is essential for tree growth. All plants compete for light and light availability is a main factor explaining differences between rain forest tree species. Light conditions differ markedly between the upper canopy and the forest floor. Rain forest trees often experience a limitation in light (Ghazoul & Sheil 2010). In the present study tree individuals that were most exposed to light showed to have both greater dbh and be higher, compared to the trees growing in a more shaded environment (Figure 3 and 4). This indicated that light availability was a limiting factor for tree growth in the study site. Other studies also report an increasing dbh growth with increasing light exposure (Clark & Clark 1992; King et al. 2005). Poorter et al. (2003) reports a significant positive relation between tree height (trees measured at 15 cm dbh) and light demand for 53 rain forest species in Liberia. Their result shows that the tallest species often grow in places with a high exposure to light and that height growth is positively correlated to light, i.e. increased light will result in increased height growth.

Species have had to develop special traits to adapt to different environmental light conditions (Ruban 2009). In my study it was seen that the investigated tree species differed in their response to light, the growth decreased with increased wood density even at same CII (Figure 3 and 4). This indicated that those of the 34 investigated tree species with lower wood densities can bear strategies that are more alike those for pioneer species. If the hypothesis is correct, species with lower wood densities may need more light for survival and growth (Swaine & Whitmore 1988). This information is important to consider when enrichment plantings are used in rehabilitation of degraded tropical rain forests.

4.2 Trade-off between growth and wood density

In my study both wood density and light availability seemed to be correlated with height growth and dbh growth (Figure 3 and 4). This because, individuals with higher light exposure generally had greater heights and dbh than other individuals in the same wood density class and the observed maximum tree height and dbh in each wood density class indicated a decreasing trend with increasing wood density. Dbh and height growth have in several studies been negatively correlated with wood density (Thomas 1996; Osunkoya et al. 2007; Wright et al. 2010). Light demanding species have low wood densities compared to shade tolerant species (Swaine & Whitmore 1988) and are reported to have the highest mean height growth in smaller diameter classes (Clark & Clark 2001). According to King (1994) light demanding species show greater or equal height growth rates compared to shade tolerant species in intermediate light levels. King et al. (2005) found that diameter growth for naturally regenerated trees in two mixed dipterocarp forests in Malaysia is determined both by wood density and light environment.

Osunkoya et al. (2007) investigated variation in wood density, wood water content, stem growth and mortality among 27 tree species in a tropical rain forest in Brunei on Borneo Island. According to their results wood density and dbh increment is negatively correlated across species, which indicate that species with low wood densities grows faster than species with high wood densities. Herault et al. (2011) reports the same result for 50 rain forest tree species in French Guiana.

It seems that the life-history of plants is partly determined by wood density, as was indicated in my results. Species with high wood densities can construct less stem volume compared to species with low wood densities with same mass wood (van Gelder et al. 2006). The construction investment for high density wood is thereby costly, but results in a steady structure and therefore species with high wood densities often are long lived. Species with low wood densities have a fast growth due to lower construction investments (van Gelder et al. 2006) but are therefore more prone to damages caused by wind, extra crown loads (King 1987), pathogens (Augspurger & Kelly 1984) and herbivores (Coley 1983). One of the main purposes of the tree's mechanical design is to bear its own weight and to withstand external forces like wind, rain and falling debris (Turner 2001; van Gelder et al. 2006). Stiffness, bending strength and compression strength are all mechanical wood properties. High values on these three properties suggest that the tree better can maintain its structure without mechanical damages. These properties increase with wood density (van Gelder et al. 2006). Species with high wood densities have slow growth rates but are instead resistant to damages and attacks (van Gelder et al. 2006; Ghazoul & Sheil 2010) which increase their survival rate (Poorter et al. 2010). Advantages with low wood density are rapid growth that will lead to outrival of competitors (van Gelder et al. 2006). Trade-offs are presumptions for species coexistence (Kneitel & Chase 2004). Trade-offs between high growth rates or properties like high wood density that increase the resistance against damages that in turn increase the survival is inevitable. Wood density and growth are very important factors for species performance and differentiation in tropical rain forests and hence related to life history strategies (Thomas 1996; Poorter et al. 2010).

The investigated tree species in this study indicated different adaptations to light depending on wood density even though they all are classified as climax species (Figure 3 and 4). They are therefore expected to differ also in other tree species traits, for example in leaf characteristics (Poorter & Bongers, 2006; Ghazoul & Sheil, 2010). Knowledge about the ecological and biological adaptions for the planted tree species in the INIKEA project is limited. This makes it difficult to match the selection of tree species to forest stand conditions in the enrichment planting program (Alloysius et al. 2010). The prerequisite for the planted trees to survive and grow is the choice of tree species for the current site conditions. Important factors to take into account are tree species requirements on temperature, rainfall and soil properties (Evans 1992). The microclimate near the forest floor is of major importance when establishing tree plantations since the requirements of different tree species differ (Whitmore 1998).

4.3 The relationship between tree species response to increased light after a shade adjustment and wood density

After the shade adjustment tree growth increased in the study site. The reason to the increased growth may be due to the increased light availability that the shade adjustment probably contributed to. But such interventions can also be expected to increase competition from fast-growing pioneer species which may have negative effects on growth for the planted trees, Species with lower wood densities showed to have higher dbh growth in comparison with species with high density wood after the shade adjustment (Figure 5). King et al. (2006) investigated 21 tree species in a tropical rain forest in Malaysia dominated by dipterocarps. According to their results the relationship between diameter growth and wood density was negative, which confirm my results. Iida et al. (2012) investigated 145 tree species in a tropical rain forest in Malaysia. According to their results stem diameter was negatively correlated to wood density. Species with low density wood can produce thicker stems than species with high wood density at lower biomass costs (Iida et al. 2012).

My results showed that horizontal crown growth and wood density was significantly negatively correlated. This result indicated that species with higher wood densities had a lower horizontal crown growth compared with species with lower wood densities after the shade adjustment (Figure 6). In general fast growing tree species produce low density wood. To prevent competition these tree species produce open-branched crowns that occupy large areas (Whitmore 1998). Crown area is positively correlated with tree height (Poorter et al. 2006). Since tree species with low wood densities in general have a rapid height growth (Swaine & Whitmore 1988) it may be expected that their crown areas are larger as a consequence of a corresponding more rapid horizontal crown expansion. On the opposite, other studies have shown that trees with high-density wood may be more effective in horizontal crown growth suggesting that species with low wood density have narrower and shallower crowns (Anten & Schieving 2010; Iida et al. 2012). By spreading the branches horizontally, shade tolerant species can capture more light in the dark understory while light demanding species grow in height instead to reach the more open canopy where light conditions are more favorable (Kohyama 1987). According to one study in a lowland forest dominated by dipterocarp trees in Malaysia there is no correlation between the ratio crown width and tree height and wood density (King et al. 2006).

The increased height growth after the shade adjustment showed no significant correlation with wood density, but a negative trend could be seen (Figure 7). According to Clark & Clark (2001) the average annual height growth for juvenile tropical trees is much less than the potential height growth. In their study trees show no height growth for some periods due to stem damages. Therefore I think tree height is a relatively uncertain measure of growth for juvenile trees. Height growth may be a safer measure for large trees that have grown out from the suppressed environment in the understory. Osunkoya et al. (2007) observed a negative trend between wood density and maximum potential tree height for 27 tree species in Brunei, on Borneo Island. According to the study by Thomas (1996) there is a significant negative association between wood density and asymptotic maximal height between 38 species in a Malaysian rain forest.

4.4 Data uncertainties and further research

Species´ specific wood densities may differ from the estimated average wood density for the genus. A more accurate value for wood density could have given higher explained variances and more significant results. According to Muller-Landau (2004) wood densities differs between sites for tree species. In her study soil fertility is one of the determining factors because higher wood densities are associated with lower soil fertility. To get more exact values on wood densities for the investigated species in my study wood densities need to be determined on the specific site.

It is generally difficult to make good estimates of light in rain forests. Patches of light on the forest floor changes during the day dependent on the position of the sun in the sky, cloudiness and canopy cover (Ghazoul & Sheil, 2010). CII was estimated subjectively which can be a source of error. Based on fisheye photos ground cover was calculated. Unfortunately ground cover did not show any significant correlation with growth for the different tree traits. This may be due to equipment failure or weaknesses in how it was used (Chan et al. 1986). A reason to why CII estimates were stronger correlated to growth than ground cover may be that subjective estimates better considers how light falls on the individual tree.

In my study the tree traits, leaved stem length, internode length and leaf size index was not significantly correlated with growth, but according to Sterck & Bongers (2001) branch extension, internode length and numbers of internodes increased due to canopy openings. Why my results did not show any growth response for leaved stem length, internode length and leaf size index after the shade adjustment may be that the time elapsed since the light adjustment was too short or not enough comprehensive for a growth response of these traits to be seen. Further research is needed to evaluate how or if these traits are affected of different canopy cover.

Additional research must be done to evaluate how the 34 different tree species will develop through ontogeny. The ultimate is to follow the tree development of species over a whole growth cycle. Important parameters to weigh into the study in the future is how site factors as slope, soil fertility and location (ridge, valley etc.) affect the growth pattern for the planted tree species.

5. CONCLUSIONS

The objectives of this study were to investigate how different canopy cover affected tree species traits for 34 tree species in an enrichment planted tropical secondary rain forest, and if tree species growth response to increased light after a shade adjustment was related to tree species specific wood densities. My results indicated that variations in light exposure and wood densities may be major determinants of growth rate variations between tree individuals and tree species. Trees with more available light were generally higher and had greater dbh than trees with less light exposure. The increased diameter growth and horizontal crown growth after the shade adjustment was correlated to wood density. Species with low wood densities showed higher diameter growth and horizontal crown growth after the shade adjustment compared to species with higher wood densities. According to this study it was indicated that light availability in the forest was a limiting factor for all tree species. By reducing canopy cover in forest stands, a higher growth rate for all tree species may be expected, particularly from species with lower wood densities. Knowledge about the ecological and biological adaptions for the planted tree species in the INIKEA Forest Rehabilitation Project is limited. This makes it difficult to match the selection of tree species to forest stand conditions in the enrichment planting program (Alloysius et al. 2010). Information from this study, on how species with different wood density, respond to light, can be used to adapt the choice of tree species for the current lighting conditions in the forest. This information can improve the rehabilitation work in INIKEA Forest Rehabilitation Project and elsewhere in Malaysia.

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APPENDICES

Appendix 1. Working schedule for the experiment area Species Demo Plot, located in the INIKEA Forest Rehabilitation Project, Sabah, Malaysia.

Working Schedule Species Demo Plot	
Date	Measure
December 5, 2008	Planting
December 18, 2008	Planting measurement
June 15, 2009	First inventory
December 15, 2010	Second inventory
December 15, 2011	Third inventory
April 10, 2012	Fourth inventory
December 15, 2012	Fifth inventory
February, 2013	Shade adjustment
June 21, 2013	Sixth inventory

Appendix 2. Regressions analyses for the 34 investigated tree species. Regressions between the difference in growth for tree species traits; dbh (A) (diameter at breast height), crown width (B) and height (C), and the difference in ground cover before and after the shade adjustment. N = number of tree individuals included in the regression analysis; Coef (C) = coefficient for predictor variable; SE Coef (C) = standard errors of the coefficients; Coef (GC) = coefficient for ground cover, P (C) = P-value coefficient; SE Coef (GC) = standard errors of ground cover; P (GC) = P-value ground cover. Regressions in MINITAB Statistical Software (2009).

(A) Regression analysis: dbh and ground cover							
Species name	**N**	**Coef (C)**	**SE Coef (C)**	**P (C)**	**Coef (GC)**	**SE Coef (GC)**	**P (GC)**
Baccaurea angulata	6	0.7191	0.1312	0.005	0.7919	0.9058	0.431
Baccaurea sp	12	0.6938	0.1411	0.001	0.361	1.049	0.737
Canarium sp	9	0.8873	0.2052	0.003	0.02	1.443	0.989
Diospyros sp	2	0.422229			-1.00293		
Dipterocarpus conformis	8	0.885	0.1613	0.002	-0.8491	0.9048	0.384
Dryobalanops keithii	9	1.0229	0.2905	0.01	0.642	4.841	0.898
Dryobalanops lanceolata	13	1.1167	0.1635	0	-2.1702	0.9414	0.042
Durio spp	8	0.6701	0.22	0.023	3.432	3.409	0.353
Heritiera sp	9	0.7148	0.1501	0.002	-0.4429	0.9102	0.641
Hopea ferruginea	6	0.5424	0.3153	0.16	-5.091	3.057	0.171
Intsia palembanica	2	0.180156			1.70038		
Koompasia excelsa	11	0.63071	0.08542	0	-0.3118	0.7855	0.701
Mangifera odorata	6	0.6012	0.1377	0.012	0.0932	0.4095	0.831
Mangifera panjang	6	0.551	0.268	0.109	0.1837	0.9996	0.863
Parashorea malaanonan	11	0.6985	0.1589	0.002	0.139	1.219	0.912
Parashorea smythiesii	4	1.4515	0.5523	0.119	4.276	2.942	0.283
Parashorea tomentella	8	0.9937	0.3181	0.02	-0.404	1.509	0.798
Pentace adenophora	3	0.7808	0.5338	0.382	0.215	1.334	0.898
Pentace laxiflora	14	1.0179	0.1917	0	1.0126	0.969	0.317
Shorea beccariana	9	0.8219	0.2011	0.005	-2.503	1.903	0.23
Shorea falciferoides	8	1.2625	0.309	0.006	-0.374	2.049	0.861
Shorea fallax	8	1.1724	0.2112	0.001	-0.425	1.652	0.805
Shorea leprosula	7	0.9059	0.3023	0.03	-0.565	1.531	0.727
Shorea leptoderma	13	0.6823	0.1651	0.002	0.653	1.478	0.667
Shorea macrophylla	14	1.0611	0.2013	0	-1.022	1.033	0.342
Shorea macroptera	10	1.3771	0.2592	0.001	0.5178	0.9743	0.61
Shorea ovalis	13	1.4241	0.2278	0	2.288	1.146	0.071
Shorea parvifolia	6	0.9134	0.3114	0.043	0.39	1.222	0.766
Shorea pauciflora	7	0.9499	0.334	0.036	-1.721	2.106	0.451
Shorea platyclados	10	0.7429	0.1553	0.001	-0.0646	0.8308	0.94
Shorea sp	7	0.787	0.1404	0.002	-1.456	1.196	0.278
Shorea xanthophylla	7	0.5912	0.1722	0.019	0.354	2.364	0.887
Sindora iripicina	3	0.5279	0.1182	0.14	-1.2032	0.5531	0.274
Walsura pinnata	8	0.4612	0.1747	0.039	-0.143	0.6907	0.843

(B) Regression analysis: crown width and ground cover							
Species name	**N**	**Coef (C)**	**SE Coef (C)**	**P (C)**	**Coef (GC)**	**SE Coef (GC)**	**P (GC)**
Baccaurea angulata	9	-0.033	0.2632	0.904	1.696	1.579	0.318
Baccaurea sp	14	0.33852	0.07457	0.001	-0.6911	0.5457	0.229
Canarium sp	15	0.0511	0.1007	0.62	-0.3844	0.7073	0.596
Diospyros sp	9	-0.1173	0.3753	0.764	0.752	1.226	0.559
Dipterocarpus conformis	12	0.2269	0.1022	0.051	-0.2602	0.7291	0.729
Dryobalanops keithii	12	0.4002	0.1129	0.005	1.5346	0.6154	0.032
Dryobalanops lanceolata	14	0.7626	0.15	0	-1.7441	0.8632	0.066
Durio spp	13	0.4528	0.2203	0.064	-5.458	2.214	0.031
Heritiera sp	17	0.22128	0.05668	0.001	-0.1164	0.2769	0.68
Hopea ferruginea	8	0.2483	0.21	0.282	-2.716	2.081	0.24
Intsia palembanica	2	0.066619			0.204045		
Koompasia excelsa	15	0.24197	0.06897	0.004	-0.4868	0.5275	0.373
Mangifera odorata	14	0.07641	0.07726	0.342	-0.0716	0.3046	0.818
Mangifera panjang	12	0.06676	0.06558	0.333	0.4915	0.3185	0.154
Parashorea malaanonan	13	0.3215	0.1464	0.05	0.5422	0.6625	0.43
Parashorea smythiesii	11	0.23097	0.08821	0.028	0.1032	0.4152	0.809
Parashorea tomentella	10	0.4004	0.1093	0.006	0.2973	0.5762	0.62
Pentace adenophora	8	0.4346	0.4913	0.41	0.739	1.802	0.696
Pentace laxiflora	17	0.3551	0.1221	0.011	1.0649	0.6676	0.132
Shorea beccariana	10	0.3202	0.2236	0.19	3.261	2.211	0.179
Shorea falciferoides	9	0.8895	0.5965	0.18	-1.46	4.122	0.734
Shorea fallax	10	0.3201	0.176	0.107	-0.205	1.44	0.89
Shorea leprosula	8	0.3207	0.2026	0.164	0.207	1.096	0.856
Shorea leptoderma	13	0.3582	0.2147	0.123	1.507	1.923	0.45
Shorea macrophylla	15	0.6345	0.1534	0.001	-1.0804	0.7832	0.191
Shorea macroptera	10	0.6889	0.2029	0.009	-0.1915	0.7829	0.813
Shorea ovalis	12	0.3887	0.1	0.003	-0.6067	0.5917	0.329
Shorea parvifolia	6	0.3754	0.1803	0.106	0.2207	0.7074	0.771
Shorea pauciflora	14	0.3269	0.1754	0.087	-0.52	1.024	0.62
Shorea platyclados	12	0.4193	0.1293	0.009	-0.2108	0.7048	0.771
Shorea sp	9	0.2121	0.1475	0.194	-1.719	1.275	0.22
Shorea xanthophylla	14	0.3365	0.06231	0	-0.1831	0.3871	0.645
Sindora iripicina	8	0.1623	0.1432	0.3	-0.7098	0.8956	0.458
Walsura pinnata	12	-0.0709	0.1076	0.411	0.4041	0.4714	0.411

(C) Regression analysis: height and ground cover							
Species name	**N**	**Coef (C)**	**SE Coef (C)**	**P (C)**	**Coef (GC)**	**SE Coef (GC)**	**P (GC)**
Baccaurea angulata	9	0.8415	0.1461	0.001	-0.4847	0.9079	0.61
Baccaurea sp	14	0.7077	0.1747	0.002	0.058	1.279	0.964
Canarium sp	15	0.6031	0.1931	0.008	-0.17	1.357	0.902
Diospyros sp	11	0.5211	0.1768	0.016	-0.4758	0.6151	0.459
Dipterocarpus conformis	12	0.6802	0.136	0.001	-0.9669	0.8728	0.294
Dryobalanops keithii	12	0.9217	0.2425	0.003	0.816	1.322	0.551
Dryobalanops lanceolata	14	0.8875	0.2623	0.005	-1.511	1.509	0.336
Durio spp	13	0.6555	0.1538	0.001	-3.395	1.546	0.05
Heritiera sp	17	0.4163	0.1419	0.01	-0.6003	0.6935	0.4
Hopea ferruginea	8	0.5596	0.2597	0.075	-1.994	2.574	0.468
Intsia palembanica	3	0.118	0.1144	0.49	1.5853	0.9057	0.33
Koompasia excelsa	15	0.6063	0.2096	0.013	1.054	1.603	0.522
Mangifera odorata	14	0.17588	0.03778	0.001	0.4481	0.1489	0.011
Mangifera panjang	14	0.2156	0.1091	0.072	0.5096	0.4698	0.299
Parashorea malaanonan	14	0.3175	0.266	0.256	1.098	1.241	0.394
Parashorea smythiesii	11	0.2223	0.1567	0.19	-1.1611	0.9447	0.25
Parashorea tomentella	11	0.9823	0.2723	0.006	2.115	1.499	0.192
Pentace adenophora	10	0.1546	0.2124	0.488	-0.5387	0.8707	0.553
Pentace laxiflora	17	1.2558	0.2327	0	2.182	1.272	0.107
Shorea beccariana	10	0.5079	0.1751	0.02	-1.389	1.731	0.446
Shorea falciferoides	9	1.3879	0.366	0.007	-0.791	2.529	0.764
Shorea fallax	10	1.2606	0.2145	0	3.639	1.755	0.072
Shorea leprosula	9	0.6048	0.2675	0.058	-1.736	1.535	0.295
Shorea leptoderma	14	0.6279	0.1353	0.001	0.831	1.254	0.52
Shorea macrophylla	16	0.9143	0.1566	0	-2.7607	0.8205	0.005
Shorea macroptera	12	1.2293	0.3496	0.006	1.441	1.426	0.336
Shorea ovalis	15	0.6451	0.2179	0.011	0.528	1.137	0.65
Shorea parvifolia	7	0.409	0.5982	0.525	0.025	2.366	0.992
Shorea pauciflora	15	0.4328	0.1296	0.005	-0.5097	0.7284	0.496
Shorea platyclados	12	0.6896	0.1569	0.001	0.5498	0.8548	0.535
Shorea sp	9	0.4981	0.225	0.062	-0.372	1.945	0.854
Shorea xanthophylla	14	0.39881	0.09409	0.001	0.0074	0.5845	0.99
Sindora iripicina	9	0.3529	0.1083	0.014	0.2598	0.3413	0.471
Walsura pinnata	14	0.1972	0.1167	0.117	0.9826	0.5439	0.096

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