Examensarbeten **2016:2**

Fakulteten för skogsvetenskap
Institutionen för skogens ekologi och skötsel

Degradation and restoration method interact to affect the performance of planted seedlings in tropical rainforest restoration

– evidence from plant functional traits

Photo: Ulrik Ilstedt

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Sveriges Lantbruksuniversitet
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Degradation and restoration method interact to affect the performance of planted seedlings in tropical rainforest restoration

– evidence from plant functional traits

Degradering och val av restaureringsmetod har effekt på planterade plantors prestation vid restaurering av tropisk regnskog

– en studie av plantors funktionella egenskaper

Julia Mellåker

Keywords / *Nyckelord:*
Dipterocarpaceae, enrichment planting, INIKEA, secondary rainforest /
Dipterocarpaceae, hjälpplantering, INIKEA, sekundär regnskog

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PREFACE

More than one year ago I got an idea from a teacher to do my master's thesis about rainforest restoration. It was a great opportunity to gain experience in international projects and tropical forestry, so during the year the idea developed into a plan and the plan was carried out. Therefore I first want to thank Ulrik Ilstedt, associate professor at SLU, for the idea and for supervision during this thesis. It was possible thanks to SIDA, for founding the field work in Malaysia through a Minor Field Study scholarship. To say everything during the trip went as planned would indeed be a lie, but thanks to helpful people all practical issues were managed. Thanks to John Tay, associate professor at Malaysian University of Sabah, David Aloysius, INIKEA project manager, and Vita Juin for guiding two lost Swedes through Malaysian bureaucracy.

During the first days in field most of the details for my study were developed and I am so thankful for all input I got from Kevin Grady, assistant research professor at Northern Arizona University, Daniel Lussetti, PhD student at SLU, and Darline Hase, PhD student at Malaysian University of Sabah. Also Petter Axelsson, researcher at SLU, who became assistant supervisor for the thesis and have helped so mush, especially in the writing process. During the data collection I really appreciated all the help I got from Albert Lojingi and his working team; Dizolkeply, Juspin, Ammin, Jemmin and Tonglee. Together we shared a lot of fun and you made leeches and the steep muddy slopes less frightening. My thesis definitely would not have been done without the help from you. I would also like to thank the girls in the kitchen for never letting me go hungry and showing me the "beach" at Camp marimba.

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Terimah kasih!
Thank you!
Tack!

ABSTRACT

A common action to save or improve biodiversity in the tropics is restoration of degraded rainforest. To understand the complex ecological structures of the forest and adapt the restoration actions after them, studies have focused on characterizing species with functional traits. Traits can be placed on a sliding scale between pioneer and climax properties and describe species life history. They can be used to predict species response in different environments, without detailed ecological knowledge for that species. The hypotheses in the study were that forest type and type of restoration treatment affect functional traits and that these traits could predict growth. Furthermore the study investigated if there was a growth-survival trade-off and if it could be predicted with functional traits. Measurements came from a field experiment in Sabah, Malaysia, where seedlings were planted with two methods within three forest types. The two treatments were line planting, where seedlings were planted in cleared lines under the canopy and gap-cluster planting, where seedlings were planted in groups in pre-existing or created gaps. The three forest types were classified based on degradation level and vegetation, forest type A was the most degraded, type B intermediate and type C the least degraded. 32 species of dipterocarps, fruit trees and other climax species were planted within the experiment. Treatments and forest types were thought to create different environmental conditions, e.g. light availability. The effects on growth were tested with a general linear model and the survival with logistic regression. Also species groups were compared with chi-square test to examine the growth-survival trade-off. The traits that were used were total height, stem diameter, crown depth, crown width, leaf stem length, total leaf area, leaf thickness, vein thickness, and leaf damage. Species was the factor that affected both growth and survival the most. Seedlings in line treatment performed similarly in all forest types, but gap-cluster planting was slightly better than line planting in forest type A and clearly outperformed line treatment in forest type B (e.g. in forest type B seedlings in gaps increased total height by average 33 % the last 9 month compared with lines 25 %). Crown depth ratio, total leaf area, and leaf stem length were clearly the traits that best predicted both height and diameter growth. In this study the growth survival trade-off was not obvious, only total height was negatively correlated with survival rate. The differences in traits due to treatments showed that the treatments created different environments for the seedlings and treatment effects were different depending on forest type. Gap-cluster planting gave higher growth in forests there the seedlings were less limited by light availability. The conclusions of this study could contribute to improved effectiveness of restoration actions in the rainforests of Borneo and be of value when planning future projects, especially regarding selection of species in enrichment plantings based on functional traits.

Keywords: *Dipterocarpaceae*, enrichment planting, INIKEA, secondary rainforest.

SAMMANFATTNING

Restaurering av degraderad tropisk regnskog har varit en vanlig åtgärd för att rädda och återskapa biologisk mångfald. För att förstå de komplexa ekologiska strukturerna i skogen och anpassa restaureringsåtgärderna efter dem har forskning fokuserat på att karaktärisera arter med hjälp av funktionella egenskaper. Egenskaper för en viss art kan placeras på en skala mellan pionjär- och klimaxegenskaper och därmed förklara artens livscykel. De kan också användas för att förutspå artens respons på miljöförhållanden, utan att ha detaljerad ekologisk kunskap om den. Hypoteserna i studien var att skogstyp och behandling påverkar funktionella egenskaper och att de kan användas för att förutsäga plantans tillväxt. Dessutom undersöktes om det fanns en tillväxt-överlevnadkompromiss och om den också kunde förutsägas av funktionella egenskaper. Mätningarna har genomförts i ett fältförsök i Sabah, Malaysia, där plantor var planterade med två olika metoder i tre olika skogstyper. De två metoderna var linjeplantering, där plantorna planterades i röjda linjer i skogen och luckplantering, där plantorna planterades i grupper i existerande eller skapade luckor. De tre skogstyperna var klassificerade utifrån degraderingsnivå och vegetation, skogstyp A var mest störd, typ B intermediär och typ C minst störd. Dessa olika faktorer har antagits skapa olika miljöförhållanden, främst olika ljusförhållanden. 32 trädarter Dipterocarper, fruktträd och andra klimaxarter var planterade i försöket. Effekten på tillväxt testades med en generell linjär modell och överlevnad med logistisk regression. Tillväxt-överlevnadkompromissen testades med ett chi2-test på olika artgrupper. De egenskaper som mättes var totalhöjd, stamdiameter, krondjup, kronbredd, bladbeklädd grenlängd, total bladarea, bladtjocklek, ventjocklek och skadad bladarea. Arttillhörighet var den faktor som till störst grad påverkade plantornas tillväxt och överlevnad. Linjeplantering gav liknande resultat i samtliga skogstyper, medan luckplantering gav något bättre resultat än linjeplantering i skogstyp A och tydligt bättre resultat i skogstyp B (t.ex. ökade plantor i luckor medelhöjden med 33 % på 9 månader, jämfört med 25 % för plantor i linjer). Krondjup, total bladarea och bladbeklädd grenlängd var de egenskaper som bäst förutspådde både höjd- och diametertillväxt. I denna studie var tillväxt-överlevnadkompromissen inte särskilt tydlig och höjd var den enda egenskap som negativt korrelerade med överlevnaden. Skillnaderna bland de funktionella egenskaperna som berodde på behandling visar att behandlingarna skapade olika miljöförhållanden för plantorna och att de varierade med skogstyp. Luckplanteringen medförde högre tillväxt i skogstyper där plantorna var mindre ljusbegränsade. Slutsatserna av denna studie kan bidra till förbättrad effektivitet av restaureringsåtgärder i regnskogen på Borneo och planering av framtida projekt, särskilt när det gäller artsammansättning i stödplanteringar baserade på funktionella egenskaper.

Nyckelord: *Dipterocarpaceae,* hjälpplantering, INIKEA, sekundär regnskog

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INTRODUCTION

Tropical rainforests are the most diverse ecosystem on earth, but they are threatened by deforestation and degradation due to human use (Turner, 1996). The primary forests on Borneo are rich in tree diversity, but selective logging in the 1970s (Siegert *et al.*, 2001) changed the structure of the forests and caused loss of species (Turner, 1996). In addition the forest became vulnerable to wild fires, due to the degraded forests' dry forest floor, caused by patchy canopy and high abundance of combustible materials (Goldammer & Seibert, 1990). Extreme weather conditions during the El Niño 1982-83 created large forest fires that degraded parts of the forest even more (Siegert *et al.,* 2001). These degraded forests lost many of the characteristic species, i.e. Dipterocarps, *Dipterocarpaceae spp.,* and are today dominated by Macaranga, *Macaranga spp*., climbers, gingers and ferns (Alloysius *et al*., 2010). These changes in tree distribution decrease the carbon storage of the forests and increase recruitment failure for species (Hector *et al.*, 2011; Whitmore, 1992). Furthermore changed tree composition affects other plant and animal communities associated to the primary forest's structure and species composition (Edwards *et al.*, 2011; Grainger, 1993). Through natural succession relying on natural regeneration alone it usually takes a long time for these secondary forests to regain their original functions and species composition (Edwards *et al.*, 2011; Lamb *et al.*, 2005).

However, this otherwise slow process could be accelerated through rehabilitation actions (Hector *et al.*, 2011; Lamb *et al.*, 2005). The specific design of these actions often depends on objectives and environmental conditions. For the least degraded forests natural regeneration is the cheapest and most effective option for enhancement and next step on the restoration staircase is to support the natural regeneration through clearing weeds and pioneer trees to increase light availability (Chazdon, 2008). In more disturbed forests further action is needed, such as enrichment planting of native species (Lamb *et al.*, 2005). Although planting is more costly than working from natural regeneration, it could be an option in areas where natural regeneration is low in diversity. The results from enrichment planting are an increase in the number of species and a reduction of the risk of large-scale recruitment failure. In this respect, seedling performance and survival are the crucial factors for the success of forest restoration (Lamb *et al.*, 2005).

Functional traits for trees have been used to predict overall plant performance for seedlings in tropical forests (Gustafsson *et al.*, 2016; Poorter & Bongers, 2006; Sterck *et al.*, 2006; Wright *et al.*, 2004). Functional traits are key attributes that determine the plant's ecological role and niche (Wright *et al.*, 2006), i.e. traits that affect reproduction, light capture, photosynthesis, defense against pests, and competitive ability. They are therefore important for understanding forest management and the success in forest restoration. Especially in the highly diverse tropics where knowledge on the ecology of many species is limited, traits might help to understand their ecological function and performance in different environments (Hector *et al.*, 2011; Chazdon, 2008; Ådjers *et al.*, 1995). Survival and growth for seedlings in rainforest understory are primarily affected by available light and nutrients, but there are also large interspecific variation (Born *et al.*, 2014). Species adaptations to different light conditions are usually described as pioneer and climax properties, but in reality it is more of a sliding scale than two opposites (figure 1) (Gustafsson *et al.*, 2016; Wright *et al.*, 2004; Clark & Clark, 1992). Individuals' adaption to different environments is caused by phenotypic plasticity, which also explains intraspecific variations (Taiz & Zeiger, 2010). General pioneer properties for trees are low wood density, high specific leaf area and high nitrogen (N) and phosphorus (P) content in foliage, while climax properties are high wood density, low total leaf area and high potassium (K) content in foliage (King *et al.*, 2006; Poorter & Bongers, 2006; Sterck *et al.*, 2006). Furthermore pioneer properties give seedlings fast response on available resources, earlier height growth and increased plasticity (Gustafsson *et al.*, 2016; Poorter & Bongers, 2006; Valladares *et al.*, 2000). Climax properties make seedlings better adapted to grow in low light understory, focusing on stability and resilience where the strategy is to outlive species of pioneer properties (King *et al.*, 2006; Ådjers *et al.*, 1995). The compromise between stability and growth is one part of the growth-survival trade-off.

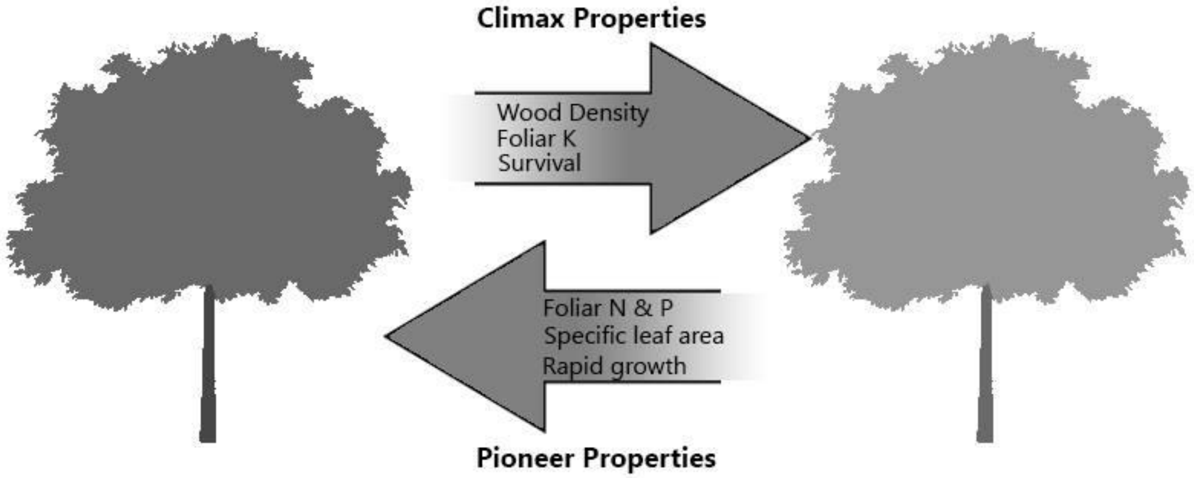

Figure 1. Schematic picture showing the sliding scale of pioneer-climax properties and the growth-survival trade-off. Adapted from Gustafsson *et al.* (2016).

The growth-survival trade-off was observed when comparing performance of species or families with different life history in the tropics (Poorter & Bongers, 2006; Sterck *et al.*, 2006; Kitajima, 1994), i.e. on different sides of the pioneer-climax scale. The species with general rapid growth showed lower survival rates in low light environments. Furthermore there is a growth-defense trade-off that indirectly contributes to survival, because species with rapid growth invest fewer resources in defense and therefore have a higher risk of mortal damage (King *et al.*, 2006; Ådjers *et al.*, 1995). Combining this with the general grouping based on functional traits, seedlings with climax properties, e.g. Dipterocarps, generally have higher survival rates than seedlings with pioneer properties, e.g. Macaranga. However detailed knowledge on within family (among species) variation in functional traits and their plasticity towards environmental variability are limited. To be able to restore and understand the tropical ecosystem, increased understanding for species groups and their response in different environments are needed. By studying a number of species in different light environments, information on how functional traits are related to growth responses is gained and could be extended to other species in the future.

This study was performed in a restoration project in Sabah, Malaysia. The level of degradation vary over the landscape and the forest has been classified into three types (Alloysius, 2015). The most degraded type (here called forest type A) has almost no tree cover and vegetation is dominated by ground vegetation, since few shading trees result in much available light. The conditions for tree regeneration are poor, because of the competition by other vegetation. The second type (called

B) has a continuous tree cover of pioneer species (mostly *Macaranga spp.*) and a relatively small amount of ground vegetation. The least degraded type (called C) consists of a mixture of tree species with pioneer and climax properties and natural good conditions for tree regeneration.

Based on light conditions in the forest types and earlier studies, some theories of the outcome of this study have been posed. In forest type A all species should have more rapid growth compared with the other forest types, because high light availability increase growth (Poorter & Bongers, 2006; Sterck *et al.*, 2006; Ådjers *et al.*, 1995). This also affects functional traits and species with pioneer properties have faster response (Gustafsson *et al.*, 2016), which indicates higher plasticity (Rozendaal *et al.*, 2006; Valladares *et al.*, 2000). Therefore the variation of functional traits should be greater in environments with high light availability, i.e. forest type A. In the low light environment, forest type C, all species are light limited and growth will be lower, also it is more likely to find differences in survival because species with climax properties are able to survive better in the shade (Poorter & Bongers, 2006; Sterck *et al.*, 2006; Ådjers *et al.*, 1995). The growth-survival trade-off should therefore be visible since species with high average growth in forest type A should have low survival in forest type C.

The two treatments in the project is line planting, where seedlings are planted in cleared lines under the canopy and gap-cluster planting, where seedlings are planted in groups in pre-existing or created gaps (Alloysius, 2015). Other studies early after planting show little differences in natural regeneration and light availability between the line and gap-cluster planting (Jansson, 2015; Waern, 2015). The theory in the project is that line planting has larger impact on the canopy because more trees, Macarangas, are removed, however the gaps are subjectively placed and thereby create more suitable planting spots (Alloysius, 2015). This should create different conditions for the seedlings and variation in seedling growth should occur between treatments.

Objectives

To address the lack of knowledge about species' functional traits and their effect on whole plant performance, 32 tree species planted in a degraded forest were studied. The study aimed to examine if treatments and forest type affect functional traits by causing different conditions for the seedlings. The study also aimed to examine if there are differences in survival between the species and if any such differences can be explained by the species' functional traits, treatment, or forest type. Furthermore tests were carried out to examine if growth and functional traits linked to growth, are negatively correlated to survival, as assumed by the growth-survival trade-off theory. The hypotheses were:

- Forest type and treatment affect functional traits.
- There are correlations between seedling growth and functional traits.
- There are differences in survival and growth between species that can be explained by functional traits.
- Species' average growth is negatively correlated to survival in consistency with the growth-survival trade-off theory.

MATERIALS AND METHODS

The data was collected within INIKEA project area, 4°37.43´N, 117°12.15´E in southern Sabah, Malaysia (Figure 2). The INIKEA project started in 1998 aiming to improve biodiversity in 18 500 ha of degraded forest through supporting natural regeneration and by enrichment planting of native tree species (Alloysius *et al.*, 2010).

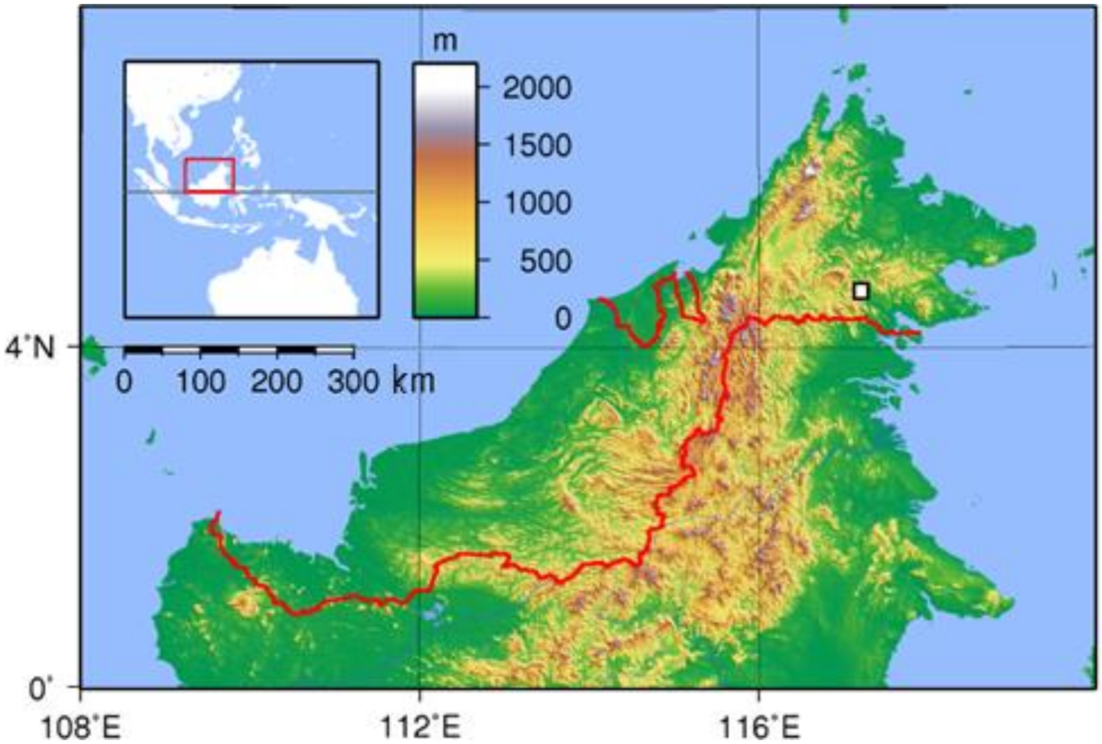

Figure 2. Map of Malaysian Borneo. The white square indicates the study location (Sadalmelik, 2007).

The three forest types that were subjectively classified by forest rangers were in this study named forest type A, B and C. The two most degraded types are normally in the project restored by two enrichment planting methods (Alloysius, 2015). Forest type A is commonly managed with line plantation and type B with gap-cluster plantations. In type C natural regeneration is supported. In total, 74 different species are planted within the project, whereof 41 species are dipterocarps, 13 non-dipterocarps and 20 fruit tree species. In the 73 hectare large Rainforest Restoration Experiment, RRE, all treatments are tested in each forest type. 21 blocks with as homogenous forest types as possible are laid out, seven blocks in each forest type (figure 3). In each block there are four plots, representing four treatments: liberation, gap-cluster plantation, line plantation and control which are randomized within each block (Alloysius, 2015). Data was only collected from the two treatments with planted seedlings. The experiment is planted in November 2013 (Alloysius, 2015). After three months the planting is inventoried, all species and locations noted and refill planting preformed. The planted plots are weeded twice per year since planting and a one year's census of growth and survival is also performed in December 2014. The management plan as whole for the experiment is available in appendix 1(Alloysius, 2015).

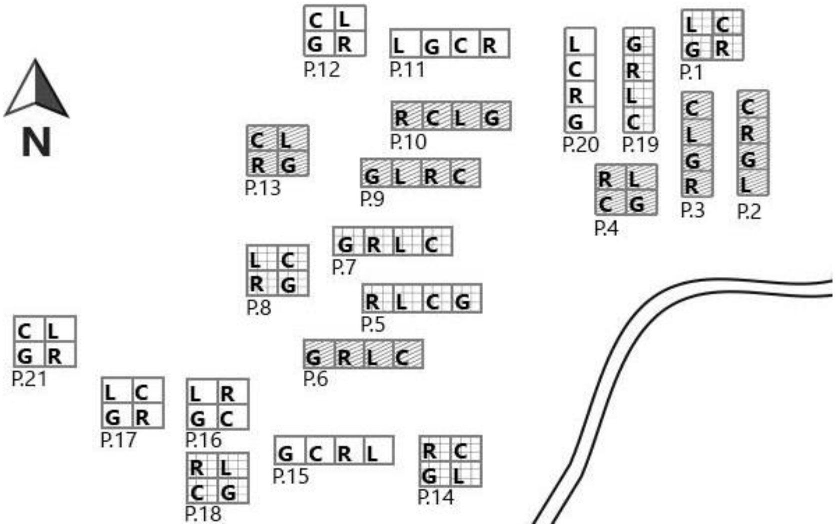

Figure 3. Schematic picture of the Rainforest Restoration Experiment, in Sabah, Malaysia. The background of the blocks indicate forest type, diagonal lines: very degraded forest called type A, checked: intermediate degraded forest called type B and clear: slightly degraded forest called type C. Letters indicate treatments location in the block, line planting (L), gap-cluster planting (G), liberation (R) and control (C). The line in the right corner is the access road.

Each treatment is performed within a 40 x 40 meter plot and each plot is planted with the same 32 species (appendix 2). In the line planting four lines, 10 m apart and 2 m wide, are cleared from pioneer trees and ground vegetation. Then 13 seedlings are planted with 3 m spacing in each line (figure 4). With the gap planting the plot is divided into 16 squares 10 x 10 m, in each square a gap is found or created by removing pioneers and ground vegetation. Then four seedlings are planted approximately one meter from the center stick in each gap. (Alloysius, 2015)

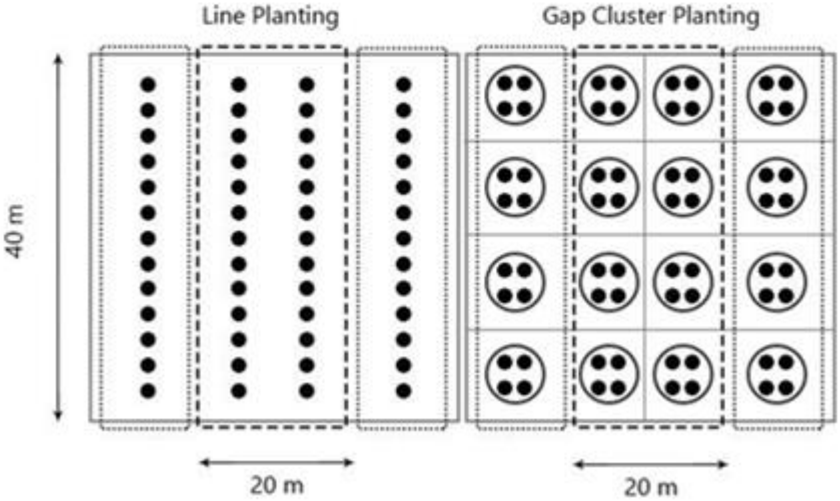

Figure 4. Schematic pictures of how seedlings were placed in line and gap-cluster planting plots. Within the dashed lines the seedling survival were inventoried. All 32 species were not represented in that area for all plots. The seedlings traits were measured within the dashed line if possible and within the dotted lines for species not present in the center.

The survival inventory was performed within a 20 x 40 m area to partly reduce edge effects of other treatments and surrounding forest. All 32 species were not represented within that area in all plots. The traits were measured for one seedling per species per plot. First, if possible, plants within the same 20 x 40 m area were chosen, then seedlings in the outer lines or gaps were selected, for the species that did not occur in the central area.

Functional traits

The inventory was performed between 26th of August and 14th of September 2015 together with local project staff. Total height (TH), stem diameter (SD), crown depth (CD), crown width (CW), leaf stem length (LSL), leaf thickness (LT) and vein thickness (VT) were measured directly in field (Table 1). Total leaf area (TLA) was estimated by digital image analysis in Digimize software (Digimizer, 2015) for five representatively selected fully developed leaves per seedling. The average leaf areas were multiplied with number of leaves for each seedling, which were counted in field. TLA was also used to calculate percentage leaf damage (LD) for each seedling. Total leaf damage area was subjectively estimated in field and thereafter divided with the calculated TLA. In the analysis CD, CW and TLA were calculated to a ratio of the total height to make it comparable between seedlings of variable size. From the census in December 2014 height and diameter values were used to calculate height and diameter growth for the last 9 months, which then where calculated to an estimation of one year's relative growth rate.

Table 1. Description of functional traits with abbreviations and explanation of measurement methods used for the data collection. Functional traits were measured for one seedling per species in each plot

Variable	Abb.	Unit	Description of variable	Description of measurement
Total height	TH	cm	Total height of the seedling from ground to tip of the leading shoot	Measured with a 2 m ruler with 1 cm accuracy
Stem diameter	SD	mm	Diameter of the stem on 10 cm height	Average of cross measurement with a caliper with 1 mm accuracy
Crown depth	CD	cm	Stem length from lowest living branch (or leaf on the stem) to the tip of the leading shoot	Measured with a measuring tape with 1 cm accuracy
Crown width	CW	cm	Diameter of the crown	Average of cross measurement at widest point of the crown with measuring tape
Leaf stem length	LSL	cm	Length from first leaf directly attached on the branch to the axis tip	Average of three representative branches measured with measuring tape
Leaf thickness	LT	mm	Thickness of the leaf between veins	Average of measurements from five representative leaves done with caliper, 0.01 mm accuracy
Vein thickness	VT	mm	Thickness of the leaf on veins	Average of measurements from five representative leaves done with caliper, 0.01 mm accuracy
Total leaf area	TLA	cm^2	Total area of all leaves on the plant	Average of five representative leaves' area estimated by photo analysis multiplied by number of leaves per plant
Leaf damage	LD	%	Percentage damaged tissue of total leaf area	In field subjectively estimated damage area per plant divided with total leaf area.

Statistical analysis

The statistical analysis was performed in the software Minitab 17. Furthermore significant level was set to $p<0.05$. Most of the analyses were done with regression in a general linear model, GLM.

$$Y_{ijln} = \tau_i + \beta_j + S_n + (\tau\beta)_{ij} + (\tau S)_{in} + (\beta S)_{jn} + X + \varepsilon_{ijln} \qquad (1)$$

The growth response (Y) was both tested as height and diameter. The predictors were treatment i's main effect (τ_i), forest type j's main effect (β_j), species n's main effect (S_n), the interactive effects of two main effects ($(\tau\beta)_{ij}$, $(\tau S)_{in}$ and$(\beta S)_{jn}$) and residuals (ε_{ijl}). When height growth were included in the survival analysis it was added as a covariate (X). The results were visualized by interval plots grouped by forest type and treatment. The correlation between the height and diameter growth and the traits were also examined in a GLM. All traits and growth numbers, except CW and CD, were transformed with natural logarithmic base when used as the response, because otherwise the residuals were not normally distributed. The growth indicators were set as the respondent and each of the traits as covariate one at a time, to investigate the traits ability to predicting seedling growth.

To investigate the differences in seedling survival in forest types and treatments a logistic regression was performed, which also included species and interaction between forest type and treatment as predictors. P was the probability for a seedling to survive and the other symbols were the same as for the equation (1).

$$P(survival) = \frac{e^{(\tau_i + \beta_j + S_n + (\tau\beta)_{ij} + \varepsilon_{ijln})}}{1 + e^{(\tau_i + \beta_j + S_n + (\tau\beta)_{ij} + \varepsilon_{ijln})}} \qquad (2)$$

To test the hypothesis if growth was negatively correlated to survival, the survival of the five species with largest average height growth were compared with the survival of the five species with lowest average height growth. Then the difference between those two groups were tested with a chi-square test. The chi-square test was also run one time for each forest type separately. Also similar groups based on traits, instead of height growth, were tested if they differed in survival. Species from all species groups were selected. Then the average survival rates for each combination of species, treatment and forest type (n=192) were calculated and put as the response variable in the GLM. To be able to compare the different factors' importance, the model was run with height growth as a covariate and species, forest type, and treatment as predictors.

RESULTS

Variation in functional traits

Forest type had a significant effect on TH, SD, CW, CD, TLA and LT (table 2). Furthermore none of the traits were affected by treatments alone, but the treatment-forest type interaction had significant effect on TH, SD and VT and tendency on LT (p 0.061). The interaction indicated that the effect of forest types on traits varied for different treatments. Species had significant effect for the traits; TH, SD, CD, TLA and LSL, furthermore the interaction forest type-species had effect on TLA and LD. The interaction effect indicated that the effect of species on the traits varied in different forest types. The degree of explanation (R^2) was in general low, but two clear groups were noted. TH, CW, TLA and SD had models with values above 9 (R^2 19.11-9.47 %) and the rest of the model have R^2 values between 1.46-5.55 %.

Table 2. Results from analyzing treatment, forest type, species and two-way interactions effect on functional traits with general linear model. R-square and P-values for all predictors and traits; for abbreviations see table 1. Values in bold indicate significant effects (P<0.05)

Response	R^2 (adj.)	P-value Treatment	P-value Forest type	P-value Species	P-value interaction Tre-For	P-value interaction Tre-Spe	P-value interaction For-Spe
ln TH	19.11	0.548	**0.012**	**0.000**	**0.003**	0.220	0.221
ln SD	9.47	0.871	**0.000**	**0.000**	**0.000**	0.104	0.145
CW	16.44	0.266	**0.034**	0.114	0.573	0.771	0.676
CD	5.55	0.109	**0.014**	**0.016**	0.168	0.382	0.054
ln TLA	9.6	0.650	**0.000**	**0.000**	0.126	0.469	**0.011**
ln LSL	4.45	0.868	0.086	**0.007**	0.435	0.646	0.397
ln LT	1.46	0.739	**0.011**	0.808	0.061	0.408	0.602
ln VT	3.68	0.823	0.054	0.468	**0.027**	0.194	0.272
ln LD	3.08	0.848	0.213	0.142	0.720	0.517	**0.011**

Gap treatment in general gave higher values for traits in forest type A and B (figure 5). In forest type C the opposite pattern occurred and line treatment gave the highest values. This visualizes the interaction effect of treatment and forest type.

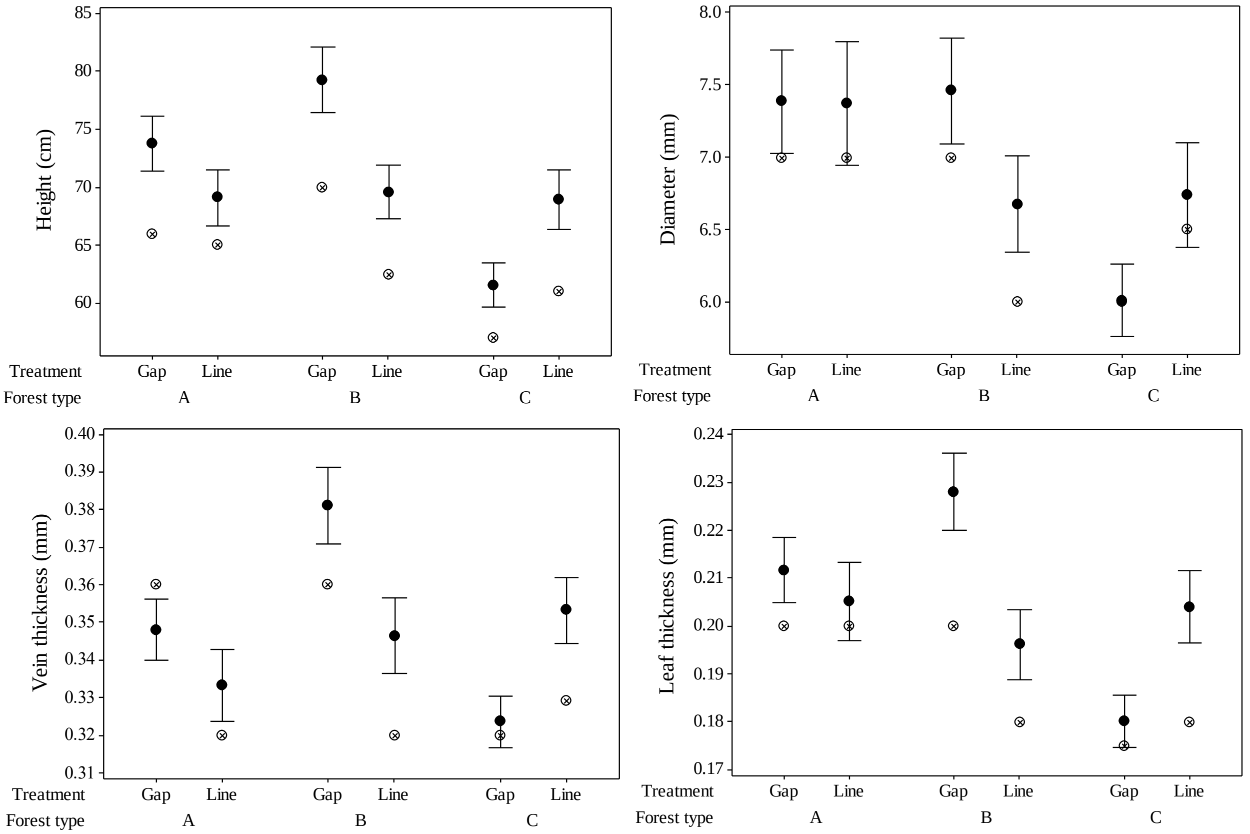

Figure 5. Interval plots for total height, stem diameter, vein thickness and leaf thickness divided on forest type, A = most degraded; C = least degraded, and treatment (gap-cluster planting or line planting). Average based on all seedlings original figures, white circles are the medians and the error bars are 95 % confidence interval.

Average values for all traits (appendix 3) showed that the combination forest type B-gap planting gave the highest values for all traits. The lowest values for most of the traits were given by the combination of forest type C-gap planting. However only TH, SD and VT were significant. Averages for all traits based on species are showed in appendix 4.

Correlation between functional traits and growth

There were correlations between most of the traits and height and diameter growth (table 3). The exceptions were LT and VT for height growth and CW, VT and LD for the diameter growth. Based on R^2 values it was clear that CD, TLA and LSL had the highest predictive power for height growth (12.33-21.58 %). For the correlations between diameter growth and traits the R^2 values were generally lower for all traits but the same distinct groups occur.

Table 3. P-values, R-square and equations for regression with general linear model. Functional traits for all seedlings as predictor (X), see table 1 for abbreviations, and yearly relative height and diameter growth rate as response (Y). Values in bold indicate significant effects ($P<0.05$)

Response	Predictor	P-value	R^2 (adj)	Equation
Height growth	CW	**0.000**	1.14	ln(Height growth) = -2.182 + 0.586 CW(ratio)
Height growth	CD	**0.000**	21.58	ln(Height growth) = -2.693 + 2.158 CD(ratio)
Height growth	TLA	**0.000**	12.33	ln(Height growth) = -2.246 + 0.024 TLA(ratio)
Height growth	LSL	**0.000**	18.83	ln(Height growth) = -2.233 + 0.0364 LSL
Height growth	LT	0.241	0.06	ln(Height growth) = -1.887 + 0.563 LT
Height growth	VT	0.107	0.26	ln(Height growth) = -1.989 + 0.618 VT
Height growth	LD	**0.001**	1.19	ln(Height growth) = -1.6971 – 2.306 LD
Diameter growth	CW	0.561	0.00	ln(Diameter growth) =-1.104 – 0.076 CW(rat.)
Diameter growth	CD	**0.000**	15.2	ln(Diameter growth) =-1.406 + 0.569 CD(rat.)
Diameter growth	TLA	**0.000**	2.31	ln(Diameter growth) =-1.262 + 0.001 TLA(rat.)
Diameter growth	LSL	**0.000**	6.24	ln(Diameter growth) =-1.390 + 0.0158 LSL
Diameter growth	LT	**0.015**	0.94	ln(Diameter growth) =-0.899 – 0.914 LT
Diameter growth	VT	0.235	0.08	ln(Diameter growth) =-0.958 – 0.361 VT
Diameter growth	LD	0.743	0.00	ln(Diameter growth) =-1.150 – 0.176 LD

CD and LSL had strong predictive power on height growth (figure 6). For CD the correlation was also visible for the three groups of species separately.

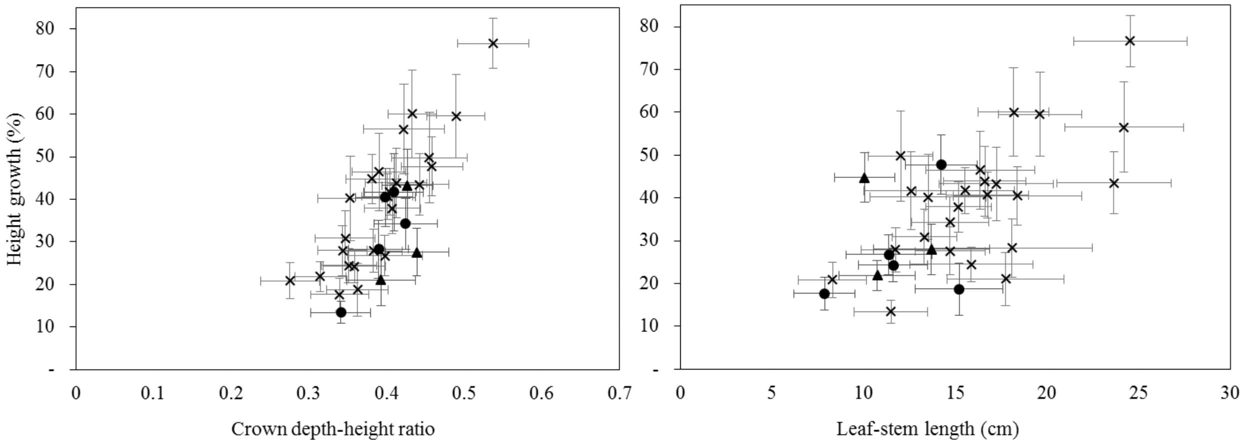

Figure 6. Scatterplot of the 32 species average for yearly relative height growth rate (Y) with predictors (X) crown depth-height ratio (crown depth divided with total height) to the left and leaf stem length (length from first leaf attached on the branch to the axis tip) to the right. Error bars show standard deviation and markers indicates tree group, x: dipterocarps, circles: fruit trees and triangles: other non-dipterocarps.

Traits, treatments and forest types effect on survival

The average survival in this study was depending on species between 39-94 % two years after planting and the forest type–treatment combinations ranging between 60-76 % in survival rate. Logistic regression showed that species had significant effect on seedling survival and forest type had a tendency to effect survival ($P<0.1$) (table 4).

Table 4 P-values from logistic regression for survival as respondent and with forest type, treatment, species and the interaction forest type-treatment as predictors for all seedlings. Values in bold indicate significant effects ($P<0.05$)

Predictors	P-value
Treatment	0.118
Forest type	0.066
Species	**0.000**
Interaction Treatment-forest type	0.996

For the two groups based on height, the higher group had significant lower survival than the lower group (table 5). When the same two groups were tested for each forest type separately, only forest type A showed significant difference between the two species groups. None of the other groupings based on other traits or actual growth gave significant differences. Furthermore the general linear model of average survival rate resulted in no significance for height growth as a covariate. Also the degree of explanation only increased marginally, from 62.00 % to 62.49 % when height growth was added as covariate in the model.

Table 5 P-values for Pearson chi-square test of difference in survival between groups based on height to investigate the existence of a growth-survival trade-off. The five species with lowest and highest average height, respectively, were creating the two groups. Forest type A = most degraded and C = least degraded. Values in bold indicate significant effects ($P<0.05$)

Groups	P-value
Height groups - All forest types	**0.049**
Height groups - Forest type A	**0.035**
Height groups - Forest type B	0.167
Height groups - Forest type C	0.969

DISCUSSION

Variation in functional traits

Forest type affected all functional traits except LSL, VT and LD. Also there were interaction effects for forest type-treatment and forest type-species. This provided clear evidence for the hypothesis that both forest type and treatment affected the expression of functional traits on the planted seedlings. For a complete understanding of these patterns one need to consider among treatment and forest type differences in a variety of environmental conditions, i.e. availability of light, competition with understory vegetation and herbivory. Forest types are clearly different in light environments (Alloysius, 2015; Jansson, 2015) which could have influenced plant performance. Although, earlier light measurements have not been able to detect differences between the planting methods on plot level (Jansson, 2015), there could still be differences for the planting spots, where weeding has been performed. Forest type B gave the highest values for all functional traits (and lowest LD), type C the lowest and type A intermediate values. These patterns are not fully supported by the theory that seedling with most light available (forest type A) should have the highest growth (Ashton *et al.*, 2006). Clearly, light availability is not the only environmental factor affecting plant performance.

Forest types differ not only in the light environment for the seedlings, but also conditions for other vegetation such as weeds and climbers (Dupuy & Chazdon, 1998; Cheke *et al.*, 1979). Seedlings are during periods competing with weeds and climbers, which slow down seedling growth (Holl, 1998). This could be difficult to notice in light measurements that have been performed close after weeding and above most of the ground vegetation. Also the maintenance actions, as weeding, increase risk of mechanic damages and mortality for the seedlings (Douterlungne *et al.*, 2015; Personal observation, 2015), especially in type A with most ground vegetation. In the more light limited forest types (forest type B and C) the tree canopy limits both the abundance of weeds and the growth of the seedlings (Dupuy & Chazdon, 1998). Furthermore forest type A was the most disturbed type, which means that logging and forest fires have had large effect on soil and vegetation. Logging causes nutrient loss and could increase erosion especially when followed by fire (Malmer, 1996), which create unfavorable condition for seedling growth. Light environment combined with soil conditions and competition from other vegetation might make forest type B the most favorable for seedling growth (cf. Ashton *et al.*, 2006; Malmer, 1996; Cheke *et al.*, 1979).

Gap planting seemed to be the better treatment in forest types A and B, i.e. high and intermediate light environment, resulting in higher growth and less leaf damage. However in forest type C, i.e. low light environment, line planting seemed to be the better treatment, resulting in higher values for all traits (except CW and diameter growth) and less damage. Gaps seemed to create clearly better condition for the seedlings in forest type B and there were also indications of improved seedling growth in forest type A. In the type with more climax trees, type C, gaps are likely to be selectively placed under the canopy because fewer Macarangas are girdled, i.e. killed (Alloysius, 2015). Planting lines are strictly placed every 10 meters and more Macarangas are removed in order to clear the lines, in contrast to gaps that are selectively placed between Macarangas (Alloysius, 2015). This could have caused more light to penetrate the canopy in line planting. In the other two forest types, A and B, there are less adult trees initially and more ground vegetation (Alloysious, 2015). Therefore seedlings are less shaded by the tree canopy, but as a result more weeds are competing for resources. Moreover the maintenance in gaps and lines has potential to create periodical differences in weed abundance. When gaps are cleared they are 5 m in diameter (Romell *et al.*, 2008) and the lines are only 2 m wide (Alloysius, 2015). Ådjers *et al.* (1995) showed that wider lines increase growth for the seedlings for most dipterocarp species. Due to the differences in cleared area, the weeds might require more time to regrow in gaps compared to lines. Also there is a theory that lines are easier to maintain, because staff follow the lines when weeding instead of needing to locate gaps (Alloysius, 2015). Thereby line planting also is considered cheaper than gap-cluster planting. This study has not been focused on the growth of competing ground vegetation, therefore further research on this subject is needed. Comparing growth of both seedlings and weeds in gaps and lines of different width should be carried out to further investigate what causes the observed variation in growth and how that knowledge could be used in practical maintenance.

The pattern displayed by the LD was inverted compared to the other traits, having the highest averages in forest type C. Furthermore LD showed significant effect for the interaction between forest type and species. Some species seem to attract more herbivores, which could be related to the defense-growth trade-off on the pioneer-climax scale (King *et al.*, 2006; Ådjers *et al.*, 1995). Kitajima and Augspurger (1989) show that seedlings in shady environments are more affected by herbivores, which were noted in forest type C. Plant –insect interactions are complex and further research is needed to understand which species are most affected of herbivory, especially because LD affected height growth negatively.

The discussed explanations are mostly based on light conditions for the seedlings. However other conditions have affected the seedlings and could have contributed to increased variation both intra- and interspecific. For example the topography makes the hydrology vary over the landscape, causing drought or water sickness for seedlings (Kozlowski, 2002), however because the lack of information about the hydrology in the plots it was disregard in this study. The same would be true for competition below ground, i.e. root competition, which could reduce seedling growth (Barberis & Tanner, 2005; Huante *et al.*, 1998). Root competition limit growth mainly by aggravated lack of water and nutrients, but this factor was not discussed further in this study.

Correlation between functional traits and growth

CD, TLA and LSL were clearly the traits that best predicted both height and diameter growth. The data supported the hypothesis that growth is correlated to functional traits, however not all. From earlier studies it is clear that pioneer properties, e.g. low wood density, high specific leaf area (SLA) and high N and P in foliage, are closely connected to rapid growth (Poorter & Bongers, 2006; Sterck *et al.*, 2006). Furthermore the difference in growth between species is larger in lighter conditions, where seedlings of pioneer properties respond faster. King and Clark (2004) and Gustafsson *et al.* (2016) confirm that CD and LSL are good predictors of growth. TLA or TLA ratio have not been used in other studies of tropical trees, however the close correlation between TLA and height growth might tell us high TLA indicates pioneer properties for an individual or a species. In other studies that have used traits to predict growth, strong correlations between traits indicating pioneer properties and faster growth has been observed. For example photosynthetic traits, as SLA, photosynthetic capacity/mass, N efficiency and dark respiration are linked to higher growth rate (Poorter & Bongers, 2006; Rozendaal *et al.*, 2006; Sterck *et al.*, 2006). Morphological traits as LSL, CW and CD are correlated to growth (Gustafsson *et al.*, 2016; King & Clark, 2004), which also was confirmed in this study. LSL was affected by neither forest type, treatment, nor the interaction between them. This was strange since it is a strong predictor of growth, which was strongly affected by forest type and treatment. The lack of response to these factors also contradict earlier findings where LSL is affected by light treatment and varied amongst light environments (Gustafsson *et al.*, 2016; King & Clark, 2004) However the measurement of LSL was not done in the same way as in the previous studies. Gustafsson *et al.* (2016) and King and Clark (2004) measure the length of displayed leaves on the stem on seedlings without branches. Whereas in this study seedlings without branches were not given any result. This also limited the number of measurements on LSL and might have caused some bias when the data was compared to the other studies.

No correlations for LT or VT and height growth were found and previous studies have not used these traits, therefore the findings are difficult to verify. It was expected that LT and VT were able to predict height growth in the darker environment, forest type C, where leaf life span is of importance for the growth (Poorter & Bongers, 2006; Rozendaal *et al.*, 2006). Because LT and VT were thought to be good predictors of leaf life spans. However the variations in height growth were generally smaller in type C (appendix 3), which aggravated to identify correlation. Furthermore size related leaf traits have lower plasticity (4-7 %) compared to SLA and photosynthetic traits (20-31 %) (Rozendaal *et al.*, 2006). This could explain why these traits were unsuccessful predictors in environments with high light availability, where seedlings respond on the available resources with increased growth (Gustafsson *et al.*, 2016; Rozendaal *et al.*, 2006).

All traits were better on predicting height growth than diameter growth, which probably was caused by the smaller variations in diameter growth between individual seedlings. Rapid diameter growth as well as height growth are classed as pioneer properties (Poorter & Bongers, 2006; Clark & Clark, 1992). Wood density being larger on the climax property edge of the scale also contributes to slower diameter growth, because more carbon is needed to increase a given volume of wood (King *et al.*, 2006). Large CW should be an indicator of a large crown that need support from a thicker stem (King, 1994), but it was not evident from this study.

When calculating growth with data from the last census, almost 20 % of the seedlings got negative figures of growth. Most likely the errors were from measurement errors or explained by different seedlings being measured. Seedlings of the planted species could occur as natural regeneration in the same area and there could be a risk of them being mixed up in weeding and census work.

Traits, treatments and forest types effect on survival

The species average survival rates, 39-94 %, and the forest type –treatment combinations 60-76 %, were similar to previous studies in the region. The survival in greenhouse trials with three dipterocarp species were 67–97% (Ashton *et al.*, 2006). Ådjers *et al.* (1995) got 35-85 % survival after two years with three dipterocarp species in field trials. Within INIKEA survival for four different dipterocarps in an shade adjustment experiment was 72–86% after 2,5 years (Romell *et al.*, 2008).

The results did not provide evidence that differences in survival could be explained by functional traits. Furthermore no clear evidence for a growth-survival trade-off was found either, only the species furthest apart on the pioneer-climax properties scale based on total height showed significant differences in survival rate. The groups based on seedlings total height showed that five species with the lowest average height had significant higher survival than the five species with highest average height. However there were no significant differences for groups based on either traits or height growth. Both Poorter and Bongers (2006) and Sterck *et al.* (2006) found clear growth-survival trade-off in field trials, as well as in modeled trials with different light environments. Poorter and Bongers (2006) also stated that long leaf life-span contribute to high survival in low light environment. In this study similar results were likely to occur in the shaded environment, forest type C. VT and LD could be used as predictors of leaf life span (Rozendaal *et al.*, 2006). High VT indicates toughness and low LD shows toughness against physical damage and herbivory. However none of them correlated with survival rate. The correlation may still exist, but may has become unclear due to that leaf life span was indirectly estimated based on other traits. Another clarifying factor might be if the seedlings in forest type C were not as light limited as expected, since the survival rate varies less between climax and pioneer property species in brighter environments (Rozendaal *et al.*, 2006).

The method and data collection was not optimal for investigating growth-survival trade-off. Data for survival and growth was not available for the same individuals, instead species averages were used. A better method would have been to collect data over time and in that way have growth data for each individual to compare with survival data for the same individual. The experimental design for the RRE is planned to get fundamental conditions for statistical analysis, with enough replicates to detect effects from combinations of forest types, treatments, and species in the order of 10-20 %, given the large within treatment variations expected in these forests. However seedlings were of different age and size when they were planted and after two years these differences have not been compensated by species characteristic growth, which could cause uncertain results. Furthermore for some of the species with high mortality the sample size became relatively small.

Conclusion

This study found that gap planting seemed to be the better treatment in more degraded areas where light availability were higher, which usually are restored by enrichment planting within INIKEA. There has been a presumption that line planting is suitable for forest type A and gap planting for forest type B. Partly because lines are easier to plant and maintain in locations with much ground vegetation. With more research on the reasons for these differences caused by treatment, together with further cost analysis, one should be able to choose the best and most cost effective method for different environmental conditions and thereby improve restoration. Furthermore after two years interspecific variations for traits were noticeable, as well as for survival rate. These results could be used to further understand the complexity of the ecosystem and improve the effectiveness of restoration actions in the rain forests. In future projects, enrichment planting could be improved by adapt species composition so that species of lower survival are planted in larger numbers, or increase the effectiveness by planting a selection of species with low mortality.

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APPENDIX 1

Table 6. Management plan for Rainforest Restoration Experiment (RRE) within the INIKEA-project Sabah, Malaysia. The experiment was set up and planted in November 2013 (Alloysious, 2015).

Weeding	Refill planting	Census
March 2014	April 2014	February 2014
September 2014		November 2014
March 2015		November 2016
September 2015		September 2023
March 2016		
September 2016		
March 2017		
September 2017		

APPENDIX 2

Table 7. Latin name, abbreviation and tree group for all species included in this study

Name Latin	Abbreviation	Tree group
Dryobalanops keithii	Dr. ke.	Dipterocarp
Dryobalanops lanceolata	Dr. la.	Dipterocarp
Dipterocarpus gracilis	Di. gr.	Dipterocarp
Shorea agamii	S. aga.	Dipterocarp
Shorea pauciflora	S. pau.	Dipterocarp
Shorea leptoderma	S. let.	Dipterocarp
Shorea falciferoides	S. fac.	Dipterocarp
Shorea seminis	S. sem.	Dipterocarp
Shorea fallax	S. fal.	Dipterocarp
Shorea argentfolia	S. arg.	Dipterocarp
Shorea xanthophylla	S. xan.	Dipterocarp
Shorea ovalis	S. ova.	Dipterocarp
Shorea gibbosa	S. gib.	Dipterocarp
Shorea acuminatissima	S. acu.	Dipterocarp
Shorea faguetiana	S. fag.	Dipterocarp
Shorea parvistipulata	S. pas.	Dipterocarp
Shorea macroptera	S. mac.	Dipterocarp
Hopea ferruginea	Ho. fe.	Dipterocarp
Shorea parvifolia	S. paf.	Dipterocarp
Shorea leprosula	S. ler.	Dipterocarp
Shorea smithiana	S. smi.	Dipterocarp
Parashorea tomentella	Pa. to.	Dipterocarp
Parashorea smythiesii	Pa. sm.	Dipterocarp
Parashorea malaanonan	Pa. ma.	Dipterocarp
Mangifera pajang	Ma. pa.	Fruit tree
Ficus benjamina	Fi. be.	Fruit tree
Baccaurea motleyana	Ba. mo.	Fruit tree
Nephelium lappaceum	Ne. la.	Fruit tree
Artocarpus odoratissimus	Ar. od.	Fruit tree
Heritiera simplicifolia	He. si.	Others
Koompassia excelsa	Ko. ex.	Others
Pentace adenophora	Pe. ad.	Others

APPENDIX 3

Table 8. Average values for survival, relative growth and traits, divided on forest type and treatments for measurements on seedlings of 32 species within the Rainforest Restoration Experiment. Forest type A = most degraded; C = least degraded and treatment (gap-cluster planting or line planting). Standard error values within brackets. Bold figures indicates the combination with largest figure and italic grey figures indicated the combination with the smallest figure per column.

Forest type	Treatment	Survival (%)	Height (cm)	Diameter (mm)	Rel. height growth (%)	Rel. diameter growth (%)	Ratio crown depth	Ratio crown width	Total leaf area (cm^2)	Leaf-stem length (cm)	Leaf thickness (mm)	Vein thickness (mm)	Leaf damage (%)
A	Total	63.78	71.6	7.4	0.28	0.31	0.40	0.68	1627	15.9	0.21	0.34	0.038
			(1.71)	(0.14)	(0.018)	(0.018)	(0.012)	(0.013)	(128)	(0.87)	(0.005)	(0.006)	(0.002)
	Gap	67.41	73.8	7.4	0.29	0.34	0.42	0.69	1716	16.9	0.21	0.35	0.040
			(2.4)	(0.18)	(0.024)	(0.024)	(0.017)	(0.017)	(161)	(1.2)	(0.007)	(0.008)	(0.004)
	Line	*60.44*	69.1	7.4	0.26	*0.27*	0.38	0.67	1527	14.7	0.21	0.33	0.036
			(2.4)	(0.22)	(0.027)	*(0.026)*	(0.018)	(0.02)	(202)	(1.25)	(0.01)	(0.01)	(0.003)
B	Total	73.89	74.9	7.1	0.29	0.46	0.42	**0.70**	1725	16.8	0.22	0.37	0.038
			(1.9)	(0.13)	(0.015)	(0.019)	(0.012)	**(0.013)**	(108)	(0.8)	(0.006)	(0.007)	(0.003)
	Gap	**76.34**	**79.3**	**7.5**	**0.33**	**0.54**	**0.44**	**0.70**	**1930**	**17.7**	**0.23**	**0.38**	0.040
			(2.9)	**(0.19)**	**(0.022)**	**(0.025)**	**(0.016)**	**(0.016)**	**(158)**	**(1.15)**	**(0.008)**	**(0.01)**	(0.005)
	Line	71.43	69.6	6.7	0.25	0.34	0.39	**0.70**	1486	15.5	0.20	0.35	0.036
			(2,3)	(0.17)	(0.020)	(0.025)	(0.016)	**(0.021)**	(141)	(1.06)	(0.007)	(0.01)	(0.003)
C	Total	69.63	65.0	6.4	0.25	0.47	0.37	0.66	1076	13.9	0.19	0.34	0.041
			(1.58)	(0.11)	(0.017)	(0.022)	(0.012)	(0.013)	(66)	(0.75)	(0.005)	(0.006)	(0.004)
	Gap	72.77	*61.6*	*6.0*	*0.24*	0.52	*0.35*	0.67	*953*	*12.4*	*0.18*	*0.32*	**0.049**
			(1.88)	*(0.13)*	*(0.022)*	(0.032)	*(0.015)*	(0.018)	*(81)*	*(0.88)*	*(0.005)*	*(0.007)*	**(0.006)**
	Line	66.48	68.9	6.7	0.26	0.41	0.38	*0.65*	1212	15.4	0.20	0.35	*0.033*
			(2.58)	(0.18)	(0.027)	(0.029)	(0.018)	*(0.02)*	(105)	(1.22)	(0.008)	(0.009)	*(0,003)*
Total		69.46	70.5	6.9	0.27	0.42	0.40	0.68	1478	15.6	0.20	0.35	0.039
			(1.1)	(0.07)	(0.009)	(0.011)	(0.007)	(0.008)	(60)	(0.47)	(0.003)	(0.004)	(0.002)

*N-value: 90 -208 for each treatment

**N-value: 197-380 for each forest type

***N-value: 689-1110 in total

APPENDIX 4

Table 8. Average values for survival, relative growth and traits for seedlings of 32 species within the Rainforest Restoration Experiment. Bold numbers indicates the five species with largest numbers and italic grey numbers indicated the five species with smallest numbers per column.

Species	Survival (%)	Height (cm)	Diameter (mm)	Rel. height growth (%)	Rel. diameter growth (%)	Ratio crown depth	Ratio crown width	Total leaf area (cm^2)	Leaf-stem length (cm)	Leaf thickness (mm)	Vein thickness (mm)	Leaf damage (%)
Ar. od.	83.33	*51.3*	6.3	0.23	0.36	*0.26*	**0.81**	1030	*8.5*	**0.37**	**0.54**	*0.011*
Ba. mo.	**94.4**	74.4	**9.5**	0.24	0.35	*0.29*	0.70	**2385**	*7.0*	**0.36**	**0.55**	0.052
Di. gr.	**91.4**	76.8	**8.9**	*0.17*	0.38	0.41	0.74	**2226**	12.1	0.21	0.39	0.031
Dr. ke.	*47.22*	70.2	**8.3**	**0.48**	0.34	0.44	**0.93**	**3027**	18.1	0.22	0.33	*0.021*
Dr. la.	69.44	**91.5**	**7.9**	0.34	0.46	0.42	0.71	**3476**	**21.9**	0.19	0.30	*0.011*
Fi. be.	*40.54*	*52.7*	*6.0*	*0.15*	*0.29*	**0.51**	0.67	*257*	*8.1*	*0.16*	*0.28*	0.035
He. si.	78.33	*50.0*	7.8	0.22	*0.28*	0.37	**0.87**	1025	-	0.22	**0.41**	**0.066**
Ho. fe.	75.76	**99.1**	7.0	**0.45**	0.48	**0.68**	0.66	1701	**25.0**	*0.10*	*0.19*	0.045
Ko. ex.	82.50	*52.6*	*5.4*	0.25	0.47	0.34	**0.81**	998	**27.7**	*0.10*	*0.19*	*0.014*
Ma. pa.	85.00	55.7	7.2	0.20	*0.28*	**0.50**	0.66	1015	12.3	0.17	0.30	0.031
Ne. la.	66.67	72.1	7.0	*0.17*	*0.33*	0.34	0.62	1289	9.8	*0.15*	*0.29*	0.044
Pa. ma.	71.88	74.7	6.7	0.22	0.39	0.40	0.64	1408	12.0	0.17	0.32	0.032
Pa. sm.	55.00	62.0	*5.6*	**0.39**	**0.58**	0.43	0.66	1183	14.0	0.17	0.30	**0.062**
Pa. to.	65.85	68.8	6.4	0.29	0.41	0.40	*0.54*	1142	17.9	0.18	0.35	**0.087**
Pe. ad.	70.83	59.6	6.7	0.25	0.36	*0.27*	0.58	1061	*7.8*	0.21	0.35	**0.053**
S. acu.	76.92	59.2	*5.8*	0.31	0.46	0.41	0.69	*885*	14.2	0.18	0.32	0.049
S. aga.	**86.49**	63.6	6.8	0.20	0.34	0.44	*0.58*	*972*	*9.5*	0.21	0.38	0.049
S. arg.	*38.89*	**115.9**	**8.4**	0.29	0.43	0.37	*0.49*	1391	19.3	0.18	0.30	*0.016*
S. fac.	**87.27**	76.0	6.0	0.26	0.36	0.46	0.57	1172	13.6	0.19	0.33	0.031
S. fag.	60.53	64.6	7.0	0.23	0.45	0.43	0.75	1624	18.3	0.21	0.36	0.036
S. fal.	69.23	56.7	6.6	*0.19*	0.44	*0.27*	0.71	*963*	11.3	0.25	**0.43**	0.034
S. gib.	48.72	66.2	*5.6*	0.25	**0.53**	0.32	0.63	*635*	14.0	*0.15*	*0.25*	0.042
S. ler.	63.33	**98.1**	6.8	0.34	**0.60**	0.37	*0.49*	1440	16.3	0.17	0.31	0.042
S. let.	**87.72**	80.3	6.3	**0.37**	0.51	**0.52**	0.67	1884	18.3	0.17	0.31	0.030
S. mac.	75.61	77.3	6.6	0.27	0.51	0.39	0.64	1898	14.5	0.21	0.35	0.034
S. ova.	64.52	*49.9*	7.0	*0.15*	*0.34*	0.32	**0.92**	1054	11.8	0.24	0.40	0.038
S. paf.	*48.48*	80.0	7.0	0.22	0.34	0.34	*0.54*	1160	14.7	0.17	0.30	**0.061**
S. pas.	*44.12*	80.1	7.1	0.28	0.51	0.38	0.58	1729	16.7	**0.26**	0.41	0.027
S. pau.	80.00	66.0	7.2	0.27	**0.54**	0.44	0.81	1827	17.7	0.19	0.32	0.043
S. sem.	75.00	**80.5**	7.4	0.26	0.49	0.33	0.68	**2287**	**19.8**	0.21	0.35	0.029
S. smi.	54.84	74.9	7.3	0.24	**0.54**	*0.30*	0.62	1100	**19.5**	**0.31**	**0.49**	0.037
S. xan.	78.79	73.3	7.1	**0.39**	0.36	**0.49**	0.72	1556	13.0	**0.26**	0.40	0.052

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