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Herbivory and its Effect on Tree Growth and Tree Survival in an Enrichment Planting Experiment in Jambi, Sumatra

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Statement of Affirmation

I hereby declare that the master thesis submitted was in all parts exclusively prepared on my own, and that other resources or other means (including electronic media and online sources), other than those explicitly referred to, have not been utilized.

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"Destroying rainforest for economic gain is like burning a Renaissance painting to cook a meal."

- E. O. Wilson -

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Abstract

Tropical rainforests are being transformed into large-scale oil palm monocultures which results in a loss of biodiversity and ecosystem functioning. Thus, enrichment planting, which experimentally increases plant diversity, is an important management strategy to conserve biodiversity in impoverished landscapes. Increased tree diversity has been hypothesized to enhance the biodiversity of all trophic levels. Within the framework of the Collaborative Research Centre 990 (CRC 990), an enrichment planting experiment was established by planting six native tree species of economic value (*Parkia speciosa*, *Archidendron pauciflorum*, *Durio zibethinus*, *Dyera polyphylla*, *Peronema canescens* and *Shorea leprosula*) systematically in varying plot sizes (5x5 m, 10x10 m, 20x20 m and 40x40m) and tree diversity levels (1, 2, 3 and 6 tree species per plot) within an oil palm plantation in the Jambi province of Sumatra. Standing herbivory of each tree individual, that was planted, was quantified 18 months after the establishment of the experiment. Despite many studies focusing on herbivory, this is the first study of standing herbivory of trees within an oil palm plantation. Here, I present the results of the quantification of herbivory with first insights on how the experimental treatments and the choice of tree species have affected leaf damage. My findings show that the experimental treatment of plot size and diversity level did not influence standing herbivory. Nevertheless, leaf damage tended to be lower in high tree diversity plots. The most important factor explaining standing herbivory was the tree species identity. Furthermore, a correlation between growth and standing herbivory was not found. The leaf damage for trees which had survived a drought was compared to the average damage of trees which had died. The comparison showed no differences but revealed a trend for a higher damage of dead trees. Further analyses for a broader understanding on the factors influencing herbivory and their interactions are needed. This knowledge can help in restoring biodiversity in oil palm landscapes in Southeast Asia.

Zusammenfassung

Tropische Regenwälder werden zu großflächigen Ölpalm-Monokulturen umgewandelt. Diese Umwandlung führt zu dem Verlust der tropischen Biodiversität und der Ökosystemfunktionen. Aus diesem Grund ist es nötig Maßnahmen für den Naturschutz zu treffen. Aufforstungsversuche durch die Anpflanzung zusätzlicher Bäume zählen zu diesen Maßnahmen. Es wird vermutet, dass eine gesteigerte Baumvielfalt positiv auf alle trophischen Ebenen wirkt. In Zusammenarbeit mit dem Sonderforschungsbereich 990, der sich mit den ökologischen und sozioökonomischen Funktionen tropischer Tieflandregenwald-Transformationssysteme auf Sumatra in Indonesien beschäftigt, wurde ein Aufforstungsversuch durchgeführt. Dazu wurden sechs einheimische Baumarten innerhalb einer Ölpalmplantage in der Provinz Jambi in Sumatra gepflanzt. Zu diesen Baumarten gehören *Parkia speciosa*, *Archidendron pauciflorum*, *Durio zibethinus*, *Dyera polyphylla*, *Peronema canescens* und *Shorea leprosula.* Diese Baumarten wurden aufgrund ihres ökonomischen Wertes gewählt. Die Pflanzungen wurden systematisch in Plots unterschiedlicher Größe (5x5 m, 10x10 m, 20x20 m und 40x40m) und Diversitätslevel (1, 2, 3 und 6 Arten) vorgenommen. Nach einer Zeit von 18 Monaten wurde die Herbivorie jedes Baumes aufgenommen. Obwohl viele Studien zur Herbivorie vorliegen, ist dies die erste Studie zur Herbivorie von Bäumen innerhalb einer Ölpalmplantage.

In dieser Masterarbeit werden die Ergebnisse der Herbivorie-Quantifizierung dargestellt. Dazu wird erklärt, inwieweit der Versuchsaufbau und die Wahl der Baumarten zum Blattverlust beitragen. Die Quantifizierung der Herbivorie zeigte, dass weder die Plotgröße noch die Diversitätslevel einen Einfluss auf die Herbivorie haben. Dennoch schien der Blattverlust, welcher durch Herbivorie verursacht wurde, geringer in den Plots mit allen sechs Arten. Die Identität der Baumart erwies sich als wichtigster Einfluss auf die Herbivorie. Einen Zusammenhang zwischen Wachstum und Herbivorie eines Baumes konnte nicht gezeigt werden. Im Anschluss an die Studie kam es zu einer längeren Dürreperiode in der Provinz Jambi. Bei dieser sind mehrere Baumindividuen vertrocknet. Der Einfluss der Herbivorie wurde getestet, indem die Werte für die überlebenden Bäume und die der vertrockneten Bäume verglichen wurde. Auch dabei konnte kein Zusammenhang festgestellt werden. Dennoch ließ sich ein Trend

erkennen, dass die Herbivorie bei den vertrockneten Bäumen leicht erhöht war im Gegensatz zu den überlebenden Baumindividuen.

Weitere Analysen der Faktoren, welche die Herbivorie beeinflussen, werden benötigt. Dieses Wissen ist hilfreich im Zusammenhang mit einer Wiederherstellung der Biodiversität in der Ölpalmlandschaft in Südostasien.

Introduction

Tropical rainforests are considered as the most diverse terrestrial ecosystems (Corley & Tinker, 2003). These ecosystems host at least two-thirds of the Earth's terrestrial biodiversity (Gardner et al., 2009). These forests are threatened by human activities. Agriculture, forestry, urbanization and infrastructure development all lead to deforestation, forest fragmentation and land-use intensification (Geist & Lambin, 2002; Gardner et al., 2009). Land use has strongly intensified due to the increasing food demand, the result of exponential increase in the world's human population and rising per capita consumption (Cohen, 1995; Godfray et al., 2010). It is estimated that areas of tropical rainforests are decreasing by 2101 km² per year (Hansen et al., 2013). This habitat loss leads to a loss of biodiversity. Additionally, the over-harvesting of timber and non-timber resources, altered disturbance dynamics (e.g. fire), changes in hydrological flows, and the invasion of exotic species form further threats to tropical biodiversity (Fitzherbert et al., 2008; Gardner et al., 2009). In addition, the variety of goods (e.g. timber, medicine, and food) and ecosystem services (e.g. water regulation for irrigation of agricultural lands, disasters, and risk reduction) provided by tropical rainforests are lost as a result of the conversion of land use (Lamb et al., 2005; Gardner et al., 2009; Moran, 2011; Wich et al., 2011).

Southeast Asia features multiple forests with high endemism rate (Sodhi et al., 2010). Due to their restricted distribution, endemic species are particularly threatened by high deforestation rates. Tropical rainforests in Southeast Asia are faced with the highest rates of deforestation worldwide (Sodhi et al., 2004; Koh & Wilcove, 2007). If the current deforestation rates continue, Southeast Asia is projected to lose 58 % of its biodiversity by 2100 (Sodhi et al., 2004; Sodhi et al., 2010). The transformation of lowland rainforest into oil palm plantations (*Elaeis guineensis*) has been identified as a major threat to biodiversity (Jepson et al., 2001; Barnes et al., 2014) and a potential driving force of climate change (Danielsen et al., 2009; Wilcove & Koh, 2010), as approximately 17 % of global greenhouse gases are emitted through deforestation (Wich et al., 2011). The establishment of oil palm plantations is one of the main causes for the high deforestation rate in Indonesia (Koh & Wilcove, 2008), which amounts approximately to 1021 km² per year (Hansen et al., 2013). At least 56 % of forest conversion is attributed to oil palm expansion (Koh & Wilcove, 2008). Sumatra's forests are particularly threatened (Margono et al., 2014). In 1985, 25 million ha, i.e. more than half of the island Sumatra (57 %), was covered with

forests (Laumonier et al., 2010). By 2007, 48 % of these forests had been lost (Laumonier et al., 2010), and by 2010, more than 70 % of the forested area of Sumatra had been converted (Margono, 2012). Oil palm agriculture is the greatest threat to biodiversity (Wilcove & Koh, 2010).

Palm oil is used for the production of food and biofuel (Fitzherbert et al., 2008; Sodhi et al., 2010), both of which are in high demand. For this reason, its production is increasing by 9 % every year (Fitzherbert et al., 2008). By 2050, the current demand of palm oil is expected to double (Corley, 2009; Moran, 2011). Oil palm is native to Africa and requires the same conditions for growth as tropical rainforests (Fitzherbert et al., 2008) and has, therefore, been successfully cultivated in Indonesia and Malaysia (Corley & Tinker, 2003). The establishment of large-scale oil palm monocultures in areas of tropical rainforests has severe consequences. Most native plant species do not occur within oil palm plantations and the abundance of vertebrates has been shown to be lower by 77 % (Danielsen et al., 2009). Species richness of invertebrates has also declined, although 31 % of invertebrate species were found in both habitats (Danielsen et al., 2009). Such species loss can negatively influence ecosystem functioning (Barnes et al., 2014). These threats to tropical rainforests and the related loss in biodiversity caused by land conversion lead to the urgent need for restoration management strategies for biodiversity and ecological functioning as well as the supply of goods and ecosystem services (Lamb et al., 2005).

Balancing the need of land for agricultural production and for biodiversity conservation is a global challenge (Harvey et al., 2008; Tscharntke et al., 2012). The restoration of forests and, with it, the restoration of ecosystem services and biodiversity is essential. One strategy for restoration management strategies is enrichment planting in impoverished landscapes. Enrichment planting is considered to combine actions against climate change and increasing biodiversity and ecosystem services (Piotto et al., 2004; Lamb et al., 2005; Paquette et al., 2009). The challenge, however, is the choice of species to plant for restoring ecosystem services, as well as the goods to provide. This is difficult and needs further development (Lamb et al., 2005). Increases in diversity can lead to higher productivity (Erskrine et al., 2006; Kelty, 2006). Furthermore, increased species richness can lead to higher abundance of all trophic levels (plants, herbivores, predators and detritivores) (Siemann, 1998; Cardinale et al., 2006). Higher plant diversity is more attractive to herbivores and a higher diversity of herbivores attracts more predators. A possible explanation for the positive effect of increasing diversity is a better

consumption of resources, due to niche partitioning (Cardinale et al., 2006). Native plant species should be used for enrichment planting. They can create conditions that are suitable for the native fauna (Lamb et al., 2005). Hence, enrichment planting with native plants might have positive effects on biodiversity.

Reducing the threats to biodiversity from oil palm agriculture is important but difficult and needs approaches regarding social, economic and ecological factors (Wilcove & Koh, 2010). Experimentally increasing the tree diversity in oil palm plantations might help to mitigate the losses in ecosystem services and biodiversity and help restoring these. Enrichment planting has never been conducted within oil palm plantations before. The first enrichment planting experiment within an oil palm plantation was established in the Jambi province of Sumatra in 2013. Investigating the effects on biodiversity and ecosystem services might help find approaches for dealing with the oil palm crisis in Southeast Asia. Positive effects on all trophic levels are hypothesized to result from increasing plant species diversity (Siemann, 1998; Cardinale et al., 2006). Hence, the investigation of herbivory is a first step of evaluating the enrichment planting experiment. Herbivores should be attracted first by the higher plant diversity. A quantification of standing herbivory might show a success of planting and choice of tree species.

Higher plant diversity might influence herbivore abundance, which in turn, might increase or decrease damages caused by herbivory. Schuldt et al. (2010) found a positive herbivory-tree diversity relationship in subtropical China. The *resource concentration hypothesis* by Root (1973) is contrary to the positive relationship between herbivory and plant diversity and states that many herbivores, especially those with a narrow host range, are more likely to find hosts that are concentrated. According to the *resource concentration hypothesis*, specialist herbivore abundances should decrease with higher diversity of plants. Whether herbivory increases or decreases with higher plant diversity needs further investigations for forest stands since most studies were conducted in grassland systems (Olff & Ritchie, 1998; Siemann, 1998; Scherber et al., 2006; Ebeling et al., 2014).

Herbivory is affected by phytochemical (e.g. alkaloids, phenolic compounds) and morphological plant traits (e.g. leaf toughness) (Corley & Barone, 1996). A trade-off between growth and defense of a plants leads to different leaf characteristics (Fine et al., 2006; Wright et al., 2010). Fast-growing species build leaves with low construction costs and, therefore, with

little investment in defense traits but high nutrient concentrations (Coley et al., 1985). Leaf characteristics of slow-developing species show contrary leaf contents (e.g. proteins, water, and fiber content). Consequently, plants which develop slowly are less attractive to insect herbivory than fast-growing species (Poorter et al., 2004). The water content of a leaf positively influences herbivory because leaves with high water content are easier to digest (Poorter et al., 2004). Light availability also affects herbivory (Coley & Barone, 1996). Leaves exposed to high light conditions, usually have higher water and nitrogen contents (Poorter et al., 2004). Leaf toughness is an important indicator for herbivory. To avoid herbivory, the nutritional quality of leaves is low, whereas the toughness is high in tropical trees. In addition, a high variety of secondary metabolites is found in the leaves of tropical forests (Coley & Barone, 1996). Secondary metabolites belong to defense traits involving toxicity to deter herbivores (Bennett & Wallsgrove, 1994). Defense mechanisms of plants against herbivory do not only include leaf morphology or phytochemicals. Rapid leaf expansion can also have protective influences. There are two different types of leaf flushing some tree species use. One, leaves are flushed during the dry season to avoid high numbers of insect herbivores or two, leaves are flushed synchronously within one species to ensure that some leaves can escape herbivory (Coley & Barone, 1996).

Herbivory can negatively affect the growth of plants because of a trade-off between growth and defense (Fine et al., 2006; Wright et al., 2010). This trade-off can result in a difference in the specific leaf area (SLA). Fewer defense traits lead to a lower leaf dry weight and, therefore, a high SLA, indicating a fast resource acquisition for optimizing the growth (Grotkopp & Rejmánek, 2007). The *plant vigor hypothesis* states that more vigorous plants are more preferred by insect herbivores (Price, 1991). Hence, more vigorous, e.g. bigger and healthier plants, are more affected by herbivory than smaller plants. The size of a plant determines insect abundance. The bigger the plant, the more insects are present (Schlinkert et al., 2015). Additionally, neighboring plants affect herbivore pressure. Plants taller than their neighbors might suffer from higher herbivory because they are more apparent (Castagneyrol et al., 2013). Furthermore, plants with unpalatable surroundings remain undetected by insect herbivores and, therefore, escape damages caused by herbivory (Baraza et al., 2006). The relationship between herbivore pressure on a plant and its neighbors has been termed associational resistance, associational defense, associational refuge, or plant-defense guild (Tahvanainen & Root, 1972; Pfister & Hay, 1988; Holmes & Jepson-Innes, 1989). Unpalatable

neighboring plants might inhibit visual (Dulaurent et al., 2012) or olfactory (Jactel et al., 2011) detection of palatable plants. The surrounding of the enrichment planting in the Jambi province are mature oil palms. Thus, they are taller and might have protective effects on the planted trees.

My master's thesis was conducted within the framework of the subproject B11 "Biodiversity enrichment in oil palm plantations: plant succession and integration" of the Collaborative Research Centre 990 (CRC 990). The main goal of the CRC 990 is to investigate how changes in species diversity across the rainforest transformation gradient result in changes of ecological and socio-economic factors. Research focuses on consequences of lower diversity in transformed systems (jungle rubber, rubber, oil palm) and compares these systems to tropical lowland forest areas as a reference. In contrast to that, the B11 project addresses the consequences of changing diversity in the opposite direction by experimentally increasing tree species diversity in oil palm plantations. To my knowledge, enrichment planting has never been conducted in an oil palm plantation before. Enrichment plantings in oil palm plantations might increase the diversity not only at the producer level, but potentially affect all trophic levels. Increases in diversity can mitigate the negative influence of agriculture on biodiversity.

In this study, I investigated different aspects of the experimental treatment, including tree species identity, plot size, diversity level, and their effects on standing herbivory. I quantified the standing herbivory of all planted trees within the experiment. I analysed the interspecific differences between the tree species and tested whether the diversity level of trees or the plot size influence herbivory. I determined the specific leaf area (SLA) for each of the six planted tree species and the change in herbivory over a time of seven weeks. Furthermore, I tested the correlation of the standing herbivory and tree growth and the effect of herbivory on tree survival.

I specifically tested the following hypotheses: 1) specific leaf area (SLA) differs among the tree species; 2) all tree species are affected by herbivory at all times; 3) herbivory differs among the tree species; 4) plot size has a positive effect on herbivory; 5) the tree diversity level has a negative effect on herbivory; 6) herbivory negatively affects the growth of a tree species; 7) tree survival is negatively influenced by herbivory.

Methods

Study Site and Experimental Design

The study was carried out within the framework of an enrichment planting experiment in an oil palm plantation owned by PT HumusIndo near Bungku in the Jambi province of Sumatra, Indonesia (01.95 ° S and 103.25 ° E, 47±11 m a.s.l.). The climate is characterized as humid tropical with a mean temperature of 26.7 ±1.0 °C. The annual rainfall amounts to 2235 ±385 mm (measured at Jambi Sultan Thaha airport; 1991-2011). The field work was conducted from May until July 2015.

In December 2013, 56 plots were established by planting tree islands according to the random partitions design by Bell et al. (2009). Across experimental plots, plot size (5x5 m, 10x10 m, 20x20 m and 40x40 m) as well as diversity (levels of 0, 1, 2, 3 and 6 tree species) and composition of six native tree species were systematically varied (Tab. 1; Tab. 2). Additionally, there are four control plots without any experimental treatment and management-as-usual.

Table 1: Planted multi-purpose tree species within the oil palm plantation of PT HumusIndo. Three tree species are mainly fruit trees (*P. speciosa*, *A. pauciflorum*, *D. zibethinus*). *D. polyphylla* produces natural latex. *P. canescens* and *S. leprosula* are used mainly for timber. These multi-purpose tree species are all of economic value and are native to the region.

Species	Family	Common Name	Key
Parkia speciosa	Fabaceae	"Petai"	A
Archidendron pauciflorum	Fabaceae	"Jengkol"	B
Durio zibethinus	Malvaceae	"Durian"	C
Dyera polyphylla	Apocynaceae	"Jelutung"	D
Peronema canescens	Verbenaceae	"Sungkai"	E
Shorea leprosula	Dipterocarpaceae	"Meranti tembaga"	F

A total of 6354 trees were planted. In order to increase light availability, 40 % of the oil palms were cut prior to planting. Dead trees were replaced during the first year after planting. Furthermore, height and diameter of each individual tree are measured every three months.

Table 2: Experimental design within the oil palm plantation of PT HumusIndo. Numbers of plots for every plot size and diversity level are shown without control plots for every plot size.

Diversity Level/ Plot Size	0 Species	1 Species	2 Species	3 Species	6 Species	Total
5x5 m	1	6	3	2	1	13
10x10 m	1	6	3	2	1	13
20x20 m	1	6	3	2	1	13
40x40 m	1	6	3	2	1	13
Total	**4**	**24**	**12**	**8**	**4**	**52**

Damage Classes

Damage classes in relation to the occurring herbivory were established to quantify the leaf damage caused by insect herbivores. I sampled ten randomly selected sun leaves per tree species on every 40x40 m single species plot on 16 and 17 May 2015. In total, I harvested 60 fully developed sun leaves. A leaf was considered as fully developed if it was completely spread and reached the full green color. I estimated the percentage of eaten leaf area (ELA) of the total leaf area (TLA). Afterwards, all leaves (without petiole) were scanned using a flatbed scanner (HP Scanjet G4050). Images were scanned with 200 dpi in black and white and saved as .jpg files. According to the calibration square within the scans, 78 pixels of the scan account for 1 cm of the real leaf. The scans were then used to determine the remaining leaf area (cm²) (RLA) and the TLA (cm²) using Photoshop CS4 (Version 11.0.2). With these measurements, the ELA (cm²) [1] and the proportion of ELA [2] which corresponds to the herbivory were calculated:

[1] $ELA = TLA - RLA$

[2] $Herbivory = \frac{ELA}{TLA}$

For validation, calculated percentages of herbivory were compared to the estimated values. The measured percentages of herbivory were used to establish a damage class scale. For the tree species *Archidendron pauciflorum*, I found many pinnae and even leaves missing and, therefore, I decided to assume a missing leaf as highest damage class. This assumption was used for the other trees as well. After scanning the leaves, they were conserved in herbar presses and stored in a wooden drying chamber at a temperature of 40 °C for four weeks.

Specific Leaf Area (SLA)

To calculate the specific leaf area (cm²/g) (SLA), I used the 60 leaves and their scanned images which I had used to establish the damage classes. In these cases, the RLA corresponds to the leaf area that is needed for calculating the SLA using the following formula.

[3] $$SLA = \frac{RLA}{Dry\,Weight}$$

After four weeks in a wooden drying chamber at 40 °C, all leaves were stored for one night in a drying chamber at 70 °C and their dry weight was determined the next day using an Acculab ALC-3100.2 scale (Sartorius group, ±0.01 g). The ratio of the measured RLA and the weight results in the SLA [3]. The average SLA for all ten leaves of one tree species was calculated and tested for differences between species using a pairwise Wilcoxon Rank Sum Test.

Minimum Leaf Number

For a reliable quantification of herbivory, it is important to investigate a sufficient number of leaves. On 16 and 17 May 2015, I estimated the percentage of ELA for 30 leaves of one tree individual per tree species except for *P. canescens*. For *P. canescens*, many trees showed a lower leaf number. Hence, I investigated all leaves of one tree (12 leaves). The leaves of *A. pauciflorum*

and *P. canescens* had to be treated differently because their leaves are pinnate leaves. The percentages of ELA for every pinna of *A. pauciflorum* were estimated, while for *P. canescens* only all pinnae on the left side of the leaf (when looking from the front) as well as the middle rip were included in the estimations (Fig. 1). The percentages of herbivory were estimated for each leaf and for further analyses, as well as for comparison reasons, translated first into the established damage class and then into the associated average percentage per class (Tab. 3).
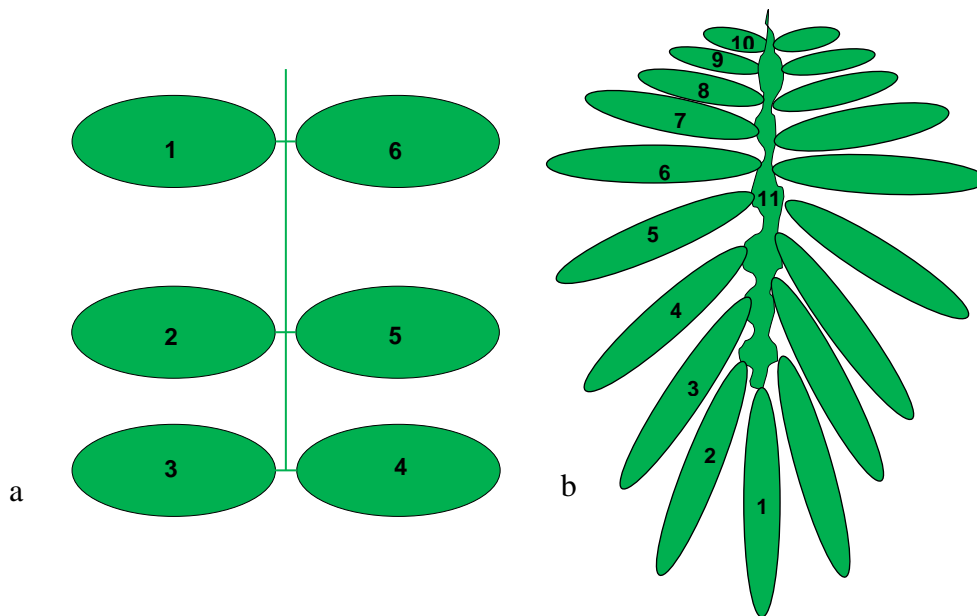
Figure 1: Schematic representation of leaves from a) *A. pauciflorum* **and b)** *P. canescens*. **Pinnae, which were included into the study, are marked with numbers. Numbers indicate the order of the estimation.**

The average percentage per class was used to calculate the mean average damage to get the damage caused by herbivory of one leaf. The change of percentage for every additional leaf was calculated which was necessary to determine the minimum leaf number to be investigated in this study.

Change in Herbivory Rate

The change in herbivory rate shows the amount of ELA in a certain time frame. I marked the third fully developed leaf for *P. speciosa*, *A. pauciflorum* and *P. canescens,* as well as the third fully developed branch for *D. zibethinus* and *S. leprosula*. I chose to investigate whole trees of *D. polyphylla* since the trees were of a small size. All marked trees were located in the single species 40x40 m plots. I estimated the damage classes (Tab. 3) for all leaves that were included in the markings starting from the top. I estimated the damage class for each pinna of *A. pauciflorum* and *P. canescens* in the exact order shown in Figure 1 and in the case of *D. polyphylla*, I estimated the herbivory clockwise. This treatment was necessary to be able to compare the same leaves from week to week. In addition, all leaves and branches were photographed using a Canon PowerShot A2500. This method was repeated once a week for seven weeks starting on 18 May 2015 and ending on 01 July 2015. The average percentage for each damage class (Tab. 3) of all leaves was used to calculate the average damage in order to receive one value per tree. The values of one tree species were again averaged and plotted against the time. Leaves which developed completely during the period I investigated the change in herbivory rate were excluded from this experiment. Thus, a change in average damage was ensured to be caused by herbivory and not by a change of leaf numbers.

Standing Herbivory

The standing herbivory, mainly caused by chewing, was determined for all planted tree species starting on 21 May 2015 and finishing on 22 June 2015. After establishing a damage class scale (Tab. 3), I determined the damage class for herbivory of the first ten fully developed leaves, starting from the top, once for every planted tree. Young leaves usually have high water contents (Townsend et al., 2008). Thus, those leaves are easier to be digested by herbivores. Furthermore, young plant tissues have the highest concentrations of nitrogen (Mattson, 1980) which is a limiting nutrient needed by herbivores. To avoid this bias, I chose to investigate the first fully developed leaves. Again, a leaf was considered as fully developed if it was completely spread and

reached the full green color. The standing herbivory was assessed by one person, except for the standing herbivory of *P. canescens.* The standing herbivory was assessed by two persons because the trees were of a tall size. The leaves of *A. pauciflorum* and *P. canescens* had again to be treated differently because of their pinnate leaves (Fig. 1). I assessed the damage class for every pinna and translated it afterwards into the average percentage. These values were then averaged in order to obtain one value per leaf. The average for all investigated leaves of one tree species was calculated to get the average damage for the whole tree. Conspicuous tree characteristics (broken trunks, located beneath oil palm), which might influence the performance of a tree, were noted. The data on average percentage of damage were statistically tested to see if there are differences among the tree species and to determine if the plot size or the diversity level have an influence on the standing herbivory. Furthermore, I tested if there was a correlation between herbivory and the growth performance of trees using the data on standing herbivory and the data on tree height and diameter. I calculated the absolute growth (cm) (H_a; D_a) [4] and relative growth (%) (H_r; D_r) [5] of the planted trees using the starting values for height (H_0) and diameter (D_0) during the establishment of the B11 experiment and the measurements obtained in January 2015 (H_2; D_2).

[4] $H_a = H_2 - H_0$ $\qquad\qquad\qquad$ $D_a = D_2 - D_0$

[5] $H_r = \frac{H_2 - H_0}{H_0}$ $\qquad\qquad$ $D_r = \frac{D_2 - D_0}{D_0}$

The growth data of January 2015 were used because the next measurement was conducted during my fieldwork. In addition to the correlation analysis of growth parameters and herbivory, I correlated the average percentage of damage for herbivory with observations of dead trees after my investigation within the time frame from July to September to see if the survival of a tree was linked to the herbivory it faced.

Data Analysis

I omitted all dead trees and all tress with none or not yet fully developed leaves from the dataset. So I only used trees with average damage for the data analysis. In order to test for differences in the SLA, I performed a pairwise Wilcoxon Rank Sum Test since the data were not normally distributed ($p < 0.01$; Shapiro-Wilk Normality Test). For the standing herbivory, my sample size exceeded the maximum number of observations allowed for the Shapiro-Wilk Normality Test. Thus, I performed a Kolmogorov-Smirnov Test to test for normality ($p < 0.01$) and therefore, a normal distribution did not apply for the average damages. The average damages per tree species, as well as per plot size or per diversity level were compared using pairwise Wilcoxon Rank Sum Tests. The stepwise linear regression approach by Bell et al. (2009) was used to determine the effect of plot size and tree diversity on the average damage caused by herbivory. In a first step, the linear effect of plot size or diversity level on the average damage was tested. In a second step, the residuals of the first model were modelled against the individual plot sizes and tree species to investigate the identity effects of each plot size and tree species on the average damage. Additionally, it was tested if there was an interaction of plot size and diversity level. Furthermore, I performed correlation analyses between growth data (height and diameter measurements) and the average damage for each tree individual. I used both absolute and relative growth data. During the months of July, August and September 2015, many trees died as a result of a dry period. I tested whether the tree mortality could be explained by a high average damage before the drought event or if the chance of survival was not correlated with the herbivory a tree faced within the enrichment planting experiment. Thus, I used the Wilcoxon Rank Sum Test. Graphics were produced using the "hexbin" package (Carr et al., 2015). All statistical analyses were conducted with R 3.1.3 (R Core Team, 2015).

Results

Overall, I quantified standing herbivory of 5758 tree individuals with a total of 54849 leaves of the six study species. The average damage of leaves amounted to 18.28 % caused by insect herbivores.

Damage Classes

The damage classes were used to simplify and enhance the fieldwork. For further analyses, the damage classes were translated into the associated average percentage per class (Tab. 3).

Table 3: Damage classes with the associated percentages of eaten leaf area (ELA) caused by herbivory. The mean percentage per damage classes was calculated and used for statistical analyses.

Damage Class	1	2	3	4	5	6
Percentage	0-<1 %	1-5 %	6-15 %	16-50 %	51-90 %	91-100 % Missing leaves
Mean Percentage of Damage Class	0.5 %	3 %	10.5 %	33 %	70.5 %	95.5 %

Specific Leaf Area (SLA)

The average SLA ranged between 118.46 cm²/g (*A. pauciflorum*) and 192.61 cm²/g (*P. canescens*) (Fig. 2). Between these two tree species, I found significant differences between the SLA (p=0.0073). The SLA of *P. speciosa*, *D. zibethinus*, *D. polyphylla* and *S. leprosula* did not

significantly differ from each other or showed differences with the SLA of *A. pauciflorum* and *P. canescens*. The variations among the ten calculated SLAs of *P. speciosa* and *P. canescens* were higher than the variations among the ten calculated SLAs of *A. pauciflorum* and *S. leprosula*. Nevertheless, there were outliers for these species.
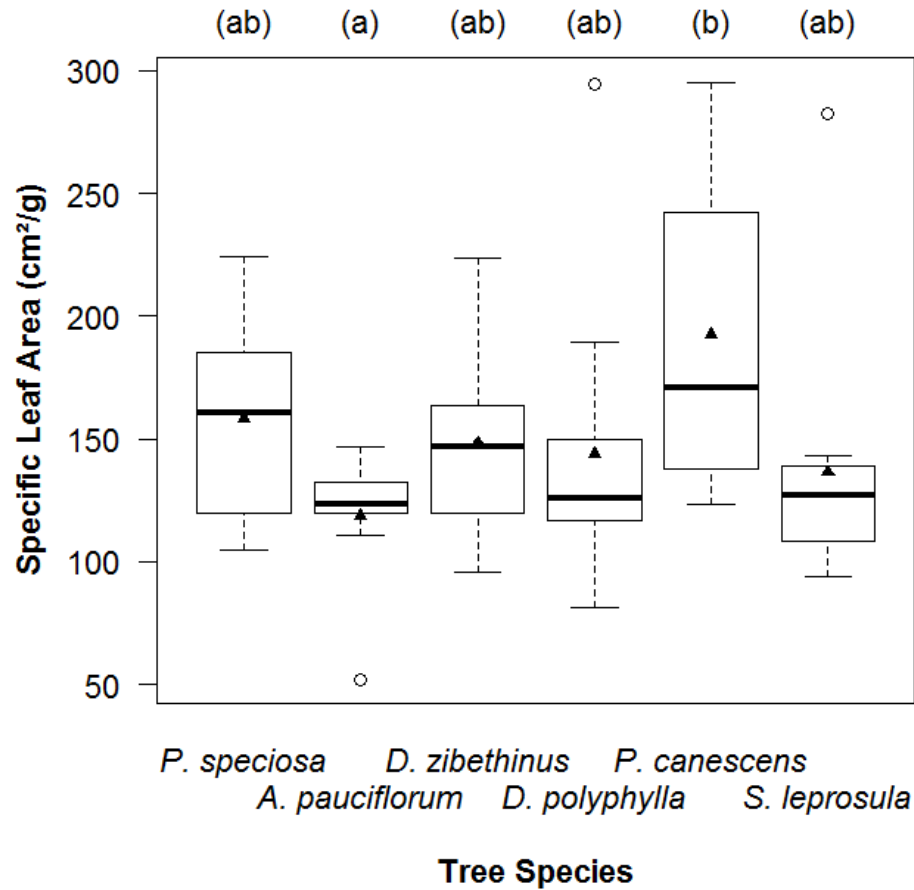
Figure 2: Specific leaf area (SLA) for each tree species. The leaf area and dry weight of ten leaves per species were measured and the SLA was calculated by dividing the leaf area by the dry weight. The mean SLA is indicated by the triangle.

Minimum Leaf Number

The average damage with every additional leaf was calculated (Fig. 3). The average damage for the individual of *P. speciosa* increased with increasing leaf number. In the beginning, the damage amounted to 0.5 % and rose up to a mean of 10.1 % by 30 leaves. With leaf 12, the damage increased strongly from 2.5 % to 8.2 %. *A. pauciflorum* started with an average damage of 80.1 % which decreased with an increasing number of leaves to 69.4 %. The first leaf of *D. polyphylla* showed an average damage of 0.5 %. The maximum average damage was reached with 2.4 % after the fourth leaf. With 30 leaves, the average damage amounted to 1.2 % which is only a small change in contrast to the other species. In the case of *D. polyphylla*, the percentage of ELA amounted to 0.5 % for the first leaf. The average damage did not change strongly with increasing leaf number until leaf 18 (2.7 %). With leaf 30, an average damage of 2.2 % was reached. The investigated tree individual of *P. canescens* had only 12 leaves attached. Hence, it was only possible to examine the average damage for 12 leaves. The first leaf showed an average damage caused by herbivores of 1.1 % which doubled to 2.4 % after leaf 12. The biggest difference in average damages with increasing leaf number could be seen for the tree individual of *S. leprosula*. The average damage stayed constant with 0.5 % for four leaves. After leaf 5, the average damage amounted to 2.5 % and reached the maximum after eight leaves with 11.1 %. With increasing leaf number, the average damage varied between 8.5 % and 10.5 %. The mean damage of all 30 leaves that I examined amounted to 8.6 %.
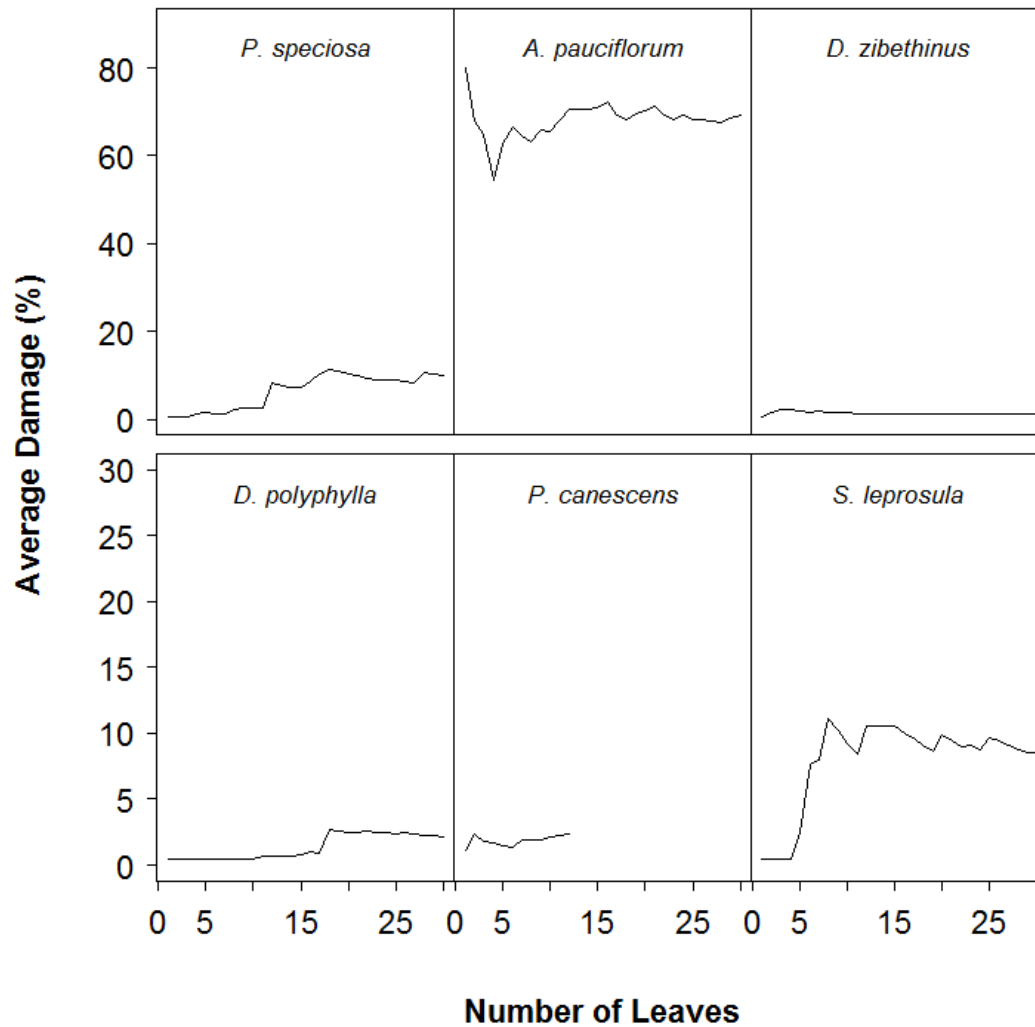
Figure 3: The change of average damage with increasing leaf number for each tree species. The cumulative mean of average damage was calculated. For all tree species, 30 leaves were examined, except for *P. canescens*. For *P. canescens*, only 12 leaves could be examined.

## Change in Herbivory Rate

There were increases in average damage for all species recognizable. Additionally, new leaves have developed over time (Fig. 4 C and Fig. 5 F). Those leaves were excluded from the estimations. In week 3, the first pinna of *P. canescens* (Fig. 5 E) started to roll because of ants. After two weeks (week 5) the pinna dried out and in week 7 and the pinna was lost. Due to the

repeated investigation, I knew the reason for the loss of the first pinna and, therefore, it was not considered as herbivory.
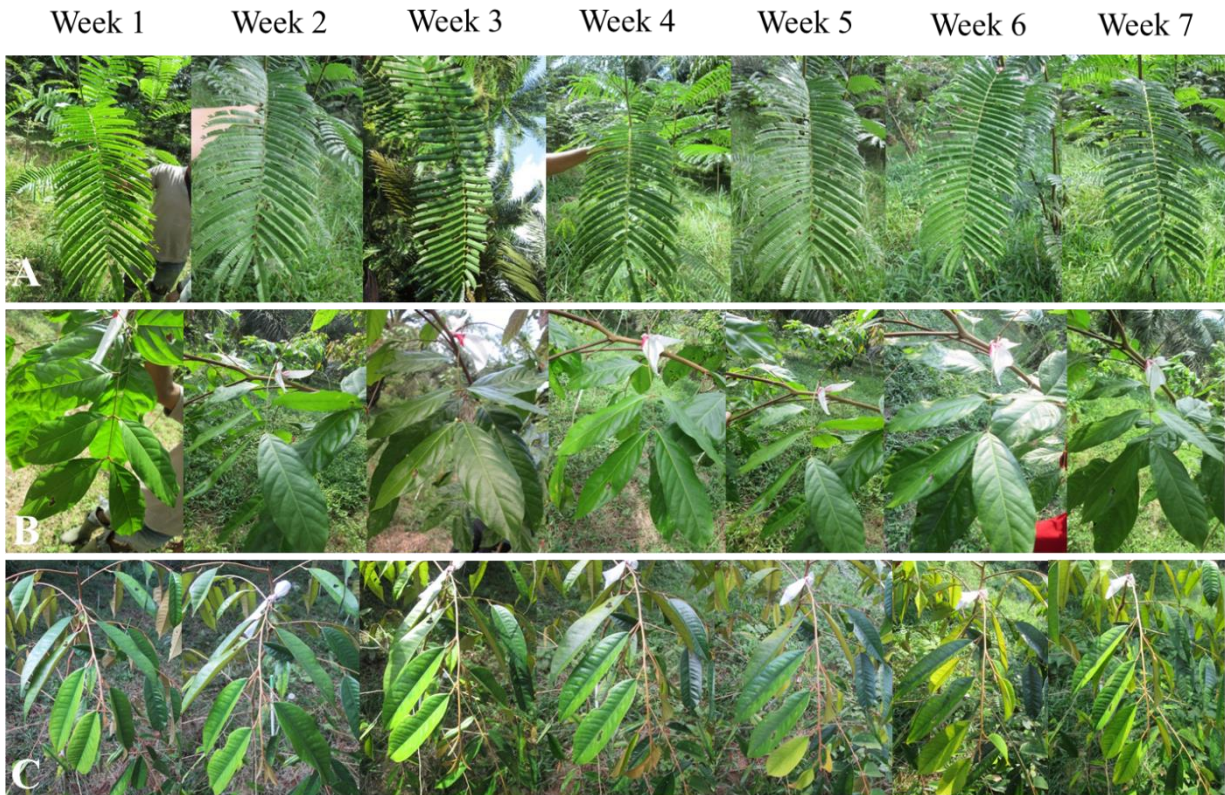
Figure 4: Time series for one individual of *P. speciosa* (A), *A. pauciflorum* (B) and *D. zibethinus* (C). Starting from the top, the third leaf of randomly chosen individuals of *P. speciosa* (A) and *A. pauciflorum* (B) were examined on damages caused by herbivory once a week for seven weeks. The leaf of *A. pauciflorum* was examined as described with Figure 1. In addition, all leaves from the third branch starting from the top of individuals of *D. zibethinus* (C) were examined for herbivory for seven weeks.
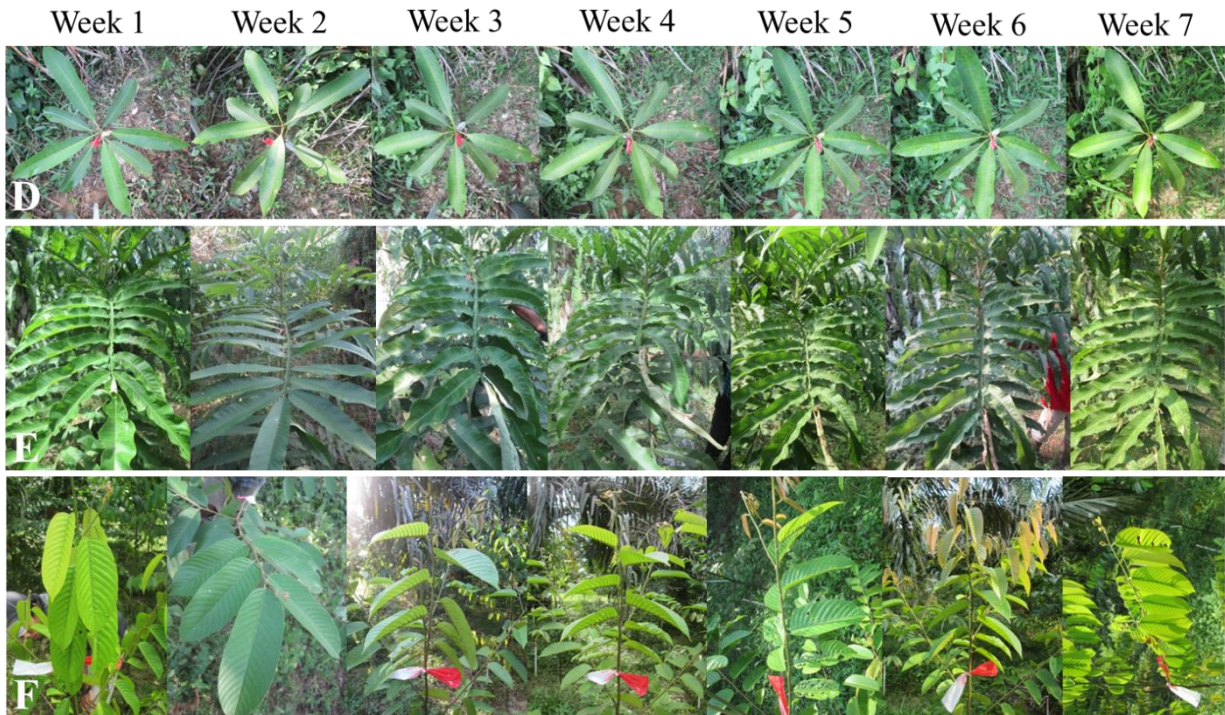
Figure 5: Time series for one individual of *D. polyphylla* (D), *P. canescens* (E) and *S. leprosula* (F). Because of the small size, all leaves of the whole individual of *D. polyphylla* (D) were examined for herbivory starting from the top and examining clockwise downwards. Starting from the top, the third leaf of randomly chosen individuals of *P. canescens* (E) was examined for damages caused by herbivory once a week for seven weeks as described with Figure 1. In addition, all leaves from the third branch starting from the top of individuals of *S. leprosula* were examined for herbivory for seven weeks.

In addition to the time series, I wanted to test the differences over time of the individuals of one species altogether (Fig. 6). Every tree species showed a higher average damage in week 7 compared to week 1. Hence, all species appeared to face herbivory. The difference of average damage varied between 11.62 % (*D. polyphylla*) and 1.25 % (*A. pauciflorum*). Although *A. pauciflorum* showed the smallest difference between the starting and the ending of the experiment, the average damage amounted to almost 50 %. The average damages of the other species ranged between 5 % and 15 % (Fig. 6).
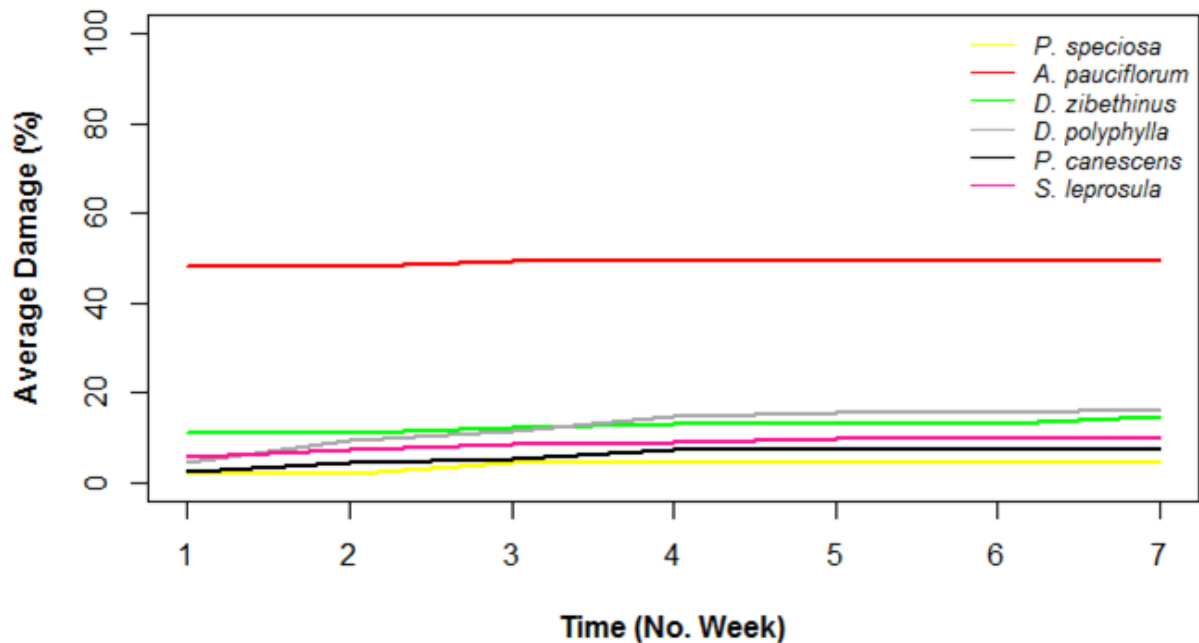
Figure 6: The change of herbivory over seven weeks of each tree species. The average damage determined for all three individuals of *P. speciosa* (yellow), *A. pauciflorum* (red), *D. zibethinus* (green), *D. polyphylla* (grey), *P. canescens* (black) and *S. leprosula* (pink) was averaged for one week and plotted against a total time of seven weeks.

Standing Herbivory

For the quantification of standing herbivory, I examined the total amount of trees (N=6354). Of these trees, 596 individuals were either dead or had no (fully developed) leaves to investigate. The average damage per species ranged between 5.06 % (*S. leprosula*) and 43.97 % (*A. pauciflorum*) (Fig. 7). All tree species showed significant differences in terms of their average damage caused by herbivory (p<0.01), except for the tree species *D. polyphylla* and *P. canescens*. The average damage of *D. polyphylla* amounted to 8.94 % and 6.89 % for *P. canescens*. The mean standing herbivory of both species did not significantly differ (p=0.25) (Fig. 7).
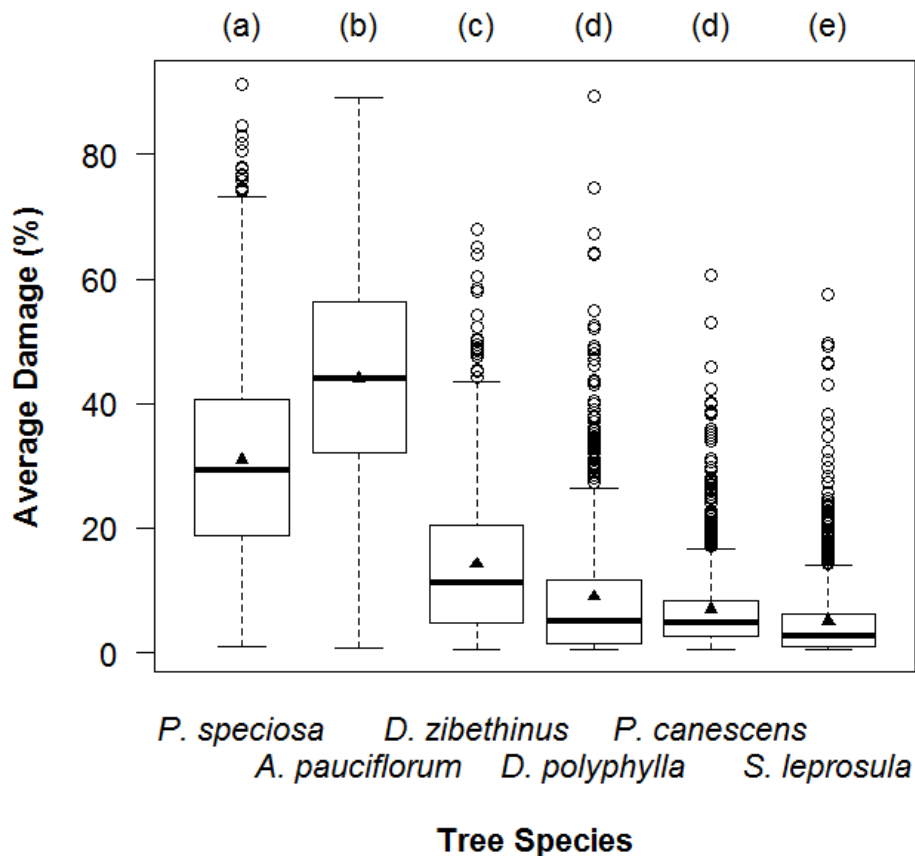
Figure 7: The average damage caused by insect herbivores for each tree species. Due to the survival and development of leaves, the number of tree individuals per tree species differed for this study. The foliar average damage for 965 individuals of *P. speciosa* and for 968 individuals of *A. pauciflorum* was calculated. 899 individuals of *D. zibethinus* and 910 individuals of *D. polyphylla* were also examined. The most trees were used for the average damage of *P. canescens* (N=1032). 984 individuals of *S. leprosula* were alive and developed leaves which were examined. The mean is indicated by the triangle.

The test for differences of leaf average damage caused by herbivory among the four different plot sizes showed that the average damage did not differ significantly between plot sizes (p>0.05) (Fig. 8). The mean average damage ranged between 16.11 % (20x20 m) and 18.95 % (40x40 m). With 16.05 % average damage, the trees within the 5x5 m plots showed almost the same herbivory as the trees within the 20x20 m plots.
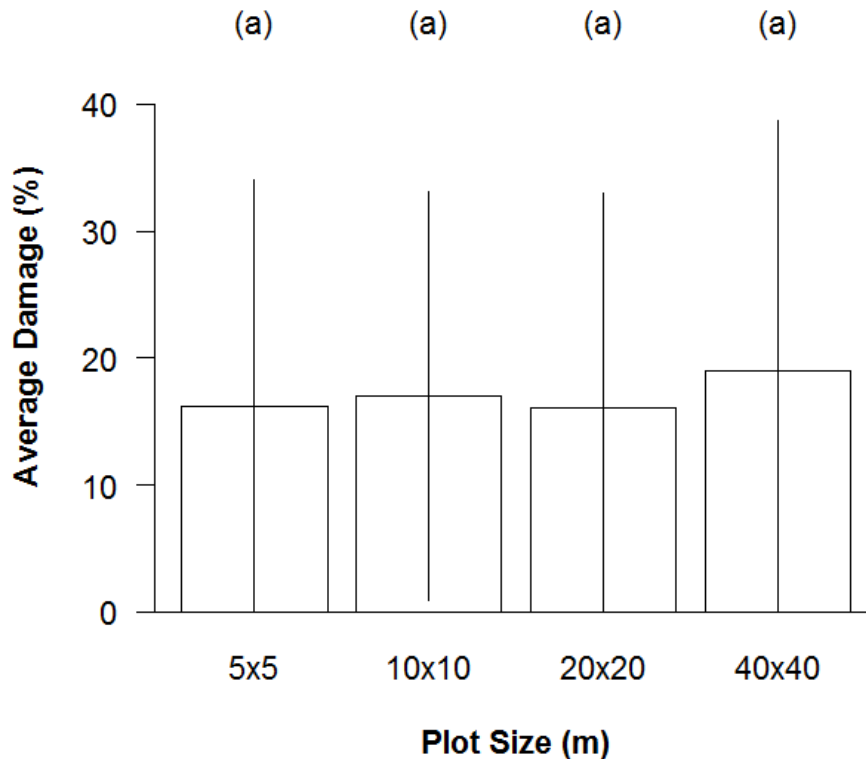
Figure 8: The average damage caused by insect herbivores for every plot size. The average damage of all living trees with leaves was calculated and averaged for all four plot sizes. Error bars give the standard deviation.

The average damage of leaves per plot size was shown for each tree species (Fig. 9). *P. speciosa* and *A. pauciflorum* had the highest average damage whereas *S. leprosula* had the lowest average damage. The mean average damage of *P. speciosa* ranged between 18.24 % (20x20 m) and 34.47 % (40x40 m). The plots with a size of 10x10 m, 20x20 m and 40x40 m showed significant differences among the occurring average damage (p<0.05). The 5x5 m plots did not differ in their average damage compared to the other plot sizes. For *A. pauciflorum*, the average damage of was slightly higher than for *P. speciosa* and varied from 27.86 % (5x5 m) to 46.12 % (40x40 m). The average damage increased with increasing plot size. The difference in average damage between the 5x5 m and 10x10 m plots was not significant because the means only differed by 0.08 %. The other plot sizes differed significantly from each other as well as from these two plot sizes (p<0.05). *D. zibethinus* faced less herbivory than *P. speciosa* or *A.*

pauciflorum. The mean average damage per plot of *D. zibethinus* ranged between 11.8 % in the 10x10 m plots and 17.32 % in the 20x20 m plots. The average damages differed significantly among 20x20 m and 10x10 m (p<0.05) or 40x40 m (p<0.01). 910 individuals of *D. polyphylla* showed a mean average damage caused by herbivory between 7.11 % (20x20 m) and 11.93 % (5x5 m). There was no significant difference between the varying plot sizes. The average damage of *P. canescens* was comparable to the average damage of *D. polyphylla* and ranged between 5.07 % (5x5 m) and 14.98 % (10x10 m). The mean of the 10x10 m plots with 14.98 % was significantly higher than the means of the other plot sizes (p<0.01). *S. leprosula* showed the lowest average damage separated by the plot sizes. The plots with a size of 20x20 m had a mean of 4.86 % and the highest mean occurred in the 5x5 m plots with 8.16 %. Still, there was a significant difference between the average damage which occurs in the 10x10 m and 40x40 m plots.
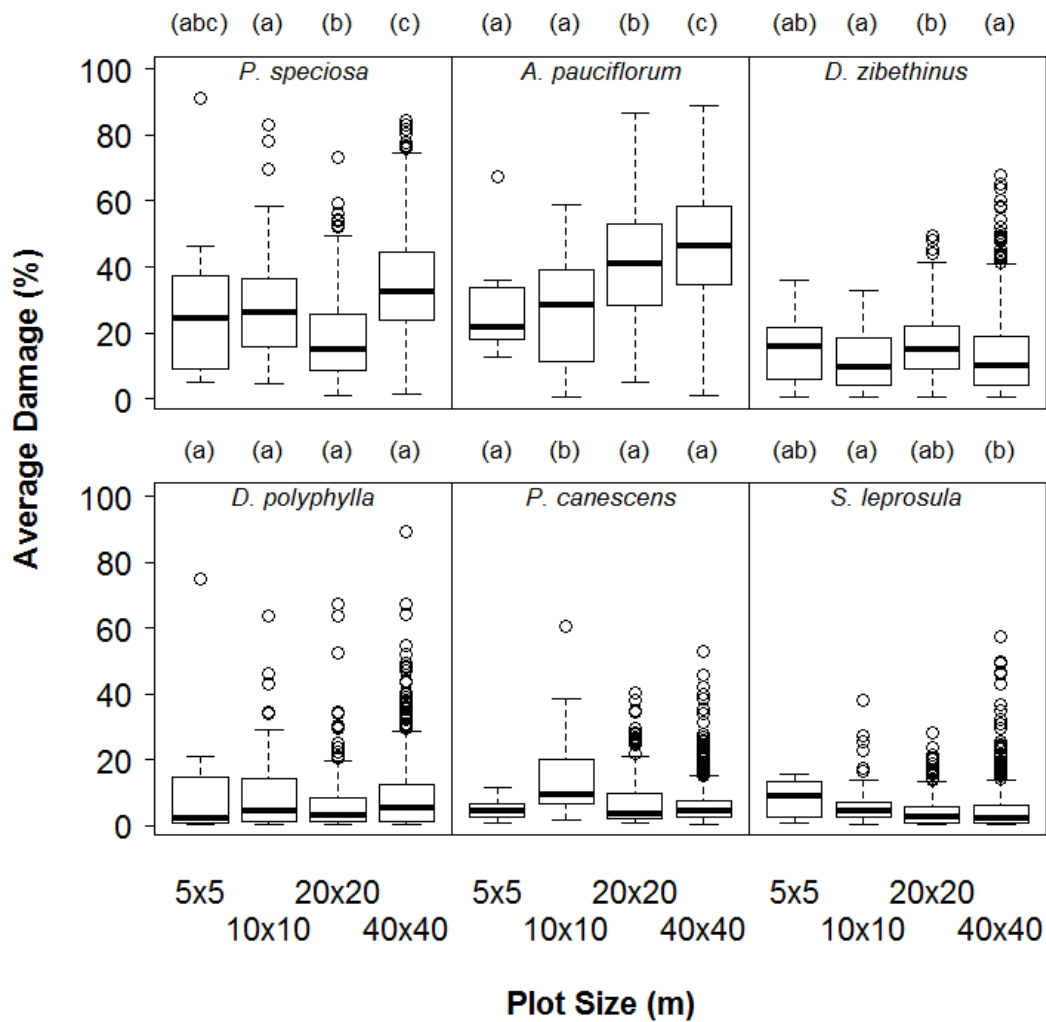
Figure 9: The average damage caused by insect herbivores for every plot size per tree species.

The average damages of single species plots and plots with a combination of two species differed significantly (p<0.05), whereas plots with three tree species showed no significant differences with lower diversity levels (Fig. 10). The lowest average damage was found in plots with all six native tree species. The average damage for the highest diversity level differed significantly from the other average damages (p<0.01).
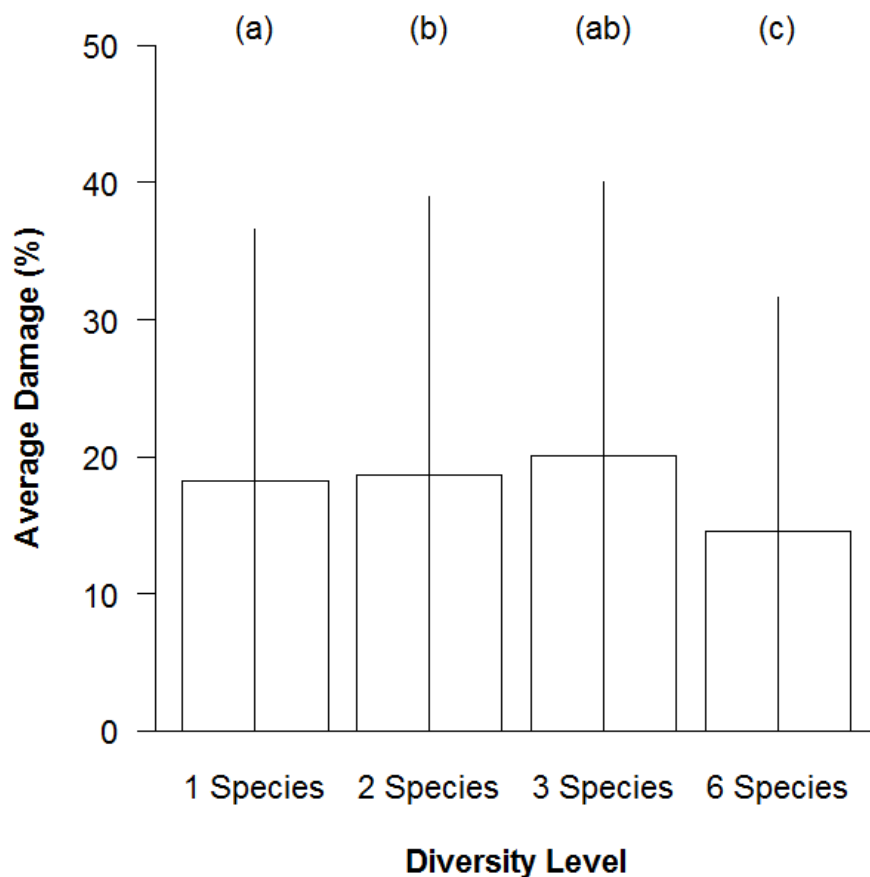
Figure 10: The average damage caused by insect herbivores for every diversity level. The average damage of all living trees with leaves was calculated and averaged for all four diversity levels. Error bars give the standard deviation.

Differences among the tree species according to the diversity level were also tested. The mean average damage of *P. speciosa* differed significantly for each diversity level (p<0.01). *P. speciosa* showed the lowest average damage for the individuals growing with the highest diversity level. The mean average damage in plots with six species amounted to 18.8 %. In contrast to that, the average damage increased with increasing diversity level from one to three species. The mean ranged between 29.2 % and 39.8 %. The mean average damage of *A. pauciflorum* was higher compared to the other species and ranged between 41.4 % (three species) and 46.6 % (two species). The difference between these diversity levels was significant with a p-value of 0.019. The average damage of *D. zibethinus* differed between the diversity levels and showed significant smaller damages in plots where all species were included (p<0.05). In plots

with all species, *D. zibethinus* showed a mean average damage of 9.9 %. The highest mean with 15 % was found in plots with only two species. Trees of the species *D. polyphylla* had a lower average damage than *P. speciosa*, *A. pauciflorum* and *D. zibethinus*. The mean average damage for the diversity levels with two and three species amounted to 8 % and, therefore, the diversity levels did not differ. The lowest average damage of *D. polyphylla* occurred for the highest diversity level with all six species with a mean of 3.1 %. The highest average damage occurs in plots with only conspecifics with a mean of 10.6 %. These means differed significantly ($p<0.01$). For *P. canescens*, the mean average damages of single species plots (6.1 %) and of plots with two species (6.4 %) did not differ significantly. However, these means differed significantly from plots with a higher diversity level ($p<0.05$). Still, mean average damages of plots with three species (9.8 %) and of plots with all six species (7.6 %) showed no differences. Compared to all study tree species, *S. leprosula* had the lowest average damage caused by herbivory. The means ranged between 4.1 % for a combination of *S. leprosula* with one other species and 7.4 % for a diversity level of three species. A significant difference could be seen for the mean average damage of single species plots with plots with two and six species ($p<0.05$).
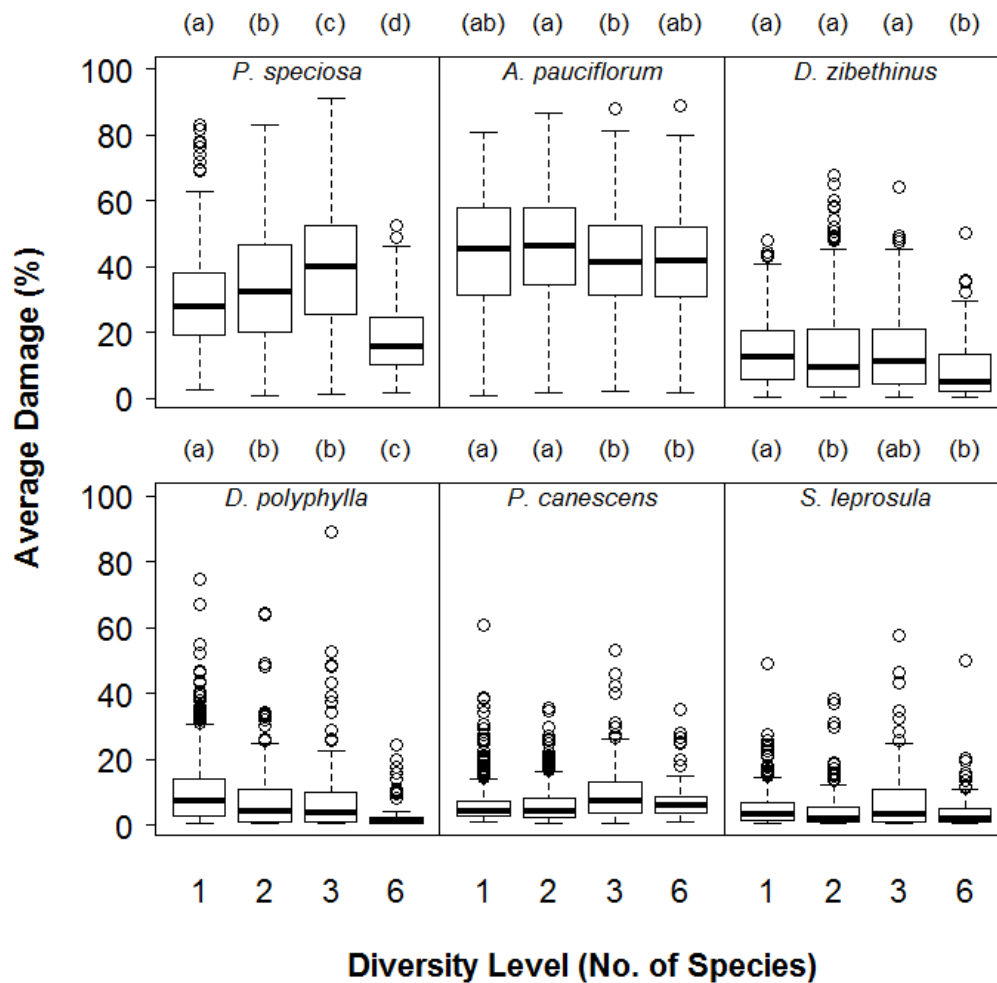
Figure 11: The average damage caused by insect herbivores for every diversity level per tree species.

Furthermore, I tested the influence of plot size and diversity level on the average damage with the stepwise linear regression model approach after Bell et al. (2009). The plot sizes did not show a linear effect and, therefore, the average damage did not increase with increasing plot size (Tab. 4). By including the different plot size identities, differences among them could not be found. The diversity levels did not show a linear effect on the occurring average damage. However, the average damage differed among tree species identities (Tab. 4). The interaction between plot size and diversity level revealed no effect. Overall, the occurring average damage caused by herbivory could mostly be explained by the tree species identity and not by the experimental treatment.

Table 4: ANOVA table of the linear models testing for the effect of plot size and tree diversity on the average damage. For modelling, the stepwise linear regression approach by Bell et al. (2009) was used to disentangle the effects of linear and identity effects of plot size and tree diversity on the average damage. Sum of Squares (SS) are shown for linear effects (LR) and identity effects (I). Levels of significance are given with 0 '*' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.**

Explanatory Variables	Sum of Squares		Mean Sq	F value	Pr (>F)	
Plot Size	SS_{LR}	36.5	36.5	0.310	0.580	
Plot Size 5x5 m	SS_I	0.8	0.8	0.007	0.935	
Plot Size 10x10 m	SS_I	1.3	1.3	0.012	0.915	
Plot Size 20x20 m	SS_I	24.8	24.8	0.212	0.647	
Plot Size 40x40 m	SS_I	8.6	8.6	0.074	0.787	
Diversity Level	SS_{LR}	8.2	8.2	0.070	0.793	
P. speciosa	SS_I	265.9	265.9	5.689	0.022	*
A. pauciflorum	SS_I	671.5	671.5	14.368	0.0005	***
D. zibethinus	SS_I	559.6	559.6	11.972	0.001	**
D. polyphylla	SS_I	450.2	450.2	9.633	0.003	**
P. canescens	SS_I	537.1	537.1	11.492	0.001	**
S. leprosula	SS_I	723.1	723.1	15.471	0.0003	***
Plot Size : Diversity Level		60.7	60.7	0.516	0.476	

In total, the growth data of 5345 tree individuals were used for the correlation analyses between average damage and the absolute height or the absolute diameter (Fig. 12). Most trees (N=5209) had a height ranging between 0 cm and 300 cm. Only 136 trees had reached a height of over 300 cm. 3546 trees had an average damage between 0 % and 20 %. The biggest diameter measured amounted to over 6 cm. Nevertheless, 4928 trees had a diameter smaller than 3 cm. The correlation analysis between both variables average damage and absolute height showed a correlation coefficient of 0.012 and, therefore, average damage was not correlated with the absolute height of a tree. The correlation coefficient for the relation between average damage and absolute diameter was slightly negative and amounted to -0.137.
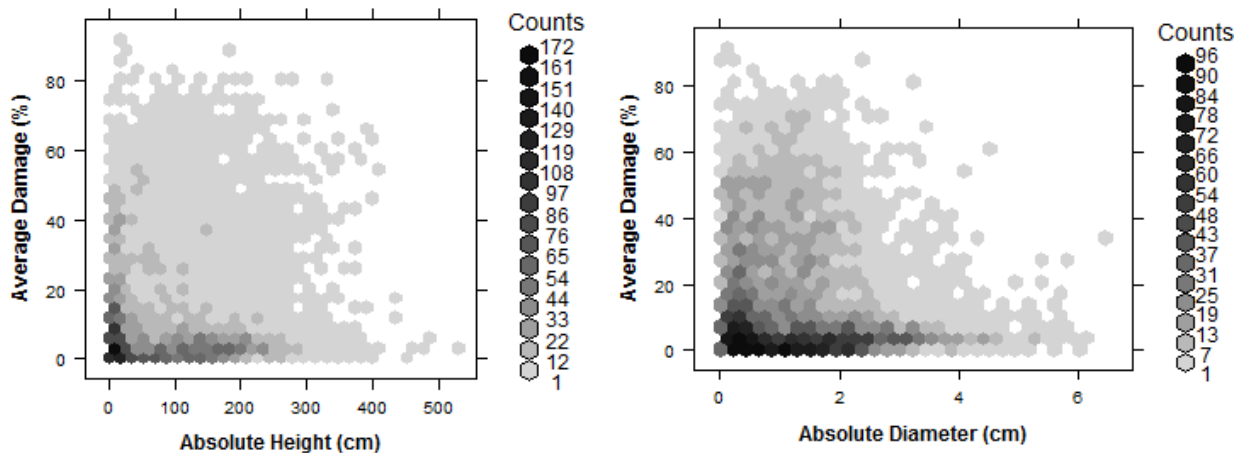
Figure 12: Hexagonally binned average damage in correlation with the absolute height (left panel) and with the absolute diameter (right panel). The average damages of all 5345 examined trees were compared with the absolute growth in height and the absolute growth in diameter from the starting of the experiment until January 2015.

The average damage per relative growth variable showed that in general, tree individuals increased their height about 10 % (N=5291) (Fig. 13). One individual grew over 20 % whereas two individuals reached an increase in height of more than 30 %. The relative diameter could be increased by up to 18 %. Still, 4525 trees grew between 0 % and 5 % in diameter. The correlation analysis for both variables relative height and average damage resulted in a correlation coefficient of 0.06. Hence, there was no correlation between the occurring herbivory and the relative height (p<0.01): The herbivory was also not correlated with relative diameter. The correlation coefficient amounted to -0.04.
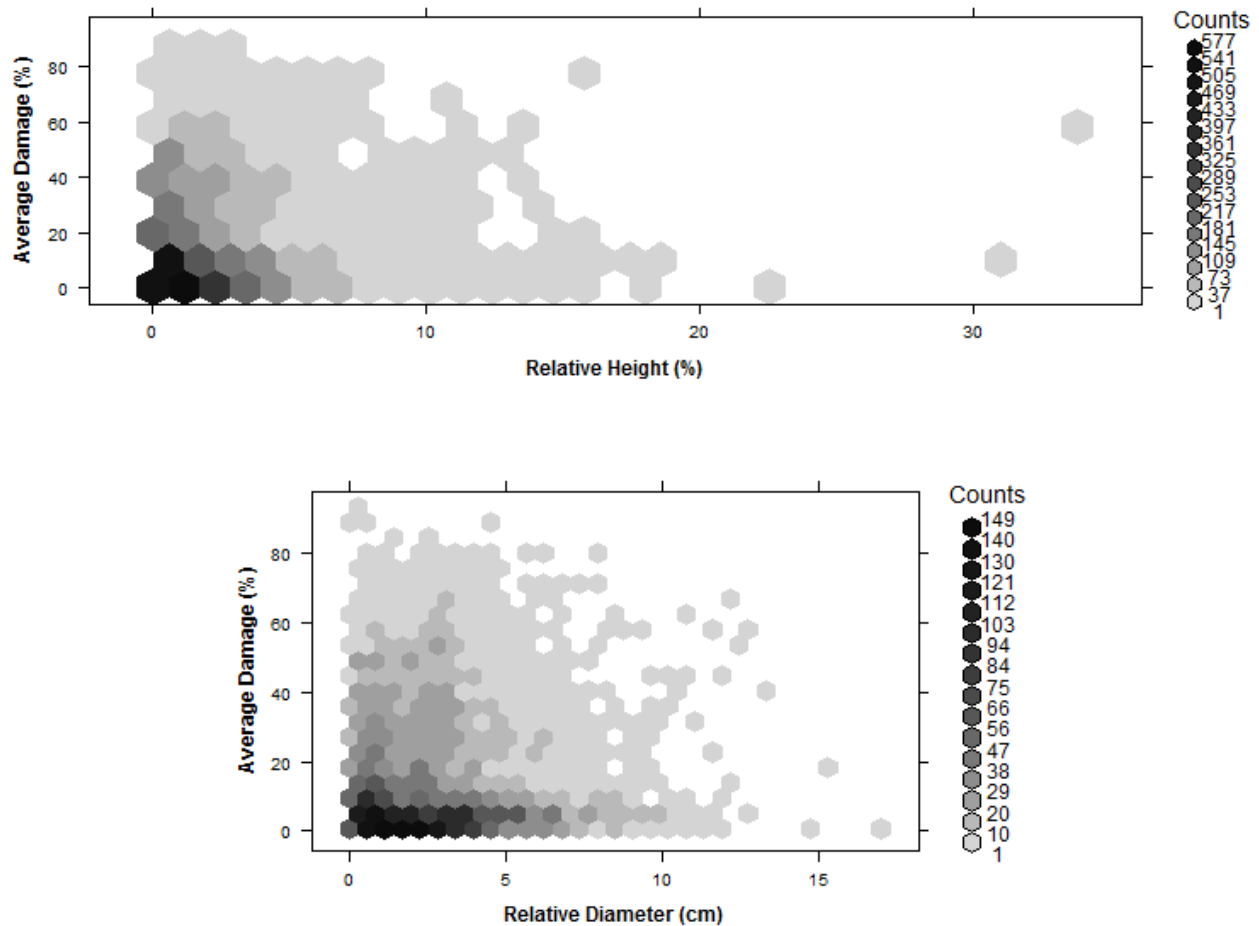
Figure 13: Hexagonally binned average damage in correlation with the relative height (upper panel) and with the relative diameter (lower panel). The average damages of all 5345 examined trees were compared with the relative growth in height and the relative growth in diameter from the starting of the experiment until January 2015.

For the time after the end of my quantification of standing herbivory (July) until September 2015, the Jambi province suffered a strong drought and many trees died. I tested if there is a relation between the average damage and the probability to survive stressful conditions. Within the three months, 564 trees died and 5194 trees survived. Differences between the average damage of alive and dead trees were significant (p<0.01) (Fig. 14). The mean for living trees resulted in an average damage of 18.9 % and for dead trees in 12.7 %. The highest average damages estimated was 91.3 % (alive) and 89.3 % (dead).
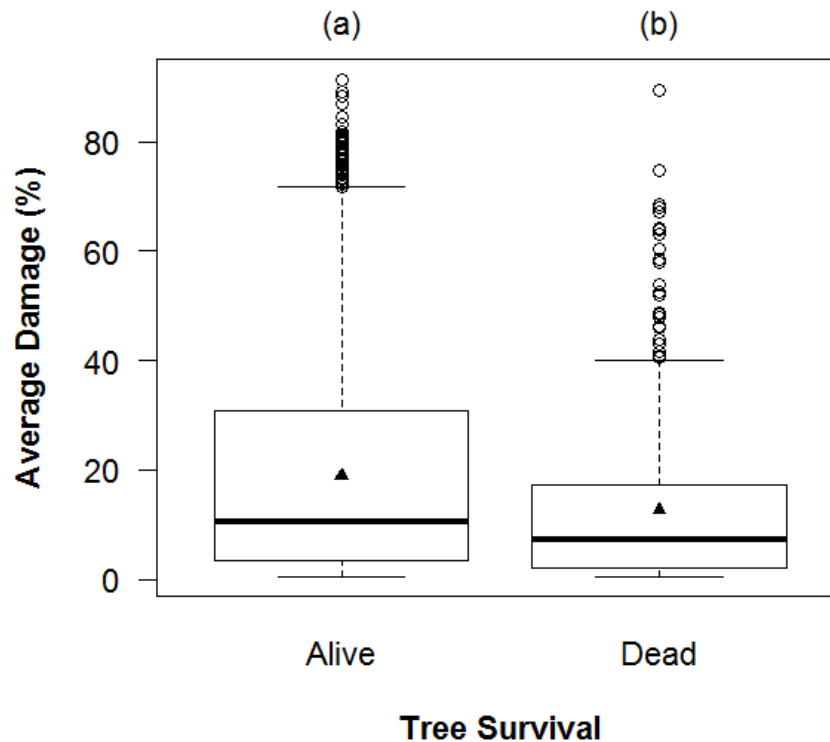
Figure 14: The average damage for trees that were still alive or died in the time frame of July to September 2015, i.e. after finishing the herbivory study. The average damage of living trees (N=5194) was compared with the average damage of trees which died (N=564) from July to September. The mean is indicated by the triangle.

The average damage for living and dead trees was also compared for each tree species (Fig. 15). The difference in average damage for living and dead trees was only significant with p<0.01 for *D. polyphylla*. The average damage of dead trees amounted to 12.17 % and was higher compared to the average damage of living trees with 7.68 %. All other tree species did not show significant differences. The mean average damage for dead trees was only smaller for *A. pauciflorum*. All other trees showed similar results whereas the average damage of dead trees was always higher compared to the average damage of still living trees. In total, 14 individuals of *P. speciosa* and three individuals of *A. pauciflorum* died during the dry period. Most tree individuals died for *D. zibethinus* (N=194) and for *D. polyphylla* (N=254). Only five individuals of *P. canescens* were not able to survive and 94 individuals of *S. leprosula* died.

Figure 15: The average damage caused by insect herbivores for living and dead trees of every tree species.
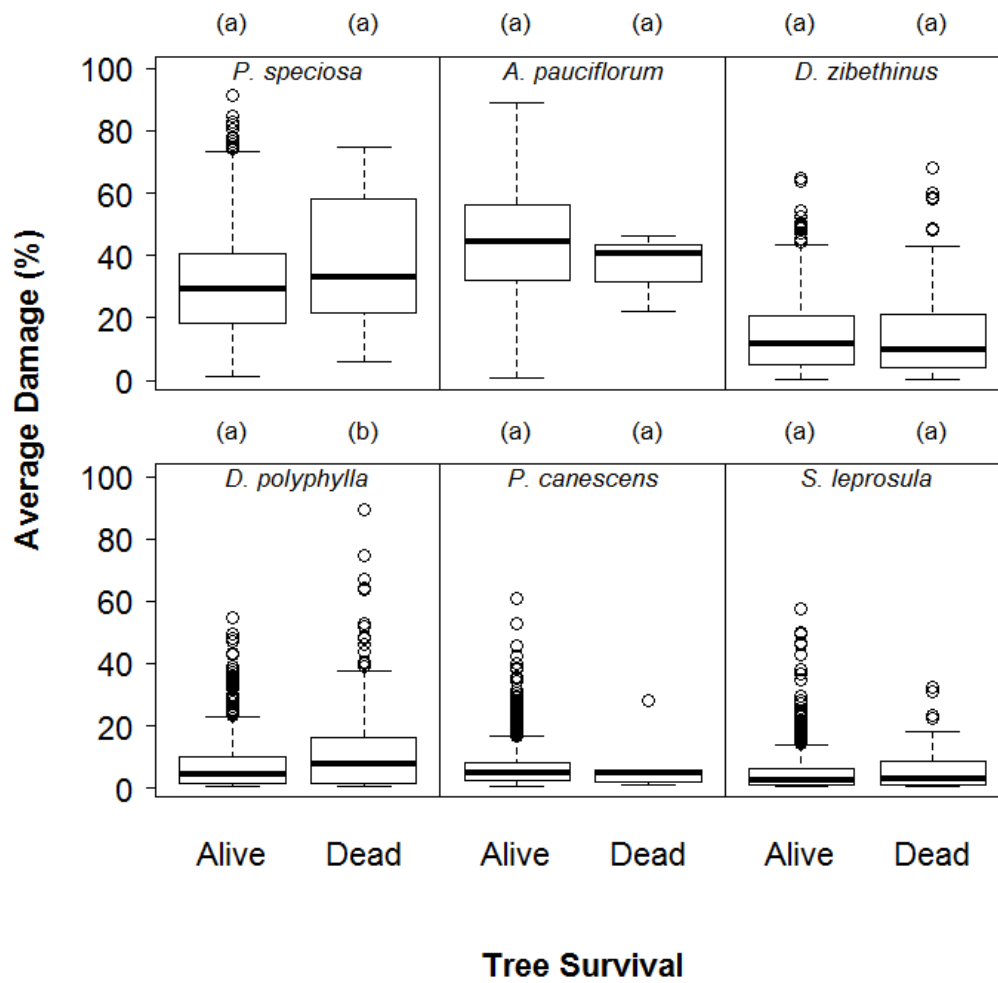
Discussion

In this study, the average damage caused by herbivory was quantified for tree individuals planted for an enrichment planting within an oil palm plantation in the Jambi province of Sumatra. The average damages were tested for differences between tree species, plot sizes and diversity levels. Furthermore, I investigated the change of herbivory rate and determined the leaf trait SLA for the six native species *P. speciosa*, *A. pauciflorum*, *D. zibethinus*, *D. polyphylla*, *P. canescens* and *S. leprosula*. Correlations between growth and herbivory, as well as survival and herbivory per tree, were tested.

For the quantification of herbivory, I first established damage classes to estimate the percentage of ELA. Quantifying damages by estimating can result in a reliable overview on the occurring herbivory or it can lead either to over- or under-estimated values. There are methods which directly measure the herbivory by sampling leaves and using programs for the measurements (Ebeling et al., 2014; Werner & Homeier, 2014). Because of the high number of trees (N=6354) I wanted to investigate, I chose to estimate the extent of herbivory. For validation, measured and estimated values for the percentage of ELA were compared. Both showed similar results which suggested that the estimation of herbivory was a suitable method to be used in the field. With regard to the measured and estimated damages, six different damage classes were established (Tab. 3). I preferred the estimation method as it was more efficient and less destructive compared to other methods (Ebeling et al., 2014; Werner & Homeier, 2014) while still producing reliable results. The damage classes facilitated the investigation of herbivory for every tree and were then translated into the average damage for further analyses.

The SLA for each tree species was calculated. This leaf trait might have an influence on herbivory. My first hypothesis states that the SLA differs among the tree species. This hypothesis was only partly confirmed. I found significant differences between the SLA of *A. pauciflorum* and *P. canescens*. The other four tree species showed similar results in their SLA and did not differ from *A. pauciflorum* or *P. canescens*. The differences between the SLAs might be explained by the different growth performances of each tree species. Fast growing species have a higher SLA than slow developing tree species (Gigon et al., 2004; Grotkopp & Rejmánek, 2007)

because slow developing species tend to have higher defense levels (Coley et al., 1985). Higher defense levels increase the weight of a leaf which decreases the SLA. An increase in growth results in less energy invested into plant defenses, leading to a trade-off between growth and defense (Fine et al., 2006; Wright et al., 2010). As a result, leaves with the same weight are taller for fast growing species than for slow developing plant species. In addition, a high SLA indicates a fast resource acquisition by the plant to optimize the growth (Grotkopp & Rejmánek, 2007). Tree species such as *P. canescens,* which showed a quick developing time, had higher SLAs in comparison to other tree species. There is not only a relationship between SLA and growth but also between SLA and leaf quality. For example, high structural component content (secondary metabolites) results in increased weight, which in turn, leads to a smaller SLA. The assumption of structural components decreasing the SLA by increasing the weight might explain the higher SLA of *P. canescens*. *P. canescens* uses the energy for growth instead of building structural components. However, the SLAs of the other species did not differ significantly from the SLA of *P. canescens* except for *A. pauciflorum*. The SLA of *A. pauciflorum* was significantly smaller meaning leaves with the same weight are smaller than leaves of *P. canescens*. The other tree species showed similar SLAs which might be explained by their shared habitat. Díaz et al. (2004) suggested that the same conditions of water and nutrient supply lead to convergent trait syndromes such as SLA. With lower water supply, nitrogen is accumulated in leaves to use higher light availability more efficiently (Cunningham et al., 1999). The leaf content of nutrients such as carbon and nitrogen influence the SLA. With higher amounts of nitrogen, leaves tend to have greater mass. The study site most likely shows impoverished soil characteristics (Allen et al., 2015) because oil palm plantations reduce freshwater availability and soil quality (Moran, 2011). As a result, the trees that were planted within the plantation grow under very similar reduced nutrient conditions. However, the SLA is correlated with many factors such as light, water, and nutrient supply (Poorter, 1999; Poorter & De Jong, 1999; Díaz et al., 2004), as well as leaf thickness and dry matter (Wilson et al., 1999). Thus, SLA is not a reliable plant trait for comparisons. It is also correlated with leaf age. Old leaves might have either higher or lower SLAs (Garnier & Freijsen, 1994). Since all leaves were randomly chosen regardless of their age, the age discrepancies between selected leaves might explain the high variation between the SLA within one species. In addition, the sampled leaves were exposed to the sun at the time of sampling but this does not implicate a total sun exposure at all times. Leaves exposed to sun light have a higher nutrient content indicating a higher photosynthesis activity and a smaller SLA

compared to shade leaves. This enhances their ability of light capturing through higher weights (Rozendaal et al., 2006). In general, plants growing under low light conditions show higher SLAs (Evans & Poorter, 2001). The leaves used for the determination of SLA were sampled mainly to establish damage classes and, therefore, showed different amounts of damage. The different amounts of damage might also be a possible explanation for the high intraspecific variations. The SLA for each species should be determined with leaves of similar characteristics with regards to sun exposure, age, and damage, to avoid variations in leaf components.

In this study, I determined the damage class for ten leaves per tree. Some trees died earlier or did not have ten (fully developed) leaves. For the determination of the number of leaves that had to be examined to reflect the overall average damage of the tree species, I first examined 30 leaves of one individual for *P. speciosa*, *A. pauciflorum*, *D. zibethinus*, *D. polyphylla* and *S. leprosula* and 12 leaves for *P. canescens*. The randomly chosen individual of *P. canescens* only carried 12 leaves. The cumulative mean average damages of the tree species were compared to each other. Ten leaves were sufficient to determine the average damage for all trees of *D. zibethinus* because the average damage did not differ strongly with increasing number of examined leaves. *A. pauciflorum* and *S. leprosula* showed high variation between the average damages even with a high number of leaves. However, the variations were higher with fewer leaves and they declined with a leaf number of ten. Thus, the average damage per tree is difficult to determine, since all leaves showed a high variation of average damage caused by herbivory. This variation declined after ten leaves, so more than ten leaves seemed to be necessary to obtain reliable data. The average damage of *P. speciosa* and *D. polyphylla* increased with increasing leaf number. After approximately 20 leaves the maximum average damage was reached. Many trees of *P. canescens,* however, barely showed a number of 20 leaves per tree. The average damage per tree should be comparable among species and needs to be adjusted to tree species with low numbers of leaves. Ten leaves have proven to be the best fitting number of leaves to be investigated.

To examine the second hypothesis, the change of herbivory was observed for seven weeks and showed small differences during the time of the first and the last observation for every tree species. The trees were affected by herbivory at all times. Thus, the hypothesis, that all tree species are affected by herbivory at all times, can be accepted. The highest overall average

damage was found for *A. pauciflorum*. The highest overall average damage does not necessarily mean that trees of the species *A. pauciflorum* suffered from more herbivory. The smallest slope between the seven quantifications of herbivory was found for *A. pauciflorum*. The observed trees were chosen randomly and the leaves which were investigated had missing pinnae. Missing leaves/pinnae were included into the study as an average damage of 95.5 % because I could not determine the reason for a missing leaf/pinna, other than the assumption of complete herbivory. *A. pauciflorum* had the highest average damage. However, the herbivory the investigated trees of this species faced was lower when compared to other species. *A. pauciflorum* tends to leaf flush. There are two different ways of leaf-flushing possible. Leaves are either flushed during the dry season to avoid high numbers of insect herbivores or leaves are flushed synchronously within one species to ensure some leaves to escape herbivory (Coley & Barone, 1996). Newly developing leaves were excluded from this study, but pinnate leaves, which were eaten during a former leaf flush, would explain the high amount of missing leaves. The biggest difference between the first and the last observation was found for *D. polyphylla* and *P. canescens*. The results from the change in herbivory rate differed, when compared to the quantification of standing herbivory (Fig. 7). The highest average damage was found for *P. speciosa*, *A. pauciflorum* and *D. zibethinus*. Hence, the results of the change of herbivory rate did not match the results of the standing herbivory. *D. polyphylla* and *P. canescens* showed some outliers with a high average damage, however, the overall average damage was lower and the average damage for both *D. polyphylla* and *P. canescens* were similar. There are many factors influencing leaf components, which consequently, influence herbivory. Leaf texture, age class, and nutritional values of leaves vary within and between individuals of trees (Lowman & Rinker, 2004, Massey et al., 2005). Varying nutritional values may also affect herbivory. For more information, the change of herbivory should be investigated for more individuals of one species and for a longer period of time to ensure different seasons are taken into account of studying herbivory. These results only show tendencies because only three individuals per tree species were investigated. The studied individuals were located within the 40x40 m single species plots. As a result, the effects of interspecific competition were excluded.

To investigate the third hypothesis, I tested the average damage per tree species for differences. All tree species except for *D. polyphylla* and *P. canescens* showed significant differences in average damage and, therefore, the third hypothesis can be accepted. The average

damage differed among the species. *A. pauciflorum* had the highest average damage with 43.97 %. The mean average damage per species was higher compared to studies of the herbivory occurring in the project "BEF China" with mean damages ranging between 3 % and 16 % (Schuldt et al., 2010). *A. pauciflorum* had many missing leaves and, because I was not able to determine the reason for the loss, missing leaves were included into the quantification of standing herbivory as the highest average damage. Thus, the high average damage can be partly explained by the high amount of missing leaves. In addition to *A. pauciflorum*, *P. speciosa* also showed a high average damage. Likewise, some leaves were missing but not in the extent as for *A. pauciflorum*. Both tree species belong to the family Fabaceae. Species of the family Fabaceae have been shown to accumulate nitrogen, because they form symbioses with N_2-fixing rhizobia bacteria (Cleveland et al., 1999; Whittington et al., 2012). Nitrogen is a valuable nutrient which is needed by herbivores (Townsend et al., 2008). Thus, trees, which accumulate high amounts of nitrogen in their leaves, should suffer more from herbivory than leaves with a lower amount of nitrogen. Additionally, *D. zibethinus* had a wide range of average damage but a much lower average damage than *P. speciosa* and *A. pauciflorum*. *D. polyphylla*, *P. canescens* and *S. leprosula* had smaller variations among the average damage of their tree individuals. *S. leprosula* showed the lowest average damage caused by herbivory. In contrast to that, Massey et al. (2006) found *S. leprosula* to have fewer defense traits against herbivores and is likely to be palatable to both specialists and generalists. Thus, *S. leprosula* is expected to have higher average damage than I have quantified. A possible explanation is that the other tree species are still more preferred than *S. leprosula*. Resource availability of tree individuals can strongly influence the occurring herbivore abundance (Whitfeld et al., 2012). Hence, the resource availability may explain average damages. In general, leaves of plants in tropical forests have low amounts of nutrients and a wide variety of secondary metabolites (Coley & Barone, 1996). Massey et al. (2005) found that under high soil quality, *S. leprosula* tends to compensate herbivory in an early life stage by producing more leaves. I quantified herbivory after nearly 18 months of establishment of the experiment. Hence, a high herbivory in the beginning might have been already compensated for which would then lead to lower herbivory. However, a possible compensation remains uncertain because the soil within palm oil plantations is expected to be impoverished (Moran, 2011; Allen et al., 2015; Dislich et al., 2015). According to Whitfield et al. (2012), total leaf biomass is the major determinant for herbivore abundance in tropical forests. A high leaf biomass represents a high amount of food and, therefore, a reduced competition among herbivores (Schlinkert et al.,

2015). Additionally, higher leaf biomass results in a more complex habitat structure and provides refuges from predators. Consequently, the herbivory of herbivorous insects is enhanced (Riihimäki et al., 2006). Palatability is a better predictor than nutritional quality of leaves (Basset, 1996; Poorter & DeJong, 1999; Poorter et al., 2004).

I assumed plot size to positively influence herbivory. According to the *resource concentration hypothesis* (Root, 1973) more individuals should occur in bigger plot sizes. Thus, host trees are more concentrated and easier to find for herbivores. The average damage is indeed higher for 40x40 m plots but the differences among plot sizes did not show significances. The identity of a neighboring species might explain the similar results. Characteristics of neighboring plants can affect herbivore pressure (Brown & Ewel, 1987; Baraza et al., 2006). An unpalatable surrounding of plants has protective influences on target plant species (Baraza et al., 2006). Bach (1980) proposed that mixed stands with a high number of unpalatable species deterred insects to leave these areas quicker. Hence, neighborhood effects can influence the growth, resource allocation patterns and damage by insect herbivores (Massey et al., 2006). Oil palms are an unattractive surrounding to herbivores because they are not native to Indonesia and should have fewer herbivorous insects feeding on their plant material. Trees in smaller plots (5x5 m and 10x10 m) with a higher probability of an oil palm as neighboring plant should show lower average damage. Nevertheless, numerous species have shown to feed on leaf tissue of oil palm (Corley & Tinker, 2003; Koh, 2008). The established plots were distributed within the oil palm plantation and, therefore, the plots might not attract many newly arriving insect herbivores. The developed gap size between oil palms has led to increased light availability, which in turn, influences the growth and the foliar chemical compounds of trees (Coley et al., 1985; Poorter, 1999; Baraza et al., 2004). I found a variation between the average damage per tree species in relation to the plot size (Fig. 9). Only the species of the family Fabaceae (*P. speciosa* and *A. pauciflorum*) showed significantly higher values for the average damage in the biggest plot (40x40 m). A higher herbivory might be explained by increased light conditions, as well as more individuals with similar palatability. More herbivores might be attracted which may lead to higher damages of leaves. The tree individuals might be able to compensate for the loss of leaf area by an increased growth due to high light levels (Eichhorn et al., 2010). For the other trees, the average damage occurring for the different plot sizes did not show strong differences and, therefore, the plot size did not influence the herbivory on *D. zibethinus*, *D. polyphylla*, *P. canescens* and *S. leprosula*.

I expected diversity level to have negative effects on herbivory. The highest average damage was found for trees growing in combinations of two and three species. There was a significant difference between the highest diversity level and all other diversity levels. The average damage caused by herbivory was smaller for plots with all six species present. The lowest average damage for plots with all six species present could be found for the species *P. speciosa*, *D. zibethinus* and *D. polyphylla,* whereas the average damage for the highest diversity level of the other three species is also one of the lowest. In contrast to the project "BEF China", all species faced higher herbivory in less diverse plots (Schuldt et al., 2010). The average damage should be higher in more diverse plots because an enhancement in plant species richness leads to an increase of species richness on all trophic levels (Siemann, 1998; Cardinale et al., 2006). Therefore, increases in tree species should lead to higher abundances of herbivores which should result in higher average damage. Schuld et al. (2010), however, found a positive relationship between plant diversity and herbivory for more species (25-68 species) than included in this study. Massey et al. (2006) found decreasing herbivory with increasing tree diversity. A possible explanation for lower herbivory with higher tree diversity might be the *resource concentration hypothesis* by Root (1973). A lower abundance of specialist herbivores is predicted resulting in lower plant damage because specialists cause more damage than generalists. With higher tree diversity the abundance of specialists decreases (Root, 1973). Furthermore, there were only four plots with a diversity level of six species, one in every plot size. The trees existed within the oil palm for only about 18 months when the quantification of herbivory started. These four plots may have not been discovered by as many insect herbivores as the other plots were. In total, there were 24 single species plots, 12 plots with a combination of two and eight plots with a combination of three species. The probability to be detected by insect herbivores is higher for those 44 plots than for the four plots with all six species.

By using the linear model approach by Bell et al. (2009), I was not able to find neither a correlation between the plot size and the average damage nor between the diversity level and the average damage (Tab. 4). Combined with the results discussed above, this shows that hypotheses four and five can be rejected. Both plot size and diversity level did not influence herbivory. The occurring average damage could mostly be explained by the tree species identity. These findings are consistent with findings of Vehviläinen et al. (2007) who found insect herbivory to be dependent mostly on host tree species. Tree characteristics seem to attract insect herbivores more than the number of individuals or species. However, these results only show tendencies and more

studies need to be carried out to be able to determine the classification of insect herbivores. The quantification of standing herbivory should be repeated several times a year to gather information on the annual patterns of herbivore abundance and their influence on the average damage. Furthermore, repeated quantifications might show age dependent differences in herbivory. In further analyses, leaf traits such as C/N ratio (see appendix), leaf toughness, and secondary metabolites should be determined to receive a broader understanding of factors influencing herbivory. A determination of herbivore insects might help explain variations in the amount of herbivory between tree species. A single quantification of standing herbivory measures the herbivory damage accumulated over the lifespan of a leaf (Poorter et al, 2004). Thus, leaf longevity plays an important role in this study which also suggests repeated quantifications.

The analyses of growth data of each tree with its associated average damage caused by herbivory revealed no correlation. Both absolute growth of height and diameter and relative growth of height and diameter showed no relation to the occurring damage (Fig. 12; Fig 13). Although it is considered that species face a trade-off between growth and defense (Fine et al., 2006; Wright et al., 2010), different studies found no correlation between growth and herbivory (Coley, 1983; Eichhorn et al., 2010; Whitfeld et al., 2012). Hence, growth is not always affected by herbivory. In contrast to that, the size of a plant determines the herbivore abundance/richness and, therefore, also the herbivory it faces. Schlinkert et al. (2015) found a positive relationship between the size of a plant and the herbivore species abundance. The increase of herbivore abundance results from the high conspicuousness and attractiveness of large plants (Schlinkert et al., 2015). *D. polyphylla* shows better growth when planted under oil palm seedlings than under mature oil palms (Tata et al., 2015). The oil palms of the study site were mature and might influence the growth negatively by reducing light availability. In this study, no correlation between tree size and herbivory could be found. The hypothesis that herbivory negatively affects tree growth did not apply in this experiment. The results do not correspond to the *plant vigor hypothesis* by Price (1991). Still, long-term influences of herbivory on seedling's growth are rare (Eichhorn et al., 2010). Thus, repeated studies on the occurring average damage might help to understand the effects of herbivory on growth and might show differences in herbivory depending on age.

From July to September 2015, 564 tree individuals died as a result of a long dry period. The average damages of still living trees were significantly higher than the average damages of

trees that died due to the drought (Fig. 15). The increased average damage for living trees of all species might be explained by the high average damage of *A. pauciflorum*. *A. pauciflorum* was the only species with a higher average damage for living than for dead trees. The average damage of dead trees for all other tree species was higher compared to the average damage of living trees. This allows the assumption of a relationship between a higher average damage caused by herbivory and the tree survival. Most individuals that died belonged to *D. polyphylla*. The survival rate of *D. polyphylla* might be enhanced by a previous inoculation with their corresponding mycorrhizal species. The inoculation of seedlings has shown to enhance the survival of *D. polyphylla* seedlings that were transplanted into degraded areas of former tropical peat swamp forests (Turjaman et al., 2006; Graham et al., 2013). Nevertheless, they normally grow on peat soils. The soil of the study site is mineral soil and, therefore, *D. polyphylla* did not perform well from the beginning on. Furthermore, this technique to enhance survival was used for *Shorea balangeran*. *S. balangeran* is from the same genus as *S. leprosula*. Thus, this method might also enhance the survival of *S. leprosula* of which 94 individuals did not survive the dry period. The inoculated mycorrhizae can supply the seedlings with additional nutrients, such as phosphates and nitrates, as well as promoting water supply and reducing the infection probability of pathogens (Rillig, 2004). A previous treatment with associated mycorrhizal species could have enhanced the survival during the drought between July and September. In addition, Eichhorn et al. (2010) found a reduced probability for dipterocarp species' seedlings to survive the following year related with damages caused by herbivory. Only damages on mature leaves led to reduced survival and damages of less than 1 % per month were sufficient to influence mortality rates (Eichhorn et al., 2010). Hence, further survival rates need to be observed to find a possible relationship between herbivory and survival. A greater impact of herbivory on survival for low light conditions was also found by Eichhorn et al. (2010). Hence, trees which did not survive might grow under lower light levels and, therefore, average damage did not necessarily need to be high to influence mortality. Thus, the hypothesis that tree survival is negatively influenced by herbivory has to be rejected although a trend might be visible. The relationship between the location and average damage of a tree needs further analysis. In addition, herbivory might indirectly reduce the survival through facilitating infection by pathogens (Bell et al., 2006). Hence, the occurrence of pathogens needs investigations.

Conclusion

Overall, this study revealed that the herbivory for the enrichment planting experiment within the oil palm plantation was mostly explained by the identity of the six native tree species *P. speciosa*, *A. pauciflorum*, *D. zibethinus*, *D. polyphylla*, *P. canescens* and *S. leprosula*. The experimental design of plot size and diversity level did not affect the average damage caused by herbivory. In contrast to the expectations, the lowest average damage was found in plots with the highest diversity level. The leaf trait specific leaf area (SLA) did not explain interspecific differences in herbivory. Furthermore, analyses of herbivory and growth, as well as herbivory and survival did not reveal any correlation. Herbivory was also not affected by tree size. However, the results suggest at least a tendency for a reduced survival probability by a high average damage caused by herbivory.

For a broader understanding of the factors that influence herbivory, further studies need to be conducted. First of all, repeated quantifications of standing herbivory are necessary to gather information about age dependent influences on herbivory. Additionally, repeated quantifications lead to information about annual patterns of insect herbivores. Studies regarding the identity of insect herbivores would present data about generalists and specialists. Furthermore, more leaf traits (e.g. C/N ratio, leaf toughness, and secondary metabolites) should be determined because they facilitate a broader understanding about which role leaf characteristics play regarding herbivory. The determination of the SLA should be repeated and for the determination, leaves with similar characteristics (age, sun exposition, and damage caused by herbivory) should be selected. Further analyses of soil characteristics should be conducted to gain a broader knowledge about the habitat.

This enrichment planting experiment is suitable for oil palm plantations because most of the six tree species showed great growth and survival ability under these conditions. Enrichment of plant species, especially of trees with an economical value, might increase the acceptance of farmers to enhance diversity within their plantations for conservation purpose. This would help to preserve the endangered and endemic biodiversity in Southeast Asia.

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Appendix

Carbon and Nitrogen Analyses

I was also interested if there was a correlation between herbivory and the carbon (C) and nitrogen (N) content of a leaf. Hence, the 60 harvested and dried leaves were sent to the Department of Soil Science, Bogor Agricultural University (IBP) for C and N analyses. In total, 2g of dried leaf matter was necessary for the analyses. Thus, I sampled additional leaves of each tree individual to reach 2g dried lead matter. Those newly sampled leaves replaced only some of the former harvested leaves, so the required leaf material was sufficient for the analyses. For *D. zibethinus*, *D. polyphylla* and *S. leprosula*, I sent mixed samples, whereas the leaves of *P. speciosa*, *P. canescens* and *A. pauciflorum* of the first experiments were used. The N analyses were conducted after the method of Kjedahl (1883) and the C amounts were determined using the loss on ignition (LOI) method (Dean, 1974). The C and N contents were then used to calculate the C/N ratio [6].

[6] $C/N = \frac{C}{N}$

Due to a long period of receiving all necessary permits for sending the leaves from Jambi to Bogor, the C and N analyses were finished only two days before the submission of this master's thesis.

Table 5: Descriptive statistics of the C/N ratio for each tree species.

Tree Species	C/N ratio (Min.)	C/N ratio (Mean)	C/N ratio (Max.)	C/N ratio (SD)
P. speciosa	24.1	31.2	44.0	6.5
A. pauciflorum	24.6	30.8	37.2	4.1
D. zibethinus	28.8	33.4	39.7	3.8
D. polyphylla	40.1	45.5	49.8	3.3
P. canescens	23.5	34.1	40.7	5.9
S. leprosula	6.5	33.3	43.1	9.9

The C/N ratio of *D. polyphylla* was significantly higher than the C/N ratio of the other tree species (p<0.01). The mean C/N ratio amounted to 45.5. The other mean C/N ratios range between 30.8 (*A. pauciflorum*) and 34.1 (*P. canescens*) and show no significant differences.
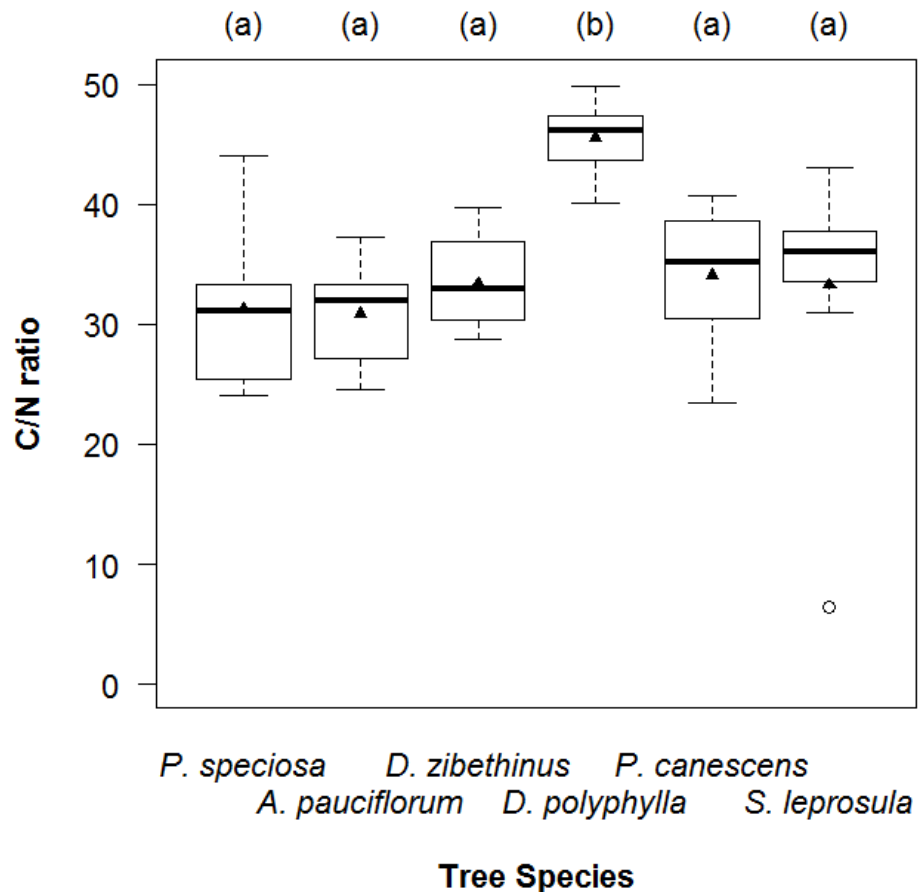
Figure 16: The C/N ratio for each tree species. The C and N content for ten leaves per species were measured and the C/N ratio was calculated by dividing C amount by the N amount. The mean C/N ratio is indicated by the triangle.

The analyses of the determined C/N ratio with their associated calculated SLA showed a negative trend with a correlation coefficient of -0.18. As a result, the SLA decreased with increasing C/N ratio. However, the C/N ratio and the SLA were not significantly correlated (p>0.05).
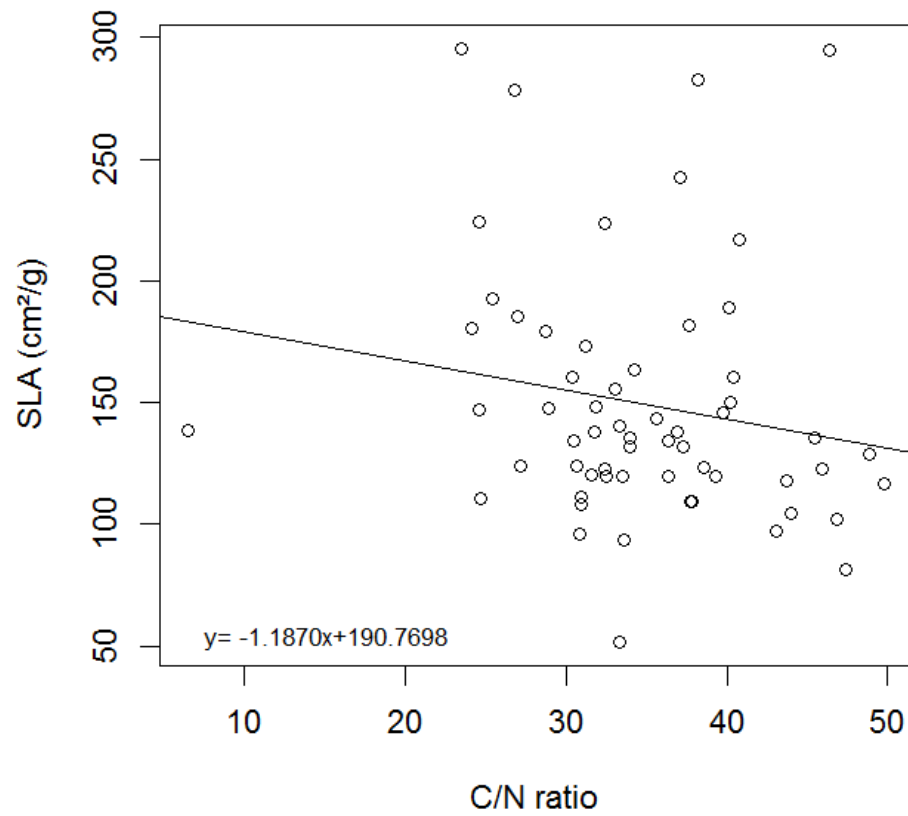
Figure 17: C/N ratio with the associated SLA of all tree species (N=60). The C/N ratio and SLA were calculated using the same ten leaves per species. The negative linear correlation of C/N ratio and SLA is given with the equation y=-1.1870x+190.7698.

Map of Study Site
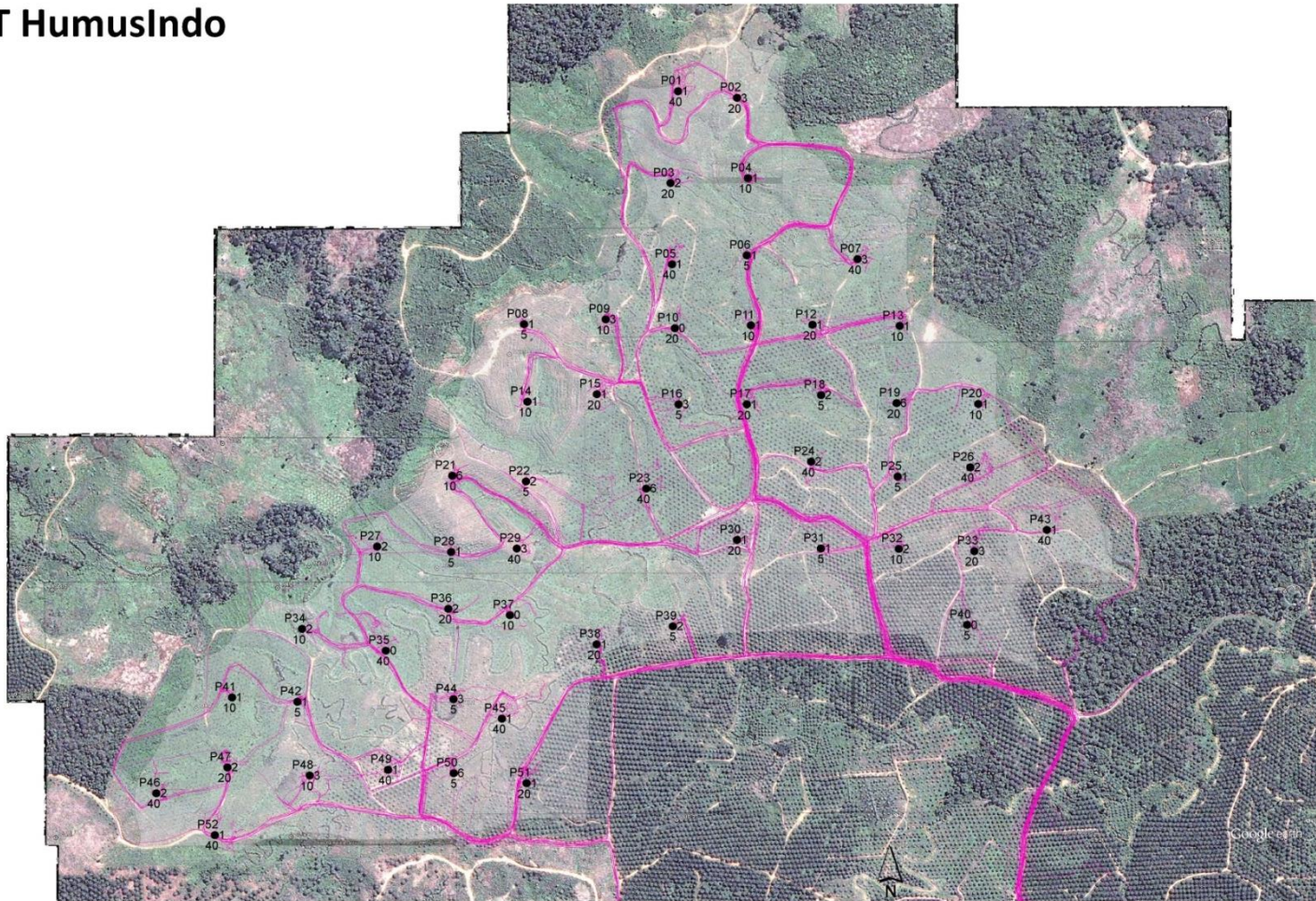
Figure 18: Map of the study site showing the locations of each plot including plot size, diversity level and plot ID.

Final Plot Design

Table 6: Experimental treatment with all 52 plots and their characteristics of plot size and diversity level. Tree species are given using the code from Tab. 1.

new_point	edge_length	div_level	combi	species	palms_cut
P01	40	1	1 sp 40	A	7
P02	20	3	3 sp 20	ACF	3
P03	20	2	2 sp 20	CD	3
P04	10	1	1 sp 10	F	1
P05	40	1	1 sp 40	B	8
P06	5	1	1 sp 5	E	0
P07	40	3	3 sp 40	AEF	8
P08	5	1	1 sp 5	F	0
P09	10	3	3 sp 10	ABD	1
P10	20	ctrl	ctrl 20		3
P11	10	1	1 sp 10	D	1
P12	20	1	1 sp 20	C	2
P13	10	1	1 sp 10	E	1
P14	10	1	1 sp 10	C	1
P15	20	1	1 sp 20	B	2
P16	5	3	3 sp 5	ACD	0
P17	20	1	1 sp 20	F	3
P18	5	2	2 sp 5	DE	0
P19	20	6	6 sp 20	ABCDEF	2
P20	10	1	1 sp 10	B	1
P21	10	6	6 sp 10	ABCDEF	1
P22	5	2	2 sp 5	BF	0
P23	40	6	6 sp 40	ABCDEF	8
P24	40	2	2 sp 40	CE	8
P25	5	1	1 sp 5	A	0
P26	40	2	2 sp 40	DF	5
P27	10	2	2 sp 10	AE	1
P28	5	1	1 sp 5	B	1
P29	40	3	3 sp 40	BCD	8
P30	20	1	1 sp 20	E	2
P31	5	1	1 sp 5	C	0
P32	10	2	2 sp 10	CF	1
P33	20	3	3 sp 20	BDE	3
P34	10	2	2 sp 10	BD	1
P35	40	ctrl	ctrl 40		7
P36	20	2	2 sp 20	AF	2
P37	10	ctrl	ctrl 10		1
P38	20	1	1 sp 20	D	3
P39	5	2	2 sp 5	AC	0
P40	5	ctrl	ctrl 5		0
P41	10	1	1 sp 10	A	1
P42	5	1	1 sp 5	D	0
P43	40	1	1 sp 40	C	8
P44	5	3	3 sp 5	BEF	0
P45	40	1	1 sp 40	E	6
P46	40	2	2 sp 40	AB	8
P47	20	2	2 sp 20	BE	2
P48	10	3	3 sp 10	CEF	1
P49	40	1	1 sp 40	F	7
P50	5	6	6 sp 5	ABCDEF	0
P51	20	1	1 sp 20	A	2
P52	40	1	1 sp 40	D	8

Raw Data and Descriptive Statistics

Table 7: Descriptive statistics of the specific leaf area (SLA) for each tree species.

Tree Species	SLA (cm²/g) (Min.)	SLA (cm²/g) (Mean)	SLA (cm²/g) (Max.)	SLA (cm²/g) (SD)
P. speciosa	104.7	158.0	224.3	39.4
A. pauciflorum	51.7	118.5	147.0	25.4
D. zibethinus	95.8	148.3	223.6	36.8
D. polyphylla	81.6	143.9	294.5	60.1
P. canescens	123.5	192.6	295.4	62.1
S. leprosula	93.7	136.3	282.7	54.4

Table 8: Raw data of the average damage for each leaf investigated to determine the minimum leaf area for each tree species.

Leaf	P. speciosa (%)	A. pauciflorum (%)	D. zibethinus (%)	D. polyphylla (%)	P. canescens (%)	S. leprosula (%)
1	0.5	80.1	0.5	0.5	1.1	0.5
2	0.5	55.5	3.0	0.5	3.6	0.5
3	0.5	58.8	3.0	0.5	0.5	0.5
4	3.0	23.8	3.0	0.5	1.3	0.5
5	3.0	95.5	0.5	0.5	0.7	10.5
6	0.5	85.1	0.5	0.5	0.5	33.0
7	0.5	53.4	3.0	0.5	5.9	10.5
8	10.5	54.7	0.5	0.5	2.0	33.0
9	3.0	85.1	0.5	0.5	1.5	3.0
10	3.0	63.8	0.5	0.5	4.5	0.5
11	3.0	95.5	0.5	3.0	2.5	0.5
12	70.5	95.5	0.5	0.5	4.4	33.0
13	3.0	69.3	0.5	0.5		10.5
14	3.0	74.7	0.5	0.5		10.5
15	3.0	72.6	0.5	3.0		10.5
16	33.0	95.5	0.5	3.0		3.0
17	33.0	18.4	0.5	0.5		3.0
18	33.0	50.5	3.0	33.0		0.5
19	0.5	95.5	0.5	0.5		0.5
20	0.5	85.1	3.0	0.5		33.0
21	0.5	85.1	0.5	3.0		0.5
22	0.5	30.5	3.0	3.0		0.5
23	0.5	45.1	0.5	0.5		10.5
24	10.5	95.5	3.0	3.0		0.5
25	3.0	45.1	0.5	0.5		33.0
26	3.0	64.4	0.5	3.0		3.0

27	3.0	63.8	0.5	0.5	0.5
28	70.5	53.4	0.5	0.5	0.5
29	3.0	95.5	0.5	0.5	0.5
30	0.5	95.5	0.5	0.5	10.5

Table 9: The cumulative mean average damage for every additional leaf to determine the minimum leaf number for each tree species.

Leaf	*P. speciosa* (%)	*A. pauciflorum* (%)	*D. zibethinus* (%)	*D. polyphylla* (%)	*P. canescens* (%)	*S. leprosula* (%)
1	0.5	80.1	0.5	0.5	1.1	0.5
2	0.5	67.8	1.8	0.5	2.4	0.5
3	0.5	64.8	2.2	0.5	1.8	0.5
4	1.1	54.6	2.4	0.5	1.6	0.5
5	1.5	62.8	2.0	0.5	1.5	2.5
6	1.3	66.5	1.8	0.5	1.3	7.6
7	1.2	64.6	1.9	0.5	2.0	8.0
8	2.4	63.4	1.8	0.5	2.0	11.1
9	2.4	65.8	1.6	0.5	1.9	10.2
10	2.5	65.6	1.5	0.5	2.2	9.3
11	2.5	68.3	1.4	0.7	2.2	8.5
12	8.2	70.6	1.3	0.7	2.4	10.5
13	7.8	70.5	1.3	0.7		10.5
14	7.5	70.8	1.2	0.7		10.5
15	7.2	70.9	1.2	0.8		10.5
16	8.8	72.4	1.1	1.0		10.0
17	10.2	69.3	1.1	0.9		9.6
18	11.5	68.2	1.2	2.7		9.1
19	10.9	69.6	1.2	2.6		8.7
20	10.4	70.4	1.3	2.5		9.9
21	9.9	71.1	1.2	2.5		9.4
22	9.5	69.3	1.3	2.5		9.0
23	9.1	68.2	1.3	2.5		9.1
24	9.1	69.4	1.3	2.5		8.7
25	8.9	68.4	1.3	2.4		9.7
26	8.7	68.2	1.3	2.4		9.4
27	8.5	68.1	1.2	2.4		9.1
28	10.7	67.5	1.2	2.3		8.8
29	10.4	68.5	1.2	2.2		8.5
30	10.1	69.4	1.2	2.2		8.6

Table 10: Mean average damage for three individuals per tree species for a period of seven weeks.

Time	*P. speciosa* (%)	*A. pauciflorum* (%)	*D. zibethinus* (%)	*D. polyphylla* (%)	*P. canescens* (%)	*S. leprosula* (%)
Week 1	1.7	3.6	1.7	1.6	1.5	1.7
Week 2	1.7	3.6	1.7	1.9	1.7	1.9
Week 3	2.0	3.7	1.8	2.0	1.8	2.0
Week 4	2.0	3.8	1.9	2.1	2.0	2.0
Week 5	2.0	3.8	1.9	2.2	2.0	2.1
Week 6	2.0	3.8	1.9	2.2	2.0	2.1
Week 7	2.0	3.8	1.9	2.2	2.0	2.1

Table 11: Descriptive statistics of the average damage for each tree species

Tree Species	Average Damage (%) (Min.)	Average Damage (%) (Mean)	Average Damage (%) (Max.)	Average Damage (%) (SD)
P. speciosa	1.0	30.9	91.3	17.0
A. pauciflorum	0.7	44.0	89.0	17.6
D. zibethinus	0.5	14.1	68.0	12.1
D. polyphylla	0.5	8.9	89.3	11.1
P. canescens	0.5	6.9	60.7	6.9
S. leprosula	0.5	5.1	57.5	6.5

Table 12: Descriptive statistics of the average damage for the different plot designs and the amount of plots with the specific characteristic and the number of trees growing in these characteristic plots (without 4 control plots).

Plot Design	No. of Plots	No. of Trees	Average Damage (%) (Min.)	Average Damage (%) (Mean)	Average Damage (%) (Max.)	Average Damage (%) (SD)
5x5 m	12	66	0.5	16.2	91.3	17.9
10x10 m	12	263	0.5	17.0	83.0	16.1
20x20 m	12	1105	0.5	16.1	86.9	16.9
40x40 m	12	4324	0.5	18.9	89.3	19.8
1 Species	24	2947	0.5	18.2	83.0	18.4
2 Species	12	1401	0.5	18.6	86.9	20.4
3 Species	8	937	0.5	20.0	91.3	20.0
6 Species	4	473	0.5	14.5	89.0	17.2

Table 13: Descriptive statistics of the average damage for each tree species regarding the different plot sizes.

Tree Species	Plot Size	Average Damage (%) (Min.)	Average Damage (%) (Mean)	Average Damage (%) (Max.)	Average Damage (%) (SD)
P. speciosa	5x5 m	5.3	27.8	91.3	24.5
	10x10 m	4.5	28.4	83.0	18.2
	20x20 m	1.0	18.2	73.3	13.2
	40x40 m	1.3	34.5	84.6	16.0
A. pauciflorum	5x5 m	12.7	27.9	67.3	15.3
	10x10 m	0.7	27.9	58.8	17.2
	20x20 m	5.1	40.6	86.9	17.3
	40x40 m	1.0	46.1	89.0	16.9
D. zibethinus	5x5 m	0.8	14.2	36.0	10.6
	10x10 m	0.5	11.8	33.0	9.7
	20x20 m	0.5	17.3	49.5	10.9
	40x40 m	0.5	13.5	68.0	12.4
D. polyphylla	5x5 m	0.5	11.9	74.7	21.0
	10x10 m	0.5	11.2	63.8	14.5
	20x20 m	0.5	7.1	67.2	10.0
	40x40 m	0.5	9.2	89.3	10.9
P. canescens	5x5 m	1.0	5.1	11.8	3.3
	10x10 m	1.7	15.0	60.7	12.0
	20x20 m	0.7	7.5	40.1	8.1
	40x40 m	0.5	6.3	52.9	5.7
S. leprosula	5x5 m	0.8	8.2	15.5	5.9
	10x10 m	0.5	7.1	38.3	8.1
	20x20 m	0.5	4.9	28.3	5.4
	40x40 m	0.5	4.9	57.5	6.6

Table 14: Descriptive statistics of the average damage for each tree species regarding the different diversity levels.

Tree Species	Diversity Level	Average Damage (%) (Min.)	Average Damage (%) (Mean)	Average Damage (%) (Max.)	Average Damage (%) (SD)
P. speciosa	1 Species	2.5	29.2	83.0	14.7
	2 Species	1.0	33.5	83.0	18.5
	3 Species	1.3	39.8	91.3	19.4
	6 Species	1.8	18.8	52.5	11.8
A. pauciflorum	1 Species	0.7	44.0	80.9	18.3
	2 Species	1.8	46.6	86.9	16.9
	3 Species	2.4	41.4	88.2	16.0
	6 Species	1.5	41.9	89.0	17.4
D. zibethinus	1 Species	0.5	14.1	48.0	9.9
	2 Species	0.5	15.0	68.0	15.0
	3 Species	0.5	14.7	64.0	13.3
	6 Species	0.5	9.9	50.3	11.2

D. polyphylla	1 Species	0.5	10.6	74.7	11.2
	2 Species	0.5	8.0	64.3	10.9
	3 Species	0.5	8.1	89.3	12.1
	6 Species	0.5	3.1	24.3	5.2
P. canescens	1 Species	0.9	6.1	60.7	6.3
	2 Species	0.6	6.4	35.4	6.0
	3 Species	0.5	9.8	52.9	9.1
	6 Species	1.0	7.6	35.1	6.7
S. leprosula	1 Species	0.5	4.9	49.3	5.1
	2 Species	0.5	4.1	38.3	5.5
	3 Species	0.5	7.4	57.5	10.1
	6 Species	0.5	4.4	49.8	6.8

Table 15: Descriptive statistics for growth. The absolute growth is the difference between the first measurement of tree height and tree diameter and the measurement conducted in January 2015. The relative growth is the ratio between the first measurement and the measurement of January 2015.

Growth Data	Absolute Height (cm)	Absolute Diameter (cm)	Relative Height (%)	Relative Diameter (%)
Growth (Min.)	1.00	0.01	0.01	0.01
Growth (Mean)	102.27	1.36	2.24	2.87
Growth (Max.)	520.00	6.47	33.80	17.00
Growth (SD.)	86.85	1.09	2.41	2.24

Table 16: Amount of planted, living and dead trees within the experimental design.

Tree Species	No. of Trees planted	No. of living Trees	No. of dead Trees or Trees with no (fully developed) Leaves (before July)	Dead Trees or Trees with no (fully developed) leaves (July - September)
P. speciosa	1059	965	94	14
A. pauciflorum	1059	968	91	3
D. zibethinus	1059	899	160	194
D. polyphylla	1059	910	149	254
P. canescens	1058	1032	26	5
S. leprosula	1058	984	74	94

Table 17: Descriptive statistics of average damage for the survival of each tree species.

Trees	Survival	Average Damage (%) (Min.)	Average Damage (%) (Mean)	Average Damage (%) (Max.)	Average Damage (%) (SD)
All	Alive	0.5	18.9	91.3	19.4
	Dead	0.5	12.7	89.3	14.7
P. speciosa	Alive	1.0	30.7	91.3	16.9
	Dead	6.0	38.9	74.7	21.1
A. pauciflorum	Alive	0.7	44.0	89.0	17.6
	Dead	22.2	36.3	46.1	12.5
D. zibethinus	Alive	0.5	14.0	65.0	11.6
	Dead	0.5	14.6	68.0	13.9
D. polyphylla	Alive	0.5	7.7	54.8	8.9
	Dead	0.5	12.2	89.3	15.1
P. canescens	Alive	0.5	6.9	60.7	6.9
	Dead	1.3	8.5	28.0	11.1
S. leprosula	Alive	0.5	5.0	57.5	6.5
	Dead	0.5	5.8	32.3	6.7