The effect of herbivory on tree performance in a reforestation experiment in La Gamba, Costa Rica

Master Thesis

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Abstract

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Herbivory, the consumption of plants by primary consumers, is a crucial part of a terrestrial food web. The high species richness in tropical rainforests leads to a higher herbivorous pressure by insects on trees, which counteract with physical and chemical defenses. These defense mechanisms might be crucial for survival of tree saplings as herbivory could have a negative impact on tree performance. I measured herbivory levels for 23 native tree species on a reforestation site in south Costa Rica and analyzed them in relation to leaf traits, growth rates and mortality rates obtained from previous studies. Herbivory levels ranged from 0.25 % to 31.42 %; the average of 7.53 % was within the range of other studies in tropical rainforests. As expected, significant differences of herbivory levels did exist between species. Herbivory correlated with specific leaf area (SLA) and chlorophyll content, which together explained about a quarter of the herbivory variations. In the subset of tree species with high wood density, herbivory correlated with SLA and leaf chlorophyll content as well. In legumes, herbivory correlated with SLA, toughness and carbon while in species with low wood density, herbivory showed no correlations. Herbivory levels had no influence on growth and mortality rate. The tree species thus appear sufficiently resistant against herbivores and suitable for reforestation projects under similar conditions.

Kurzfassung

Besenbäck, Elisa. 2018. Der Einfluss von Herbivorie auf die Performance der Bäume eines Wiederaufforstungsversuches in La Gamba, Costa Rica. Masterarbeit an der Universität für Bodenkultur Wien:

Herbivorie, die Ernährung von Primärkonsumenten durch grüne Pflanzen, ist ein wesentlicher Bestandteil eines terrestrischen Nahrungsnetzes. Die höhere Artenvielfalt in tropischen Regenwäldern führt zu einem höheren Druck von Insekten auf Bäume, die sich wiederum durch physische und chemische Verteidigungsmechanismen zur Wehr setzen. Diese Verteidigung kann für den Baum überlebenswichtig sein, da Herbivorie einen negativen Einfluss auf die Fitness eines Baumes haben kann. Von 23 heimischen Baumarten einer Wiederbewaldungsfläche im Süden von Costa Rica wurde die Herbivorie quantifiziert und im Zusammenhang mit Blatteigenschaften, Wachstums- und Mortalitätsraten von früheren Untersuchungen analysiert. Herbivorielevel reichten von 0,25 % bis 31,42 %, der Durchschnitt von 7,53 % bewegte sich im Rahmen der Ergebnisse anderer Studien in tropischen Regenwäldern. Wie erwartet unterschieden sich die Herbivorielevel zwischen den Arten signifikant. Herbivorie korrelierte mit der spezifischen Blattfläche (SLA) und dem Chlorophyllgehalt, die gemeinsam etwa ein Viertel der Unterschiede erklärten. In der Untergruppe von Arten mit hoher Holzdichte korrelierte Herbivorie ebenfalls mit SLA und Chlorophyllgehalt. Bei Leguminosen korrelierte Herbivorie mit SLA, Reißfestigkeit und Kohlenstoffgehalt während bei Arten mit niedriger Holzdichte keine Korrelationen gefunden wurden. Das Herbivorielevel hatte keinen Einfluss auf Wachstums- und Mortalitätsrate. Die Baumarten scheinen daher ausreichend resistent gegenüber Herbivoren und folglich geeignet für zukünftige Wiederbewaldungsprojekte unter ähnlichen Bedingungen zu sein.

Abbreviations

Abbreviation		Unit
A	abundance	%
C	carbon content	%
CHL	chlorophyll content	SPAD
G	growth rate	m/year
H	herbivory level	%
HDspecies	high wood density species	
LDMC	leaf dry matter content	mg g^{-1}
LDspecies	low wood density species	
M	mortality rate	yr^{-1}
N	nitrogen content	%
S	severity	%
SLA	specific leaf area	mm^2 mg^{-1}
THI	leaf thickness	mm
TOU	leaf toughness	N/cm leaf width

1 Introduction

1.1 Plant-animal-interactions in the tropical rainforest ecosystem

A tropical rainforest is a complex ecosystem in which animals and plants interact. Their interactions are a vital and natural part of ecosystem functioning and can be depicted through a food web (Figure 1). Excluding carnivorous plants, the relationship between animals and plants in regards to food is those of the eater (herbivore) and the eatable (host). We call this “predation” of plants herbivory. It appears that herbivory was the initial interaction from which other interactions evolved, like the dispersal of propagules and the pollination of flowers, both an advantage for the plant (Mabberley 1992).

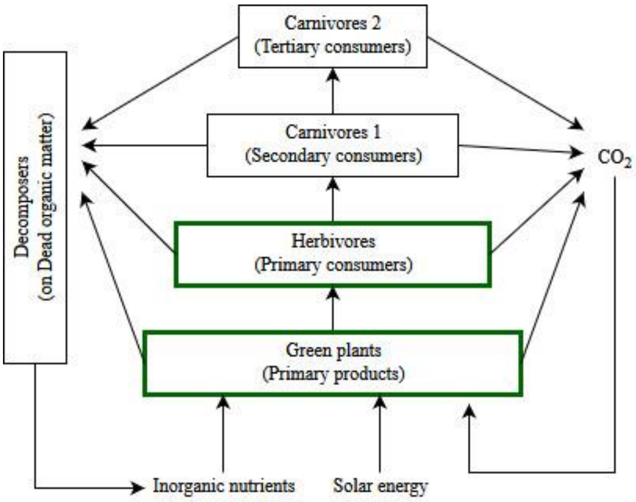


Figure 1: Tropical food web with arrows showing the flow of matter/energy; relevant levels for herbivory are marked in green (adapted from Nair 2007).

Early explorers first realized the latitudinal gradient in species diversity on earth with the highest diversity found in the equatorial tropics (Ghazoul & Sheil 2010). It is believed that globally tropical rainforests host about 50 % of the world’s species covering just about 8 % of the Earth’s land surface (Whitmore 1998). The forest in the Golfito region belongs to the Neotropics. A feature of the Neotropics is their high diversity in plants and animals, exceeding species diversity in Asian or African tropics (Ghazoul & Sheil 2010, Nair 2007, Werger & Lieth 1989).

The more stable climate conditions, the higher productivity, the age, and the larger area compared to other climatic regions not only explain the high plant diversity but also favor higher pest diversity. Therefore, biotic interactions, especially between plants and their herbivores, are stronger. Herbivore diversity and host specificity, which are not investigated in this study, as well as herbivory occurance and herbivory rates are generally higher in the tropics than in temperate regions, as are abundance and herbivory rates (Coley & Kursar 2014, Dyer & Coley 2002, Leigh et al. 2004, Schemske et al. 2009). Kursar & Aide (1991) report average herbivory rates of 7.5 % in temperate forests and 10.9 % in tropical forests. Similar rates for temperate forests are reported by Coley & Barone (1996) with 7.1 %. However, their findings for tropical wet forests differ and distinguish between shade tolerant species with herbivory rates of 11.1 % and gap specialists with a rate of 48 %. At the same time, Kursar & Aide (1991) report higher levels of plant defenses against herbivores in tropical forests and thus hold higher herbivore pressure accountable for the higher rates rather than lower defenses.

1.2 Herbivory

Nearly all parts of a tree are a potential source of food for animals. While the tracks left behind by herbivores feeding on leaves or shoots are noticeable, damage on other parts is not always visible. For example, root feeders, like nematodes, and phloem feeders might also have great negative impact on a tree. Furthermore, mammals and a range of invertebrates might consume the bark or stem-miners can afflict the stem (Ghazoul & Sheil 2010, Mabberley 1992).

Compared to permanently available parts of a tree, leaves with a limited live span are more attractive to herbivores due to the higher nutritional value, especially the higher protein content (Turner 2004). Furthermore, a large proportion of tropical forest insects are leaf feeders (Nair 2007). For example, Mathur & Singh (1961, cited in Nair 2007) reported that 137 out of 174 insects found on teak trees in India and its adjacent countries were leaf feeders. At the same time, the most important leaf consumers are insects (Ghazoul & Sheil 2010). This was also proven for expanding leaves where the share of damage due to insects on young leaves is > 95 % (Kursar & Coley 2003). Insects feed on leaf tissue in different ways, which result in total or partial destruction of the leaf. Accordingly, folivorous insects belong to different functional feeding guilds. *Leaf chewers* eat the leaf lamina either from the edge or by leaving holes. *Leaf mining insects* feed on the parenchyma cells while the epidermal cells remain. *Leaf skeletonizers* selectively graze the green leaf tissue while the vein network remains. *Leaf tiers* and *leaf rollers* form shelters from the leaf and might additionally graze from within (Nair 2007, Paul et al. 2012, Speight & Wylie 2001). The harm to the tree through defoliation varies depending on factors like age of the leaves, severity of defoliation, position on the canopy, the season of the occurrence, and the current stress of the tree (Speight & Wylie 2001).

Most of the damage to the leaves caused by herbivores occurs during expansion (Kursar & Coley 2003). According to Coley & Aide (1991), the rate of herbivory (loss per time) on expanding leaves in tropical shade tolerant species is 5-100 times the rates of mature leaves. Hence, up to 75 % of all herbivorous damage occurs during this period of expansion. Considering the average lifespan of a shade tolerant tree’s leaf of 2.5 years, the largest proportion of damage occurs in just 4 % of the lifespan (Coley & Kursar 2014, Coley & Kursar, 1996).

Both young leaves of pioneer tropical trees and of shade tolerant tropical trees suffer higher herbivory rates than the mature leaves. In shade tolerant trees the rate is just three times higher, while young leaves of pioneer trees are up to almost 25 times more affected (Coley 1983a). Aide (1993) reports a 27 % loss of the potential leaf area of young leaves during the first month of their life. Damage on young leaves has a much higher impact on plant productivity than damage on mature leaves due to a decrease in photosynthetic capacity, leaf nitrogen, and stomatal conductance with leaf age (Aide 1993).

1.1.1. Defense mechanisms of leaves against herbivores

Herbivores have been present throughout the evolution of tropical trees, which therefore developed different strategies and mechanisms of defense over time (Coley 1987, Spight & Wylie 2001). Defenses of host plants include physical and chemical mechanisms or combinations of both. Without the plants evolving these defense mechanisms, the loss of leaf area would be significantly higher than it actually is (Coley & Kursar 1996).

Constitutive vs. induced defense

Defenses of plants may be either constitutive or induced by the attack. Constitutive defenses are preventive, the defense mechanisms are present in the leaf no matter if there is an attack or not. As for induced defense, the plant is able to identify if an insect starts feeding and releases different kinds of signals that start the defensive reaction. Whether the defense is preventive or reactive is due to benefit versus cost, as plant defense mechanisms are expensive. The available resources can therefore be used either for growth or for defense. Thus, an investment in defensive mechanisms without a herbivorous attack might be a waste of resources (Fürstenberg-Hägg et al. 2013). Accordingly, induced defenses are advantageous if (1) the defense costs are high and if (2) there is a variance in time or space and the tree is not under permanent attack or if (3) there are tradeoffs between the defense against herbivores and other enemies or different herbivore species and the defense against the one promotes the other. While the reduced costs are an advantage, the plant may suffer high damage during the time necessary to establish the defense after the start of the attack (Frost et al. 2008).

Direct defense vs. indirect defense

Direct defense describes physical barriers of a plant that deter the herbivores from causing damage as well as chemical compounds (generally secondary metabolites) that are repellent, anti-nutritional or toxic to the herbivores. The plant's food quality for the herbivores decreases. If a plant attracts the natural enemies of the potential herbivores as a defense strategy, it is referred to as *indirect defense*. Therefore, the plants release a blend of volatiles, provide food like extrafloral nectar and fruit bodies or serve as housing by providing shelter or nesting sites. Both direct and indirect defenses can be either constitutive or induced. (Bruinsma et al. 2009, Dicke & Sabelis 1988, Fürstenberg-Hägg et al. 2013, War et al. 2012). In the next chapter, leaf traits will be discussed in regards to their value for direct defense.

1.2.1.1 Defensive traits

Leaf toughness

Leaf toughness is a physical defense against chewing insects and seems to be one of the most effective defense mechanisms of leaves against herbivores. The idea is simply that insect defoliators, especially small insects, are unable to feed on and digest the tough leaf tissue. Large amounts of cellulose, lignin and other cell wall compounds make the leaves tough. The process of toughening can only start when the leaf has reached its final size and there is no need for the cells to expand further. As toughness appears to be of such importance, leaves toughen as soon as physiologically possible, and it takes just days for the leaf to reach its full toughness, no matter how long the expansion takes (Figure 2 – Coley 1987, Coley 1983b, Kursar & Coley 2003, Massad 2012, Spight & Wylie 2001).

Pubescence

Hairs or trichomes on the surface may have different purposes, including water retention or increased resistance to mammals (especially spines). Furthermore, hairy leaves are also a way to keep the insects from damaging the leaves. This could be because either the insects are too small in relation to the hairs to reach the surface of the leaf or they are not strong enough to fight their way through the hairs.

This defensive trait affects the epidermis and is in many cases a simple but effective method that prevents the leaf from damage. Nevertheless, Coley (1983a) found pubescence as the only positively related trait to herbivory not because the hairs make the leaf attractive to herbivores but because pubescence negatively relates to all other defenses. Pubescence seems to be an easily visible and notable defense characteristic that enables to identify poorly defended leaves. However, hairs or trichomes offer no protection against leaf mining insects and larvae. These specially adapted animals tunnel in the parenchyma between the two layers of the epidermis (Coley 1983a; Spight & Wylie 2001).

Specific leaf area (SLA) and leaf area (LA)

Higher herbivory damage was recorded for leaves with lower specific leaf area (SLA) by Coley (1983b) comparing two tree taxa in Panama and by Cooke et al. (1984) investigating four species (out of two families) in Malaysia. Myster (2002) reported a proportionally higher loss of leaf area to herbivores for larger leaves (higher LA) of *Inga*.

Nitrogen content

Nitrogen content is a factor of high influence on the attractiveness of a leaf to potential herbivores. Higher nitrogen content means higher nutritional value. A leaf has the highest nitrogen concentration during its expansion (Figure 2) (Aide 1993, Kursar & Coley 1991). High protein levels and the absence of secondary cell walls in growing cells cause the high nitrogen content (Kursar & Coley 2003). Plant organic nitrogen levels are crucial for herbivores; they even influence their growth rates and reproductive potentials. Thus, nitrogen level is an important factor to consider in pest ecology and epidemiology (Spight & Wylie 2001).

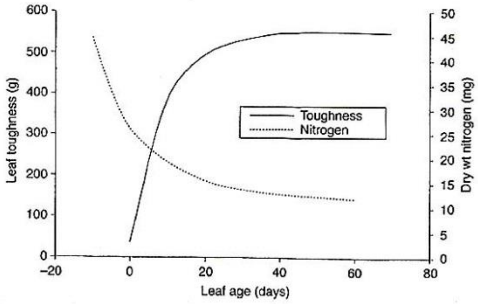


Figure 2: Toughness and nitrogen content as functions of leaf age of the rainforest tree *Ouratea lucens* in Panama (curves are fitted by Spight & Wylie 2001 after data of Kursar & Coley 1991; leaf age at full leaf expansion is 0 days).

Secondary metabolites

Secondary metabolites are not essential for the development of a plant, its growth or reproduction. Nevertheless, every plant owns a set of secondary metabolites of which some might play an important role as a defense mechanism (Coley 1987). Secondary metabolisms deter or even poison the herbivorous insects (Spight & Wylie 2001). The diversity of secondary metabolites is higher in the tropics than in temperate regions (Coley & Barone 2006). Increased concentrations of secondary metabolites correlate with higher levels of herbivory (Myster 2002) and can either be a reaction to the herbivory attack or a constitutive defense strategy (Karban et al. 1997). Besides alkaloids (e.g. nicotine and morphine) and highly toxic cyanogenic glycosides, phenolics are present in plants (Bernays et al. 1994). Especially phenols are an important secondary compound in regard to herbivory (Coley 1987), with tannins turning out to be of special interest as defensive trait. Nevertheless, the costs of tannin production result in lower growth or reduced leaf production (Coley 1983; Coley 1986, Sagers & Coley 1995).

1.2.1.2 The special case of young leaves

As already stated in chapter 1.2, leaves suffer the highest damage from herbivores when they are young. One possible explanation for this is that they are less fibrous and less tough. Therefore, they are easier to chew and to digest for the animals. The second explanation would be the higher nutritional value. Young leaves tend to have a higher water content, and the nitrogen content per mass is 2-4 times higher than of mature leaves (Coley 1983a, Coley & Kursar 1996, Kursar & Coley 2003, Spight & Wylie 2001, Turner 2004). One more aspect, evaluated by Kursar & Coley (2003), is the lower chemical defense of young leaves. According to their investigations, quickly expanding leaves contain an even lower amount of effective secondary metabolisms than slowly expanding leaves. That is why they are preferred by herbivores. To counteract the high damages, trees developed different kinds of strategies to protect their young leaves from herbivores, mostly phenological ones, which differ from the defense strategies for mature leaves (Coley 1983a).

Synchronous leaf expansion

The idea of synchrounous leaf expansion is that through the production of a great amount of newly flushed leaves at one time the produced biomass exceeds the amount that herbivores are able to consume and therefore reduces the herbivorous damage (Aide 1993). Investigations in different tropical trees showed that leaves that expanded at other times than during peak months suffered two to four times more damage than leaves flushed during peak months (Aide 1991, Aide 1993). Besides the oversaturation of the herbivores, also their temporal delay might cause the reduced herbivory rate: the peak of herbivory occurs chronologically after the peak of leaf production. Accordingly, the grazing rate is low before the herbivory peak is reached (Aide 1993).

Rapid leaf expansion

A study of ten species of five families shows that the above mentioned time gap between the peak of leaf production and the peak of herbivory is just two weeks in average (with two exceptions) (Lamaree et al. 2014). As a consequence, leaves have these two weeks of advantage to develop to a stage where they are less attractive to herbivores or where defense mechanisms are established.

According to Aide (1993) it takes 4-50 days for the leaf to expand from 20 % of its size to full size. The findings of other studies suggest leaf expansion periods of 10 to 40 days (Kursar & Coley 2003) or of less than six weeks (42 days) (Lamaree 2014). During expansion, on average, leaves double in size every five days whereas the fastest expanding species double in size every day (Coley & Kursar 1996).

In order to expand that rapidly, the leaves need high levels of enzymes for a fast construction. This means, the faster the leaves expand, the higher is the content of nitrogen and the more attractive are the leaves to herbivores. In addition, the quickly expanding leaves are less tough than slowly expanding leaves. These two factors may explain why Coley & Kursar (1996) and Kursar & Coley (2003) found higher herbivory rates and more damage on quickly expanding leaves. Surprisingly, the positive correlation between expansion rate and herbivory was still present after removing the two influence factors nitrogen content and leaf toughness through statistical modelling (Coley & Kursar 1996). As soon as a leaf reaches its full size it beginns to toughen. At the same time, the nitrogen content drops and the leaf is now less attractive to herbivores (Kursar & Coley 2003).

Delayed greening

Rapid leaf expansion often goes along with a delayed greening of the leaves. With such species, the young leaves appear white, red or pink due to their low chlorophyll content. This is caused by a delay of the chloroplast development, which increases rapidly as the leaf is expanded and toughens. The loss of potential photosynthesis during the time of expansion is outweighed by the otherwise wasted energy necessary for the development of the chloroplasts of potentially grazed leaf area. Species with delayed greening additionally have lower nitrogen contents at a given point of expansion compared to early greening species. As a consequence, trees with delayed greening lose fewer resources for a given amount of leaf damage (Coley & Kursar 1996, Coley & Kursar 1991, Kursar & Coley 2003).

1.3 Differences in herbivory quantities

Herbivory damage can be quantified either as leaf area removed per defined time, which is referred to as herbivory rate, or as missing leaf area at a certain point of time, called herbivory level. The variation in herbivory rates is high. The area removed by insects from a single measured leaf per day varies from 0.0003 % to 2.8 % in a tropical rainforest in Panama (Coley 1983a) or from 0.07 % to 0.99 % leaf area removed per month in Malaysia (Eichhorn et al. 2010). In one-time evaluations herbivory levels ranged from 6.15 % to 13.44 % of removed leaf area per species in Malaysia (Cooke et al. 1984) and from 0.9 % to 8.5 % in Bolivia (Poorter et al. 2004). Tree species of an Ecuadoran forest caught in a litter-trap showed herbivory levels from 2.49 % to 29.46 % (Cardenas et al. 2014). It needs to be considered that in contrast to other one-time evaluations all the leaf live-time damage is included here.

1.3.1 Interspecific

Differences in the quantity of herbivory depend on the tree species (Coley 1983a). Evidence of significant differences in herbivory rates and levels between species is given in numerous studies. These include investigations of two species in Puerto Rico (Myster 2002), of five species in Puerto Rico (Schowalter 1994), in Malaysia (Eichhorn et al. 2010), and in Panama (Paul et al. 2012), 15 species in Bolivia (Poorter et al. 2004), 28 species in Ecuador (Cardenas et al. 2014), 31 species in Costa Rica (Schnetzer 2014), and 47 tree species in Panama. For the latter, variations of more than three orders of magnitude in herbivory were observed (Coley 1987).

The difference of the defense mechanisms respectively their combination explains about 70 % of herbivory rate differences among the mature leaves of different species. Fiber resp. toughness and nutritional measures appeared to be the best indicators for herbivory quantity in the study of Coley (1987) where tannins, lignin, fiber, cellulose, water content, pubescence, and nitrogen explained 70 % of herbivory variations. Schuldt et al. (2012) included also geographical range characteristics and was able to explain 70.3 % of interspecific herbivory variation with leaf dry matter content (LDMC), mean local abundance, climatic niche breadth, and niche marginality.

Differences in herbivory are also evident between early successional species with less leaf damage and late successional species with more damage (Myster 2002, Schonwalter 1994). Contrary findings were reported by Poorter et al. (2004). They found a decrease in herbivory rates with increasing successional index and similar herbivory levels for early and late successional species, with a peak for the middle successional species. Higher herbivory rates do not inevitably mean lower fitness. If a pioneer tree and a shade tolerant tree suffer the same amount of herbivory damage, in terms of removed leaf area, the impact on the pioneer tree will be much smaller. Pioneer trees are able to cope with higher herbivory rates because their leaves are cheaper in terms of resource consumption and they have higher growth rates (Coley 1983a).

Myster (2002) found more herbivourous damage on *Inga* leaves than on *Cecropia* leaves. He suggested that the fixation of nitrogen by the tree and the consequently nutrient richer leaves could be a reason for attracting more insects and leading to higher rates of herbivory in leguminous species. The interspecific variation in leaf tissue loss due to herbivores in woody plants is already obvious during leaf expansion. Kursar and Coley (2003) observed herbivory rates during expansion time ranging from 20 % to 60 % of missing leaf area.

1.3.2 Intraspecific

Differences in herbivory levels of individuals within a certain species determine their success and thus the development of anti-herbivore defenses. As herbivory may influence reproduction and tree performance, intraspecific variations contribute to plant selection and accordingly contribute to the evolutionary process of a species (Coley 1983a).

The study of an understory shrub species in Costa Rica showed intraspecific variations in herbivory rates with single values ranging from 0.00 to 25.95 % (Marquis 1984). A high intraspecific variation in herbivory levels was also reported by Cardenas et al. (2014) for 28 investigated species.

Contrary findings exist from a comparison of *Trichilia* and *Cecropia* in Panama. Intraspecific variations in herbivory levels are similar for both species although they differ in life history, defenses and herbivory levels (Coley 1983b). A research on *Inga* and *Cecropia* delivered equal leaf losses for the individuals within one species (Myster 2002).

1.4 Herbivory and tree performance

The loss of leaf tissue reduces the tree’s rate of carbon fixation and means a loss of the plant’s resources (Marquis 1984). The loss of leaf material to total defoliation in extreme cases can be substantial for a tree and will negatively affect a tree’s performance (Turner 2004). Decreased growth rates, reproduction and competitive fitness as well as higher tree mortality are the consequences (Aide 1993, Coley & Barone 2016, Coley & Barone 1996).

For my study, only growth rates and mortality rates define the tree performance, and I look at it from an interspecific point of view.

1.4.1 The effect of herbivory on the growth rate

There are two possible relations of herbivory and growth rate: the damage causes either reduced growth, or the investment in defense results in fewer resources for growth and thus lower growth rates (Coley et al. 1985). The latter is supported by a study that shows a negative correlation between growth rates and investments in defense (Coley 1988) and is explained by the growth-defense tradeoff theory.

The theory of *growth-defense tradeoffs* builds on the assumption that a tree (or a plant in general) has a limited pool of resources to use either for growth or for defense. Investing more into the one will result in fewer resources for the other. As growth and defense both are essential for the tree in order to survive and reproduce, the growth-defense tradeoffs have high ecological, agricultural, and economic consequences (Huot et al. 2014). Based on the growth-defense tradeoff theory Coley et al. (1985) suggest that trees with slow growth rates and high investments in defense mechanisms are favored in low nutrient habitats by natural selection. At the same time, trees with high growth rates and low levels of defense are favored in nutrient rich environments.

In a reforestation in Costa Rica, negative impacts of herbivory damage on tree growth in the first six month after planting were still evident five years later (Massad 2012). Experiments on the understory shrub *Piper arieianum* with imitated herbivory damage concluded that ≥ 30 % defoliation had great influence on the growth within the next two years for small and medium size plants, compared to control plants. Growth of large plants suffered no decline by the herbivore damages. These findings might be due to the higher absolute biomass of large plants and the accompanying higher compensation capacity (Marquis 1984). Trees of a reforestation in south Costa Rica showed a negative correlation between herbivory level and growth rates in two studies (Feldmeier 2017; Schnetzer 2014), but here herbivory was only bases on rough semi-quantative estimates.

There are also studies that found no connection between herbivory and reduced growth for saplings or seedlings as in two investigated tree species in Puerto Rico (Myster 2002), five species in Malaysia (Eichhorn et al. 2010) or 32 woody species in Panama (Aide 1993). Eichhorn et al. (2010) realized that just studies reporting a high herbivorous damage observed a decrease in growth rates due to herbivory. Obviously, a tree can cope with the loss of a small portion of biomass, and only excessive herbivorous damage has a negative impact on growth (Nair 2007).

Saplings which were protected from insecticides, which resulted in lower herbivore pressure, grew faster compared to unprotected individuals on a former pasture in Panama (Plath et al. 2010) and in a forest in Panama as well (Pearson et al. 2003). Lower herbivory rates and 10 times higher growth rates were also found in plants in protected environments compared to exposed plants of the understory shrub *Psychotria horizontalis* in Panama (Sagers & Coley 1995).

1.4.2 Herbivory and mortality

Through increased mortality caused by high amounts of herbivorous leaf damage, herbivores have a high selective power (Coley 1985). Four out of five species in Malaysia showed that greater herbivorous damage on mature leaves causes higher mortality within the following year. Findings also indicated that herbivory might contribute to different survival rates among different light habitats (Eichhorn et al. 2010). In one out of three species in Panama, higher herbivory rates increased the probability of trees to die (Pearson et al. 2003). Finca La Bolsa, a reforestation site close to my research area, was investigated two times within four years. Both times herbivory had no impact on mortality and there was no influence of herbivory from 2012 on mortality in 2016 (Feldmeier 2017, Schnetzer 2014). A correlation between herbivory and mortality was neither present in Puerto Rico (Myster 2002) nor in Panama (Plath et al. 2010). In accordance, in a study in Australia, Doust et al. (2008) describe herbivory as a very unlikely factor to explain mortality rates.

A negative relationship of herbivory against mortality with a missing connection between herbivory (in terms of defoliation) and reduced growth might be caused by herbivores feeding on other parts of the plant (e.g. roots, bark or stem). Another idea suggests that damages by herbivores might facilitate pathogens leading to future mortality (Eichhorn et al. 2010). Defoliation can be the start of the process of herbivorous attacks on the whole tree (Spight & Wylie 2001).

1.5 The project COBIGA – Corredor Biológico La Gamba

After big losses of primary forest areas in Costa Rica because of clearings for plantations and pastures, the country has nowadays a high share of protected land. Around 27.5 % (as of 2014) of the country's terrestrial area is under protection (Trading Economics 2017). The current issue discussed by environmentalists is the fact that the protected forest areas are single patches with missing connectivity and genetic exchange. Biological corridors represent a suitable solution to that problem: artificial but close-to-nature forest belts that connect the isolated forests. Concepts of such corridors may vary a lot in dimension, from the Meso-American Biological Corridor linking North and South America via Central America to small local corridors (Weissenhofer et al. 2016).

The two National Parks in the Region of Golfo Dulce, Corcovado National Park and Piedras Blancas National Park are already, but not sufficiently, connected through the *Reserva Forestal Golfo Dulce*. The high biodiversity in the lowland rainforests of the Golfo Dulce region is also due to the floral and faunal exchange with the enclosed highland rainforests of Fila Cal. In difference to the lowland rainforest, protected through the two national parks mentioned above, there is no protection for the mountain rainforest. This initial situation initiated the project COBIGA – Corredor Biológico La Gamba, in which international as well as national organizations work together. The aim is to protect the mountain rainforest and to create a connection to the lowland rainforests while ensuring a sustainable development of the region (Weissenhofer et al. 2016).

The corridor is supposed to connect the biggest possible patches of forest with the most minimal effort. Special focus during the planning phase was put on the closing of forest glades, the reforestation of former pastures and plots along rivers. Where possible, natural succession should create the connecting forest bends. On some plots, e.g. former pastures due to their compacted soil, reforestation is essential to create a new forest. Altogether, 45 hectares were reforested with 37,500 trees of more than 200 species until June 2016. Two areas, *Finca La Bolsa* and *Finca Amable*, owned by the *Rainforest of the Austrians* (*Regenwald der Österreicher*), are objects of different kinds of scientific research by the *University of Vienna* and the *University of Natural Resources and Life Science Vienna* (Weissenhofer et al. 2016).

Another aspect of the COBIGA Project is the function of the newly established secondary forest as CO_2 sink from the atmosphere. The *University of Natural Resources and Life Science Vienna* conducts this reforestation project on 14.6 hectares of the future corridor. This reforested area should sequester 4,400 tons of CO_2 within 30 years (Universität für Bodenkultur Wien n.d.).

1.6 Aim of this work

This research investigates the effect of herbivory on the performance of different tree species in the reforestation site Finca Amable in La Gamba (Costa Rica) to answer the following research questions:

1) Are there significant differences in herbivory levels between the species?
2) Can leaf traits explain the differences in herbivory levels?
3) Does the herbivory level influence growth and mortality of the trees?

The findings should contribute to the design and species selection for further reforestations.

2 Methods

2.1 Study area

The village of La Gamba (8°42’33’’N-83°11’04’’W) is situated in the southwest of Costa Rica in the district of Golfito in the Golfo Dulce region (Figure 3). The Municipality of La Gamba is bordered by the Piedras Blancas National Park to the north and west, by the Refugio de Vida Silvestre Golfito to the south and southeast, and by the Inter-American Highway to the east (Klingler 2008).

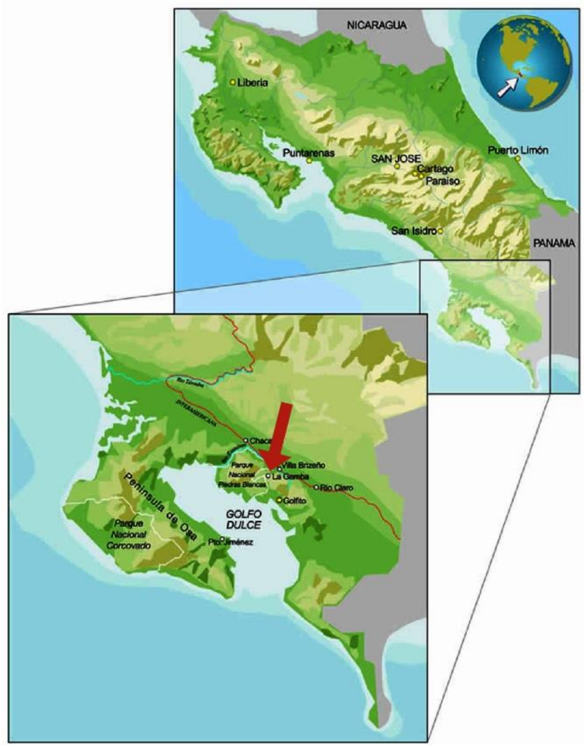
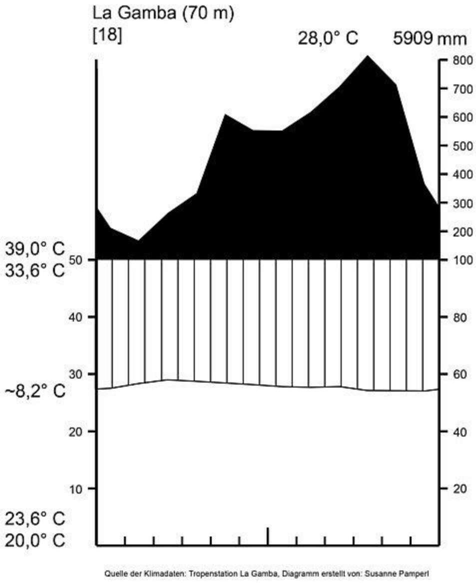


Figure 3: The Golfo Dulce region (adapted from Weissenhofer et al. 2008a)

Meteorological data collected at the *Tropenstation La Gamba* (La Gamba Field Station) between 1999 and 2016 gives a good insight into the climate of the local rainforest (Esquinas rainforest). With rain on about 300 days a year and an annual precipitation of almost 6,000 mm, it is one of the wettest lowland rainforests not just in Costa Rica but also in all of Central America. The rainy season lasts from May to November and dry season is from December to April. Dry season in the Esquinas rainforest does not follow the common definition, as there is still rain (but less) and no water deficit (see Figure 4). During the drier months, some trees drop their leaves. Due to La Gamba’s location in the equatorial zone, there is little variation in temperature throughout the year. The average temperature is 28.3 C. (Weissenhofer & Huber 2008; Tropenstation La Gamba n.d.)



Quelle der Klimadaten: Tropenstation La Gamba, Diagramm erstellt von: Susanne Pamperl

Figure 4: Climate diagram, Tropenstation La Gamba (La Gamba field station) 1998-2016 (source: Tropenstation La Gamba, Susanne Pamperl; comma signifies dot)

Due to the humid climate and the orographic formation, the Golfo Dulce region is very rich in flora and fauna. The intensified agricultural exports and livestock industries during the last century led to a decline of primary and secondary forest area, which shrunk to the protected areas like the two national parks, a forest reserve, and national wildlife refuges (Weissenhofer et al. 2008b).

2.2 Study site

Finca Amable is a reforestation site on a former pasture in the village of La Gamba. The total area is 13.7 hectares. It borders with the Piedras Blancas National Park along the river in the north, palm oil plantations, pastures, and an unpaved road. Until the end of the year 2015, 10,700 tree seedlings of more than 200 different native tree species had been planted (Weissenhofer et al. 2016). The area consists of 11 sectors, which were continuously replanted, starting with sectors 1 to 4 along the road to La Gamba in 2012. Afterwards sectors 5 and 6, 7 to 9 and, most recently, the final sectors 10 and 11 followed (see Figure 5).

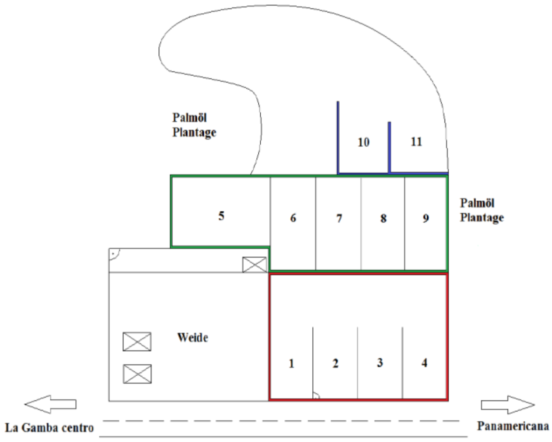


Figure 5: The reforestation site *Finca Amable*: arrangements of the sectors 1 to 11. (Source: Katharina Schwarzfurtner)

The study area features trial plots with a specific plant design in order to investigate the effect of functional diversity. Different combinations of high wood density tree species (> 0.5 g/cm³), low wood density tree species (< 0.5 g/cm³) and legumes were planted in the trial plots. Each plot consists of six rows with six trees each. The distance between the rows ist 4 m, and trees within a row are separated by 3.5 m. The 36 trees per plot are of nine different species, four individuals each. Plots without planting were established as reference areas with natural regeneration (Figure 6) (Kleinschmidt et al. 2016; Kleinschmidt 2013). For this study, research took place at the 24 plots from sectors 1 to 6 because of the higher age of the trees and the related bigger size and higher number of leaves.

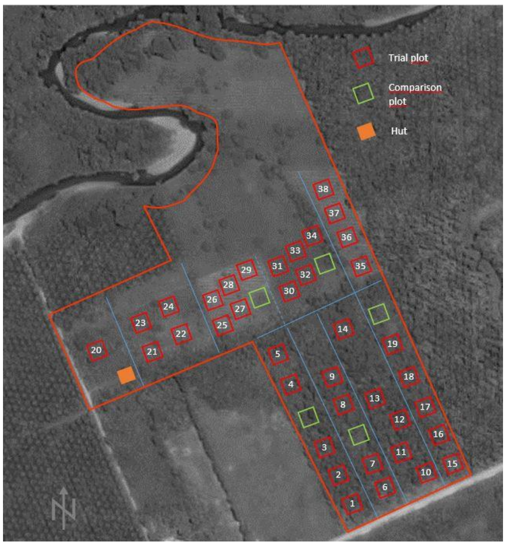


Figure 6: Arrangements of the trial plots in the sectors 1 to 9 at Finca Amable. Sector borders in blue; trial plots are red squares with numbers; comparison plots are green squares. (adapted from Kleinschmidt)

2.3 Measurement of herbivory levels

With reference to Paul et al. (2012) and Dawson et al. (2008), herbivory was quantified multiplying the **abundance A** (proportion of leaves damaged) and the **severity S** (proportion of missing leaf area per damaged leaf). I calculated herbivory levels for three branches per tree as abundance x severity. By calculating the mean of these three measurements, I received the **herbivory level H** per tree as percent of missing leaf area at one point of time (Schowalter 1994). In the case of compound leaves, one leaflet was considered as unit; in case of single leaves, the whole leaf was considered (Poorter et al. 2004). The term “leaf” in the context of the collected data refers to the unit and includes both, the leaflets and the single leaves. The number of species where either leaf or leaflet was used for herbivory measurements, also per functional group, is given in Table 1.

Table 1: Number of leaves and leaflets used as unit for herbivory measurements overall and per functional group. HD = high wood density, LD = low wood density

	leaf	leaflet
All species	9	14
HD species	6	3
Legumes	0	7
LD species	3	4

2.3.1 Sampling and data collection

Data collection took place from 2 February to 22 February, 2016. During this time, herbivory abundance of the trees was recorded in the field, and the leaves for the evaluation of the herbivory severity were collected and scanned. The processing of the leaf scans was done from December 2016 to March 2017.

All species with a planting abundance of more than 25 individuals on all trial plots of Finca Amable were taken into account. From these 26 species, three had to be excluded for various reasons (individuals of *Schizolobium parahyba* were too high to reach the leaves, *Buchenavia costaricensis* and *Licania operculipetala* had just four individuals big enough in the relevant sectors) leaving 23 species for investigation (Table 2).

Table 2: Selected species, their functional group, leaf anatomy and unit for herbivory measurements; excluding reasons for excluded species. HD = high wood density, LD = low wood density, Leg = legumes

N° planted trees	selected species	functional group	leaf anatomy	unit
30	*Anacardium excelsum*	LD	simple leaf	leaf
62	*Aspidosperma spruceanum*	HD	simple leaf	leaf
30	*Astronium graveolens*	HD	odd-pinnate, mostly opposite	leaflet
27	*Pachira sessilis*	LD	digitate	leaflet
46	*Brosimum utile*	HD	single leaf	leaf
33	*Bursera simaruba*	LD	odd-pinnate, opposite; up to 9 leaflets	leaflet
29	*Calophyllum longifolium*	HD	simple leaf	leaf
34	*Castilla tunu*	LD	Simple leaf	leaf
37	*Cedrela odorata*	HD	even-pinnate; 10-22 opposite leaflets	leaflet
27	*Cojoba arborea*	Leg	pair-pinnate	leaflet
62	*Hieronyma alcherneoides*	HD	simple leaf	leaf
41	*Lonchocarpus macrophylla*	Leg	odd-pinnate, opposite	leaflet
49	*Minquartia guianensis*	HD	simple leaf	leaf
32	*Ormosia macrocalix*	Leg	odd-pinnate, opposite	leaflet
46	*Peltogyne purpurea*	HD	even pinnate (2 leaflets)	leaflet
47	*Platymiscium curuense*	Leg	odd-pinnate (5 leaflets)	leaflet
36	*Dussia macroprophyllata*	Leg	odd-pinnate, opposite	leaflet
43	*Spondias mombin*	LD	odd-pinnate, opposite	leaflet
29	*Tachigali versicolor*	Leg	even-pinnate, opposite	leaflet
49	*Terminalia amazonia*	HD	simple leaf in rosettes	leaf
27	*Virola koschnyi*	LD	simple leaf	leaf
65	*Vitex cooperi*	LD	odd-pinnate (3-5 opposite leaflets)	leaflet
40	*Zygia longifolia*	Leg	bi-pinnate; Y pinnae (6 leaflets per leaf)	leaflet
	excluded species	**reason**		
26	*Buchenavia costaricensis*	just 4 individuals big enough in sectors one to six		
46	*Inga sp.*	after determining the species the abundance of each species is < 25		
26	*Licania operculipetala*	just 4 individuals big enough in sectors one to six		
38	*Schizolobium parahyba*	all trees in sectors one to six are too high to reach leaves		

All existing trees per species were put in an Excel table and assigned with a random number using the function *RAND()*. The individuals were ranked descending afterwards using those numbers. For the random sample, the first five alive trees higher than 1 m of each species from plot 1 to 6 were selected, beginning from the top of the table. Information on height was obtained from the 2015 measurements for plot one to four and the 2016 measurements for plot five and six (Kleinschmidt 2017). In a next step, it was ensured that for every species a maximum of two individuals originate from the same plot and that the five sampled trees originate at least from three different sectors. Exceptions of this sector regulation were

Terminalia amazonia, Spondias mombin, Castilla tunu, Pachira sessilis and *Virola koschnyi,* as they were just present in two sectors (Table 2). Additionally, *Virola koschnyi* just provided big enough individuals in two plots leading to three individuals from the same plot in the sample. If a tree appears to be unsuitable for herbivory level determination or dead in the field, the next individual from the random list replaced it. This occurred due to the bad performance of the tree and therefore a too small number of adult leaves (< 30 leaves), or because it was impossible to cut branches from higher trees as they had just a few due to their growth form.

Abundance

Three branches per tree were taken into account to evaluate the abundance. I chose the branches from the bottom, the middle and the top of the tree and from different sides (Figure 7).

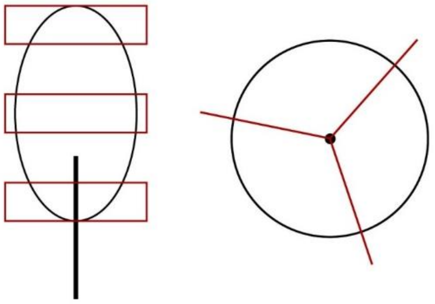


Figure 7: Position of the branches for herbivory determination on the tree vertically and horizontally.

If a tree was too tall to reach the top even with scissors on a stick, I used the highest possible branch (about 6-7 m) and took the middle one from in between. If the growth form was umbrella-shaped like *Bursera simaruba* the three branches were chosen from three different spots in the crown. If a tree did not have three countable branches due to its growth form, the leaves were chosen from the different levels of the main shoot. The first 15-25 leaves per branch (ideally around 20 depending on growth form and leaf shape) starting from the end of the branch were taken into account. Counting started with those leaves appearing mature according to color, thickness, shape, and surface. If a tree had less than 60 leaves in total, all leaves were counted. Just leaves actually missing leaf tissue were considered affected. The share of damaged leaves of the total number of counted leaves was recorded. From all three branches, the abundance of herbivory per tree was derived calculating the average of the percentage of damaged leaves per branch.

Severity

From the affected leaves counted for abundance, the first one, the last one, and the middle one of each branch – nine leaves per individual – were collected. If one branch did not have three damaged leaves this number was accordingly lower. If the damage of a leaf was so severe that the shape was not visible anymore, a close-by leaf, which appeared to have about the same size and shape, was also collected as reference for the potential size of the affected leaf (Eichhorn et al. 2010). Afterwards, all leaves were scanned with the Canon scanner *CanoScan LiDE 120*. The single scans at a solution of 400 dpi were saved as high quality JPEG files. Some leaves were bigger than the scanner, so I cut them into pieces and scanned them separately (Figure 8). I further processed the scans in *Adobe Photoshop CS5* by increasing contrast and removing the petiole to get two versions of each scan: one showing the existing leaf area and one showing the potential leaf area by adding missing outlines or using the reference leaf (Figure 8). Dead leaf tissue that seemed to originate from herbivores was minimal and therefore ignored.

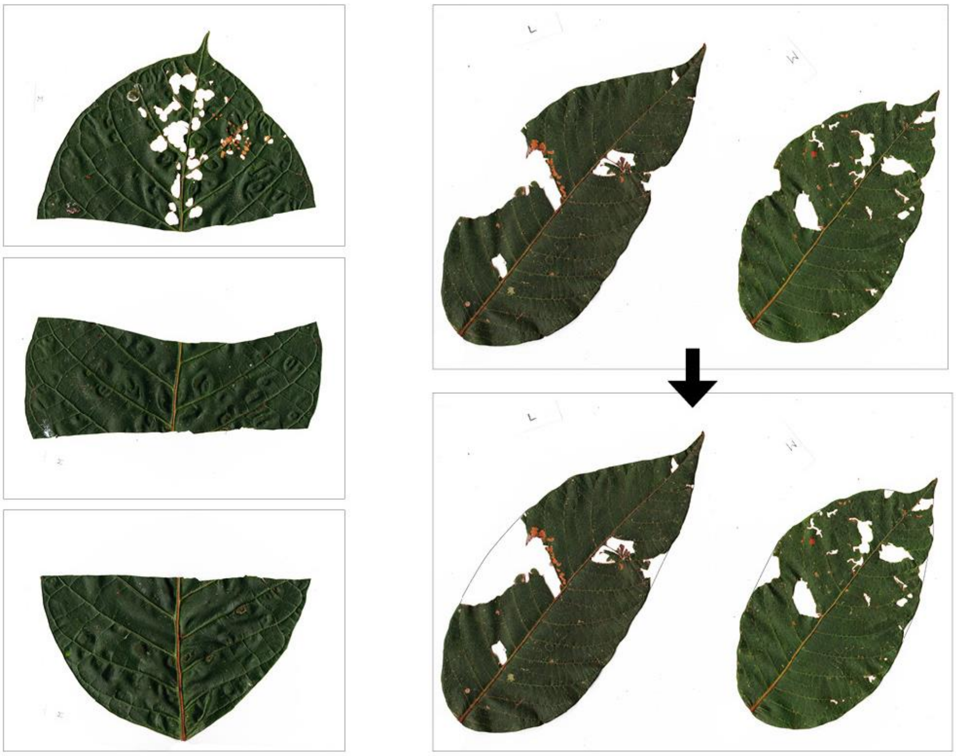


Figure 8: Leaf scans – a big cut leaf scanned in three pieces (left), and an example of leaves before and after adding the lines of the potential leaf area (right).

The existing leaf area was calculated using *ImageJ* by excluding holes in the area analysis of the original scans. The potential leaf area was generated using the scans with the added outlines and including the holes in the area analysis. With this data, the percentage of missing leaf area was calculated.

2.3.2 Growth rate and leaf traits

Leaf trait data – except for LA – were obtained from Hackl (2016) and Eletzhofer (2017). They conducted the measurements on sun-exposed leaves in April 2015 and February 2016. The trees for the measurements originated from the same plots of Finca Amable as the individuals for my herbivory quantification. The number of cases for measurements of leaf traits varied from a minimum of one individual to a maximum of twelve individuals. Kleinschmidt & Hietz (unpublished) evaluated growth and mortality rates for all trees of the reforestation experiment (Table 3).

Table 3: n per species and trait: L-TH, CHL, L-TG, LDM, SLA, N and C (Eletzhofer 2017; Hackl 2016); LA (own data); G and M (Hietz & Kleinschmidt unpublished).

species	L-TH	CHL	L-TG	LDM	SLA	N	C	LA	G	M
Anacardium excelsum	7	11	7	6	7	5	5	45	142	130
Aspidosperma spruceanum	10	12	8	8	8	6	6	45	240	116
Astronium graveolens	6	6	6	5	6	5	5	29	150	112
Brosimum utile	4	6	4	4	4	2	2	16	175	118
Bursera simaruba	5	5	5	4	5	5	5	45	155	66
Calophyllum longifolium	6	8	7	6	6	6	6	37	136	66
Castilla tunu	3	3	3	3	3	2	1	29	119	97
Cedrela odorata	5	5	5	5	5	4	4	42	143	126
Cojoba arborea	6	7	2	7	7	8	8	41	129	64
Dussia macroprophyllata	4	4	4	4	4	4	4	45	121	54
Hieronyma alchorneoides	10	10	10	10	10	8	8	45	277	133
Lonchocarpus macrophylla	6	5	6	5	5	4	4	44	169	107
Minquartia guianensis	7	9	7	7	7	3	3	41	206	119
Ormosia macrocalix	6	6	6	5	6	3	3	45	126	47
Pachira sessilis	5	5	5	5	5	5	5	43	92	65
Peltogyne purpurea	7	10	7	6	7	7	7	43	176	96
Platymiscium curuense	4	4	4	4	4	3	3	35	159	139
Spondias mombin	5	5	5	5	5	4	4	43	162	100
Tachigali versicolor	4	4	4	4	4	3	3	45	139	77
Terminalia amazonia	6	8	6	6	6	4	4	42	174	75
Virola koschnyi	4	4	4	4	4	4	4	44	103	89
Vitex cooperi	3	3	3	3	3	3	2	45	267	120
Zygia longifolia	7	11	7	7	7	4	4	45	168	158

Chlorophyll content

The chlorophyll content expresses the “greenness” of a leaf. Chlorophyll content per unit relates to the photosynthetic capacity of a plant and depends on nutrient availability and environmental factors like stress due to drought, cold or salinity. The chlorophyll content was measured using the *SPAD 502 Plus Chlorophyll Meter* (Konica Minolta, Osaka, Japan) (Eletzhofer 2017, Hackl 2016). The SPAD measures how much light of the wavelength absorbed by chlorophyll is passing through the leaf tissue (Palta 1990). In the field, the value was measured six times per leaf, three times leaf margin on both sides of the midrib (Figure 9), in order to minimize measuring errors. Measurements on leaf-veins were avoided. In the end, the mean of the six values was calculated using the function *average* of the *SPAD 502* (Eletzhofer 2017, Hackl 2016).

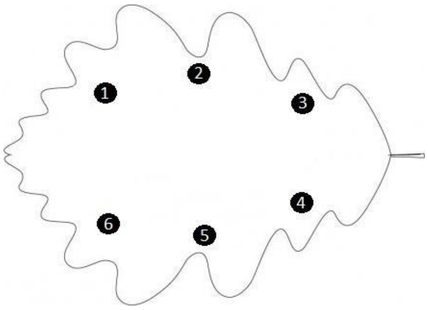


Figure 9 : Example for the six SPAD measurements on a leaf (Hackl, 2016).

Leaf thickness

Leaf thickness was measured with an analogue micrometer to 0.01 mm. Two measurements per leaf were averaged. Leaf-veins were avoided. (Eletzhofer 2017; Hackl 2016)

Leaf toughness

A self-made construction including two clips, one mounted to an electronic force gauge (Sauter FK25 – Sauter GmbH, Balingen, Germany) and the other mounted to a screw was used to measure toughness. A 5x1 cm piece of leaf lamina was cut out from the central section of the leaf, but away from the midrib. After clamping the narrow ends of this piece into the two clips, the leaf was slowly stretched using the screw until it ripped apart. The force gauge stores the maximum force, which is the force in Newton necessary to tear the defined area of leaf lamina apart (Eletzhofer 2017, Hackl 2016).

Leaf area (LA)

The only trait captured myself and directly measured on the same leaves used for herbivory measurements is the *leaf area*, which, in this research, refers to one leaf or leaflet. I converted the number of pixels from the scans of the (potential) leaf area in cm².

Specific Leaf Area (SLA)

SLA describes the ratio of leaf area to leaf dry mass. A low SLA indicates a thick lamina, high tissue density or both. In this case, leaf area refers to the whole compound leaf and was measured by Hackl (2016) and Eletzhofer (2017). They scanned the single leaf or all leaflets of compound leaves after collection and evaluated the leaf area with Photoshop or Image J. Thereafter the leaves where dried at 80 °C in the dry chamber of the field station La Gamba for at least 48 hours. The dried leaves' weight without petiole and rachis was measured to 1 mg.

Leaf Dry Matter Content (LDMC)

LDMC is a measure for the ratio of dry weight to saturated weight of a leaf. The dry weight was measured using the method described for SLA. Saturation weight was measured right after returning from the leaf collection to the field station. For transportation, the leaves were stored in black plastic bags. Efforts were made to saturate leaves by placing them on damp paper or putting the petioles into water (Eletzhofer 2017, Hackl 2016).

Carbon (C) and Nitrogen (N)

The content of C and N were derived from dried leaf samples. They were ground in the *Mixer Mill MM2* (Retsch GmbH, Haan, Germany) and the necessary amount weighed accurate to 1 µg. With mass spectroscopy (DeltaPLUS, Finningan MAT, Bremen, Germany) the content of C and N in percent was measured at the Department of Microbiology and Ecosystem Science of the University of Vienna (Eletzhofer 2017).

Tree growth

Trees were measured in 2013, 2015 and 2016 using a marked pole and a laser rangefinder for taller trees, and *growth* rates were calculated as height growth in meter per year (Kleinschmidt 2017).

Mortality

Mortality rate indicates the probability of an individual of a certain species to die. Mortality rates for the 2017 measurements were calculated using the formula

$$\textit{mortality rate} = \log(n_0) - \log(n_1) / dt_{mean}$$

n_0 is the number of living trees at the first inventory (or planted trees) and n_1 is the number of living trees at the second inventory. Dt_{mean} is the mean time between the two inventories in years (Hietz & Kleinschmidt unpublished).

2.4 Data storage

In the field, data was recorded on paper and afterwards the records were entered into a *Microsoft Excel2013* spreadsheet. The leaves were marked on their surface and transported in zip lock bags. The scans of the leaves were stored as JPG files.

2.5 Data analysis

IBM SPSS Statistics 24 was used for data analysis. I tested the distribution of the data using a Kolmogorov-Smirnov-Test, considering $p < 0.05$ as a significant deviation from a normal distribution (Bühl 2014). All averages were calculated using the mean and the standard deviation (SD) as measure of dispersion. To ensure normally distributed data, some of the data was transformed prior the analysis as shown in Table 4. The closest approximation in a qq-plot to a normal distribution for herbivory data was achieved using the log(asin(sqrt(x))+0.01) transformation. Consequently, I applied the transformation also for abundance and severity.

Table 4: Applied data transformations to achieve normally distributed data

variable	applied transformation
severity	log(asin(sqrt(x))+0.01)
abundance	log(asin(sqrt(x))+0.01)
herbivory	log(asin(sqrt(x))+0.01)
L-THI	sqrt(x)
mort	log(x)
LA	log(x)

To calculate correlations between herbivory levels and traits, growth and mortality, a Pearson-test was used. For correlations on intraspecific variation data (between herbivory level and range, minimum and maximum), I used the Spearman's rank correlation coefficient.

The classification of the tree species in the functional classes of high wood density (> 0.5 g/cm³), low wood density (< 0.5 g/cm³) and legumes was borrowed from Kleinschmidt et al. (2016) and was already defined for the planning of the planting design for the Finca Amable reforestation.

I used a Welch test for the comparison of herbivory levels between species because of missing variance homogeneity and one-way ANOVAs for the comparison of likewise transformed herbivory levels between functional groups. With one-way ANOVA for repeated measurements, I analyzed the differences between herbivory, severity and abundance of top, bottom and middle branches. In case of missing sphericity, a correction using the Epsilon of Greenhouse Geissler was applied. I used a multiple regression to test how much abundance, severity and functional group influence herbivory levels (in relative numbers) and to test how much of herbivory variations are explained by the traits.

3 Results

3.1 Herbivory levels

3.1.1 Interspecific

Almost two thirds of the cases (14 out of 23) were within the range of 0-5 % herbivory level. The maximum for all other 5 %-classes up to 35 % were only three species per class (Figure 10). Severity as well showed the species in the 0-5 %-class with a constant decrease ending at the 30-35 %-class. I observed different frequency patterns for abundance, where I found between one and three species in most of the 10 %-classes. Two exceptions were the 50-60 %-class counting six species and the 80-90 %-class counting four species. Severity showed a stronger correlation with herbivory (r = 0.962, p = <0.001) than abundance (r = 0.487; p = 0.018).

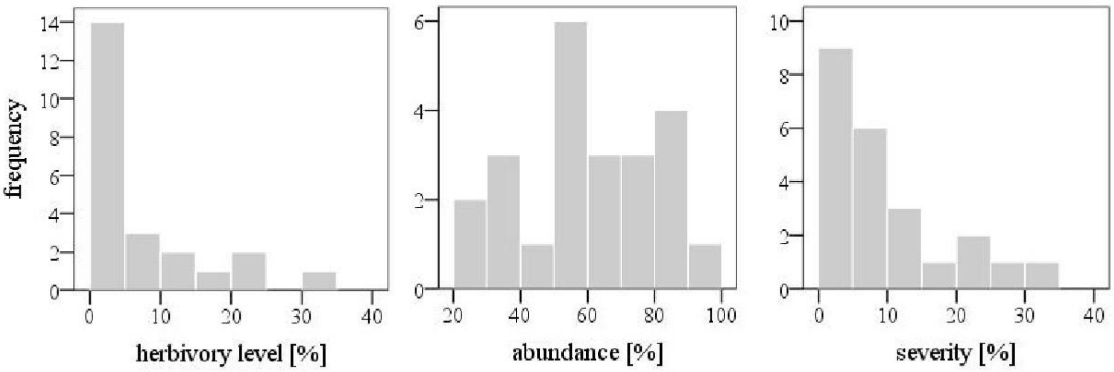


Figure 10: Frequencies of herbivory level, abundance and severity per species grouped in 5 %-classes for herbivory and severity and in 10 %-classes for abundance.

A multiple regression (corr. $R^2 = 0.975$) proofed that severity (beta-coefficient = 0.904, $p < 0.001$) is a stronger predictor for herbivory than abundance (beta-coefficient = 0.181, p = 0.001; Table 5).

Table 5: Coefficients of the multiple regression. Effects of severity, abundance and species on herbivory level.

	Non-standardized coefficients		standardized coefficients		
	regression coefficientB	**standard error**	**Beta**	**T**	**Sig.**
(constant)	-17.807	2.894		-6.154	.000
severity	.904	.036	.915	25.421	.000
abundance	.181	.044	.160	4.126	.001

dependent variable: herb

The herbivory levels of the 23 tested species ranged from 0.25 % (*Astronium graveolens*) to 31.42 % (*Pachira sessilis*) (Figure 11). The average herbivory level was 7.53 ± 8.14 % (mean ± SD). Looking at the three functional groups, the LDspecies (grey) accounted for the highest as well as for the lowest overall herbivory level resulting in a mean of 8.42 ± 10.81 % (SD). HDspecies (blue) ranged from 0.55 % to 15.46 % with a mean of 5.03 ± 5.01 % (SD). Legumes (orange) showed herbivory levels ranging from 1.30 % to 22.79 %, the mean was 9.87 ± 8.72 % (Figure 12).

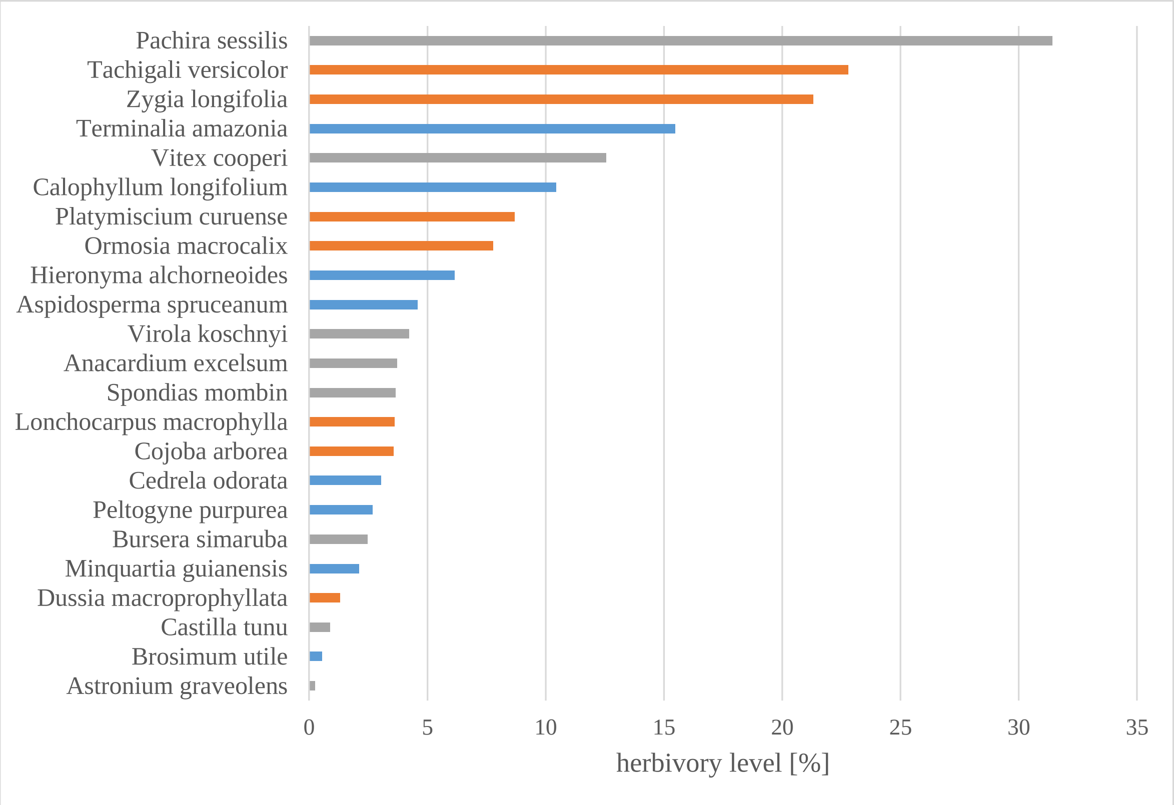


Figure 11: Average herbivory levels per species (mean). n per species = 5; blue = HDspecies; grey = LDspecies; orange = legumes

Herbivory levels between the species showed highly significant differences F(22, 33.321) = 7.781, p < 0.001 (Table 6). The three functional groups had no significant influence on herbivory levels F(2, 20) = 1.033, p = 0.374 (Table 7). Furthermore, legumes did not differ in herbivory levels from other trees (HD plus LD species) F(1, 21) = 1.382, p = 0.253; neither did HDspecies differ from LDspecies (legumes excluded) F(1, 14) = 0.645, p = 0.435.

Table 6: Welch-Test – Differences of herbivory levels between species

	Statistics[a]	Df1	Df2	Sig.
Welch-Test	7.781	22	33.321	.000

Asymptotic F-distributed

Table 7: One-way Anova – Influence of functional groups on herbivory level

Herbivory

	Sum Sq	Df	Mean Sq	F	p
between groups	.128	2	.064	1.033	.374
within the group	1.242	20	.062		
total	1.370	22			

Looking at H separated according to the functional groups, legumes showed a much higher range than HD and LD species but HD species had one outlier (outside 1.5 times the height of the box) and LD species one extreme (outside 3 times the height of the box). The median H for legumes is about twice as high as for the other two groups. All three groups were left-skewed (Figure 12).

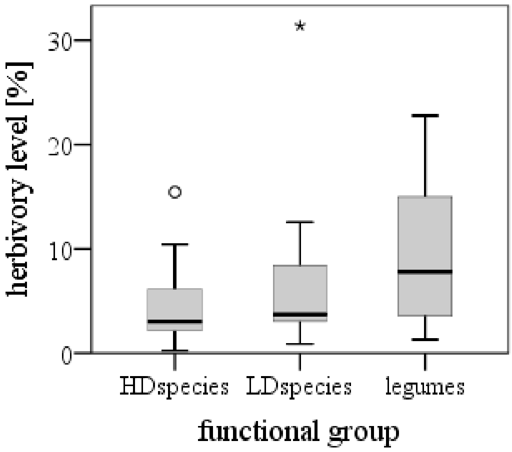


Figure 12: Boxplot of the herbivory levels of the three functional groups. $n_{HDspecies}$ = 9; $n_{LDspecies}$ = 7; $n_{legumes}$ = 7. O = outlier (outside 1.5 times the height of the box) * = extreme (outside 3 times the height of the box).

3.1.2 Intraspecific

In average herbivory levels of the five trees per species were found in a range of 15.28 % ± 16.48 % (mean ± SD). Intraspecific variations of herbivory levels per tree showed coefficients of variation (CV) from 30.40 % (*Cojoba arborea*) to 185.60 % (*Calophyllum longifolium*) averaging in 92.41 % ± 44.62 % (mean ± SD). In nine cases, statistic outliers (values outside the whiskers, resp. more than 1.5 times the height of the box) caused a wide range (Figure 13). The functional group had no significant influence on the CV (r = -0.126[i]; p = 0.567) maximum (r = 0.202; p = 0.356) or minimum (r = 0.268; p = 0.217) herbivory level per species (Spearman-Rho).

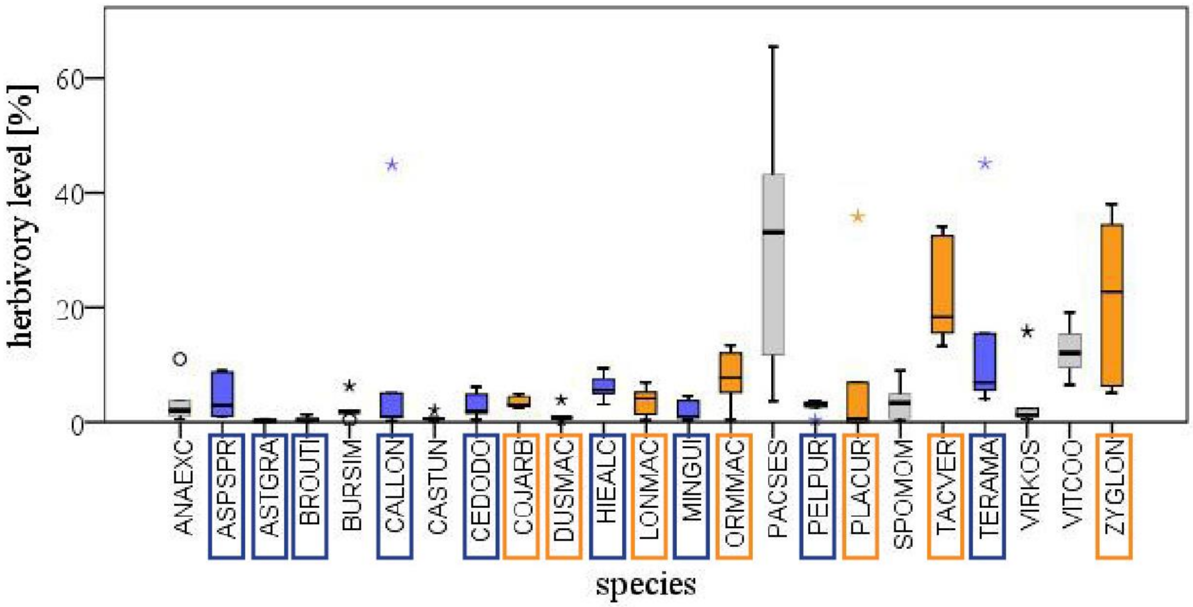


Figure 13: Boxplot showing the herbivory levels measured for the five individuals per species. Colors indicating the functional groups: blue = HDspecies; orange = legumes; grey = LDspecies. O = outlier (outside 1.5 times the height of the box) * = extreme (outside 3 times the height of the box).

The bottom, middle and top branches of all tested trees showed no significant differences in herbivory levels F(2, 214) = 0.215; p = 0.807 (Table 8), severity F(2, 226) = 0.282; p = 0.755 and abundance F(1.852, 196.256) = 0.229 (Table 9); p = 0.778 (Table 10).

Table 8: Tests of Within-Subjects Effects of a one-way ANOVA with repeated measurements – influence of branch position on herbivory levels

source		**sum Sq Typ III**	**Df**	**mean Sq**	**F**	**Sig.**
position	**sphericity assumed**	.048	**2**	.024	**.215**	**.807**
	Lower bound	.048	1.000	.048	.215	.644
error (position)	**sphericity assumed**	23.939	214	.112		
	lower bound	23.939	107.000	.224		

Table 9: Tests of Within-Subjects Effects of a one-way ANOVA with repeated measurements – influence of branch position on severity.

source		sum Sq Typ III	Df	mean Sq	F	Sig.
position	**sphericity assumed**	.058	**2**	.029	**.282**	**.755**
	lower bound	.058	1.000	.058	.282	.596
error (position)	**sphericity assumed**	23.194	226	.103		
	lower bound	23.194	113.000	.205		

Table 10: Tests of Within-Subjects Effects of a one-way ANOVA with repeated measurements – influence of branch position on abundance. Assumption of sphericity violated.

source		sum Sq Typ III	Df	mean Sq	F	Sig.
position	**Greenhouse-Geisser**	.027	**1.852**	.015	**.229**	**.778**
	lower bound	.027	1.000	.027	.229	.633
error (position)	**Greenhouse-Geisser**	12.441	196.265	.063		
	lower bound	12.441	106.000	.117		

3.2 Leaf traits

All values in this chapter refer to Table 11.

Leaf thickness ranged from 0.09 mm (*Cojoba arborea*) to 0.48 mm (*Calophyllum longifolium)* with an average of 0.22 ± 0.08 mm (mean ± SD). HD species had thicker leaves, on average 0.26 ± 0.09 mm, than LD species (0.20 ± 0.04 mm) and legumes (0.18 ± 0.07 mm).

Chlorophyll content ranged from 34.92 *(Bursera simaruba)* to 59.67 (*Zygia longifolia)* with an average of 45.58 ± 6.16 (mean ± SD). HD species and legumes showed higher contents (47.45 ± 6.33 and 46.67 ± 6.65), LD species showed lower contents (42.09 ± 4.56).

Toughness ranged from 1.57 N (*Astronium graveolens)* to 6.43 N (*Tachigali versicolor).* The average was 3.69 ± 1.45 N (mean ± SD). Toughness for the functional groups was 2.96 ± 0.72 N (LD species), 3.90 ± 1.57 N (HD species) and 4.16 ± 1.71 N (legumes).

Leaf dry matter content (LDMC) ranged from 285.54 mg g^{-1} (*Hieronyma alcherneoides*) to 500.9 mg g^{-1} (*Tachigali versicolor*) with a mean of 375.61 ± 55.18 mg g^{-1} (mean ± SD).

LDMC showed little differences between the functional groups: 360.20 ± 42.75 mg g^{-1} (LDspecies), 378.00 ± 53.22 mg g^{-1} (HD species) and 387.95 ± 71.40 mg g^{-1} (legumes).

Specific leaf area (SLA) ranged from 6.85 mm^2 mg^{-1} (*Calophyllum longifolium*) to 23.08 mm^2 mg^{-1} (*Dussia macrophylla*). In average, the SLA is 13.68 ± 3.50 mm^2 mg^{-1} (mean ± SD). HD species (12.45 ± 3.35 mm^2 mg^{-1}) and LD species (12.90 ± 2.04 mm^2 mg^{-1}) showed quite similar values while the SLA of legumes was higher (16.03 ± 4.05 mm^2 mg^{-1}).

Nitrogen content (N) ranged from 1.39 % (*Calophyllum longifolium*) to 3.75 % (*Dussia macrophylla*) with a mean of 2.40 ± 0.65 % (mean ± SD). The values of the functional groups are 1.97 ± 0.39 % (LD species), 2.22 ± 0.60 % (HD species) and 3.05 ± 0.40 % (legumes).

Carbon content (C) ranged from 42.79 % (*Castilla tunu)* to 51.48 % *(Tachigali versicolor).* The average C was 47.40 ± 1.99 % (mean ± SD). LD species had an average C content of 45.64 ± 2.00 %, HD species had a C content of 47.71 ± 0.99 % and legumes had an average C content of 48.75 ± 1.82 %.

Leaf/leaflet area (LA) ranged from 0.30 cm^2 (*Cojoba arborea*) to 669.70 cm^2 (*Brosimum utile*) resulting in a mean of 121.64 ± 164.87cm^2 (mean ± SD). LD species showed the lowest average LA with 141.50 ± 140.07cm^2. HD species reached a LA of 157.14 ± 229.78 cm^2 and legumes had an average of 56.12 ± 47.79cm^2.

Table 11: Leaf traits of the 23 investigated species, sorted according to their functional class (high wood density, low wood density, legumes): Mean ± SD of thickness, chlorophyll content, toughness, leaf dry matter content (LDMC), specific leaf area (SLA), nitrogen content (N), carbon content (C) and leaf area (LA). n for each trait see Chapter 2.3.2

	Sc. name	THI [mm]	CHL [rel.value]	TOU [N]	LDMC [mg g^{-1}]	SLA [mm^2 mg^{-1}]	N [%]	C [%]	LA [cm2] *
high wood density	*Aspidosperma spruceanum*	0.26 ± 0.05	49.21 ± 9.03	5.78 ± 1.2	326.04 ± 98.1	11.28 ± 1.6	1.8 ± 0.27	48.04 ± 1.32	60.43 ± 7.44
	Astronium graveolens	0.19 ± 0.06	36.3 ± 6.84	1.57 ± 0.47	392.75 ± 40.36	18.9 ± 2.56	2.62 ± 0.43	48.9 ± 1.31	20.41 ± 6.21
	Brosimum utile	0.21 ± 0.04	39.83 ± 5.25	5.38 ± 0.3	396.85 ± 68.44	12.88 ± 2.98	2.5 ± 0.32	47.81 ± 0.32	669.70 ± 152.56
	Calophyllum longifolium	0.48 ± 0.06	46.81 ± 6.13	5.45 ± 1.72	343.09 ± 42.96	6.85 ± 1.37	1.39 ± 0.25	49.01 ± 0.92	122.68 ± 33.21
	Cedrela odorata	0.22 ± 0.03	50.82 ± 4.76	2.29 ± 0.52	394.99 ± 65.87	15.3 ± 4.44	3.26 ± 0.4	47.65 ± 1.45	35.5 ± 12.17
	Hieronyma alcherneoides	0.31 ± 0.04	56.13 ± 4.95	2.47 ± 1.09	285.54 ± 22.35	10.86 ± 2.39	2.72 ± 0.3	47.02 ± 3.93	414.47 ± 186.83
	Minquartia guianensis	0.21 ± 0.06	52.24 ± 9.06	4.56 ± 0.7	374.52 ± 19.99	13.52 ± 3.55	2.18 ± 0.51	47.8 ± 4.88	58.67 ± 6.38
	Peltogyne purpurea	0.22 ± 0.02	44.33 ± 7.68	4.53 ± 0.52	461.17 ± 43.7	11.8 ± 1.48	1.75 ± 0.3	47.5 ± 1.37	13.68 ± 6.13
	Terminalia amazonia	0.24 ± 0.03	51.34 ± 7.03	3.01 ± 0.94	427.02 ± 45.03	10.67 ± 1.18	1.76 ± 0.44	45.68 ± 5.82	18.76 ± 5.16
legumes	*Cojoba arborea*	0.09 ± 0.04	49.54 ± 7.28	2.44 ± 0.94**	430.4 ± 46.83	19.61 ± 3.8	2.78 ± 0.2	49.34 ± 1.67	0.3 ± 0.04
	Dussia macrophylla	0.1 ± 0.03	45.25 ± 7.62	1.91 ± 0.24	347.27 ± 58.18	23.08 ± 4.16	3.75 ± 0.53	46.46 ± 0.57	51.17 ± 15.52
	Lonchocarpus macrophyllus	0.21 ± 0.06	39.16 ± 8.59	4.62 ± 1.67	313.1 ± 61.1	15.62 ± 3.36	3.11 ± 0.41	47.11 ± 1.21	51.53 ± 25.55
	Ormosia macrocalyx	0.25 ± 0.03	47.31 ± 4.61	4.8 ± 0.73	359.27 ± 25.31	13.07 ± 2.91	3.03 ± 0.14	49.06 ± 0.26	74.37 ± 20.65
	Platymiscium curuense	0.19 ± 0.09	43 ± 4.73	3.1 ± 0.2	319.57 ± 44.38	16.03 ± 3.39	3.35 ± 0.63	47.47 ± 1.09	63.98 ± 15.61
	Tachigali versicolor	0.23 ± 0.04	42.72 ± 5.39	6.43 ± 1.37	500.9 ± 78.09	12.15 ± 3.83	2.52 ± 0.46	51.48 ± 4.71	144.22 ± 42.59
	Zygia longifolia	0.24 ± 0.02	59.67 ± 5.86	5.78 ± 2.07	445.16 ± 34.58	12.62 ± 5.42	2.84 ± 0.17	50.34 ± 0.83	7.30 ± 2.36
Low wood density	*Anacardium excelsum*	0.18 ± 0.06	42.25 ± 4.84	4.36 ± 0.77	373.08 ± 35.94	10.09 ± 1.67	1.73 ± 0.23	45.74 ± 2.85	168.92 ± 44.33
	Bursera simaruba	0.19 ± 0.04	34.92 ± 6.97	2.53 ± 0.62	347.92 ± 68.37	14.47 ± 3.4	2.05 ± 0.45	47.54 ± 1.75	31.24 ± 3.12
	Castilla tunu	0.24 ± 0.07	41.13 ± 5.62	2.2 ± 0.77	381.17 ± 30	11.29 ± 2.76	1.96 ± 0.34**	42.79 **	433.51 ± 169.29
	Pachira sessilis	0.21 ± 0.01	41.84 ± 8.79	3.42 ± 1.94	379.06 ± 35.18	12.81 ± 2.07	2.18 ± 0.45	43.8 ± 2.55	64.65 ± 56.91
	Spondias mombin	0.16 ± 0.06	40.62 ± 9.05	2.78 ± 0.71	291.07 ± 58.1	16.32 ± 4.92	1.61 ± 0.13	45.32 ± 1.35	45.06 ± 11.29
	Virola koschnyi	0.2 ± 0.14	43.53 ± 16.07	2.78 ± 0.57	422.83 ± 45.85	12.46 ± 1.92	1.57 ± 0.33	48.57 ± 2.61	240.02 ± 44.47
	Vitex cooperi	0.27 ± 0.05	50.33 ± 1.79	2.64 ± 0.75	326.26 ± 68.76	12.86 ± 3.27	2.69 ± 0.51	45.75 ± 1.12**	36.63 ± 8.49

	Sc. name	**THI [mm]**	**CHL**	**TOU [N]**	**LDMC [mg g^{-1}]**	**SLA [mm^2 mg^{-1}]**	**N [%]**	**C [%]**	**LA [cm2] ***
all species	*Mean ± SD*	0.22 ± 0.08	45.58 ± 6.16	3.69 ± 1.45	375.61 ± 55.18	13.68 ± 3.50	2.40 ± 0.65	47.40 ± 1.99	121.64 ± 164.87
	Min - Max	0.09-0.48	34.92-59.67	1.57-6.43	285.54-500.90	6.85-23.08	1.39-3.75	42.79-51.48	0.30-669.70
	Mean ± SD HDspecies	0.26 ± 0.09	47.45 ± 6.33	3.90 ± 1.57	378.00 ± 53.22	12.45 ± 3.35	2.22 ± 0.60	47.71 ± 0.99	157.14 ± 229.78
	Mean ± SD legumes	0.18 ± 0.07	46.67 ± 6.65	4.16 ± 1.71	387.95 ± 71.40	16.03 ± 4.05	3.05 ± 0.40	48.75 ± 1.82	56.12 ± 47.79
	Mean ± SD LDspecies	0.20 ± 0.04	42.09 ± 4.56	2.96 ± 0.72	360.20 ± 42.75	12.90 ± 2.04	1.97 ± 0.39	45.64 ± 2.00	141.50 ± 140.07

Table 12: Tree traits (growth rate, mortality rate) per species, the overall mean and the mean per functional group.

	species	n_{Growth}	Height growth [m/year] mean	$n_{Mortality}$	Mortality rate$_{2017}$ mean
high wood density	*Aspidosperma spruceanum*	240	0.49838495	116	0.33339892
	Astronium graveolens	150	1.63780168	112	0.06999734
	Brosimum utile	175	0.41903743	118	0.32012389
	Calophyllum longifolium	136	0.9472959	66	0.27296385
	Cedrela odorata	143	1.62066505	126	0.02998741
	Hieronyma alcherneoides	277	1.90610002	133	0.05557789
	Minquartia guianensis	206	0.30593546	119	0.38064588
	Peltogyne purpurea	176	0.57862705	96	0.05727264
	Terminalia amazonia	174	1.61568088	75	0.15218252
legumes	*Cojoba arborea*	129	1.96422037	64	0.01368679
	Dussia macroprophyllata	121	1.365533	54	0.08778908
	Lonchocarpus macrophyllus	169	1.96207163	107	0.02831509
	Ormosia macrocalyx	126	0.73877808	47	0.0776858
	Platymiscium curuense	159	1.58111793	139	0.01205894
	Tachigali versicolor	139	0.85552771	77	0.21219073
	Zygia longifolia	168	1.08284583	158	0.01841354
low wood density	*Anacardium excelsum*	142	2.71882273	130	0.00711316
	Bursera simaruba	155	1.89274497	66	0.07999724
	Castilla tunu	119	0.67505451	97	0.59718945
	Pachira sessilis	92	1.13229523	65	0.45335391
	Spondias mombin	162	2.11291792	100	0.03108629
	Virola koschnyi	103	0.65444197	89	0.24173925
	Vitex cooperi	267	1.65039383	120	0.06018222
all species	*Mean ± SD*	23	1.3 ± 0.65		0.16 ± 0.17
	min-max		0.31-2.72		0.01-0.60
	HDspecies (mean ± SD)	9	1.06 ± 0.63		0.19 ± 0.14
	Legumes (mean ± SD)	7	1.36 ± 0.50		0.06 ± 0.07
	LDspecies (mean ± SD)	7	1.55 ± 0.77		0.21 ± 0.23

The **height growth** ranged from 0.31 m/year (*Minquartia guianensis)* to 2.72 m/year (*Anacardium excelsium*) with a mean of 1.3 ± 0.65 m/year (mean ± SD). The functional group of HD species grows the slowest with just 1.06 ± 0.63 m/year on average, followed by legumes with a height growth of 1.36 ± 0.50 m/year and LD species growing 1.55 ± 0.77 m/year on average (Table 12).

Mortality rate until 2017 was 0.16 ± 0.17 (mean ± SD) in average, where the lowest value was evident for *Anacardium excelsum* (0.01) and the highest value for *Castilla tunu* (0.60). The functional group of legumes showed a comparatively low mortality rate (0.06 ± 0.07) while the other two groups are quite similar with 0.19 ± 0.14 (HD species) and 0.21 ± 0.23 (LD species) (Table 12).

3.3 Correlations and regressions

Table 13: Pearson-Correlation of the leaf/tree traits and herbivory, abundance and severity for all species (n = 23). Correlation coefficient in the right top half, p-value in the left bottom half. Significant correlations are bold, * significant on the 0.05 level; ** significant on the 0.01 level

	H	A	S	CHL	TOU	LDMC	SLA	THI	LA	N	C	G	M
H	1	**.487***	**.962****	**.453***	0.374	0.111	**-.417***	0.344	-0.117	-0.066	0.114	0.046	-0.063
A	0.018	1	0.286	0.176	0.292	-0.055	-0.339	0.184	**.454***	-0.054	-0.109	-0.104	0.265
S	0.000	0.185	1	**.510***	0.350	0.212	-0.370	0.317	-0.297	-0.041	0.198	0.032	-0.116
CHL	0.030	0.422	0.013	1	0.175	0.074	-0.221	0.250	-0.238	0.161	0.216	-0.126	-0.115
TOU	0.078	0.177	0.101	0.423	1	0.280	**-.527****	**.424***	0.170	-0.202	**.484***	**-.458***	0.174
LDMC	0.615	0.803	0.330	0.738	0.196	1	-0.079	-0.173	-0.281	-0.114	**.423***	-0.355	0.126
SLA	0.048	0.113	0.083	0.310	0.010	0.719	1	**-.824****	**-.456***	**.651****	0.052	0.272	-0.337
THI	0.108	0.400	0.141	0.250	0.044	0.429	0.000	1	**.449***	-0.373	0.071	-0.289	0.367
LA	0.596	0.030	0.168	0.274	0.438	0.195	0.029	0.032	1	-0.185	-0.269	-0.270	**.466***
N	0.766	0.806	0.853	0.462	0.355	0.604	0.001	0.080	0.399	1	0.199	0.162	-0.385
C	0.605	0.619	0.364	0.321	0.019	0.045	0.814	0.748	0.215	0.364	1	-0.220	-0.159
G	0.834	0.636	0.884	0.567	0.028	0.097	0.209	0.182	0.213	0.461	0.313	1	**-.747****
M	0.775	0.221	0.599	0.601	0.426	0.566	0.116	0.085	0.025	0.070	0.468	0.000	1

SLA and CHL explain 24.2 % of variation in herbivory (corr. $R^2 = 0.242$; Table 14, Table 15). The model of a multiple regression to test the influence of leaf traits as predictors for herbivory is not significant F(10, 12) = 1.255, p = 0.350

Table 16).

Table 14: Multiple Regression, model summary - Variation of herbivory explained by CHL and SLA

R	**R-Sq**	**corr. R-Sq**	**standard error of the estimator**
.557^{a}	.311	,242	,21732

independent variables: (constants). SLA_mean. chloro_mean

Table 15: Multiple regression, coefficients – individual effect of SLA and chlorophyll

	not standardised coefficients		**standardised coefficients**	**T**	**p**
	regression coefficientB	**standard error**	**Beta**		
(constant)	-1,03	0,435		-2,369	0,028
chlorophyll	0,015	0,008	0,379	1,99	0,06
SLA	-0,024	0,014	-0,333	-1,751	0,095

dependent variable: herbAsinSqur

Table 16: ANOVA – test for significance of the model of leaf traits influencing herbivory levels

	Sum Sq	**Df**	**Mean Sq**	**F**	**p**
regression	.700	10	.070	1.255	.350^{b}
not standardized residues	.670	12	.056		
total	1.370	22			

dependent variable: herbAsinSqur

independent variables : (constants), thoughness_mean, LAlog, N_mean, chloro_mean, LDMC_mean, MortLog, C_mean, ThickSqrt, growth, SLA_mean

Table 17: Pearson-Correlation of the leaf/tree traits and herbivory, abundance and severity for high wood density species (n = 9). Correlation coefficient in the right top half, p-value in the left bottom half. Significant correlations are bold, * significant on the 0.05 level; ** significant on the 0.01 level

	H	*A*	*S*	*CHL*	*TOU*	*LDMC*	*SLA*	*THI*	*LA*	*N*	*C*	*G*	*M*
H	1	0.383	**.965****	**.762***	0.181	-0.224	**-.801****	0.619	-0.062	-0.479	-0.495	0.180	0.068
A	0.309	1	0.178	0.637	0.244	-0.544	-0.407	0.131	0.639	0.097	-0.520	-0.041	0.229
S	0.000	0.648	1	**.717***	0.109	-0.058	**-.709***	0.550	-0.260	-0.465	-0.446	0.180	-0.046
CHL	0.017	0.065	0.030	1	-0.038	-0.448	-0.458	0.301	0.118	0.016	-0.543	0.212	-0.057
TOU	0.640	0.527	0.779	0.923	1	-0.070	-0.609	0.354	0.311	-0.647	0.226	**-.869****	**.773***
LDMC	0.562	0.130	0.882	0.226	0.858	1	0.287	-0.550	-0.624	-0.113	-0.231	-0.183	-0.190
SLA	0.009	0.277	0.032	0.216	0.082	0.454	1	**-.809****	-0.313	**.690***	0.182	0.206	-0.400
THI	0.075	0.737	0.125	0.431	0.350	0.125	0.008	1	0.362	-0.470	0.256	0.073	0.224
LA	0.875	0.064	0.500	0.762	0.415	0.073	0.413	0.338	1	0.201	0.115	-0.120	0.334
N	0.192	0.804	0.207	0.968	0.060	0.771	0.040	0.202	0.604	1	-0.016	0.456	-0.583
C	0.175	0.151	0.229	0.130	0.559	0.550	0.639	0.506	0.769	0.968	1	-0.282	0.165
G	0.643	0.916	0.642	0.584	0.002	0.638	0.594	0.851	0.759	0.217	0.462	1	**-.703***
M	0.862	0.553	0.906	0.884	0.015	0.625	0.286	0.562	0.380	0.100	0.671	0.035	1

Table 18: Pearson-Correlation of the leaf/tree traits and herbivory, abundance and severity for <u>legume</u> species (n = 7). Correlation coefficient in the right top half, p-value in the left bottom half. Significant correlations are bold, * significant on the 0.05 level; ** significant on the 0.01 level

	H	*A*	*S*	*CHL*	*TOU*	*LDMC*	*SLA*	*THI*	*LA*	*N*	*C*	*G*	*M*
H	1	0.483	**.953****	0.357	**.848***	0.617	**-,902****	0.748	0.177	-0.730	**.825***	-0.568	0.089
A	0.272	1	0.257	0.004	**.828***	0.376	-0.586	0.651	0.545	-0.363	0.421	-0.531	0.624
S	0.001	0.578	1	0.482	0.712	0.686	**-.811***	0.581	-0.091	**-.798***	**.880****	-0.478	-0.057
CHL	0.432	0.994	0.273	1	0.165	0.447	-0.171	0.037	-0.528	-0.243	0.441	-0.282	-0.309
TOU	0.016	0.021	0.073	0.724	1	0.529	**-.926****	**.865***	0.367	-0.716	0.732	-0.587	0.371
LDMC	0.140	0.406	0.089	0.315	0.223	1	-0.377	0.085	-0.262	**-.787***	**.919****	-0.420	0.332
SLA	0.006	0.167	0.027	0.715	0.003	0.405	1	**-.933****	-0.327	0.692	-0.684	0.553	-0.150
THI	0.053	0.113	0.172	0.937	0.012	0.855	0.002	1	0.563	-0.410	0.408	-0.559	0.196
LA	0.704	0.205	0.846	0.224	0.418	0.570	0.474	0.188	1	0.252	-0.148	-0.509	0.537
N	0.063	0.423	0.031	0.599	0.071	0.036	0.085	0.361	0.586	1	**-.910****	0.234	-0.109
C	0.022	0.346	0.009	0.322	0.061	0.003	0.090	0.363	0.751	0.004	1	-0.538	0.268
G	0.183	0.220	0.278	0.540	0.166	0.348	0.198	0.192	0.244	0.613	0.213	1	-0.660
M	0.849	0.134	0.904	0.500	0.413	0.466	0.749	0.674	0.214	0.816	0.561	0.107	1

Table 19: Pearson-Correlation of the leaf/tree traits and herbivory, abundance and severity for <u>low wood density</u> species (n = 7). Correlation coefficient in the right top half, p-value in the left bottom half. Significant correlations are bold, * significant on the 0.05 level; ** significant on the 0.01 level

	H	*A*	*S*	*CHL*	*TOU*	*LDMC*	*SLA*	*THI*	*LA*	*N*	*C*	*G*	*M*
H	1	**.755***	**.991****	0.441	0.368	-0.050	0.088	0.215	-0.564	0.477	-0.028	0.029	-0.076
A	0.050	1	0.715	0.472	0.078	0.472	-0.124	0.373	-0.146	0.340	0.285	-0.466	0.166
S	0.000	0.071	1	0.370	0.368	-0.083	0.097	0.222	-0.619	0.529	-0.040	0.079	-0.091
CHL	0.322	0.285	0.414	1	0.068	-0.020	-0.290	0.618	0.020	0.489	-0.090	-0.125	-0.072
TOU	0.417	0.868	0.417	0.884	1	0.133	-0.385	-0.404	-0.133	-0.198	0.055	0.587	-0.337
LDMC	0.915	0.284	0.859	0.967	0.746	1	-0.677	0.118	0.679	-0.243	0.168	-0.577	0.523
SLA	0.851	0.790	0.836	0.529	0.311	0.095	1	-0.342	-0.658	-0.064	0.207	0.108	-0.317
THI	0.644	0.409	0.632	0.139	0.386	0.802	0.452	1	0.110	**.838***	-0.341	-0.468	0.411
LA	0.188	0.754	0.138	0.966	0.891	0.094	0.108	0.814	1	-0.415	-0.248	-0.511	0.569
N	0.279	0.455	0.222	0.265	0.654	0.599	0.891	0.019	0.354	1	-0.258	-0.059	0.056
C	0.952	0.535	0.933	0.848	0.971	0.719	0.655	0.454	0.592	0.577	1	0.135	-0.607
G	0.951	0.292	0.866	0.790	0.155	0.175	0.818	0.289	0.241	0.900	0.773	1	**-,809***
M	0.872	0.722	0.846	0.878	0.460	0.228	0.488	0.360	0.182	0.905	0.148	0.028	1

The presented data in the scatterplots was the original data, while R² results from the analysis with partly transformed data (see methods section).

3.3.1 Leaf thickness

Herbivory, severity, abundance, growth, and mortality showed no significant relation to leaf thickness. This was true for the whole set of tested species and for all the functional groups.

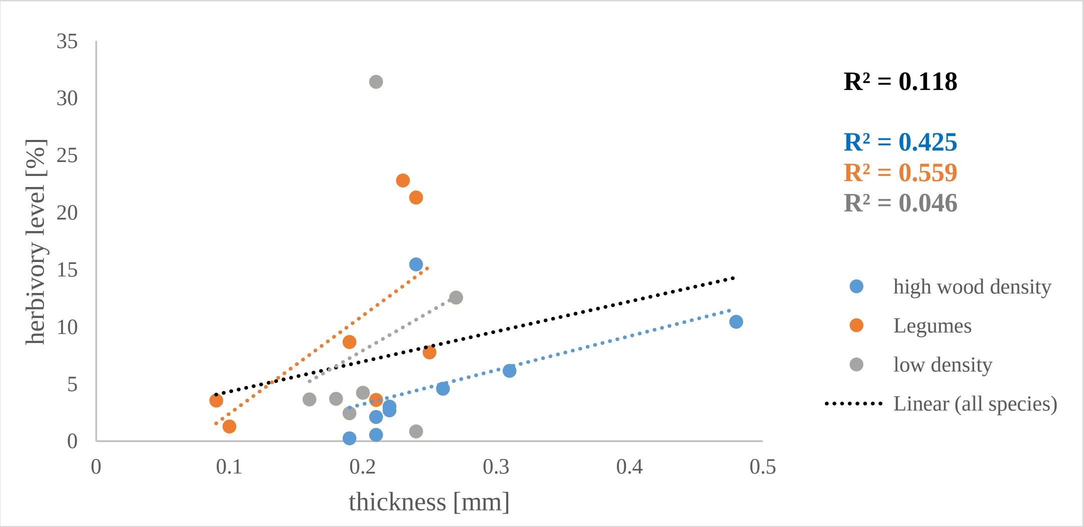


Figure 14: Correlation between herbivory level [%] and leaf thickness [mm] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation.

3.3.2 Chlorophyll content

The chlorophyll content had a low but significant influence on herbivory levels (r = 0.453; p = 0.030) and on the severity of herbivory (r = 0.510; p = 0.013). The same observations were present for the HD species with a correlation of CHL and H (r = 0.762; p = 0.017) and a CHL and S (r = 0.717; p = 0.030).

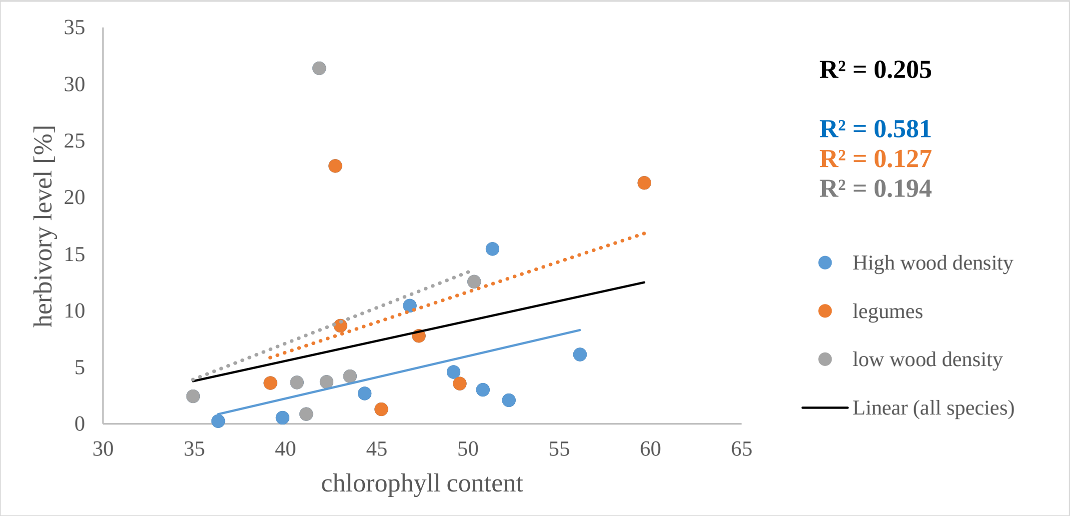


Figure 15: Correlation between herbivory level [%] and chlorophyll content on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation, drawn through line = significant correlation.

3.3.3 Leaf toughness (TOU)

Leaf toughness and herbivory were only correlated in legumes (r = 0.848; p = 0.016). Within this functional group also abundance (r = 0.828; p = 0.021) was correlated with TOU. TOU also correlated with C in all species (r = 0.484; p = 0.019).

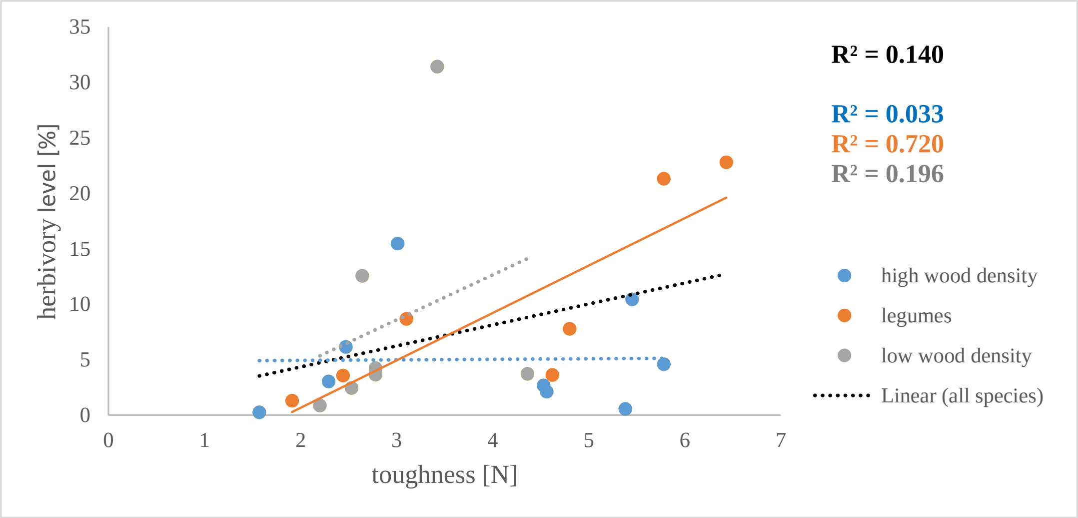


Figure 16: Correlation between herbivory level [%] and leaf toughness [N] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation, drawn through line = significant correlation.

3.3.4 Leaf dry matter content (LDMC)

LDMC had no correlation with H, S or A and with G or M. LDMC correlated with C contents in all species (r = 0.423; p = 0.045) and in legumes (r = 0.919; p = 0.003) where it also correlated negatively with N content (r = -0.787; p = 0.036).

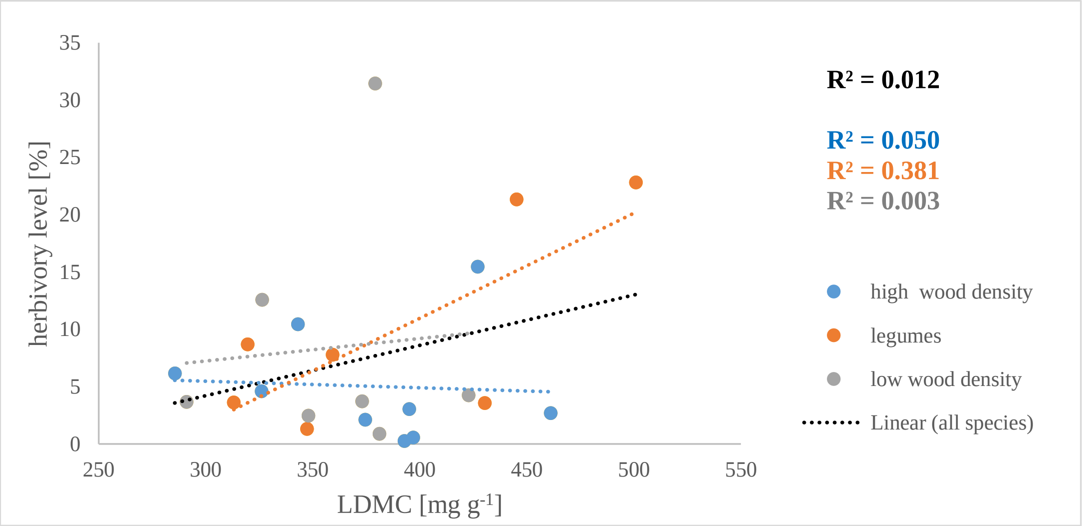


Figure 17: Correlation between herbivory level [%] and leaf dry matter content [mg g^{-1}] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation.

3.3.5 Specific leaf area (SLA)

There was a significantly negative correlation between SLA and herbivory (r = -0.417; p = 0.048). The same negative correlation existed for HD species (r = -0.801; p = 0.009) and for legumes (r = -0.902; p = 0.006). For these two groups, the negative correlation was also identifiable in regard to the severity (HD species: r = -0.709, p = 0.032; legumes: r = -0.811, p = 0.027). Furthermore, SLA had a correlation with N contents in all species (r = 0.651, p = 0.001) and in HD species (r = 0.690, p = 0.040).

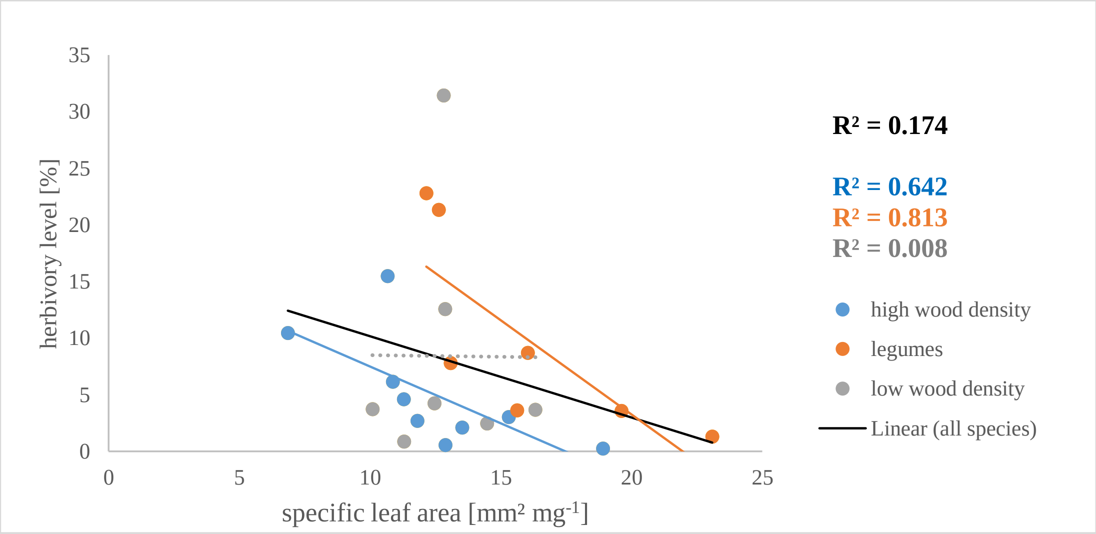


Figure 18: Correlation between herbivory level [%] and SLA [$mm^2\ mg^{-1}$] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation, drawn through line = significant correlation.

3.3.6 Nitrogen content

N negatively correlated with S in legumes (r = -0.798, p = 0.004). No other correlations regarding herbivory or growth and mortality existed. See the respective chapter for correlations regarding SLA and LDMC. N showed also a negative correlation with C in legumes (r = -0.910; p = 0.004) and with THI in LD species (r = 0.838; p = 0.019).

Nitrogen content appeared to be significantly different for legumes and not-legumes F (1, 21) = 18.111, p = < 0.001 explaining 43 % (corr. $R^2 = 0.437$) of the variation.

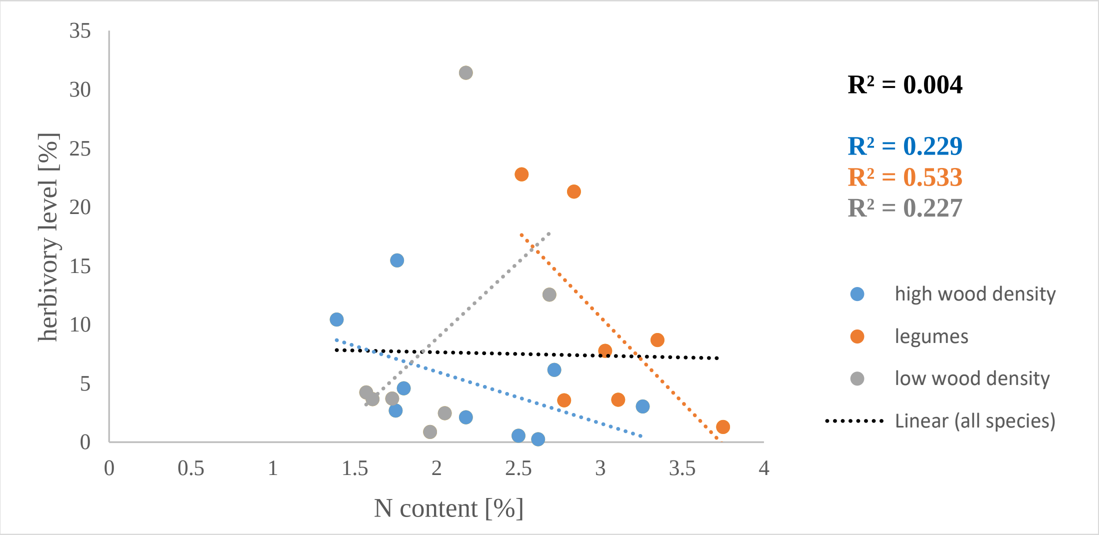


Figure 19: Correlation between herbivory level [%] and N content [%] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation.

3.3.7 Carbon content

A relation between herbivory and C was just found for the legume species (r = 0.825, p = 0.022). The correlation between severity and C was even stronger here, and more significant (r = 0.880; p = 0.009). I mentioned correlations of C with LDMC, TOU and N already in the respective chapters

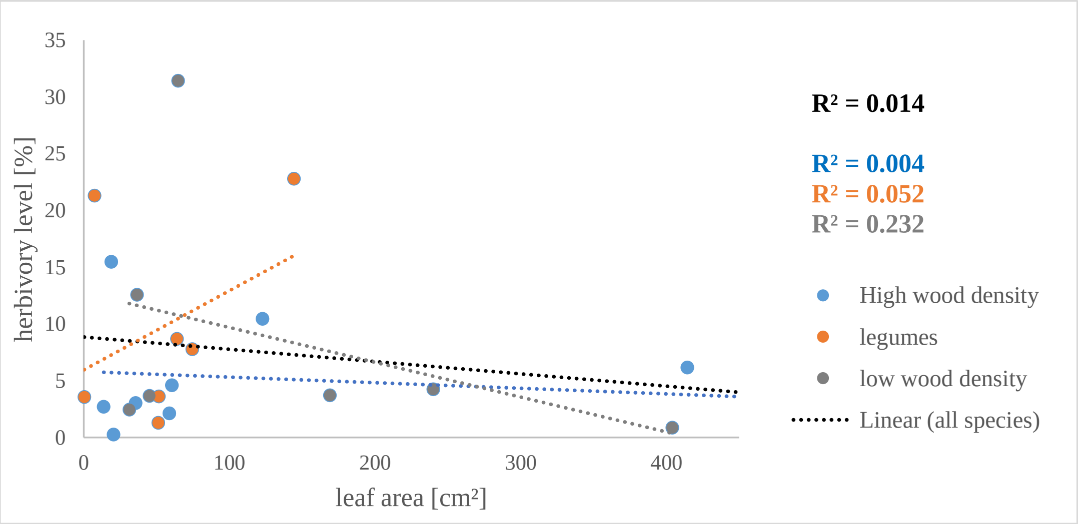


Figure 20: Correlation between herbivory level [%] and C content [%] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation, drawn through line = significant correlation.

3.3.8 Leaf area

Leaf area was an influencing trait on abundance (r = 0.454; p = 0.030) and mortality (r = 0.466; p = 0.025). LA had no correlations within the functional groups.

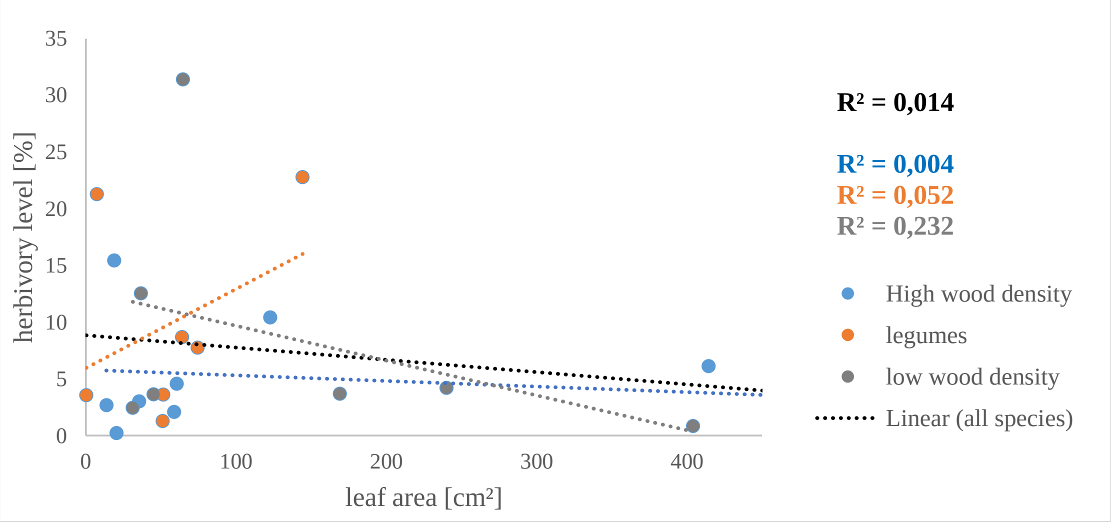


Figure 21: Correlation between herbivory level [%] and LA [cm²] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation.

3.3.9 Growth and mortality

Herbivory, severity or abundance did not correlate with either growth or with mortality. Growth was negatively correlated with mortality (r = -0.747; p = < 0.001). In addition to all species this correlation was also found for HD species (r = -0.703; p = 0.35) and for LD species (r = -0.943; p = 0.001). Growth was negatively correlated with toughness for all species (r = -0.458; p = 0.028). This negative correlation was more significant for just the HD species (r = -0.869; p = 0.002). I also found a high and significantly positive correlation between mortality and toughness for HD species (r = 0.773, p = 0.015). Furthermore, mortality correlated with LA (r = 0.466; p = 0.025) for all species.

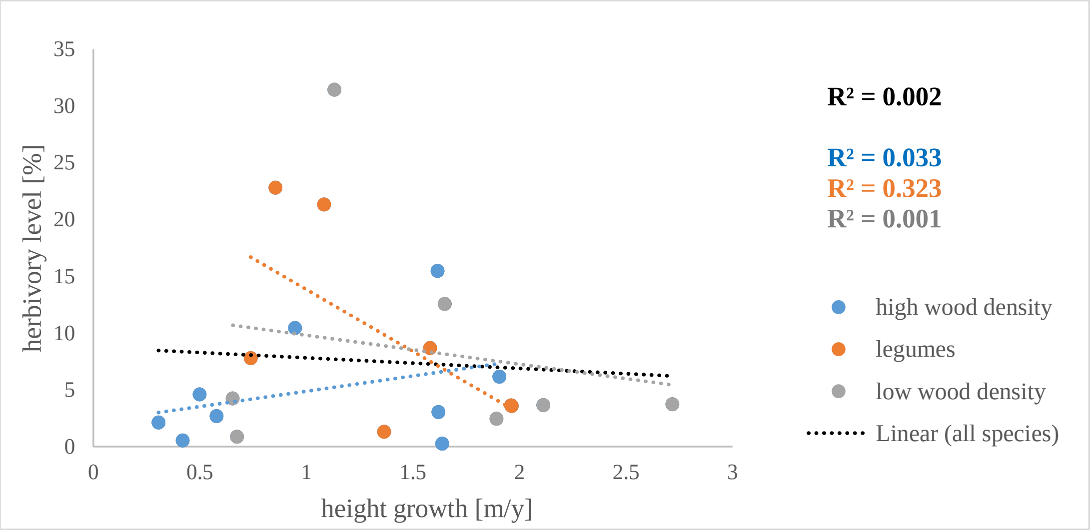


Figure 22: Correlation between herbivory level [%] and growth [m/y] on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation.

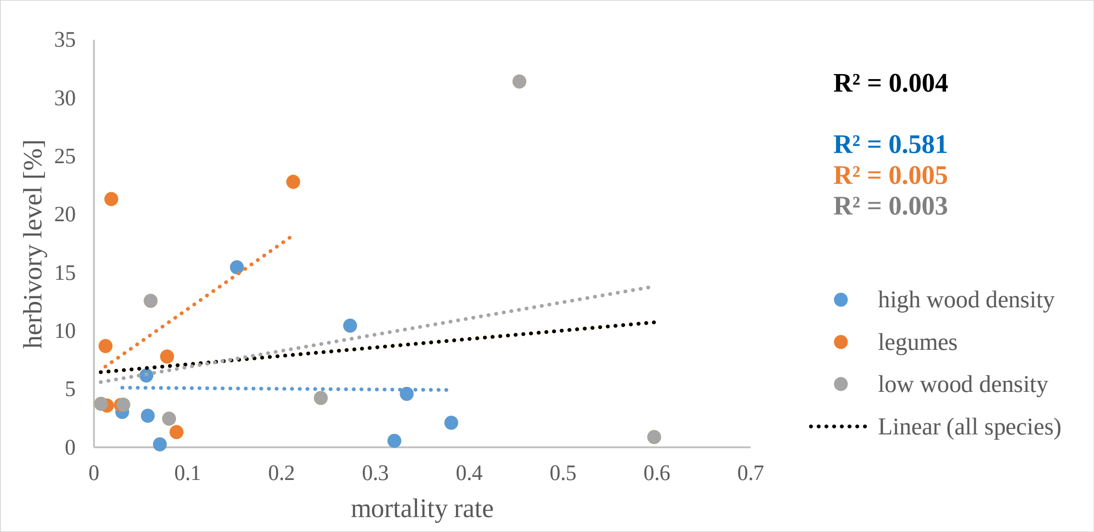


Figure 23: Correlation between herbivory level [%] and mortality rate on the species level for all species (n = 23) and sorted in functional groups. ($n_{highDensity}$ = 9; $n_{lowDensity}$ & $n_{legumes}$ = 7), dotted line = not significant correlation.

3.3.10 LA, severity and abundance

A Spearman-correlation confirmed the influence of LA on severity of herbivory. The negative correlation was weak but showed a high significance (r = -0.294; p = 0.001). The scatterplot depicts that high severity stroke only small leaves and that bigger leaves had low levels of severity (Figure 24). The analysis also showed a correlation between LA and the abundance of herbivory (r = 0.284; p = 0.002): bigger leaves are more likely to be attacked by herbivores. LA ranges from 0.3 cm² to 669.7 cm² (chapter 3.2). The median is just 58.67 cm² and therefore lower than the average (121.64 cm²).

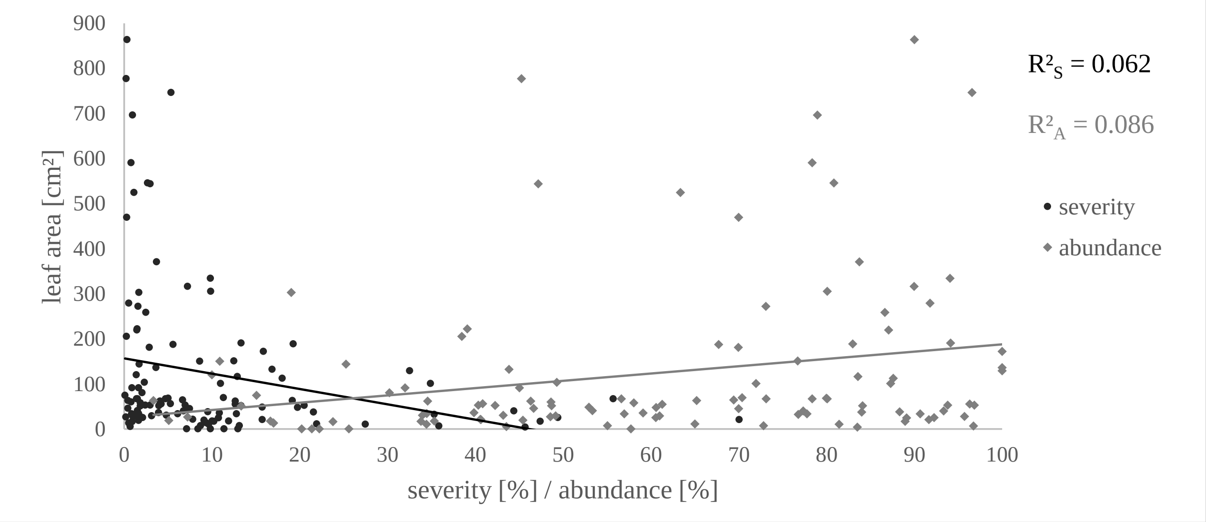


Figure 24: Linear regression of LA and severity as well as LA and abundance per tree. n = 115

4 Discussion

4.1 Critical reflection on methods

The total damage caused by herbivores might be up to five times higher (Lowman 1984) than evaluated with the method of a one-time evaluation. A study review by Coley & Barone (1996) also found underestimates between 38 % and 60 % in one-time evaluations compared to long-term evaluations. One possible explanation is that fully eaten leaves are not considered. Furthermore, the different lifetimes of the leaves respectively time that a leaf was exposed to herbivores are not taken into account (Coley 1987, Coley & Barone 1996, Lowman 1984). Leaf lifetimes in tropical trees range from 3 months for early successional species to 3.2 years for the latest successional species (Poorter 2001). Concluding herbivory levels from one-time evaluations would therefore lead to underestimated herbivory for early successional species and overestimated herbivory for late successional species (Poorter et al. 2004). A disadvantage of these two methods used in research is the incomparability of herbivory levels and rates. Nevertheless, one-time evaluations are regularly used in herbivory research (Chapter 2.3), and because of the limited time, it was a suitable method for this study. As stated in Chapter 1.2, most of the lifetime herbivorous damage (about 75 %) occurs during the period of expansion. By using mature leaves for the evaluation of herbivory levels, I ensured that at least this main share of leaf loss was considered.

The analyzed unit had a big variation in size. For instance, the simple leaves of *Brosimum utile* were on average 669.70 cm² large compared to sub-leaflets of *Cojoba arborea* averaging 0.3 cm² in size. Paul et al. (2012) also reported that bigger leaves show higher herbivory levels. In his study on five species, LA accounted for 27.3 % of herbivory variation. In accordance with Myster (2002), herbivores preferably attack larger leaves than smaller leaves. This is evident for my study in high abundance (the share of attacked leaves) found just on branches with large individual leaves and a positive correlation between LA and abundance on the species level. Additionally, I found that small leaves show the highest severities, which is a stronger predictor for the herbivory level than abundance. Though not statistically significant, legumes had the lowest LA (actually leaflets) and the highest herbivory. By using the same area of leaf tissue of each tree for herbivory measurements (Paul et al. 2012), such bias could be avoided. The use of the whole leaf instead of leaflets as reference unit would also be an alternative approach. The challenge here might be the high number of leaflets of some species’ leaves like *Cojoba arborea* with a rough estimate of 1.500 leaflets on a single compound leaf (National Parks Board, Singapore 2013).

Not every feeding guild causes a loss of tissue (Chapter 1.2) but just the missing leaf area was relevant for calculating the herbivory level. Therefore, an underestimation of herbivory would be possible but is unlikely as there was no damage by rollers and hardly any damage by miners was observed in the field. Fungal infections and pathogens were not considered in this analysis but would be an interesting feature for further investigation with regard to herbivory and leaf traits.

Herbivory levels and leaf traits in this study originate from different leaves and even different individuals of a species (except for LA that was measured on the leaf scans for severity quantification). For this reason, in theory, it is not possible to distinguish between constitutive and induced defenses (Fürstenberg-Hägg et al. 2003). In reality, induced defenses are predominantly chemical compounds, which were not determined in this study. A bias is therefore not likely.

4.2 Herbivory

Severity correlates stronger with herbivory level than abundance. A possible explanation therefore might be the high proportion of small leaves in the sample because the same amount of lost leaf area results in much higher severity in small leaves than in bigger leaves.

Herbivory levels of individuals within a species spread on average over 15.28 %, which is less than observed for a single species by Marquis (1984) with 25.95 %. Functional groups have no influence on intraspecific variations. According to Coley (1983a), herbivorous damage on individual plants is neither predictable nor constant and might be caused by changing effectiveness of defensive mechanisms over time.

The average herbivory level of 7.53 % is lower than the average herbivory level in other tropical forests (Kursar & Aide 1991). It is also at the lower end of the herbivory levels observed by Cooke et al. (1984) but on the higher end of herbivory levels observed by Poorter et al. (2004). A comparison of absolute numbers with studies that evaluated herbivory rates (leaf area lost per period) instead of herbivory levels (leaf area lost at a point of time) is not possible (see chapter 4.1). Findings of both evaluation methods regarding interspecific variations are similar and in accordance with this study: Differences in herbivory rates and levels between species do exist (Eichhorn et al. 2010, Myster 2002, Porter et al. 2004, Schowalter 1994). It needs to be mentioned that these studies investigate just two to five species, which is clearly fewer than in my study. In a Panamanian forest, differences between 47 species reached more than three orders of magnitude (Coley 1987), which corresponds with my findings presenting herbivory levels per species from 0.25 % to 31.42 %. Legumes had the highest, but not significantly, herbivory level (9.87 %) of the three functional groups, which is still below or within respectively slightly above (Poorter et al. 2004) the range of herbivory levels reported in the studies already mentioned. Significant differences between the functional groups were not observed.

To test reported differences in herbivory between pioneer and shade tolerant trees (Myster 2002, Porter et al. 2004, Schowalter 1994), data for HD species and LD species was investigated. Low wood density is characteristic for pioneer trees and high wood density is characteristic for shade tolerant trees (Muller-Landau 2004). Correspondingly, HD species had the lowest growth rates (1.06 m/year) – also characteristic for shade tolerant trees – and LD species had the highest growth rates (1.55 m/year), as expected of pioneer species. The two groups of HD species and LD species displayed no differences in herbivory levels. My findings disagree with Myster (2002) and Schonwalter (1994), who reported that pioneer trees suffer less damage by herbivores than shade tolerant trees. At the same time, it is not consistent with Poorter et al. (2004), who reported the opposite relation between herbivory and successional status. Still, my findings correspond to one result of Poorter et al.'s study: Herbivory levels for early and late successional species are similar. Additionally, they describe a peak of herbivory in middle successional species. Their explanation is that pioneers have a low leaf lifespan and shade tolerant trees are less attractive to herbivores.

> **Research Question 1: Are there significant differences in herbivory levels between the species?**
>
> Significant differences in herbivory levels between the 23 tested tree species do exist.

4.3 Defensive mechanisms

Surprisingly little correlations were found between herbivory and leaf traits (Figure 25). The only influencing traits on herbivory for the whole species sample are chlorophyll and SLA. They explain 24.2 % of the variations in herbivory levels.

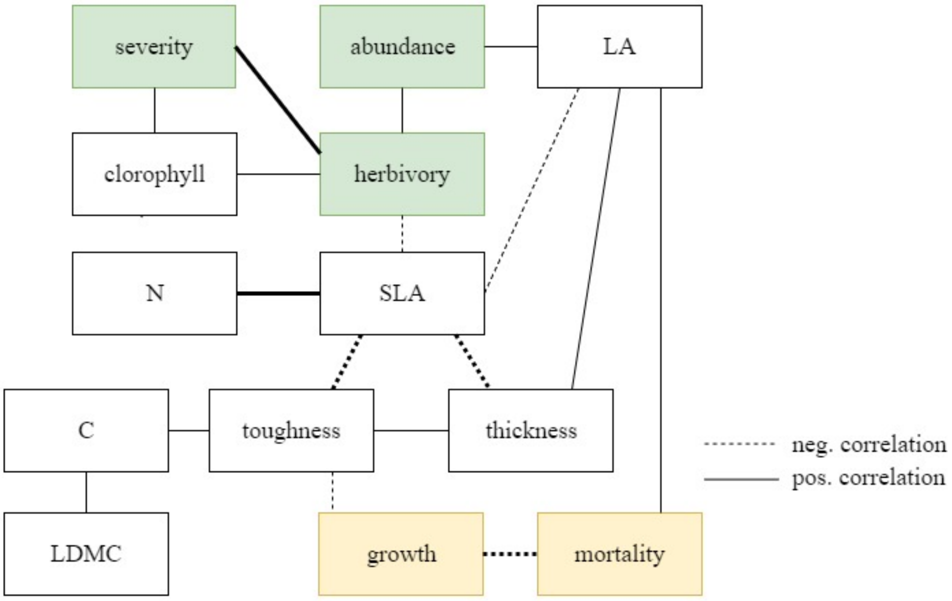


Figure 25: Diagram showing the significant correlations present for all species (n = 23). Thin line: significant on the 0.05 level, bold line: significant on the 0.01 level

Chlorophyll

A higher chlorophyll content appeared to be even a stronger predictor for higher herbivory levels for HD species. Chlorophyll content is a good predictor for the chloroplast development. In young leaves, some species delay the development of the chloroplasts until they are tough to keep the losses of resources through the high amount of defoliation on young leaves low (Kursar & Coley 2003). The correlation of higher herbivory and higher chlorophyll content found in mature leaves suggests that there is also another factor related to chlorophyll content resp. chloroplasts that plays a role in plant herbivore interactions. Koski et al. (2017) found lower chlorophyll contents in the undamaged leaves of herbivory affected trees compared to unaffected trees. This finding implies that chlorophyll content is a trait that reacts to herbivory not just on the leaf level but on the tree level. A lower chlorophyll content either may be a reactive defensive mechanism or is the attempt of the tree to lose fewer resources to herbivores as described for delayed greening.

Furthermore, chlorophyll content correlates positively with severity for all species (Figure 25) and HDspecies (Figure 26) leading to the suggestion that the “greenness” of a leaf does not influence whether it is attacked by an herbivore or not, but once it is attacked the amount of damage appears to be higher if the chlorophyll content is higher.

SLA & toughness

SLA negatively correlates to herbivory (Figure 25). This finding is in accordance with other studies (Coley 1983; Cooke et al. 1984; Poorter et al. 2004). Poorter et al. (2004) reported similar findings. They used SLA to conclude to toughness: higher SLA means less tough leaves. Cooke et al.'s (1984) findings reported significantly higher SLA in younger leaves that are known to be less tough. In the current study as well, a negative correlation between SLA and toughness was present. Paul et al. (2012) reported tougher leaves to have lower SLA.

Toughness appeared to influence herbivory levels just in legumes (Figure 27). Contrary to my expectations and experiences from another reforestation site in Costa Rica (Massad 2012), the correlation is a positive one. I have two possible hypotheses to explain higher herbivory in tougher leaves for legumes respectively higher herbivory for leaves with low SLA: (1) The high amount of herbivorous damage already occurred to the expanding leaf before toughening. This is likely to be true as up to 75 % of the lifetime damage of a leaf happens during expansion (Coley & Kursar 2014, Coley & Kursar 1996). (2) Leaf toughness is often discussed as an adaption to abiotic stress (Coley 1987), and stress may result in higher herbivory rates (Eichhorn et al. 2010). Legumes did show the highest toughness of all functional groups (4.16 N). At the same time, legumes had the lowest mortality rate and were close to the overall mean regarding the growth rate. More abiotic stress for legumes than for the other functional groups is thus not likely. Accordingly, the first explanation is accurate or the reason for the negative correlation of herbivory level and toughness is caused by something else.

Nitrogen

Legumes had the highest nitrogen content (3.05 %). The significantly higher nitrogen content of legumes' leaves is the result of their fixation of nitrogen. According to Myster (2002), these leaves are more attractive to herbivores because of a higher nutritional value. My findings contradict this idea and the findings of Paul et al. (2012), as there was no correlation between herbivory and nitrogen content. As for legumes, I even identified a negative correlation between severity and N content. Interestingly, N in legumes showed a strong negative correlation with C. C in turn positively correlated with herbivory (Figure 27). The other functional groups did not show similar relations. This suggests that through the detour of C the high N of legumes might even result in reduced herbivory levels. A positive correlation of herbivory and C contents was also reported from a subtropical forest (Schuldt et al. 2012). A study on red oak in the United States, the allocation of foliar C as a consequence of herbivory was confirmed (Frost & Hunter 2008).

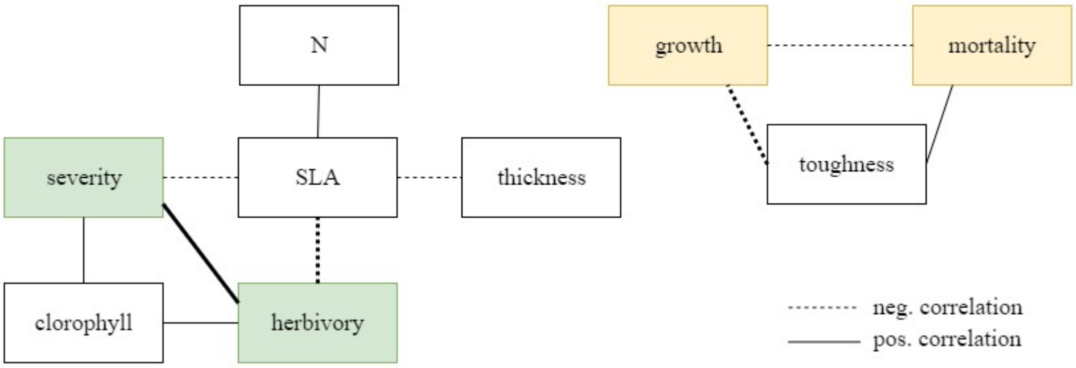


Figure 26: Diagram showing the significant correlations present for HD species (n = 9). Thin line: significant on the 0.05 level, bold line: significant on the 0.01 level

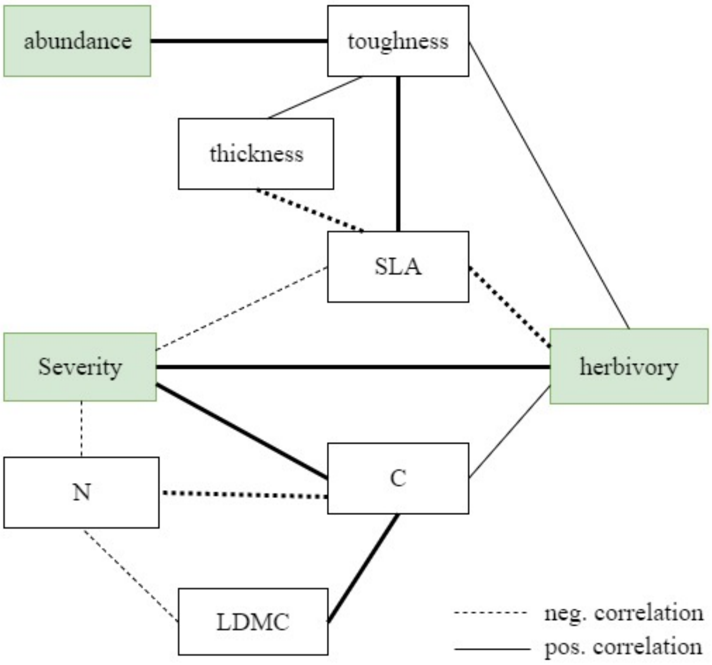


Figure 27: Diagram showing the significant correlations present for Legumes (n = 7). Thin line: significant on the 0.05 level, bold line: significant on the 0.01 level

Contrary to my findings that just explain 24.2 % of herbivory by leaf traits, Coley (1987) could explain up to 70 % of herbivory variations with defensive leaf traits. Her set of tested traits contained just two traits that I also tested: toughness and nitrogen. Among her investigated traits were tannins, fiber, lignin, cellulose, pubescence, and water content. Hence, chemical defenses might have a higher influence on herbivory levels than physical ones. It is also possible that I investigated traits not as important for defense or at least not vital for the tested species or the condition present at Finca Amable. This is supported by a study from Panama, which used a subset of my traits and found just little explanation (Paul et al. 2012). Furthermore, all trees were planted in the same habitat, which might be closer to the ecological optimum for some species but less optimal for others. Less-than-ideal abiotic factors induce stress to the tree that consequently is not able to develop the defensive traits fully. As a result, some species might suffer higher herbivory (Eichhorn et al. 2010) or some species may show unexpected variations in defenses. Coley (1987) discusses a number of studies ascertaining that habitat variations influence defensive mechanisms.

> **Research question 2: Can leaf traits explain the differences in herbivory levels?**
> The investigated leaf traits explain just 24.2 % of variations in herbivory levels between the species.

4.4 Growth and mortality

The average growth rate was 1.3 m/year. The lowest growth rates were observed for HD species and the highest growth rates for LD species. These findings are in accordance with the expected higher growth for pioneers (LD species) as this is part of their life strategy and the conditions in Finca Amable are more favorable for pioneers than for late successional species (HD species). In line with this assumption is the fact that *Anacardium excelsium*, belonging to the group of LD species, shows the highest growth rate (2.72 m/year) and at the same time the lowest mortality rate (0.01). Surprisingly, in my study the mortality rate was the highest for LD species, just slightly less for HD species and comparably low for legumes with just about one third of the other rates.

I was expecting that high herbivory influences a tree’s performance in terms of decreased growth rates or increased mortality rates (Aide 1993, Coley & Barone 1996, Turner 2004). In my research I could not identify a correlation between herbivory and growth or mortality, not for the group of all tested species nor for any functional group. These findings are in accordance with other studies missing a relation between herbivory and growth (Aide 1993, Eichhorn et al. 2010, Myster 2002) and herbivory and mortality (Doust et al. 2008, Myster 2002, Plath et al. 2010). Therefore, I could not confirm the growth-defense tradeoff theory (Coley 1987) for the reforestation at Finca Amable.

According to Eichhorn et al. (2010), studies identifying a relation between growth and herbivory were generally dealing with higher herbivory rates. In an experiment on the Neotropical understory shrub *Piper arieianum,* the critical amount of herbivory to cause long-term growth reduction appeared to be 30 % defoliation (Marquis 1984). I found only *Pachira sessilis* with > 30 % defoliation. The growth rate of 1.13 m/y was just slightly below the overall average (1.30 m/y) but far below the average of LD species (1.55 m/y), to which *P. sessilis* belongs. The relatively low impact of a high herbivory level on growth could be reasoned by the lower investment in leaves and leaf defensive mechanisms by pioneers and the accordingly lower loss of resources in case of higher leaf tissue loss. One could reason that the missing correlation of herbivory and growth in HD species contradicts this argument. Alternatively, studies determine whether the herbivory at one point influences growth rates or mortality at another point, often some years in the future (e.g. Eichhorn et al. 2010, Massad 2012, Marquis 1984). However, such an influence can just be tested by comparing single trees rather than species averages.

The negative correlation between growth rates and mortality rates present in the current study indicates that slow growing species are more likely to die back. Again, this would mean that the conditions at the former pasture of Finca Amable are more favorable for fast growing pioneer species. Herbivory has a higher impact on small and medium trees with regard to future growth deficits than on larger trees, which have a higher compensation capacity due to their higher biomass (Marquis 1984). In a case of a reforestation site, at the time of planting all samplings would have the same precondition. Faster growing species reach a size where herbivory has no longer a negative impact on their future growth earlier. Slow growing species remain much longer in a size where herbivory decreases their growth. This decrease of growth keeps them even longer in the critical size resulting in an even higher competitive disadvantage. My own findings showed a negative correlation between growth and mortality (for all species, HD species and LD species) implying that slowly growing, small trees are more likely to die. Alternatively, to look at it from another point of view, the low growth rates could be the effect of a previous herbivore attack. Either the caused damage might have weakened the tree or was the entrance point for a fungus or a disease (Eichhorn et al. 2010), which finally killed the tree.

Research question 3: Does the herbivory level influence growth and mortality of the trees?

Herbivory levels appeared not to have an influence on growth and mortality.

5 Conclusion

The applied method for herbivory assessment has its limitations but is commonly used in research and was suitable for the preconditions of this research. The ascertained herbivory levels averaging 7.53 % are similar to previous studies. As expected, significant differences in herbivory levels do exist between the species but not between functional groups. Surprisingly, successional status showed no influence on herbivory. Chlorophyll content and SLA were the only traits tested that showed a correlation with herbivory. For the functional sub-groups, the relations were different, which may relate to the fact that different species use different sets of defensive traits. Chlorophyll and SLA only accounted for about a quarter of the interspecific herbivory variations. This is low, compared to other researches, which could explain up to 70 % of the variations. Therefore, I assume that other traits than the investigated ones have more bearing on herbivory. Especially chemical traits are of high importance as defensive characteristics.

Herbivory had no negative influence on growth or mortality, implying that other aspects, like abiotic factors, might play a more important role in the performance of trees. It seems that functional groups as well as early and late successional species differ in their defensive mechanisms and their tree performance in connection to herbivory. Herbivory seems not to be a major problem for the performance of any of the investigated tree species at the reforestation site Finca Amable. As far as herbivory is concerned, the 23 tree species could be recommended for further reforestations under similar conditions.

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