Master Thesis

Assessment of allometric relationships of tropical trees in Costa Rica

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Abstract

Tropical forests are characterized by high biodiversity, particularly of trees. Measuring growth characteristics of tree species is a daunting task, making a standard growth formula for all tree species rather imprecise. Instead studies describing individual species` specific growth strategies and their response to the local environment would provide better estimates of growth and biomass and potentially more insight into ecological processes.

The quantitative relationships between two or more key characteristics of trees by using extensive measurements from a selection of one species to generalize the entire species population is known as tree growth allometry. Past research has indicated the need for further studies regarding the differing relationships between diameter and height growth. Pioneer tree species tend to grow quickly, while on the other end of the spectrum, late successional species tend to favor shade in their juvenile periods and grow slowly. After decades these slow-developing trees will overtake the pioneer species which had provided the shade necessary for their early development.

During the months of March and April of 2018, height, diameter, crown dimensions, and the distance between neighboring trees were measured for populations from over 100 native tree species planted between 2012 and 2015 in a reforestation project (COBIGA) in La Gamba, Costa Rica. We used these measures to calculate tree allometric relationships and competition or shading by neighbors. We quantified the species' habitat preference with data on their occurrence in old-growth and young forests and asked if growth strategies are related to habitat preference. Specifically, we tested the following hypotheses: I) Species differ in their allometric relationships, II) Pioneer trees, which tend to be shade-intolerant, invest relatively more in height growth than old-growth specialists and that trees with high wood density, which tend to be shade-tolerant species from old-growth forest, should be able to support a crown with a relatively thinner stem (higher H/D), and III) pioneer trees respond to shading with increased height growth (higher height/diameter ratio) compared to old-growth specialists.

Results showed significant differences in species' allometric height/diameter relationships. The height/diameter slope was also found to have a relationship with a species' successional classification, being either more closely related to pioneer (low height/diameter slope) or climax (high height/diameter slope) species. Significant neighboring effects were found for certain species. Smaller trees with greater height/diameter slopes were more affected by higher neighboring index values.

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1 Introduction

Tropical forests are characterized by high biodiversity and rapid growth. Old growth tropical forests in different parts of the world have been known to contain an astonishing 150-300 tree species per hectare (Sollins, 1998; De Oliveira et al. 1999). The specific growth strategies of differing tree species are dependent on several factors including an individual's genetic heritage, environment, stage of development, and actions by man (Picard et al., 2012). Genetic factors such as wood density and growth strategies of species dictate where on the growth gradient a particular species can be found. On one end are the pioneer species which typically need plenty of light to germinate and grow quickly to fill in a natural or man-made forest gap, and on the other end of the gradient are the climax specialist which germinate in the rainforest understory and grow slowly looking for a canopy gap in order to overtake pioneer species or other slower climax species for ultimate survival as part of the primary succession process (Swaine et al. 1988). Environmental factors that have been shown to affect tree growth are light radiation, soil structure and nutrient make-up, temperature, elevation, and rainfall (King et al. 2005, Clark et al. 2003, Powers et al. 2009, Homeier et al. 2010). Genetics coupled with environmental factors therefore determine how a species reacts and develops to adulthood. Certain species prefer to focus growth in one or more areas such as width of trunk, overall height, or the canopy width and height. These growth strategies have helped a particular species find its niche in an ecosystem and contribute to the abundant biodiversity found in the tropical rainforest.

Growth of trees, or biomass accumulation, is an essential part of ecological studies due to its link with global carbon stocks and sinks (Ketterings et al. 2001). Below, in Figure 1, we see a model of how CO_2 cycles through a general forest ecosystem. Understanding how reforestation programs or deforestation affect carbon balances is essential to a greater understanding of linkages between local ecology and worldwide climate changes. In particular, secondary tropical forest are an integral part of tropical ecosystems, whether developing from natural disasters such as hurricanes or more increasingly by anthropogenic disturbances such as logging or forest conversion to agricultural lands (Hughes et al. 1999). These secondary rainforests have rapid rates of above ground biomass and in turn have the potential to become large carbon sinks especially during the beginning stages of succession. However, as Hughes (et al. 1999) points out previous land use dictates the ability and rate of biomass accumulation.

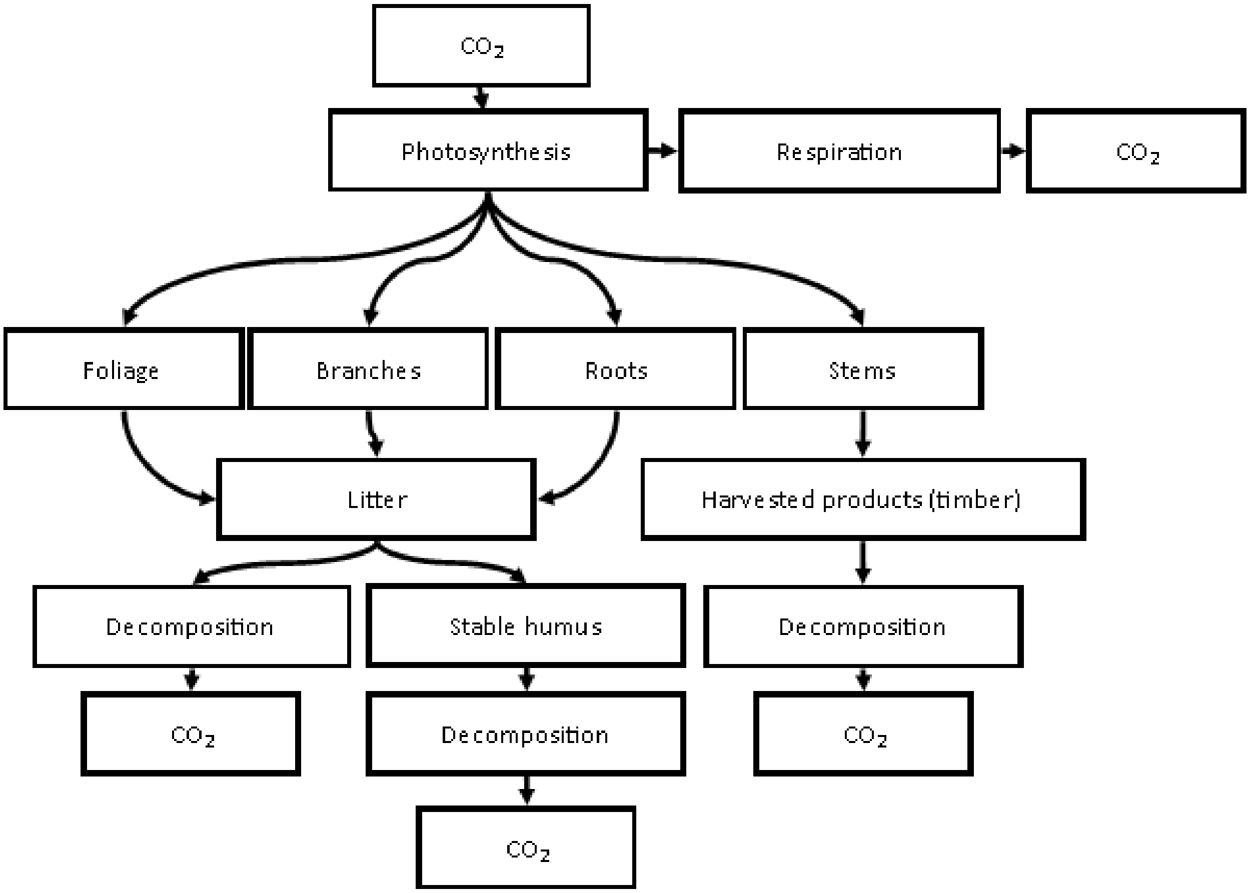


Fig. 1: Diagram of fluxes and carbon stocks in a typical forest ecosystem (Nabuurs & Mohren, 1993, modified)

The sub-discipline of functional ecology links processes within a given population, community, and ecosystem to performance traits such as growth, metabolism, and reproduction (McGill et al. 2006). Various growth strategies are utilized when functional traits respond accordingly based on differing environmental gradients (Westoby & Wright, 2006). Past research has indicated the need for further studies regarding the differing relationships between diameter, height, and crown area to calculate aboveground biomass (Feldpausch et al. 2012; Chave et al. 2005). However, currently forest biomass estimates routinely utilize only diameter measurements (Feldpausch et al. 2012) or a constant height-diameter relationship during a ground census (Drescher et al. 2011), and therefore could be imprecise on what the actual growth rate is for the selected forest area. A more concise model formed from utilizing additional measurements of structural variables such as total tree height, crown height, and crown width coupled with specific regional biome classifications would greatly reduce error in allometric growth equations to assess biomass (Brown, 1997; Feldpausch et al. 2012; Goodman et al. 2014).

Confirmation of biomass allometric models also relies greatly on data from direct destructive harvesting of trees. These harvest sites vary due to environmental variations and vegetation type and a classification system proposed by Brown (1997) was used to classify forest systems into three categories of dry, moist, and wet in accordance with the Holdridge life zone system (Holdridge, 1967). This more concise classification has advanced carbon accounting through allometric equations.

Measuring growth characteristics of tree species is a daunting task, making a standard growth formula for all tree species imprecise. Instead studies describing individual species' specific growth strategies and their response to the local environment would provide better estimates of growth and biomass and potentially more insight into ecological processes. The study of tree allometrics can be utilized to distinguish relationships per species between measurements of different parts of the studied tree. By understanding growth relationships between different structural parts of a species, a more precise estimation of a tree's life cycle can be constructed. Gould (1966 p. 587) defines allometry in a very simplistic way as "the study of size and its consequences". Allometric growth ratios such as height to DBH (diameter at breast height) or DBH to crown area vary across different species, species age, regions or biospheres, and other ecological factors. By understanding specific species' allometry, and the factors that dictate growth habits, this could help improve our understanding of more accurate biomass data along with understanding differentiation of regional environmental effects on growth and forest ecology.

The current study aims to discuss growth parameters of tropical tree species and to look at allometric relationships intra and interspecies in the studied reforestation plot located in La Gamba, Costa Rica. By assessing the allometric growth correlations in this specific biome, my hopes are that ecological processes can be better understood and that this information will be utilized in future reforestation projects.

1.1 Allometrics

1.1.1 An introduction to allometry

Allometry as defined by Gould is "the differences in proportions correlated with changes in absolute magnitude of the total organism or of the specific parts under consideration" (p. 587, 1965). The study of allometry was first conceived by Otto Snell in 1892 and further emphasized by famed evolutionary biologist D'Arcy Thompson and Julian Huxley in the early part of the 20th century. Allometric scaling has been used as a key biological tool for fauna as well as flora and helps to correlate size changes in two or more parts of an organism or group of organisms that have differing growth rates. For example, a certain species of tree may develop a short trunk with a very slight increase in height and girth annually but also has extensive branching growth in regard to crown height and width can be measured and correlated with a proper scaling formula. An example can be seen in Figure 2 in which body size of a fiddler crab develops at a certain rate while the claw size develops at a faster rate therefore creating an allometric ratio that favors claw size. The formula usually applied is a power function such as $f(x) = kx^a$ (Longo & Montevil, 2014). This field of study can be narrowed further into two areas pertaining to size differences in ontogenic development of a particular species or analysis of interspecies variations.

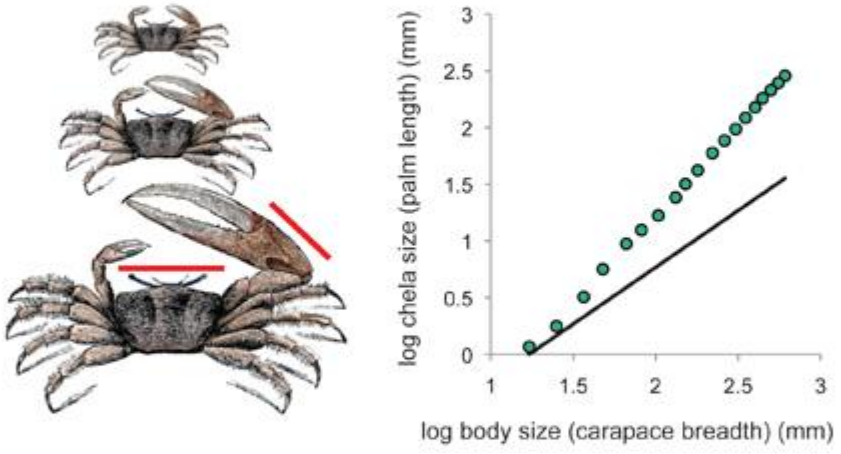


Fig. 2: Allometric relationship between chela (claw) size and body size of a developing fiddler crab (*Uca pugnax*). (Shingleton, 2010)

1.1.2 Allometry application

The study of allometry within the tropical forest environment is important because this enables quantification of carbon fluxes associated with plant growth dynamics including woody vegetation (Jara et al. 2015).

Loss in forest cover, either through forest degradation or complete deforestation resulted in 7 to 14% of total global anthropogenic CO_2 emissions from 2000 to 2005 with Latin America accounting for 54% of these emissions (Harris et al. 2012). The Reducing Emissions from Deforestation and Forest Degradation (REDD) program, which was setup by the United Nations in 2008, creates incentives for forest conservation and enhancing forest carbon stocks. One critical piece of this program hinges on the consistent ground-based monitoring, reporting, and verification (Chave et al. 2014). The ground census data for a particular area is used to convert biometric measurements into biomass values using an allometric model (Brown, 1997). However, use of generalized allometric models to assess above ground biomass have been viewed as a qualitative issue in differing localized environments (Chave et al. 2014; Skole et al. 2011; Drescher et al. 2011). This is because environmental factors such as precipitation, temperature, and seasonality differ greatly among geographical locations even if the rainforest are considered to be classified as similar in population and spatial tree density. These variances affect tree growth throughout its lifespan. One factor pointed out by Chave (et al. 2005; 2014) about one of his earlier studies is that the inclusion of height into the allometric model would greatly reduce inaccuracies in carbon stock estimates. This outcome was also found in a study by Drescher (et al. 2011) that inclusion of height measurements would improve the outcomes of biomass equations, and goes further to suggest that local location, environment, and forest structure should be incorporated into allometric models. However, due to closed canopies it can be quite challenging to obtain an accurate height measurement to portray the actual forest system correctly (Larjavaara & Muller-Landau 2013). One solution, proposed by Sullivan (et al. 2018), is to take a limited sampling of heights per species with a focus on larger diameter individuals and to use these measurements to examine allometrics. Larjavaara & Muller-Landau (2013) go on to assess two height measurement techniques, the 'tanget' and 'sine' methods. The tangent method which measures horizontal distance from the tree along with the angle to the top at a distance of at least one tree height away was found to overestimate height. The sine method which utilizes laser measurements to the top and base of the tree in relation to the angle from the horizon was found to underestimate height measurements, but was recommended by the author because of its faster application ability and lesser variation amongst differing technicians. Hunter (et al. 2013) point out the difficulty in using a range finder to obtain height measurements, implying that due to obstacles an underestimation is likely to occur due to the laser inadvertently striking a lower branch or leaf; furthermore, identifying the correct tree pinnacle point is difficult to pick out from the forest floor.

1.2 Growth dynamics

Topical forest ecology is a complex system with many interlacing factors that can influence one another. There are two main groups of factors that influence a tree's growth (1) the environment's biotic and abiotic resources and (2) the genetics of a given species (HilleRisLambers et al. 2012). Figure 3 demonstrates how the community assembly theory of species can be affected by a range of spatiotemporal scales. First, the environment creates distinct biogeographic populations through different climate and growth zones. Secondly, neighborhood competitive interactions contribute to local coexistence. This therefore results in a local community that is specialized to its local environment and biota. Community assembly is a constant process in which neighborhood interactions and feedback influence species make-up and growth. Although a single species has a specific range for growth potential, environmental factors greatly contribute to a specific tree's overall growth performance and allometry. The environmental factors are broad and ranging from differences in climactic conditions to soil nutrient content. Perhaps the environmental factor that most affects the allometry of a specific tree is competition from neighboring trees, and more specifically competition for the valuable resource of photosynthetic light. Drescher (et al. 2011) found strong evidence of environmental effects on height/diameter (H/D) relationships in tropical forests, with rainfall and temperature being highly significant factors along with altitude correlations.

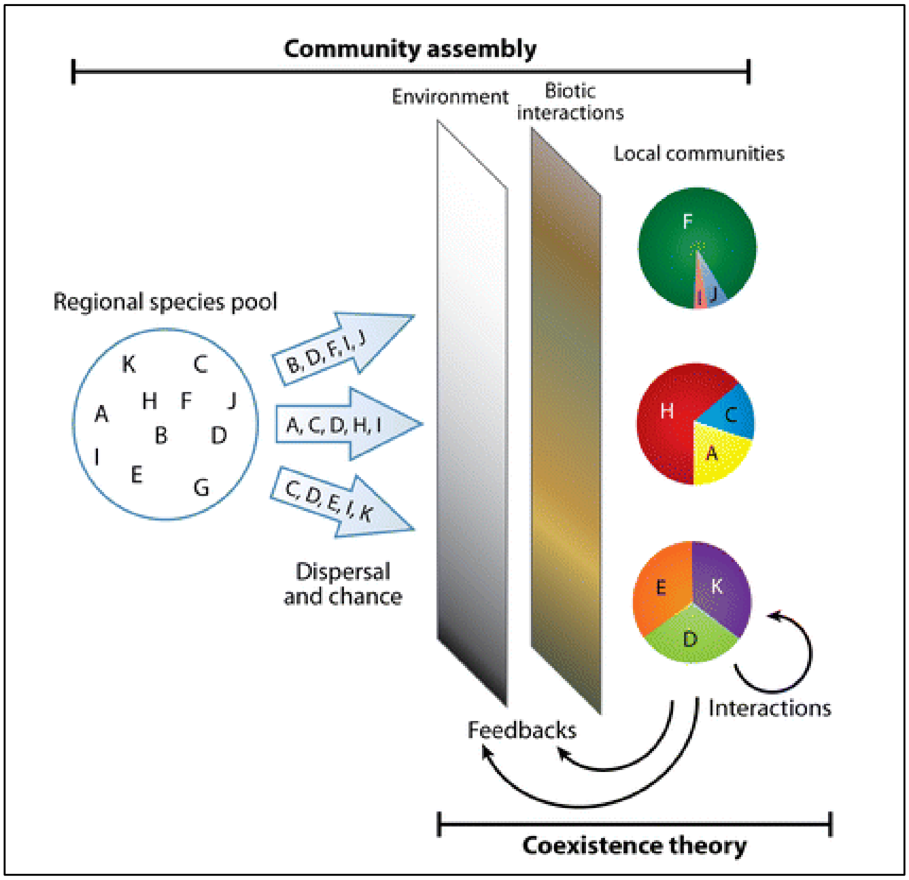


Fig. 3: Diagram of influences on community assembly (HilleRisLambers et al. 2012)

The genetics of a tree species, however, dictate the range in which growth traits may differ in a given environment. There are an estimated 40-53,000 tree species in the tropics (Slik, et al. 2015). This huge variation in genetics signifies that tree species have evolved over time in order to fill a specific niche in an ecosystem. In diverse eco-systems differing tree species allocate their resources in a heterogeneous manner creating both conflicting and symbiotic relationships. On a temporal scale, tree communities are also exclusive during different periods of forest development. There are species that quickly inhabit an opened area and others are found only in existing forest that populate much later in the successional process. We will look more into how a tree displays its growth traits on a successional gradient later in this chapter.

1.2.1 Environmental effects on allometry

1.2.1.1 Light

Access to light is widely regarded to be one of the more important environmental factors driving the growth of tropical trees (Rüger et al. 2011; King et al. 2005; Poorter, 2001). Trees respond to differing light gradients in various methods considering that generally 1 to 5% of the sun's photo-synthetically active radiation reaches the rainforest floor for developing seedlings (Clark et al. 1996; Chazdon & Pearcy, 1991). The higher into the canopy that a tree can grow dictates the amount of light availability as shown in a study by Montgomery (& Chazdon, 2001) in which at 1m mean diffused light transmittance equaled 2%, and at a height of 9 meters over 10% became available as shown in Figure 4. Surprisingly, in this study, old growth forest canopies exhibited a higher percentage of light diffusion between 1m and 6.5m. This result was contributed to the physical structure of the second growth forest. Not only were there more woody shrubs and saplings, but mid sized trees in the second growth study area possessed varying allometry and crown sizes. This implies a more complete horizontal and vertical coverage of the canopy area compared to old growth tropical forest. Shade tolerant species are able to germinate and develop slowly in understory light conditions whereas pioneer species must wait for a canopy gap to

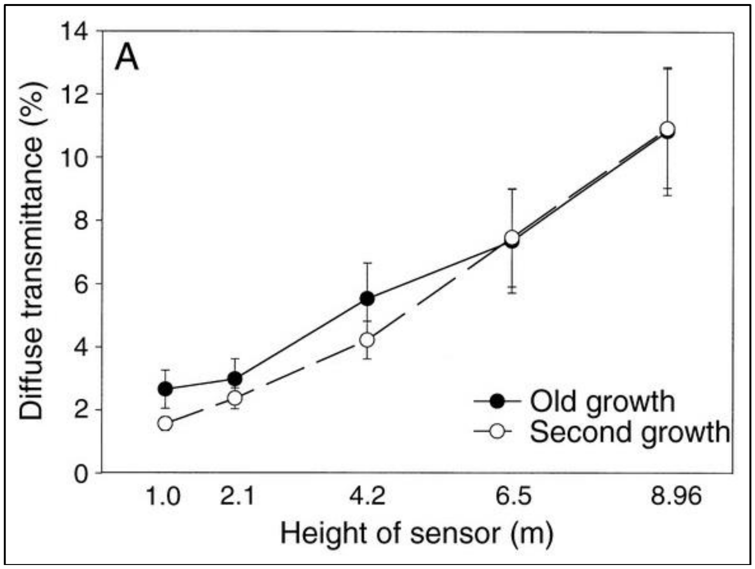


Fig. 4: Patterns of vertical light availability in an old-growth forest and a 15–20 year old second-growth forest at La Selva Biological Station, in the Caribbean lowlands of northeastern Costa Rica. Diffuse transmittance at five heights above the forest floor (Montgomery & Chazdon, 2001)

occur in order to take advantage of the necessary light for growth and ultimate survival (Veneklaas & Poorter, 1998; Montgomery & Chazdon, 2001). Canopy gaps, which form when a tree is removed from the canopy naturally or un-naturally, create opportunities for a varied species mix and are necessary for pioneer species to exist in mature forests (Hubbell et al. 1999). Tree saplings that are in the lower levels and receive limited light tend to have higher biomass in their leaves and achieve a higher leaf area per mass, while reducing self-shading by developing wider crowns (Poorter, 1999; 2001). These specialized shade tolerant leaves also have slower respiration and photosynthetic rates, which enables these species to invest less in maintenance and enables potential relative growth rates to be enhanced (Oberbauer et al. 1985). In a tropical moist forest in Costa Rica, growth in a pioneer species (*Heliocarpus appendiculatus*) was found to be more plastic than growth in a small gap specialist (*Dipteryx panamensis*) in changes in irradiance levels (Fetcher et al. 1983).

1.2.1.2 Precipitation

Tropical rain forests are categorized by maintaining at least 100 mm of rainfall every month with possible dry periods lasting a few days to weeks (Whitmore, 1998). Hydraulic limitation theory defines water availability as a direct contributor or inhibitor of tree height growth through hydraulic resistance, especially in taller trees with longer branches (Yoder et al. 1994). Lines (et al. 2012), points out that there is in fact a pattern of reduced tree height for a given diameter with an increase in aridity. She argues that the biomechanical constraint of hydraulic transport in cooler temperatures limits branch length in order to avoid embolism risk. Drescher (et al. 2011) also backs this claim that a longer dry season is associated with shorter trees with thicker trunks in order to increase water transport with higher sap-wood cross-sectional area. Furthermore, a correlation between longer dry-seasons and crown diameter at a given diameter were shown to increase. This is thought to be caused by greater trunk size supporting a larger "top-heavy" canopy.

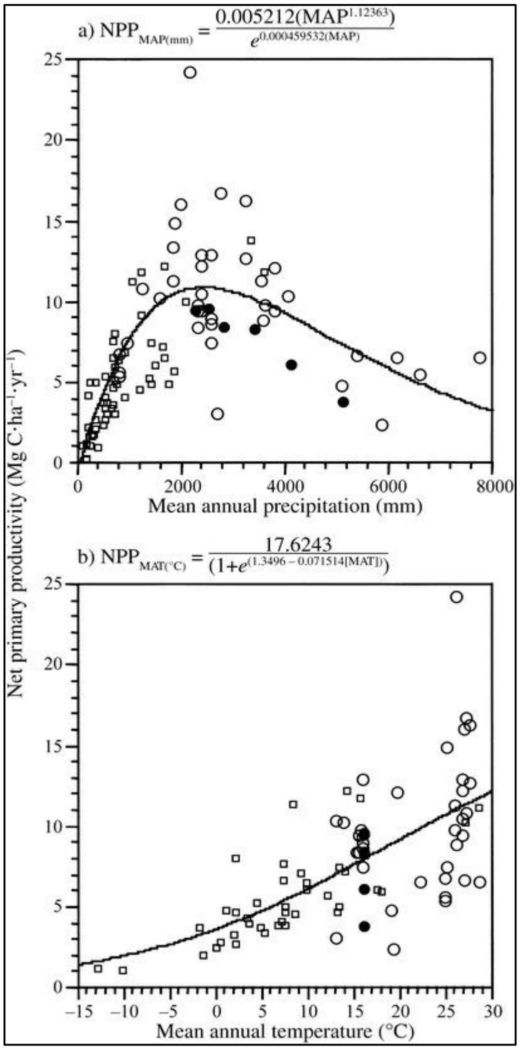


Fig. 5: The relationships between net primary productivity and (a) mean annual precipitation and (b) mean annual temperature (Schuur, 2003)

Sufficient moisture levels for survival and growth differ by tree species on a wide range. Overall precipitation rates from 1960 to 1998 in tropical areas have decreased due to global climate change, with certain exceptions (Malhi et al. 2004). However, future global climate model predictions indicate that for most tropical wet forests, precipitation will increase (Smithson, 2001). With this increase of precipitation, forest growth in the form of net primary production (NPP) is expected to decrease at a certain threshold (approximately 2,200mm) as shown in Figure 5, through the effects of decreasing radiation inputs, increased leaching of nutrients, and reduction of available oxygen in the soil (Schuur, 2003).

1.2.1.3 Temperature

Average temperatures in tropical forest have been increasing in recent years (Wagner et al. 2014; Malhi et al. 2004; Clark et al. 2003). Annual tree growth in Costa Rica has been shown to have a negative relationship with warmer mean yearly temperature and instead has shown drastic increases of annual growth during cooler years (Clark et al. 2003). However, tropical trees still need higher temperatures than temperate trees. Cunningham (& Read, 2002) show that while temperate tree species maintain photosynthesis at high rates over wider ranges of temperatures, tropical species require a narrower range of high temperatures for maximum rates of photosynthesis. This vulnerability of tropical trees to a smaller preferred temperature could become an issue as warming trends continue. Temperature effects on H/D allometrics is usually coupled with change in elevation and will be further discussed in the following section.

1.2.1.4 Elevation and topography

Elevation and topography gradients in a tropical biome, though poorly understood, correlate with environmental growth factors such as temperature, wind exposure, soil hydrology, and nutrient supply (Homeier et al. 2010). Topography has dynamic effects on drainage and water retention in soils. Surface water flows from higher elevations causing drier conditions on upper slopes and water accumulation is higher in valleys or on more level areas of soil. Whitmore (1998) points out that the biggest change from tropical lowland forest to upper montane forest is the gradual decrease in tree height. In valleys or lower elevations trees are generally taller at a given diameter than ones found higher on mountainsides due to decreasing temperatures, lack of nutrients, low radiation, and proper soil chemical or physical conditions (Homeier et al. 2010; Breckle et al. 2005; Bruijnzeel & Veneklaas, 1998). Root systems are also affected heavily by differing elevations. Graefe (et al. 2008) shows in her study, that fine roots in the lower elevation gradients tend to have higher root turnover with a mean of about one year compared to mid-montane forest. The high level of root turnover signifies higher levels of nutrient cycling and carbon re-entering the soil (Gill & Jackson, 2000).

1.2.1.5 Soil substrate

Another factor that stems from elevation changes is the mineral and nutrient characteristics of the soil. Soil composition and its structural characteristics could limit or promote growth in tropical forests. The rapid exchange of nutrients is possibly best described by Whittaker, that “The tropical rain forest thus has a relatively rich nutrient economy perched on a nutrient-poor substrate” (1975, p. 271). Grubb (1977) speculates that while lack of phosphourous (P) limits growth in lowland rainforest, nitrogen plays a large limiting role in growth of montane tropical forest.

In a study in Borneo, a decreased H/D relationship of tree species was shown to be affected by differing substrate compositions, although elevation was also an added factor in the study (Aiba & Kitayama, 1999). Nutrient deficiency was a suggested reason for the stunting of trees in higher elevations. Furthermore, Aiba (& Kitayama, 1999) found that tree allometry has a marked difference in soil substrate from low elevations with non-ultrabasic substrate where trees have slender trunks with greater height versus high elevation ultrabasic substrate in which larger trunk size and lower heights reflect the variance in biomass allocation and resulting allometry. Drescher (et al. 2011) attributes partial H/D variability to soil physical conditions and states that without soil physical restraints, trees are more slender in trunk diameter and especially at smaller diameters.

Species' distributions have been shown to favor particular soil gradients in wet tropical forest (Powers et al. 2009; John et al. 2007). According to Sollins (1998 p. 23), the most influential soil physical and chemical properties on tropical rainforest species composition are "P availability, Al toxicity, depth to water table, amount and arrangement of pores of different sizes, and availability of base-metal cations, micronutrients (e.g., B, Zn), and N". Topography and parent material strongly influence P availability in soil; with volcanic rock possessing double the amount of P as quartz diorite parent material, and 2.5× higher amounts in valleys than on ridges (Mage & Porder, 2013).

Soil properties also have been found to change drastically depending on temporal scales (Sollins, 1998; Newberry et al. 1988). Differences in dry and wet season nutrient or pH values create the problem of correlating a particular soil classification to tree growth in regards to time and length of studies. Instead annual pattern inferences should be made to understand soil dynamic of a forest stand.

Besides temporal scales, spatial considerations should be made as well. Decomposition rates of organic material have been shown to be higher in lowland forest than in montane tropical forests, where soil organic matter decomposes much more slowly (Jenny, 1950). Shuur (2003), points out one reason for this is that with increasing precipitation levels in the tropics decomposition rates decreased due to slow diffusion of oxygen through saturated pores, which in turn means less nutrients availability from decomposed organic matter.

1.2.1.6 Competition

Competition comes in many forms and can contribute to a species access of abiotic resources such as light from tree-fall gaps, ground-water, or nutrients (Hubbell et al. 2001). Abiotic resource competition starts during the seedling and sapling stages where negative feedback affects species in high densities or near conspecific adults (Mangan et al. 2010; Packer et al. 2000; Peters 2003). Tree competition in reforested pastures, such as the current study, could be affected both positively and negatively by existing tall grasses. Negative aspects are relatively clear, being competition for above and below ground resources that are needed for development (Kambatuku et al. 2011). However, competing tree saplings or other vegetation have been shown to facilitate positive effects on certain seedlings in early stages of growth by creating accommodating microclimates through shade or increased moisture (Barbosa et al. 2014).

Allometric variability from competition has been shown to be a consequence of competition. Trees in closer proximity to each other generally have a larger mean H/D relationship compared to less dense forest in order to seek out light (Forrester et al. 2017). Crown projection area was also shown to decrease with increased competition in this same study.

Measurement of how neighboring trees affect the growth of surrounding trees has been studied in the past by creating a neighboring indices (Daniels, 1976; Hegyi, 1974). While calculating a neighboring index for a target tree, several variables should be included to an allometric formula in order to assess the degree to which the target tree may be affected by neighbors. Perhaps the most important factor is the diameter of the neighboring tree (Forrester et al. 2017).

Biotic competition from neighboring trees is perhaps also a driver in forest ecology to maintain high biodiversity levels (Hubbell et al. 2001). Studies have demonstrated an amplification of species diversity through the varied responses to light gap disturbances (Denslow, 1980; Hartshorn, 1978). Each tree species specializes in varying growth strategies to capture sunlight and to develop. More will be discussed on how these species are differentiated and classified in the following chapters. Wills (et al. 1997) proposes a “species herd-immunity” theory in which certain rare tree species are protected from host-specific pathogens or predators due to these trees being protected by a dense and biodiverse community therefore isolating the pathogen and avoiding attack or disease. It has been shown that pioneer species, or gap specialists, are more vulnerable from neighboring tree competition and especially in conspecific areas than their shade-tolerant counterparts (Hubbell et al. 2001). Adding to this, neighboring trees in a particular radius from a central focus tree affect the growth through a number of positive or negative factors including shading, competition for water and nutrients, and litter or nitrogen fertilization (Bhadoria et al. 2018).

1.3 Genetic factors and relating allometry

Over a very long period of time, continental drift and subsequent evolution created profound changes in flora and fauna to form rain forests of today with their diverse composition (Whitmore, 1998). Genetic factors that define a species along a gradient from pioneer to climax species categories come from trade-offs of resource allocation in order to achieve particular growth strategies (Hubbell et al. 1999; Enquist et al. 1999). Species differ greatly along this gradient based on particular adaptations made over time and space.

1.3.1 Growth strategies

Life-history growth strategies of tropical trees dictate how a plant allocates resources to different organs in order to grow, survive, and reproduce; and are reflected by anatomical and morphological traits (Rüger et al. 2012). These growth strategies amongst the different vegetation levels change in relation to the ontogenic development and environmental factors (Valladares et al. 2016). Table 1 shows the usual characteristics defining pioneer and climax tree species and how certain characteristics such as height growth or branching may affect allometric scaling.

Table 1: Main characteristics of pioneer and climax species in tropical rain forests (Whitmore, 1998, modified)

	Pioneer	Climax
Common alternative names	Light-demander, (shade-) intolerant, second-growth	Shade-bearer, (shade-) tolerant, primary-growth
Germination	Only in canopy gaps open to the sky which receive some full sunlight	Usually below canopy
Seedlings	Cannot survive below canopy in shade, never found there	Can survive below canopy, forming a ‘seedling bank’
Seeds	Usually small, produced copiously and more or less continuously, and from early in life	Often large, not copious, often produced annually or less frequently and only on trees that have (almost) reached full height
Soil seed bank	Many species	Few species
Dispersal	By wind or animals, often for a considerable distance	By diverse means, including gravity, sometimes only a short distance
Dormancy	Capable of dormancy (‘orthodox’) commonly abundant in forest soil as a seed bank	Often with no capacity for dormancy (‘recalcitrant’), seldom found in soil seed bank
Growth rate	Carbon fixation rate, unit leaf rate, and relative growth rates high	These rates lower
Light compensation point	High	Low
Height growth	Fast	Often slow
Branching	Sparse, few orders	Often copious, often several orders

Growth periodicity	Indeterminate ('sylleptic'), no resting buds	Determinate ('proleptic'), with resting buds
Leaf life	Short, one generation present, viz. high turn-over rate	Long, sometimes several generations present so slow turn-over rate
Herbivory	Leaves susceptible, soft, little chemical defense	Leaves sometimes less susceptible due to mechanical toughness or toxic chemicals
Wood	Usually pale, low density, not siliceous	Variable, pale to very dark, low to high density, sometimes siliceous
Ecological range	Wide	Sometimes narrow
Longevity	Often short	Sometimes very long

1.3.2 Climax tree species

Climax species are described as being "… self-perpetuating, in a state of dynamic equilibrium" (Whitmore 1998, p. 117). This is because climax trees are able to germinate and grow below a closed forest canopy although only a few survive to reach higher than one meter due to lack of precious sunlight (Whitmore, 1998). Swaine (et al. 1988) note that there are variations in this subgrouping of species in relation to the amount of solar radiation needed for growth, by which one extreme needs more solar radiation and grows quickly with higher seedling mortality. These species referred to as light hardwoods (LHW) produce a paler and less dense wood. On the other side of the spectrum are the heavy hardwoods (HHW) which require very little solar radiation in order to grow due to slow development. The HHW is darker in color and much denser. One benefit of LHW species, as noted by the author, is that these trees regenerate favorably after timber extraction versus HHW which are less likely to naturally regenerate.

Baraza (et al. 2004) note that leaves from shade tolerant trees are a bit fewer but larger in order to increase total leaf area; while shoot/root ratios are higher in shade tolerant seedlings.

Herbivory effects are more prevalent in the understory where shade tolerant plants develop due to a more favorable environment for insects and pathogens (Baraza et al. 2004). However, most of these climax species invest more energy into defenses to combat leaf consumption.

1.3.3 Pioneer tree species

Pioneer species germinate and quickly grow in a forest gap while suppressing species that lag behind in speed of vertical growth with a single layered canopy (Whitmore, 1998). However, below this canopy climax species germinate and wait for a pioneer individual's death in order to be released into the higher canopy and take over as part of the cycle of secondary succession (Whitmore, 1998). These light demanding species exhibit a resource acquisition strategy with traits such as high specific leaf area and low wood density (Poorter et al. 2008; Wright et al. 2010); and therefore are expected to be less accepting of crowding by neighboring trees (Lasky et al. 2014).

Swaine (et al. 1998) clearly defines tropical pioneer tree characteristics but acknowledges that not all pioneers fall under his classification system as seen in Table 2.

Table 2: Characteristics of pioneer tropical tree species (Swain et al. 1988)

i.	Seeds only germinate in canopy gaps open to the sky and which receive some full sunlight	ii.	Growth indeterminate with no resting buds
iii.	Plants cannot survive in shade - young plants never found under a closed forest canopy	iv.	Branching relatively sparse
v.	Seeds small and produced copiously and more-or-less continuously	vi.	Leaves short-lived
vii.	Seeds produced from early in life	viii.	Rooting superficial
ix.	Seeds dispersed by animals or wind	x.	Wood usually pale, low density, not siliceous
xi.	Dormant seeds usually abundant in forest soil (especially fleshly-fruited species). Seeds orthodox (no recalcitrant species known)	xii.	Leaves susceptible to herbivory; sometimes with little chemical defense
xiii.	Seedling carbon-fixation rate high; compensation point high	xiv.	Wide ecological range (7); phenotypically plastic
xv.	Height growth rapid.	xvi.	Often short-lived.

1.3.4 Wood density

Wood density is a key biotic trait for assessing a species role in the global carbon cycle (Chave et al. 2006). As shown in the previous chapter wood density is a predictor of where a tree species is classified on the successional gradient, where slow-growth species generally produce high density wood, while pioneers trade low wood densities for rapid growth to reach the higher canopy level.

Wood density of a particular species has been found to be a major genetic factor for variation in growth strategies (King et al. 2005). However, wood density per particular species varies under differing environmental conditions (Donegan et al. 2014). Overall a negative relationship in wood density and growth rate have been found in the tropics (Enquist et al. 1999). King (et al. 2006) explain this in a threefold manner that "…(a) species with low-density wood tend to be less shade-tolerant and are therefore restricted to brighter-than-average microsites; (b) the thickness of the peripheral shell of stem wood corresponding to a given biomass increment is inversely proportional to wood density, so that diameter growth rates vary inversely with wood density, all else being equal; and/or (c) light-wooded species require less biomass to support their crowns, i.e. they have lower support costs, and are therefore able to achieve greater crown extension per unit of synthesized biomass, which enhances future light interception and growth.". In this way tree diameter and crown extension allometric variability is suggested to be affected by differing wood density characteristics that a tree species demonstrates as part of its growth strategy.

Trade-offs have been found in pioneer species to enhance growth in which these species develop trunks with lower wood density and higher concentrations of nutrients dedicated to leaves for photosynthetic energy conversion (King et al. 2006). Furthermore, wood density and a species' life history traits are connected through the physiological role of transporting sap, and also a mechanical role of supporting an extensive canopy and resistance of being pushed over by climactic factors (Chave et al. 2006).

1.3.5 Leaf characteristics

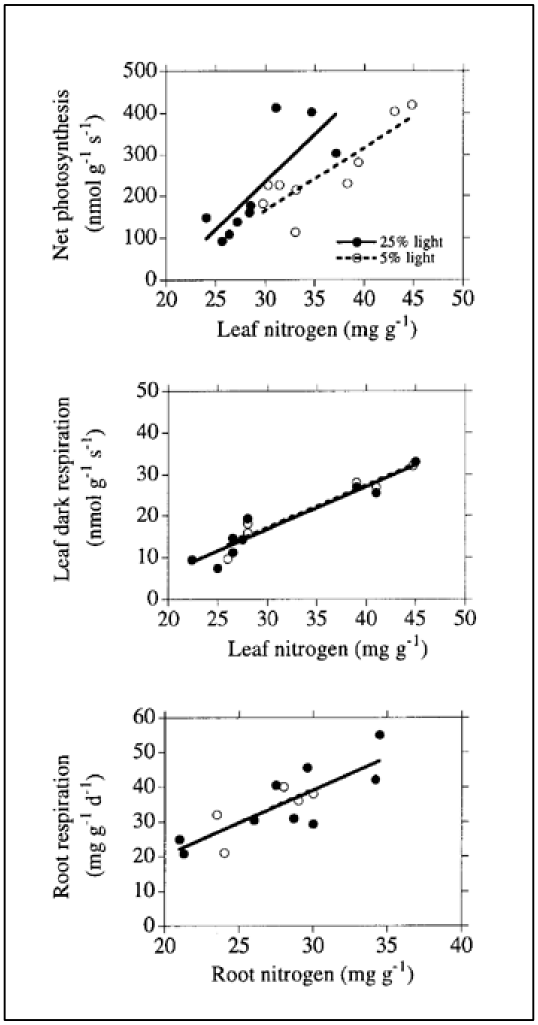


Fig. 6: Leaf tissue structure relating to respiration (Reich et al., 1998)

Support costs also include leaf traits in the growth trade-off scheme. Leaf traits of a particular species vary according to particular environmental conditions (Martínez-Garza, et al. 2005) and have been shown to affect plant growth by affecting tissue structure, and chemical and metabolic activity (Reich et al. 1998). More specifically, species' CO_2 exchange and tissue nitrogen concentrations have been shown to correlate (Reich et al. 1998). Higher leaf or root N was attributed to higher levels of respiration (see Figure 6).

In areas of higher mean temperatures and greater solar radiation plants develop thicker leaves in order to capitalize on higher potential photosynthesis rates; furthermore, these dense leaves also contribute to extra leaf water storage during times of water stress (Niinemets, 2001). Species successional status was also shown to be a factor in herbivory effects, where colonizing species with rapid growth of leaves with less defenses were shown to be damaged six times more rapidly than shade tolerant or old-growth species (Coley, 1983). The pioneer species were shown, in the same study, to exhibit softer leaves, lower concentrations of fiber and phenolics, higher nitrogen and water levels, shorter leaf lifespan, and a faster growth rates making their leaves a more desirable target for herbivory. By investing in rapid growth, defenses have been traded and neglected resulting in higher mortality rates. These low morphological support costs therefore reflect poor survival rates (Kitajima, 1994).

Trees growing in lower light levels have been generalized as having larger leaves with lower dry leaf weight, density, and water content than trees in more sunlit areas (Martínez-Garza, et al. 2005). In an Australian study by Pickup (et al. 2005) a relationship was found between wood density and leaf size, where higher wood density was correlated to larger leaves and lower wood density meant that leaves were generally smaller. This could be explained by the trade-off theory that smaller leaves with higher photosynthesis output would be utilized more by low density and fast-growing tree species, while slow growing, high density species would opt for larger and longer lasting leaves.

2 Objectives and Hypothesis

2.1 Objectives

1. One objective of this research is to understand the relationships between tree growth and neighboring effects by evaluating tree allometrics, specifically the relationships between tree diameter and height.
2. Another objective is to look at any differences in allometric relationships among species, and then further looking into intra-species variations and understanding the causes. These allometric variables will include height, diameter, and crown dimensions.

2.2 Hypothesis

1. Tropical tree species differ in their allometric relationships





2. Pioneer trees, which tend to be shade-intolerant, invest relatively more in height growth than old-growth specialists and trees with high wood density, which tend to be shade-tolerant species from old-growth forest, support a crown with a relatively thinner stem (higher H/D)

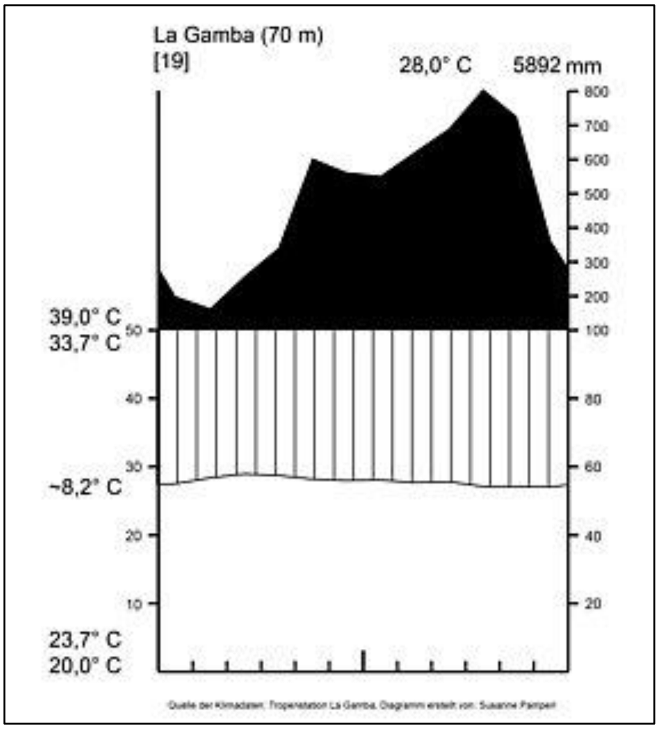
3. Pioneer trees respond to shading with increased height growth (higher H/D) compared to old-growth specialists

3 Methods

3.1 Site Conditions

The reforestation area, known as La Finca Amable (N 8.714153, W -83.173638), is located just outside the village of La Gamba, Costa Rica (Fig. 7). This area receives approximately 6000mm of rain per year, with mean annual temperature of 28.3°C as seen in Figure 8 (La Gamba, 2017). La Gamba is one of the wettest lowland forest in Central America due to its geographic location bordering the Fila Cruces mountain range and has an average of 276 rainy days per year (Weissenhofer & Huber, 2008).

Fig. 7: The reforestation area within the black outline is known as La Finca Amable and is comprised of over 6000 native individual trees from over 100 species



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

Fig. 8: Climate diagram 1998 – 2017 (La Gamba 2018)

La Finca Amable is part of the Biological Corridor La Gamba (COBIGA) project, which aims to connect the lowland forest areas of Piedras Blancas National Park with the Talamanca mountain rainforest to the North. This connection between lowland and mountain ecosystems builds on the already strong biodiversity for both flora and fauna. Between the years 2012 and 2015, 6000 individual trees consisting of over 100 native tree species were planted in a converted cattle pasture. Species were selected based on soil type, local weather conditions, topography, and specific desired ecological characteristics. Spacing between saplings was approximately 4.5m x 4.5m, making the reforestation areas about 500 trees per hectare. The reforestation area is divided up into 12 different sectors, and each sector contains a certain amount of plot areas which are made up of a 6 x 6 tree layout. In the first three years, tree saplings were managed by cleaning surrounding grasses in a radius of one meter and other spontaneous vegetation several times a year.

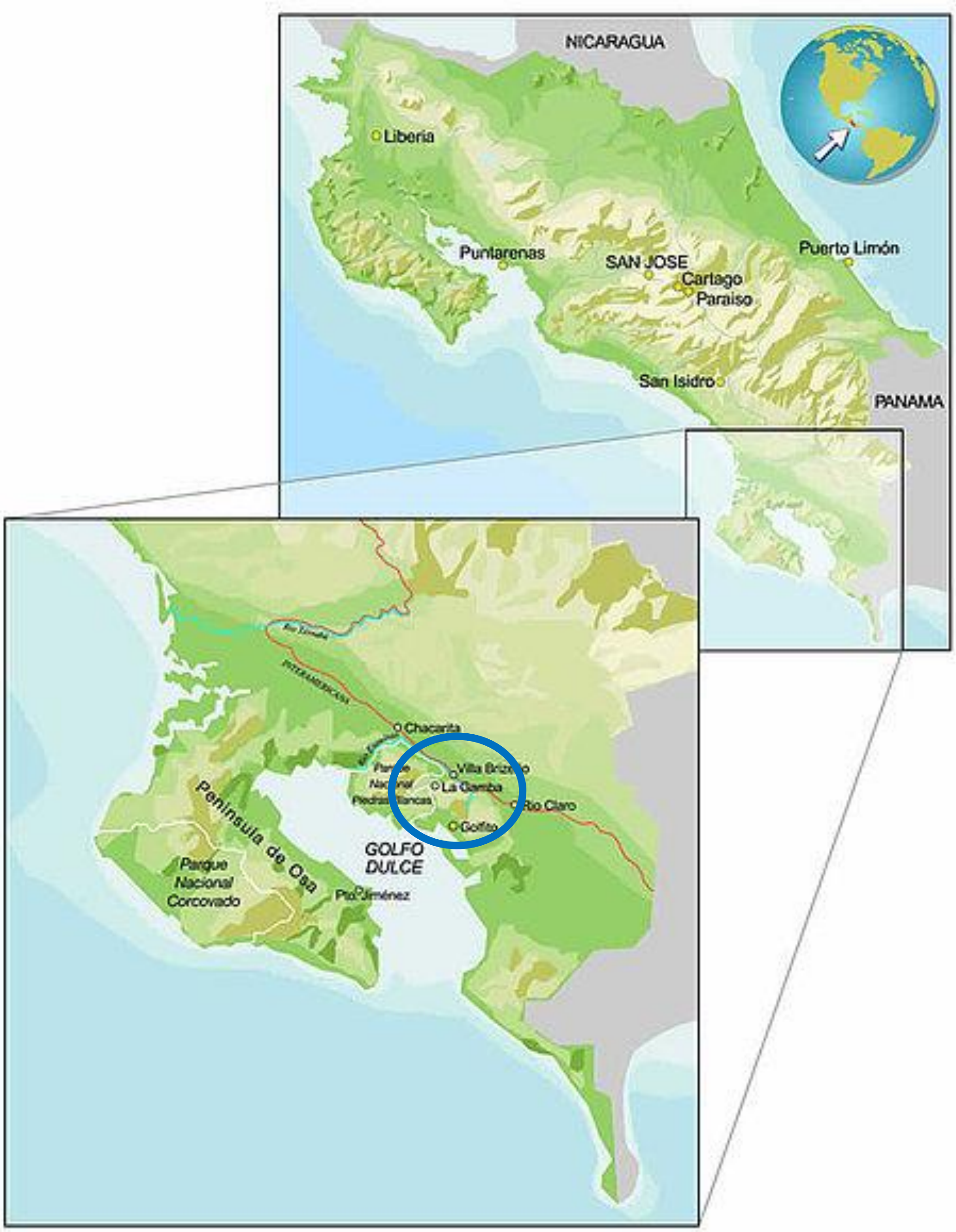


Fig. 9: Map of Costa Rica and the Golfo Dulce region (Weissenhofer et al. 2008)

3.2 Data Collection

Fig. 10: Our reflective tool (toilet paper roll with reflective 3M tape mounted on a pole at breast height) used to create a reference point for tree position measurement (Own photo)

Fig. 11: Our field equipment used for height, diameter, crown, and position measurements (Own photo)

During the months of March and April of 2018, my working partner, Katharina Schwarzfurtner, and I recorded individual tree positions along with total tree height and lower crown limit measurements with a TruPulse 350R laser paired with the program Field-Map using a Getac electronic mapping tool. Positions were calculated by using green-filtered laser measurements from each tree to various centrally located reference points in the sectors. The reference points were marked with a flag and a reflective tape was used to reflect the laser beam, as shown in Figure 10. The distances between the reference points were then taken and plotted with the corresponding trees in order to create a complete tree map of the entire studied area (Fig. 12). Circumference measurements >15cm were taken with a measuring tape at breast height, and diameter of trees with <15cm with a measurement caliper. Individuals with branching lower than breast height were measured for circumference or diameter below the lowest branch collar. Radial crown measurements were manually taken for the 32 most common species with tape measure in the cardinal directions, North, East, South, and West. These measurements were then used to calculate a mean diameter per tree by taking the average of all four directions. Trunk length (crownbase) was calculated measuring the vertical distance from the lower crown limit (first major branching along trunk) to the base of the targeted tree. Similarly, crown vertical length was calculated by measuring the distance between the lower crown limit and the top of the canopy. All measurement tools can be seen in Figure 11. Notes were also taken for any irregularities during the process such as incorrect tree identification based on the existing map and fallen or toppled tree due to neighboring trees or spontaneous vine growth.

At the end of Finca Amable data collection, my colleague and I achieved the following measurements:

- 3,836 individuals for total height, DBH, and relative positioning
- 1,875 individuals for crownbase height
- 751 individuals for canopy widths (N-S, E-W)

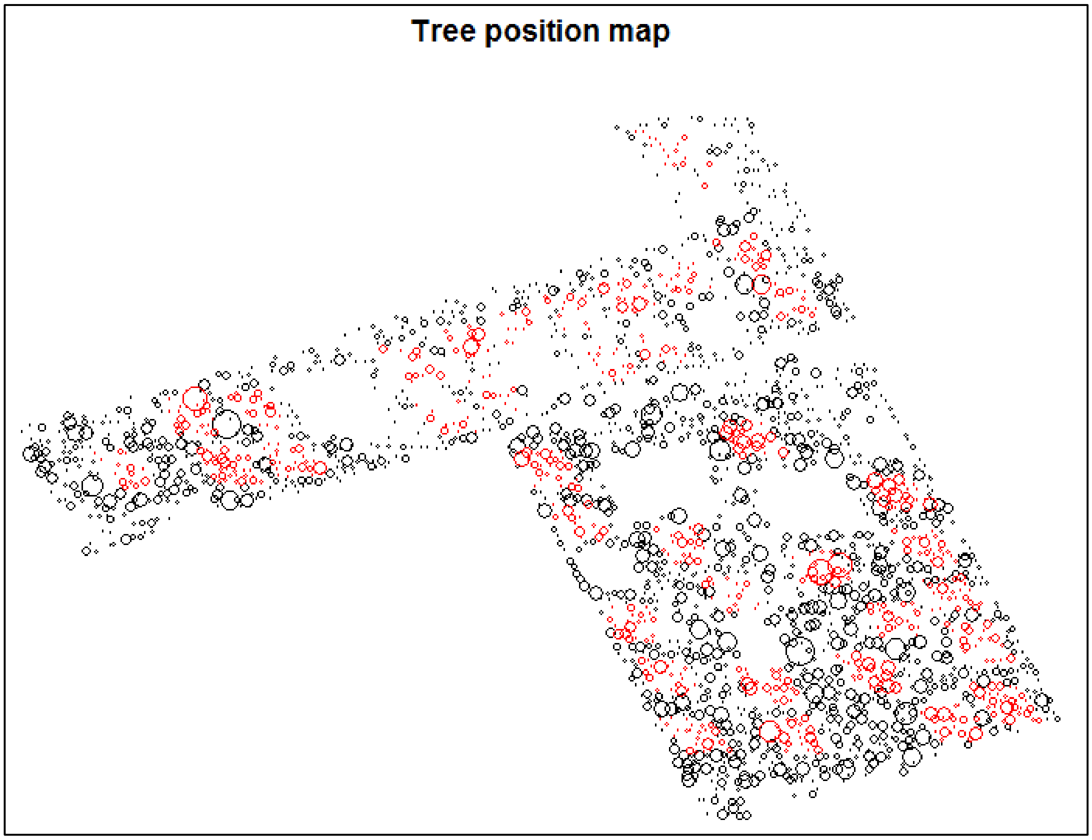


Fig. 12: Finca Amable map created from relative positions of all trees in the 2018 census. Trees marked in red represent the different plot areas. Larger circles represent larger DBH measurements

3.3 Data Analysis

Position and height data were imported to Excel from the Field-Map software and DBH and crown measurements were manually input into an Excel spreadsheet. Statistically analysis was done by using R studio (version 3.3.3). Finca Amable census data from previous research beginning in 2013 was used to in addition to look at tree growth and resource allocation over a period of time (Bence, 2017; Kleinschmidt, 2017). Measurements of the study area in the previous years include diameter and height measurements from a select number of trees, mainly in the plot areas within the sectors. Two selections of data were used for analysis. The first from only the 2018 data and the second being a combination of census data from 2013-2018. The data was chosen from the entire data pool and filtered for species with ≥30 individuals that were measured for DBH and height, diameter measurements were included that were taken between 1m and 1.3m in height, and without irregularities such as ambiguous tree identification or severe damage. Figure 13 shows how certain trees due to low branching were measured for diameter at a lower level and therefore were excluded from the analyzed data to avoid discrepancies in data output. One species that should be pointed out is *Inga sp.* which had 122 individuals measured and was one of the top ten most populated species. However, due to its natural shape, branching usually occurred quite low (under breast-height) on the trunk and therefore only 27 individuals were able to be accounted for once filtered for DBH measurements taken between 1m and 1.3m.

Fig. 13: Demonstration of differing diameter measurements due to low branching (Own photo)

To describe the height/diameter relationship the equation H = a + b(dbh) was used instead of the common log transformed equation, log(H) = a + b*log(dbh). Across the range of tree sizes measured, the non-transformed equation provides a better linear fit than the log:log transformed equation, presumably because the trees are still relatively young and of similar sizes in general. Figure 14, shows the difference in the two growth models for two species on differing sides of the pioneer/climax growth gradient. As the trees continue to increase in size, height should plateau as diameter growth continues to increase. In this case a log:log scale will be more relevant for such a study.

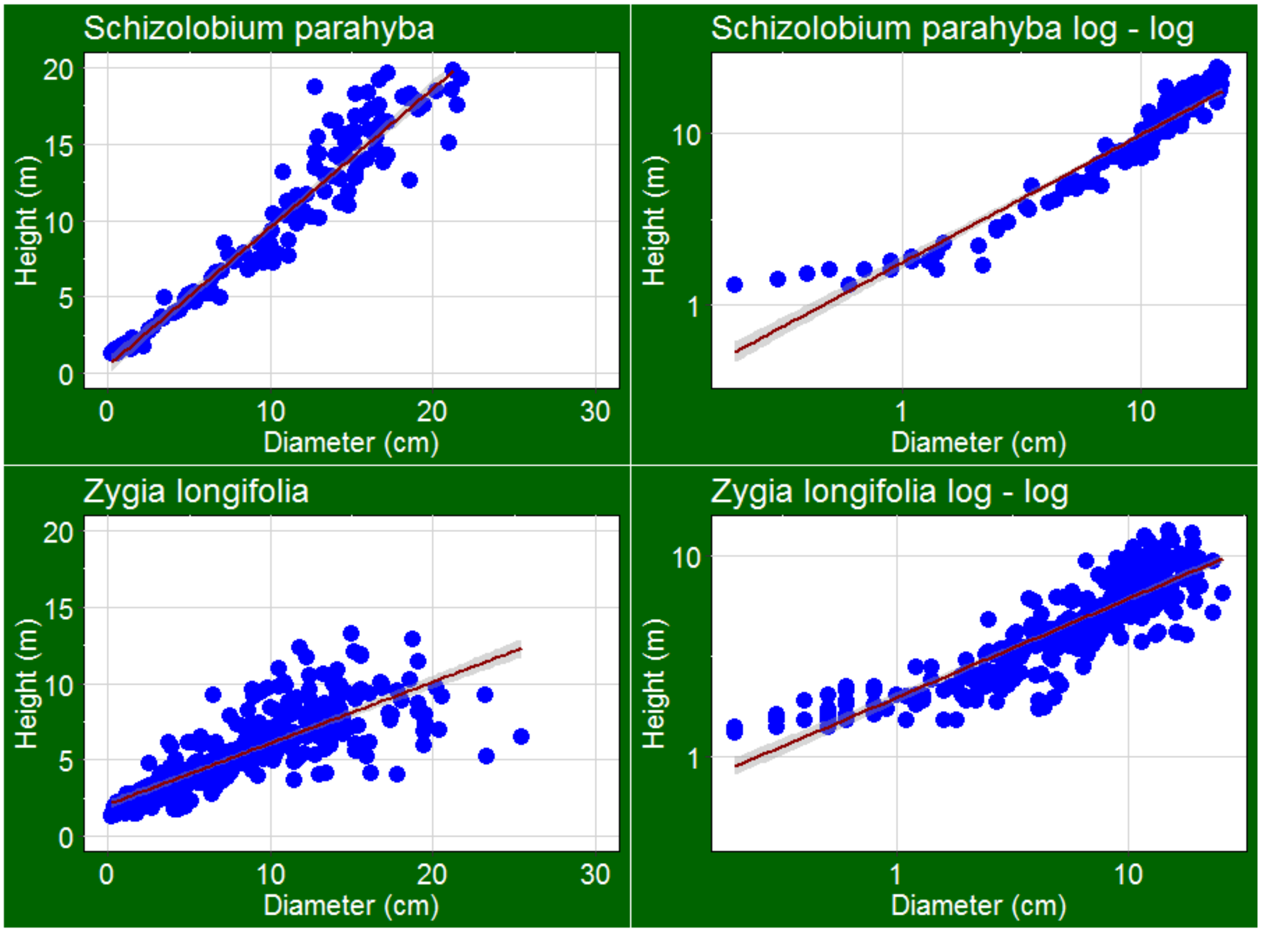


Fig. 14: Height/Diameter relationship between the pioneer species, *Schiyolobium parahyba*, and the climax species, *Zygia longifolia*. The left two plots show the non-log transformed data, while the two on the right show the log-log relationship

The slope of the H/D regression (coefficient 'b') was then extracted per species and used to analyze the relationship between allometry and wood density as well as a scaling where each species was classified on a species successional gradient. Wood density data were obtained from the TRY Plant Trait Database (Kattge et al. 2011). To classify species along a successional gradient, where on one end are the pioneer species and the other old-growth specialist species, we created a range between '0' and '1' based on existing literature (Chazdon et al. 2011). To calculate this successional value, the total number of individuals recorded from old-growth forests were divided by the number of individuals found in second-growth forest plus old-growth forest. Therefore, if there were no records in old-growth forest the value would be closer to '0', and closer to '1' if there were a greater number of individuals found in old-growth forest.

$$\mathrm{NI}i = \sum_{j=1}^{n} \frac{\left(\frac{d\mathrm{bh}j}{\mathrm{D}ij}\right)}{d\mathrm{bh}i}$$

Shading responses where formulated by using a neighbor index (NI). Factors contributing to a NI value included the distance to neighboring tree (D_{ij}), size of neighbor (dbhj), and target tree size (dbhi). The effect of NI on the H/D relationship was tested in one model involving all species, DBH, NI and their interactions to test if trees generally responded to competition (NI) by changing their growth strategy (H/D). In addition, separate models testing the effect of NI and DBH on H/D were run for each species.

4 Results

In the following sections the proposed hypothesis will be tested regarding genetic and environmental characteristics of the studied area. First, we look at how species differ in their growth strategy of investing more in height or diameter growth. We also look into crown dimensions in relation to tree height and diameter. Secondly, we look at the genetic factors of tree species including wood density and successional classification to further investigate what factors play a role in allometric differentiation and the growth strategies. Finally, neighborhood effects are looked at in order to find what effects competition, mainly in the form of competition for sunlight, plays in growth strategies. Table 3 displays the studied species' census information from 2018 as well as wood density, successional classification, and coefficient b (H/D slope). The studied species includes only those that have been filtered to avoid bias from irregular tree measurements as described in chapter 3.3. Generally maximum height was greater in pioneer or secondary-growth species with lower successional classification values. *Spondias mombin* exhibited the greatest maximum height, at 19.9m, as well as the largest DBH measurement, of 33.3cm. The shortest maximum height of just 6.3m was seen in the dense-wooded and late-successional species *Minquartia guianensis*. Not all species' densities were found in the TRY wood density database and therefore were excluded from the density analysis.

Table 3: Species with at least 30 individuals measured for height and diameter. List includes: height standard deviation (h.sd), diameter standard deviation (d.sd), minimum height (h.min), maximum height (h.max), minimum diameter (d.min), maximum diameter (d.max), number of individuals per species (n), coefficients a & b, successional classification (class), and wood density value (wd)

2018 Filtered data characteristics

Species	h.sd m	d.sd cm	h.min m	h.max m	d.min cm	d.max cm	n	a	b	class	wd g/cm3
Acosmium panamense	2.07	2.2	2.6	12.9	2.9	12.1	59	4.32	0.25	0	0.81
Anacardium excelsum	3.80	6.3	3.3	19.8	4.4	30.4	101	5.76	0.38	0.382	0.38
Astronium graveolens	3.35	3.9	1.8	17.4	1.0	22.0	74	3.13	0.62	0.352	0.85
Brosimum utile	1.81	1.3	1.5	8.8	0.9	6.4	45	0.12	1.24	0.783	0.5
Bursera simaruba	2.99	3.9	2.3	18.6	1.0	18.8	48	3.48	0.50	0.126	0.34
Calophyllum longifolium	2.80	2.8	1.4	13.0	0.6	11.3	32	1.85	0.85	0.931	0.55
Cedrela odorata	3.27	6.3	2.2	18.7	1.0	30.2	97	4.75	0.39	0.246	0.44
Ceiba pentandra	2.2	6.7	4.3	14.9	5.5	35	41	3.58	0.26	0.768	0.3
Cojoba arborea	2.97	3.7	3.6	15.7	2.7	16.6	52	4.65	0.53	NA	0.74
Croton schiedeanus	4.21	7.0	1.8	17.4	0.8	28.4	39	5.26	0.37	0.424	0.53
Handroanthus sp.	2.23	4.7	3.2	11.8	3.6	27.8	34	3.10	0.38	0.085	NA
Hieronyma alchorneoides	3.63	4.9	2.0	19.3	1.5	24.5	136	3.75	0.59	0.204	0.64
Lonchocarpus macrophyllus	3.43	3.9	2.4	19.8	0.9	17.8	116	3.02	0.60	0	NA
Lonchocarpus sp.	3.6	4.6	1.51	15.02	0.5	18.46	31	2.92	0.53	NA	NA
Luehea seemannii	3.15	5.7	5.0	19.3	4.8	29.0	46	6.62	0.28	0.294	0.43
Minquartia guianensis	1.34	1.5	1.6	6.3	0.5	5.4	37	1.32	0.82	0.93	0.73
Ormosia macrocalyx	2.24	2.3	1.5	12.7	0.7	13.1	45	1.19	0.89	0.812	0.61
Peltogyne purpurea	1.65	2.2	1.6	9.6	0.7	11.8	51	1.99	0.53	0.844	0.79
Platymiscium curuense	2.58	2.9	1.8	15.8	1.1	17.2	151	2.95	0.63	0.088	NA
Schizolobium parahyba	3.28	3.1	8.36	24.08	10	22.1	38	3.65	0.76	0.191	0.39
Simarouba amara	2.34	3.1	2.7	10.8	2.2	16.1	37	2.40	0.61	0.438	0.38
Spondias mombin	3.47	6.7	3.2	19.9	3.4	33.3	84	4.89	0.31	0.268	0.39
Symphonia globulifera	1.99	1.9	1.7	8.5	0.7	8.3	31	1.41	0.93	0.892	0.59
Tachigali versicolor	4.51	5.0	2.4	18.5	1.9	21.5	40	2.11	0.82	0.946	0.53
Tocoyena pittieri	2.49	3.0	2.1	13.3	0.9	12.1	37	1.56	0.66	0.708	NA
Virola koschnyi	3.67	4.6	1.5	16.0	0.9	17.0	40	1.66	0.74	0.633	0.41
Vitex cooperi	2.53	4.7	1.8	12.7	0.6	21.6	46	2.58	0.46	0.567	NA
Zygia longifolia	2.64	4.6	2.4	13.2	1.2	20.2	42	3.02	0.43	NA	0.68

4.1 Species allometric differentiation

4.1.1 Height/Diameter relationship

Looking all census data from 2013 to 2018 in Figure 15, the height/diameter relationship was shown to be a significant factor amongst differing species with a p-value equaling <0.05. At a given diameter some tree species are taller or shorter than others. This of course was an expected result and differences in tree stature are plainly visible when walking through any forest. Some species, even at a somewhat young age, are already in a size range where the H/D is no longer linear. For example, *Inga sp*. seems to be decreasing in height extension after 15m quite quickly while increasing its diameter size constantly. In general, increasing DBH indicates an increase in height as well. Although certain species with an upward sloped line, such as *Brosimum utile* and *Symphonia globulifera*, tended to focus on height growth in comparison to DBH, meaning that these species have a higher H/D slope. Another group of trees with a more horizontal line focused their growth on extending trunk size compared to height growth such as *Ceiba pentandra* and *Acosmium panamense* which show a lower H/D slope.

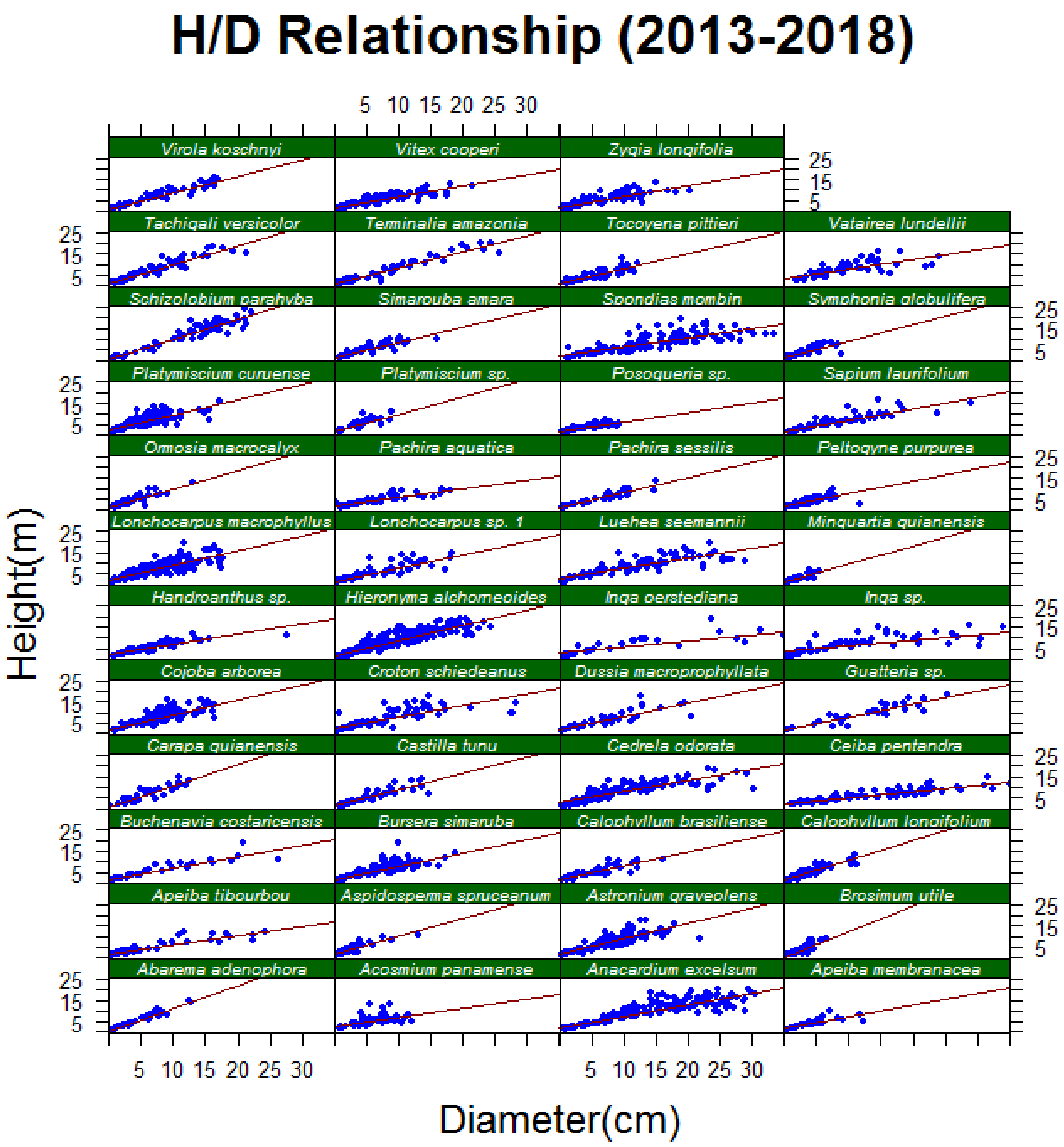


Fig. 15: Height/Diameter relationships for trees species with at least 30 individuals during the census years between 2013-2018

Table 4: Anova summary for Fig. 15. Here tree height is correlated to diameter, species, as well as a combination of diameter and species between 2016 and 2018. All correlations are significant with p >0.05

	DF	Sum Sq	Mean Sq	F value	p
Diameter	1	41955	41955	13225.95	<2e-16***
Species	46	4209	91	28.84	<2e-16***
Diameter:Species	46	3478	76	23.84	<2e-16***
Residuals	3628	11509	3		

A closer look at the 2018 data in Figure 16 reveals how certain species are developing slowly with very little height or diameter growth. Species such as *Brosimum utile* and *Minquartia guianensis,* which are both considered as climax species, also had the lowest measurements for maximum DBH. This portrays the climax tree growth strategy or perhaps the conditions were not appropriate for juvenile growth. An example would be too much sunlight in early growth stages compared to the natural climax species development under deep shade of a closed canopy.

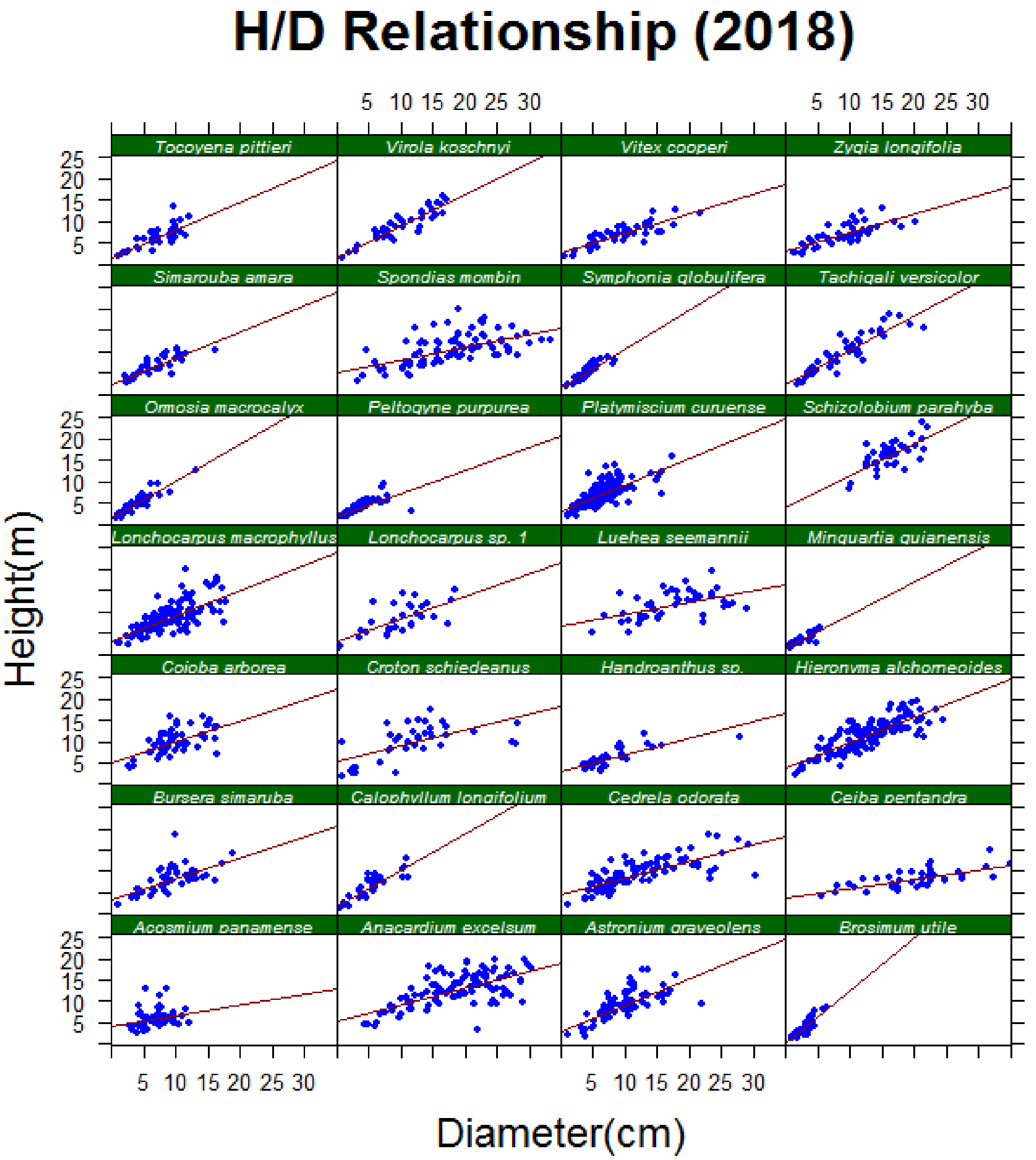


Fig. 16: Height/Diameter relationships for trees species with at least 30 individuals during the 2018 census

Table 5: Anova summary for Fig. 16, Here tree height is correlated to diameter, species, as well as a combination of diameter and species during the 2018 census. All correlations are significant with p >0.05

	DF	Sum Sq	Mean Sq	F value	p
Diameter	1	15617	15167	3450.513	<2e-16***
Species	27	3394	126	27.771	<2e-16***
Diameter:Species	27	876	33	7.172	<2e-16***
Residuals	1496	7124	5		

4.1.2 Crown shape relating to allometry

Crown vertical and horizontal size as well as crownbase length in comparison with height and diameter will be looked at in this subchapter.

The crown diameter correlation to DBH per species was shown to be significant with $p < 0.05$. In general, a positive relationship was shown in which the larger the DBH per species meant that the crown diameter also increased in a very linear fashion (Fig. 17). This increase was quite distinct per species and included such differences as *Bursera simaruba*, which maintained similar small sized crown diameters regardless of DBH, and opposingly to a species such as *Minquartia guinensis*, which increased crown diameter greatly with an increase in DBH.

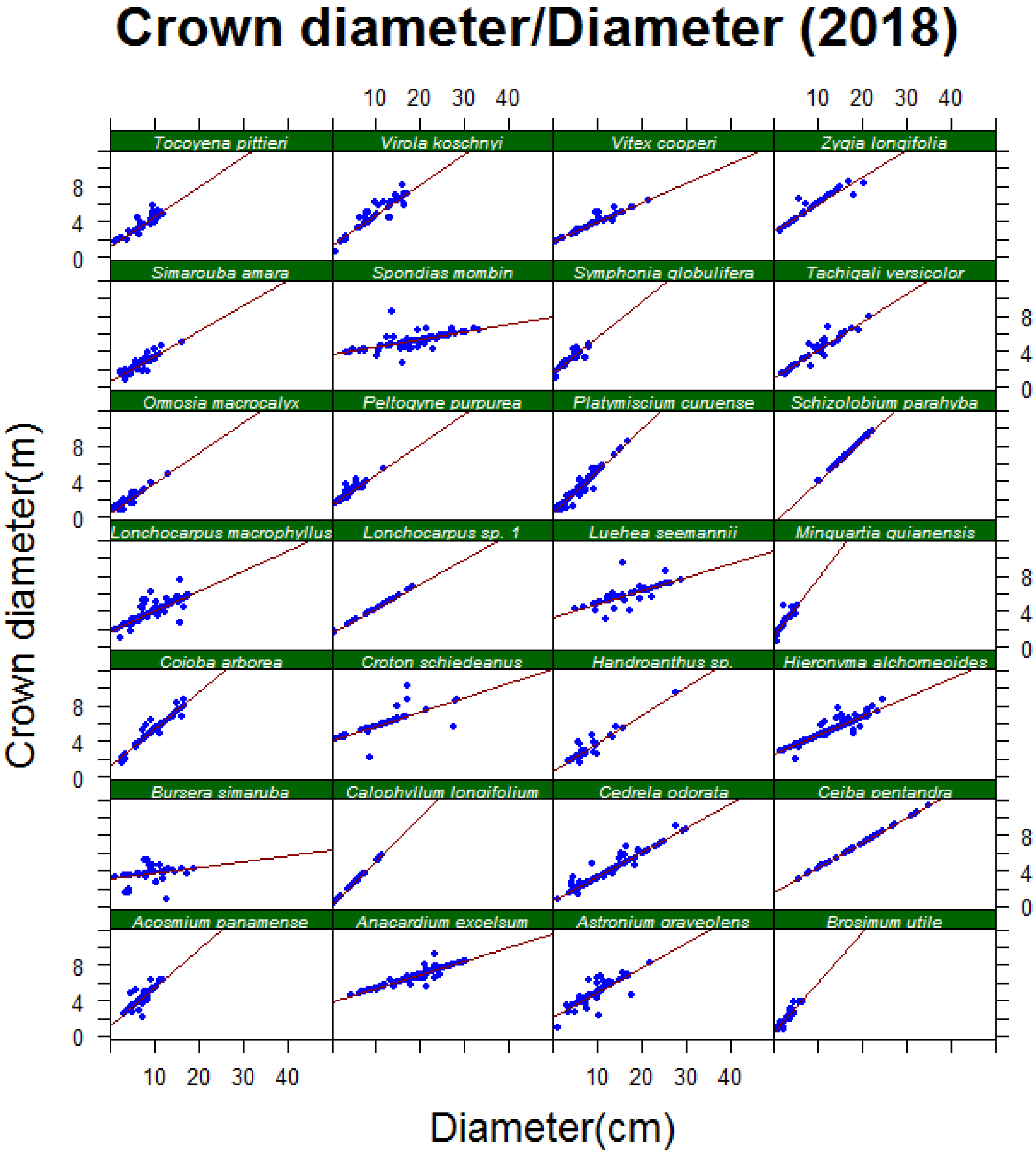


Fig. 17: Crown diameter in relation to diameter (DBH) measurements from the 2018 census

Table 6: Anova results for Fig. 17 detailing the significant correlations for crown diameter with diameter (or DBH), species, and diameter with species. All correlations are significant with p >0.05

	DF	Sum Sq	Mean Sq	F Value	p
Diameter	1	4158	4158	18075.81	<2e-16***
Species	27	705	26	113.46	<2e-16***
Diameter:Species	27	375	14	60.44	<2e-16***
Residuals	1571	361	0		

Crown diameter in relation to total tree height was also shown to increase linearly for all species. However certain species such as *Bursera simaruba* and *Spondias mombin* contributed less in crown diameter growth than others.

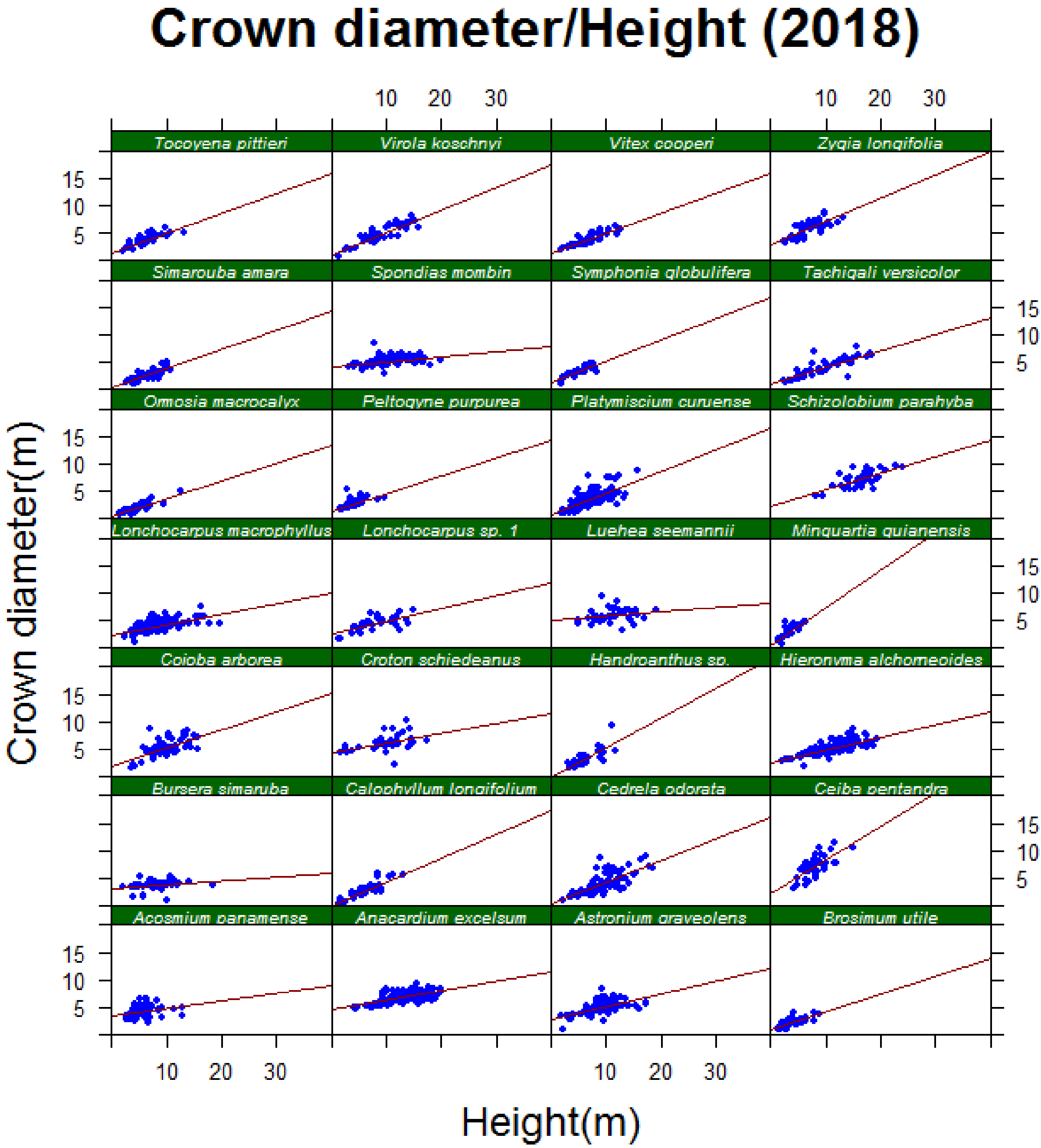


Fig. 18: Crown diameter in relation to total tree height measurements from the 2018 census

Table 7: Anova results for Fig. 18 detailing correlations between crown diameter with tree height, species, and height with species. All correlations are significant with p >0.05

	DF	Sum Sq	Mean Sq	F Value	p
Height	1	2954.2	2954.2	3562.78	<2e-16***
Species	27	1131.2	41.9	50.529	<2e-16***
Height:Species	27	211.9	7.8	9.466	<2e-16***
Residuals	1571	1302.6	0.8		

An increase in total tree height in relation to the vertical height of the canopy was also found to increase consistently as seen in Figure 19. All regression lines tended to maintain a similar slope and therefore a clear growth strategy trend between species could not be formulated.

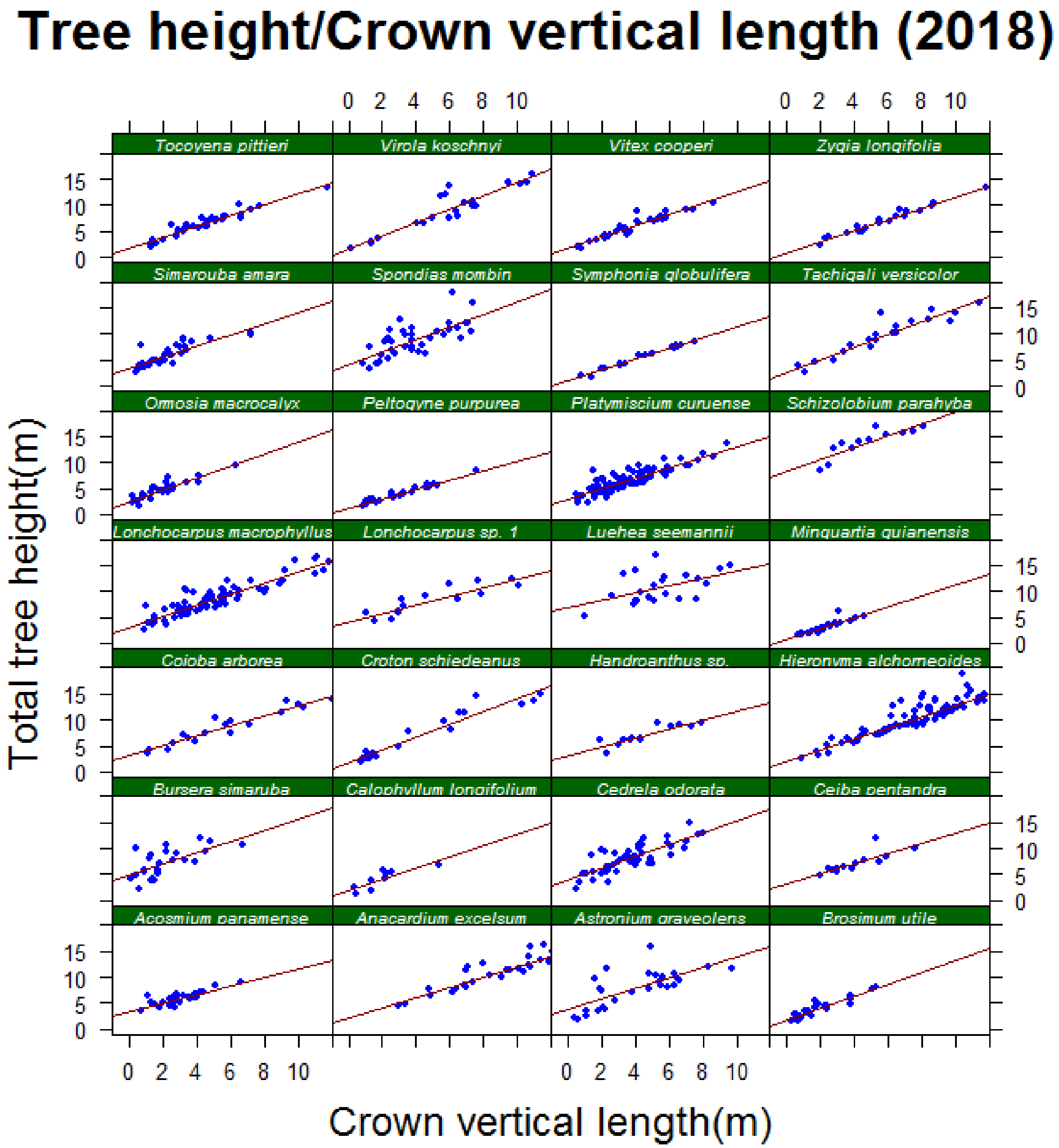


Fig. 19: Total tree height/crown vertical length relationship for trees species during the 2018 census

Table 8: Anova summary for Fig. 19. Here total tree height is correlated to height of crown (vertical length), species, and height of crown with species. Height of crown and species correlations are significant with p >0.05

	DF	Sum Sq	Mean Sq	F Value	p
Crown vertical length	1	8332	8332	4308.36	<2e-16***
Species	27	1458	54	27.918	<2e-16***
Crown veretical length:Species	27	57	2	1.097	0.336
Residuals	795	1537	2		

Total tree height when compared to the crownbase, or trunk length, was quite different among all species. Three main groups can be extracted from the analysis. The first group, which includes *Symphonia globulifera* and *Vitex cooperi*, maintains a nearly constant crownbase with an increase in total height. The second group which displays a different growth strategy develops a long, branchless trunk with an increase in tree height. Examples for this group are *Spondia mombin* and *Bursera Simaruba*. A third group falls somewhere in between the first two, meaning that measurements vary greatly intraspecies, most likely dependent on environmental conditions. This more spontaneous group includes the species *Lonchocarpus macrophyllus*, *Platymiscium curuense*, *Hieronyma alchomeoides*, and *Anarcadium excelsium*.

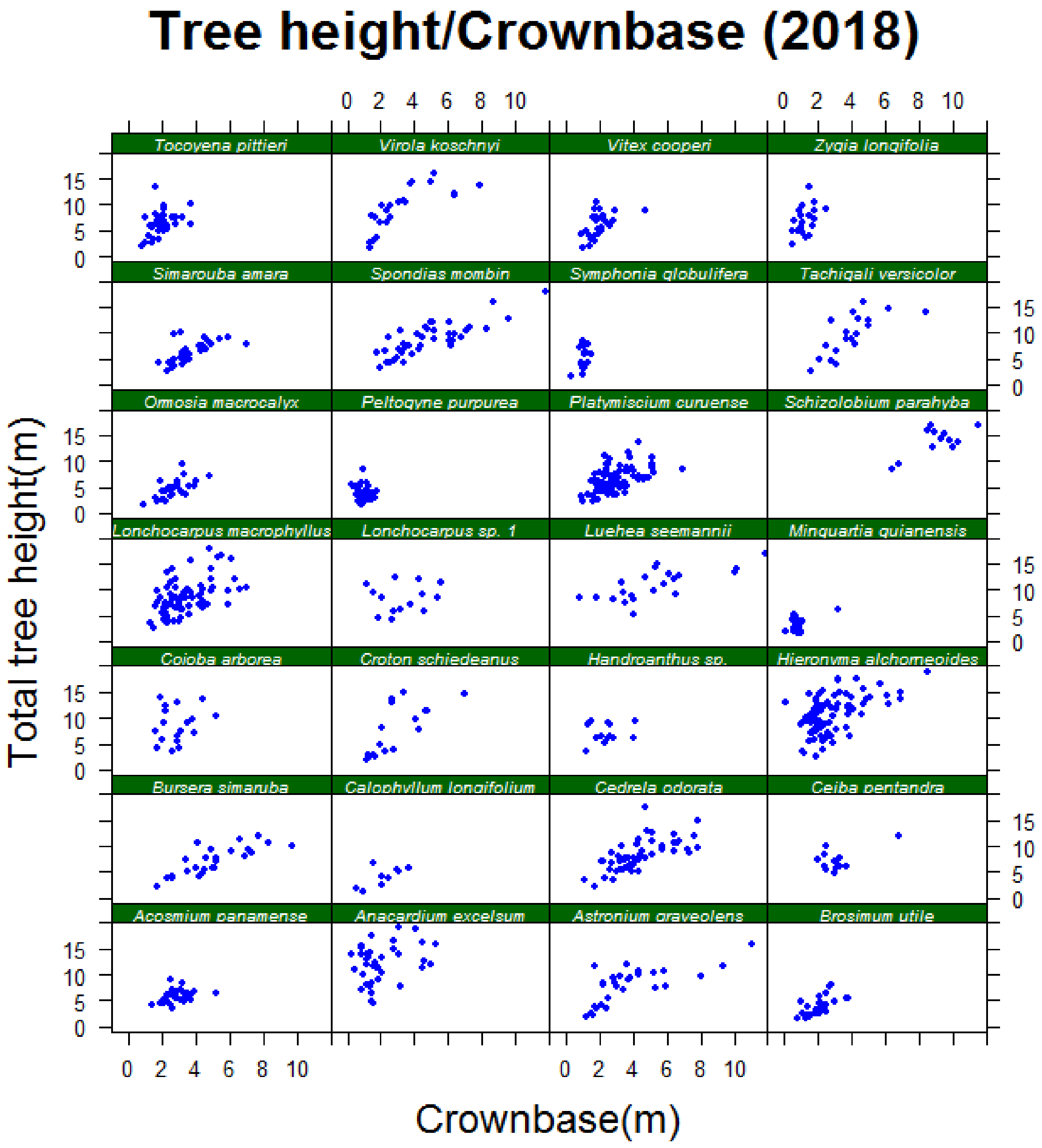


Fig. 20: Total tree height in relation to crownbase (trunk length) measurements from the 2018 census

Table 9: Anova results for Fig. 20. Here total tree height is correlated to crownbase, species, crownbase with species. Crownbase and species correlations are significant with p >0.05

	DF	Sum Sq	Mean Sq	F Value	p
Crownbase	1	3411	3411	625.548	<2e-16***
Species	27	3426	127	23.274	<2e-16***
Crownbase:Species	27	212	8	1.442	0.0686
Residuals	795	4335	5		

4.2 Genetic growth variables

In this subchapter we now look at how genetic variables such as wood density and species successional stage correlate to the slope of the H/D (coefficient b) per species.

In Figure 21, the H/D slope and wood density values are shown to not have a significant relationship. The linear regression results in a p-value of 0.42 and Pearson r^2 equaling 0.03. Trees with higher density were expected to have a higher H/D slope. This increased density would enable them to have a thinner stem diameter at a given height in order to support their canopy. This outcome was not shown in the present study and may stem from the fact that the forest plot is still developing and looking at the H/D slope from the juvenile trees may not be the same as later in the species' development. However, there is a slight trend, based on the regression line in Figure 21 for high wood density individuals to also exhibit a slightly higher H/D slope with several exceptions.

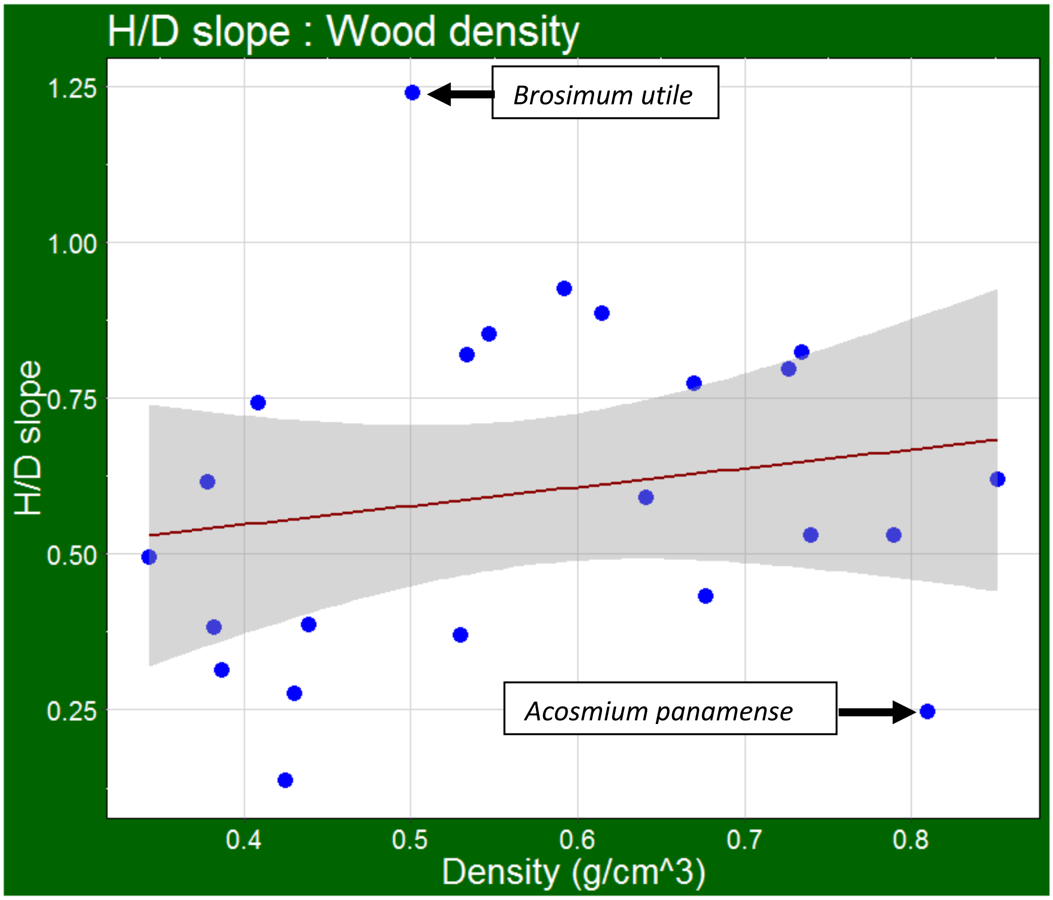


Fig. 21: H/D slope/Wood density relationship per species with at least measured 30 individuals during the 2018 census

Table 10: Linear regression summary of Fig. 21. Here H/D slope is correlated to wood density. No significant relationship is found with p = 0.42 and multiple R-squared = 0.03

	Estimate	Std. Error	t value	p
(Intercept)	0.4266	0.2166	1.970	0.0622
Density	0.3015	0.3657	0.824	0.4189

Multiple R-squared: 0.03135
Adjusted R-squared: -0.01477

The analysis of each species' H/D slope value in relation to its assigned value for successional class between pioneer (0) and climax (1) classification resulted in a positive relationship between the H/D slope and successional class with a p-value of 0.0009. An increased value for H/D slope came with an increase as well for successional class value.

Pioneer species had significantly lower H/D relationship than the old growth specialist as seen in Figure 22. This significance contradicts the second hypothesis that pioneer trees would invest more in height growth than old-growth specialists. Instead it seems that climax species tend to have greater height at a given diameter than pioneer species. Although, the majority of pioneers did have higher mean heights, they also exhibited greater diameter measurements making their H/D relationship much lower after analysis. However, an important result is that different tree species, due to their genetic make-up, do in fact utilize growth strategies related to their typical habitat along a successional gradient.

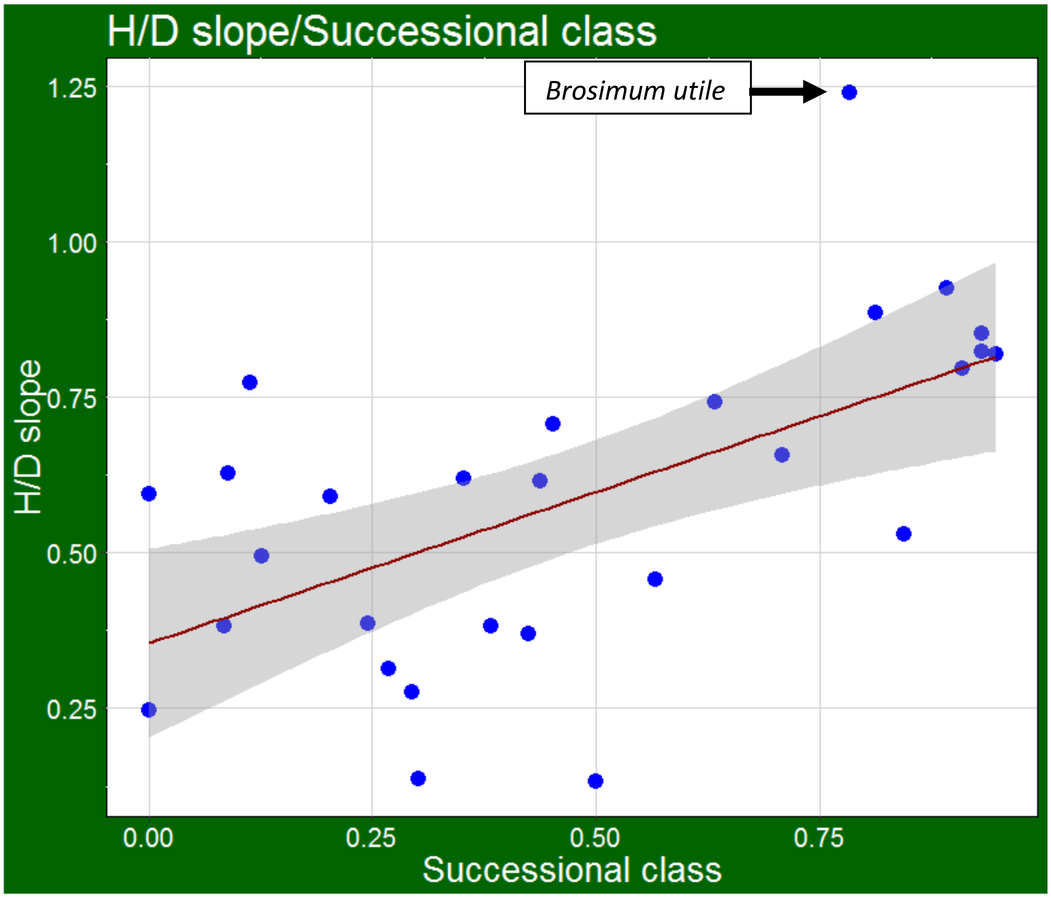


Fig. 22: Relationship between the H/D slope and successional class for species with at least measured 30 individuals during the 2018 census

Table 11: Linear regression summary of Fig. 22. Here H/D slope is correlated to the successional classification of the studied species. Successional class correlations are significant with p >0.05 and multiple R-squared = .35

	Estimate	Std. Error	t value	p
(Intercept)	0.35446	0.07378	4.804	5.63e-05***
Successional class	0.48735	0.13051	3.734	0.000931***

Multiple R-squared: 0.3491
Adjusted R-squared: 0.3241

While comparing a species wood density to its successional class value no significant relationship was found with a p-value of 0.38. The trend line does show a general increase in density as the successional class value increases, meaning higher wood density for climax related species. However, certain species like *Acosmium panamense* and *Astronium graveolens* are strong exceptions to this trend in that these species have extremely high wood density values however are classified on the pioneer side of forest succession. Furthermore, these two species also exhibited smaller statures than other pioneer or second-growth species perhaps implying that height growth was indeed limited to a small degree. On the other side is *Virola koschnyi* which has very low wood density but is considered to be closer to the climax end of the successional gradient. However, the overall result goes against my hypothesis and shows that even though a tree species may have higher wood density, this does not indicate whether or not a species will contribute more growth into diameter or height expansion.

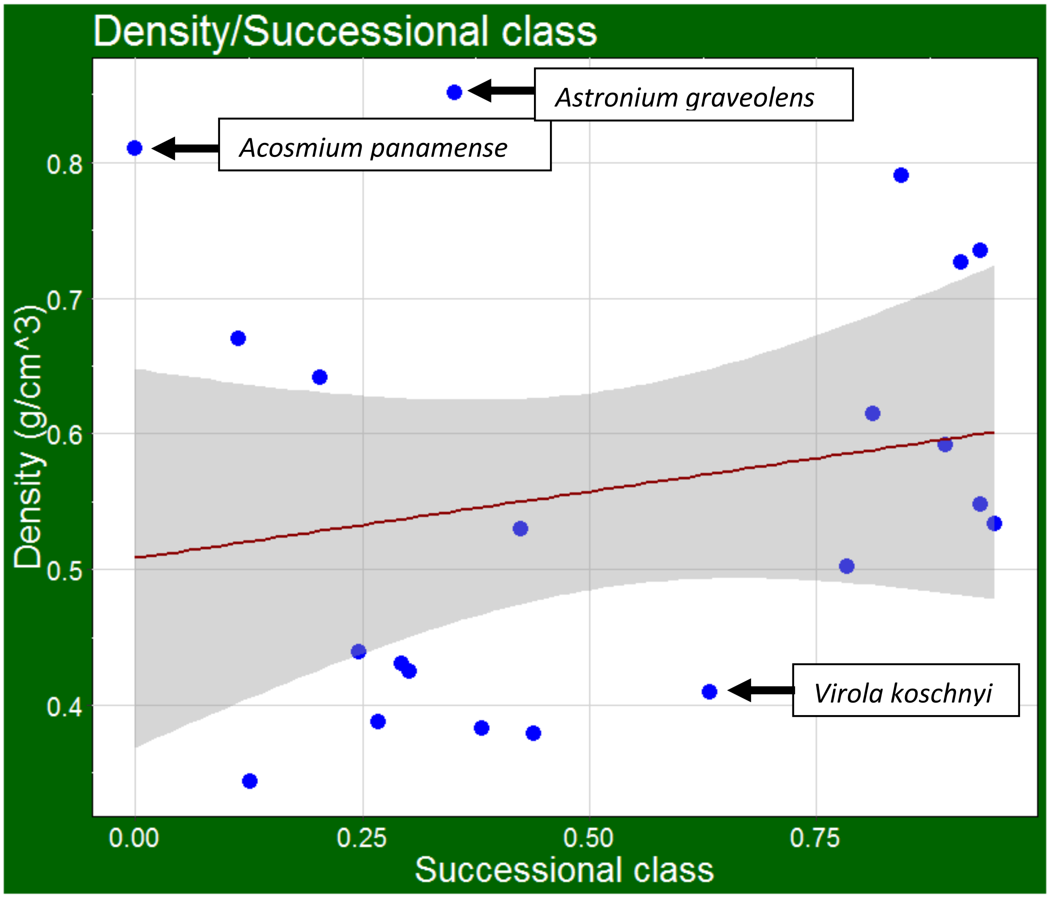


Fig. 23: Density (g/cm^3)/Successional class relationship per species with at least measured 30 individuals during the 2018 census

Table 12: Linear regression summary of Fig. 23. Here density is correlated to the successional classification of the studied species. Successional class correlations are found to not be significant with p = 0.38 and multiple R-squared = 0.04

	Estimate	**Std. Error**	**t value**	**p**
(Intercept)	0.50830	0.066665	70627	3.38e-07***
Successional class	0.09829	0.11037	0.897	0.384

Multiple R-squared: 0.04007
Adjusted R-squared: -0.01046

4.3 Effects of shading on tree allometry

In many species' cases the H/D increase with neighboring effect was shown to be significant (Fig. 26), suggesting that trees tend to invest more in height growth due to competition for resources such as light or nutrients. This trend not only applies to pioneer species but also to slower growing climax species as well (Fig. 24). In fact, it was found that as the neighboring index increases all climax species show an increased H/D ratio. This result goes against my third hypothesis that pioneers respond to competition with increased H/D ratio compared to old-growth specialists. Instead, all tree species to a certain degree responded to shading with an increased H/D slope (Fig. 25). A full list of NI and DBH significance values per species are listed in the appendix (Table 18). However, it must be noted that the H/D relationship is generally higher in trees at smaller sizes.

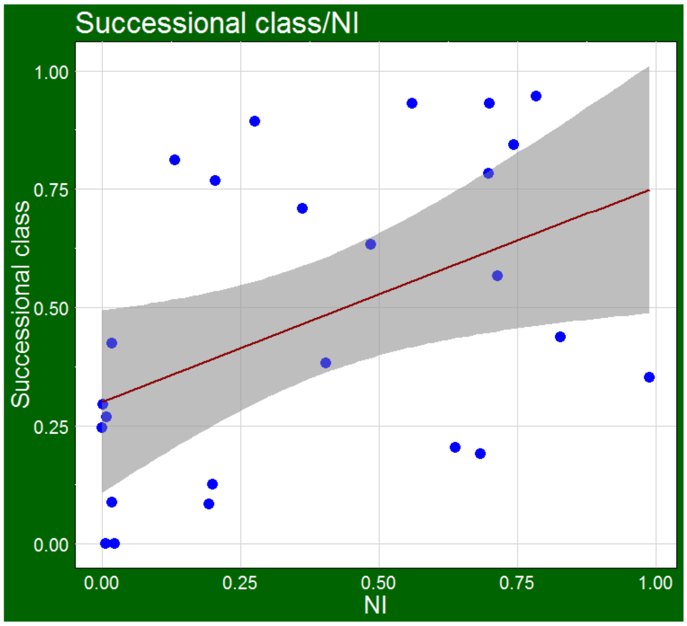


Fig. 24: Successional class/NI relationship per species with at least measured 30 individuals during the 2018 census

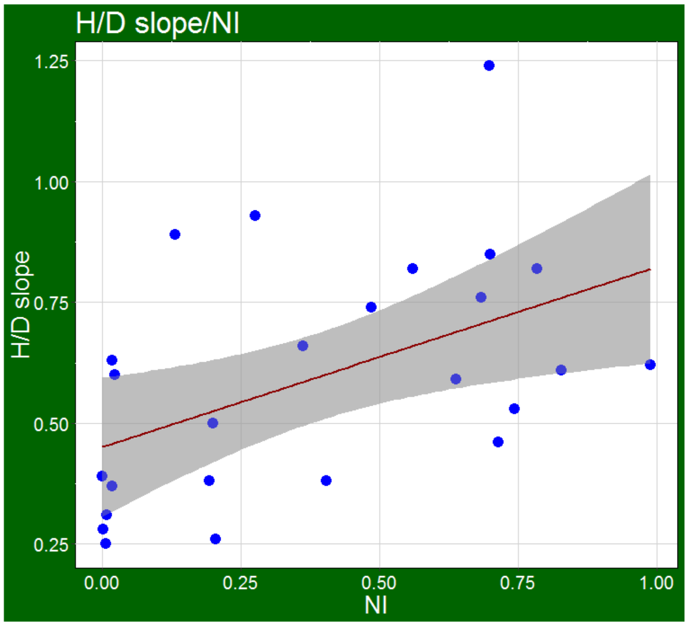


Fig. 25: H/D slope/NI relationship per species with at least measured 30 individuals during the 2018 census

Table 13: Linear regression summary of Fig. 24. Here successional class is correlated to the NI of the studied species. NI correlations are found to be significant with p = 0.0230 and multiple R-squared = 0.2052

	Estimate	Std. Error	t value	p
(Intercept)	0.30134	0.09296	3.242	0.0036**
NI	0.45318	0.18600	2.436	0.0230*
Multiple R-squared: 0.2052				
Adjusted R-squared: 0.1706				

Table 14: Linear regression summary of Fig. 25. Here H/D slope is correlated to the NI of the studied species. NI correlations are found to be significant with p = 0.0133 and multiple R-squared = 0.2382

	Estimate	Std. Error	t value	p
(Intercept)	0.45077	0.06946	6.489	1.27e-06***
NI	0.37270	0.13899	2.682	0.0133*
Multiple R-squared: 0.2382				
Adjusted R-squared: 0.205				

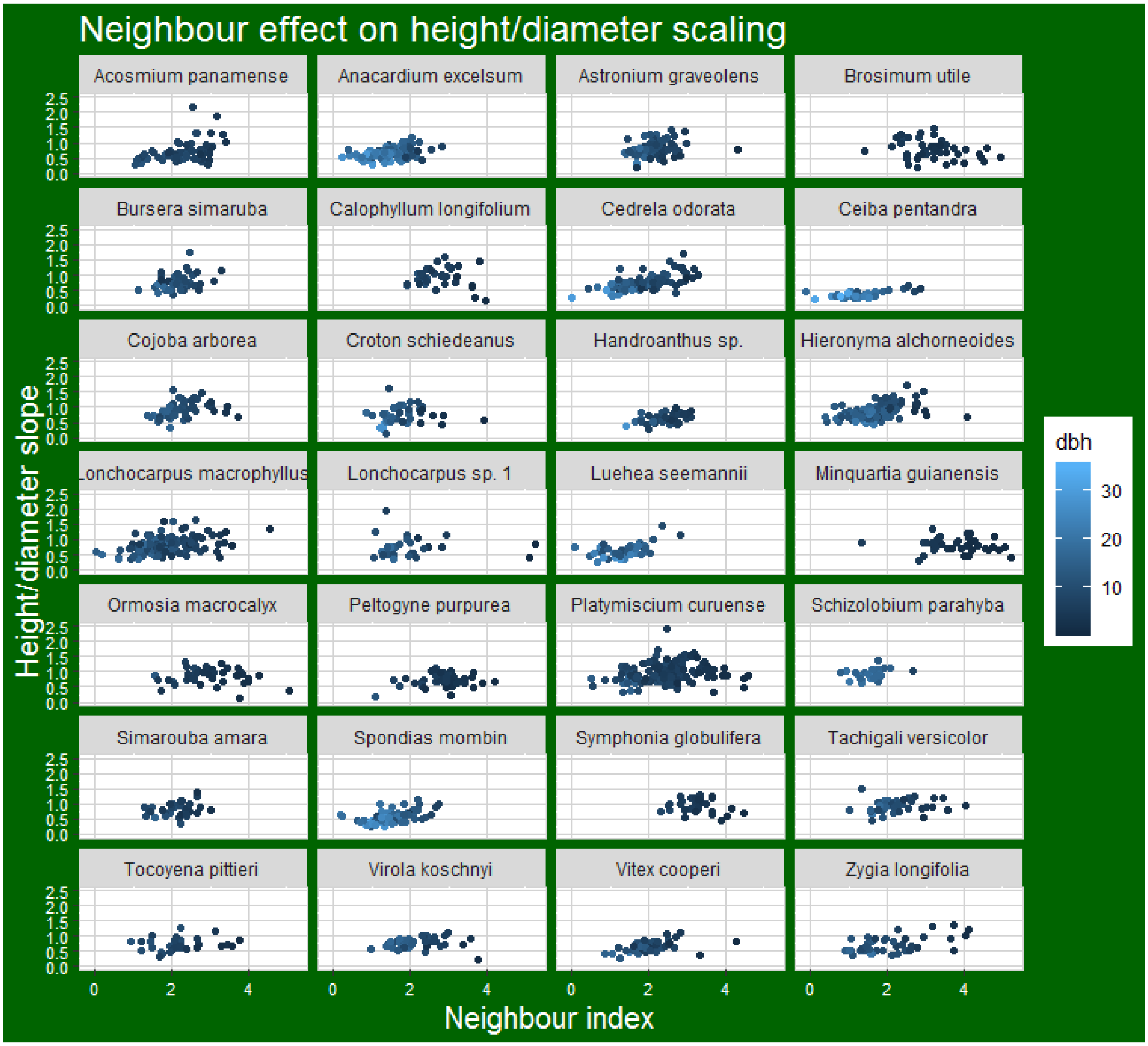


Fig. 26: Height/Diameter in relation to neighboring index value for the 2018 census. Individuals with larger DBH measurements are represented by light blue points and individuals with narrower DBH are represented by dark blue points

Table 15: Result of a linear model testing the effect of tree size (DBH), species and neighbor index - including their interactions on the height/diameter correlation

	DF	**Sum Sq**	**Mean sq**	**F value**	**p**
DBH	1	20.44	20.443	313.571	<2e-16***
Species	27	18.31	0.678	10.405	<2e-16***
NI	1	0.52	0.523	8.017	0.0047**
DBH:Species	27	10.93	0.405	6.206	<2e-16***
DBH:NI	1	3.82	3.822	58.617	3.46e-14***
Species:NI	27	66.14	2.450	37.575	<2e-16***
DBH:Species:NI	27	1.91	0.071	1.088	0.3454
Residuals	1465	95.51	0.065		

5 Discussion

In this section we begin with an overview of limitations to the present study. Next, is a short review of previous studies findings compared to that of this study and what the implications for similar or differing results may be. Lastly, the dynamics that differentiate allometric growth patterns in the Finca Amable study area are discussed.

5.1 Limitations of the present study

Several problematic issues arose during the research and data collection that will be addressed in this section. The first issue was the timeframe for data collection. The 2018 planned census was the most ambitious with the addition of individual tree mapping by means of laser and crown measurement data of all trees in the research area. However, due to technical difficulties, time limitations and thick spontaneous vegetation only 3,836 trees were measured for DBH, height, and position. Furthermore 20-30 individuals of the top 32 species were measured for crown radiuses, in order to estimate for the remaining trees. While not all trees were fully measured, especially for crown widths, we did measure enough individuals to properly investigate the data obtained.

For the data analysis, to avoid bias, a large number of individuals were not taken into account because the diameter measurement was not taken at breast height due to lower branching. Individuals of specific species such as *Zygia longifolia*, *Bunchosia nitida*, *Inga sp*. and *Vitex cooperi* among others, were frequently measured below breast height. Some of these species had enough filtered individuals to be analyzed but others, even though in large numbers, were not studied due to a species' characteristic low branching. Taking these additional individuals into account would help greatly in this study and further analysis into how to incorporate these irregular diameter values would be quite valuable.

One issue in overall project methodology was how to calculate height. In previous years, height measurements of trees that were < 4m were taken with a measurement pole, whereas in the 2018 census a laser was used for all height measurements due to the fact that many of the trees had grown well over the range of what could be measured with a pole. Furthermore, navigating a long pole through the current regeneration area would have been impossible. The laser tool that was used was viewed as a much easier device in practice. However, the laser system was not without its own problems. For certain areas of dense growth, the top of the canopy was difficult to find with the laser and therefore could have resulted in incorrect measurements. A comparison at the end of the data collection was completed on a group of 20 random trees to compare the laser height measurements to a pole system. The results show a slight increase in variability as the tree height increases (see appendix, table 16). Future research in this study plot may want to look at alternative methods either with a tangent method (as discussed in Chapter 1.1.2) or through drone measurements. As the forest continues to grow, height measurements will become an even greater issue.

Being that the area had previously been a pasture for cattle, signalgrass (*Brachiaria*) was still thriving and creating competition for some of the slower growing tree species. Other competition came from various lianas and pioneer species including naturally occurring Yarumo (*Cecropia sp*.). Figure 27 shows examples of these two species within the reforestation area. In sectors 6 – 10, grasses and vines were in many cases overtaking smaller trees and stunting their growth and presumably would result in eventual mortality. During the measurement process, cleaning and maintenance was conducted not only to obtain precise measurements, but also to maintain tree health. This maintenance took quite a bit of time and is recommended to have continued past the first three years, especially where grasses still have a strong presence. Once trees have established and create a solid canopy, grasses and weak pioneers naturally die back due to lack of resources. The older sectors of 1-5 created such a dense canopy that

Fig. 27: (top left) Grasses, *Brachiaria*, still competing for sunlight sometimes reaching 3 meters tall. (bottom left) Various other vegetation mixed with grasses left from the previous cattle pasture. (right) *Cecropia sp*. were more common in the older sectors and reached heights of 5 meters. (Own photos)

there were virtually no grasses persisting, however *Cecropia sp*. Remained and even flourished in certain areas up to heights of 3 – 4m.

Another aspect to this research was the naturalness of the studied stand of trees. A characteristic of the regeneration area that should be noted is the experimental layout of Finca Amable versus the natural growth succession of a rainforest. All trees in this project were planted around the same time and thus directly had sufficient and homogeneous sunlight for growth whether pioneer or climax species. This is not a natural state of development, especially for climax species which would more than likely grow much faster with the ample sunlight during the early stages of life than a naturally developing climax species that waits for its opportunity to break through a canopy gap sometimes spanning decades. However, as this particular research was a part of a reforestation experiment, we know that all trees were planted approximately around the same time period and therefore may not count as a bias for our study. In fact, looking at how trees react on a basis of equality for space, light, and moisture gives us a fairly clear view of how utilizes its resources and varies in allometry.

5.2 Study implications

5.2.1 H/D variation

Species differed in growth patterns. The species investigated range along a successional gradient, where old-growth specialist, for the most part, grew more slowly. These species that more closely resembled climax species were generally shorter with a higher H/D slope value and produced a narrower trunk at a given diameter since the canopy was not as developed yet and therefore less structural support was needed (King, 1996). Species included *Symphonia globulifera, Tocoyena pittieri, Minquartia guianensis, Ormosia macrocalyx, Peltogyne purpurea, Brosimum utile*, and *Calophyllum longifolium*. On the other side were the pioneer to secondary-growth species that quickly grew vertically in order to capitalize on the open canopy for sunlight (Poorter et al. 2003). The allocation of resources to new growth extending upwards in comparison to increasing wood density and strength clearly shows the pioneer growth strategy. The current study also found that this substantial increase in height growth also came increased diameter sizes to accommodate such top-heavy canopies with generally less dense wood structure resulting in a lower H/D slope value. These species included *Acosmium panamense, Anacardium excelsum, Astronium graveolens, Bursera simaruba, Cedrela odorata, Cojoba arborea, Croton schiedeanus, Hieronyma alchorneoides, Lonchocarpus macrophyllus, Spondias mombin, Platymiscium curuense,* and *Luehea seemannii.* There were three species, *Virola koschnyi, Vitex cooperi, Simarouba amara*, which were in the middle of the successional spectrum, otherwise known as generalist, which displayed similar growth patterns in height and diameter. Overall, this outcome reflects previous results from research in the tropics by King (1996), Poorter (et al. 2003) and Kohyama (et al. 2003).

5.2.2 Crown allometry

Crown diameter in relation to DBH was shown to have a positive relationship and strong correlation per species (Fig. 17). The general trend, however, is that species more closely related to pioneers tend to maintain less variations in crown diameters with increasing DBH. However, for most climax or late-successional species with increasing DBH comes also an increase in crown diameter.

While comparing crown diameter to height, similar results were found compared to DBH. Pioneer species maintained similar crown diameter sizes even with increases in total tree height. *Bursera simaruba* was a strong example of this showing an almost horizontal regression line with increasing height for as much as 20m as seen in Figure 18.

Total tree height related positively to crown vertical length (Fig. 19). No clear differentiation is seen regarding the canopy height in relation to total tree height. However, total tree height compared to its crownbase (trunk) height varies widely within a single species as well as among differing species. This variety in tree height compared with crownbase indicates different growth and light capture strategies. Certain trees maintain a very similar crownbase length even as they increase in total height such as *Zygia longifolia* and *Symphonia globulifera*. The opposing strategy is to maintain a long clear stem with a shorter canopy, which was displayed by *Spondias mombin, Simarouba amara*, and *Luehea seemannii*. This strategy to drop low branches, known as self-pruning, is generally viewed to decrease self-shading. In a Liberian rain forest study of tree architecture, Poorter (et al. 2003) found that shade-tolerant species may not favor reduction of canopy depth in order to reduce self-shading. This is explained by the fact that these species generally have lower photosynthetic light compensation points for their leaves and should be able to maintain more leaf layers in similar low light conditions. He goes on to mention that light-demanding species tend to maintain shallow crowns due to the high turnover of petioles, leaves, and branches which in turn means that energy is allocated toward a higher place in the canopy rather than producing and maintaining long-lived branches and leaves. King (1996), also found similar results in Costa Rica where adult individuals of small-statured species were characterized by deeper crowns than those of large-statured species.

5.2.3 Wood density

Although there was no significant relationship, higher wood density tended to be found in trees species classified as being slow-growth specialist and therefore had a higher H/D slope relationship compared to the pioneer species which had lower wood density and a lower H/D relationship. Previous studies in dry and seasonally wet tropical forest have detailed this finding and explain it by differing species' resource allocation strategies (Enquist et al. 1999; Muller-Landau, 2004).

Density was found to not be a good predictor of a species' H/D relationship. Similar results were found in Indonesia by Kohyama (et al. 2003) in which a wide range of phylogenetic groups were accessed for relationships between wood density, growth rate, and size. To compete in a tropical environment, higher wood density species take the strategy of increasing height to avoid being overtaken. In this case, the trade-off of less diameter growth with higher wood density is explained by mortality mitigation. Building upon a strong foundation may take more time, but a higher survival rate is guaranteed. King (et al. 2006) found similar results in a study of Malaysian lowland forest in which he observed negative relationships between mortality rates and tree support and wood density. In the same study, King (et al. 2006) also concludes that stem diameter increased just slightly with decreasing wood density values, indicating that low density species do not necessarily develop substantially thicker stems to account for their light and weaker wood. Dreschner (et al. 2011) also found stem density not to be an important factor in H/D allometry and instead suggested stand basal area to be the major driver regarding vegetation structure effects.

Wood density has also been shown to vary by geographic location quite substantially (Muller-Landau, 2004). Fearnside (1997) gives the example of *Carapa guianensis* in the Brazilian Amazon, which was recorded to have densities ranging from 0,43 g/cm^3 to 0,569 g/cm^3 in two different research areas that were separated by less than 500 kilometers. Perhaps further analysis of the species' wood densities of Finca Amable would also show variations from the values that were used in this analysis from the TRY plant trait database. Although a slight increase or decrease will more than likely not create any significance toward a stronger correlation between wood density and H/D relationship.

5.2.4 Successional classification relating to allometry

H/D slope correlated quite significantly with successional classification as seen in Figure 22. We can conclude that successional class contributes greatly to how a species develops and could be used as a predictor for H/D relationships per secies. Pioneer species with lower successional class values maintained lower H/D slopes, meaning that with greater height extension it was necessary to also produce a wider trunk diameter to support such a tall structure. Climax species favored a higher H/D slope and exhibit more growth in height while relying on a thinner stem. This finding contradicts my hypothesis that pioneers invest more in height growth at a given diameter.

There were several unexpected exceptions to how a species develops based on the successional class predictions. For most pronounced example is the species *Tachigali versicolor,* which is classified on the successional scale at 0.946 meaning that it is almost completely found mature in old-growth tropical forest and also has a typical H/D slope value for this successional classification. This quick growing species was found to be taller than any other climax species with a maximum height of 18.5m, and mean height of 9.83m. However, compared to the pioneer species its DBH was not as large at a given height suggesting that its growth strategy was predominately to grow vertically quite quickly and to invest in radial trunk growth once above any competition from pioneer species. Poorter (et al. 2005) also found similar results when studying *Tachigali vasquezii* in an old-growth tropical forest in Bolivia. He explains that the monocarpic characteristic of these species, meaning that they only flower and seed once in their lifetime and then die creating a canopy gap for their freshly produced seeds, is the reason for quick vertical growth into the higher canopy layer. The reproductive strategy creates a necessity for monocarpic species to increase in height quickly to ensure survival at a seedling or sapling stage in order to avoid extinction.

5.2.5 Neighboring effects

Shading and crowding by neighbors were also shown to be significant factors in the H/D relationship. Species with smaller DBH measurements were generally more affected by neighboring effects than species which had higher diameters. This is because the higher a species' DBH indicates, generally, that height is also larger. With this increased height an individual is likely to have less overhead canopy. Similar results were found in Puerto Rico where smaller trees showed increased sensitivity to crowding (Uriarte et al. 2004). Another result, which contradicts my third hypothesis that pioneer trees respond to shading with increased height growth (higher H/D) compared to old-growth specialist species, was found in which old-growth species with higher H/D slopes were significantly correlated to have higher NI values (Fig. 25). In other words, the climax species' growth strategy was to focus resources on height growth and especially in cases of stronger competition from neighboring trees.

Interesting neighboring effects from rainforest in Panama, Borneo, and Puerto Rico, found that in conspecific tree neighborhoods, growth was shown to be negatively affected to a higher degree compared to trees with no conspecific neighbors (Hubbell et al. 2001; Stoll & Newbery, 2005; Uriarte et al. 2004). The neighboring effects for conspecific individuals was shown to decrease dramatically at a range of 12 – 15m from the target tree (Hubbell et al. 2001). This is argued to be a driver of diversity in mature forest by species creating competition for conspecifics and creating space for differing and possibly rare species. Due to the lack of entire conspecific tree neighborhoods in the current study, this neighboring effect could not be tested. However, the incorporation of species type into the neighboring model would be of great interest.

Competitive effects from neighboring trees are not only applicable to tropical ecosystems. In a European study, Forrester (et al. 2017) showed that trees in a more competitive environment have a larger mean height compared to individuals with less competition.

5.3 Allometric relationships

At this stage differentiation between pioneer and climax species is seen primarily in the height differences. Pioneers have developed quickly with greater height but also greater DBH in most cases to support this height growth. As the successional process proceeds species such as *Brosimum utile* and *Ormosia macrocalyx* are expected to develop by increasing in height at first and secondly in diameter growth to support their large structure. Although in this study some exceptions were documented such as the monocarpic species, *Tachigali versicolor*. Crown growth dynamics were viewed as a strong predictor of successional class among species, especially total tree height in comparison to crownbase height. Neighboring effects were shown to affect a species H/D relationship, especially in climax species which respond to competition with increased height growth.

On a spatial scale, La Finca Amable is quite a unique regeneration plot in regards to its climate and could be a factor in distinct allometric growth strategies that differ from other nearby tropical rainforest. Similarities in flora and environmental conditions were noted to significantly decrease at a distance of approxiamtley 40 km in an old-growth Costa Rican rain forest (Sesnie et al. 2009). The bordering Fila Cruces mountain range creates extremely wet conditions for the lowland forest around it. This wet climate with constantly warm temperatures ensures ample opportunity for growth, even in the dry season for many of the evergreen species such as the highly populated and well established *Zygia longifolia*.

6 Conclusion

Understanding a tropical tree species' biomass allocation and allometry over a life-time is essential for estimating biomass accumulation as trees grow. This biomass, which is used in carbon balance estimates, should be as precise as possible for such an essential study regarding climate change scenarios. With evolving allometric models, the importance of specific classifications based on environmental and genetic factors is of great importance. The inclusion of species height measurements has also been shown to be an important variable in allometric equations. However, the most effective method to obtain height measurements is a matter of discussion and will need to be looked at more closely.

Results show that a species' growth strategy dictates how it distributes its resources and therefore varies in allometry. These varying species are found to fall along a successional gradient where pioneer species were found to focus on quick height growth and outward with increased diameter growth in the first years of development and usually had a lower H/D slope while most late-successional species, which were still quite short, maintained a higher H/D slope. Wood density, in the end, was a poor predictor of a species' allometric growth habits, although is slightly correlated to species' successional class. Neighboring effects on the H/D relationship were tested in a model with the factors of all species, DBH, and neighboring index value resulting in significant results. This means that trees do respond to competition by changing their growth strategy in terms of their H/D. Another model was run separately to test the effect of neighboring index and DBH on H/D to further look at certain species. The results show more significant results for a few tree species, and limited correlations for others.

Continued census measurements should be carried out in the restoration area of La Finca Amable to understand how allometric growth strategies vary among species over an entire lifespan and through the successional process. As trees continue to develop, allometric relationships should change in order to strategically allocate resources in different parts of the tree structure. Further recommendations include a more precise height measurement tool, longer census time-frame, and replanting of rare species that perished due to spontaneous competition.

7 References

Aiba, S. I., & Kitayama, K. (1999). Structure, composition and species diversity in an altitude-substrate matrix of rain forest tree communities on Mount Kinabalu, Borneo. *Plant Ecology*, 140(2), 139-157.

Baraza, E., Gómez, J. M., Hódar, J. A., & Zamora, R. (2004). Herbivory has a greater impact in shade than in sun: response of Quercus pyrenaica seedlings to multifactorial environmental variation. *Canadian Journal of Botany*, 82(3), 357-364.

Barbosa, E. R., van Langevelde, F., Tomlinson, K. W., Carvalheiro, L. G., Kirkman, K., de Bie, S., & Prins, H. H. (2014). Tree species from different functional groups respond differently to environmental changes during establishment. *Oecologia*, 174(4), 1345-1357.

Bence, M. (2017). Tree growth and survival in reforestation plot Finca Amable, La Gamba, Costa Rica. MSc. Thesis, Szent István University.

Bhadouria, R., Srivastava, P., Singh, S., Singh, R., Raghubanshi, A. S., & Singh, J. S. (2018). Effects of Light, Nutrient and Grass Competition on Growth of Seedlings of Four Tropical Tree Species. *Indian Forester*, 144(1), 54-65.

Breckle, S. W., Breckle, U., Homeier, J., & Scheffer, A. (2005). Mineral deficiencies in a pine plantation in southern Ecuador. *Ecotropica*, 11, 79-85.

Brown, S. (1997). Estimating biomass and biomass change of tropical forests: a primer (Vol. 134). Food & Agriculture Org.

Bruijnzeel, L. A., & Veneklaas, E. J. (1998). Climatic conditions and tropical montane forest productivity: the fog has not lifted yet. *Ecology*, 79(1), 3-9.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T. and Lescure, J.P. (2005). Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, *145*(1), pp.87-99.

Chave, J., Muller-Landau, H. C., Baker, T. R., Easdale, T. A., Steege, H. T., & Webb, C. O. (2006). Regional and phylogenetic variation of wood density across 2456 neotropical tree species. *Ecological applications*, 16(6), 2356-2367.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C. and Henry, M. (2014). Improved allometric models to estimate the aboveground biomass of tropical trees. *Global change biology*, *20*(10), pp.3177-3190.

Chazdon, R. L., & Pearcy, R. W. (1991). The importance of sunflecks for forest understory plants. *Bioscience*, 41(11), 760-766.

Chazdon, R.L., Chao, A., Colwell, R.K., Lin, S.Y., Norden, N., Letcher, S.G., Clark, D.B., Finegan, B. and Arroyo, J.P., 2011. A novel statistical method for classifying habitat generalists and specialists. *Ecology*, *92*(6), pp.1332-1343.

Clark, D. A., Piper, S. C., Keeling, C. D., Clark, D. B. "Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000." *Proceedings of the National Academy of Sciences* 100.10 (2003): 5852-5857.

Clark, D. B., Clark, D. A., Rich, P. M., Weiss, S., & Oberbauer, S. F. (1996). Landscape-scale evaluation of understory light and canopy structures: methods and application in a neotropical lowland rain forest. *Canadian Journal of Forest Research*, 26(5), 747-757.

Coley, P. D. (1983). Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological monographs*, 53(2), 209-234.

Cunningham, S., & Read, J. (2002). Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. *Oecologia*, 133(2), 112-119.

Daniels, R. F. (1976). Simple competition indices and their correlation with annual loblolly pine tree growth. *Forest Science*, 22(4), 454-456.

Drescher, M., Fyllas, N.M., Feldpausch, T.R., Lewis, S.L., Salim, K.A., Metcalfe, D.J., Kemp, J., Nilus, R., Mitchard, E.T.A., Baker, T.R. and Fearnside, P.M., 2011. Height-diameter allometry of tropical forest trees.

Enquist, B. J., West, G. B., Charnov, E. L., & Brown, J. H. (1999). Allometric scaling of production and life-history variation in vascular plants. *Nature*, 401(6756), 907.

Fearnside, P. M. (1997). Wood density for estimating forest biomass in Brazilian Amazonia. *Forest ecology and management*, *90*(1), 59-87.

Feldpausch, T.R., Lloyd, J., Lewis, S.L., Brienen, R.J., Gloor, M., Monteagudo Mendoza, A., Lopez-Gonzalez, G., Banin, L., Abu Salim, K., Affum-Baffoe, K. and Alexiades, M., 2012. Tree height integrated into pantropical forest biomass estimates. *Biogeosciences*, pp.3381-3403.

Fetcher, N., Strain, B. R., & Oberbauer, S. F. (1983). Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. *Oecologia*, 58(3), 314-319.

Forrester, D. I., Benneter, A., Bouriaud, O., & Bauhus, J. (2017). Diversity and competition influence tree allometric relationships–developing functions for mixed-species forests. *Journal of Ecology*, 105(3), 761-774.

Gill, R. A., & Jackson, R. B. (2000). Global patterns of root turnover for terrestrial ecosystems. *New phytologist*, 147(1), 13-31.

Goodman, R. C., Phillips, O. L., & Baker, T. R. (2014). The importance of crown dimensions to improve tropical tree biomass estimates. *Ecological Applications*, 24(4), 680-698.

Gould, S. J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews*, 41(4), 587-638.

Graefe, S., Hertel, D., & Leuschner, C. (2008). Estimating fine root turnover in tropical forests along an elevational transect using minirhizotrons. *Biotropica*, 40(5), 536-542.

Grubb, P. J. (1977). Control of forest growth and distribution on wet tropical mountains: with special reference to mineral nutrition. *Annual Review of Ecology and Systematics*, 8(1), 83-107.

Harris, N.L., Brown, S., Hagen, S.C., Saatchi, S.S., Petrova, S., Salas, W., Hansen, M.C., Potapov, P.V. and Lotsch, A., 2012. Baseline map of carbon emissions from deforestation in tropical regions. *Science*, *336*(6088), pp.1573-1576.

Hartshorn, G. S. (1978). Tree falls and tropical forest dynamics. *Tropical trees as living systems*, 617, 638.

Hegyi, F. (1974). A simulation model for managing jack-pine stands simulation. *RoyalColl. For, Res. Notes*, 30, 74-90.

HilleRisLambers, J., Adler, P. B., Harpole, W. S., Levine, J. M., & Mayfield, M. M. (2012). Rethinking community assembly through the lens of coexistence theory. *Annual review of ecology, evolution, and systematics*, 43, 227-248.

Holdridge, L. R. (1967). Life zone ecology. Tropical Science Center, San José, Costa Rica.

Homeier, J., Breckle, S. W., Günter, S., Rollenbeck, R. T., & Leuschner, C. (2010). Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. *Biotropica*, 42(2), 140-148.

Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. and De Lao, S.L., 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, *283*(5401), pp.554-557.

Hubbell, S. P., Ahumada, J. A., Condit, R., & Foster, R. B. (2001). Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research*, 16(5), 859-875.

Hughes, R. F., Kauffman, J. B., & Jaramillo, V. J. (1999). Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology*, 80(6), 1892-1907.

Hunter, M. O., Keller, M., Victoria, D., & Morton, D. C. (2013). Tree height and tropical forest biomass estimation. *Biogeosciences*, *10*(12), 8385-8399.

Jara, M.C., Henry, M., Réjou-Méchain, M., Wayson, C., Zapata-Cuartas, M., Piotto, D., Guier, F.A., Lombis, H.C., López, E.C., Lara, R.C. and Rojas, K.C., 2015. Guidelines for documenting and reporting tree allometric equations. *Annals of Forest Science*, *72*(6), pp.763-768.

Jenny, H. (1950). Causes of the high nitrogen and organic matter content of certain tropical forest soils. *Soil Science*, 69(1), 63-70.

John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M. and Foster, R.B., 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences*, *104*(3), pp.864-869.

Kambatuku, J. R., Cramer, M. D., & Ward, D. (2011). Savanna tree–grass competition is modified by substrate type and herbivory. *Journal of Vegetation Science*, 22(2), 225-237.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B., Wright, I.J. and Cornelissen, J.H.C., 2011. TRY–a global database of plant traits. *Global change biology*, *17*(9), pp.2905-2935.

Ketterings, Q. M., Coe, R., van Noordwijk, M., & Palm, C. A. (2001). Reducing uncertainty in the use of allometric biomass equations for predicting above-ground tree biomass in mixed secondary forests*. Forest Ecology and management*, 146(1-3), 199-209.

King, D. A. (1996). Allometry and life history of tropical trees. *Journal of tropical ecology*, *12*(1), 25-44.

King, D. A., Davies, S. J., Supardi, M. N., & Tan, S. (2005). Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Functional ecology*, 19(3), 445-453.

King, D. A., Davies, S. J., Tan, S., & Noor, N. S. M. (2006). The role of wood density and stem support costs in the growth and mortality of tropical trees. *Journal of Ecology*, 94(3), 670-680.

Kitajima, K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98(3-4), 419-428.

Kleinschmidt, S. (2017). *Growth of native tree species related to successional habitat preference and functional traits in a reforestation trial in Costa Rica.* MSc. Thesis*,* Universität Wien

Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T., & Kubo, T. (2003). Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. *Journal of Ecology*, *91*(5), 797-806.

La Gamba. http://www.lagamba.at/en/tropical-field-station/scientific-data-of-the-golfo-dulce-region/. (Accessed: 30.05.18)

Larjavaara, M., & Muller-Landau, H. C. (2013). Measuring tree height: a quantitative comparison of two common field methods in a moist tropical forest. *Methods in Ecology and Evolution*, 4(9), 793-801.

Lasky, J. R., Uriarte, M., Boukili, V. K., & Chazdon, R. L. (2014). Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. *Proceedings of the National Academy of Sciences*, 201319342.

Lines, E. R., Zavala, M. A., Purves, D. W., & Coomes, D. A. (2012). Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. *Global Ecology and Biogeography*, 21(10), 1017-1028.

Longo, G., & Montévil, M. (2014). Scaling and scale symmetries in biological systems. *In Perspectives on Organisms* (pp. 23-73). Springer, Berlin, Heidelberg.

Mage, S. M., & Porder, S. (2013). Parent material and topography determine soil phosphorus status in the Luquillo Mountains of Puerto Rico. *Ecosystems*, 16(2), 284-294.

Malhi, Y., & Wright, J. (2004). Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 359(1443), 311-329.

Mangan, S. A., Schnitzer, S. A., Herre, E. A., Mack, K. M., Valencia, M. C., Sanchez, E. I., & Bever, J. D. (2010). Negative plant–soil feedback predicts tree-species relative abundance in a tropical forest. *Nature*, 466(7307), 752.

Martínez-Garza, C., Pena, V., Ricker, M., Campos, A., & Howe, H. F. (2005). Restoring tropical biodiversity: leaf traits predict growth and survival of late-successional trees in early-successional environments. *Forest Ecology and Management*, 217(2-3), 365-379.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in ecology & evolution*, 21(4), 178-185.

Montgomery, R. A., & Chazdon, R. L. (2001). Forest structure, canopy architecture, and light transmittance in tropical wet forests. *Ecology*, 82(10), 2707-2718.

Muller-Landau, H. C. (2004). Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica*, *36*(1), 20-32.

Newbery, D. M., Alexander, I. J., Thomas, D. W., & Gartlan, J. S. (1988). Ectomycorrhizal rain-forest legumes and soil phosphorus in Korup National Park, Cameroon. *New Phytologist*, 109(4), 433-450.

Niinemets, Ü. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, 82(2), 453-469.

Oberbauer, S. F., & Strain, B. R. (1985). Effects of light regime on the growth and physiology of Pentaclethra macroloba (Mimosaceae) in Costa Rica. *Journal of Tropical Ecology*, 1(4), 303-320.

Packer, A., & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, 404(6775), 278.

Peters, H. A. (2003). Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology letters*, 6(8), 757-765.

Picard, N., Saint-André, L., & Henry, M. (2012). Manual for building tree volume and biomass allometric equations: from field measurement to prediction. *Manual for building tree volume and biomass* *allometric equations: from field measurement to prediction, FAO; Food and Agricultural Organization of the United Nations (2012)*.

Pickup, M., Westoby, M., & Basden, A. (2005). Dry mass costs of deploying leaf area in relation to leaf size. *Functional Ecology*, 19(1), 88-97.

Poorter, L. (1999). Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Functional ecology*, 13(3), 396-410.

Poorter, L. (2001). Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. *Functional Ecology*, 15(1), 113-123.

Poorter, L., Bongers, F., Sterck, F. J., & Wöll, H. (2003). Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology*, *84*(3), 602-608.

Poorter, L., Zuidema, P. A., Peña-Claros, M., & Boot, R. G. (2005). A monocarpic tree species in a polycarpic world: how can Tachigali vasquezii maintain itself so successfully in a tropical rain forest community?. *Journal of Ecology*, 93(2), 268-278.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G., Harms, K.E., Licona, J.C., Martinez-Ramos, M., Mazer, S.J. and Muller-Landau, H.C. (2008). Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, *89*(7), pp.1908-1920.

Powers, J. S., Becknell, J. M., Irving, J., & Perez-Aviles, D. (2009). Diversity and structure of regenerating tropical dry forests in Costa Rica: Geographic patterns and environmental drivers. *Forest Ecology and Management*, 258(6), 959-970.

Reich, P. B., Walters, M. B., Tjoelker, M. G., Vanderklein, D., & Buschena, C. (1998). Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. *Functional Ecology*, 12(3), 395-405.

Rüger, N., Berger, U., Hubbell, S. P., Vieilledent, G., & Condit, R. (2011). Growth strategies of tropical tree species: disentangling light and size effects. *PLoS One*, 6(9), e25330.

Rüger, N., Wirth, C., Wright, S. J., & Condit, R. (2012). Functional traits explain light and size response of growth rates in tropical tree species. *Ecology*, 93(12), 2626-2636.

Schuur, E. A. (2003). Productivity and global climate revisited: the sensitivity of tropical forest growth to precipitation. *Ecology*, 84(5), 1165-1170.

Sesnie, S. E., Finegan, B., Gessler, P. E., & Ramos, Z. (2009). Landscape-scale environmental and floristic variation in Costa Rican old-growth rain forest remnants. *Biotropica*, *41*(1), 16-26.

Singleton, A. (2010). Allometry: the study of biological scaling. *Nature Educ. Knowl*. 3 (10): 2.

Skole, D. L., Samek, J. H., & Smalligan, M. J. (2011). Implications of allometry. *Proceedings of the National Academy of Sciences*, *108*(4), E12-E12.

Slik, J.F., Arroyo-Rodríguez, V., Aiba, S.I., Alvarez-Loayza, P., Alves, L.F., Ashton, P., Balvanera, P., Bastian, M.L., Bellingham, P.J., Van Den Berg, E. and Bernacci, L., 2015. An estimate of the number of tropical tree species. *Proceedings of the National Academy of Sciences*, *112*(24), pp.7472-7477.

Smithson, P. A. (2002). IPCC, 2001: climate change 2001: the scientific basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change, edited by JT Houghton, Y. Ding, DJ Griggs, M. Noguer, PJ van der Linden, X. Dai, K. Maskell and CA Johnson (eds). Cambridge University Press, Cambridge, UK, and New York, USA, 2001. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 22(9), 1144-1144.

Sollins, P. (1998). Factors influencing species composition in tropical lowland rain forest: does soil matter?. *Ecology*, 79(1), 23-30.

Stoll, P., & Newbery, D. M. (2005). Evidence of species-specific neighborhood effects in the Dipterocarpaceae of a Bornean rain forest. *Ecology*, *86*(11), 3048-3062.

Sullivan, M.J., Lewis, S.L., Hubau, W., Qie, L., Baker, T.R., Banin, L.F., Chave, J., Cuni-Sanchez, A., Feldpausch, T.R., Lopez-Gonzalez, G. and Arets, E., 2018. Field methods for sampling tree height for tropical forest biomass estimation. *Methods in Ecology and Evolution*, *9*(5), pp.1179-1189.

Swaine, M. D., & Whitmore, T. C. (1988). On the definition of ecological species groups in tropical rain forests. Vegetatio, 75(1-2), 81-86.

Uriarte, M., Canham, C. D., Thompson, J., & Zimmerman, J. K. (2004). A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. *Ecological Monographs*, *74*(4), 591-614.

Valladares, F., & Niinemets, Ü. (2008). Shade tolerance, a key plant feature of complex nature and consequences. *Annual Review of Ecology, Evolution, and Systematics*, 39, 237-257.

Veneklaas, E. J., & Poorter, L. (1998). Growth and carbon partitioning of tropical tree seedlings in contrasting light environments. *Inherent variation in plant growth: physiological mechanisms and ecological consequences*, 337-362.

Wagner, F., Rossi, V., Aubry-Kientz, M., Bonal, D., Dalitz, H., Gliniars, R., Stahl, C., Trabucco, A. and Herault, B., 2014. Pan-tropical analysis of climate effects on seasonal tree growth. *PLoS One*, *9*(3), p.e92337.

Weissenhofer, A., & Huber, W. (2008). The climate of the Esquinas rainforest. A. Weissenhofer, W. Huber, V. Mayer, S. Pamperl, A. Weber, G. Aubrecht. (eds.), 59-62.

Westoby, M., & Wright, I. J. (2006). Land-plant ecology on the basis of functional traits. *Trends in ecology & evolution*, 21(5), 261-268.

Whitmore, T. C. (1990). *An introduction to tropical rain forests*. Clarendon Press, Oxford.

Whittaker, R. H. (1975). *Communities and Ecosystems*. Macmillan Publishing Co., New York.

Wills, C., Condit, R., Foster, R. B., & Hubbell, S. P. (1997). Strong density-and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences*, 94(4), 1252-1257.

Wright, S.J., Kitajima, K., Kraft, N.J., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., Díaz, S. and Engelbrecht, B.M., 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, *91*(12), pp.3664-3674.

Yoder, B. J., Ryan, M. G., Waring, R. H., Schoettle, A. W., & Kaufmann, M. R. (1994). Evidence of reduced photosynthetic rates in old trees. *Forest Science*, 40(3), 513-527.

8. Tables

Table 18: Neighboring index and dbh significance values per species

9. Figures

Fig. 1: Diagram of fluxes and carbon stocks in a typical forest ecosystem (Nabuurs & Mohren, 1993, modified)

Fig. 2: Allometric relationship between chela (claw) size and body size of a developing fiddler crab (*Uca pugnax*). (Shingleton, 2010)

Fig. 3: Diagram of growth influencers in a particular environment (HilleRisLambers et al. 2012)

Fig. 4: Patterns of vertical light availability in an old-growth forest and a 15–20 year old second-growth forest at La Selva Biological Station, in the Caribbean lowlands of northeastern Costa Rica. Diffuse transmittance at five heights above the forest floor (Montgomery & Chazdon, 2001)

Fig. 5: The relationships between net primary productivity and (a) mean annual precipitation and (b) mean annual temperature (Schuur, 2003).

Fig. 6: Leaf tissue structure relating to respiration (reich et al., 1998)

Fig. 7: The reforestation area within the black outline is known as Finca Amable and is comprised of over 6000 native individual trees from over 100 species

Fig. 8: Climate diagram 1998 – 2017, La Gamba 2018

Fig. 9: Map of Costa Rica and the Golfo Dulce region (Weissenhofer et al. 2008)

Fig. 10: Our reflective tool (toilet paper roll with reflective 3M tape mounted on a pole at breast height) used to create a reference point for tree position measurement (Own photo)

Fig. 11: Our field equipment used for height, diameter, crown, and position measurements (Own photo)

Fig. 12: Finca Amable map created from relative positions of all trees in the 2018 census. Trees marked in red represent the different plot areas. Larger circles represent larger DBH measurements

Fig. 13: Demonstration of differing diameter measurements due to low branching (Own photo)

Fig. 14: Height/Diameter relationship between the pioneer species, *Schiyolobium parahyba*, and the climax species, *Zygia longifolia*. The left two plots show the non-log transformed data, while the two on the right show the log-log relationship

Fig. 15: Height/Diameter relationships for trees species with at least 30 individuals during the census years between 2013-2018

Fig. 16: Height/Diameter relationships for trees species with at least 30 individuals during the 2018 census

Fig. 17: Crown diameter in relation to diameter (DBH) measurements from the 2018 census

Fig. 18: Crown diameter in relation to total tree height measurements from the 2018 census

Fig. 19: Total tree height/crown vertical length relationship for trees species during the 2018 census.

Fig. 20: Total tree height in relation to crownbase (trunk length) measurements from the 2018 census

Fig. 21: H/D slope/Wood density relationship per species with at least measured 30 individuals during the 2018 census

Fig. 22: Relationship between the H/D slope and successional class for species with at least measured 30 individuals during the 2018 census

Fig. 23: Density (g/cm^3)/Successional class relationship per species with at least measured 30 individuals during the 2018 census.

Fig. 24: Successional class/NI relationship per species with at least measured 30 individuals during the 2018 census

Fig. 25: H/D slope/NI relationship per species with at least measured 30 individuals during the 2018 census

Fig. 26: Height/Diameter in relation to neighboring index value for the 2018 census. Individuals with larger DBH measurements are represented by light blue points and individuals with narrower DBH are represented by dark blue points

Fig. 27: (top left) Grasses, *Brachiaria*, still competing for sunlight sometimes reaching 3 meters tall. (bottom left) Various other vegetation mixed with grasses left from the previous cattle pasture. (right) *Cecropia sp*. were more common in the older sectors and reached heights of 5 meters. (Own photos)

10. Appendix

Table 16: Comparison between pole and laser measurement (Fieldmap H) systems resulting in an average discrepancy of 10cm.

Tree ID	Fieldmap (H)	Pole (H)	Difference
2561	4,55	4,5	0,05
2624	2,32	2,15	0,17
2658	4,52	4,15	0,37
2716	5,14	4,10	1,04
2727	2,35	2,30	0,05
2763	2,71	2,35	0,36
2771	3,86	3,80	0,06
2772	2,43	2,30	0,13
2777	3,15	3,10	0,05
4880	2,64	3,1	-0,46
4882	2,54	2,75	-0,21
4884	3,64	3,6	0,04
4895	4,07	4,1	-0,03
4897	5,03	4,8	0,23
4943	2,14	2	0,14
4958	3,26	3,7	-0,44
4963	3,48	3,3	0,18
5033	3,19	3,2	-0,01
5035	4,01	3,7	0,31
5037	2,07	2,05	0,02
5050	3,52	2,9	0,62
5066	4,64	4,4	0,24
5090	2,02	2,1	-0,08
5122	2,53	2,7	-0,17
5129	2,2	2,1	0,1
5133	2,64	2,9	-0,26
5176	4,38	4,50	-0,12
5182	5,45	4,50	0,95
5186	3,71	3,80	-0,09
5187	2,46	2,25	0,21
5188	2,77	3,05	-0,28
5201	2,81	2,80	0,01
5238	4,24	3,70	0,54
5258	2,22	2,40	-0,18
5372	2,25	2,05	0,2
5421	4,12	4,10	0,02
5424	2,18	2,00	0,18
		AVG	**0,10648649**

Table 17: Full list of species with corresponding number of measured individuals per species for the 2018 census. Highlighted species were used for analysis

Species	Number of individuals per species studied
Zygia longifolia	194
Platymiscium curuense	181
Croton schiedeanus	164
Hieronyma alchorneoides	164
Lonchocarpus macrophyllus	150
Anacardium excelsum	149
Cedrela odorata	133
Inga sp.	122
Vitex cooperi	122
Acosmium panamense	93
Peltogyne purpurea	93
Astronium graveolens	92
Spondias mombin	87
Luehea seemannii	86
Cojoba arborea	65
Brosimum utile	55
Handroanthus sp.	55
Inga oerstediana	55
Bursera simaruba	52
Tocoyena pittieri	52
Minquartia guianensis	51
Ormosia macrocalyx	51
Symphonia globulifera	50
Simarouba amara	45
Virola koschnyi	44
Tachigali versicolor	43
Ceiba pentandra	42
Aspidosperma spruceanum	41
Lonchocarpus sp. 1	40
Schizolobium parahyba	39
Calophyllum longifolium	38
Terminalia amazonia	37
Vatairea lundellii	36
Carapa guianensis	35
"Desconocido"	34
Apeiba tibourbou	34
Castilla tunu	34
Calophyllum brasiliense	32
Guatteria sp.	32
Andira inermis	31
Bunchosia nitida	31
Sterculia recordiana	31
Dussia macroprophyllata	29
Pachira aquatica	29
Sapium laurifolium	29
Posoqueria sp.	27
Posoqueria sp. 1	26
Buchenavia costaricensis	25
Elaeis oleifera	25
Ficus sp.	24
Macrolobium hartshornii	20
Pseudima costaricensis	20
Virola guatemalensis	20
Apeiba membranacea	19
Genipa americana	18
Inga barbourii	18
Swartzia panamensis	18
Amphitecna isthmica	17

Diphysa americana	17
Pachira sessilis	17
Abarema adenophora	16
Albizia saman	16
Dilodendron costaricense	16
Inga punctata	16
Ocotea insularis	16
Cupania livida	14
"Sangrillo"	13
Cojoba sophorocarpa	13
Hymenaea courbaril	13
Guatteria amplifolia	12
Acacia allenii	11
Brosimum alicastrum	9
Ochroma pyramidale	9
Platymiscium sp.	9
Terminalia ivorensis	9
Tetragastris panamensis	9
"Zapote"	8
Aspidosperma myristicifolium	8
Licania operculipetala	8
Terminalia bucidoides	8
Handroanthus chrysanthus subsp. chrysanthus	7
Blighia sapida	6
Gliricidia sepium	6
Erythrina fusca	5
Handroanthus impetiginosus	5
Lonchocarpus sp. 2	5
"Aguacatillo"	4
"Palma"	4
"Zapotillo"	4
Brosimum lactescens	4
Caryocar costaricense	4
Clusia magnifolia	4
Dalbergia retusa	4
Ficus maxima	4
Inga acuminata	4
Inga pezizifera	4
Pterocarpus officinalis	4
"Aguacatillo rosa"	3
"Chaperno frijolillo"	3
"Jaboncillo"	3
"Quizarrá"	3
Asterogyne martiana	3
Casearia arborea	3
Cassia grandis	3
Coccoloba sp.	3
Guarea guidonia	3
Handroanthus ochraceus subsp. ochraceus	3
Ormosia coccinea	3
Perebea hispidula	3
Williamodendron glaucophyllum	3
"Manzana rosa"	2
Artocarpus heterophyllus	2
Beilschmiedia pendula	2
Brosimum sp.	2
Byrsonima crispa	2
Caryodaphnopsis burgeri	2

Cochlospermum vitifolium	2
Cordia cymosa	2
Couratari guianensis	2
Couratari sp.	2
Dialium guianense	2
Licania platypus	2
Otoba novogranatensis	2
Pouteria torta	2
Protium aracouchini	2
Sloanea obtusifolia	2
Trichilia septentrionalis	2
Unknown	2
"Leptobotriosa"	1
"Mabea"	1
"Otro"	1
"Probado"	1
"Volador"	1
Annona mucosa	1
Billia columbiana	1
Brosimum costaricanum	1
Calatola costaricensis	1
Carludovica drudei	1
Cryosophila guagara	1
Durio zibethinus	1
Elaeis guineensis	1
Enterolobium schomburgkii	1
Ficus nymphaeifolia	1
Geonoma scoparia	1
Inga bella	1
Inga densiflora	1
Inga ruiziana	1
Inga spectabilis	1
Iriartea deltoidea	1
Lacmellea panamensis	1
Lansium parasiticum	1
Lecythis mesophylla	1
Mangifera foetida	1
Myroxylon balsamum	1
Prioria copaifera	1
Protium sp.	1
Qualea paraensis	1
Ruptiliocarpon caracolito	1
Sloanea medusula	1
Trichospermum mexicanum	1
Trichospermum sp.	1
Vantanea barbourii	1
Virola surinamensis	1
Vochysia allenii	1
Zygia unifoliolata	1
Total individuals	**3836**

Table 18: Neighboring index and dbh significance values per species

		NI				DBH			
Species	**n**	**Estimate**	**SE**	**t-value**	**p**	**Estimate**	**SE**	**t-value**	**p**
Acosmium panamense	59	0.0169	0.0061	2.7627	0.0058	-0.0059	0.0179	-0.3306	0.7410
Anacardium excelsum	101	0.0097	0.0116	0.8352	0.4037	-0.0108	0.0045	-2.3866	0.0171
Astronium graveolens	74	0.0000	0.0034	0.0147	0.9883	-0.0095	0.0074	-1.2892	0.1975
Brosimum utile	45	0.0006	0.0015	0.3886	0.6976	0.1435	0.0326	4.3969	0.0000
Bursera simaruba	48	0.0112	0.0087	1.2822	0.2000	-0.0211	0.0106	-1.9856	0.0473
Calophyllum longifolium	32	-0.0020	0.0053	-0.3858	0.6997	-0.0080	0.0191	-0.4154	0.6779
Cedrela odorata	97	0.0189	0.0052	3.6514	0.0003	-0.0109	0.0045	-2.4199	0.0156
Ceiba pentandra	41	0.0154	0.0121	1.2716	0.2037	-0.0032	0.0068	-0.4659	0.6414
Cojoba arborea	52	-0.0125	0.0064	-1.9647	0.0496	-0.0471	0.0119	-3.9388	0.0001
Croton schiedeanus	39	-0.0123	0.0052	-2.3696	0.0179	-0.0210	0.0061	-3.4483	0.0006
Handroanthus sp.	34	0.0126	0.0097	1.3041	0.1924	-0.0049	0.0101	-0.4870	0.6264
Hieronyma alchorneoides	136	0.0017	0.0037	0.4703	0.6382	-0.0192	0.0045	-4.2550	0.0000
Lonchocarpus macrophyllus	116	0.0051	0.0022	2.2785	0.0228	-0.0160	0.0059	-2.7355	0.0063
Luehea seemannii	46	0.0414	0.0130	3.1973	0.0014	-0.0127	0.0060	-2.1092	0.0351
Minquartia guianensis	37	-0.0007	0.0012	-0.5834	0.5597	0.0094	0.0326	0.2889	0.7727
Ormosia macrocalyx	45	-0.0023	0.0015	-1.5114	0.1309	-0.0049	0.0170	-0.2908	0.7712
Peltogyne purpurea	51	0.0011	0.0033	0.3280	0.7429	0.0219	0.0190	1.1499	0.2504
Platymiscium curuense	151	-0.0035	0.0015	-2.3805	0.0174	-0.0349	0.0073	-4.7572	0.0000
Posoqueria sp.	34	0.0117	0.0083	1.4032	0.1608	-0.0391	0.0222	-1.7597	0.0787
Schizolobium parahyba	38	0.0095	0.0234	0.4079	0.6834	-0.0150	0.0161	-0.9300	0.3525
Simarouba amara	37	0.0028	0.0129	0.2166	0.8285	-0.0235	0.0161	-1.4590	0.1448
Spondias mombin	84	0.0293	0.0109	2.6813	0.0074	-0.0061	0.0048	-1.2586	0.2084
Symphonia globulifera	31	-0.0045	0.0041	-1.0918	0.2751	-0.0059	0.0348	-0.1690	0.8658
Tachigali versicolor	40	0.0012	0.0044	0.2744	0.7838	-0.0022	0.0092	-0.2403	0.8101
Tocoyena pittieri	37	0.0057	0.0063	0.9129	0.3614	0.0057	0.0190	0.3013	0.7632
Virola koschnyi	40	-0.0046	0.0065	-0.6988	0.4848	-0.0062	0.0125	-0.4967	0.6195
Vitex cooperi	46	0.0013	0.0034	0.3661	0.7143	-0.0147	0.0079	-1.8726	0.0613
Zygia longifolia	42	0.0035	0.0035	1.0176	0.3091	-0.0279	0.0113	-2.4629	0.0139

Affidavit

I hereby swear that I have compiled this work without external help and without using sources and aides other than those permitted and that the sources have been cited verbatim or quoted textually in the places indicated.

This work has not been submitted in the same or similar form to any other examiners as a form of examination. I am aware that offenders may be punished ('use of unauthorized assistance') and that further legal action may ensue.

Zachary West

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