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SPECIES SELECTION AND PLANTATION MANAGEMENT IN ENRICHMENT PLANTING WITH NATIVE TIMBER SPECIES IN THE PANAMA CANAL WATERSHED

Abigail A. Marshall
The University Of Montana

SPECIES SELECTION AND PLANTATION MANAGEMENT IN ENRICHMENT PLANTING

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By

ABIGAIL ANN MARSHALL

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Approved by:

Scott Whittenburg, Dean of The Graduate School
Graduate School

Dr. Cara Nelson, Chair
Department of Ecosystem and Conservation Sciences

Dr. Jefferson S. Hall
Smithsonian Tropical Research Institute

Dr. Anna Sala
Division of Biological Sciences

Dr. Stephen Siebert
Department of Forest Management

Species selection and plantation management in enrichment planting with native timber species in the Panama Canal Watershed

Chairperson: Dr. Cara Nelson

ABSTRACT

Large areas of the Panama Canal Watershed have been converted to monocultures of teak (*Tectonia grandis*), a non-native timber species that is generally not providing hoped-for economic and ecological benefits of Forest Landscape Restoration. Enrichment planting offers a potential strategy for revitalizing these underperforming plantations through the addition of high-value, native species to the understory, but more information is needed to guide implementation and management in this region and other tropical areas. I assessed the performance of six promising native species (*B. crassifolia, D. retusa, D. oleifera, H. alchorneoides, P. pinnatum, T. amazonia*) as an enrichment planting in teak plantations, and specifically considered how light availability, crowding pressure and annual fertilization affected seedling performance, I measured survival and growth for the first 30 months post-planting for ~3,000 seedlings; half received annual fertilization and half did not. I found that growth rate did not significantly affect survival among- or within-species, except for a positive relationship for *D. oleifera.* Overall seedling survival was high (83%), and, while species varied widely, there was not a strong effect of light, crowding or fertilization on survival. In contrast, overall growth of species was significantly affected by these factors.. Across all species growth was negatively related to crowding and positively related to light availability and fertilization. There were among-species differences; while all but one species (*D.* oleifera) were negatively affected by crowding, only half responded positively to light availability (*D. retusa, P. pinnatum,* and *B. crassifolia*) and fertilization *(D. retusa, P. pinnatum,* and *T. amazonia).* My findings suggest that all study species except for *B. crassifolia,* which suffered unacceptably high mortality, have high potential for use in enrichment planting in Panama teak plantations. Among-species differences in response to fertilization and growing environment highlight the need for continued studies to establish specific silvicultural guidelines for species in the enrichment planting context.

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I met Dr. Jefferson Scott Hall during my Peace Corps service through using one of his neotropical tree guides in a community reforestation project. In the last 5 years I can't think of anyone that has contributed more to the sustainable management of the Panama Canal Watershed; his deep commitment to place and work in the realms of both research and policy is inspiring and exemplary. Throughout this study he challenged me but also believed in me, and I am honored to have been a part of the Agua Salud project.

My other committee members Dr. Anna Sala and Dr. Steve Siebert are also wonderful scientists and wonderful humans. They were insanely accommodating to my extended timeline and supportive in all stages of the writing process, and each brought an important perspective from their respective focuses of plant physiology and tropical social-ecological systems.

I am so lucky for my friends and family; their love and support got me through and also made what could have been a rough patch into a genuinely enjoyable experience. I'm grateful to my Peace Corps community in Panama for first teaching me about native trees of Panama, for the other many Panamanians and STRI folks I learned from and worked with along the way.

The University of Montana's College of Forestry is on the traditional lands of Indigenous peoples, including the Selis, Ksanka, and Qlispé. Many others, including Blackfeet, Nez Perce, Shoshone, Bannock, and Coeur D'Alene, had and continue to have a crucial presence in the area. These tribes are holders of tremendous knowledge of these lands, and this knowledge has a vital place in future stewardship. I want to acknowledge the role of policies related to conservation and forestry in the historical and ongoing exclusion of indigenous people from their lands and resources in Montana and elsewhere. The UM's FCFC is positioned to support de-colonization by empowering indigenous-led research, employing indigenous faculty, and making Indian Education a priority for all UM students.

I also want to acknowledge the land and people of my research site in what is now the Eastern Panama Canal watershed. The historical inhabitance of these so-called "Cuevan lands" is complex and has included ancestors of the Guna tribe as well as the Embera and Wounaan tribes. The Smithsonian Tropical Research Institute does not have an institutional land acknowledgement and I was not able to consult members of these tribes prior to this presentation, but nonetheless would like to acknowledge the many people whose care and knowledge of these beautiful, forested hills and river valleys pre-dates colonialism. Western science has much to learn from this deep knowledge of place that is ever-evolving within modern indigenous groups in Panama.

TABLE OF CONTENTS

1   Introduction

Despite global increases in tree plantation establishment, Latin America is lagging behind: smaller gains in planted forest area are projected for this region compared with other places in the tropics (Korhonen et al. 2020). This is especially concerning for the Panama Canal Watershed (PCW) (Dale et al. 2005)**,** given the critical role of forest cover in stabilizing year-round water supply necessary for Canal function (Ibáñez et al. 2002; Ogden et al. 2013) and its critical role in maintaining local and regional biological corridors (Hall et al.). Planted forests are a major component of ongoing forest landscape restoration (FLR) initiatives that seek to strategically increase tree cover in degraded or deforested landscapes like the PCW, and on a larger scale the Bonn Challenge (Dave et al. 2019). Incorporating a diversity of native species can increase ecological integrity and ecosystem service provisions of planted forests in comparison to the monoculture plantations of non-native species that are more common in the tropics, but barriers including lack of silvicultural knowledge have limited implementation (Messier et al. 2021).

Tropical forests have exceptional potential for carbon sequestration and biodiversity conservation (Benayas et al. 2009; Laurance et al. 2012; Chazdon et al. 2016), yet continue to decline due to national policies and larger economic forces that contribute to expanding agriculture, timber harvesting and growing infrastructure (Geist and Lambin 2002). Plantation forestry has been heralded as a "win-win" that both provides opportunity for rural landowners to generate income and also preserves the ecosystem services of natural forest cover (FSC et al. 2012; Kissinger et al. 2012), but these potential benefits are not always realized. Factors that limit the socio-economic benefits of plantations for low-resource producers include insecure land rights and long return times on initial financial investments (Sinacore, K. et al.; Brown et al. 2008; Brancalion et al. 2012), as well lack of technical support and access to markets (Shyamsundar et al. 2018). Ecologically, plantations can contribute to a heterogeneous landscape (Barlow et al. 2007) and increase per-area productivity to facilitate conservation and minimize over-harvesting of natural forests in other areas (Parrotta et al. 1997; Paquette and Messier 2010), as well as enhancing benefits of natural forests by buffering edges and increasing connectivity amongst forest fragments (Brockerhoff et al. 2008). However, studies of understory plant biodiversity and wildlife habitat within plantations present mixed findings (Cusack and Montagnini 2004; Barlow et al. 2007; Bremer and Farley 2010; McFadden and Dirzo 2018). Understory development can be variable and different than natural stands (Aubin et al. 2008), and

may provide inferior habitat for native species (Brockerhoff et al. 2008). Plantation establishment and management practices are critical factors in determining ecological benefits (Aubin et al. 2008; Paquette and Messier 2010), and active management of plantation understory may be necessary to encourage a future forest trajectory that is similar to reference plant communities in natural forest (Parrotta et al. 1997).

Incorporating a diversity of native tree species can increase the ecological and social value of planted forests in comparison to exotic monocultures that are still widespread, throughout the tropics (Payn et al. 2015; Messier et al. 2021). Past studies comparing single- and mixed-species stands have shown that greater species richness can contribute to higher productivity due to lower intra-specific competition (Piotto et al. 2010; Mayoral et al. 2017), greater above- and below-ground carbon sequestration and storage in both the short- and long-term (Redondo-Brenes 2007; Davis et al. 2012), lower water use (Sinacore et al. 2019), reduced herbivory (Jactel and Brockerhoff 2007), and improved soil conditions due to nutrient cycling (Montagnini and Porras 1998). Although exotic species can facilitate natural regeneration, especially in highly degraded areas (Griscom and Ashton 2011), native species that are adapted to local conditions and the local soil microbiome (i.e. presence of symbiotic mycorrhizae) can provide greater ecological benefits and, especially in light of decreased management costs, may be more cost effective (Sinacore, K. et al.; Piotto et al. 2010; Griess and Knoke 2011). In addition to comparable wood production with even the most highly-productive exotic species (Amazonas et al. 2018), native species can also provide fruits, nuts and other non-timber forest products that are important to rural livelihoods (RRB et al. 2017). In comparison with exotics, native species offer additional social advantages in meeting cultural needs and helping maintain traditional forest values (Davis et al. 2012).

Enrichment planting is an evidence-based, low-risk strategy for incorporating native species and increasing both ecological and economic value of timber plantations (Ashton et al. 1997; Paquette et al. 2006a; Millet et al. 2012; Ouédraogo et al. 2014). In enrichment planting, valuable species are planted into the understory of already-established plantations or natural forests (Paquette et al. 2009). Potential ecological benefits of enrichment plantings include increasing structural diversity and facilitating natural regeneration (Lamb et al. 2005; Griscom and Ashton 2011). Although enrichment planting can be done with native or exotic species, ecological benefits are generally higher when native species are used. Economically, land managers can benefit through staggered harvest rotations: combining early seral species, which are a quicker return on investment due to fast growth

rates, with late successional species, which have longer harvest rotation, allow for several commercial harvests instead of just one and thereby provide a more sustained income with lower economic risks (Piotto et al. 2004; Lamb et al. 2005). Additionally, enrichment planting in already-established plantations lowers startup costs and requires less additional maintenance labor (Keefe et al. 2012)

The widespread adoption of enrichment planting and integration of native species into FLR are limited by critical knowledge gaps (Paquette et al. 2006b; Hall et al. 2011a; Schneider et al. 2014). Specifically, there is a lack of information on species-specific performance in plantation or enrichment planting settings (Wishnie et al. 2007; Schweizer and Brancalion 2020), as well as best practices for overstory management and fertilization. Outcomes of mixed-species plantings are difficult to predict due to unique and understudied site requirements of native tropical species (Redondo-Brenes and Montagnini 2006). Some species that perform poorly in open-grown conditions may do better in an enrichment planting setting (Kelty 2006), and differences in growth rates among species, even species of similar successional status, is an important consideration for land managers given that it affects rotation times (Kammesheidt 2011). On the other hand, although fast-growing species are often viewed as a priority for enrichment planting and assumed to be the best performers (Charles et al. 2018; Craven et al. 2009), relationships between growth and survival have not been tested for most species. Poor survival can greatly reduce or negate financial benefits for land managers so field trials are a critical first step before widespread planting of native species (Keefe et al. 2012).

Another gap in knowledge is the extent to which the performance of individual planted trees depends on the neighborhood environment in which it is growing. Interactions among pre-established vegetation and newly-planted seedlings can range from facilitation, through amelioration of harsh growing conditions and increased nutrient availability, to suppression through competition for above- and below-ground resources (Kelty and Cameron 1995; Forrester et al. 2006; Rappaport and Montagnini 2014). Overstory density has been shown to negatively affect enrichment planting growth, but species differ in their response to levels of crowding (Ramos and del Amo 1992; Ashton et al. 1997; Forrester et al. 2005). While the partially-shaded conditions of an enrichment planting setting can improve seedling survival of later-succession species when compared with full-sun conditions (Ashton et al. 1997; Cole et al. 2011), these same shaded conditions may inhibit the growth of more heliotrophic species (Hooper et al. 2002a). This variation among species, or niche

differentiation, can allow for more effective utilization of available light, water and nutrients in a mixed species plantation than in a homogenous monocultures (Kelty and Cameron 1995). The "complimentarity effect" from differential resource use among species can increase overall stand productivity, but improper species and site combinations can also suppress growth of desired species (Loreau and Hector 2001; Redondo-Brenes and Montagnini 2006). Quantifying the effects of crowding from neighboring trees on species targeted for enrichment plantings can improve understanding of appropriate planting densities in mixed plantations, and additional assessment of light availability can help disentangle shade responses from below-ground resource competition (Canham et al. 2004).

There is also limited information on post-establishment fertility requirements of native trees in plantations. A one-time, localized application of inorganic Nitrogen-Potassium-Phosphorus (N-P-K) fertilizer during or shortly-after planting is a common practice (Smethurst 2010) that has been shown to positively affect establishment and initial growth for a variety of tree species across different regions and plantation systems, including timber production in the tropics (Chamshama and Hall 1987; Cochran et al. 1991; Wang et al. 2008; Oskarsson and Brynleifsdóttir 2009; Cicek et al. 2010). In addition to the initial fertilizer treatment, however, some managers use regular application of inorganic N-P-K in the years following planting; the efficacy of these regular applications has not been well studied and results have been mixed (Smethurst 2010). Although fast-growing, high-production timber species have generally shown a positive growth response to fertilization (e.g. Albaugh et al., 2004; Coyle et al., 2016; Giardinaet al., 2003), there is also evidence that species adapted to low-nutrient soils or that exhibit less plasticity in response to increased soil fertility may grow well on infertile sites or may not benefit from supplemental fertilization (Carpenter et al. 2004; Stape et al. 2008; Smethurst 2010). Response to increased nutrient availability differs widely and unpredictably among species and depending on site conditions (McDonald et al. 2003). Given the cost of fertilization and low profit margins for plantation forests, information on its impact on growth of native tree species is critical. Furthermore, excessive N fertilization of plantations can result in potentially negative ecological consequences such as leaching (Georgiadis et al. 2017), acidification (Wright et al. 2011; Santiago et al. 2012), and decreased soil microbial activity (Treseder 2008).

The Panama Canal Watershed (PCW) – a nexus of social, economic, cultural and ecological interest – is an important focus area for improved management and, therefore, an ideal case study in FLR. The Canal is a key international trade route: In 2019 there were 13,785 transits connecting 160

countries, and domestically the Canal contributed nearly $3 billion to Panama's economy and employed 9,701 workers (Autoridad del Canal de Panama 2019). The area in and around the PCW is the most densely-populated of the country and home to an increasingly large percentage of the country's population (MINERPA 2021), which has resulted in a rapid decline in forest cover throughout the second half of the 20th century (Dale et al. 2003). Forests provide key hydrologic functions, including erosion prevention, flood mitigation and year-round fresh water supply (Noordwijk et al. 2017; Zhang et al. 2017; Peña-Arancibia et al. 2019; Adamowicz et al. 2019); these functions are crucial in the PCW, where seasonal high- and low-flows routinely threaten Canal operations (Ibáñez et al. 2002). Furthermore, natural forests of the PCW have a "sponge-effect" allowing for water infiltration, which regulates both base flow during the dry season and maximum runoff during storms (Ogden et al. 2013). In addition to hydrological function, PCW forests provide other key ecosystem services including wildlife habitat and carbon sequestration (Hall et al.; Ibáñez et al. 2002)

The transfer of Canal management from the United States to Panama at the end of 1999 sparked a number of laws incentivizing forestry in the PCW (Hall et al. 2015), resulting in a flurry of commercial plantation establishment (Dale et al. 2003). From these early days to present, the vast majority of PCW plantations are monocultures of teak (*Tectona grandis)* - an exotic timber species that is highly valuable but ill-suited to the area's infertile, poor-drainage clay soils (Stefanski et al. 2015). Similar to other types of exotic monoculture plantations worldwide, there is evidence that PCW teak plantations are not achieving the hoped-for economic and ecological benefits. In appropriate growing conditions, exotic timber species such as teak are economically attractive to land managers seeking high productivity under short harvest rotations, consistent genetics, and high-value timber with an established market (Kumar BM 2005; Pérez and Helsingin yliopisto 2005; FSC et al. 2012). However, the PCW largely does not provide appropriate growing conditions and teak have generally not yielded the hoped-for financial return (Stefanski et al. 2015). Lack of economic benefit for private landowners offers a possible explanation for the lower-than-predicted establishment and upkeep of PCW plantations despite decades of government- and NGO-led programs and subsidies (Dale et al. 2003). Additionally, there is evidence that these plantations are not achieving other desired forest functions such as water resource balancing, soil conservation and carbon sequestration (Kraenzel et al. 2003; Cernusak et al. 2007; Fernández-Moya et al. 2014).

Prior studies (e.g. Sinacore et al.; Piotto et al. 2010; Griess and Knoke 2011) suggest that using native species in PCW FLR efforts can provide greater economic and ecological benefits, but more information is needed to guide implementation and management. This study contributes to a small but growing body of literature (e.g. Piotto et al. 2010b; Plath et al. 2011; Hall et al. 2011a; Schneider et al. 2014) that seeks to evaluate the survivorship and growth performance of valuable native species in plantations. It builds on preliminary research (Marshall et al. 2020) by including a broader range of species with varying life history strategies, as well as a greater variety of teak plantation conditions. Specifically, we studied variability in the performance of six native species (*B. crassifolia, D. retusa, D. oleifera, H. alchorneoides, P. pinnatum, T. amazonia*) valued for timber and fruit, and the factors that are predictive of these species' performance as an enrichment planting in Panama Canal Watershed teak plantations. My research addresses the performance of these species in an enrichment planting setting and, specifically, the following questions:

1) To what extent do seedling survival and growth (basal diameter, height, total biomass, relative growth rate) vary by species and is growth predictive of survival?
2) To what extent is seedling survival or growth (basal diameter) related to crowding, light availability, or other site conditions, and do these relationships vary by species?
3) To what extent does annual application of chemical N-P-K fertilizer affect seedling survival or growth and do results vary by species?

2   Materials and Methods

2.1   Study Site

This study was conducted in the province of Colon, Panama on the Caribbean (Eastern) side of the central Canal basin within an approximately 10-km radius (Longitude: 9°11'55"N to 9°17'02"N and Latitude: 79°41'01"W to 79°47'07"W). Six enrichment planting areas were established in existing monoculture teak (*Tectona grandis)* plantations **[Figure 1]**. Two of the planting areas are privately-owned near the towns of El Limon and El Giral. The remaining four are within the 30-ha teak plantation in the Smithsonian Tropical Research Institute's Agua Salud research site (Stallard et al. 2010), an approximately 15-km^2 area near the town of Frijolito. To complement enrichment plantings and represent traditional open-grown plantation establishment conditions, an additional planting area was established in an Agua Salud pasture, and cattle were henceforth excluded from the site. Given the lack of replication, this site was not included for statistical analysis but rather as anecdotal comparison.

Figure 1: *Study area locations (stars) in the Eastern Panama Canal watershed, within an approximately 10-km radius (Longitude: 9°11'55"N to 9°17'02"N and Latitude: 79°41'01"W to 79°47'07"W).   Two planting areas are in privately-owned teak plantations near the towns of El Limon and El Giral. The remaining four areas are located within the 30-ha teak plantation in the Agua Salud research site.*
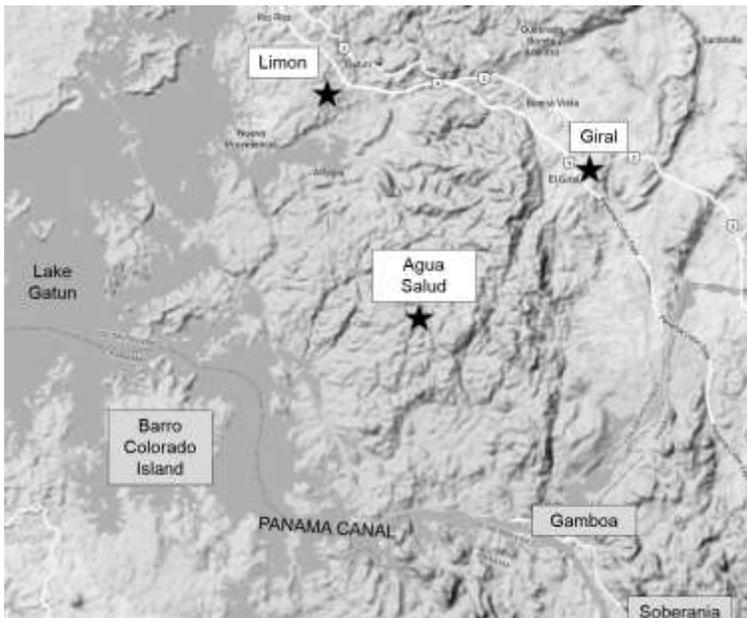
Climate is seasonal humid tropical and similar across planting areas. Daytime high temperature averages 32°C year-round, and annual rainfall averages 2,700 mm and typically is received almost exclusively during the wet season from May to mid-December (Ogden et al. 2013). The initial planting year of this study followed an historic El Niño drought, one of the three driest periods of the last century in the PCW (Sinacore et al. 2019). After 2016, precipitation remained within normal range for the duration of the study. Planting area soils are acidic, highly-weathered Oxisol and Inceptisol clays typical of the surrounding PCW. Initial soil sampling, conducted in 2016 (prior to fertilizer treatment application), confirmed that levels and variation in mineral and macronutrient content among Agua Salud planting areas in this study was similar to variation among private plantations and that the sites are representative of low-fertility sites in the PCW **[Table 1, detailed sampling protocol and methods available in Supplementary]**. Findings of extensive prior soil testing of the Agua Salud plantation are further described in publications including (Hassler et al. 2011; Mayoral et al. 2018; van Breugel et al. 2019).

Table 1: *Mean (SE) soil characteristics for all study planting areas: 2 located in private teak plantations (LI=Limon, GI=Giral), 4 located within the Agua Salud research site (AS 1-4); and the open-grown pasture comparison area (OG, italics). n= number of plots sampled; pH= soil acidity (BaCl$_2$ method); ECEC= effective cation exchange capacity; Al= aluminum (a measure of potential toxicity); C= total carbon; N= total nitrogen content (including all inorganic and organic forms); P=phosphorus; K= potassium; Ca=calcium; Mg=magnesium. Data were collected in 2016.*

AREA	n	pH	ECEC (cmolc/kg)	Al (% sat.)	C (%)	N (%)	P (mg/kg)	K (cmolc/kg)	Ca (cmolc/kg)	Mg (cmolc/kg)
LI	4	5.20(0.18)	15.82(1.4)	0.28(0.1)	3.79(0.21)	0.29(0.01)	1.52(0.13)	0.20(0.03)	12.76(1.48)	2.53(0.25)
GI	10	4.58(0.09)	9.87(1.36)	8.70(3.4)	2.11(0.14)	0.14(0.01)	2.03(0.11)	0.23(0.03)	6.41(0.96)	2.62(52)
AS1	12	4.54(0.08)	8.78(0.65)	11.04(3.43)	3.24(0.07)	0.25(0.01)	1.90(0.11)	0.20(0.03)	5.34(0.68)	2.02(0.17)
AS2	12	4.46(0.05)	8.57(0.36)	8.88(2.45)	3.34(0.06)	0.26(0)	1.50(0.03)	0.34(0.02)	4.62(0.35)	2.38(0.14)
AS3	12	4.47(0.08)	10.57(0.82)	10.53(3.72)	3.31(0.08)	0.26(0.01)	1.68(0.11)	0.33(0.04)	6.56(0.87)	2.56(0.23)
AS4	12	4.38(0.03)	9.26(0.66)	9.43(2.29)	3.18(0.14)	0.25(0.01)	1.45(0.06)	0.32(0.04)	5.23(0.51)	2.69(0.27)
OG	*9*	*4.40(0.06)*	*9.27(0.64)*	*10.29(3.03)*	*3.11(0.11)*	*0.23(0.01)*	*1.36(0.05)*	*0.44(0.07)*	*4.81(0.47)*	*2.59(0.27)*

2.2 Plantation Characteristics

The age of teak plantations ranged from 11-25 years at the time of measurement in January 2019. Although teak were initially planted at a regular 3-m spacing, thinning treatments as well as mortality created variability in tree spacing in all planting areas. One year after enrichment planting stem density averaged 64% of the original planting density across all planting areas (Hall, unpublished data). The growth of teak in the Agua Salud plantations is classified as well below average, based on site index curves established for Central American teak (Keogh 1982; Hall 2013), and observations from the more fertile soils of the Panama Este and Darien provinces (Fennica et al. 2020). Given low growth rates, teak at Aqua Salud are not projected to be financially profitable within a 20-year rotation (Sinacore, K. et al.; Hall 2013). In the private plantations, teak growth is similarly poor, though trees are older and thus, on-average, slightly larger **[Table 2].**

Table 2: *Number of 12-seedling experimental plots (n), plantation age (Age, years after initial teak planting), mean (SE) number of teak trees per hectare (TPH) and quadratic mean diameter (QMD) of teak at the last measurement period (30-months after enrichment planting; January 2019) for all study planting areas. See Table 1 caption for planting area codes.*

Area	n	Age (yrs)	TPH (#)	QMD (cm)
LI	16	15-16	425(28)	20(1.0)
GI	37	23-25	452(31)	16(0.5)
AS1	48	11	749(33)	13(0.4)
AS2	48	11	934(26)	8(0.2)
AS3	48	11	628(25)	11(0.3)
AS4	48	11	785(26)	10(0.2)

2.3 Study Species

The six study species were selected from a list of species with high potential or broader interest for commercial production based on existing literature and author communications with land managers (Breugel et al. 2011; also see below) **[Table 3]**. Species had shown high survivorship and good growth on low fertility, moist sites across a rainfall-soil fertility matrix (Hall and Ashton 2016).

Table 3: _Shade tolerance and site and fertilization requirements for each of the six study species, based on the pre-existing literature._

Species	Shade tolerance	Site and fertilization requirements
Byrsonima crassifolia	**Shade intolerant;** well-adapted to exposed conditions for germination and early growth (Hooper et al. 2002a)	Above-average growth and survival on infertile sites; consistent growth across fertile/infertile sites and moderate to high survival overall (Hall and Ashton 2016)
Dalbergia retusa	**Shade- and small-gap tolerant**; faster initial growth in shaded conditions but taller in full sun over time (Augspurger 1984); can grow in open conditions (Craven et al. 2011)	Consistent and above-average survival and growth across fertile/infertile sites; above-average height on infertile sites (Hall and Ashton 2016); nitrogen fixer (Batterman et al. 2018), but does not always nodulate (Gei and Powers 2015)
Dipteryx oleifera	**Gap specialist** (Balderrama and Chazdon 2005); late-successional species, but seedling growth and survival high at high light levels(Hooper et al. 2002a; Schmidt 2009); may grow better in moderate shade (Hall and Ashton 2016)	Overall below-average growth and moderate to poor survivorship ;in full sunlight slightly better growth on fertile sites (Hall and Ashton 2016); legume but non-nitrogen fixing (Moreira et al. 1992)
Hyeronima alchorneoides	**Gap specialist** (Clark and Clark 1992); seedling growth and survival higher with increasing light availability (Balderrama and Chazdon 2005)	Widely varied survival and growth across sites, ranging from below to above average; specially high performance in infertile, wet conditions (Hall and Ashton 2016); higher growth in ultisols versus inceptisols (Delgado et al. 2003)
Platymiscium pinnatum	**Moderately shade tolerant**; initial seedling growth highest in partial shade (Davidson et al. 2002); can persist and grow in partial to deep shade (Hall and Ashton 2016)	Good survivorship and growth in infertile sites; overall high survivorship and consistent growth across sites (Hall and Ashton 2016); nitrogen-fixer (de Faria et al. 2010)
Terminalia amazonia	**Shade- and small-gap tolerant**, slow growth in shade, much faster growth in sun (Augspurger 1984); long-lived pioneer (Nichols 1994)	Especially high growth in wet infertile conditions (Hall and Ashton 2016); exceptional ability to access nutrients on acidic, low-phosphorus clays;

Byrsonima crassifolia (Malpigheaceae)

B. crassifolia, commonly known in Panama as "nance," is a highly-valued, multiuse species across its broad neotropical range, from central Mexico to central South America (Correa A. 2010). There is archaeological evidence of human use of the species in Panama over 4,000 years ago (Cooke and Ranere 1992). Compounds in the bark, roots and leaves are used medicinally, and fruits are sold commercially for culinary use in desserts and drinks (Correa A. 2010). The dense wood is highly-valued in rural areas for firewood and small-scale construction (Love and Spaner 2005; Garen et al. 2011), and when forests are cleared for agriculture *B. crassifolia* is commonly protected and left standing (Aguilar and Condit 2001). The primary source of *B. crassifolia* timber and fruit is natural regeneration, although there is some planted commercial production on the Pacific coast of Mexico (Duarte 2011). *B. crassifolia* is considered to be "incipiently domesticated," as cultivated populations don't differ genetically from wild populations (Croft 2012). It is typically found in savanna and open pastures (Correa A. 2010) and is considered to be highly shade intolerant (Hooper et al. 2002a). *B. crassifolia* has a deep, radical root system, providing access to deeper, more consistent moisture sources and allowing the species to maintain fruit production under drought conditions (Torres et al. 2018) and also on infertile soils (van Breugel et al. 2011).

Dalbergia retusa (Fabaceae)

Of the species tested in this study, *D. retusa* produces the highest-value wood, and is most commonly referred to by the tradename 'rosewood' in reference to the distinctive scent (UNEPWCMC 2015) and locally known as "cocobolo." *D. retusa* has long been used in indigenous artisanry throughout the species' Central American range, and is now one of the most prized woods worldwide for fine artisan work, especially as tonewood for musical instruments (Vardeman and Runk 2020). Illegal logging has greatly decreased its abundance in natural dry tropical primary and secondary forests, prompting a CITES restriction on all *Dalbergia* species and listing as a vulnerable species on the IUCN Red List; it accounted for 35% of the total value of worldwide plant and animal seizures from 2005-2014 (UNODC 2020). In Panama, the Emberá and Wounaan indigenous groups use the dense and rot-resistant wood for carvings and household tools, which they sell commercially, but historically avoided overharvesting by utilizing fallen limbs or roots. A surge in illegal logging, fueled by international demand and a developing high-volume trading market, led to rampant poaching from indigenous-managed forests in Eastern Panama which peaked in 2014-15 but is ongoing despite nationaland international protections (Vardeman and Runk 2020). Increasing

plantation production is therefore a high priority to mitigate continued threat to natural populations. Given the high value and cultural importance of this species, Panamanian farmers have expressed especially strong interest in cultivation of *D. retusa* (Garen et al. 2011; Hall et al. 2011b). In a study comparing plantations of native timber species to teak in the PCW, *D. retusa* was far more productive than teak by all measures (Sinacore, K. et al.; Sinacore 2018). The species consistently achieves high growth and survival across a range of environmental conditions including dry and infertile sites (Craven et al. 2013; Soderlund 2016; Hall and Ashton 2016), but in full-sun conditions *D. retusa* tends to have a wide-spreading, multi-stemmed growth form that is not ideal for timber; identifying strategies for improving growth form is a management priority (Mayoral et al. 2017). In addition to its cultural and economic importance, *D. retusa* is ecologically valuable as a leguminous tree species and exceptionally strong nitrogen fixer through associations with rhizobia bacteria (Batterman et al. 2018). High-nutrient leaf litter can enhance soil fertility in the surrounding forest floor (Paul et al. 2012; Gei and Powers 2013; but see also Quesada-Ávila et al., in press). *D. retusa* is also very drought tolerant (Sinacore et al. 2019); the species has high water use efficiency (Cernusak et al. 2007) and avoids drought by losing its leaves during the dry season (Sinacore et al. 2019).

Dipteryx oleifera (Fabaceae)

D. oleifera (pseudonym *D. panamensis*) is most commonly known as "Almendro," Spanish for almond, in reference to its large, nutrient-dense, abundant seeds. These seeds are an important food source for many birds and mammals, and for this critical ecological role *D. oleifera* is considered a "keystone species" of tropical wet forests throughout Central America (Schmidt 2009). *D. oleifera* is also highly-valued for its beauty and high-quality, dense timber (Aguilar and Condit 2001), which is used for construction (Tenorio et al. 2016). *D. oleifera* is not widely grown in plantations, and commercial harvesting from natural forests has decreased its abundance and prompted its listing as a CITES threatened species (Schmidt 2009). Growth and survival were relatively low in previous growing trials, but in some cases high-quality compensated for low-quantity wood production in overall value estimation (Tilkia and Fisherb 1998; Redondo-Brenes and Montagnini 2006). *D. oleifera* has been found to have higher survival and growth under nurse trees versus in open-grown plantations (van Breugel et al. 2011). Despite being large seeded and considered shade tolerant, *D. oleifera* has displayed a strong, positive growth response to increased light and also has been observed to grow faster on high fertility sites (De Steven 1988; Delgado et al. 2003; Balderrama and

Chazdon 2005). Though a member of the legume family, this species does not appear to form root nodules or to fix nitrogen (Montagnini 2000).

Hyeronima alchorneoides (**Euphorbiaceae**)

H. alchorneoides (spelling variant *Hieronyma*) is one of the most widely used native species in Costa Rican commercial timber plantations (De Los Santos-Posadas et al. 2011), and is increasingly planted throughout its Central and South American range. It is a tall, canopy tree that primarily grows in low-elevation, humid forests (Flores 1993). In Panama, the species is commonly known as "zapatero" or "pilon" and is valued in rural communities for construction and firewood (Aguilar and Condit 2001). Its wood has high commercial value for its excellent density, workability and rot resistance (Tenorio et al. 2016), though one study found plantation-grown wood was inferior to natural sources (Roque and Leandro 2009). While this species was the top performer in a 13-year study of native timber species in Costa Rican plantations (Ewel et al. 2015), another long-term Costa Rican plantation study found growth was below average compared to other study species (Fonseca et al. 2012).

Platymiscium pinnatum (**Fabaceae**)

Platymiscium pinnatum is culturally valued and a traditional timber tree in Panama, where it is commonly known as "quira" (Klitgaard 2005). While its dense, attractive wood is commercially valuable, there is very little plantation cultivation of *P. pinnatum* (Fournier 1993). Despite strong interest among Panamanian farmers in planting this species (Hall et al. 2011b), there is very little published research on its growth and survival in plantations, and the results that are available show contrasting trends: in Costa Rican plantations, *P. pinnatum* had relatively high survival but low growth after 5 years (Leopold et al. 2001), whereas in Ecuador it was one of the top performing species after 2 years (Villacís et al. 2016). This species is a strong candidate for enrichment planting trials due to its shade tolerance: a greenhouse study identified *P. pinnatum* as a later-successional species that performs best under shaded conditions rather than full light (Davidson et al. 2002). *P. pinnatum* has high water-use efficiency, comparable to a C4 grass (Cernusak et al. 2007). The same study also observed nodulation, suggesting nitrogen fixation, though it was less pronounced than it was on *D. retusa,* the other N-fixing species included in my study.

Terminalia amazonia (Combretaceae)

T. amazonia has the longest legacy and most widespread current use in commercial timber plantations of the 6 study species (Nichols 1994). Natural regeneration occurs in both pastures and forests, and typically in wetter sites (Hall and Ashton 2016). This species may be less well-known outside of the regions in which it is common: in a survey of farmers in Rio Hato and Los Santos, both drier areas of Panama, the majority didn't recognize or express interest in this species (Hall et al. 2011b), while in another study in the Las Pavas area of the PCW, a wetter climate, participants reported preferentially protecting *T. amazonia* during field clearing and burning (Aguilar and Condit 2001). The straight bole and narrow crown typical of *T. amazonia* is excellent for timber production. The common name "Amarillo" refers to the light, yellow-colored wood that is high quality (Flores 2009), though quality of plantation wood may be inferior to natural sources due to reduced heartwood content (Roque and Leandro 2009). Numerous studies across Latin America have noted the exceptionally high performance of *T. amazonia* across a variety of site conditions (Chiu and Snow; Cusack and Montagnini 2004; Piotto 2007), and height index curves have been established for Costa Rica (Montero et al. 2003; De Los Santos-Posadas et al. 2006). Early growth of this species is notably slower relative to other native species, but after the first couple of years *T. amazonia* seems to "take off" (Craven et al. 2011; Sinacore et al. 2019). In a study comparing growth in mixtures versus monocultures, *T. amazonia* had the highest growth of any study species and performed better in mixtures than monocultures due to lower intra-specific competition (Mayoral et al. 2017). *T. amazonia*'s improved performance when surrounded by smaller neighboring trees (of different species) suggests this species was sensitive to the effects of crowding. Along the same lines, *T. amazonia* survival was positively related to plantation spacing when grown in pure plantations (Montero et al. 2003).

2.4 Experimental Design

2.4.1 Plot Layout

Each of the four Agua Salud planting areas were subdivided into 48 contiguous, variably sized plots, with 8 plots for each of the 6 species. Each plot was randomly assigned one of the 6 study species and had 12 seedlings of this species **[Supplementary Figure 1]**, planted at least 6 m apart (to avoid among-seedling interactions) and at least 1 m away from teak trees. Where possible, plots were planted in 4 rows of 3 to form ~18 x 24 m (ca. 432 m2) rectangular plots, but plot shape and size frequently deviated to maintain a 6-m buffer from plantation edges. Due to space constraints and

landowner preference, the two planting areas that are privately owned have fewer plots and do not include all study species: the Giral plantation contains 41 plots and 5 of the 6 study species (*B. crassifolia* was not planted)*;* and the Limon plantation contains 16 plots and 4 of the 6 study species (*P. pinnatum* and *H. alchorneoides* were not planted)*.*

2.4.2 Planting Media and Protocol

All seedlings were grown in tubettes at the Futuro Forestal (www.futuroforestal.com) nursery in Las Lajas, in the Chiriqui province of Panama (see also Roman et al. 2012). Exact seedling age at planting time varied depending on species-specific phenology of seed production and germination requirements, but all seedlings were less than 1-year-old when outplanted. Pre-planting seedling size differed significantly among species for all measures (p-values <0.001) **[Supplementary Table 1]**. Immediately prior to planting, seedlings across all species had mean stem length of 34.6±1.2 cm, mean root collar of 4.1±0.18 mm and mean dry biomass of 2.8±0.23 g.

One to two months prior to planting, understory vegetation was cut with machetes and, immediately prior to planting, a 1-m diameter circle was cleared to bare dirt around each seedling planting site. Similar clearing was repeated 2-3 times annually for the duration of the study. At the time of planting, each seedling received 90g of 12-24-12 NPK dry, granular chemical fertilizer (10.8g N, 21.6g P, 10.8g K) and one handful of organic material (composted cow manure and forest duff), incorporated with loose dirt at the bottom of the planting hole. *B. crassifolia, T. amazonia, D. retusa,* and *D. oleifera* were planted in August 2016; *H. alchorneoides* and *P. pinnatum,* for which planting stock was initially unavailable, were planted in July-August 2017. Only seedlings with good vigor and without evidence of foliar disease were planted.

2.4.3 Fertilizer Treatment

For each species, half of plots were chosen to receive annual fertilization (treatment group); the remaining half received no additional fertilization following planting (control group). Assignment to fertilizer treatment or control was done by subjectively stratifying treatments across topographic conditions to ensure their even distribution throughout each planting area; in other words, I ensured that both treatment and control plots were spread across upper to lower hill positions for each species. For the fertilization treatment plots, 100g of 12-24-12 N-P-K fertilizer was applied once annually at the start of the rainy season, beginning the first year after planting. For each planted

seedling in treated plots, the fertilizer was split evenly between two ~15 cm-deep holes dug 15-20 cm uphill from the base of the seedling, and covered with a layer of soil.

2.5   Sampling

2.5.1 Survival and Growth of Native Seedlings

In order to assess survival and growth of enrichment planting seedlings, seedling status (alive or dead), height (m) and basal diameter (BD, cm) were recorded 6 months post planting and then annually during the dry season (January) from 2017-2020 for 2,976 seedlings in all planting areas (n= 6 species x 2 levels of fertilizer x 216 to 264 seedlings/planting area). Height was measured from the soil surface vertically to the highest point of main photosynthetic tissue, excluding leaves (Pérez-Harguindeguy et al. 2013). For each seedling with BD ≤5 cm, 2 BD measurements were made with digital calipers from opposite sides of the stem (to account for irregularly-shaped stems) and averaged; for larger seedlings, a single measurement was made with a diameter tape. For trees with multiple stems at or below 5 cm above the root collar, the tallest stem was measured and BD was recorded below the branching point. Final measurements were taken ~42 months post-planting (after 3 full growing season) for species planted in 2016 and ~30 months post-planting (following 2 full growing seasons) for species planted in 2017.   Analyses were done on the 30 month post-planting data only, since 42 month data were only available for a subset of species.

BD relative growth rate (RGR), a common and widely-used metric for growth comparison, was calculated for the time between initial and final post-planting measurements using the standard equation (FISHER 1921):

$$RGR = [ln(M_2) - ln(M_1)]/(t_2 - t_1)$$

where M_1 and M_2 are initial (6 month) and final (30 month) BDs, respectively, and t_2-t_1 is the number of years (2) between measurements.

Total biomass (TB, kg), which reflects both growth and wood density for each species, was estimated using an equation developed through direct measurement of native tree species growing in PCW plantations (Sinacore et al. 2017):

$$TB = -2.586 + (2.456 * BD * ln(BD)) + (0.915 * BD * ln(WSG))$$

where *BD* is the individual BD measurement (cm) of a given seedling and *WSG* is the wood-specific gravity of the species as approximated based on compiled results of prior studies in the region (Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., and Chave 2009; ICRAF 2020). This equation was developed with 6-year-old trees and its reliability for younger seedlings is unknown, , but it is is best measure available for among-species comparison of same-aged seedlings.

2.5.2 Crowding Pressure

Crowding pressure from teak overstory trees was assessed for one centrally-located target seedling per plot using a 6-m fixed-radius subplot (Berger et al. 2008). Target seedlings were located in the center of the plot, so that the subplot would fall within the larger plot boundaries. For each teak within the subplot, DBH (cm) and distance (m) were measured from the target seedling. Distance was measured two ways: ground distance and slope-corrected distance. Measurements proved highly correlated (Adj R^2 =0.97) and only ground distance was used in the final analysis. Because seedlings were planted at 6-meter spacing, and understory vegetation was removed, only overstory teak trees (and not other seedlings) fell within the subplot radius.

Total crowding pressure for each target seedling was calculated as

$$\text{Crowding pressure} = \left(\sum_{i=1}^{n}\left(\frac{DBH_i}{Dist_i}\right)\right)/100$$

where i=1….n neighboring teak, DBH=diameter (cm) of main teak bole at 1.35 m above soil surface, and Dist=ground distance (m) from base of target seedling to base of teak trunk closest to seedling. Crowding pressure increases with increasing DBH of each teak neighbor and decreases with increasing distance from the target seedling, and the combined effects of all neighbors provide an estimate of both below-ground and above-ground interactions (Fichtner et al. 2015). The summed effects of all neighbors was divided by 100 to keep values within the same order of magnitude of other variables for more easily-interpretable coefficient estimates.

2.5.3 Light Availability

In order to partition the above-ground effects of crowding from below-ground effects such as competition for nutrients and water, light availability was measured for each seedling using hemispherical photography. Photos were taken with a CI-110 Plant Canopy Imager, positioned directly above seedlings at a height of 1 m, in early morning, late afternoon or during overcast

weather to avoid direct sunlight. These data were collected in January 2018, when seedlings were still too short to affect light availability of one another and teak overstory had not begun to drop leaves as occurs later in the dry season on some sites. CID™ Plant Canopy Image Analysis software was used to calculate the transmission coefficient for the ray penetrations (or the fraction of visible sky) used to represent PAR (Mailly 2017). Software assessment of each photo was checked for accuracy, and incorrect classification was revised when possible or else excluded from the final analysis.

2.6 Statistical Analysis

2.6.1 Survival and Growth

Survival and growth were compared among species (Q1) using ANOVA models, with separate models for each response variable (BD, BD RGR, height and TB). ANOVA assumptions confirmed with standard diagnostic plots. Significant differences were further explored using Tukey's Honest Significant Differences method. Survival was calculated at the plot level as the % of the 12 planted seedlings still living after 30 months. Growth was assessed as plot-level mean±SE of each response variable at 30 months. For these analyses only seedlings in control plots (no post-planting fertilization) were used because there were significant differences in BD between fertilizer treatments for all species combined (p-value=0.04) and for some, but not all, individual species.

The relationship between survivorship and growth was assessed using linear regression, with a model for all species as well as separate models for each species. For these and subsequent models, BD was selected as the primary response variable representing growth because it was strongly related to height (Adj R^2 = 0.72, p-value<0.001), and the height data had more error due to factors such as machete or herbivore damage, seedling position, and observer bias. RGR and TB were considered but not used as the primary response variable due to the applied nature of this study; actual, achieved growth and variation may be the most useful measure for land managers and others interested in assessing the performance of these particular species. Additionally, most seedlings were not measured at planting so RGR does not account for growth prior to the first measurement at 6 months post-planting; BD is the only direct measurement (TB was calculated with equations based on BD) that accounts for the full study period.

2.6.2 Effect of Growing Environment and Fertilizer

The effects of growing environment (Q2) and fertilizer (Q3) on enrichment planting survival and growth were assessed using linear mixed effects models (LMM), with separate models for each response variable (survival and BD). LMMs for all species combined and for each species individually were constructed. For these LMMs, fertilizer treatment (2 levels) and species (6 levels; only in the all-species models) were included as categorical fixed effects and either crowding pressure or transmission coefficient was included as a continuous fixed effect. I did not use both crowding and transmission coefficient in the same LMMs because, due to the collinearity of these variables, neither was significant when included together in the same model (P>0.7) **[Supplementary Figure 2]**. Planting area (6 levels) was included as a random intercept to account for the hierarchical data structure and potential among-area variation in planting conditions not captured by crowding or light measures. The importance of among-area variance was confirmed by using the likelihood-ratio test to compare LMMs with the null model containing only the fixed effects (Harrison et al. 2018). Treating planting area as a random effect allows for broader inference from these data, which aligns with this study's goal of informing management of poorly-performing teak plantations throughout the PCW. Distribution of data was examined both visually and using descriptive statistics produced with the fitdistrplus R package (Delignette-Muller 2014) **[Supplementary Figure 3]**.

LMMs initially included all possible interactions among fixed effects, as other studies have found among-species differences in response to fertilizer application (i.e. Lawrence, 2003; Smethurst, 2010) and light availability (i.e. Falster, Duursma, & FitzJohn, 2018; Hooper, Condit, & Legendre, 2002a; Rappaport & Montagnini, 2014), and soil nutrient availability may affect light or crowding responses (i.e. Coates, Lilles, & Astrup, 2013). Insignificant interactions were successively eliminated based on the Likelihood Ratio Test (LRT), which uses the Chi square distribution to test the significance of fixed effects and interactions. The Akaike's information criterion (AIC) was compared for these nested models. This approach was appropriate for testing hypotheses related to the importance and potential interaction of specific fixed effects (rather than maximizing global predictive power of the entire model), given that the random effect was the same across all potential models and there were relatively few parameters (Gruber et al. 2011).

Model interpretation and validation

The explanatory power (effect size) of fixed effects within the all-species LMM and each single-species LMM was assessed by comparing the marginal R^2 of models both with and without each fixed effect. In linear regression, R^2 values are a standard and intuitive way of assessing the amount of variance explained by study variables, but in LMM it is important to differentiate between the Conditional R^2, the overall variance explained by both fixed and mixed effects, and the Marginal R^2, the variance explained by only fixed factors (Harrison et al. 2018). Said values were calculated using methods established by Nakagawa and Schielzeth (2013; Nakagawa et al. 2017), and the effects of each variable were portioned by comparing marginal R^2 of nested models both with and without each fixed effect using the piecewise SEM R package (Lefcheck 2016). Standard model diagnostics were conducted using the sjPlot R Package (Lüdecke 2020) to confirm assumptions of data distribution and error structure. Final models were cross-validated using a K-fold method of resampling that accounted for hierarchical data structure: 10 mutually-exclusive subsets were created using pooled data from all planting areas and including observations from each area within each subset or "fold." Each of the 10 folds was then used as a "testing set" for models developed based on the 9 remaining "training sets" (Yang and Huang 2014).

3   Results

3.1   Survival and Growth (Q1)

Overall mean±SE survival at 30 months post-planting was 83±2% across all control plots, all species and all planting areas. Survival varied significantly among species (p-value<0.001), ranging from a mean of 98±1% for *P. pinnatum* to 47±3% for *B. crassifolia* [**Table 4**]. With *B. crassifolia* excluded from analysis, the overall survival of all other enrichment planting seedlings was above 90% after 30 months. *D. oleifera* had the second lowest survival (72±5%) of any other species. Rates of survival among the remaining 4 species were not significantly different (p-values=0.07-0.99).

Table 4: *Mean (SE) survival and growth for the six study species (and all species overall, bold) across all control (i.e. no annual fertilization) plots within all planting areas at 30 months post-planting. n= total number of plots per species; survival= percent of the 12 planted seedlings within each plot that were alive; BD= mean basal diameter (cm) of all living seedlings on the plot; RGR= relative growth rate of BD of all living seedlings from 6-30 months post-planting; height= mean vertical distance (m) from soil surface to the highest point of main photosynthetic tissue for all living seedlings; TB= mean total biomass (kg)/seedling based on all living seedlings.*

Species	n	Survival(%)	BD(cm)	RGR(BD)	Height(m)	TB(kg)
B. crassifolia	20	47(3)	2.64(0.16)	0.71(0.03)	1.19(0.08)	5.36(0.72)
D. retusa	22	97(1)	2.91(0.13)	0.54(0.03)	1.79(0.09)	7.76(0.68)
D. oleifera	22	73(5)	1.45(0.14)	0.49(0.04)	0.99(0.11)	2.87(0.35)
H. alchorneoides	20	88(4)	3.42(0.31)	0.51(0.03)	2.66(0.29)	10.12(1.68)
P. pinnatum	19	98(1)	2.74(0.16)	0.54(0.02)	2.00(0.13)	6.87(0.72)
T. amazonia	22	92(2)	2.08(0.08)	0.49(0.02)	1.35(0.05)	3.47(0.33)
Overall	**125**	**83(2)**	**2.52(0.09)**	**0.54(0.01)**	**1.65(0.08)**	**6.06(0.41)**

Across all species and planting areas, mean±SE BD in control plots at 30 months was 2.52±0.09 cm, mean BD RGR was 0.54±0.01 per year, mean height was 1.65±0.08 m, and mean seedling TB was 6.06±0.41 kg. There were significant among-species differences for all measures of growth (p-values all <0.001). *H. alchorneoides* had the largest BD (3.42±0.31 cm), height (2.66±0.29 m) and seedling TB (10.12±1.68 kg); *D. oleifera* had the smallest values of all three measures (1.45±0.14 cm BD, 0.99±0.11 m height, 2.87±0.35 kg TB). BD RGR was significantly higher for *B. crassifolia* (0.71±0.03 per year, p-value<0.001) than for any other species, but did not differ significantly among the other 5 species (p-values=0.16-0.99) **[Figure 2].**
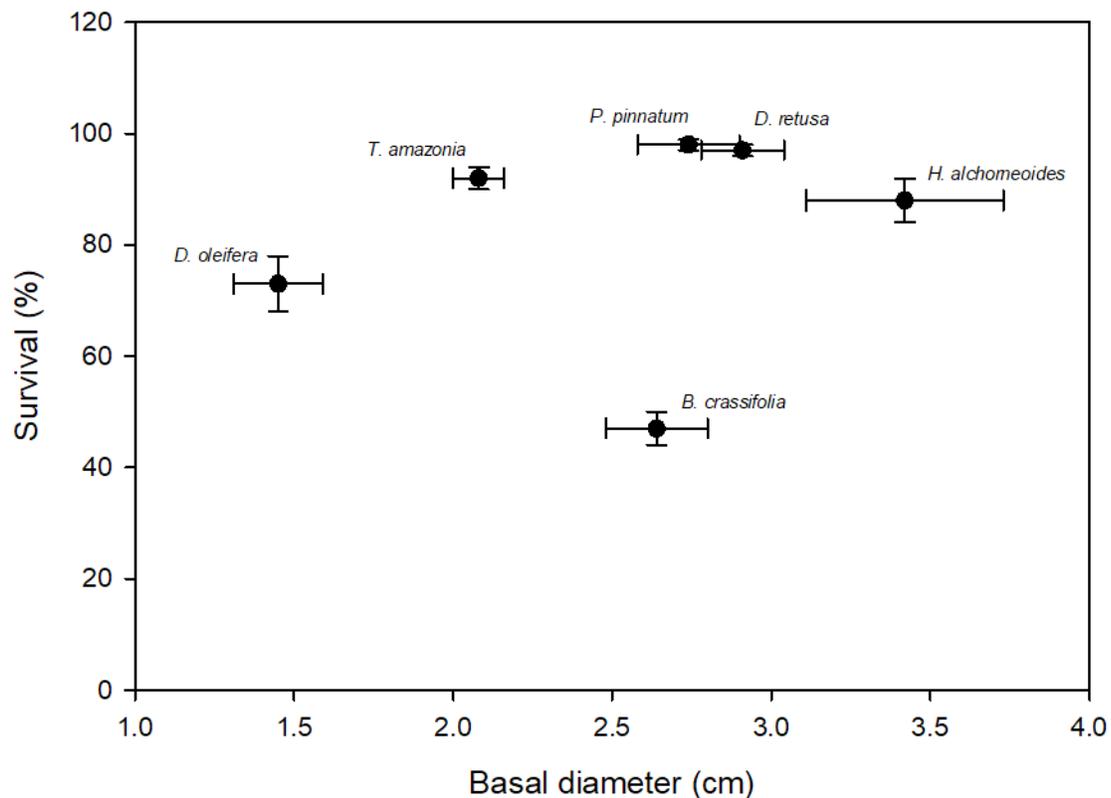

Figure 2: *Mean (SE) survival (%) and growth (30-month basal diameter, cm) for the 6 enrichment planting species across all control (i.e. no annual fertilization) plots within all planting areas. Species names are above corresponding points. There was not a significant relationship between survival and growth across all species.*

For all species combined, there was not a significant relationship between survival and growth (p-value=0.65 Figure 2). Within species, there was a positive relationship between survival and growth for *D. oleifera*: plots with seedlings with greater BD also had higher survival (Adj. R^2=0.42, p-value<0.01). For the other 5 species, however, survival and growth were not significantly related (p-values=0.09-0.25).

3.2   Effect of Growing Environment (Q2)

Across all planting areas, crowding pressure on individual target seedlings ranged from 0.03 to 0.61, averaging 0.26 **[Supplementary Figure 4A].** Crowding pressure was not predictive of survival for all species combined (p-value=0.12) nor for any individual species (p-values=0.06-0.86).

Across all planting areas, transmission coefficients (light availability) for individual seedlings spanned the spectrum from full sun (1.0) to highly shaded (0.03); plot-level mean transmission coefficients ranged from 0.28-0.83, averaging 0.51 **[Supplementary Figure 4B]**. For all species combined, light availability was not predictive of survival (p-value=0.88). In single-species models light availability was significantly and negatively related to survival for *D. oleifera* and *H. alchorneoides* (p-values<0.001) but was not significantly related to survival for the remaining 4 species (p-values=0.39-0.83).

Both crowding pressure and light availability explained a significant amount of variation in growth (30-month basal diameter) for all species combined and for some, but not all, species when considered separately**.** Crowding pressure was significantly negatively correlated with growth of all species together, but explained <2% of variability (p-value=0.009) **[Supplementary Table 3]**. There was not a significant crowding x species interaction in the multispecies growth model (p=0.1). However, in single-species models, crowding had a significant effect on growth of 5 of 6 species (*D. oleifera* was the exception*;* p-value=0.85) **[Table 5A]**. *B. crassifolia* was the most negatively impacted (p-value=0.008): crowding explained 22% of variation in growth (after accounting for the effects of fertilizer and planting area, see below). For the remaining 4 species, crowding accounted for a significant but smaller percent of variation in growth: 7% for *P. pinnatum,* 9% for *D. retusa,* 10% for *H. alchorneoides,* and 11% for *T. amazonia* (p-values<0.05) **[Figure 3]**.
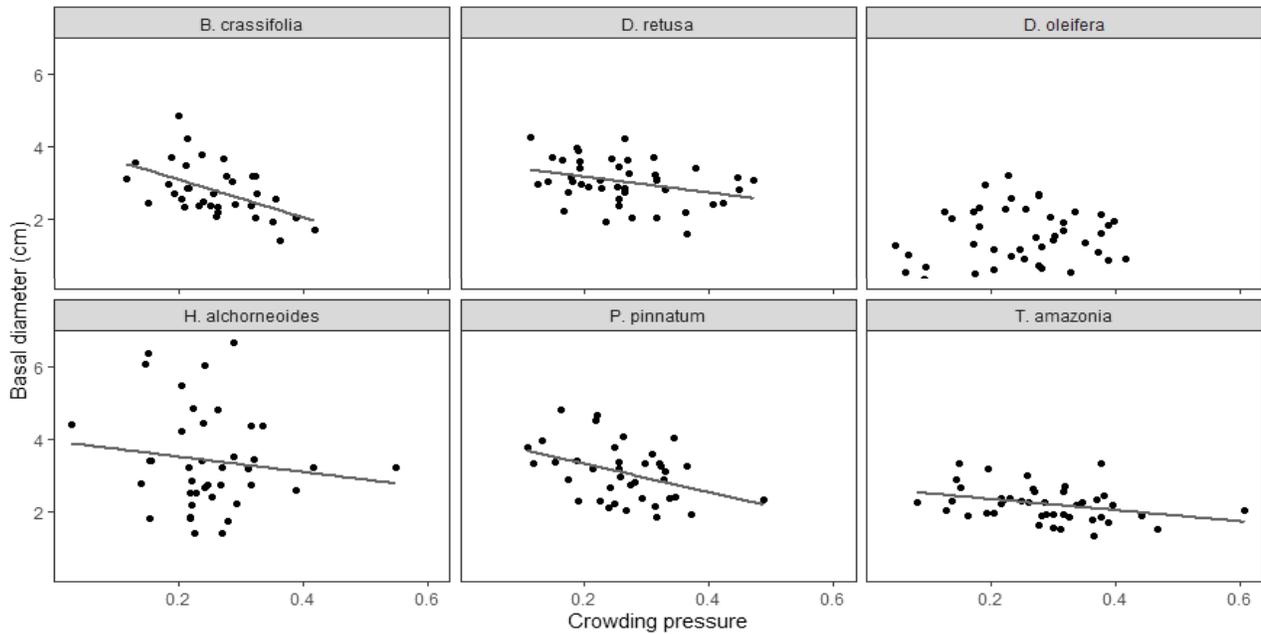
Figure 3: *Effect of crowding pressure from teak on seedling growth (30-month basal diameter, cm) for each of the 6 enrichment planting species. Basal diameter values are plot-level means (n= 12 seedlings). Crowding pressure values are for one target seedling per plot. There were significant, negative relationships (P<0.05) for all species except for D. oleifera.*
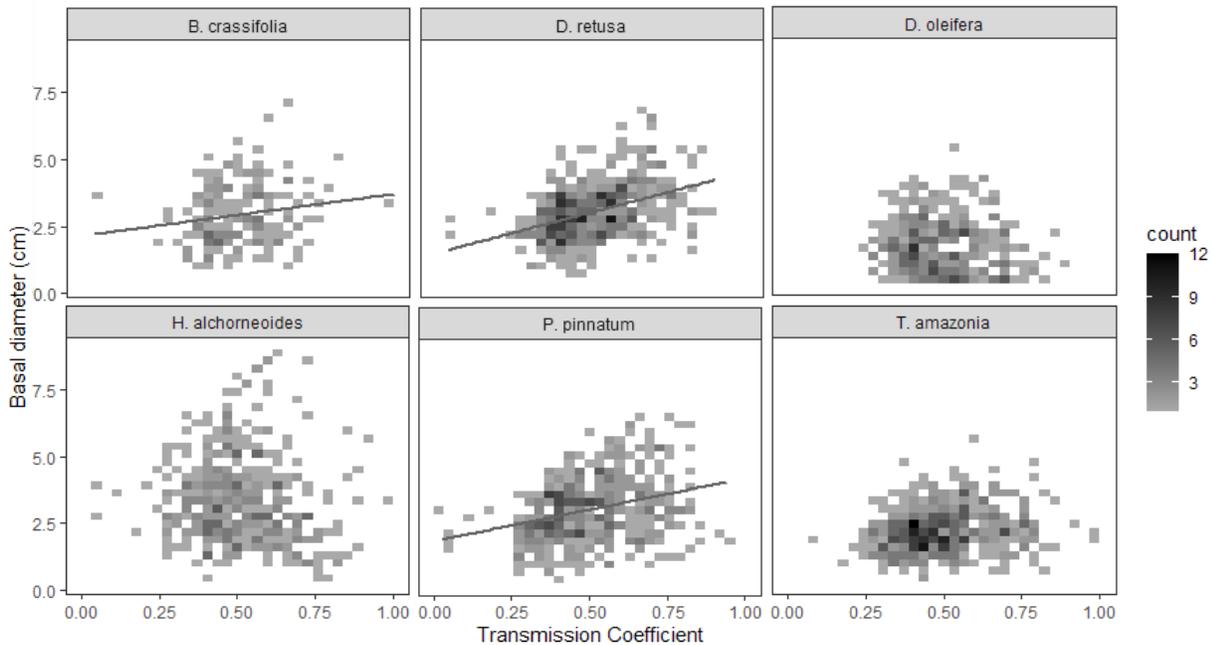
Figure 4: *Effect of light availability (transmission coefficient) on seedling growth (30-month basal diameter, cm). Due to a large number of observations, data are presented as binned counts: graph area was divided into x,y grid cells (30x30 rectangles). Shading of each grid cell represents the number of individual seedlings (n=1-12) with values of light availability and growth that fall within that cell; lighter shading denotes fewer seedlings and dark shading denotes a higher number of seedlings. Light availability was significantly related to growth of B. crassifolia, D. retusa, and P. pinnatum but not the other 3 species.*

29

Table 5: *Summary statistics for the effect of growing environment and fertilizer on BD, with separate tables for crowding pressure (**A**) and light availability (**B**). n=number of observations (plots); β=coefficient estimates; p= p-values (<0.05 bolded); σ²=random effect variance (the variance explained by planting area); ICC=intra-class correlation coefficient (the proportion of the total variance explained by the random effect); Marginal R^2 is the proportion of variance in BD explained by fixed effects only and conditional R^2 is the proportion of variation explained by the full model (fixed and random effects). Confidence intervals for coefficient estimates available in* **Supplementary Table 4, A and B**.

(A)

	B. crassifolia		D. retusa		D. oleifera		H. alchorneoides		P. pinnatum		T. amazonia	
n	35		43		43		40		38		43	
Predictors	β	p	β	p	β	p	β	p	β	p	β	p
(Intercept)	3.95	**<0.001**	3.45	**<0.001**	1.43	**<0.001**	4.76	**<0.001**	3.62	**<0.001**	3.44	**<0.001**
Fixed effects												
Fertilization	0.14	0.526	0.22	0.142	0.23	0.229	-0.02	0.951	0.52	**0.015**	0.32	**0.009**
Crowding pressure	-1.51	**0.008**	-0.67	**0.027**	0.03	0.937	-1.71	**0.01**	-1	**0.03**	-0.46	**0.023**
Random effect												
Planting area												
σ²	0.35		0.22		0.35		0.72		0.34		0.14	
ICC	0.06		0.33		0.32		0.62		0.23		0.19	
Marginal/ Conditional R^2	0.266 / 0.306		0.127 / 0.415		0.025 / 0.340		0.103 / 0.657		0.237 / 0.410		0.211 / 0.359	

(B)

	B. crassifolia		D. retusa		D. oleifera		H. alchorneoides		P. pinnatum		T. amazonia	
n	33		42		42		39		39		44	
Predictors	β	p	β	p	β	p	β	p	β	p	β	p
(Intercept)	1.12	0.166	0.95	**0.015**	2.01	**0.001**	2.82	**0.022**	1.28	**0.019**	1.49	**<0.001**
Fixed effects												
Fertilization	0.22	0.328	0.26	**0.035**	0.19	0.287	-0.05	0.877	0.63	**0.001**	0.27	**0.03**
Transmission coefficient	3.21	**0.05**	3.77	**<0.001**	-1.12	0.295	1.09	0.573	2.85	**0.003**	1.22	0.085
Random effect												
Planting area												
σ²	0.35		0.14		0.32		0.87		0.3		0.14	
ICC	0.22		0.28		0.33		0.52		0.37		0.21	
Marginal/ Conditional R^2	0.219 / 0.389		0.470 / 0.616		0.046 / 0.363		0.010 / 0.525		0.335 / 0.583		0.168 / 0.339	

Light availability was significantly positively correlated with growth of all species together and explained ~2.7% of variability in growth (p-value-0.003) **[Supplementary Table 3]**. There was a significant light availability x species interaction in the multispecies growth model (p<0.001). For 3 of 6 species (*D. oleifera, H. alchorneoides,* and *T. amazonia*) light did not significantly affect growth (p>0.05) **[Table 5B]**. Light availability explained 43% of variation in growth for *D. retusa,* 21% for *P. pinnatum,* and 20% for *B. crassifolia* (p-values<0.03) **[Figure 4]**.

There were significant effects of planting area on enrichment planting growth not accounted for by crowding or light. For all species combined, planting area had a significant effect on growth (p-values<0.01), but explained only a small percent of variation in the multi-species model (7% and 9% for the crowding and light models respectively) **[Supplementary Table 3]**. The effect size of planting area varied among individual species. In individual species models, planting area was significant for 5 of 6 species when crowding was included (the exception was *B. crassifolia,* p-value=0.19) **[Table 5A]** and for all models that included light **[Table 5B]**. Different planting areas affected species differently: no area was the most or least productive across all species. Planting area had the largest effect for *H. alchorneoides,* explaining over 50% of variation in growth in both crowding and light models (p-value<0.05). For other species, the effect was smaller, explaining between 15-33% of variation in growth in both the crowding and light models (p-value<0.05). In contrast with growth, enrichment planting survival was not significantly different among planting areas after accounting for the effects of crowding and light (p-values=0.06-0.52).

3.3   Effect of Fertilization (Q3)

There was no difference in survival between fertilized and control (unfertilized) plots for all species together or for any species individually (p-values=0.11-0.96), with the exception of *B. crassifolia* in the model that also included crowding (p-value=0.023). However, fertilizer had a significant effect on growth: for all species combined, BD was 11% higher for fertilized plots versus control plots (p-value=0.04). Growth response to fertilization differed among species **[Figure 5]**. In individual species models, fertilization significantly affected mean BD of *P. pinnatum* and *T. amazonia* in both the models that included light and those that included crowding (p-values=0.001-0.03) and *D. retusa* in the crowding model only (p-value=0.035), but did not have a significant on mean BD of the other species (p-values=0.14-0.95) **[Table 4A]**. BD of *P. pinnatum* fertilized seedlings was 22% larger on-

average than control seedlings, 13% larger for *T. amazonia* and 8% larger for *D. retusa*. In the multispecies model there was a significant interaction between fertilization and light availability (p-value=0.011).
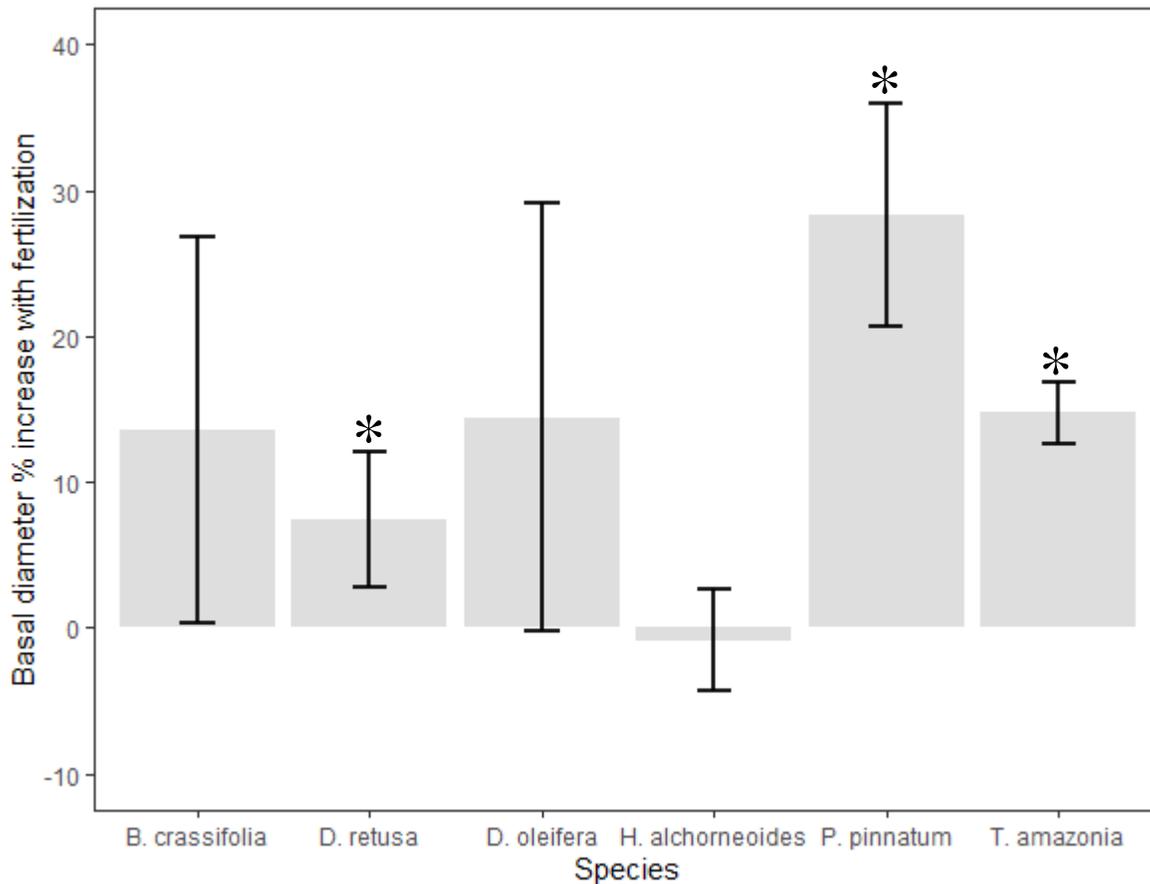

Figure 5: *Mean (SE) % increase in seedling growth (30-month basal diameter, cm) between fertilizer and control treatments (calculated as [((treatment/control)-1)*100]) among all planting areas. Fertilizer treatment seedlings received applications of chemical N-P-K fertilizer once annually; control seedlings were not fertilized after planting. Annual application of chemical fertilizer significantly increased basal diameter for D. retusa, T. amazonia and P. pinnatum (indicated with *) but not the other 3 species.*

4   Discussion

Many native neotropical species have long been utilized by rural communities of Panama practicing sustained-use forestry and stewardship of natural forests (Aguilar and Condit 2001). These species remain culturally valued today (Garen et al. 2009; Paquette and Messier 2010) and have high potential for financial profitability (Sinacore, K. et al.; Griess and Knoke 2011), yet have been underutilized in larger-scale FLR projects in the PCW and other regions. In order to better integrate

native species into FLR efforts, there is a need for information on the species and management approaches that will be financially and ecologically appropriate. Specifically, land managers need evidence on whether enrichment planting can offer a potential path forward to recoup sunk costs of already-established and underperforming teak plantations. My results indicate that native timber species are capable of establishing and growing in an enrichment planting setting within teak plantations, aligning with more recent research (Wolfe et al. 2015) that challenge longstanding dogma that teak plantations inhibit understory growth (Healey and Gara 2003). Among-species differences in responses to crowding, light availability and fertilization highlight the continued need for species-specific silvicultural information to inform enrichment planting projects.

4.1   Survival and Growth (Q1)

All of the study species were selected for their relatively high survival in growth trials and other previous studies (e.g. Park et al. 2010; Breugel et al. 2011; Hall and Ashton 2016), and overall they achieved similarly high survival in the enrichment planting context (with the exception of *B. crassifolia* and, to a lesser extent, *D. oleifera*). Variation in conditions across sites and planting years makes growth comparison to previous studies difficult, but overall the early results are promising. While average growth of enrichment planting species is far below, for example, projected 3-year growth for teak in Panama on fertile sites (Ross 2013), the wood of these species is similar to far greater in financial value (Schmidt 2009, Vardeman and Runk 2020, Tenorio et al. 2016). Furthermore, adding in these trees as an enrichment planting to an already-established plantation minimized startup costs and labor (Keefe et al. 2012). The additional ongoing maintenance of these trees, clearing understory plants around the base, was likely lower than in the traditional open-grown establishment conditions due to shading from teak overstory (Hooper et al. 2002a). A full financial assessment is beyond the scope of this study, but early results suggest that the addition of high-value native species could change the profitability of underperforming teak plantations such as the Agua Salud plantation, which was not projected to financially break even prior to enrichment planting (Hall 2013; Sinacore et al., in review).

In the same planting year, an open-grown site (previously a cattle pasture) was established as a comparison planting **[Supplementary Table 7]**. Though, due to lack of replication, I was unable to test for differences in growth between the enrichment plantings and this open-grown planting area, I anecdotally noted that survival was 8 % lower, but 30-month BD was 24% higher in the open grown site compared to the enrichment planting areas. This trade-off in growth versus survival has been

widely documented in enrichment planting (i.e. Forrester et al. 2005; Paquette et al. 2006a; Redondo-Brenes and Montagnini 2006), and future research should include a replicated open-grown comparison site to investigate present observations.

In the restoration context, growth is often used as a proxy for fitness and the fastest-growing species and individuals are often assumed to have the highest survival (Charles et al. 2018; Craven et al. 2009). However, I did not find a significant relationship between survival and growth among species. The species that achieved the highest BD growth after 30 months, *H. alchorneoides,* ranked 4th in survival while the smallest species in absolute growth, *D. oleifera,* ranked 5th. The species with the lowest survival (*B. crassifolia*) had the highest RGR but the two species that tied for 2nd highest RGR (*P. pinnatum* and *D. retusa*) had the 1st and 2nd highest survival, respectively. And within individual species, the only significant relationship between survival and growth was a positive correlation for *D. oleifera* seedlings; growth did not predict survival for individuals of any other species. This suggests that growth may not be the best predictor of fitness and practitioners should be careful to avoid overreliance on growth as a measure of plant performance. though some level of mortality is acceptable given that pre-commercial thinning is typically necessary in plantations to avoid over-crowding. One caveat to comparing and integrating my research with existing literature relating survival and growth is that seedlings were transplanted, so these results do not reflect germination or initial establishment.

4.2   Effect of Growing Environment (Q2)

While crowding had a fairly consistent negative effect on growth for all but one species (*D. oleifera*), species responses to light availability ranged widely. Crowding reflects below-ground competition for water and nutrients in addition to light, while light availability is a measure of a strictly aboveground resource. Differences in species responses to crowding versus light suggests that these below-ground interactions may be important and that seedlings are not exclusively light limited. This aligns with a preliminary enrichment planting trial in Agua Salud teak plantations (Marshall et al 2020) which found that crowding explained more variation in enrichment planting growth than light alone, though among-species differences in response to growing environment in the present study caution against over-generalizing. If the negative effects of crowding were driven by nutrient competition, I would expect that the species that responded positively to fertilizer would also have responded negatively to crowding, and this was not always the case. The finding that crowding

effects were not explained by either light or nutrients (fertilization) points to the complexity of resource competition among forest trees.

Shade tolerance based on previous studies and conventional wisdom was not a good predictor of species responses to light availability. The 3 species that did not have a significant positive growth response to light spanned the range of shade tolerance from low (*T. amazonia)* to moderate *(H. alchorneoides)* to high (*D. oleifera*). Interestingly, across all species, trees with the highest growth were in partial shade (0.5-0.75 transmission coefficient). This aligns with previous findings that partial shade rather than fully open grown conditions can be optimal for mid- and later-successional species (Ashton 1995; Marshall et al. 2020)

Interestingly, the effect of planting area on all species together explained less variation in growth than for most species individually, indicating that there was no universal "best" or "worst" planting area for all species. This finding speaks to the complex relationship between site conditions and the unique requirements of different species. *H. alchorneoides* growth was by far the most affected by planting area, whereas *B. crassifolia* was the least-affected, which is consistent with prior findings that this species grows well even on very harsh sites where few other tree species are found (Jimenez Madrigal 2002). While the effect of aspect on light and moisture availability in the tropics is less important than in the Northern hemisphere (Méndez-Toribio et al. 2017), slope position and gradient can be an important factors (Mayoral et al. 2018). These factors, as well as soil nutrient status, were not assessed in my study but are valuable future research directions.

4.3   Effect of Fertilization (Q3)

The observed growth increase associated with annual fertilization for some of the study species is interesting from both a management and ecological perspective. Among-species differences highlight that growth benefits from application of supplemental fertilization cannot be generalized (Xia and Wan 2008) and should be experimentally evaluated for individual species in field conditions similar to those of management interest (Smethurst 2010).

Strong early growth can give tree seedlings a greater competitive advantage against understory weeds (Craven et al. 2009), thus if fertilizer increases seedling growth it could potentially reduce management effort. In addition, if the positive growth response to fertilizer of *D. retusa, P. pinnatum* and *T. amazonia* continue over time, trees that receive fertilization could be significantly larger at harvest, thereby increasing profits of these high value of these species. Furthermore, trees could

reach merchantable harvest size more quickly, benefiting land managers by shortening rotation times for a faster return on investment. I intentionally tested the most affordable and widely-available chemical fertilizer (12-24-12 NPK) in order to assess whether this low-cost option was a worthwhile management investment. At the application rate of 100g annually, the per-tree cost of fertilizing for the first 10 years is 1 kg fertilizer plus labor. Given the high-value wood of study species, very minimal growth increases would be required to break even financially on the investment.

The lack of growth increase from fertilization for half of the species in this study is a notable finding, especially given the low-fertility soils of planting areas in this study. This contrasts with the strong response to fertilizer of many exotic timber species such as teak, even in sites with more productive soils (Kumar BM 2005; Smethurst 2010; Jerez and de Andrade Coutinho 2017). There was also no significant difference in variability in growth between seedlings in fertilized and unfertilized plots. This was surprising given that there were differences in nutrient availability among plots even within the same planting areas. If plot nutrient status was a major driver of differences in growth, one might expect to see lower variability in growth (i.e. more consistent growth) with fertilization. However, I did not find that to be the case. .

The small to insignificant effect size of fertilization for study species not only provides useful and important information for the management of these particular native species, but also ties in to recent research on soil nutrient limitations in tropical forests. Of the 3 macronutrients supplied by the chemical fertilizer, phosphorus is of particular interest given that this is generally considered to be the most limiting nutrient in tropical soils (Hedin et al. 2009) and soil testing confirmed low levels of phosphorus in this study's planting areas. The phosphorus affinity, or growth response to phosphorus availability, of tree species has been identified locally as one of the strongest predictors of tropical forest community composition (Condit et al. 2013; Zalamea et al. 2016). Conveniently, a previous assessment of growth responses to phosphorus availability in lowland tropical forest species in Panama included 5 of the 6 study species (all except *D. retusa*) (Condit et al. 2013). All 3 species that didn't have a significant growth response to fertilization in the present study (*B. crassifolia, D. oleifera,* and *H. alchorneoides*) were also found by Condit et al (2013) to have below-average affinity to phosphorus. Furthermore, *P. pinnatum,* which had by far the largest positive response to fertilizer in this study, was found by Condit et al (2013) to have an above-average phosphorus affinity. The positive fertilizer response of both nitrogen-fixing species, *P. pinnatum* and *D. retusa,* adds support to the focus on phosphorus (rather than nitrogen) limitation and aligns with previous

findings that low levels of available phosphorous have been found to limit the growth of nitrogen-fixing trees (Batterman et al. 2013).

The significant effect of fertilizer on *T. amazonia* growth complicates this tidy story. According to Condit et al (Condit et al. 2013), this species has an especially low phosphorus affinity (i.e. grows well on sites low in phosphorus), and for other pioneer species in Panama, though not *T. amazonia* specifically, distribution across a natural phosphorus gradient was predictive of growth response to phosphorus (Zalamea et al. 2016). Yet in my study, *T. amazonia* had the second-largest positive response to fertilization. A previous study of *T. amazonia* response to fertilization in Costa Rica (Carpenter et al. 2004) found that, similar to this study, fertilized *T. amazonia* was significantly larger after 2 years. After 8 years, Carpenter et al. (2004) found there was no longer a significant difference between fertilized and unfertilized trees, though there were important differences in soils of the study site and experimental design: different from my study, Carpenter et al. (2004) only applied the fertilizer treatment for the initial 2 years post-planting. The same Costa Rica study also tested interplanting *T. amazonia* with nitrogen-fixing species *Inga edulis* and found this increased *T. amazonia* growth and foliar nitrogen content (Nichols and Carpenter 2006). These findings suggest that nitrogen can be a limiting factor in *T. amazonia* growth, so it's possible that the positive response to fertilization in the present study is due to additional nitrogen availability rather than to phosphorous.

A meta-analysis of growth response to fertilization in tropical seedlings (Lawrence 2003) found that light-demanding species were more likely to respond positively to fertilization compared with shade-tolerant species. In my study, shade tolerance (based on previous studies) was not strongly predictive of fertilizer response: whereas the light-demanding species *B. crassifolia* had no response to fertilization, the more shade-tolerant species *P. pinnatum* had the greatest growth response. Regardless of a given species' shade tolerance, the significant light availability X fertilization interaction in the multispecies model suggests that seedlings are better able to utilize additional nutrients at higher light levels. In their review of interacting above- and below-ground resource constraints, Coomes and Grubb (2000) note that the minimum light availability at which seedlings respond to increased nutrient availability varies among species and is related to both shade tolerance and response to nutrient supply. The light levels in their reviewed studies (2-45% of full daylight) fall within the spectrum of light availability tested in my study.

4.4   Performance by Species

B. crassifolia

B. crassifolia had by far the lowest survival; this is different than the full-sun PRORENA growth trials, where the species achieved moderate to high survivorship (van Breugel et al. 2011). Growth of surviving individuals was strong, however: though it wasn't the largest in absolute measures after 30 months, *B. crassifolia* had the highest RGR of any study species. While the cause of mortality for these seedlings was undetermined, significant foliar damage was observed suggesting that pest and disease may have played a role. Pre-planting seedlings were small and with less woody growth than other species at planting, which could help explain high early mortality but not continued high mortality throughout the study. Additionally, researchers noted prior to planting some trays and individuals showed signs of what appeared to be post-emergence damping-off; seedlings with obvious above-ground signs of disease were avoided but it's possible that below-ground damage was undetected. When collecting root samples from second-year seedlings researchers noted large, unusual galls on *B. crassifolia* roots, further suggesting some type of pest. In addition and to the great inconvenience of sampling crews, defoliation by the highly-venomous caterpillar *Megalopyge opercularis* was observed more frequently on *B. crassifolia* than any other species. Another possible explanation could be seed source: in Panama cultivated *B. crassifolia* is genetically indistinguishable from native populations, likely because there has been little to no artificial selection (Croft 2012). Given this high genetic diversity and phenotypic variability of the species (Correa A. 2010), it's possible that seedlings in this study came from a population that is less vigorous than the species overall.

B. crassifolia is considered to be shade intolerant (Hooper et al. 2002a) and has a lower wood density than my other study species; these characteristics are associated with a syndrome of lower survival but higher growth rate (Ruger et al. 2012), which aligns with what I observed. Given the low shade tolerance of *B. crassifolia*, the relatively weak response to light availability was surprising. In contrast, this species had the highest relative growth response to crowding: Reducing average crowding pressure by half would increase this species' average 30-month BD by an estimated 23% based on coefficient estimates for single-species models. The relatively high proportion of growth variation explained by crowding pressure suggests that a resource other than light may be limiting growth of *B. crassifolia*, which is contrary to expectations given that this species is thought to be

highly drought-tolerant (Torres et al. 2018) and performs best in infertile soils (Hall and Ashton 2016).

D. retusa

The strong growth of *D. retusa* in this study (second highest BD and TB after 30 months) aligns with robust performance in a preliminary enrichment planting trial at the Agua Salud research site (Marshall et al. 2020) and other past observations (i.e. Mayoral et al 2017); in another study comparing *D. retusa* and *T. amazonia* growth under similar full-sun, plantation conditions, *D. retusa* initially outperformed *T. amazonia* but growth slowed considerably after the first two years. This slowdown was not observed in this study: *D. retusa* was the tallest and had the largest TB and second-largest BD after 42-months (*H. alchorneoides* and *P. pinnatum* not included for this final measurement).

Light explained more variation in growth for *D. retusa* (43%) than any other potential predictor for any other species, while crowding explained far less (9%). *D. retusa* performed well despite low fertility and drought conditions in other studies (i.e. Craven et al. 2013; Soderlund 2016; Hall and Ashton 2016), which aligns with my findings that crowding pressure, which reflects competition for belowground resources including water and nutrients, had a relatively small effect. The large response to light availability when separated from other effects of crowding is harder to explain. This contrasts with findings from a preliminary enrichment planting study that *D. retusa* achieved highest growth at intermediate light levels (Marshall et al. 2020). One potential consideration is the branching tendency of this species and the way BD was measured: if there were multiple stems at or below 5 cm height, a single BD measurement was taken below the lowest branching point. This could explain why mean BD was lower for single-stemmed versus multi-stemmed seedlings (p-value=0.001). I hoped that partial shade would improve growth form and indeed found that mean light availability was lower for single-stemmed trees than trees with multiple stems (p-value<0.001), so it's possible that the increased branching with increased light could explain some of the strong positive correlation between light and BD. Height was not related to light availability (p-value=0.13), though interestingly multi-stemmed trees were taller on-average than single-stemmed trees (p-value<0.001).

D. oleifera

D. oleifera performed poorly relative to other species in this study: survival was the second-lowest (after *B. crassifolia*) and growth was far lower than other species. Interestingly there was a positive correlation between growth and survival across plots for *D. oleifera* seedlings (Adj. R^2=0.42, p-value<0.01) but not for any other species (p-values=0.09-0.25); it's possible that both growth and survival were affected by a factor that was not identified in this study, such as a below-ground disease or pest. While *D. oleifera* was by far the smallest after 30 months, in later intervals (18-30 months and 30-42 months) RGR was above-average compared with other species. Given the slow-but-steady growth pattern of this species (Schmidt 2009), low early survival and growth may not be indicative of longer-term performance. This species also has exceptionally high wood density (Tenorio et al. 2016), which is often associated with slower growth (Ruger et al. 2012).

The negative relationship between *D. oleifera* survival and light availability contrasts with previous findings that this species achieves consistent survival across varying light levels (Balderrama and Chazdon 2005). *D. oleifera* was the only species that did not show a significant growth response to either light or crowding, and this contrasts with previous findings. *D. oleifera* is naturally-occurring across a range of light conditions (De Steven 1988; Clark and Clark 1992; Butterfield and Mariano 1995; Schmidt 2009), but a previous study found that growth is maximized at higher light availability (Balderrama and Chazdon 2005). *D. oleifera* responded positively to thinning treatments in single-species plantation trials (Schmidt 2009), suggesting some sensitivity to crowding. It's possible that the growth of *D. oleifera* was strongly affected by an unidentified or unmeasured factor such as disease or moisture availability, and therefore the effects of the predictors considered in this study were less evident.

H. alchorneoides

This species achieved by far the highest growth in all final values at 30 months of growth, though did not have the highest RGR. This aligns with strong performance in previous studies and, more generally, the rapid early growth strategy of emergent species (Butterfield and Mariano 1995; Balderrama and Chazdon 2005; Hall and Ashton 2016). Additionally, *H. alchorneoides* seedlings were the largest on-average at planting, which is known to strongly benefit early establishment and growth (Riikonen and Luoranen 2018). While *H. alchorneoides* is considered to have dense wood (Roque and Leandro 2009), it was on the lower end of these study species (all selected for especially

high-value timber) and the relatively higher initial growth aligns with this ranking given that denser wood is often associated with slower growth (Ruger et al. 2012).

The negative relationship between light availability and survival for *H. alchorneoides* contrasts with findings from a previous study in Costa Rica (Balderrama and Chazdon 2005) that survival for this species increased at higher light levels. In another Costa Rican study, *H. alchorneoides* achieved consistently high survival across a spectrum of shade conditions including mature forest (Piotto 2007). *H. alchorneoides* was the most affected by crowding: this explained 10% of BD growth variation and reducing average crowding pressure by half would increase average 30-month BD by an estimated 20%. In contrast, the effect of light availability was not significant. Lack of light response is consistent with a previous study in Costa Rica in which *H. alchorneoides* was the only species capable of sustaining growth as an enrichment planting in mature forest conditions and achieved consistently high growth in pasture, secondary and mature forest (Piotto 2007). However, a different Costa Rican study found the opposite: *H. alchorneoides* growth was strongly affected by light availability (Balderrama and Chazdon 2005).

P. pinnatum

P. pinnatum achieved the highest survival of any species and slightly above-average growth. High survival aligns with previous findings (Davidson et al. 2002; Hall and Ashton 2016). The exceptionally dense wood of this species (Klitgaard 2005) means that biomass accumulation is higher than for similarly-sized trees of other species. Given that high wood density is associated with lower intrinsic growth rate (Ruger et al. 2012), it's impressive that this species achieved higher-than-average growth

P. pinnatum growth was more strongly related to light availability than crowding, which was not entirely expected given this species is considered shade-tolerant (Davidson et al. 2002; Klitgaard 2005). Interestingly, in the full-sun comparison site, five of the six species had lower survival but higher growth while *P. pinnatum* was the exception in both cases: survival was 2% higher and growth was the same for full-sun versus enrichment planting seedlings.

T. amazonia

The relatively unremarkable performance of *T. amazonia* is in itself remarkable given the standout performance of this species in prior studies. Survival was relatively high but *T. amazonia* growth was below-average for all measures compared to other study species. Importantly, though, other

studies have noted a rapid increase in growth rates after the initial 2 years (Craven et al. 2011; Sinacore et al. 2019). Even 42-months post-planting, however, *T. amazonia* growth was still below average for all species in my study.

The lack of a significant relationship between *T. amazonia* growth and light availability was especially surprising given that the leaf traits and natural distribution of this species are typical of a more light-demanding species (Craven et al. 2011). This is also different than preliminary enrichment planting results from Marshall et al (2020) that show a positive relationship between light availability and *T. amazonia* growth. Previous research suggests that this species, while a strong competitor, is also sensitive to competitive pressure (Montero et al. 2003; Craven et al. 2009; Mayoral et al. 2017), but my results don't support this: The negative effects of crowding on *T. amazonia* growth were slight, similar to *P. pinnatum, D. retusa,* and *H. alchorneoides.* Given that early growth is not indicative of longer-term trends for this species, it's possible that the effects of light and crowding are not yet apparent for this species but will become more pronounced over time.

4.5 Conclusion

Results from this study provide critical information for land managers in need of an alternative to the largely unprofitable teak plantations that dominate the PCW (Stefanski et al. 2015) and other areas of the globe. My hope is that these findings support increased integration of culturally, ecologically, and in some cases even economically valuable native species into PCW FLR efforts, thereby encouraging much-needed community participation (Oestreicher et al. 2009). Findings are broadly relevant, even outside the region, for informing the increasingly-popular but under-researched strategy of enrichment planting and the use of native species in FLR efforts (Paquette et al. 2006a; Redondo-Brenes and Montagnini 2006; Hall et al. 2011a, a; Messier et al. 2021). Specifically, understanding enrichment planting dynamics in the early growth period is especially important given that teak (as is often the case with overstory species) are faster-growing and will be harvested prior to the maturation of enrichment planting species. However, while my findings are valuable for the management of early enrichment planting projects, longer-term studies are needed to assess how older, larger trees may respond to growing conditions and fertilizer, and how responses and overall performance vary among-species differences in performance. Additional studies are also necessary to understand the effect of planting year and pre-planting growing conditions. Each species in my study was assessed for a single planting and from planting stock grown by one nursery (though from varied genetic sources); year-to-year weather variation and nursery conditions are important factors that

42

may affect performance. These studies are critical for silvicultural guidelines for species with diverse values, such as those selected for this study, and should continue to be a high priority for researchers seeking to inform FLR management in the PCW and elsewhere.

Additionally, this research provides insight into more basic ecological questions related to biotic interactions among forest trees. For example, effects of crowding pressure were not captured by aboveground dynamics (variation in light) alone: some species responded more strongly to just the aboveground effect of light availability, whereas others were most affected by the combined above- and belowground effects captured in my estimate of crowding pressure. My study did not disentangle belowground competition for water and soil nutrients, and exploring these dynamics is a valuable area of future research for informing enrichment planting management.

The finding that higher phosphorus affinity was generally predictive of positive fertilizer response for my species (except for *T. amazonia*) aligns with the idea that phosphorus is the most limiting nutrient in tropical soils (Hedin et al. 2009) and a major shaping force of these forest communities (Condit et al. 2013; Zalamea et al. 2016). It will be interesting to see whether the early benefits of fertilization continue as trees mature, though even the initial positive response is an important finding for successful management of FLR projects (Charles et al. 2018; Craven et al. 2009). Longer-term measurements will give a better picture of how enrichment planting affects the financial profitability of teak plantations, as well as ecological effects of the resulting increased biodiversity.

5   Bibliography

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6   Supplementary Materials

Supplementary Table 1

Pre-planting measurements were collected for 10 representative seedlings of each enrichment planting species. Stem length (cm) was measured from root collar to farthest extent of main photosynthetic tissue) and root collar diameter (mm) is the average of 2 measurements taken opposite one another with digital calipers. To assess total dry biomass (g), 10 individuals of each species were harvested and cleaned, and all plant parts (above- and belowground) were dried and weighed.

Species	n	Stem Length (cm)	Root collar (mm)	Dry biomass (g)
B. crassifolia	10	31.74	3.88	1.08
D. oleifera	10	35.34	3.92	1.51
D. retusa	10	34.26	3.71	3.28
H. alchorneoides	10	35.52	4.42	5.26
P. pinnatum	10	35.92	4.26	1.92
T. amazonia	10	35.00	4.20	3.99

Means (standard errors) are from plot-level data at 42 months post-planting, measurements and calculations are the same as Table 4 for 30-month data. 42-month measurements are not available for *H. alchorneoides* or *P. pinnatum* because of later planting date. Both control and treatment fertilization groups for each species are displayed here on separate rows.

Species	Fertilization	n	BD(cm)	Height(m)	TB(kg)
B. crassifolia	Control	20	3.72(0.26)	1.62(0.13)	10.68(1.39)
B. crassifolia	Treatment	16	4.03(0.31)	1.80(0.15)	12.52(1.64)
D. retusa	Control	22	3.67(0.20)	2.34(0.13)	11.92(1.14)
D. retusa	Treatment	22	3.88(0.16)	2.60(0.12)	12.96(0.89)
D. oleifera	Control	22	2.20(0.17)	1.62(0.17)	5.3(0.71)
D. oleifera	Treatment	22	2.55(0.24)	1.85(0.22)	7.4(1.01)
T. amazonia	Control	22	2.66(0.11)	1.77(0.07)	5.96(0.5)
T. amazonia	Treatment	23	3.08(0.13)	2.12(0.10)	7.85(0.62)
Overall	**Control**	**86**	**3.05(0.09)**	**1.85(0.06)**	**8.42(0.47)**
Overall	**Treatment**	**83**	**3.34(0.09)**	**2.12(0.07)**	**9.99(0.47)**

Supplementary Table 3

Multispecies LMMs were constructed to consider the effects of either crowding or light availability on enrichment planting growth for all species together; these models were constructed similarly to single-species LMMs (Table 5, A and B) and additionally included species as a fixed effect. Fixed effects estimates were calculated for a no-intercept model (no "default" species), whereas an intercept model was used to calculate ICC and marginal/conditional R^2 values.

Predictors	Crowding Pressure			Light Availability		
	Estimates	CI	p	Estimates	CI	p
Spp. [*B. crassifolia*]	3.02	2.54 – 3.50	**<0.001**	1.82	1.16 – 2.49	**<0.001**
Spp. [*D. retusa*]	3.30	2.83 – 3.78	**<0.001**	2.05	1.39 – 2.70	**<0.001**
Spp. [*D. oleifera*]	1.83	1.37 – 2.30	**<0.001**	0.56	-0.09 – 1.22	0.092
Spp. [*H. alchorneoides*]	3.64	3.17 – 4.11	**<0.001**	2.35	1.68 – 3.02	**<0.001**
Spp. [*P. pinnatum*]	3.31	2.82 – 3.80	**<0.001**	2.09	1.43 – 2.74	**<0.001**
Spp. [*T. amazonia*]	2.53	2.04 – 3.02	**<0.001**	1.28	0.63 – 1.92	**<0.001**
Fertilization	0.23	0.04 – 0.42	**0.017**	0.24	0.05 – 0.43	**0.014**
Crowding pressure	-1.54	-2.69 – -0.40	**0.009**			
Light availability				1.65	0.58 – 2.72	**0.003**

Random effect- Planting Area

σ^2	0.53
ICC	0.16
N	6 $_{AREA}$
n	239
Marginal R^2/ Conditional R^2	0.407 / 0.501

Supplementary Table 4

Confidence intervals (CI) for single-species LMM fixed effects estimates (β) were omitted from **Tables 5 A and B** due to space constraints and are presented here for both crowding pressure **(A)** and light availability **(B)** estimates.

4A

Predictors	B. crassifolia β	B. crassifolia CI	D. retusa β	D. retusa CI	D. oleifera β	D. oleifera CI	H.alchorneoides β	H.alchorneoides CI	P. pinnatum β	P. pinnatum CI	T. amazonia β	T. amazonia CI
(Intercept)	3.95	2.95 – 4.94	3.45	2.84 – 4.07	1.43	0.66 – 2.19	4.76	3.17 – 6.35	3.62	2.73 – 4.51	2.45	2.03 – 2.87
Fertilization	0.14	-0.30 – 0.58	0.22	-0.08 – 0.51	0.23	-0.15 – 0.60	-0.02	-0.58 – 0.54	0.52	0.11 – 0.93	0.32	0.09 – 0.56
Crowding pressure	-4.73	-8.13 – -1.33	-2.11	-3.97 – -0.25	0.09	-2.21 – 2.39	-5.38	-9.40 – -1.36	-3.1	-5.94 – -0.33	-1.43	-2.66 – -0.21

4B

Predictors	B. crassifolia β	B. crassifolia CI	D. retusa β	D. retusa CI	D. oleifera β	D. oleifera CI	H.alchorneoides β	H.alchorneoides CI	P. pinnatum β	P. pinnatum CI	T. amazonia β	T. amazonia CI
(Intercept)	1.12	-0.49 – 2.72	0.95	0.19 – 1.72	2.01	0.85 – 3.16	2.82	0.43 – 5.22	1.28	0.22 – 2.34	1.49	0.77 – 2.21
Fertilization	0.22	-0.23 – 0.66	0.26	0.02 – 0.50	0.19	-0.17 – 0.56	-0.05	-0.69 – 0.59	0.63	0.26 – 1.00	0.27	0.03 – 0.51
Light availability	3.21	-0.00 – 6.43	3.77	2.35 – 5.19	-1.12	-3.26 – 1.01	1.09	-2.79 – 4.98	2.85	1.00 – 4.70	1.22	-0.17 – 2.61

## 6.1   Supplementary Table 7

Achieved survival and growth and percent difference of full-sun comparison site versus enrichment planting areas. Means were compared for survival (%) and basal diameter (BD, 30-month, cm) and relative growth rate of BD (RGR, from 6-30 months). Negative percentages indicate mean for full sun was lower.

| Species	Fertilization	Full-sun Survival	Survival % difference	Full-sun BD	BD % difference	Full-sun RGR	RGR % difference
B. crassifolia	Control	0.44	-6%	4.255	61%	0.84	18%
B. crassifolia	Treatment	0.58	49%	3.23	9%	0.77	0%
D. retusa	Control	0.9	-7%	2.995	3%	0.72	33%
D. retusa	Treatment	0.86	-9%	3.702	18%	0.75	32%
D. oleifera	Control	0.53	-27%	2.665	84%	0.82	67%
D. oleifera	Treatment	0.5	-30%	1.906	13%	0.68	26%
H. alchorneoides	Control	0.78	-11%	3.491	2%	0.6	18%
H. alchorneoides	Treatment	0.94	3%	5.047	48%	0.71	37%
P. pinnatum	Control	1	2%	2.746	0%	0.58	7%
P. pinnatum	Treatment	0.94	-4%	2.962	-12%	0.76	21%
T. amazonia	Control	0.9	-2%	2.582	24%	0.56	14%
T. amazonia	Treatment	0.92	-3%	3.189	35%	0.68	28%
Overall	**Control**	**0.76**	**-8%**	**3.12**	**24%**	**0.69**	**28%**
Overall	**Treatment**	**0.79**	**-5%**	**3.34**	**20%**	**0.72**	**22%**

Supplementary Figure 1

A representation of the arrangement of six 12-seedling plots (dotted white lines show borders). In an effort to maximize planting space, the 12-seedling plots were arranged contiguously, with 6-m spacing between seedlings in adjacent plots as well as within plots. Seedlings were most often planted in 3 rows of 4, but due to topography and plot edges, plot shape was frequently irregular.
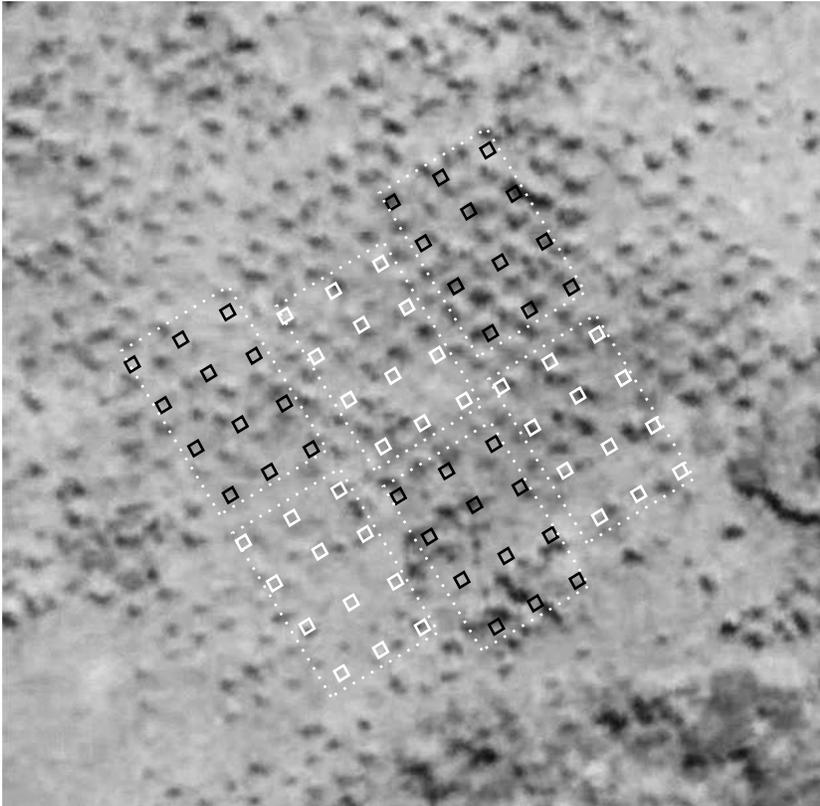
Relationship between plot means of crowding pressure and light availability (transmission coefficient), with separate graphs for each of the 6 planting areas. Across all plots in all planting areas there was a negative relationship between light availability and crowding pressure (Adj R^2 =0.27, p-value<0.01).

Relationship between crowding and light availability
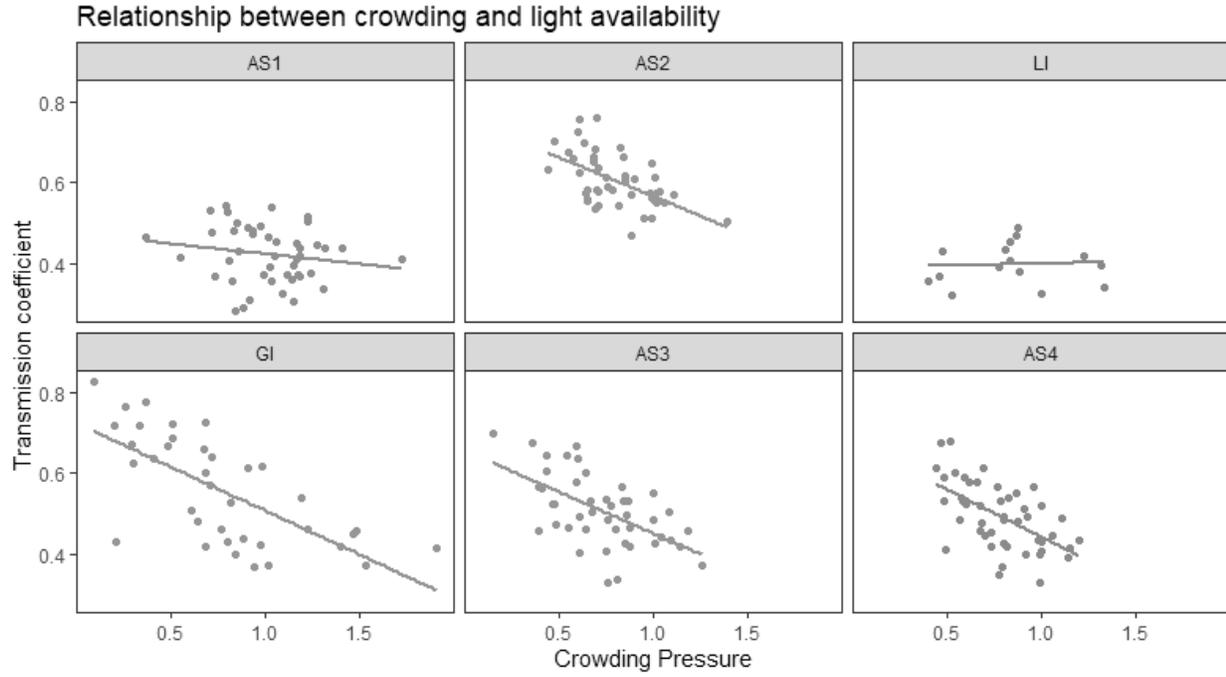
Distribution of enrichment planting basal diameter (30-month, cm) within all planting areas, separated by species. These distributions were used along with other diagnostics to confirm LMM assumptions.
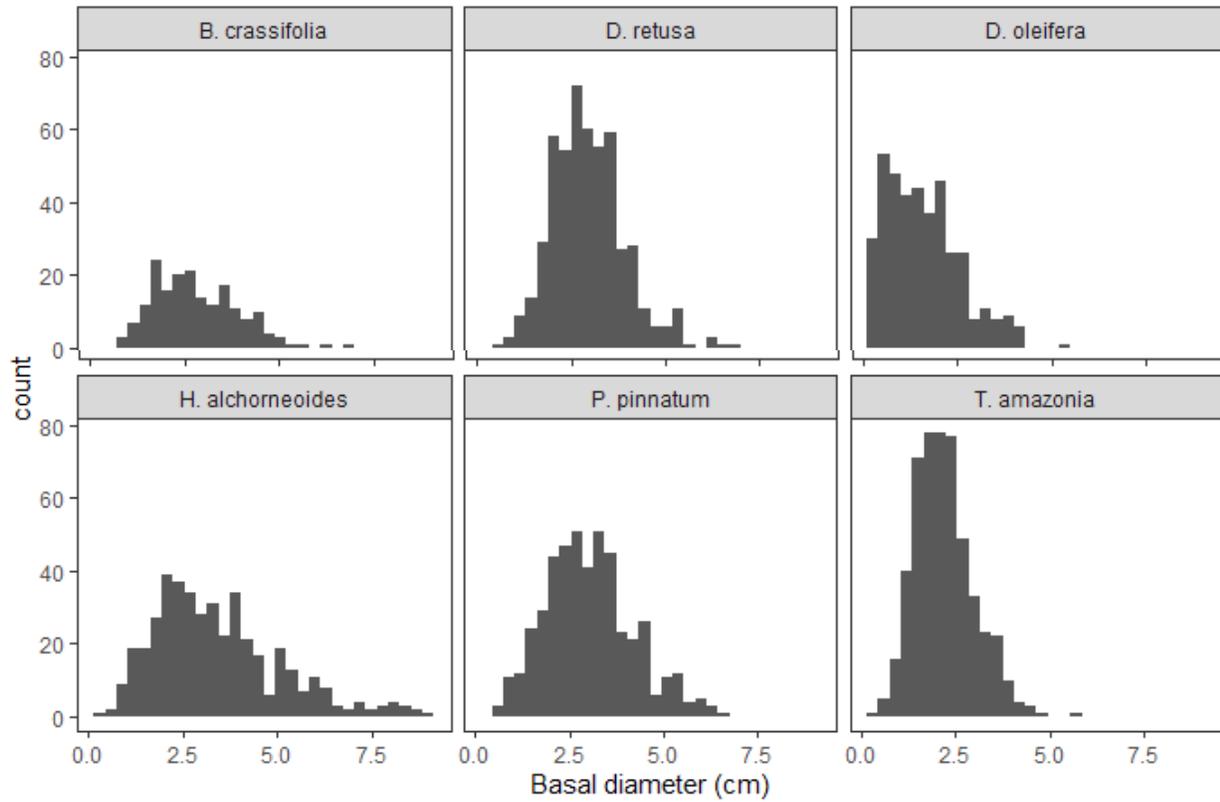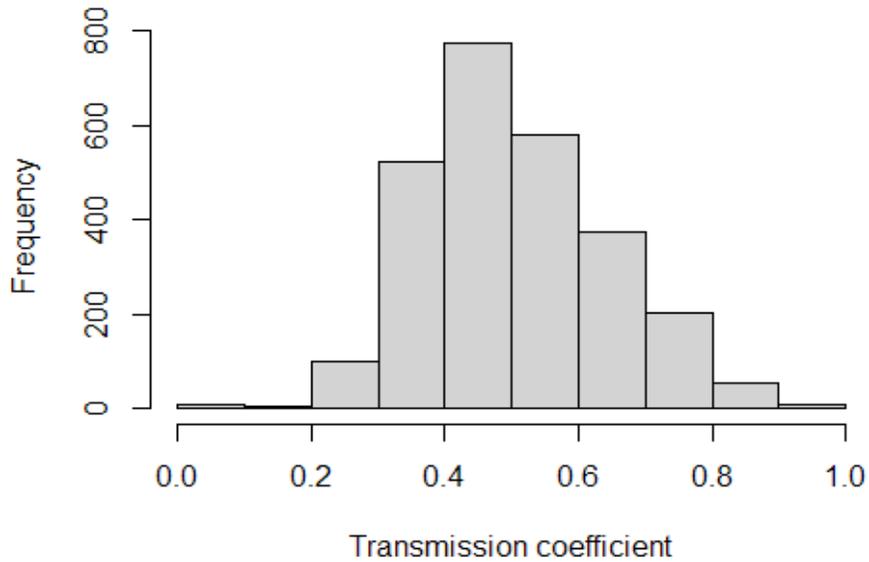
Supplementary Figure 4

Distribution of growing environment measurements of crowding pressure from teak (A) and transmission coefficient (B) within all planting areas.

4A
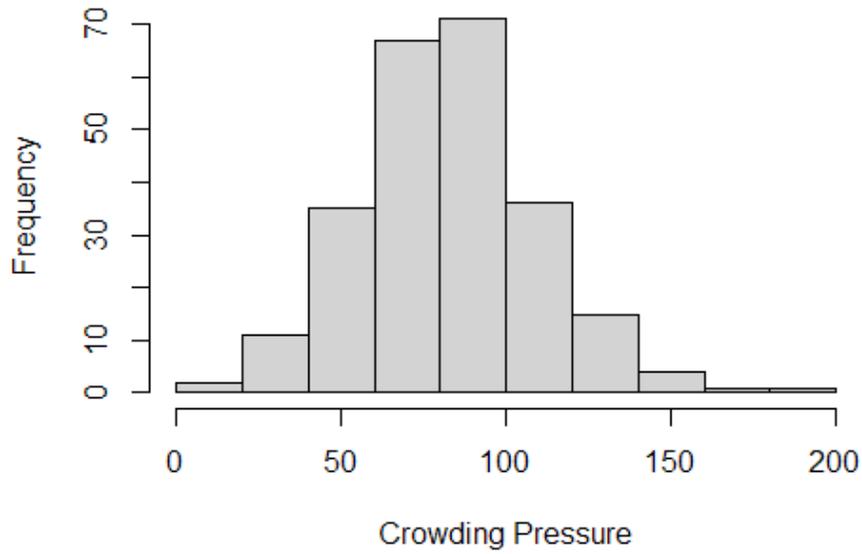
4B

Supplementary Methods

Soil Sampling Protocol

To confirm that soil nutrients and variation among planting areas are representative of the broader PCW, initial sampling was conducted in 2016 prior to the initial fertilizer treatment application. Soils were collected from 71 plots systematically dispersed across each planting area. Within each sampled plot, 5 sub-sample soil cores of the top 15 cm were bulked and analyzed at the Smithsonian Tropical Research Institute soil lab for total C:N, pH, cations and phosphorus using a Mehlich-III extraction **[Supplementary Table 3]**.

Teak Growth

The subplot measurements taken to assess crowding pressure from teak were also used to characterize and compare teak growth among plantations **[Table 2]**. Quadratic mean diameter (QMD) was calculated as

$$QMD = \sqrt{(\sum \quad dbh_i^2/n)}$$

where dbh is the DBH of tree i within 6-m subplots and n is the total number of teak in the subplot.

Replanting Protocol

Due to high early morality, dead *B. crassifolia* seedlings were replanted in November 2016. In 2017, following continued high mortality (28%), dead *B. crassifolia* were not replanted but rather replaced with either *Carapa guianensis* or *H. alchorneoides*. *D. oleifera* seedlings also experienced high mortality (27%) during the 2017 dry season and were replanted with a new batch of *D. oleifera* seedlings in 2017. Less than 30% of replanted *B. crassifolia* seedlings survived to the second growing season and by the 4th year survival was lower than 10%. In contrast, survival of the 2017-planted *D. oleifera* seedlings much higher than the original "batch" (86% after 30 months). All replanted seedlings were noted and excluded from the statistical analysis to minimize the compounding effects of planting year and microsite location. All other species had high early survival and were not replanted.