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VARIATION IN PLANT WATER USE, GROWTH, AND WATER-USE EFFICIENCY OF PLANTED MIXTURES AND MONOCULTURES: TOWARD PROPER SPECIES SELECTION FOR REFORESTATION EFFORTS IN THE SEASONALLY DRY TROPICS

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VARIATION IN PLANT WATER USE, GROWTH, AND WATER-USE EFFICIENCY OF PLANTED MIXTURES AND MONOCULTURES: TOWARD PROPER SPECIES SELECTION FOR REFORESTATION EFFORTS IN THE SEASONALLY DRY TROPICS

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DISSERTATION

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This dissertation has been examined and approved in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Natural Resources and Earth Systems Science by:

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On August 8, 2018

Original approval signatures are on file with the University of New Hampshire Graduate School.

DEDICATION

To Margaret Chanda, from whom I inherited my interest in teaching and to the trees that accompanied me on this journey and reminded me that “nothing is softer or more flexible than water, yet nothing can resist it (Lao Tza)”.

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TABLE OF CONTENTS

LIST OF FIGURES

Figure 1-6. Water use efficiency for each treatment (stand level; WUE_S [kg L^{-1}]). DR monoculture: *D. retusa* monocultures, Mixed: mixed stands, TA monoculture: *T. amazonia* in monocultures. Solid horizontal lines inside boxes correspond to the median and the dashed lines to the mean for all sites. The lower and upper box boundaries correspond to the first and third quartiles. Letters indicate significant differences in average WUE_S based on linear model and lease square means pairwise comparison**.**

Figure 1-7. Leaf-level water use efficiency (WUE, A_{max} / leaf transpiration) for each treatment during dry season 2015. Letters denote significant differences among treatments based on ANOVA and post-hoc Tukey test. DR mono: *D. retusa* trees in monocultures; DR mixed: *D. retusa* trees in mixtures; TA mono: *T. amazonia* in monocultures TA mixed: *T. amazonia* in mixtures.

Figure 1-8. Leaf-level photosynthesis (A_{max}, µmol CO_2 $m^{-2}s^{-1}$) during five different dry season sampling dates for 2015. Error bars represent standard errors of the mean for each treatment and sample date. DR mixture: *D. retusa* trees in mixtures; DR monoculture: *D. retusa* trees in monocultures; TA mixture: *T. amazonia* in mixtures TA monoculture: *T. amazonia* in monocultures.

Figure 1-9. Leaf-level conductance (g_s, mol H_2O $m^{-2}s^{-1}$) during five different dry season sampling dates for 2015. Error bars represent standard errors of the mean for each treatment and sample date. Missing data during March 3rd and March 20th due to *D. retusa* monocultures leaf senescence. Missing data Marc 3rd for *T. amazonia* monocultures due to equipment errors. DR mixture: *D. retusa* trees in mixtures; DR monoculture: *D. retusa* trees in monocultures; TA mixture: *T. amazonia* in mixtures TA monoculture: *T. amazonia* in monocultures.

Figure 2-1. Weekly averages of (a) sap flux density (J_s; $gm^{-2}s^{-1}$), (b) vapor pressure deficit (VPD; kPa), (c) radiation (µmol $m^{-2}s^{-1}$), (d) volumetric water content (VWC, %), and weekly sum of (e) precipitation (mm $week^{-1}$). Colored lines represent averages of individual trees for the four treatments. DR monoculture: *D. retusa* trees in monocultures; DR mixture: *D. retusa* trees in mixtures; TA monoculture: *T. amazonia* in monocultures TA mixture: *T. amazonia* in mixtures. Shaded area represents the dry season. Black horizontal line in (a) signifies the ENSO event. Soil data not available before December 2014.

Figure 2-2. Mean daily sap flux density (J_s) by treatment and water year. Capitalized letters represent significant differences by water year based on ANOVAs and post-hoc Tukey tests ($p < 0.001$) and small letters represent significant differences treatments of the same water year based on ANOVAs and post-hoc Tukey tests ($p < 0.001$). Error bars are standard errors of the mean.

Figure 2-3. Relationship between normalized J_s and (a) vapor pressure deficit (VPD, kPa) and (b) radiation (µmol $m^{-2}s^{-1}$). Lines represent relationship between VPD or radiation and normalized J_s by treatment (DR mixed, *D. retusa* in mixtures; DR monoculture, *D. retusa* in monocultures; TA mixed, *T. amazonia* in mixtures; TA monoculture (*T. amazonia* in monocultures). Significant logarithmic relationship between radiation/VPD and normalized J_s for 2014 only.

Figure 2-4. Hysteresis of normalized sap flux density (J_s) by normalized vapor pressure deficit (VPD) and treatment (top x-axis). For each treatment, hystresis loops divided by water year (normal years: Wet 2014 and Dry 2015; drought years: Wet 2015 and Dry 2016). Clockwise hysteresis occurring during 2014 wet season for all treatments and a counterclockwise figure-eight hysteresis for all treatments in during the 2015 wet season and 2016 dry season. Hourly time stamps for dawn, midday, and dusk included in figure.

Figure 2-5. (a) Diameter at breast height growth from 2014 to 2016 (DBH; cm) versus sap flux density (J_s) by treatment and (b) average DBH_{growth} (cm) for 2014-2016 and 2015-2016 by treatment. Letters (b) represent significant differences by year for each treatment based on ANOVAs and post-hoc Tukey tests. The * below TA mono and TA mixed boxplots in (b) represent significant differences in DBH growth between the two years. Horizontal lines inside the boxes (b) represent the median while the upper and lower box boundaries represent the first and third quartiles. Dots represent points that fall beyond these ranges.

Figure 2-6. Midday water potential (Ψ_L; MPa) by treatment for each year during the dry season. The 2014 and 2015 dry seasons represent normal dry seasons while the 2016 dry season represents a drought dry season. Treatments include: (a) *D. retusa* monocultures, (b) *D. retusa* mixtures, (c) *T. amazonia* monocultures, and (d) *T. amazonia* mixtures. Letters represent significant differences by treatment for each year. Based on ANOVA and post-hock Tukey test. No data available for *Dalbergia retusa* in 2016 because leaves had not fully flushed during sampling campaign.

Figure 2-7. (a) Pre-ENSO Conditions (2014/5 dry season) and (b) ENSO Conditions (2016 dry season) pre-dawn leaf water potential (Ψ_{pd} MPa) and midday leaf water potential (Ψ_{md} MPa). Solid black line represents 1:1 line. Significance of slopes based on linear regression shown by (*): *0.05 significance, ***0.0001 significance. The slope (σ) shown for all treatments during Pre-ENSO Conditions (including TA mono, which was not significant). During the ENSO Conditions, neither *D.* retusa treatment showed a significant relationship between Ψ_{pd} and Ψ_{md}. Values of σ closer to zero represent more isohydric behavior while slopes closer to 1 represent more anisohydric behavior (Martínez-Vilalta et al., 2014). Points represent leaf water potentials for an individual tree. Measurements were taken during the dry season of 2014, 2015, and 2016 every three weeks starting in February and ending in April. *Dalbergia retusa* did not fully flush leaves during the sampling period in 2016 and had minimal leaves in 2015.

Figure 3-1. Time since establishment (or age in years) versus stand volume (m^3ha^{-1}). Stand volume is projected stand volume based on mean annual increment of diameter at breast height and mean annual increment of height of trees in each of the four treatments. Gray shading represents projections while the non-shaded area represents estimates from data. Projections are shown to rotation age. Declines in stand volume signify pre-commercial thinning, commercial thinning, or final harvest.

Figure 3-2. Modeled net present value* [US$ ha^{-1}] function of (a) all treatments by the interest rate [*r*, %] and (b) all treatments by *r* with a varying y-axis. Note the change in y-axis of the treatment plots changes with treatment.

LIST OF TABLES

Table 3-5. Stand transpiration [mm day^{-1}] for four study treatments. Treatments include: *D. retusa*, *T. amazonia*, and *T. grandis* monocultures, and *D. retusa* and *T. amazonia* mixtures.

Table B-1. ANCOVA table of generalized linear model results of mean normalized sap flux density by mean normalized vapor pressure deficit (VPD). Treatment and Water Year included as factors.

Table C-1. Costs per hectare associated with managing each treatment. Costs are broken down by year and include costs of fire protection, pruning, and manual cleaning when applicable.

Table C-2. Actual (gray shading) and modeled (white background) stand development of *Terminalia amazonia* monocultures across projected rotation length (25 years). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

Table C-3. Actual (gray shading) and modeled (white background) stand development of *Dalbergia retusa* monocultures across projected rotation length (30 years). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

Table C-4. Actual (gray shading) and modeled (white background) stand development of *Tectona grandis* across projected rotation length (25 years). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

Table C-5. Actual (gray shading) and modeled (white background) stand development of mixed plots of *T. amazonia* and *D. retusa* across projected rotation length (25 years and 30 years, respectively). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

ABSTRACT

VARIATION IN PLANT WATER USE, GROWTH, AND WATER-USE EFFICIENCY OF PLANTED MIXTURES AND MONOCULTURES: TOWARD PROPER SPECIES SELECTION FOR REFORESTATION EFFORTS IN THE SEASONALLY DRY TROPICS

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In recent years, there has been a trend towards reforesting previously degraded areas by planting trees. While plantations offer an opportunity to restore ecosystem functions and diversity, most reforested plantations currently consist of monocultures, or single-species systems. Originally planted to provide wood for both global and regional markets, monocultures provide only a few goods and services and reduce plant biodiversity in comparison to multi-species systems, like forests. An alternative to the current plantation design is planting mixed species systems that not only diversify a plantation, but provide an opportunity to enhance ecosystem services that include non-timber forest products, carbon sequestration, and increased

soil fertility. There is also evidence that mixed species stands tend to be more resilient to disturbances and climate change than monocultures.

Both anthropogenic and environmental stresses put pressure on tropical forests. Plantations, however, provide a means of decreasing anthropogenic pressures on forests by providing timber products, among other goods and services. Despite the increase in popularity of plantations, research still does not fully understand how certain plantation species might affect resource use (i.e., nutrient abundance and water quantity). While a growing body of research has begun to include studies on how resource use might change when species are planted in monocultures and mixtures, additional research is needed in areas where soils are severely degraded. In the seasonally dry tropics of Panama, how species in monocultures and simplified mixed species systems respond to changes in water availability is also of importance because survival of the dry season is central to the longevity of the species and the stand.

In Panama, the Agua Salud Project offers a unique opportunity to explore the dynamics of reforested areas that were previously degraded, with a specific emphasis on understanding ecosystem services provided by forests and how these services change with land use change. Like most deforested areas, the Agua Salud Project plantations are planted on sub-marginal lands with poor soil. In 2008, native species plantations were established in two blocks which had previously been cleared 40 years before. The spatial arrangement of the species in the mixed species stands allows for isolation of interactions between species so we can test both interspecific interactions and how species strategies vary in monocultures and simplified mixed systems. Understanding the link between species diversity and water use dynamics is a crucial first step toward proper selection of species that balance the tradeoffs between growth and transpiration.

In addition to selecting species that regulate water well in this region, choosing species that are economically valuable in such a way that they can compete financially with the commonly planted non-native *Tectona grandis* (teak), is necessary to transition away from planting non-natives and towards planting native species. In addition to ecophysiological characteristics of these species when planted in different combinations, we provide information about how the native species will compete financially against teak and whether mixtures or monocultures are more lucrative operationally.

INTRODUCTION

High global rates of tropical deforestation are increasingly being countered by the establishment of new forested areas through tree planting (FAO, 2001). This trend provides a unique opportunity to restore many of the critical ecosystem services and functions that have diminished as a result of past land uses (i.e., agriculture and cattle herding practices) (Hall et al., 2011). Historically, the majority of forest plantations have involved single species; for example, in Latin America, monocultures represent nearly 99% of all planted lands prior to 2004 (Evans and Turnbull, 2006). Although these single-species plantations can be highly productive, they provide limited goods and services (Plath et al., 2011), reduce plant biodiversity (Healy et al., 2008), and may negatively affect soil quality (Lamb et al., 2005; Wishnie et al., 2007). However, recent years have witnessed a growing emphasis on planting mixed species systems, a trend that is expected to continue and intensify in the near future as the benefits of mixed species over monocultures is further recognized (Ashton and Ducey, 1996; Lamb et al., 2005; Paquette and Messier, 2010).

A primary motivation for promoting mixed-species plantings world-wide is the provision of multiple ecosystem services beyond wood and fiber, including carbon sequestration (Erskine et al., 2006; Montagnini, 2000), enhanced soil fertility (Bauhus et al., 2000), and improved water supply (Munoz-Pina et al., 2008). Plantations of native species have the potential to become popular on degraded lands where cattle ranching and agriculture do not provide much economic value or where non-native tree species have performed poorly. However, one tradeoff with planting trees instead of using the land for these purposes is that trees require greater quantities of water than short stature vegetation types (i.e., grasslands, pasture, and crops). This can be potentially detrimental in an area like the Panama Canal Watershed (PCW) during the dry season, when water resources are limited. For example, in 1998, a strong El Niño caused water levels in the Panama Canal to fall six meters below the normal level. As a result, The Panama Canal Authority (ACP; Spanish acronym) imposed draft restrictions, forcing some shipping companies that could not lighten their loads to reroute vessels through the Suez Canal or to use train routes across the United States. In contrast, during the wet season, severe flooding during storm events can suspend boat transit through the Panama Canal. In 2010 a storm dropped 760 millimeters of rain in one day in the upper Chagres River (the main river that feeds the Panama Canal), causing areas around the Panama Canal to flood. For only the fourth time in 100 years of the canal, the operation suspended ship transit and opened the locks to ease runoff (Robert Stallard, personal communication, March 2015). Even though the PCW faces significant changes in water abundance throughout the year, certain land uses can enhance regulation of hydrologic flows that may ease extreme water fluctuations. Agua Salud Project researchers have found that dry season runoff from a forested catchment receded more slowly than that of a pasture catchment and that peak runoff rates from the pasture were 1.7 times greater than those of the forest catchment (Ogden et al., 2013). This "sponge-effect" theory (whereby forested areas absorb water in the wet season and supply water in the dry season) provides an important rationale for conserving and expanding forested lands around the PCW to help prevent too little or too much water from affecting the Panama Canal operations.

Roughly 46,500 hectares of secondary forests exist within the buffer zone of the Panama Canal (URS Holdings, 2007) and the area of tree cover has been increasing as land conversion from pasture to plantation increases (ACP, 2014). This conversion could help turn land into "sponge-like" forested mosaics, but evidence of the sponge-effect of plantations is poorly understood. However, evidence suggests that planting trees in mixtures (as opposed to monocultures, which are more typical due to easier management) will enhance overall growth, or net primary productivity (NPP), through complementary and facilitative interactions (Erskine et al., 2006), while also providing important hydrological regulation. However, one study of native species in Panama did not find differences in sapling height nor stem diameter between two-year-old monocultures and mixed plantations (Plath et al., 2011), but these stems were not yet interacting aboveground and so the effect of complementary interactions between species is likely underrepresnted. In contrast, a second study in Australia examining acacias and eucalypts planted in monocultures and mixtures 9.5 years old, found stand-level tree biomass was highest in mixed plots (Bauhus et al., 2004), which was attributed to species' interactions. Bauahus et al., (2004) suggested that complementary interactions through diversity of canopy structure, leaf phenology, and light acquisition, can be selected to intentionally increase NPP. For example, canopy architectural diversity in mixed species plots where canopy stratification exists can increase light interception by different trees species and enhance NPP of the stand (Menalled et al., 1998, Stenberg et al., 1994). Alternatively, trees that drop leaves and flush asynchronously reduce competition for light and growing space which can also increase NPP (Kozlowski et al., 1991). Aside from complementary interactions, facilitative interactions such as those provided by nitrogen fixing trees can increase NPP at the tree- and stand-level through increases in nitrogen availability to non-fixing trees. A study by Batterman et al., (2013a) showed that in secondary tropical forests, nitrogen-fixing trees were extensive and returned nitrogen to the soil that was then available to neighboring trees. Increased nitrogen, along with other key nutrients in the soils has the potential to enhance tree growth (Richards et al., 2010; Russo et al., 2008). Thus, trees planted together with ecological traits that result in complementary and/or facilitative interactions, can promote stands that are more productive than their monoculture counterparts.

However, studies have also shown that highly productive trees use more water (Law et al., 2002; Zhang et al., 2004). This may pose a problem during the dry season, when the PCW receives less than 400 millimeters of precipitation during a four-month period and both the Panama Canal and local communities compete for freshwater resources. However, highly productive trees could use similar or reduced quantities of water for the same level of NPP if complementary and facilitative interactions exist such that water-use efficiency (WUE, i.e., the amount of carbon gained per water loss) is greater. This is possible when a species accumulates more nitrogen (N) in its leaves for a given transpiration rate and thus is able to have higher photosynthetic capacity and a higher leaf-level photosynthetic water-use efficiency (Cernusak and Aranda, 2007). Trees that are N-fixers or trees that grow adjacent to N-fixers, can potentially maintain higher NPP and water-use efficiency compared to trees that are not N-fixers or are not surrounded by N-fixers.

Trees face a constant tradeoff between CO_2 uptake and water loss so finding species or a combination of species that maximize CO_2 uptake and minimize water loss is a challenge. Trees that are water-use efficient find an optimum efficiency whereby stomatal aperture varies during the day in a manner that minimizes transpiration and maximizes photosynthesis (Kozlowski et al., 1991). In general, trees that are not water-use efficient will often maintain the stomata open, releasing water, and respond slowly to extended dry periods. Trees that are water-use efficient have greater stomatal control and will close their stomata during periods of extreme dryness, typically experiencing less water stress (Laio et al., 2001). Although trees grown in climates that face dry periods are adapted to survive these conditions, climate projections suggest greater intensity and duration of droughts to which these plants may not be well adapted. However, there is some evidence that mixtures that combine species with complementary interactions may be more water-use efficient than monoculture counterparts and thus more able to be resilisent to extreme dry conditions. Combining an N-fixer with a species that does not fix N might allow the non-fixer to maintain higher levels of photosynthesis per unit water lost (Bunce et al., 1977).

One challenge we face is finding a balance between restoring degraded lands to productivity while also maintaining water reservoirs during the dry season and flood mitigation services during the wet season. Although research exists at the watershed scale related to land use and the “sponge-effect”, a major knowledge gap exists in understanding the quantity of water planted trees use in both wet and dry seasons and whether this quantity is altered through careful planting designs and species selections.

Further, a second knowledge gap exists in the management of productive native species plantations and the differences between monoculture and mixed stands. This disconnect is conspicuous as we see that *Tectona grandis* plantations (known commonly as teak, a valuable non-native timber species) are still abundant and make up 90% of plantations in Panama alone even though teak requires substantial amounts of water and nutrients to be productive (Griess and Knoke, 2011) and often is ill adapted to the low nutrient soils that exist in the PWC. A few studies have shown that teak does not grow as well as other native species, such as *Terminalia amazonia*, nor is it as economically valuable as another native species, *Dalbergia retusa* (Griess and Knoke, 2011; Piotto, 2008), yet adaptation of native species plantations is slow. It is important to fill this knowledge gap through research that examines how growth of native species compares to that of a popular planted exotic species.

A third knowledge gap exists in understanding the value of planting teak monocultures versus monocultures or mixtures of native species on low-nutrient soils. Research has shown that teak grown on nutrient poor soils in Panama delays rotation length until 30 years, whereas a typical rotation on good soils is 15 years (Chaturvedi and Raghubanshi, 2015). Further, little research has assessed the economic value of two native species, *T. amazonia* and *D. retusa*, planted in mixtures. While a push toward a multi-species plantation exists, little is understood about whether a multi-species plantation can exceed the financial benefits of their monoculture counterparts. Here, we look at these questions and focus on the non-native to native species comparison and whether plantation design can enhance the net present value of a species.

My overarching questions are: *Can planting design (monocultures versus two-species mixtures) of native tree species be used to restore ecological processes in degraded lands and what are the subsequent trade-offs between wood production, C sequestration, transpiration, and hydrologic regulation. How does species vary in their physiological responses to drought? Can native species be economically as viable as non-native species and does plantation design affect financial viability of native species.* The dissertation that follows is divided into three chapters:

- Chapter 1 – Carbon and water tradeoffs: Are mixed-species plantations more water-use efficient than monocultures?
- Chapter 2 – Effects of El Niño on tree water use responses and water stress: Do complementary interactions in mixed species tree plantations enhance resistance to drought over monocultures?
- Chapter 3 – Can planted native tree species compete with teak plantations financially and in terms of both carbon sequestration and water regulation?

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CHAPTER 1

CARBON AND WATER TRADEOFFS: ARE MIXED-SPECIES PLANTATIONS MORE WATER-USE EFFICIENT THAN MONOCULTURES?

ABSTRACT

Evidence that certain mixed species plantings are more productive than monocultures is well documented in the literature. Less attention has been paid to assessing the tradeoff between carbon acquisition and water loss, although research designs are increasingly including this aspect, as it is critically important for selecting species in reforestation areas that experience water deficits in order to maximize growth and minimize transpiration. We selected two species (*Terminalia amazonia* and *Dalbergia retusa*) planted in mixtures and monocultures located in central Panama to assess the effect of mixing species on growth, water use, and water-use efficiency. We also explored the effect climate variables and soil volumetric water content (VWC) have on sap flux density (J_s) in different treatments and the underlying mechanism acting at the leaf and tree levels. Although mixtures overyielded compared to monocultures, this effect was not significant. Mean stand-level transpiration (E), however, was significantly greater ($p < 0.0001$) in *T. amazonia* monocultures (3.5 mm day^{-1}) than mixtures (1.5 mm day^{-1}) or *D. retusa* monocultures (0.2 mm day^{-1}). *Dalbergia retusa* monocultures had the highest stand-level water use efficiency (WUE_S), followed by mixtures and *T. amazonia* monocultures. Even though we found that *T. amazonia* had significantly greater Q and leaf-level WUE than *D. retusa*, no significant differences in tree-level Q or tree WUE (WUE_T) between treatments of the same species was found. In the monocultures, radiation was the strongest predictor of J_s during the wet season, but transitioned during the dry season to VWC and VPD for *D.* retusa and *T. amazonia*, respectively. Vapor pressure deficit (VPD) was the strongest predictor of J_s for *D. retusa* in the mixtures (0.71-0.93) while a combination of VPD and radiation was the strongest predictor of J_s for *T. amazonia* in the mixtures. These findings provide new insights into relationships between carbon and water tradeoffs in monocultures and mixtures and provide useful information for species selection for reforestation initiatives geared toward maximizing the benefit of carbon sequestration and water regulation. However, our results show that species selection matters and that the dominance of one tree species might override the complementary interactions that would otherwise increase WUE in mixtures.

1.1 INTRODUCTION

Concerns over deforestation and climate change, in addition to international agreements, have propelled efforts to promote tree planting globally and encouraged reforestation on degraded lands to improve ecosystem services (Chazdon, 2003; Paquette et al., 2018). However, reforestation initiatives typically focus primarily on marginal lands with low soil fertility and high soil compaction, where natural regeneration processes are slow (Paul et al., 2015). Historically, many landowners in Central America have planted monocultures of *Tectona grandis* (teak) for timber production (Evans and Turnbull, 2006). In Panama, it is estimated that there are 55,000 ha of planted teak (Kollert and Chrubini, 2012) despite teak being poorly adapted to the infertile and acidic clay soils found across most of the country (Calder, 2002; Hase and Foelster, 1983). For these reasons, there is a growing interest in exploring the use of native species that are productive in the marginal lands where teak is commonly planted. Two species of important timber value and proven to grow well on relatively infertile soils are *Terminalia amazonia* and *Dalbergia retusa* (Mayoral et al., 2017).

In the past, monocultures have been favored over mixed-species stands for both restoration and timber production due to their greater management simplicity and (assumed) greater productivity (Nichols et al., 2006). In recent decades, however, evidence has emerged to suggest that mixed plantings may be more productive than monocultures (Montagnini, 2000; Piotto, 2008), providing a benefit that might offset the added challenges of mixed planting management. Not all studies have found enhanced productivity in mixtures (Chen et al., 2016; Underwood et al., 2014). Some studies have even found mixed results, as seen in a review of over 18 different species combinations in Panama (Mayoral et al., 2017). These conflicting findings suggest that greater information is needed regarding the optimization of favorable interspecific interactions (Loreau et al., 2001; Menalled et al., 1998; Trenbath, 1974) and a greater understanding regarding the mechansims that affect positive or negative interactions between species. While information regarding species' ecological requirements when planted in monocultures exists (Hall and Ashton, 2016), less is known about the interactions among species or subsequent individual species' productive capacity when planted in mixtures.

Hypothesized greater growth rates and productivity of native mixtures (or even native monocultures that are more productive than non-native alternatives) also raise concerns about potential unintended (and often negative) consequences for water resources (Bruijnzeel, 2004; Jackson et al., 2009). A case for promoting mixtures over monoculture plantings is based in the fundamental hypothesis that mixed, or more diverse systems, that include species with complementary adaptive strategies of contrasting functional traits, can increase resource use and/or efficiency (Binkley et al., 2004). Increased resource use efficiency or resource use in mixtures would theoretically support greater productivity, or overyielding (Ewel et al., 2015; Mayoral et al., 2017), which occurs when production in mixtures exceeds predictions based on monocultures yields of the component species (Hooper and Dukes, 2004). However, greater productivity can lead to greater water use by individual trees (Law et al., 2002) when increased growth is associated with increased sapwood area to transport water. For this reason, increased stand level transpiration (*T*) is also possible in mixed stands, especially if species have complementary functional traits such as different water uptake strategies due to root partitioning, or different leaf phenologies, allowing for a temporal partitioning of light acquisition (Ewel et al., 2015) and/or water uptake (Forrester et al, 2010). A reduction in competition for resources in complementary mixed stands can lead to overall greater resource use, however, strong facilitative interactions (i.e., nitrogen fixing) between species in mixtures can also lead to greater water-use efficiency (WUE), whereby units of carbon gained per units of water loss are greater (Forrester et al., 2010). This can be achieved by inclusion of nitrogen (N) fixing species in mixed plantings, as N-fixers can increase soil N availability and leaf-level N concentrations for non-N fixers, thereby increasing instantaneous leaf water use efficiency (WUE_L) due to increased photosynthetic capacity without increases in transpiration (Cardinale et al., 2002; Craven et al., 2011, 2007; Forrester and Bauhus, 2016). Craven et al., (2013) used carbon isotope methods for native species in Panama further showed that WUE can increase in more water stressed sites, but this was found in a common garden experiment on very young trees. Notwithstanding, there is still uncertainty whether complementary interactions among species with different functional traits will result in shifts in WUE in mixtures and monocultures.

Mixing species can also enhance growth by creating more favorable microclimates due to canopy stratification. For example, a species that is partially shaded during the hottest or driest part of the day or year, might be able to maintain higher levels of transpiration compared to trees whose canopies are in direct sunlight where radiation intensity might force stomatal closure. Other studies have shown that VPD can be a strong predictor of tree water use (Q) or sap flux density (J_s) in plantations (Alvarado-Barrientos et al., 2014), but radiation, volumetric water content (VWC), and precipitation likely drive some patterns of J_s, depending on a combination of canopy position, site characteristics, and neighboring species.

Our work focuses on two native timber species, *Terminalia amazonia* and *Dalbergia retusa*, planted in monocultures and two-species mixtures (hereafter; mixtures) at the Agua Salud study site in Panama (Mayoral et al., 2017). These species were specifically selected for their contrasting functional traits. While both are long lived pioneers (LLP), *D. retusa* is dry season semi-deciduous, a N-fixer, sends lateral roots, and has high leaf water-use efficiency (WUE_L) (Cernusak and Aranda, 2007). In contrast, *T. amazonia* is evergreen, sends both lateral and deeper roots, and has high transpiration rates (Kunert et al., 2010). Of the two species, *T. amazonia* has significantly higher growth rate than *D. retusa*. After only seven years of growth, mean height of *T. amazonia* was 10.0 m while *D. retusa* was 5.0 m (Mayoral et al., 2017). These contrasting traits make these two species ideal for exploring the potential to enhance complementary interactions that enhance growth, water use, and water-use efficiency in mixtures versus monocultures.

The objective of this study was to determine whether mixing species with complementary functional traits could achieve increased stand level productivity, total water use, and WUE compared to monocultures. Additionally, we sought to understand the underlying mechanisms and interactions at the tree and leaf levels to explain stand level responses. Specifically, we test the following three hypotheses:

(1) Complementary interactions in more diverse stands lead to higher growth, water use, and WUE.
(2) At the tree and leaf level, both species will exhibit increased increment growth, water use, and WUE in mixtures compared to monocultures.
(3) Daily J_s will be driven by changes in VPD and radiation over changes in soil moisture for monocultures, where canopy-atmosphere coupling is high and driven by VWC (or precipitation) in mixtures where canopy-atmosphere coupling is lower.

1.2 METHODS

1.2.1 Site Description

The study was conducted in the Agua Salud Project site within the Panama Canal Watershed (9°13’ N, 79°47’W, 330 m amsl). Our work focused on the 114 hectares (ha) native species plantation that was established in 2008 in two separate blocks 3 km distant from each other. Although the plantation has a total of 21 treatments, we focus on 3 treatments – monocultures of *Dalbergia retusa*, monocultures of *Terminalia amazonia*, and two-species mixtures of *D. retusa* and *T. amazonia*. These treatments were selected primarily because *D. retusa* and *T. amazonia* have contrasting functional traits related to water, nutrient, and light acquisition that would enable us to test our hypotheses regarding complementary interactions, while we were also limited to a single study system due to logistical and equipment constraints. Sap flow measurements are costly and labor intensive, which constrained our study design and required us to prioritize the three treatments that would best enable us to test our hypotheses and make broader generalizations related to growth, water use, and WUE of monocultures and mixed plantings. Prior to plantation establishment, the land was cleared of forest in the 1970s with the predominant land use being cattle grazing (Weber and Hall, 2009). The topography is characterized by short and steep slopes (Hassler et al., 2011) and the soils are silt clay to clay with pH values of 4.67 ± 0.27 (in $CaCl_2$) and 5.8 ± 0.23 (in H_20) (Mayoral et al., in review). Mean daily maximum and minimum temperatures are 32 and 23°C, respectively (http://striweb.si.edu/esp/physical_monitoring/descrip_bci.htm).

Plots of monocultures of *D. retusa* (n = 12), monocultures of *T. amazonia* (n = 11), and mixtures of both species (n = 13) at six years of age were randomly distributed across two blocks. Within each plot, trees were planted in 42 x 36.5 m plots of 15 x 15 individuals. Measurements were taken in the core plot comprised of 9 x 9 trees (27 x 23.4 m). Mixtures were established in a spatially explicit design that isolates interactions between individual trees of different species, whereby individuals of *D. retusa* was completed surrounded by an individual of *T. amazonia* in a hexagon configuration and vice versa (Figure 1-1). Trees planted within the same row have 3 m spacing, while trees between rows have 2.6 m spacing. This novel planting design enabled us to test interactions between two species (for more details, see Mayoral et al., 2017). Since tree establishment in 2008, four yearly understory cleanings occurred from May through August to prevent additional competition with the planted trees.

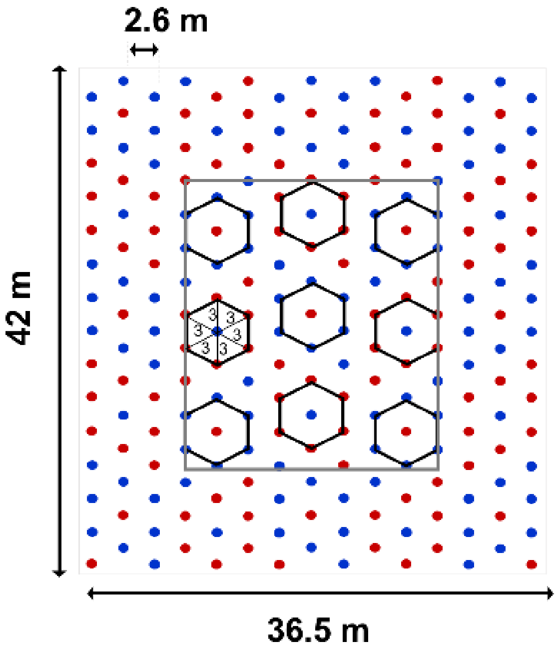

Figure 1-1. Spatial planting pattern of the two target species combinations, including trees of both species with heterospecific neighbors, indicated by the points within dashed lines. Monoculture plots with each species not shown. Each plot consists of 15 x 15 trees (42 x 36.5m), and includes a buffer zone of three rows around a core plot of 9 x 9 trees (27 x 23.4 m; central rectangle).

1.2.2 Sampling design

The sampling was designed to estimate water use and growth and physiological responses of monocultures and mixtures of *D. retusa* and *T. amazonia*. Between June and August of 2014 and 2015, the height (m) and diameter at breast height (DBH, cm, measured 1.3 m above ground) of all trees (n = 2916) within the core of the study plots were measured (hereafter referred to as plantation trees).

In February 2014, we established subplots within a subset of the monocultures and mixtures to measure sap flow in selected trees (hereafter referred to as sap flow trees) (Table 1-1). We selected seven subplots for the study, two within monocultures of *D. retusa*, two within monocultures of *T. amazonia*, and three within mixtures distributed across the two study blocks, that best represented the mean DBH across all plots. In June 2014, we added a fourth subplot in the mixtures. Within monoculture and mixture plots, we selected 8 trees per plot for sap flow measurements based on the following criterion: 1) The trees had to be of DBH similar to plot mean DBH; 2) The trees had to be interacting aboveground, without competing directly for light; 3) For each plot, all eight trees had to be within a 10 m radius of each other so the sap flow cables could connect to them. Within the mixtures, we added a fourth criteria: 4) Trees had to be either one of the *center* or *surrounding* trees. For example, each mixture had sap flow sensors installed in one center *T. amazonia* and 3 of the 6 surrounding *D. retusa* in that hexagon group, and vice versa. We visited each site at least twice a week to download data, check sensors, and replace broken sensors. We changed the battery of each station at least once a week. A total of 64 sap flow trees were measured; however, 49 trees were used for analyses due to sensor errors and biotic factors, including mortality due to canopy wind damage (1 tree) or sensor malfunction due to ant attacks (4 trees) or thermocouple erosion from humidity (10 trees). If these sensor errors resulted in 20% of the data missing, we excluded the tree from the analyses.

We analyzed data from June 15, 2014 through June 15, 2015. Tree-level biomass and water use estimates were based on data obtained from individual sap flow trees. Stand-level measurements were scaled using plot inventories (Mayoral et al. 2017) and the relationship between DBH and sapwood area for each treatment was analyzed following Hernandez-Santana et al. (2015). Briefly, we measured the DBH of 30 trees across the plantation (20 *D. retusa* and 20 *T. amazonia*) and took a core from each measured tree to calculate the amount of sapwood area and heartwood. We did not find heartwood for the range of DBH sampled and thus could directly relate DBH. We assigned water use values to each tree in the full inventory based on DBH using treatment derived equations for each species and treatment:

D. retusa monocultures: $y = 0.06277x - 0.1571$ ($R^2 = 0.58$, $p = 0.009$) (eq. 1)
D. retusa mixtures, $y = 0.12571x - 0.44432$ ($R^2 = 0.54$, $p = 0.02$) (eq. 2)
T. amazonia monocultures: $y = 0.15489x - 1.01002$ ($R^2 = 0.58$, $p = 0.001$) (eq. 3)
T. amazonia mixtures: $y = 0.11819x - 0.51214$ ($R^2 = 0.50$, $p = 0.009$) (eq. 4)

where y is Q and x is DBH.

Table 1-1. Tree characteristics of the sap flow trees. DR mono: *D. retusa* in monocultures, DR mixed: *D. retusa* in mixtures, TA mono: *T. amazonia* in monocultures, TA mixed: *T. amazonia* in mixtures. Mean diameter at breast height [DBH; cm], N: number of trees sampled, SE: standard error of the mean.

Treatment	N	DBH [cm]	SE
DR mono	16	4.33	0.23
DR mixed	16	5.59	0.34
TA mono	16	11.13	0.63
TA mixed	16	10.84	0.6

1.2.3 Micrometeorological & soil moisture data

Two distinct meteorological (MET) stations located within the Agua Salud Project study area collected local climate data for the 2014-2015 study period. From June 2014 through January 2015, MET data were collected from a tower managed by the Autoridad del Canal de Panamá (Meteorology and Hydrology Branch, Panama Canal Authority, Republic of Panama), while data after February 2015 were collected from a tower managed by the Smithsonian Tropical Research Institute. Climate data from the towers included air temperature (ºC) and relative humidity (RH, %) using an HMP60 (Vaisala, Vantaa, Finland), and precipitation (mm) using a 260-250-A tipping bucket (NovaLynx, CA, USA). Vapor pressure deficit (VPD, kPA) was calculated from the air temperature and RH data based on Allen et al., (1998). Small gaps in the dataset exist due to either sensor malfunction (< 1 week) or during the renovation of the tower and update of the sensors (~ 1 month).

According to the Panama Canal Authority, the start and end dates of the wet and dry seasons were the following: The 2014 dry season began December 21, 2013 and ended May 6, 2014 and the 2014 dry season began December 14, 2014 and ended up May 16, 2015 (Paton, 2016). Cumulative rainfall was 2203 mm for 2014 and 1810 mm for 2015 (Meteorology and

Hydrology Branch, Panama Canal Authority, Republic of Panama). Generally, about 80% of the average annual precipitation falls between May and mid-December. An El Niño-Southern Oscillation (ENSO) event, which resulted in the third longest dry season on record in Panama started toward the end of this study's sampling period in June (Paton, 2016).

Soil volumetric water content (VWC) was measured using DeltaT PR2 sensors (DeltaT, Cambridge, United Kingdom) at six soil depths (100, 200, 300, 400, 600, and 1000 mm) starting in December 2014 and thus only captures the dry season and the beginning of the wet season in 2015 for the data reported herein. At monoculture sites, 3 trees with sap flow sensors were randomly selected. An soil moisture access tube was placed 0.5 m in a random cardinal direction from the bole of the selected tree (12 access tubes across monocultures). In the mixtures, 12 access tubes were positioned 0.5 m from the bole of the tree (48 access tubes across mixtures). Each center tree had three access tubes and each surrounding tree had one access tube in the mixtures. Soil moisture measurements were collected for each tube every 1-4 days. A mean weekly VWC was calculated for the upper three depths for each treatment – 100 mm, 200 mm, and 300 mm. Lower depths were excluded because they did not change significantly throughout the year (Appendix A, Figure A-1).

1.2.4 Biomass measurements

Tree-level aboveground biomass (AGB, kg) was estimated following Miller et al. (2017) using species-specific allometric equations based on excavation data from a nearby site (Sinacore et al., 2017). We estimated AGB for *D. retusa* using the equation:

$$\mathrm{AGB} = 2.400 \times \log(DBH) - 1.299 \quad (\mathrm{R}^2 = 0.84, \mathrm{RMSE} = 0.59) \qquad \text{(eq. 5)}$$

We estimated AGB of *T. amazonia* using the equation:

$$\mathrm{AGB} = 1.735 \times \log(DBH) - 0.262 \text{ (R}^2 = 0.74\text{, RMSE} = 0.35\text{)} \qquad \text{(eq. 6)}$$

Stand-level estimates of AGB were calculated for each plot and then converted to kg m^{-2}. Aboveground stand and tree biomass growth was calculated as the difference in AGB between the 2015 and 2014 inventories.

1.2.5 Tree sap flux density (J_s) and water use (Q)

Sap flow was measured using the heat ratio method (HRM) (Burgess et al. 2001). On each study tree, one sensor was installed 1.30 m above the base of the tree facing north. Each sensor contained three probes (a heater probe and two temperature probes, installed equidistantly upstream and downstream from the heater probe, 0.6 cm). Each temperature probe contained three thermocouples located at 0.5, 1.7, and 3.0 cm from the bark of the tree. A heat pulse was automatically sent to the heater probe every 15 minutes. The speed of the heat (*Vh*) was calculated every 15 minutes according to Burgess et al. (2001):

$$V_h = \frac{k}{x}\ln(v_1 \,/\, v_2)3600 \qquad \text{(eq. 7)}$$

where *k* is the thermal diffusivity of green (fresh) wood, *x* is the distance in centimeters between the heater and either temperature probe, and v_1 and v_2 are increases in temperature from initial temperature at equidistant points downstream (v_1) and upstream (v_2). Heat pulse velocities were corrected (Vc) for errors (probe misalignment and wounding) following Burgess et al. (2001):

$$V_c = bV_h + \mathrm{c}V_h^2 + \mathrm{d}V_h^3 \qquad (\mathrm{eq.}\,8)$$

where b, c, and d are coefficients round in Table 1 of Burgess et al., (2001). Estimates of each tree's daily sap flux density (J_s) were obtained from Vc (Green et al., 2003) based on the period from June 15, 2014 through June 15, 2015:

$$J_s = \frac{\rho_d}{\rho_s}\left(\mathrm{MC} + \frac{C_{dw}}{C_s}\right)V_c \qquad (\mathrm{eq.}\,9)$$

where ρ_d is the density of sapwood, ρ_s is the density of water, MC is the volumetric water content of the sapwood, C_{dw} is the thermal conductivity of dry wood, and C_s is the thermal conductivity of water. For comparison of J_s among treatments and species, we used the outer most thermocouple position (closest to the bark) which has the fastest J_s and is positioned in the newest wood.

To calculate sap flow we first calculated the cross-sectional sapwood area (determined using cores, described above) and divided that area into three concentric annuli delimited by the midpoint between the three measurement depths of the sensors. The sap flow corresponding to each annulus was estimated by multiplying the area of the annulus by J_s at each thermocouple depth. The water use (Q) for the tree was estimated by adding the values from the three concentric annuli.

1.2.6 Water use (Q), transpiration (E), and water-use efficiency (WUE)

We modeled a linear relationship between DBH and water use (Q) (equations 1-4) for each treatment and used this equation to estimate tree Q of plantation trees for which we did not have sensors installed. For all trees across all study plots, we summed the Q for each tree in a plot and multiplied this value by the stand sapwood area divided by stand ground area of the plot to calculate stand transpiration (E; mm day^{-1}). Stand-level water use efficiency ($\mathrm{WUE_S}$) was estimated by dividing the stand-level aboveground biomass growth for each plot between June 2014 to June 2015 by the stand-level transpiration for each plot. To calculate tree water-use efficiency ($\mathrm{WUE_T}$), we divided aboveground biomass growth between June 2014 and June 2015 by the mean Q of the tree within the same period.

1.2.7 Leaf-level photosynthesis (A_{max}), stomatal conductance (g_s), and WUE

We measured leaf-level instantaneous photosynthesis (A_{max}), stomatal conductance (g_{s}), and transpiration using a LI-6400 Portable Photosynthesis System (LICOR Biosciences Inc, Lincoln, NE, U.S.A) during the dry season of 2015 every two weeks from February through April for all sap flow trees. Photon flux density was set to 1800 µmol^{-2}s^{-1} to measure net photosynthetic capacity (A_{max}) and transpiration measurements. Instantaneous $\mathrm{WUE_L}$ was calculated as the division of leaf A_{max} and leaf transpiration. Three leaves per sap flow tree were measured between 09:00 and 11:30 am, with 10 measurements taken per leaf. Sun leaves were selected and 10 measurements per leaf were averaged. The three samples per tree were then averaged to estimate the leaf transpiration and A_{max}, and g_{s} for each tree.

1.2.8 Statistical analyses

Leaf-, tree-, and stand-level measurements that did not meet normality tests were log- or square root transformed for analyses and back-transformed for all figures. To assess differences in leaf-level g_s and A_{max} among treatments and measurement periods a MANOVA and post-hoc Tukey test were used. An ANOVA and post-hoc Tukey test was used to assess differences for tree- and stand- Q, WUE_T, and E between treatments. The exception was that WUE_S was not transformed because the transformations did not result in a normal distribution. To test for differences in WUE_S among treatments, we performed a non-parametric Kruskal-Wallis test and a pairwise Wilcox test with a Bonferroni correction.

To compare mean daily J_s by treatment, we used a repeated mixed effects model where treatment was a fixed effect and tree was a random effect using the *lmer* package in R (R Core Team, 2017). We performed a two-way ANOVA and post-hoc Tukey test to test for significant differences of J_s among the treatments at the tree level. We analyzed the relative importance (RI) of MET variables (VWC, VPD, radiation, precipitation) on J_s by season and treatment using the LMG method, which is the R^2 contribution averaged over the orderings among regressors, and the LAST method, which is each variable’s contribution when included last using the *relaimpo* package in R (R Core Team, 2017). All MET variables, except precipitation were log transformed to meet normality assumptions. We were unable to include VWC as a predictor in the wet season of 2014, but included it in the dry season of 2015, where the VWC dataset was complete.

1.3 RESULTS

1.3.1 Soil and MET data influencing sap flux density (J_s)

The soil moisture data set represents the period between December 2014 and June 2015 when cumulative rainfall was just over 1500 mm. During January 2015 through June 2015, the cumulative rainfall was just over 300 mm, which is typical of that time of year. Volumetric water content (VWC; %) varied by treatment during the dry season. The lowest VWC occurred during the end of the dry season, around April, decreasing to less than 10% VWC in the *T. amazonia* mixtures (Figure 1-2d). The highest WVC was recorded during the end of the wet season of 2014, with a VWC of > 25%. *Dalbergia retusa* mixtures had significantly higher VWC than *D. retusa* monocultures, *T. amazonia* monocultures, and *T. amazonia* mixtures ($p < 0.001$), while the latter three were not significantly different from each other.

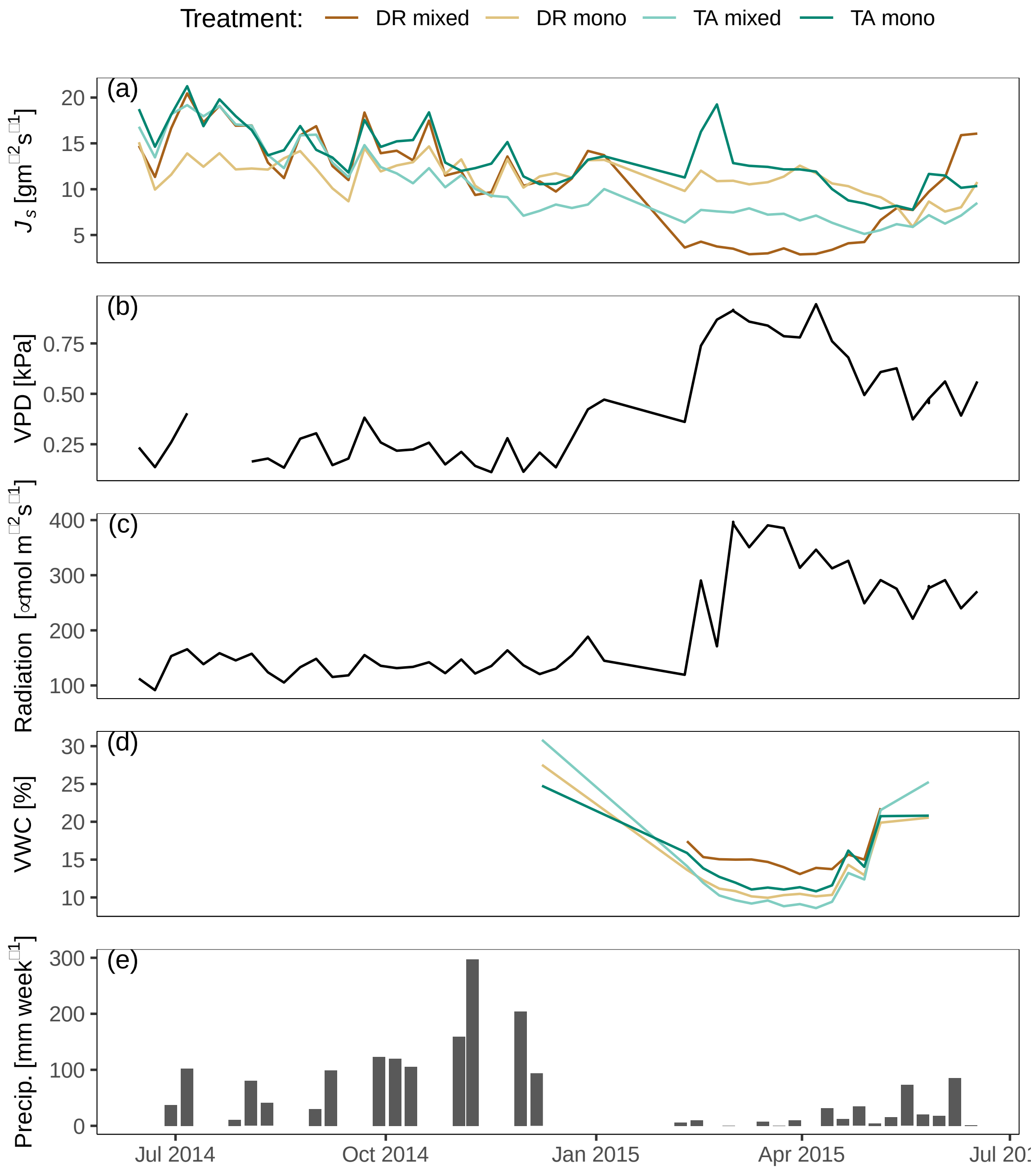

Figure 1-2. Weekly averages of (a) sap flux density (J_s; gm^{-2}s^{-1}), (b) vapor pressure deficit (VPD; kPa), (c) radiation (µmol m^{-2}s^{-1}), (d) volumetric water content (VWC, %), and weekly sum of (e) precipitation (mm week^{-1}). Colored lines represent averages of individual trees for the four treatments. DR mixed: *D. retusa* trees in mixtures; DR mono: *D. retusa* trees in monocultures; TA mixed: *T. amazonia* in mixtures TA mono: *T. amazonia* in monocultures. Soil data not available before December 2014.

The full generalized linear model that included treatment, VPD, radiation, and precipitation and the interaction of each meteorological variable with treatment, found significant effects of all variables and interactions in predicting daily J_s, with two exceptions: the interaction with radiation for the *D. retusa* in mixtures and the interaction with precipitation for the *D. retusa* in monocultures. For the mixture treatments, VPD exhibited the strongest correlation with J_s for trees planted in mixtures, according to the RI evaluation, ranging from 40-93% (Table 1-2). In *D. retusa* monocultures, radiation and VWC were the strongest predictors of J_s. In *T. amazonia* monocultures, radiation was the strongest predictor in the wet season and VPD was the strongest predictor in the dry season. While there was no difference in the strongest predictor for *D. retusa* in mixtures between seasons, *D. retusa* in monocultures transitioned from radiation in the wet season to VWC in the dry season (Table 1-2). Monocultures of *T. amazonia* also transitioned, but from radiation in the wet season to VPD in the dry season.

Table 1-2. Relative Importance Metrics. Treatment includes four study treatments: DR mixed: *D. retusa* trees in mixtures; DR mono: *D. retusa* trees in monocultures; TA mixed: *T. amazonia* in mixtures TA mono: *T. amazonia* in monocultures. Predictor variables include: VPD: vapor pressure deficit, VWC: volumetric water content (not included in the wet season of 2014 because dataset incomplete), precipitation, and radiation. Relative importance values sum to 1.00 for each predictor by treatment.

Treatment	Method	Predictor	Wet 2014 Rel. imp. (%)	Dry 2015 Rel. imp. (%)
DR mixed	LMG	VPD	0.79	0.81
	LMG	Radiation	0.20	0.04
	LMG	Precipitation	0.01	0.00
	LMG	VWC	na	0.15
	LAST	VPD	0.71	0.93
	LAST	Radiation	0.28	0.06
	LAST	Precipitation	0.01	0.00
	LAST	VWC	na	0.02
DR mono	LMG	VPD	0.47	0.03
	LMG	Radiation	0.53	0.00
	LMG	Precipitation	0.00	0.00
	LMG	VWC	na	0.98
	LAST	VPD	0.39	0.00
	LAST	Radiation	0.61	0.00
	LAST	Precipitation	0.00	0.00
	LAST	VWC	na	1.00
TA mixed	LMG	VPD	0.49	0.44
	LMG	Radiation	0.50	0.50
	LMG	Precipitation	0.01	0.00
	LMG	VWC	na	0.01
	LAST	VPD	0.48	0.40
	LAST	Radiation	0.48	0.58
	LAST	Precipitation	0.04	0.00
	LAST	VWC	na	0.02
TA mono	LMG	VPD	0.43	0.73
	LMG	Radiation	0.55	0.01
	LMG	Precipitation	0.01	0.00
	LMG	VWC	na	0.26
	LAST	VPD	0.28	0.83
	LAST	Radiation	0.68	0.01
	LAST	Precipitation	0.04	0.00
	LAST	VWC	na	0.14

Methods are LMG (overall model contribution averaged over orderings of predictors) and LAST (model contribution given all other predictors already included in the model). Analyses were divided by season (dry season 2014 and wet season 2015). Gray shading represents highest relative importance value by treatment, method, and season.

1.3.2 Tree and stand level water use, transpiration, and WUE

Mean hourly tree water use (*Q*) varied by treatment and aboveground biomass (AGB) increment growth (kg yr^{-1}) (Figure 1-3a). *Terminalia amazonia* in mixtures had significantly higher *Q* than all other treatments. Hourly *Q* was significantly greater for *T. amazonia* in mixtures ($p < 0.001$) than *T. amazonia* in monocultures and either *D. retusa* treatment (Figure 1-3b). Mean hourly *Q* for *T. amazonia* in mixtures and monocultures was 6.59 ± 0.42 L h^{-1} and 4.93 ± 10.50 L h^{-1}, and for *D. retusa* mixtures and monocultures, 1.05 ± 0.14 L h^{-1} and 0.82 ± 0.06 L h^{-1} , respectfully (Figure 1-3a). *Dalbergia retusa* in the monocultures had significantly greater WUE_T than *T. amazonia* in the monocultures ($p = 0.04$) while *Dalbergia retusa* WUE_T in the mixtures was not significantly different from WUE_T from *T. amazonia* in either treatment (Figure 1-4).

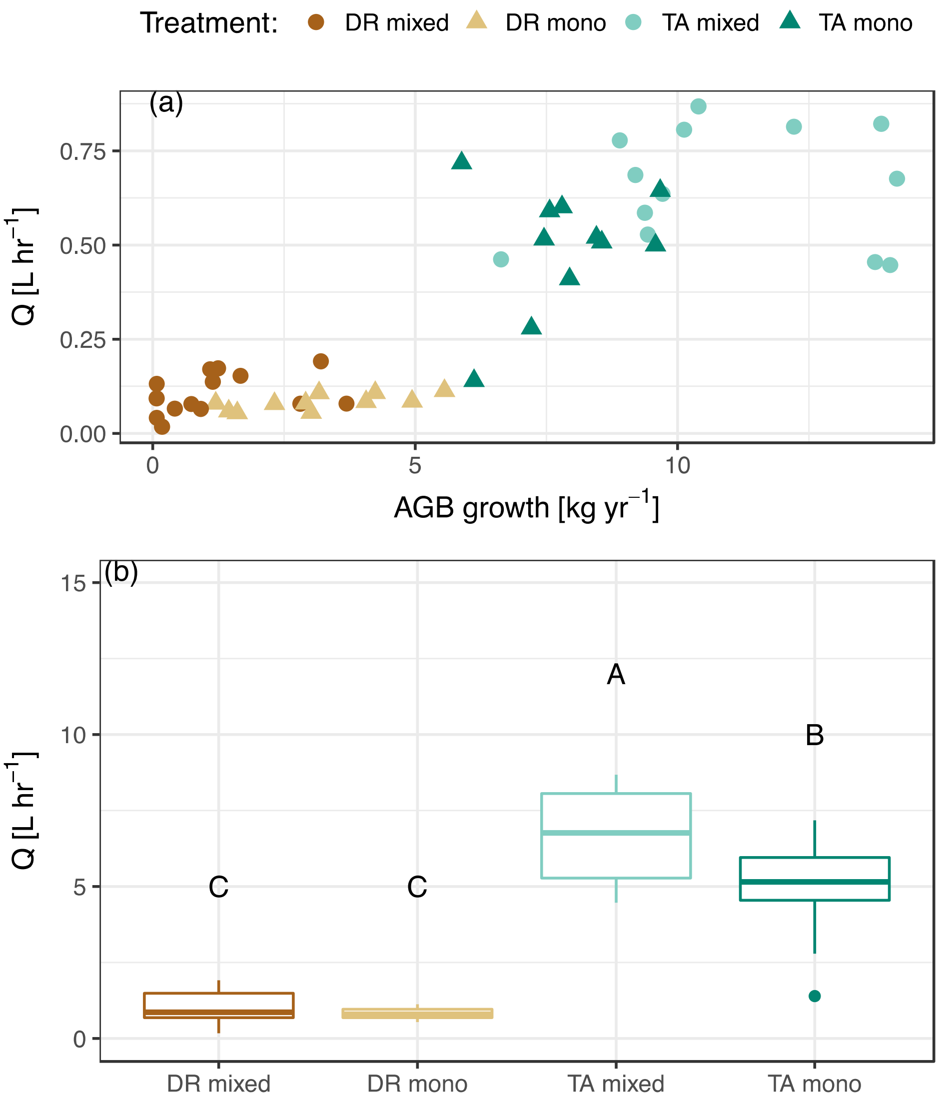

Figure 1-3. Average tree-level whole-tree sap flow (Q, L hr^{-1}) of sapflow trees compared to tree aboveground biomass (AGB) growth (kg yr^{-1}). Mean Q and tree AGB growth were calculated from June 15, 2014 through June 15, 2015. Points represent individual trees. The treatments include: DR mixed: *D. retusa* trees in mixtures; DR mono: *D. retusa* trees in monocultures; TA mixed: *T. amazonia* in mixtures TA mono: *T. amazonia* in monocultures.

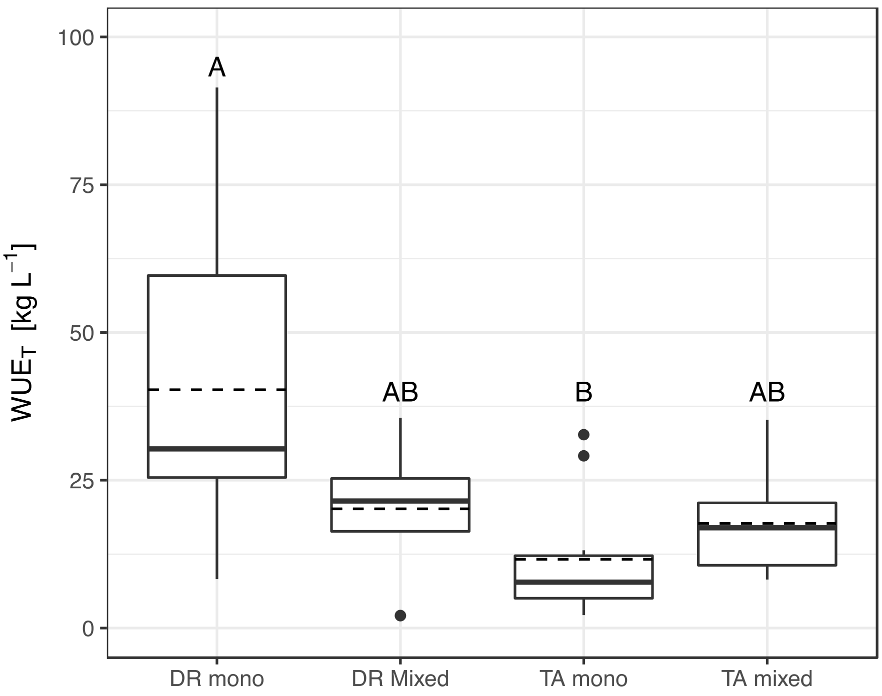

Figure 1-4. Tree-level water use efficiency (WUE, kg L^{-1} water transpired) for each treatment. DR mono: *D. retusa* in monocultures, DR mixed: *D. retusa* in mixtures, TA mono: *T. amazonia* in monocultures, TA mixed: *T. amazonia* in mixtures. Letters denote significant differences among treatments based on ANOVA and post-hoc Tukey test. Solid horizontal lines inside boxes correspond to the median and the dashed lines to the mean. The lower and upper box boundaries correspond to the first and third quartiles.

At the stand level, *E* was significantly different among treatments ($p < 0.001$) (Figure 1-5). *E* was highest in the *T. amazonia* monocultures (mean = 3.38 ± 0.43 mm day^{-1}), followed by the mixtures (mean = 1.73 ± 0.29 mm day^{-1}), and the *D. retusa* monocultures (mean = 0.20 ± 0.07 mm day^{-1}) (Figure 1-5b). The yearly AGB increment growth for the stand also had a significant effect on *E* ($R^2 = 0.72$, $p < 0.001$) (Figure 1-5a). Water use efficiency of the stand (WUE_S) was significantly different among two of the three treatments (Figure 1-6). WUE_S of *D. retusa* monocultures > mixtures ≥ *T. amazonia* monocultures ($p < 0.001$ and $p = 0.320$, respectively) (Figure 1-6).

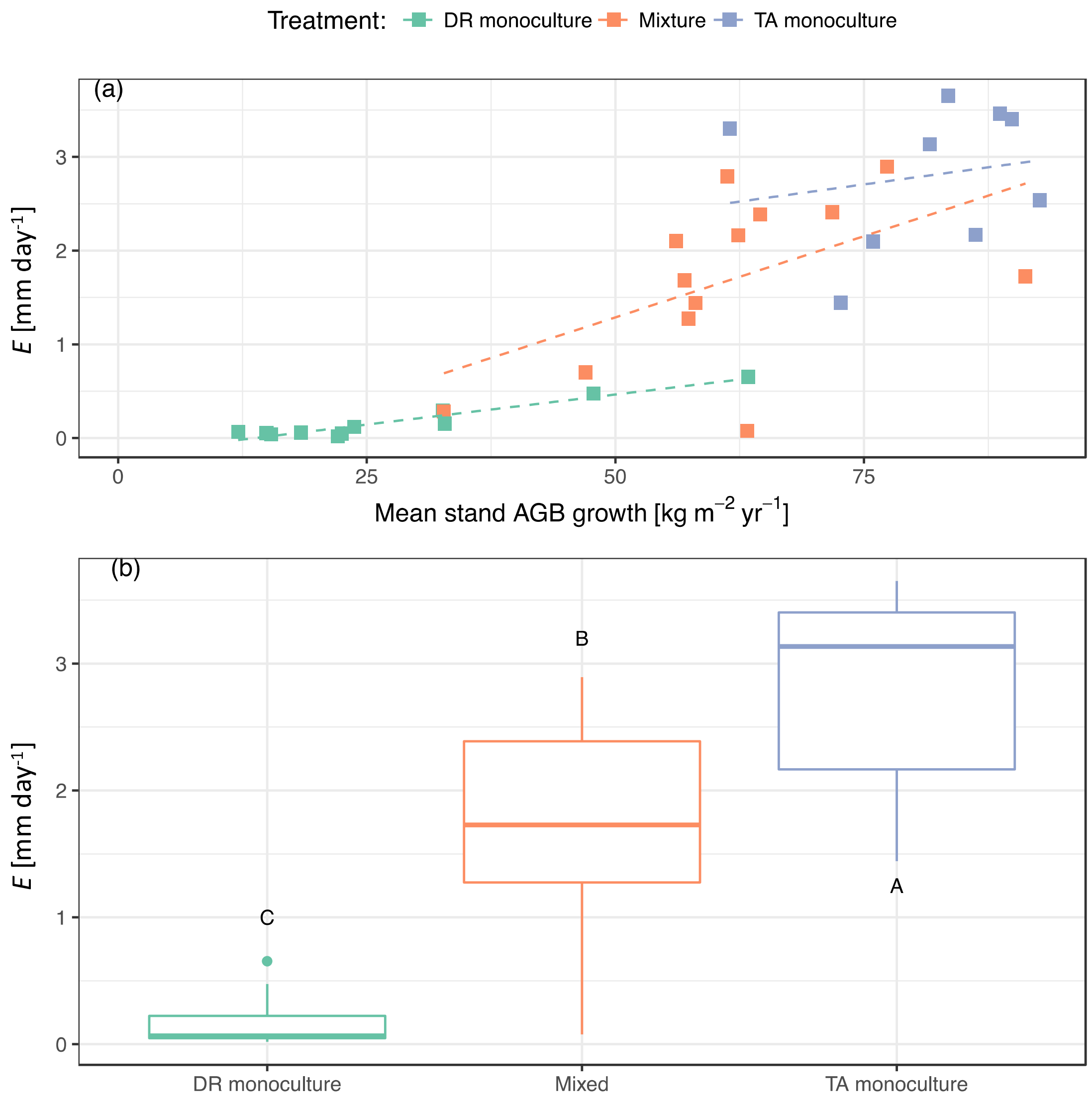

Figure 1-5. Stand-level transpiration (*E*, mm day^{-1}) by (a) mean stand aboveground biomass growth (AGB growth; kg m^{-2}yr^{-1}) and (b) treatment for all stands in Agua Salud plantation. DR monoculture: *D. retusa* monoculture (n = 12); Mixed: *D. retusa* and *T. amazonia* two-species mixture (n = 13); TA monoculture: *T. amazonia* mixture (n = 11). Points represent means for individual plots where sap flow measures were taken and modeled transpiration for other sites (27.0 m by 23.4 m) and dashed lines represent generalized linear model for each treatment. For the boxplot, solid horizontal lines inside boxes correspond to the median daily transpiration. The lower and upper box boundaries correspond to the first and third quartiles. Letters indicate significant differences in average *E* based on linear model and lease square means pairwise comparison.

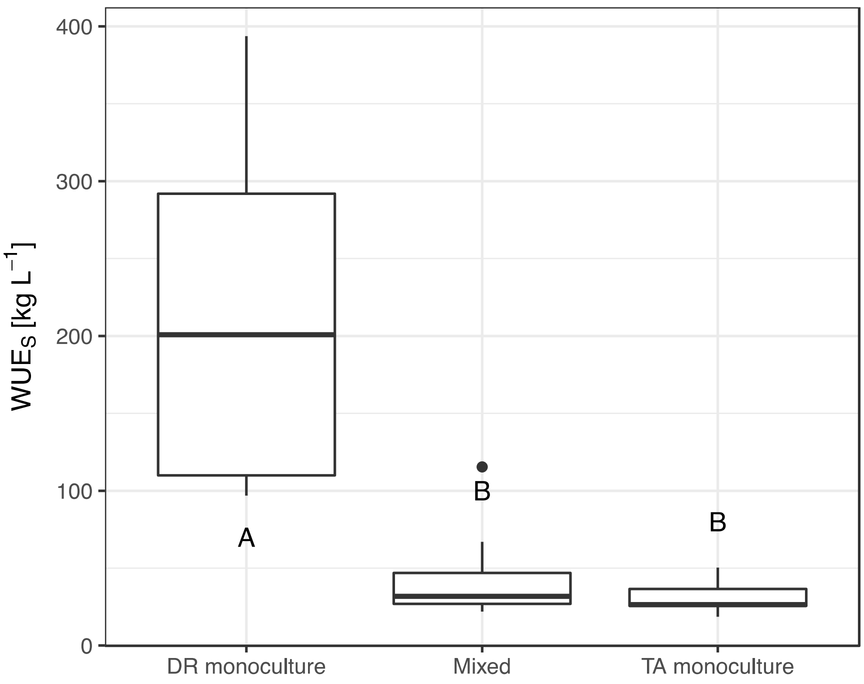

Figure 1-6. Water use efficiency for each treatment (stand level; WUE$_S$ [kg L^{-1}]). DR monoculture: *D. retusa* monocultures, Mixed: mixed stands, TA monoculture: *T. amazonia* in monocultures. Solid horizontal lines inside boxes correspond to the median and the dashed lines to the mean for all sites. The lower and upper box boundaries correspond to the first and third quartiles. Letters indicate significant differences in average WUE$_S$ based on linear model and lease square means pairwise comparison**.**

1.3.3 Leaf-level photosynthesis (A_{max}), conductance (g_s), and WUE

WUE$_L$ differed by species (Figure 1-7), with *Terminalia amazonia* in the mixtures having significantly greater WUE$_L$ than *T. amazonia* in the monoculture and the two *D. retusa* treatments. At all sampling periods, A_{max} differed significantly by species, with *T. amazonia* always having greater A_{max} than *D. retusa* ($p < 0.008$) (Figure 1-8). From February 23rd through March 20th, A_{max} was not significantly different between monocultures and mixtures of *T. amazonia*. *Dalbergia retusa* in monocultures had significantly higher A_{max} than *D. retusa* in mixtures except for on April 15. Leaf-level g_s was significantly different ($p < 0.008$) by treatment for all sample periods except for March 20th. Leaf-level g_s patterns closely followed A_{max}, except that g_s of *T. amazonia* in mixtures followed a similar pattern (declines early in dry season and increases late in dry season) to g_s of *D. retusa* rather than *T. amazonia* in monocultures which increased after March 3 (Figure 1-9).

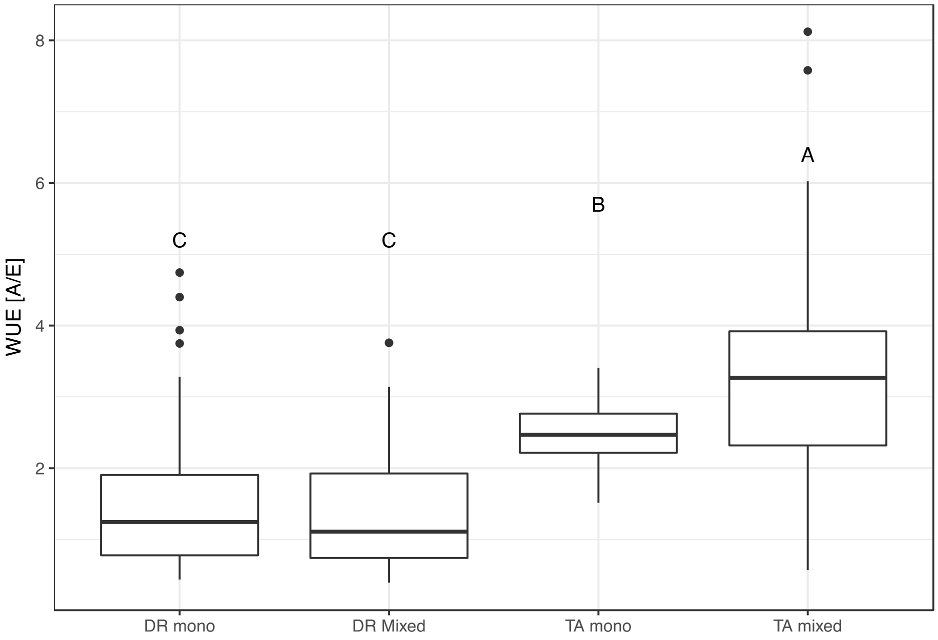

Figure 1-7. Leaf-level water use efficiency (WUE, A_{max} / leaf transpiration) for each treatment during dry season 2015. Letters denote significant differences among treatments based on ANOVA and post-hoc Tukey test. DR mono: *D. retusa* trees in monocultures; DR mixed: *D. retusa* trees in mixtures; TA mono: *T. amazonia* in monocultures TA mixed: *T. amazonia* in mixtures.

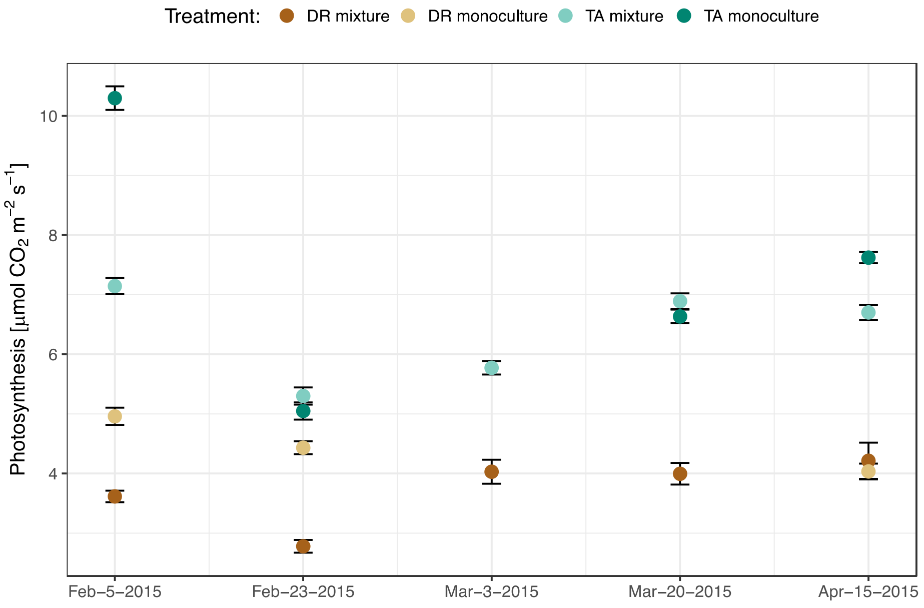

Figure 1-8. Leaf-level photosynthesis (*A*$_{max}$, µmol CO$_2$ m^{-2}s^{-1}) during five different dry season sampling dates for 2015. Error bars represent standard errors of the mean for each treatment and sample date. DR mixture: *D. retusa* trees in mixtures; DR monoculture: *D. retusa* trees in monocultures; TA mixture: *T. amazonia* in mixtures TA monoculture: *T. amazonia* in monocultures.

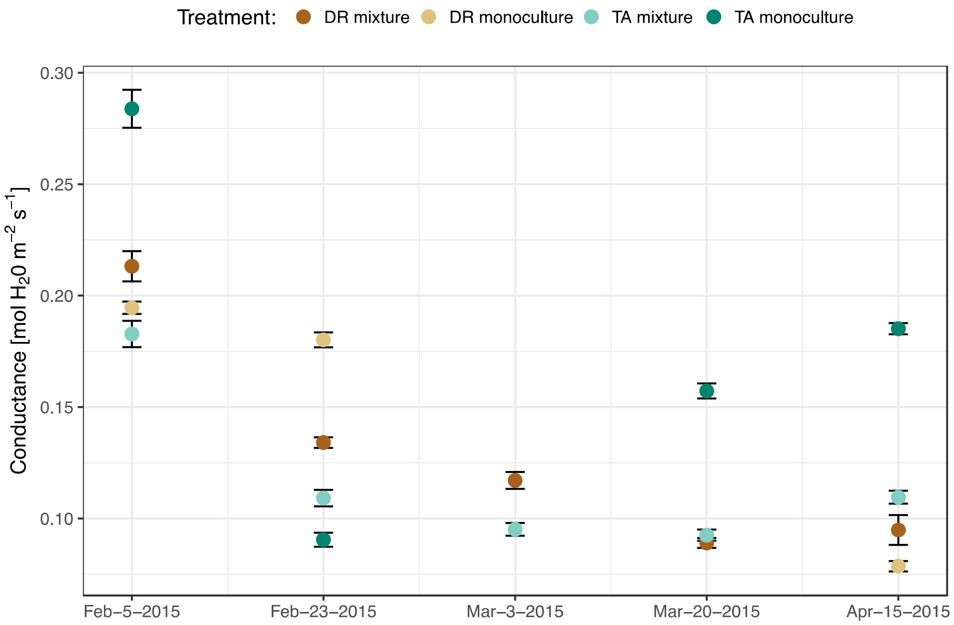

Figure 1-9. Leaf-level conductance (*g_s*, mol H_2O $m^{-2}s^{-1}$) during five different dry season sampling dates for 2015. Error bars represent standard errors of the mean for each treatment and sample date. Missing data during March 3rd and March 20th due to *D. retusa* monocultures leaf senescence. Missing data Marc 3rd for *T. amazonia* monocultures due to equipment errors. DR mixture: *D. retusa* trees in mixtures; DR monoculture: *D. retusa* trees in monocultures; TA mixture: *T. amazonia* in mixtures TA monoculture: *T. amazonia* in monocultures.

1.4 DISCUSSION

1.4.1 Mixtures use more water than monocultures, but not always.

There is evidence that forests or plantations that combine species with complementary functional traits lead to enhanced stand-level resource use efficiency (Forrester et al., 2016). While stand-level WUE$_S$ for mixtures in this study was greater than for the *T. amazonia* monocultures, *D. retusa* monocultures had greater WUE$_S$ than the mixtures (Figure 1-6) and so does not fully support the resource-use efficiency-diversity theory. One reason may lie in the fact that *T. amazonia* was so much more productive than *D. retusa* such that there was not an opportunity for complementary interactions to occur. This 'dominant species effect' may have been stronger than the complementary interactions (Loreau et al 2001) between these two species. Higher transpiration of *T. amazonia* monocultures suggests that any complementary interactions in the mixtures may have been outweighed by the the dominance of *T. amazonia*. While diameter is generally strongly correlated with water use (Meinzer et al., 2001) it does not always correlate well, as seen in temperate broad-leaf forests (Hölscher et al., 2005). Kunert et al., (2012) found that two- and three-species Panamanian mixtures had higher annual stand transpiration compared to monocultures, but that this was mostly a function attributing this to larger diameters in mixtures. Since we only found that *T. amazonia* had larger diameters in mixtures (and not *D. retusa*), this discrepancy may explain the lower stand level transpiration in mixtures versus *T. amazonia* monocultures.

1.4.2 Mixtures Tree-level interactions and climate variables help explain stand-level results.

Annual stand transpiration is an important factor to consider when designing a plantation, but how trees behave and how this might change depending on climatic variation, is an important consideration when selecting species for areas where precipitation, radiation, or VPD changes throughout the course of a year. We found strong evidence that *T. amazonia* might have benefitted *D. retusa* in the mixtures. The partial shading from *T. amazonia* may have ameliorated microclimate conditions for *D. retusa* such that evaporation from the upper soil depths was less pronounced in the mixtures, where *D. retusa* generally accesses water. Further, *D.* retusa in the mixtures received less radiation, which may have made it less suspeptible to high radiation that is common in the dry season. This concept was illustrated in the fact that the *J*s of *D. retusa* monocultures was primarily influenced by radiation during the wet season (~60%) and VWC during the dry season (~99%), while J_s of *D. retusa* in mixtures (which are partially shaded) was primarily influenced by VPD regardless of the season (Table 1-2), but not radiation or VWC. VWC having a small influence on J_s for D. retusa in the mixtures may have also been related to the fact that it was planted with *T. amazonia*, which accesses water at deeper soil depths than *D. retusa*. Interestingly, this trend seemed to be related to treatment. We found a similar trend for *T. amazonia*, where the J_s of monocultures was primarily driven by radiation in the wet season and VPD during the dry season while *T. amazonia* in the mixtures were influenced by a combination of VPD and radiation.

1.4.3 Leaf-level measurements cannot explain our tree-level results

We expected to find that WUE_L would be higher for *D. retusa* than *T. amazonia* and that the *T. amazonia* in mixtures would have higher WUE_L than in monocultures due to its association with the N-fixing *D. retusa*. WUE_L, however, diverges from our tree-level WUE_T results (Figure 1-4, Figure 1-7). Mainly, *T. amazonia* had higher WUE_L than *D. retusa* The partial shading from *T. amazonia* may have ameliorated microclimate conditions for *D. retusa* such evaporation from the upper soil depths was less pronounced in the mixtures. There is evidence in other plantations that N-fixing species benefit non-fixing species. A notable example is plantations of *Eucalyptus globulus* and *Acacia mearnsii* where mixtures were more water use efficient than monocultures due to greater increases in canopy photosynthetic capacity that were linked to increases in N availability (Forrester et al. 2010). *Dalbergia retusa* is a known N-fixer (Batterman et al., in review), and we find evidence at the leaf-level that *T. amazonia* benefits from the association with *D. retusa*, in having higher WUE_L (Figure 1-7). Yet these results do not directly scale to the tree, as we find no significant difference between *T. amazonia* WUE_L by treatment (Figure 1-4).

The different trends in WUE observed at the leaf and tree scales underscores the difficulty in reconciling the ecological meaning of instantaneous leaf-level measurements with integrated tree-level measurements derived over annual time scale. It has been established that upscaling from leaf to tree or stand incorporates a certain level of uncertainty (Hernandez-Santana et al., 2015; Looker et al., 2016). For our study, we identify six areas of uncertainty in scaling from leaf to tree. First, our leaf-level measurements were taken from February through April 2015, during the peak of the dry season while tree measurements were taken and averaged annually. Leaf-level dry season behavior is unlikely to imitate the aggregate of wet and dry season tree-level data. Second, the correlation might be poor because growth (or dry matter production) depends largely on leaf area, leaf duration, and leaf exposure, all of which vary throughout the growing season and the life of the tree (Perez et al 2013). Third, not all photosynthate is used for producing new tissue. Some is used for respiration or production of other secondary substances (Ryan and Yoder, 1997), and would thus not directly contribute to the WUE calculation, which uses an allometric equation to determine AGB from DBH. Fourth, although we worked in a plantation, which is more uniform than a forest, trees of the same species still differ in their leaf area and crown area depending on neighboring trees, which would not be integrated into the leaf-level measurements, but would be for tree-level water use. Fifth, leaf-level measurements were taken on fully exposed sun leaves while tree-level measurements integrate sun and shade leaves. Finally, leaf-level measurements were also taken in a chamber where fans eliminated the boundary layer surrounding the leaf which acts as a resistant to water vapor diffusion, and thus could overestimate leaf photosynthesis compared to open grown trees where conditions change are are not always at ideal levels for maximum photosynthesis (Cavaleri and Sack, 2010).

Interestingly, however, at the species level, our $A_{\max}$ results do support the species differences in growth we observed at the whole tree scale, with higher $A_{\max}$ associated with higher growth rates (Figure 1-3, Figure 1-8). The high $A_{\max}$ of *T. amazonia* were similar to those found in another study in Panama (Craven et al., 2011). During the dry season, $A_{\max}$ in the Craven et al., (2011) study was just over 5.0 µmol CO_2 m^2s^{-1} while the $A_{\max}$ in our study was just over 6.0 µmol CO_2 m^2s^{-1} on average. In a second study, both species showed significantly higher WUE in dry sites compared to wetter sites (Craven et al., 2013), suggesting that these two species have adaptive strategies to minimize water loss in drier environments. *Dalbergia retusa* is semi-deciduous in the dry season, losing leaves to prevent desiccation. Leaves that do not senesce may be poor at regulating stomatal openings and could have been represented in our data. In addition to avoiding water deficits by dropping leaves, reducing $A_{\max}$ may be a strategy of *D. retusa* in the dry season to avoid additional moisture stress. Craven et al., (2013) used C^{13}

isotopes methods that show *D. retusa* and *T. amazonia* have similar WUE_L (Craven et al., 2013). It is important to note that the trees in that study were 2-year old plantation grown, and not yet interacting aboveground and were kept in ideal conditions for growth. In contrast, our study focused on 8-year old trees that were interacting aboveground and likely belowground.

Concern over species' ability to tolerate drought conditions, especially given current predictions of longer and more intense dry periods, gives importance to species ability to adapt to soil moisture deficits. Reduction in conductance (g_s), or the degree of stomatal opening, is associated with a species ability to reduce water loss. *Dalbergia retusa*, which has been previously found to have strong stomatal control (Craven et al., 2013), showed a steady decline in g_s over the dry season, regardless of treatment (Figure 1-9). Notably, while *T. amazonia* in the mixtures showed a steady decline in g_s, *T. amazonia* in monocultures showed an initial decline and then a steady increase in g_s throughout the dry season (Figure 1-9). In Panama, faster growing species, like *T. amazonia* typically reduced water loss via a reduction in g_s during the dry season (Lawlor and Cornic, 2002), exhibiting a drought avoider strategy (Larcher, 2003). However, we only saw that trend for the mixtures, suggesting that *T. amazonia* in mixtures might be trying to limit water loss. With increasing tree stature, trees must adjust to greater hydraulic resistance to water flow in the xylem. They can do this by closing stomata and increasing specific leaf area to limit water loss (Rijkers et al., 2000). *Terminalia amazonia* in the mixtures shows a non-significant trend toward greater productivity and could explain the reduction in g_s. Alternatively, *T.* amazonia could have had greater water availability in mixtures (from reduced competition or complementary interactions), thus, did not need to open stomata as much to maintain water uptake (more WUE). Species need the adaptive capacity to tolerate seasonal droughts in Panama to minimize drought-related injury and mortality. At the leaf-level, the mixtures *T. amazonia* are reducing g_s more than the *T. amazonia* monocultures, lending evidence to greater stomatal regulation in the mixtures than the monocultures. The changes in g_s over the dry season also follow closely with the J_s trends over the dry season. There is an initial decline in both g_s and J_s for all treatments, but then *T. amazonia* in the monocultures has an increase in both J_s and g_s in mid-March (which may have been necessary in order to extract more water from drying soils) while the other treatments do not have an increase until April or May (Figure 1-2, Figure 1-9).

1.4.4 Management and ecosystem services.

From a management perspective, monocultures of *T. amazonia* might be easier to manage than mixed-species plots, especially if the objective is to grow high quality timber. However, benefits may be gained through mixed plantings. Over longer time periods, planting *T. amazonia* with a N-fixer like *D. retusa* might also enhance productivity (Batterman et al. in review). In fact, it has recently been shown that *D. retusa* is fixing significantly more N than any other N fixer in the experimental plantation (Batterman et al. in review).

When selecting species to plant, it is becoming increasingly important to consider the implications on water availability and the potential tradeoff with carbon acquisition. This is particularly important in the dry season, when there is less than 300 mm of precipitation from December through April (http://striweb.si.edu/esp/physical_monitoring/descrip_bci.htm). The difference in stand level transpiration by treatment is significant. *Terminalia amazonia* in the monocultures used an average of greater than 3.5 mm day^{-1}. In comparison, mixtures used an average of just more than 1.5 mm day^{-1} while *D. retusa* monocultures used 0.2 mm day^{-1} (Figure

1-5b). Over the course of a year or rotation, these water uses can become increasingly significant.

However, species selection is ultimately about optimizing tradeoffs. In selecting mixed species stands, carefully selecting species to optimize productivity and WUE should consider the potential for complementary interactions (Cardinale et al., 2007). Interspecific mixing has also been shown to increase ecosystem functioning through facilitative interactions (Cardinale et al., 2002). The key is to find species whose positive interactions outweigh any negative interactions due to competition (Binkley et al., 2004). Avoiding high performing species that may override any potential complementary interactions is important if both species in the mixtures are equally valuable to the landowner.

If the goal is to maximize water-use efficiency of the plantation, *D. retusa* is the obvious choice as at the stand-level, it is significantly more water-use efficient than the mixture or *T. amazonia* monoculture. If the goal is to minimize plantation transpiration, *D. retusa* would again be the best choice. Mixtures would also be an option as they use significantly less water per day than *T. amazonia* monocultures. An additional benefit of the mixture is that *T. amazonia* is productive and can reach maturity sooner than *D. retusa* does on the soils in the Panama Canal Watershed. To maximize complementary interactions combining a high-performing species, like *T. amazonia*, with a slower grower (*D. retusa*) is not advised in these conditions.

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CHAPTER 2

EFFECTS OF EL NIÑO ON TREE WATER USE RESPONSES AND WATER STRESS: DO COMPLEMENTARY INTERACTIONS IN MIXED SPECIES TREE PLANTATIONS ENHANCE RESISTANCE TO DROUGHT OVER MONOCULTURES?

ABSTRACT

Severe and prolonged droughts are becoming increasingly common, yet the effects of drought on specific species and species combinations are poorly understood. We took advantage of the 2015-2016 El Niño Southern Oscillation (ENSO) event in central Panama to test differences in drought response related to growth and water use in monocultures and mixtures of *Terminalia amazonia* and *Dalbergia retusa*, comparing the response to pre-ENSO conditions of 2014. Mean daily sap flux density (J_s, $gm^{-2}s^{-1}$) declined significantly during the 2015/2016 ENSO drought for all trees in monocultures and mixtures. J_s during the dry seasons (drought and non-drought years) was significantly greater for trees in mixtures than monocultures. During 2014, leaf water potential (Ψ_L, MPa) was significantly more negative for *T. amazonia* than *D. retusa*, but no differences in Ψ_L were observed between monocultures and mixtures. Toward the end of the drought in 2016, Ψ_L of *T. amazonia* in monocultures was significantly more negative than *T.*

amazonia in the mixtures. In 2015, the Ψ_L of *D*. retusa in the monocultures was more negative than in the mixtures, but this was not significant. Among all treatments, VPD and radiation were the main drivers of J_s before the ENSO event and transitioned to VWC at the end of the ENSO conditions. Our results suggest that complementary interactions in mixed species plantations affect water regulation and moisture stress of trees in ways that enhance resistance to drought compared to monocultures. These findings have implications for designing reforestations for climate change adaptation and reduced susceptibility to drought.

2.1 INTRODUCTION

Climate change scenarios predict that rainfall and soil moisture levels will decline throughout the seasonally dry tropics (Allen et al., 2017). In Panama, drought conditions occur on 5-7-year time scales during El Niño Southern Oscillation years (ENSO). In the Panama Canal Watershed, dry conditions also occur annually between mid-December and mid-April, with less than 200 mm of precipitation typically falling during the dry season (Ogden et al., 2013). Water use patterns by tropical trees are altered during the dry season (Kunert et al., 2010), but the pattern can vary by species, depending on complex interactions between species' leaf phenology, rooting depth, physiology, solar radiation, vapor pressure deficit, and soil moisture availability (Kunert et al., 2012; Schwendenmann et al., 2015, 20 10). Less is known about water use patterns during a prolonged drought.

Reforestation efforts are increasingly emphasizing the potential benefits of planting species mixtures over monocultures, such as higher biodiversity, greater productivity, and economic diversification, as well as potential benefits through improved climate change adaptation (Nichols et al., 2006), but understanding species response to drought is a crucial and understudied element to reforestation efforts. The functional diversity hypothesis, which posits that interactions among trees with complementary functional traits can increase total resource availability, resource use efficiency, and stand productivity (Binkley et al., 2004), has been broadly supported and used to promote mixed species plantations over monocultures (Piotto et al., 2010). In theory, species diversity should be positively correlated with ecosystem resistance – the ability to remain unchanged when disturbed, and resilience – the capacity to recover structure and function following a disturbance (Bellard et al., 2012). However, how such species interactions occurring within mixed species plantations affect resistance and resilience to disturbance and extreme events, such as drought, is poorly understood (Pretzsch et al., 2013). While some studies suggest enhanced resistance and resilience in mixed species plantations (Forrester et al., 2010; Kunert et al., 2012), other studies have found contradictory results (Jucker et al., 2014). For instance, studies have demonstrated significantly enhanced stem increment growth during drought (i.e., resistance) when growing in mixtures compared to monocultures (Lebourgeois et al., 2013; Pretzsch et al., 2013). However, Jucker et al. (2014) showed that mixed plantations of Iberian pine and oak species overyielded (where mixtures exceed yields of monocultures of each species), but this overyielding effect diminished during drought (Jucker et al., 2014). In this study, the observed overyielding by mixtures was attributed to complementary light use strategies during favorable growth years that were outweighed by more fierce competition for water during drought years. Our previous work in Panama demonstrated that mixtures of *T. amazonia* and *D. retusa* were more productive than monocultures (although they did not significantly overyield), while mixtures had greater transpiration than *D. retusa* monocultures. However, more productive (or larger) stands with greater biomass and leaf area typically require more water to sustain metabolic functions during a drought, and thus may reach physiological thresholds of drought response sooner than less productive stands (Bretfeld et al., 2018). More work is needed to disentangle the complex relationships between species diversity, complementarity, and drought response.

Some of the contradictory findings related to drought response reported above may be explained by site-environment interactions. Across broad climate gradients, more positive effects of species richness on tree growth occur on drought-prone sites, while these relationships are more inconsistent or lacking on favorable sites (Jucker et al., 2016). Our work on two species –

Terminalia amazonia and *Dalbergia retusa* – did not support the diversity-complementary hypothesis (Chapter 1), in that mixtures were not more water use efficient than the monocultures. Although this result may be a response of the dominance effect where a high yielding species planted with low yielding species diminishes any strong complementary interacxtions between species (Roscher et al., 2007). Regardless, these treatments had not yet experienced a significant drought, which may change intraspecific and interspecific interactions suggested by Jucker et al., (2016).

One approach to elucidate the role of complementary interactions in mediating drought resistance and resilience is through experiments using mixed species and monoculture plantations specifically designed to combine species with complementary functional traits. It has been broadly established that water use patterns by tropical trees are altered during the dry season (Kunert et al., 2010), and that these pattern can vary by species, depending on species' particular adaptations to moisture stress, such as leaf phenology, rooting depth, hydraulic traits, and stomatal regulation (Kunert et al., 2012; Schwendenmann et al., 2015, 2010).

Variation in species' responses to drought can be characterized along a continuum of drought avoidance to drought tolerant behavior in terms of stomatal regulation, ranging from drought avoidance (isohydric behavior), in which stomata close at a threshold water potential to minimize transpiration, to drought tolerance (anisohydric behavior), in which stomatal closure is less severe and transpiration continues at relatively high rates (McDowell et al., 2008; McDowell, 2011). Leaf water potential (Ψ_L) measured during midday (Ψ_{md}) is a proxy for degree of physiological stress (Pérez-Harguindeguy et al., 2013) and can be used to compare levels of moisture stress among species. Some studies suggest that deciduous trees tend to be better able to prevent hydraulic failure via stomatal closure (i.e., isohydric behavior) or leaf abscission

(Hoffmann et al., 2011), while evergreen species tolerate (or attempt to tolerate) lower Ψ_L, as indicated by steep decreases in hydraulic conductance with decreases in Ψ_L (i.e., anisohydric behavior) (Hernandez-Santana et al., 2016).

Stomatal regulation is not the only mechanism by which trees can avoid or tolerate moisture stress. Deep roots that can access deep water sources allow trees to maintain high levels of transpiration and growth despite moisture deficit in the upper soil horizon (Meißner, 2012). Some evidence suggests that larger or more productive trees allocate a greater amount of resources to roots than to aboveground structures and processes, compared to smaller or less productive trees (Schwendenmann et al., 2010), and would thus be able to tolerate drought (i.e., maintain high transpiration) if able to access deeper soil water storage. In theory, high transpiration rates could also occur in mixtures where drought conditions may be less intense than in monocultures due to variable rooting depths (Pretzsch et al., 2013). Consequently, monocultures may be more vulnerable to drought and mixtures more resistant to drought if complementary and facilitative interactions outweigh competitive ones and if access to water in mixtures is sufficient throughout the drought. Mixtures may allow for shifts in the threshold conditions required to trigger certain physiological responses (e.e., stomatal closure or plant mortality) by increasing the buffering capacity. Support for the theory that functional diversity can lead to greater resistance to drought is an area of active research (Forrester et al., 2010; Kunert et al., 2012). However, few studies have been able to test whether resistance to drought (i.e., maintaining growth rates and transpiration rates of non-drought years), is possible during a prolonged drought.

The ENSO event in 2015/2016 provided a adventitious opportunity to study the response of a young plantation of monocultures and two-species mixtures and explore how water use patterns and physiological responses to moisture stress change over time in response to a prolonged drought. We selected two species with contrasting phenology and physiology hypothesized to generate complementary interactions when growing in mixture. *Terminalia amazonia* is evergreen, with lateral and deeper roots, low water-use efficiency (Cernusak and Aranda, 2007), and is considered to be more drought tolerant due to sustained transpiration during dry periods (i.e., anisohydric tendencies) (Kunert et al., 2010). *Dalbergia retusa* is semi-deciduous, with lateral roots, high water-use efficiency, and has isohydric tendencies (Borchert et al., 2002). We measured growth, sap flux density (J_s), and moisture stress of *T. amazonia* and *D. retusa* in monocultures and mixtures over a 2.5-year period (1-year pre-ENSO and 1.5-years during ENSO) to assess the response of trees to an extreme drought. The experimental design was such that we could isolate interactions between the species (see Figure 1-1 for details). We hypothesized the following:

1. (1) Trees growing in mixtures would have greater resistance and resilience to drought compared to trees growing in monocultures due to complementary interactions resulting in greater total water availability to trees in mixtures,
2. (2) Controls on J_s would transition from VPD and radiation to soil moisture as the drought progresses and competition for resources increases, and would occur more quickly (i.e., lower threshold) in monocultures and less quickly in mixtures (due to greater buffering capacity)?
3. (3) Species with isohydric tendencies will experience earlier thresholds of leaf water potential compared to species with anisohydric tendencies, with the behaviors becoming more pronounced (i.e., diverging) during the drought.

2.2 METHODS

2.2.1 Site Description

The study was conducted in the Agua Salud Project site within the Panama Canal Watershed (9°13' N, 79°47'W, 330 m amsl). We focused on 3 of the plantation treatments – monocultures of *Dalbergia retusa*, monocultures of *Terminalia amazonia*, and two-species mixtures of *D. retusa* and *T. amazonia*. Within each plot, trees were planted in 45 x 39 m plots of 15 x 15 individuals. The core plot, where inventory measurements were taken, was comprised of 9 x 9 trees (27 x 23.4 m). Mixtures were established in a spatially explicit design that isolated interactions between individual trees of different species, whereby an individual of *D. retusa* was completed surrounded by an individual if *T. amazonia* in a hexagon configuration and vice versa; see Figure 1-1 in Chapter 1 for more details. These species combinations were selected because *D. retusa* and *T. amazonia* have contrasting functional traits that we hypothesized would promote complementary interactions when grown together. Prior to plantation establishment, the land was cleared of forest in the 1970s with the predominant land use being cattle grazing (Weber and Hall, 2009). The topography is characterized by short and steep slopes (Hassler et al., 2010; Mayoral et al. in review) and the soils are silt clay to clay with pH values ranging of 4.67 ± 0.27 (in $CaCl_2$) and 5.8 ± 0.23 (in H_2O) (Mayoral et al., in review).

2.2.2 Sampling design

Sap flux density (J_s) and moisture stress were measured for trees growing in monocultures and mixtures of *D. retusa* and *T. amazonia* at 6,7, and 8 years of age. Seven subplots were established in February of 2014, two within monocultures of *D. retusa*, two within monocultures of *T. amazonia*, and three within mixtures. In June 2014, we added a fourth subplot in the mixtures. In each subplot, we measured sap flow on eight selected trees (hereafter referred to as sap flow trees). These subplots were selected because they were representative of the mean DBH across all plots. Within monoculture plots, we selected 8 trees per plot in the buffer zone for sap flow measurements. Selected trees met the following criteria: 1) of similar DBH to the mean plot DBH; 2) had crowns interacting aboveground; 3) located within a 10 m radius (the maximum length of the sap flow cables) of each other. Within the mixtures, we selected 8 trees per plot (4 *D. retusa* and 4 *T. amazonia*) based on these same criteria, plus one additional criterion: 4) Each mixture had sap flow sensors installed in one center *T. amazonia* and 3 of the 6 surrounding *D. retusa* in that group, and vice versa. We selected a total of 64 sap flow trees. For more information on the study design and experimental setup, see Chapter 1 (Figure 1-1).

2.2.3 Micrometeorological & soil moisture monitoring

Climate data were obtained from two meteorological (MET) stations located within the Agua Salud Project. From June 2014 through January 2015, MET data were collected from a tower managed by the Autoridad del Canal de Panamá (Meteorology and Hydrology Branch, Panama Canal Authority, Republic of Panama), while after February 2015 data were collected from a tower managed by the Smithsonian Tropical Research Institute. Climate data from the towers included air temperature (ºC) and relative humidity (RH, %) using an HMP60 (Vaisala, Vantaa, Finland), and precipitation (mm) using a 260-250-A tipping bucket (NovaLynx, CA, USA), vapor pressure deficit (VPD, kPa) was calculated from the air temperature and RH data following Allen et al. (1998). Small gaps (< 1 month) in the dataset exist due to either sensor malfunction or during the renovation of the tower and sensors. The start and end of the dry seasons, as well as the ENSO event, are documented by Paton (2016) and the seasons and ENSO event are highlighted in Figure 2-1.

Soil volumetric water content (VWC) was measured using DeltaT PR2 sensors (DeltaT, Cambridge, United Kingdom) at six soil depths (100, 200, 300, 400, 600, and 1000 mm) starting in December 2014. At monoculture sites, 3 trees with sap flow sensors were randomly selected. An access tube was placed 0.5 m distant from the bole of the tree in a random cardinal direction from the bole of the tree. In the mixtures, 12 access tubes were positioned 0.5 m from the bole of the tree. Each center tree had three access tubes and each surrounding tree had one access tube. Soil moisture measurements were collected for each tube every 1-4 days. A mean VWC was averaged for the first three soil depths (where season changes were obvious) and included in the models below. An ANOVA with a post-hoc Tukey test was performed to analyze mean VWC difference between treatments and depths.

2.2.4 Sap flow and growth

Sap flow was measured using the heat ratio method (HRM) (Burgess et al., 2001). On each tree, one sensor was installed 1.30 m above the base of the tree facing north. Each sensor contained three probes (a heater probe and two temperature probes, installed equidistantly upstream and downstream from the heater probe, 0.6 cm). Each temperature probe contained three thermocouples located at 0.5, 1.7, and 3.0 cm from the bark of the tree. A heat pulse was automatically sent to the sensors every 15 minutes. The speed of the heat (V_h) was calculated every 15 minutes according to Burgess et al., (2001):

$$V_h = \frac{k}{x}\ln(v_1 \,/\, v_2)3600 \qquad (\text{eq. } 1)$$

where *k* is the thermal diffusivity of green (fresh) wood, *x* is the distance in centimeters between the heater and either temperature probe, and v_1 and v_2 are increases in temperature from initial temperature at equidistant points downstream (v_1) and upstream (v_2). Heat pulse velocities were corrected (*Vc*) for errors (probe misalignment and wounding) following Burgess et al. (2001):

$$V_c = bV_h + \mathrm{c}V_h^2 + \mathrm{d}V_h^3 \qquad \text{(eq. 2)}$$

where b, c, and d are coefficients round in Table 1 of Burgess et al., (2001). Estimates of each tree's daily sap flux density (J_s) were obtained from *Vc* (Green et al., 2003) based on the period from April 1, 2014 through May 15, 2016:

$$J_s = \frac{\rho_d}{\rho_s}\left(\mathrm{MC} + \frac{C_{dw}}{C_s}\right)V_c \qquad \text{(eq. 3)}$$

where ρ_d is the density of sapwood, ρ_s is the density of water, MC is the volumetric water content of the sapwood, C_{dw} is the thermal conductivity of dry wood, and C_s is the thermal conductivity of water. We visited each site at least twice a week to download data, check sensors, and replace broken sensors. We changed the battery of each station at least once a week.

For comparison of J_s among treatments and species, we used the outer most thermocouple position (closest to the bark) which has the fastest J_s and is in the newest wood. For each sap flow tree, we measured the diameter at breast height (DBH, cm) each year between March and April. Diameter at breast height growth ($\mathrm{DBH}_{\mathrm{growth}}$, cm) was calculated as the difference between DBH in 2016 and DBH in 2014.

2.2.5 Leaf water potential (Ψ_L)

On all trees installed with sap flow sensors, we measured leaf water potential (Ψ_L, MPa) predawn (Ψ_{pd}) and midday (Ψ_{nd}) using a pressure chamber (PMS Instrument Company, Albany, OR, USA). During the dry season (which runs from late December through mid-April), we measured water potential on 3 branches of each sap flow tree every 2-3 weeks. In a few cases where trees grew too tall to collect leaves via a pole pruner (i.e., 4 trees in 2016 in one of the sites), Ψ_L was not measured. Finally, we did not collect leaves for *D. retusa* in either treatment during 2016 because the leaves had not fully flushed during the sampling period and if we had cut the few leaves that remained it would have affected J_s measurements.

We plotted Ψ_{pd} versus Ψ_{md} in relation to a 1:1 line. Based on the theoretical framework outlined in by Martinez-Vilalta et al., (2014), we calculated the slope of the linear line for each of the treatments for Pre-ENSO conditions (2014) and ENSO conditions (2015/2016). The slopes (σ) of the lines represent isohydric and anisohydric behavior (Coble et al., 2017; Martinez-Vilalta et al., 2014). In this framework, four distinct behaviors exist: strict isohydric ($\sigma = 0$), partial isohydric ($0 < \sigma < 1$), strict anisohydric ($\sigma = 1$), and extreme anisohydric ($\sigma > 1$). While this strict definition is useful when assessing larger datasets, as seen in Martinez-Vilalta et al., (2014), we use this framework as a relative comparison among the treatments to characterize the behavior of the species and treatments in pre-ENSO and ENSO conditions.

2.2.6 Statistical analyses

A total of 54 of the 64 trees were used for analyses. In the final data analysis, trees were excluded for the following reasons: (1) One tree died during the study due to canopy wind damage and (2) Other trees were removed from where greater than 20% of the data for that tree were missing due to broken sensors. We divided our data by ‘water years’ which were as follows: wet 2014 (normal wet season), dry 2015 (normal dry season), wet 2015 (drought wet season), and dry 2016 (drought dry season), to better assess the effect of drought on our measured variables.

To test for differences in DBH growth by treatment we ran an ANOVA with a post-hoc Tukey test. We performed an ANCOVA and post-hoc Tukey test to test for J_s differences by treatment. All J_s values were square-root transformed for analyses to meet normality standards and back transformed for figures. J_s and VPD were normalized for the hysteresis loop comparison by season, treatment, and year. Normalization of J_s was calculated by dividing each mean daily J_s by the maximum value of J_s. We computed normalized VPD with the same method. We ran a multivariate comparison to examine the effects of treatment, VPD, radiation, VWC, precipitation, and the interactions between treatment and meteorological variables on daily J_s. All variables, except for VWC and precipitation were log transformed to meet normality assumptions for the analyses. Relative importance metrics of environmental predictors were calculated using the R-package *relaimpo* (Grömping, 2006). Calculating relative importance values is a method that can be used when some of the regressors in a model are correlated, which is the case with our data. We calculated relative importance using two methods – LMG and LAST. LMG calculates the R^2 contribution averaged over orderings among regressors and LAST calculates each variables contribution when included last.

Ψ_{md} and Ψ_{pd} were calculated by averaging 3 leaves per tree over the course of 3-4 sampling periods during each dry season of 2014, 2015, and 2016. To compare differences of Ψ_L by treatment and year, we used a MANOVA and post-hoc Tukey test. We created a linear model for the relationship between Ψ_{pd} and Ψ_{md} for each treatment before and during the ENSO event. The slopes of the lines were used to compare relative behavior of the species and treatments. All metrics were performed using the statistical software R (R Core Team, 2017).

2.3 RESULTS

2.3.1 Micrometeorological and soil moisture conditions

The 2015-2016 year experienced an El Niño-Southern Oscillation (ENSO) event, which resulted in the third longest dry season on record since data collection began in 1925 in Panama (Paton, 2016). Generally, about 80% of the average annual precipitation falls between May and mid-December. Mean daily maximum and minimum temperatures are 32 and 23°C, respectively (http://striweb.si.edu/esp/physical_monitoring/descrip_bci.htm).

Precipitation in 2014, 2015, and 2016 totaled 2092 mm, 1473 mm, and 3071 mm, respectively in the Agua Salud Project site (STRI Physical monitoring unit). The 2015 precipitation was 30% less than the 2014 annual precipitation and 45% less than the 30-year mean annual precipitation for the region of 2700 mm (Ogden et al., 2013). Radiation during the wet season of the 2015 El Niño year was 41% times higher on average than the radiation during the wet season of 2014 (Figure 2-1c). VPD was 30% higher during the 2015 wet season (Figure 2-1b).

During the dry season of 2015 (which is the start of VWC sampling), the mean VWC was significantly higher for *D. retusa* monocultures ($p < 0.0001$) than *T. amazonia* monocultures or mixtures (Figure 2-1d). There was no significant difference between mean VWC for tubes within the same treatment over the study period. The mean VWC for all treatments combined was significantly lower during the dry season of 2016 (23.1 ± 0.18%) than the dry season of 2015 (25.2 ± 0.186) ($p < 0.001$) (Figure 2-1d).

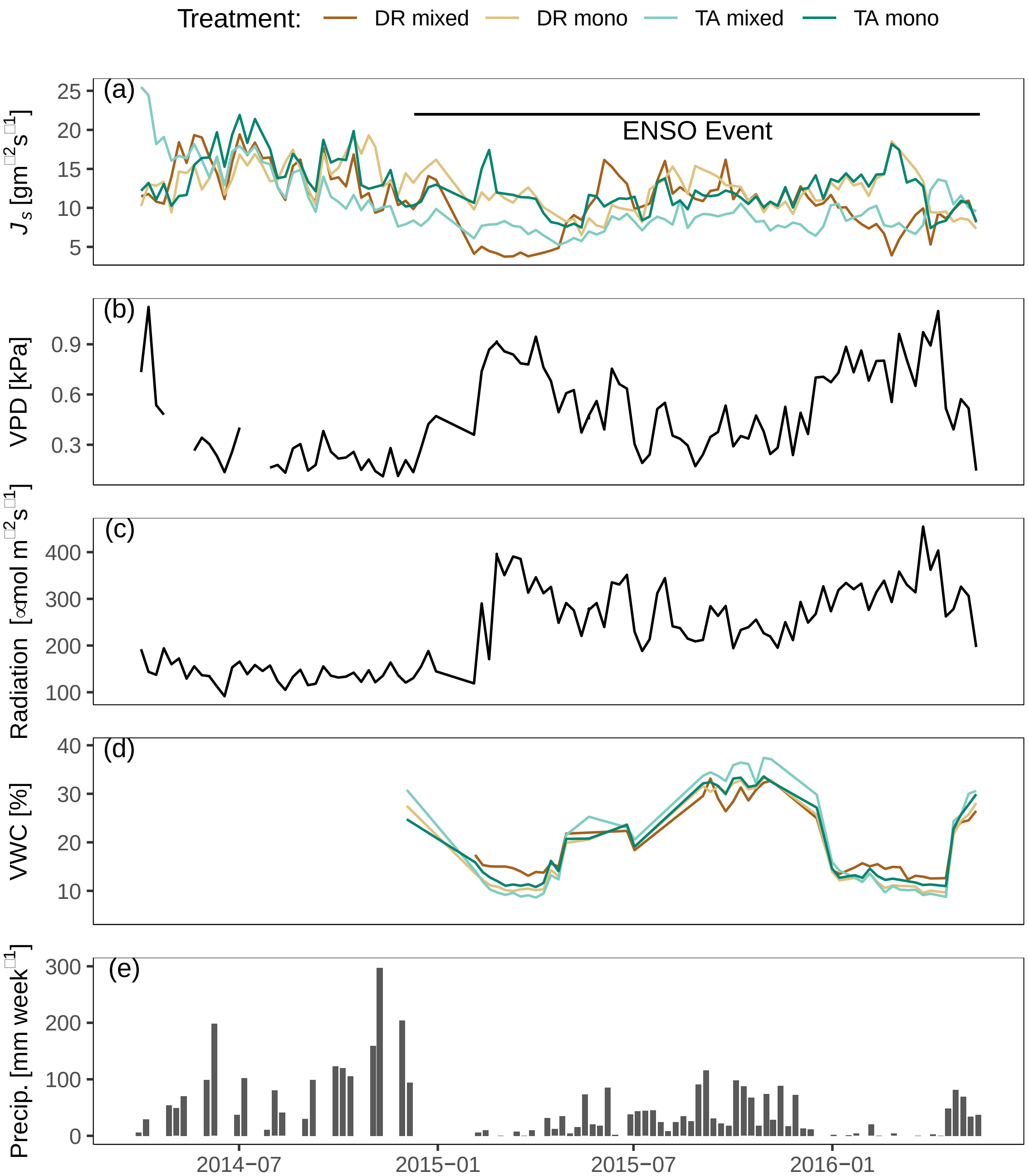

Figure 2-1. Weekly averages of (a) sap flux density (J_s; gm^{-2}s^{-1}), (b) vapor pressure deficit (VPD; kPa), (c) radiation (μmol m^{-2}s^{-1}), (d) volumetric water content (VWC, %), and weekly sum of (e) precipitation (mm week^{-1}). Colored lines represent averages of individual trees for the four treatments. DR monoculture: *D. retusa* trees in monocultures; DR mixture: *D. retusa* trees in mixtures; TA monoculture: *T. amazonia* in monocultures TA mixture: *T. amazonia* in mixtures. Shaded area represents the dry season. Black horizontal line in (a) signifies the ENSO event. Soil data not available before December 2014.

2.3.2 Sap flux density patterns and relationship with microclimate

Sap flux density (J_s) varied by season water year and among treatments. The highest mean J_s for all treatments occurred during the normal wet season of 2014 (Figure 2-2). During the normal dry season of 2015, both *D. retusa* and *T. amazonia* planted in the mixtures maintained higher J_s than when in the monocultures. The trees planted in mixtures also signicantly had higher J_s in the drought dry season of 2016 than the trees planted in monocultures ($p < 0.001$) (Figure 2-2). During the start of the drought (wet season 2015), *T. amazonia* had significantly lower J_s than the other three treatments ($p < 0.001$), the only water year where J_s of *T. amazonia* was significantly lower than that of the other three treatments.

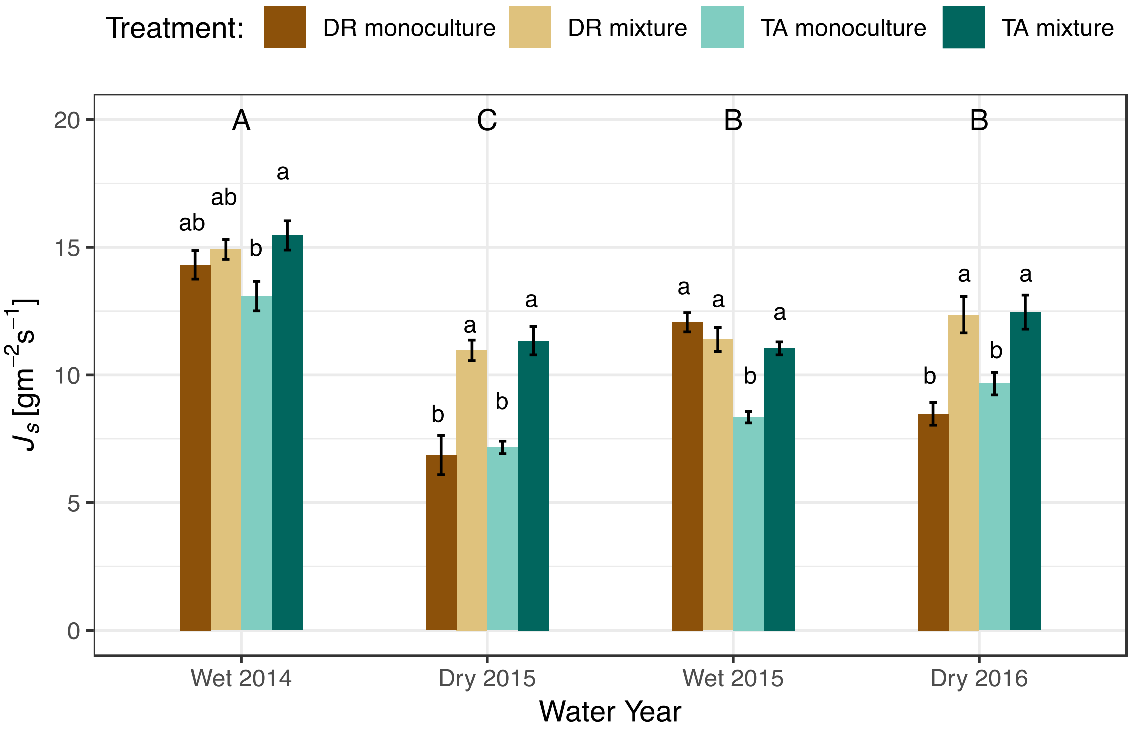

Figure 2-2. Mean daily sap flux density (J_s) by treatment and water year. Capitalized letters represent significant differences by water year based on ANOVAs and post-hoc Tukey tests ($p < 0.001$) and small letters represent significant differences treatments of the same water year based on ANOVAs and post-hoc Tukey tests ($p < 0.001$). Error bars are standard errors of the mean.

Both VPD and radiation had a significant logarithmic relationship with J_s during 2014 ($p < 0.0001$) (Figure 2-3). At VPD higher than 0.25 kPa, trees in the mixtures maintained significantly higher J_s than that in the monocultures. During both 2015 and 2016, we found a non-significant logarithmic relationship between J_s, radiation, and VPD. The relative importance of VPD, VWC, precipitation, and radiation on J_s varied by season and treatment (Table 2-1). In the monocultures, J_s of *D. retusa* was influenced by radiation and VPD during the wet seasons and VWC during the dry seasons. In monocultures of *T. amazonia*, J_s was influenced by radiation and VPD in the wet season of 2014 and dry season of 2015, respectively (Table 2-1). During the wet season of 2015 and dry season of 2016, VPD and VWC exerted similar controls on J_s. In mixtures, J_s of *D. retusa* was originally influenced by VPD, but during the wet season of 2015 and dry season of 2016, VWC had the greatest influence (0.74-0.97). In mixtures of *T. amazonia* J_s was strongly influenced by VPD and radiation in 2014 and the dry season of 2015, but then transitioned to VWC having the greatest influence during the wet season of 2015 and the dry season of 2016, when VWC had the greatest influence on J_s. (0.63-0.92).

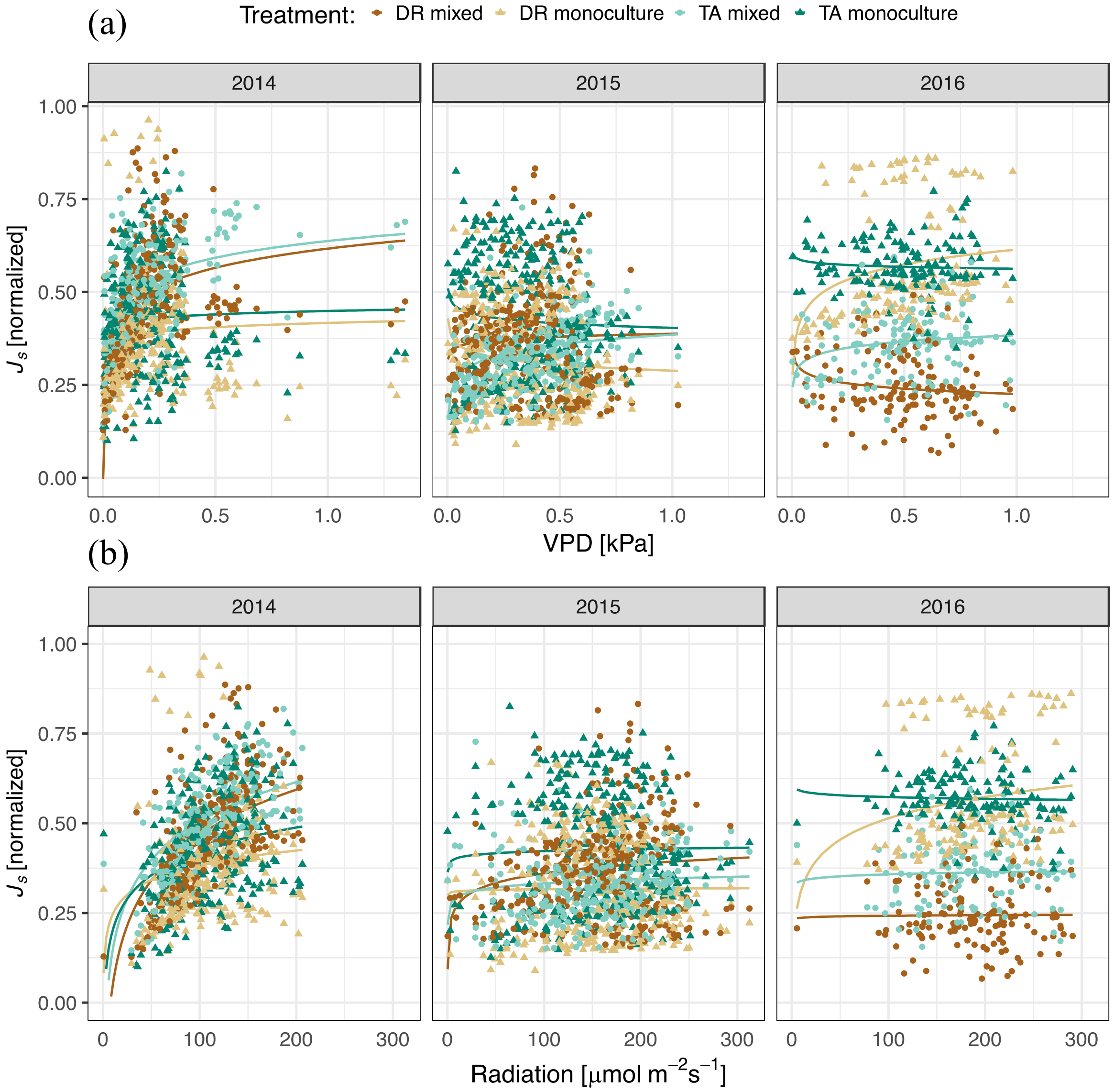

Figure 2-3. Relationship between normalized J_s and (a) vapor pressure deficit (VPD, kPa) and (b) radiation (μmol $m^{-2}s^{-1}$). Lines represent relationship between VPD or radiation and normalized J_s by treatment (DR mixed, *D. retusa* in mixtures; DR monoculture, *D. retusa* in monocultures; TA mixed, *T. amazonia* in mixtures; TA monoculture (*T. amazonia* in monocultures). Significant logarithmic relationship between radiation/VPD and normalized J_s for 2014 only.

Table 2-1. Relative Importance Metrics of Sapflux Density. Treatment includes four study treatments: DR mono: *D. retusa* trees in monocultures; DR mixed: *D. retusa* trees in mixtures; TA mono: *T. amazonia* in monocultures TA mixed: *T. amazonia* in mixtures. Predictor variables include: VPD: vapor pressure deficit, VWC: volumetric water content, precipitation, and radiation. Relative importance values sum to 1.00 for each predictor by treatment. VWC was not included in wet season 2014 analyses because dataset is not complete. Gray shaded boxes highlight metric with the highest relative importance value by treatment, method, predictor, and season.

Treatment	Method	Predictor	Wet 2014 Rel. imp. (%)	Dry 2015 Rel. imp. (%)	Wet 2015 Rel. imp. (%)	Dry 2016 Rel. imp. (%)
DR mixed	LMG	VPD	0.79	0.81	0.09	0.20
	LMG	Radiation	0.20	0.04	0.05	0.05
	LMG	Precipitation	0.01	0.00	0.00	0.01
	LMG	VWC	na	0.15	0.87	0.74
	LAST	VPD	0.71	0.93	0.08	0.00
	LAST	Radiation	0.28	0.06	0.05	0.03
	LAST	Precipitation	0.01	0.00	0.00	0.00
	LAST	VWC	na	0.02	0.87	0.97
DR mono	LMG	VPD	0.47	0.03	0.43	0.10
	LMG	Radiation	0.53	0.00	0.52	0.10
	LMG	Precipitation	0.00	0.00	0.00	0.00
	LMG	VWC	na	0.98	0.05	0.80
	LAST	VPD	0.39	0.00	0.29	0.12
	LAST	Radiation	0.61	0.00	0.53	0.12
	LAST	Precipitation	0.00	0.00	0.00	0.00
	LAST	VWC	na	1.00	0.19	0.76
TA mixed	LMG	VPD	0.49	0.44	0.13	0.25
	LMG	Radiation	0.50	0.50	0.04	0.10
	LMG	Precipitation	0.01	0.00	0.00	0.01
	LMG	VWC	na	0.01	0.83	0.63
	LAST	VPD	0.48	0.40	0.07	0.00
	LAST	Radiation	0.48	0.58	0.00	0.08
	LAST	Precipitation	0.04	0.00	0.00	0.01
	LAST	VWC	na	0.02	0.92	0.91
TA mono	LMG	VPD	0.43	0.73	0.42	0.15
	LMG	Radiation	0.55	0.01	0.12	0.05
	LMG	Precipitation	0.01	0.00	0.00	0.00
	LMG	VWC	na	0.26	0.45	0.80
	LAST	VPD	0.28	0.83	0.42	0.23
	LAST	Radiation	0.68	0.01	0.11	0.09
	LAST	Precipitation	0.04	0.00	0.00	0.00
	LAST	VWC	na	0.14	0.48	0.67

Methods are LMG (overall model contribution averaged over orderings of predictors) and LAST (model contribution given all other predictors already included in the model). Analyses were divided by season (dry season 2014 and wet season 2015). Gray shading represents highest relative importance value by treatment, method, and season.

For all treatments, a clockwise hysteresis was present between normalized hourly J_s and normalized vapor pressure deficit (VPD) for the 2014 wet season (Figure 2-4). For the 2015 wet season and 2016 dry season (drought year), a counterclockwise figure-eight hysteresis was present between normalized hourly J_s and normalized VPD (Figure 2-4). For each treatment, the hysteresis slope was significantly influenced by treatment and water year (Appendix B, Table B-1). Hysteresis slopes were significantly steeper in during the 2014 wet season than in 2015 or 2016 for all treatments.

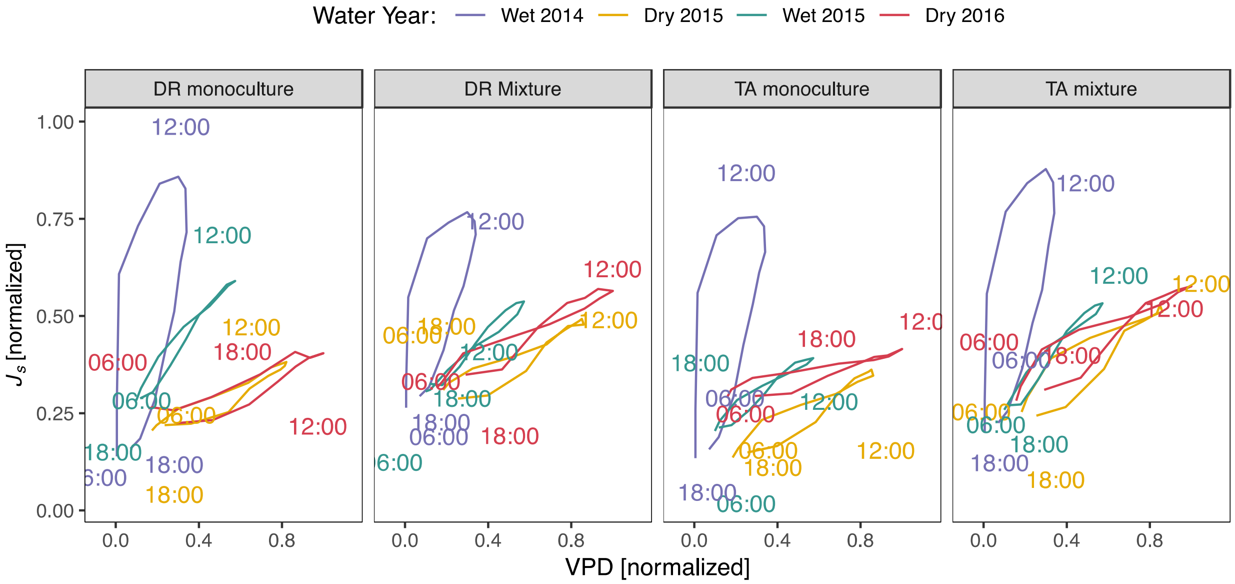

Figure 2-4. Hysteresis of normalized sap flux density (J_s) by normalized vapor pressure deficit (VPD) and treatment (top x-axis). For each treatment, hystresis loops divided by water year (normal years: Wet 2014 and Dry 2015; drought years: Wet 2015 and Dry 2016). Clockwise hysteresis occurring during 2014 wet season for all treatments and a counterclockwise figure-eight hysteresis for all treatments in during the 2015 wet season and 2016 dry season. Hourly time stamps for dawn, midday, and dusk included in figure.

Growth (DBH, cm) from 2014 to 2016 varied by species and treatment (Figure 2-5). *Terminalia amazonia* in the mixtures had significantly greater DBH growth than any other treatment, while *D. retusa* in the mixtures had the least growth than the other treatments (Figure 2-5b). Growth was significantly correlated to J_s for all treatments and years ($p < 0.001$).

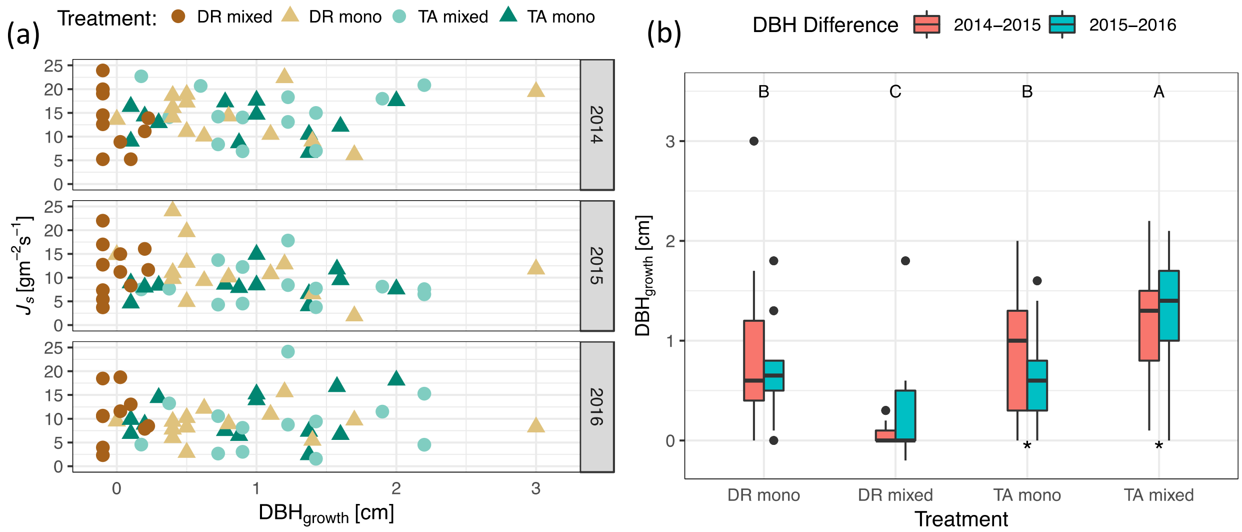

Figure 2-5. (a) Diameter at breast height growth from 2014 to 2016 (DBH; cm) versus sap flux density (J_s) by treatment and (b) average DBH$_{growth}$ (cm) for 2014-2016 and 2015-2016 by treatment. Letters (b) represent significant differences by year for each treatment based on ANOVAs and post-hoc Tukey tests. The * below TA mono and TA mixed boxplots in (b) represent significant differences in DBH growth between the two years. Horizontal lines inside the boxes (b) represent the median while the upper and lower box boundaries represent the first and third quartiles. Dots represent points that fall beyond these ranges.

The average Ψ_{md} of *D. retusa* in mixtures and monocultures in 2014 was -3.2 and -3.5 MPa, respectively, with no significant difference between the two ($p = 0.35$) (Appendix B, Figure B-1). *Dalbergia retusa* trees growing in mixtures and monocultures showed a significant decrease of Ψ_{md} from 2014 to 2015 ($p < 0.001$, $p = 0.02$, respectively) (Figure 2-6a,b). Ψ_{md} of *T. amazonia* in monocultures declined from 2014 to 2015 and 2016, but there was no difference between 2015 and 2016 ($p < 0.001$). In contrast, the Ψ_{md} of *T. amazonia* in the mixtures declined from 2014 to 2015 but then increased significantly in 2016 compared to 2015 (Figure 2-6). Mean

Ψ_{md} during the dry season of 2014 was significantly lower for *T. amazonia* than *D. retusa* ($p < 0.001$).

The relationship between Ψ_{pd} and Ψ_{md} was linear for all treatments except *T. amazonia* monocultures prior to the ENSO event (Figure 2-7a). The slope (σ) of the line for *D. retusa* in mixtures was greater than 0.5 while the σ of *D. retusa* in monocultures was less than 0.5. During ENSO conditions, *T. amazonia* in mixtures and monocultures had a σ greater than 1.00 (Figure 2-7b).

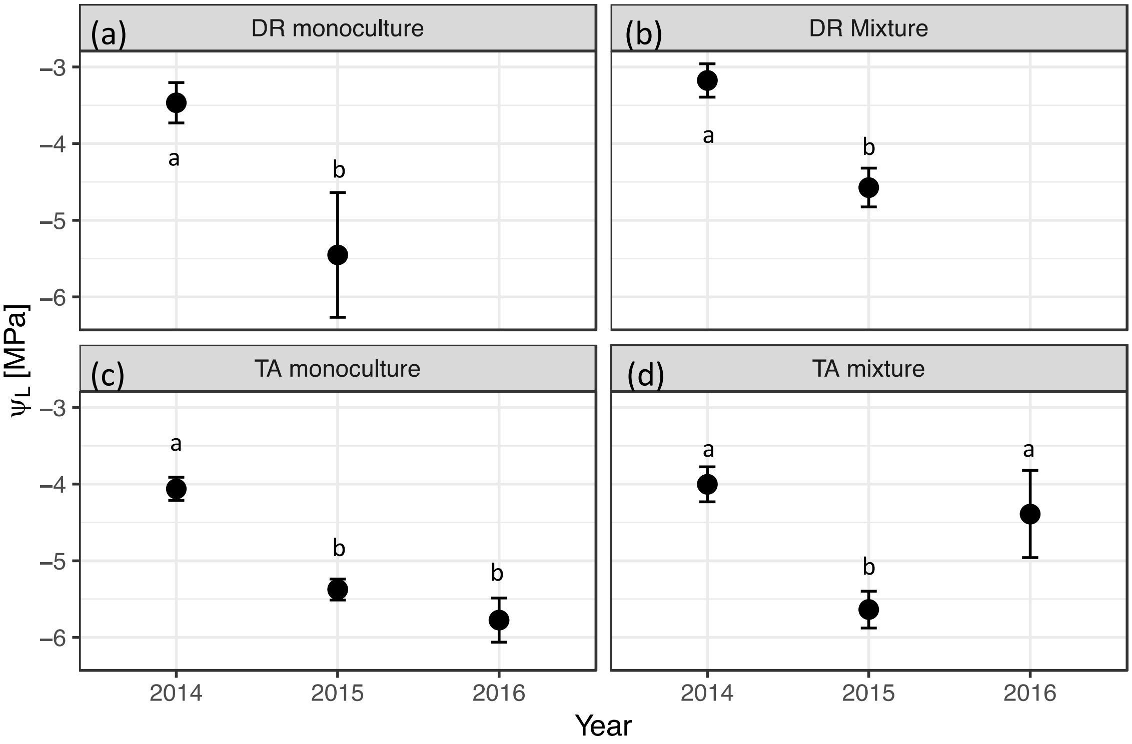

Figure 2-6. Midday water potential (Ψ_L; MPa) by treatment for each year during the dry season. The 2014 and 2015 dry seasons represent normal dry seasons while the 2016 dry season represents a drought dry season. Treatments include: (a) *D. retusa* monocultures, (b) *D. retusa* mixtures, (c) *T. amazonia* monocultures, and (d) *T. amazonia* mixtures. Letters represent significant differences by treatment for each year. Based on ANOVA and post-hock Tukey test. No data available for *Dalbergia retusa* in 2016 because leaves had not fully flushed during sampling campaign.

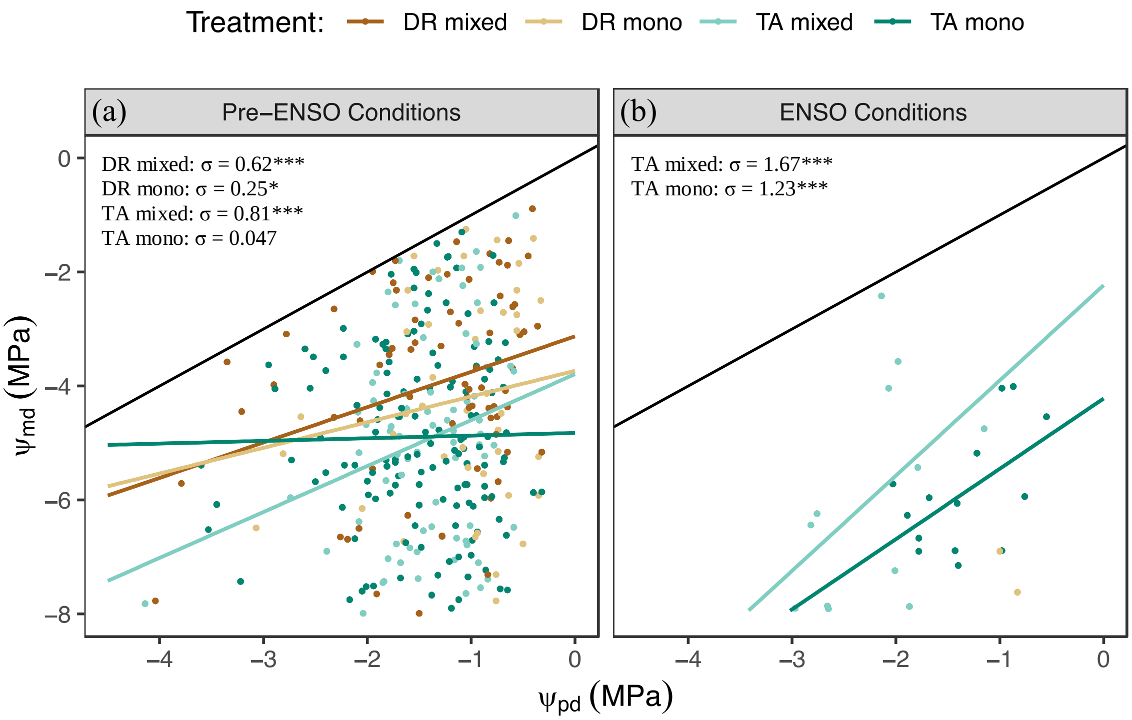

Figure 2-7. (a) Pre-ENSO Conditions (2014/5 dry season) and (b) ENSO Conditions (2016 dry season) pre-dawn leaf water potential (Ψ_{pd} MPa) and midday leaf water potential (Ψ_{md} MPa). Solid black line represents 1:1 line. Significance of slopes based on linear regression shown by (*): *0.05 significance, ***0.0001 significance. The slope (σ) shown for all treatments during Pre-ENSO Conditions (including TA mono, which was not significant). During the ENSO Conditions, neither *D.* retusa treatment showed a significant relationship between Ψ_{pd} and Ψ_{md}. Values of σ closer to zero represent more isohydric behavior while slopes closer to 1 represent more anisohydric behavior (Martínez-Vilalta et al., 2014). Points represent leaf water potentials for an individual tree. Measurements were taken during the dry season of 2014, 2015, and 2016 every three weeks starting in February and ending in April. *Dalbergia retusa* did not fully flush leaves during the sampling period in 2016 and had minimal leaves in 2015.

2.4 DISCUSSION

2.4.1 Drought resistance stronger in mixtures than monocultures

We hypothesized that trees in mixtures would be more resistant to drought than trees planted in monocultures. We found this to be true where J_s of the trees in mixtures was less than those planted in mixtures during the drought period (Figure 2-2). We also found evidence of this resistance during a normal dry season, where trees in mixtures still maintained higher J_s than those planted in monocultures. One reason that trees in mixtures may have been able to maintain higher J_s than trees in monocultures is if total soil moisture is greater in the mixed plantings. However, we did not find differences in VWC that could explain differences in J_s. Although the roots of both *T. amazonia* and *D. retusa* are generally in the upper 40 cm of the soil, there is evidence that *T. amazonia* sends deeper roots that are deeper than the length of our soil probes. *Terminalia amazonia*'s ability to access deeper water storage that is unlikely to change dramatically during a drought, could help *T. amazonia* maintain high J_s. Further, *T. amazonia* in mixtures had higher growth rates than any other treatment (Figure 2-5b). Giardina et al., (2018) showed that taller trees are often less sensitive to changes in precipitation or VWC than shorter trees, largely due to greater access to deeper soil water storage. There is evidence that during a drought, trees put more resources into roots than the aboveground compartment to access deeper soil layers. During both dry seasons in our study, soil VWC in the upper 40 cm was significantly lower for *D. retusa* in the monocultures compared to the mixtures, which suggests that *D. retusa* monoculture trees may have experienced greater competition for soil water, leading to declines in J_s. Alternatively, *D. retusa* in monocultures were also exposed to full radiation throughout the day, which may have led to greater stomatal closure to prevent hydraulic failure, contributing to the reduced J_s. In contrast, *D. retusa* in mixtures were partially shaded, making the microclimate conditions less severe during the drought conditions.

Indeed, microclimate conditions did influence changes in J_s across seasons and years. Our second hypothesis, that radiation and VPD would exert the strongest controls on J_s in monocultures early in the drought and later switch to VWC was supported (Table 2-1). Both J_s of *T. amazonia* in the mixtures and monocultures was driven largely by VPD and radiation prior to the drought event, but by the end of the drought event, VWC was the primary driver of J_s. The pattern for *D. retusa* was particularly interesting as well. While J_s in *D. retusa* in the mixtures was driven by VPD (even during the first dry season of 2015), VWC was the main driver of J_s starting during the first wet season of the ENSO event (2015). In contrast, J_s for *D. retusa* in mixtures was primarily driven by VWC during both dry seasons, but a combination of VPD and radiation during the wet seasons. Evidence from work in a nearby secondary forest suggests that older canopy trees are often more coupled with the atmosphere than younger trees that are primarily driven by soil interactions (Bretfeld et al., 2018). Arguably, *T. amazonia* behaved like an older canopy tree, where J_s was primarily driven by VPD and radiation. However, this behavior changed during the drought, where *T. amazonia* transitioned from being controlled by atmospheric drivers to soil drivers. This suggests that generalizations about the effect of different MET variables on J_s should be be closely considered under different climatic conditions as well.

The transition from regulation of VPD on J_s to regulation of VWC on J_s was particularly obvious in the hysteresis of VPD and J_s over the course of the ENSO event. A strong hysteresis suggested regulation of stomatal to prevent hydraulic failure (Bretfeld et al., 2018; Sevanto et al., 2014). While each treatment showed a strong hysteresis during the normal wet season of 2014, where J_s declined in the afternoon, there was not a strong hysteresis from the dry season of 2015 onward, suggesting other mechanisms are influencing J_s as well. Radiation during the wet season of 2015 was 41% higher than the wet season of 2014, and could have contributed to partial stomatal closure to prevent hydraulic failure or increased conductance if water is not limiting.

2.4.2 Mixtures may be less water stressed than monocultures, but it is species-specific

Our hypothesis that mixtures would be more moisture stressed than monocultures, as indicated by lower midday water potential, is only partially supported. Though *Terminalia amazonia* was significantly more water stressed than *D. retusa* (Appendix B, Figure B-1) during a normal dry season, during the dry season of 2015, only *D. retusa* in mixtures was significantly less water stressed than the other three treatments. This could be partially influenced by the greater VWC in the *D. retusa* mixtures, or the more favorable microclimate conditions (i.e., lower radiation). By 2016, however, we saw significant differences in Ψ_{md} for the first time between *T. amazonia* mixtures and monocultures, with the mixtures being significantly less water stressed than the monocultures. Based on our work that suggests *T. amazonia* in mixtures are larger than those in the monocultures, we suspect that rooting depths of *T. amazonia* in the mixtures was deeper and helped prevent *T. amazonia* from becoming overly water stressed at the end of the drought.

One explanation for this trend could be that since *D. retusa* sheds its leaves, the *T. amazonia* in the mixtures could recover quickly by foraging for unexploited nutrients. Additional nutrients provided by *D. reutsa* may have also allowed *T. amazonia* to maintain higher DBH growth than all the other treatments. This interspecific facilitation has been shown in some mixtures of European tree species in South Germany (Pretzsch et al., 2013), but not all mixtures have shown positive responses to mixing (Forrester et al., 2016), underlining the importance of species selection. These results suggest that simply mixing species will not necessarily result in complementary or facilitative interactions. However, careful selection of species for traits that might enhance favorable interactions can lead to better predictions of complementary and faciliatiave interactions.

2.4.3 Species-specific characterization across isohydry-anisohydry spectrum

It is important to note that within this anisohydric-isohydric framework there are critical thresholds that determine isohydric or anisohydric behavior, based on the slope of the line between midday and predawn leaf water potentials (Martinez-Vilalta et al., 2014). Further, many studies have shown that species operate on a continuum of spectrum of behaviors (Klein 2014, Roman et al 2015). Prior research suggested that stomatal regulation of water potential would be stronger in *D. retusa* than *T. amazonia*. We hypothesized that that the mixtures would behave closer to isohydric species than anisohydric species (i.e., have greater control of stomata) during a drought. We did find that *D. retusa* showed more isohydric behavior than *T. amazonia* prior to the ENSO event (Figure 2-7). However, both species had slopes (relationship between Ψ_{md} and Ψ_{pd}) less than 1 which suggests isohydric behavior. The greater stomatal control exhibited by *D.* retusa in monocultures compared to mixtures may have been due to different microclimate conditions. In the monocultures of *D. retusa*, radiation was greater than the radiation *D. retusa* experienced in the mixtures (because of shading from *T. amazonia*). As such, *D. retusa* in the monocultures may have needed to regulate stomatal openings better to prevent hydraulic failure. Since *D. retusa* did not flush leaves during the final dry season (at the end of the drought), *D. retusa* may delay flushing during extreme drought years to prevent hydraulic issues related to dryness. This tends to be the case in the temprate zone where semi-deciduous and deciduous species have been shown to delay leaf flushing or have early leaf abscission to avoid drought conditions (Hoffmann et al 2011). *Terminalia amazonia*, however, behaved very differently before and during the ENSO event. We had predicted that *T. amazonia* would have more isohydric behavior during the drought, but found it to move in the direction of anisohydric behavior.

The lower stomatal control observed for *T.* amazonia growing in mixtures versus monocultures may have been due to the deeper rooting depth of *T. amazonia*, that allowed *T. amazonia* access to deeper sources of water. In some cases, there is strong evidence trees osmotically adjustduring drought, which could also explain why *T. amazonia* tolerated declines in soil water potential. Osmotic adjustment theoretically maintains turgor-dependent processes at lower water potentials and delays desiccation (Schwendenmann et al., 2010). This does not explain the differences we saw between treatments

The isohydric and anisohydric framework also makes assumptions that isohydric species are more drought avoidant while anisohydric ones are more drought resistant, this assumption may not fully explain a species resilience to drought. For instance, generally anisohydric species are characterized as being more vulnerable to hydraulic failure (Martinez-Vilalta et al., 2014), a combination of growth rates, wood specific gravity, and vessel wall strength can change a species ability to be resilient to drought. Some studies suggest that fast-growing tropical trees have high rates of drought-included mortality, particularly from hydraulic failure (McDowell, 2011). This is based in the fundamental theory that slower growing trees, which typically have higher wood specific gravity (Wright et al 2004), have more robust xylem that are less susceptible to cavitation (Eller et al., 2018). Both *T.* amazonia and *D.* retusa have high wood specific gravity and this may have buffered them from issues of caviation. However, faster growing species, which generally have faster turnover of xylem vessels, may prevent cavitation through capitance, which reflects the stored water in the stem that can protect xylem from drops in soil potential (Meinzer et al., 2008). Stem refilling in drought-stressed trees is also common, especially in regions with a strong dry season (Pfautsch and Adams, 2013).

2.5 CONCLUSIONS

Our results provide strong incentive for selecting *T. amazonia* and *D. retusa* for plantation forestry in the seasonally dry tropics of Panama. In both treatments, the species not only survived the drought, which is an important consideration as droughts are predicted to increase in intensity and duration in the future (Allen et al., 2010), but were able to resistant drought when planted in mixtures. Due the projected increase in drought duration and severity, our results provide incentive for planting mixture over monocultures. *Terminalia amazonia* in mixtures were less stressed than when planted in monocultures while *Dalbergia retusa* was less water stressed than *T. amazonia* overall. *Dalbergia retusa* even delayed leaf flushing during the drought year, showing that it may shift water regulation strategies depending on the duration or severity of a drought to prevent hydraulic failure.

Our work also emphasizes that species mixtures may increase the buffering capacity such that species in mixtures can maintain higher J_s than in monocultures during dry periods. Unfavorable conditions, such as limited water supply, may enhance complementary interspecific interactions (Pretzsch et al., 2013), providing a strong rationale for selecting mixed plantings over monoculture plantings. However, we do not have evidence that VWC became limiting to growth or water use of the study species, and thus further exploration into how water limitation may affect water regulation of planted mixtures and monocultures is necessary.

Even though *T. amazonia* and *D. retusa* reduced Js during the drought compared to a normal year, a potential negative consequence is that if trees in mixtures continue to use more water than monocultures, they may be more susceptible to hydraulic failure than monocultures.

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CHAPTER 3

CAN PLANTED NATIVE TREE SPECIES PLANTATIONS COMPETE WITH TEAK PLANTATIONS FINANCIALLY AND IN TERMS OF BOTH CARBON SEQUESTRATION AND WATER REGULATION?

ABSTRACT

Terrestrial ecosystems provide a great deal of goods and services that benefit human well-being. Plantations provide timber, but also support regulatory services like carbon (C) sequestration and water regulation. International agreements and payment for ecosystem services programs are putting a value on C storage, but pricing on water regulation is less common even though issues of water quanity and quality are becoming increasingly important. The present study compares growth, economic viability, C storage, and transpiration of native species (*Dalbergia retusa* and *Terminalia amazonia*) in monoculture and mixed plantations to a non-native species (*Tectona grandis*) in monoculture plantations. *Dalbergia retusa* in monocultures outperformed all other plantations economically, with a net present value of unique revenues and costs (NPV*) of 318,836 US$ ha^{-1} at 6% interest. *Dalbergia retusa* also had the highest mean C storage over the rotation (78.50 t C ha^{-1}) and lowest transpiration rates (0.20 mm day^{-1}). Mixed plantings of the native species ranked second in terms of NPV*, C storage, and transpiration rates. These projections provide evidence that native species can not only compete financially with *T. grandis*, but they can compete in terms of C storage and lower transpiration rates as well.

3.1 INTRODUCTION

Tree plantations are considered an economical way to promote reforestation of degraded tropical lands (Paul et al., 2015), but only recently has information become available regarding species survival and growth under different precipitation and soil fertility conditions (Hall and Ashton, 2016; Mayoral et al., 2017). Plantations also represent an alternative strategy to decrease pressure on natural forests for timber production and represent a significant carbon (C) sink (Griscom and Ashton 2011). In fact, it is estimated that one hectare of sustainable forest plantation could offset 5-20 ha of deforestation (Dixon, 1995). Plantations continue to support communities in terms of carbon sequestration that rely on timber trade as an important source of income and continue to grow in popularity in the tropics.

In Panama, total forest cover is 4,666,096 ha, 65,457 ha (< 2%) of which is in plantation (FAO 2015). Although plantations account for less than 2% of Panama's forest cover, the emphasis is on the non-native species. For example, in 2012 over 2,744 ha of non-native species were planted, compared to just under 542 ha of native species (FAO, 2015). Even though roughly 90% of plantations are comprised of *Tectona grandis* due to its high economic value globally (FAO, 2010), this non-native species is not adapted to the nutrient poor soils that exist on most lands available for reforestation in Panama. Although *T. grandis* has been shown to grow well in India (Chaturvedi and Raghubanshi, 2015), the growth rates in the Panama Canal Watershed (PCW), where major reforestation efforts are being promoted, are poor. Since *T. grandis* is ill adapted to the PCW soils, a rotation age of 25 years or more is common in Panama (Silver et al., 2000; Stefanski et al., 2015), 10 years longer than the rotation age in parts of India

(Chaturvedi and Raghubanshi, 2015). The increased rotation length of *T. grandis* on poor quality sites is often not considered before establishment of a *T. grandis* plantation in Panama.

In addition to species selection, designing the plantation is another central consideration to plantation management. The current plantation designs include monocultures planted in 3 m by 3 m spacing (Wishnie et al., 2007). Although monocultures are easier to manage, they have the potential to be particularly susceptible to insect outbreaks. Planting mixtures has not only been shown to reduce insect damage risk (Plath et al., 2011), but mixed planting could potentially space out revenue streams through time if species with different rotation ages are selected (Ashton and Kelty, 2017). Additionally, with timber markets notably volatile, diversifying the plantation species might buffer against this volatility and reduce financial risk to the landowner and hedge against unexpected mortality due to climate changes or pathogens (Piotto et al., 2010). A potential additional benefit is that mixed plantings may reduce the need for intermediate treatments, such as pruning, if trees that are combined act as 'trainers', keeping the stems straight and branch free.

Few plantation species can compete economically with *T. grandis* when it sells for prices seen outside of Panama (900 \$US m^{-3}) (Chaturvedi and Raghubanshi, 2015), however, *T. grandis* in Panama sells closer to 300 \$US m^{-3} (Stefanski et al., 2015). Two potential alternatives, that are valuable and native to Panama include *Dalbergia retusa* and *Terminalia amazonia*, both of which have been shown to grow well on infertile or degraded soils (Mayoral et al., 2017). While *D. retusa* has a longer rotation lengths than *T. grandis* by 5-10 years (Chaturvedi and Raghubanshi, 2005), the price per cubic meter is significantly higher. Additionally, *D. retusa* does not necessarily need to grow straight, as would be typically required of most commercial trees, because it is used primarily as a craft wood. In contrast, *T. amazonia* is a fast-growing species that can reach rotation age in 20 years or fewer. International markets are not as developed as for the previous two species, but *T. amazonia* can be used in similar applications as *T. grandis*, and thus has a strong potential to supplement or replace *T. grandis* in some markets.

Given the history of planting *T. grandis* in Panama, the net present value (NPV) of native species in monocultures or mixtures would have to considerably exceed the NPV of *T. grandis* for a small landowner to feel comfortable choosing one of the native species. An emerging strategy, however, to motivate landowner decision-making is through markets like Payment for Ecosystem Services (PES) that put a price on services such as carbon (C) sequestration or water regulation. International programs like REDD+ place a heavy emphasis on the benefit of C-sequestration of forests and plantations and markets for water already exist in Mexico (Hall et al., 2015) and could become more popular in the next few decades as water resources become more limiting. Average C storage by agroforestry globally has been estimated to be between 9 and 63 t C ha^{-1} depending on the region (Schroeder 1994), with temperate regions typically resulting in higher C storage due to longer rotation lengths. However, there is considerable variability in C storage among species within the same region. For example, *T. amazonia* in 10-year old plantations in Panama stored 82.5 t C ha^{-1} while two other species, *Virola koschnyi* and *Dipteryx panamensis* stored 37.0 and 102.6 t C ha^{-1}, respectively (Montagnini and Nair, 2004).

Water markets are less developed, but scientific evidence already demonstrates the important role trees play in water regulation. Evidence from the Panama Canal Watershed that forested landscapes act as sponges – absorbing water during the wet season (flood mitigation) and releasing water during the dry season (alleviating water shortages) (Ogden et al., 2013) lends insite into the potential benefit of forested areas. Plantations are a valuable component in the water cycle and selected species should be considered in landscape management decisions for both hydrologic and economic reasons. In addition to an economic comparison among *T. grandis, T. amazonia, D. retusa,* and *T. amazonia/D. retusa* mixtures, the quantity of C stored and the annual transpiration (*E*) are two key factors that may make one plantation more desirable than another. While C storage is often cited in the literature, annual transpiration of plantations is more difficult to obtain. Our paper approaches plantation species selection from an economic, C storage, and transpiration perspective to open the possibility for future PES schemes in the PCW and addresses the following:

(1) Can monocultures and mixtures of native species outcompete *T. grandis* monocultures financially on infertile sites?
(2) Can native species of *T. amazonia* and *D. retusa* store more C than *T. grandis* over the course of a rotation?
(3) Can native monoculture and mixed plantations of *T. amazonia* and *D. retusa* transpire less water than *T. grandis* monocultures?

3.2 METHODS

3.2.1 Site Description

The study was conducted in the Agua Salud Project site within the Panama Canal Watershed (9°13’ N, 79°47’W, 330 m amsl). The topography is characterized by short, steep slopes (Hassler et al., 2011; Mayoral et al., in review) and the soils are silt clay to clay with pH values ranging from 4.4 to 5.8 (van Breugel and Hall, 2008). We worked in a 75 ha native species plantation and

30 ha *Tectona grandis* plantation that were established in 2008 (Appendix C, Figure C-1 & Figure C-2). We focused on two of the native species – *Terminalia amazonia* and *Dalbergia retusa* for their hypothesized physsiologicaly complementary interactions (Chapters 1 & 2) and market value both nationally and internationally. Plots of monocultures of *D. retusa* (n = 12), monocultures of *T. amazonia* (n = 11), mixtures (n = 13), and monocultures of *T. grandis* (n = 21) were randomly distributed across two blocks. Each native species plot had a measured core plot comprised 81 trees planted in 3 m by 3 m spacing (see Chapter 1 Figure 1-1). The teak plots were 25 m by 25 m with trees also planted in 3 m by 3 m spacing. Prior to plantation establishment, the land was cleared of forest in the 1970s and the subsequent predominant land use was for cattle grazing (Weber and Hall, 2009). Since tree establishment in 2008, yearly understory cleanings occurred from May through August to prevent additional competition with the planted trees.

3.2.2 Sampling design

The sampling design to estimate stand volume, net present value, equal annual annuity, carbon sequestration, and transpiration employed a combination of intensive and extensive measurements. Diameter at breast height (DBH) and height (H) in the core of the plots were measured every year in the native species plantations starting the year after planting. For the teak plantations, DBH and H were measured in the core area every year starting in 2014 in the plots were transpiration was also measured (4 plots).

3.2.3 Volume, Net Present Value (NPV), Equal Annual Annuity (EAA) projections

We used inventory data (DBH) through year 8 for volume calculations. After year 8, we modeled DBH growth to predict to predict future DBH until the selected harvest age. Mean annual DBH increment (MAI_D) and mean annual height increment (MAI_H) by species and treatment at the study site during the first 8 years were used to predict future years (Table 3-1). We calculated basal area for each tree (BA, m^2) from DBH at each site and then multiplied by 0.5, based on the equation by Petit and Montagnini (2004), to calculate volume, which is the application of a basal area to volume ratio. To calculate stand volume at each age, we multiplied the tree volume by the number of trees in the plot at each age class. We selected three distinct rotation ages based on growth projections. Since the study sites are on marginal lands, the MAI was lower than that of other sites in Panama (Hall et al., 2011) and thus the rotation ages were longer than reported elsewhere in the literature. We selected a rotation age of 30 years for *D. retusa*, 25 years for *T. amazonia*, and 25 years for *T. grandis*. We assumed 1,111 trees were planted per hectare (based on 3 m by 3 m spacing) at the initial plantation establishment. At each successive age, we estimated native species mortality of 2% based on site specific mortality rates (Mayoral et al., 2017). We selected a 2% mortality for the teak as well to assume each species had an equal probability of survive throughout the rotation.

Table 3-1. Summary of inventory data for each treatment. Diameter at breast height [DBH, cm] and height [m] of trees are means with standard deviations. Mean annual increment [MAI height; m] and MAI [DBH; cm] are projected MAIs calculated based on 8 years of inventory data on plantations.

Species	Treatment	DBH [cm]	Height [m]	MAI [Height; m]	MAI [DBH; cm]
D. retusa	Monoculture	3.34 (1.00 - 8.1)	4.22 (1.43 - 8.76)	1.2	0.9
	Mixed	2.98 (1.00 - 7.7)	3.97 (1.18 - 7.42)		
T. amazonia	Monoculture	8.13 (1.05 - 18.2)	8.87 (2.14 -15.07)	1.8	1.7
	Mixed	9.36 (1.10 - 18.1)	8.88 (1.87 - 14.29)		
T. grandis	Monoculture	8.06 (0.90 - 14.1)	7.21 (0.78 - 13.93)	1.2	0.9

All removals were forecasted based on our own modeled growth and general timing of harvests noted in studies across Panama. Trees were removed during a pre-commercial thinning (PCT) and commercial thinning (CT) (Table 3-2) in all treatments. The timing (7 years) of the PCT for *T. amazonia* was selected because growth had stalled on the plantation by age 7 (Mayoral et al., 2017). We selected a PCT at age 8 for *T. grandis* based on the mean performance across our *T. grandis* sites. Finally, *D. retusa* did not have a decline in the growth rate within the study period (8 years) so we used the projected growth and evidence from Griess and Knoke (2011) to select a PCT at 9 years of age. All CT and harvest ages were selected based on the forecasted growth rates in this study and the density and volume at which CT took place in the Griess and Knoke (2011) study in Panama. The percentage of trees removed for each treatment is detailed in Table 3-2. A final harvest removed all remaining trees at the end of the rotation age of the stand. A merchantable volume was estimated for CT and final harvest by subtracting 33% of the total standing volume. Although many studies estimate a 15% reduction to calculate merchantable volume from standing volume, we chose the more conservative estimate of 33% based on Piotto et al., (2010) harvesting experience in Central America. The difference between calculated standing volume and merchantable volume exists due to the ratio of heartwood to sapwood, harvesting breakage, and non-merchantable boles, tops, or limbs. Details outlining the forecasting of tree DBH, tree volume, and stand volume estimates are outlined in Appendix C, Table C-2-5.

Table 3-2. Summary of age for pre-commercial thinning (PCT), commercial thinning (CT), harvest, and standing value by treatment. TA: *T. amazonia*; DR: *Dalbergia retusa*. Percentages in parentheses under PCT and CT represent the percentage of trees harvested.

Species	Treatment	PCT [age; years]	CT [age; years]	Harvest [age; years]	Stand Value [US$]
D. retusa	Monoculture	9 (30%)	18 (45%)	30	2000 $US / ton
T. amazonia	Monoculture	7 (40%)	14 (50%)	25	200 $US /$m^3$
D. retusa & T. amazonia	Mixed	8 (40%)	16 (30%)	TA 25 | DR 30	TA 200 $US /$m^3$ | DR 2000 $US/ton
T. grandis	Monoculture	8 (30%)	18 (45%)	25	300 $US / m^3

To calculate the value of harvested timber, we selected conservative price estimates (Table 3-2) from Oficina Nacional Forestal de Costa Rica (National Foretry Office of Costa Rica) and Stefanski et al., (2015). To calculate net present value (NPV), we used the following equation:

$$\text{NPV} = -C_0 + \sum_{t=1}^{T} \frac{Rt - Ct}{(1+r)^t} \qquad \text{(eq. 1)}$$

where $-C_o$ is the initial cost of plantation establishment, where R_t and C_t are the revenues and costs in year *t*, *r* is the discount rate, and *t* is the year of each rotation age. Costs associated with site preparation, intermediate management (fire control, cleanings, pruning, PCT, and CT), and final harvest were based on observed costs from the study plantation and estimated costs based on other studies of nearby sites (Griess and Knoke, 2011) and costs on the study plantation (Jefferson Scott Hall, personal communications). For more information on costs, see Appendix

C, Table C-1. NPV is calculated for unique revenues and costs for each management system (NPV*). NPV* comparisons among investments represents the relative profitability of the investment compared to an alternative, with the higher NPV* representing the more profitable investment. Because the rotation length of the different treatments varied, we adjusted for investment duration by calculating the equivalent annual equivalent (EAE) using the following formula based on (Möhring and Rüping 2008):

$$EAE = \frac{r \times NPV}{1-(1+r)^{-t}} \qquad \text{(eq. 2)}$$

where NPV is the net present value (eq. 1), r is the interest rate per period, and t is the number of years. To test for the sensitivity of NPV* and EAE to changes in r, we calculated NPV* and EAE changing r from 4% to 15% in increments of 1%. Costs were only included in the NPV* calculation if they were either (1) different among the treatments, (2) occurred at different intervals, or (3) if the duration of the cost differed. As such, the NPV* and EAE are relative NPV* and EAE among the treatments, and not necessarily the actual value of the different plantations. We selected a uniform standing timber value of US $200/m^3 for CT outputs (ITTO, 2016). The standing timber value of final harvests for *Tectona grandis* and *T. amazonia* was 300 US$ m^{-3} and 200 US$ m^{-3}, respectively. The standing timber value of *Dalbergia retusa* was based on t ha^{-1}, and was estimated to be 2,000 US$ t^{-1}. The timber price realized for each species was based on market reports and the timber market report from ITTO and Stefanski et al., (2015).

3.2.4 Uncertainty and sensitivity analysis

Any plantation is susceptible to damage from insect outbreaks, volatile timber markets, or extreme climatic events that influence ultimate revenues from harvesting. One or a combination of these factors can be changed in a manner that can influence the value in a positive (optimistic) or negative (pessimistic) direction. We investigated fluctuations in NPVs for a given treatment based on assumptions of rising cash outflows for stand establishment and intermediate treatments occurring alongside decreasing cash inflows after harvesting and vice versa. We selected two optimistic scenarios: increasing cash inflows and decreasing cash outflows by 50% (Optimistic 1) and 25% (Optimistic 2) of those used in base scenario calculations of NPV. Two pessimistic scenarios assumed a decrease in cash inflows and an increase in cash outflows by 50% (Pessimistic 1) and 25% (Pessimistic 2) of the base scenario.

3.2.5 Carbon sequestration estimates

To estimate carbon (C) storage of each treatment, we calculated the aboveground biomass for the *D. retusa* and *T. amazonia* based on species-specific biomass equations for the region (Sinacore et al., 2017). We converted the aboveground biomass into C storage per hectare by multiplying the biomass of each hectare by 0.5 based on Brown and Lugo (1982). To calculate the C storage of *T. grandis*, we used a species-specific equation from a nearby site (Kraenzel et al., 2002). We summed the total aboveground biomass per plot at each age and converted into tons of C per hectare. Instead of using the final C storage value at harvest age, we calculated the mean C storage over the course of the plantation to compare among treatments. We chose this method rather than summing over the entire rotation length for the following reasons: (1) C sequestration and storage is generally highest early in the rotation (1-10 years) (Montagnini and Nair, 2004), and thus summing beyond those years could lead to overestimates of C storage; and (2) Short-rotation plantations have a high capacity for C sequestration but a short-term capacity for C storage (Kraenzel et al., 2002), resulting in better estimates of C storage potential if examined as a mean storage over time. Ideally, we would consider the mean C storage over multiple rotations, but our study is limited to a one rotation projection. Additionally, the common denominator for all rotation ages would be 150 years, a time from which land use is likely to change.

3.2.6 Stand transpiration

Stand transpiration (E, mm day^{-1}) was calculated for each plot based on a subset of observations. We selected four monocultures of *T. grandis,* two monocultures each of *T. amazonia* and *D. retusa*, and four mixtures (50% *T. amazonia* and 50% *D. retusa*) for instrumentation of sap flow sensors. In the 12 selected plots, we selected eight trees per plot to measure sap flow every fifteen minutes from June 15, 2014 until June 15, 2015. For more detail on the calculation of stand transpiration for the native species and *T. grandis,* see Chapter 1 and Sinacore et al., in prep, respectively. Briefly, stand E for each treatment was calculated by averaging E of plots of the same treatment, calculated as millimeters per hectare. This is calculated on an area basis in the same manner that precipitation calculations are derived.

3.2.7 Value, carbon sequestration, and transpiration comparison

Although we projected both stand value and C sequestration for a rotation, we were unable to do the same for E because both size, climatic variation, and density influence transpiration rates, such that uncertainty would be too great (Berry et al., 2017; Vertessy et al., 1995). We present transpiration when the plantation was 6 years old. To compare C storage among treatments, we used the mean storage over the course of the rotation. To compare financial performance across treatments, we employed EAE with a real intereat rate, *r*, of 6% (Duffy et al., 2001).

3.3 RESULTS

3.3.1 Volume and carbon storage

At 25 years of age, monocultures of *T. amazonia* and *T. grandis* reached around 675 m^3 ha^{-1} and 200 m^3 ha^{-1}, respectively. Monocultures of *D. retusa* reached less than 250 m^3 ha^{-1} after 30 years of age. Before the final harvest of *T. amazonia* in the mixtures, the mixtures had over 500 m^3 ha^{-1} at age 25. At age 30, *D. retusa* in the mixtures totaled around 250 m^3 ha^{-1} (Figure 3-1a). Converted to C storage, *D. retusa* monocultures had the highest C storage at the end of the rotation, over 200 t C ha^{-1}, followed closely by mixtures of *D. retusa* and *T. amazonia* (Figure 3-1b). The lowest C storage of all the treatments was *T. grandis,* which has less than 50 t C ha^{-1} at the end of the rotation. Mean C storage over the rotation was 78.5, 45.33, 38.68, and 17.41 t C ha^{-1} for *D. retusa* monocultures, mixtures, *T. amazonia* monocultures, and *T. grandis* monocultures, respectively.

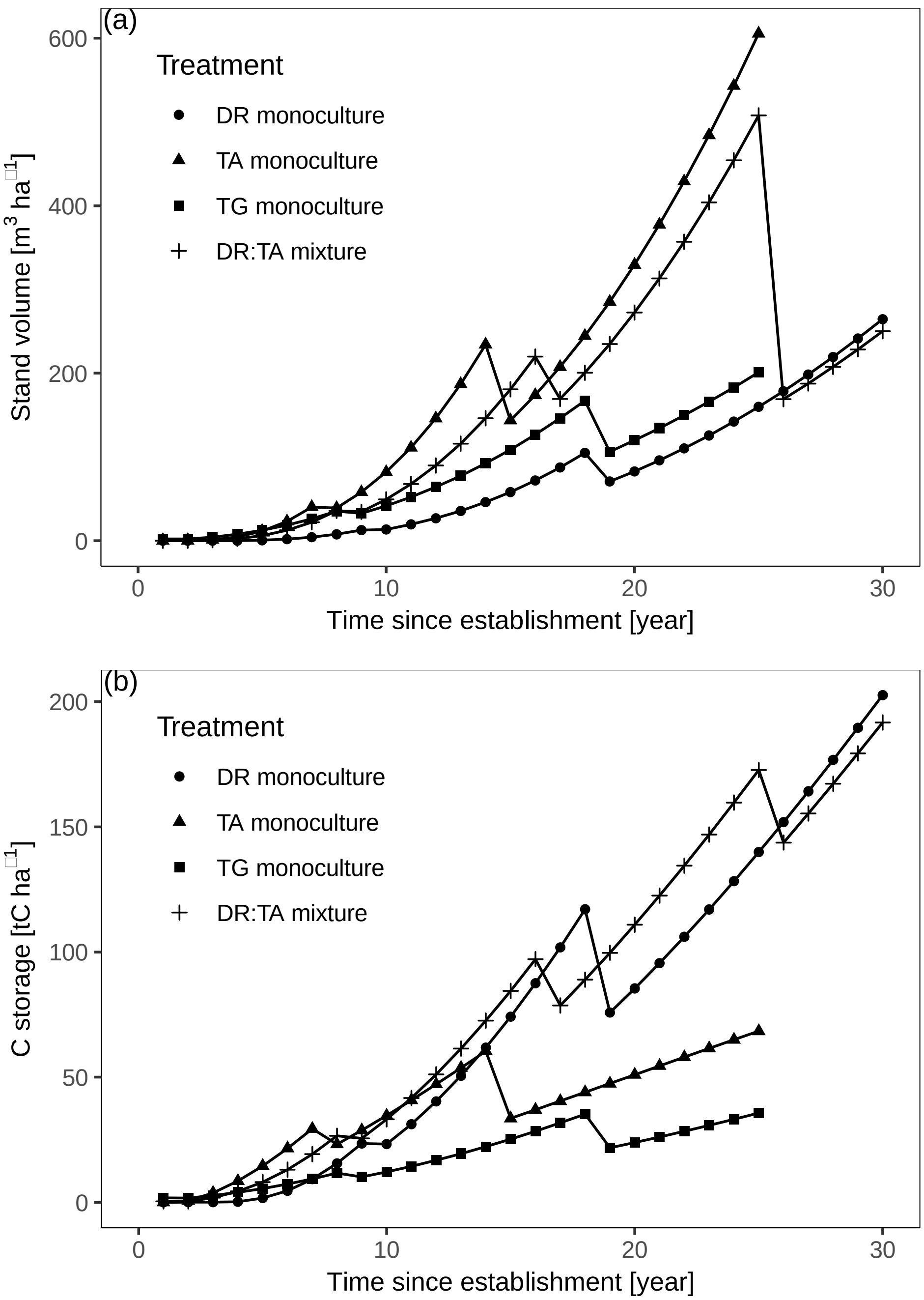

Figure 3-1. Time since establishment (or age in years) versus stand volume (m^{3}ha^{-1}). Stand volume is projected stand volume based on mean annual increment of diameter at breast height and mean annual increment of height of trees in each of the four treatments. Gray shading represents projections while the non-shaded area represents estimates from data. Projections are shown to rotation age. Declines in stand volume signify pre-commercial thinning, commercial thinning, or final harvest.

3.3.2 Net present value (NPV), equal annual equivalent (EAE), and sensitivity*

After the final harvest, NPV* and EAE estimates of the treatments from highest to lowest were *D. retusa* monoculture > DR:TA mixture > *T. amazonia* monoculture > *T. grandis* monoculture (Figure 3-2, Figure 3-3, Table 3-3, Table 3-4). The NPV* at 6% was highest in *D. retusa* monocultures (318,836 US$ ha^{-1}) and mixtures (317,199 US$ ha^{-1}). NPV* did not fall below zero throughout the range of interest rates used except for *T. grandis*, which declined below 0 US$ ha^{-1} at 12% (Table 3-3). The same trends were obtained for the EAE at different interest rates for each treatment. *Dalbergia retusa* monocultures had the highest EAE followed closely by mixtures (Table 3-4).

Optimistic 1 and Optimistic 2 projections of NPV* and EAE changed the relative value of the species (Figure 3-2b). If scenarios arise such that *T. amazonia* monocultures have an increase in market value, the NPV* of *T. amazonia* monocultures becomes more competitive with *D. retusa* monocultures or the mixtures. *Tectona grandis*, however, even with optimistic projections remains lower than *T. amazonia* (Figure 3-2b, Figure 3-3b). We did not find any site differences for NPV* or EAE in terms of ranking at each interest rate.

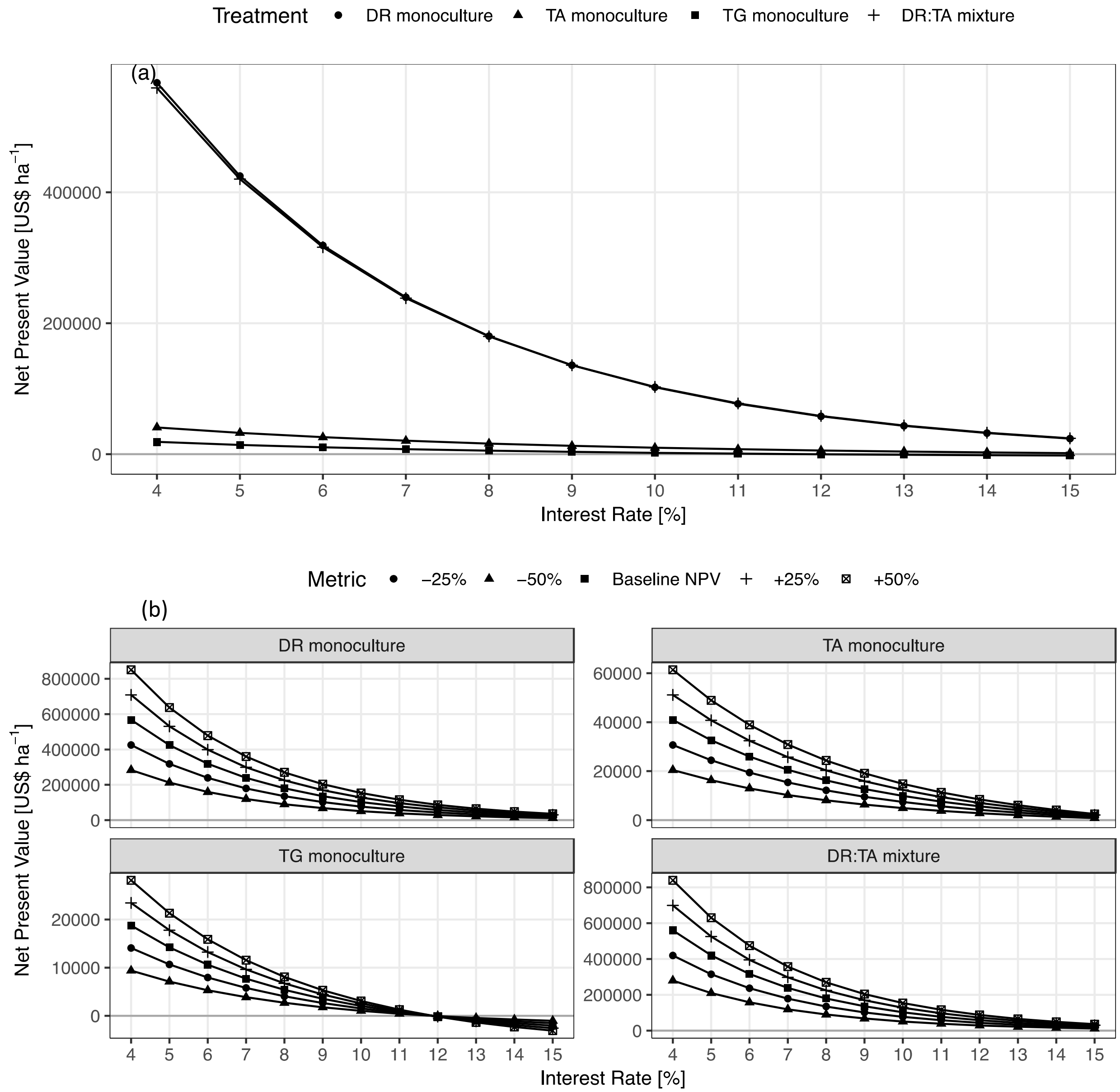

Figure 3-2. Modeled net present value* [US$ ha^{-1}] function of (a) all treatments by the interest rate [*r*, %] and (b) all treatments by *r* with a varying y-axis. Note the change in y-axis of the treatment plots changes with treatment.

Table 3-3. Baseline net present value (NPV*) of treatments with changing interest rate. Treatments include: *D. retusa*, *T. amazonia*, and *T. grandis* monocultures, and *D. retusa* and *T. amazonia* mixtures.

Interest rate [%]	Net present value [US $/ha]			
	D. retusa monoculture	*T. amazonia* monoculture	*T. grandis* monoculture	*D. retusa & T. amazonia* mixture
4	567,229	40,922	18,749	559,410
5	424,862	32,599	14,203	420,148
6	318,836	25,932	10,585	316,199
7	239,650	20,572	7,697	238,376
8	180,346	16,245	5,386	179,940
9	135,811	12,737	3,532	135,932
10	102,276	9,883	2,042	102,695
11	76,959	7,551	841	77,521
12	57,797	5,639	-129	58,400
13	43,256	4,065	-913	43,837
14	32,196	2,764	-1,548	32,715
15	23,763	1,686	-2,064	24,198

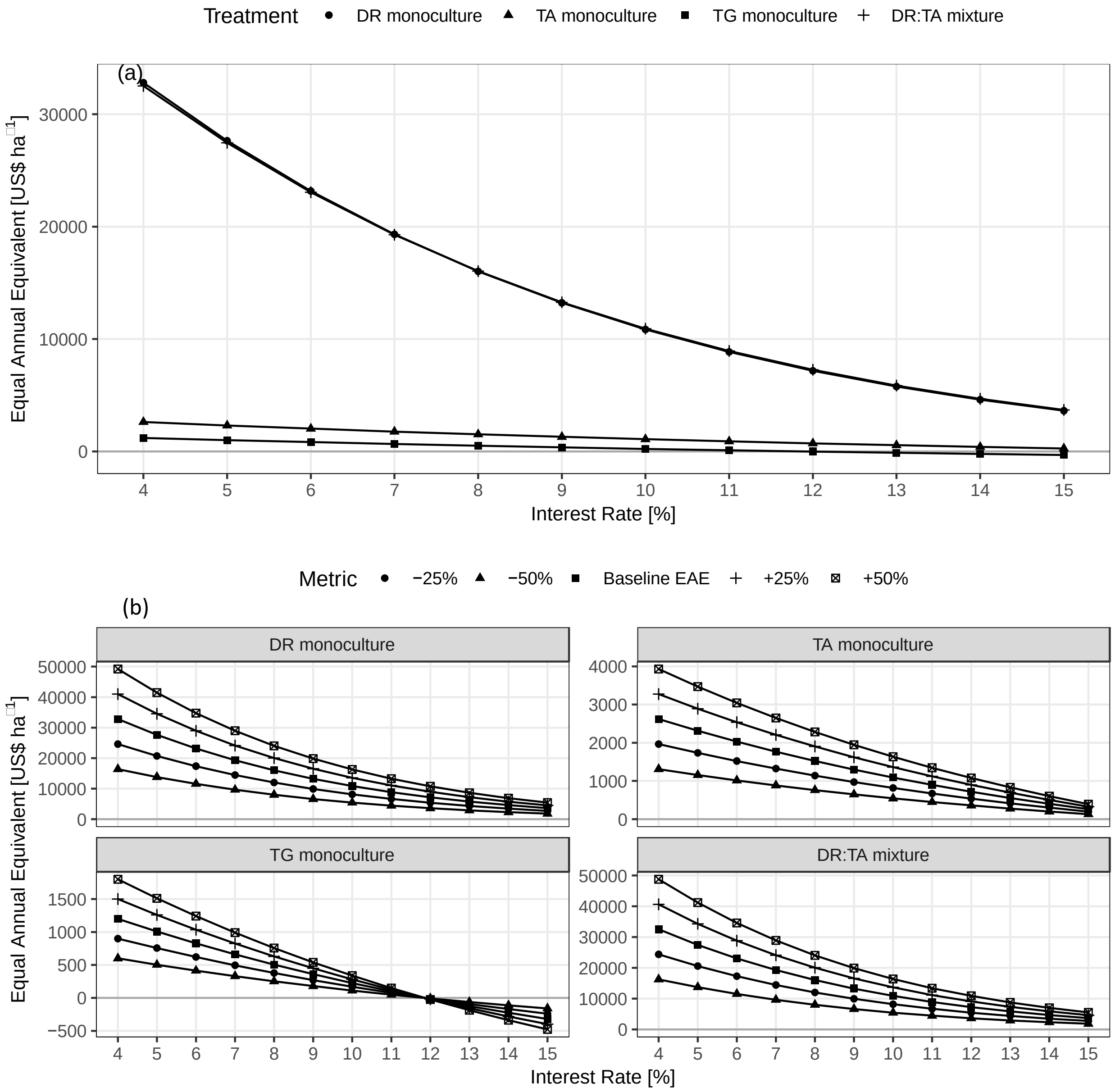

Figure 3-3. Modeled equal annual equivalent [US$ ha^{-1}] function of (a) all treatments by the interest rate [*r*, %] and (b) all treatments by r with a varying y-axis. Note the change in y-axis of the treatment plots changes with treatment.

Table 3-4. Baseline equal annual equivalent (EAE) of treatments with changing interest rate. Treatments include: *D. retusa*, *T. amazonia*, and *T. grandis* monocultures, and *D. retusa* and *T. amazonia* mixtures.

Interest rate [%]	Equal Annual Equivalent [US $/ha]			
	D. retusa monoculture	*T. amazonia* monoculture	*T. grandis* monoculture	*D. retusa & T. amazonia* mixture
4	32,803	2,620	1,200	32,512
5	27,638	2,313	1,008	27,455
6	23,163	2,029	828	23,066
7	19,313	1,765	660	19,281
8	16,020	1,522	505	16,037
9	13,219	1,297	360	13,271
10	10,849	1,089	225	10,923
11	8,852	897	100	8,938
12	7,175	719	-16	7,266
13	5,771	555	-125	5,860
14	4,598	402	-225	4,680
15	3,619	261	-319	3,691

3.3.3 Stand transpiration

Mean stand transpiration from June 15, 2014 through June 15, 2015 was lowest in *D. retusa* monocultures (0.20 mm day^{-1}) and highest in *T. grandis* monocultures (4.14 mm day^{-1}) (Table 3-5). The second highest transpiration was in *T. amazonia* monoculture (3.38 mm day^{-1}) while the two species mixtures fell intermediate (1.73 mm day^{-1}).

Table 3-5. Stand transpiration [mm day^{-1}] for four study treatments. Treatments include: *D. retusa*, *T. amazonia*, and *T. grandis* monocultures, and *D. retusa* and *T. amazonia* mixtures.

Treatment	Stand transpiration [mm/day]
D. retusa monoculture	0.20
T. amazonia monoculture	3.38
D. retusa & T. amazonia mixture	1.73
T. grandis monoculture	4.14

3.3.4 EAE, carbon storage, and transpiration comparison

A conceptual ranking system of transpiration, C storage, and EAE (at 6%) were used to rank treatments based on those three metrics. *Dalbergia retusa* monocultures ranked highest in terms of both EAE and C storage (Figure 3-4). *Dalbergia retusa* monocultures also had the lowest stand transpiration of all the treatments. The treatment with the lowest ranking was *T. grandis* monocultures. *Tectona grandis* monocultures had the highest stand transpiration of all the treatments and the lowest mean C storage and lowest EAE (Figure 3-4).

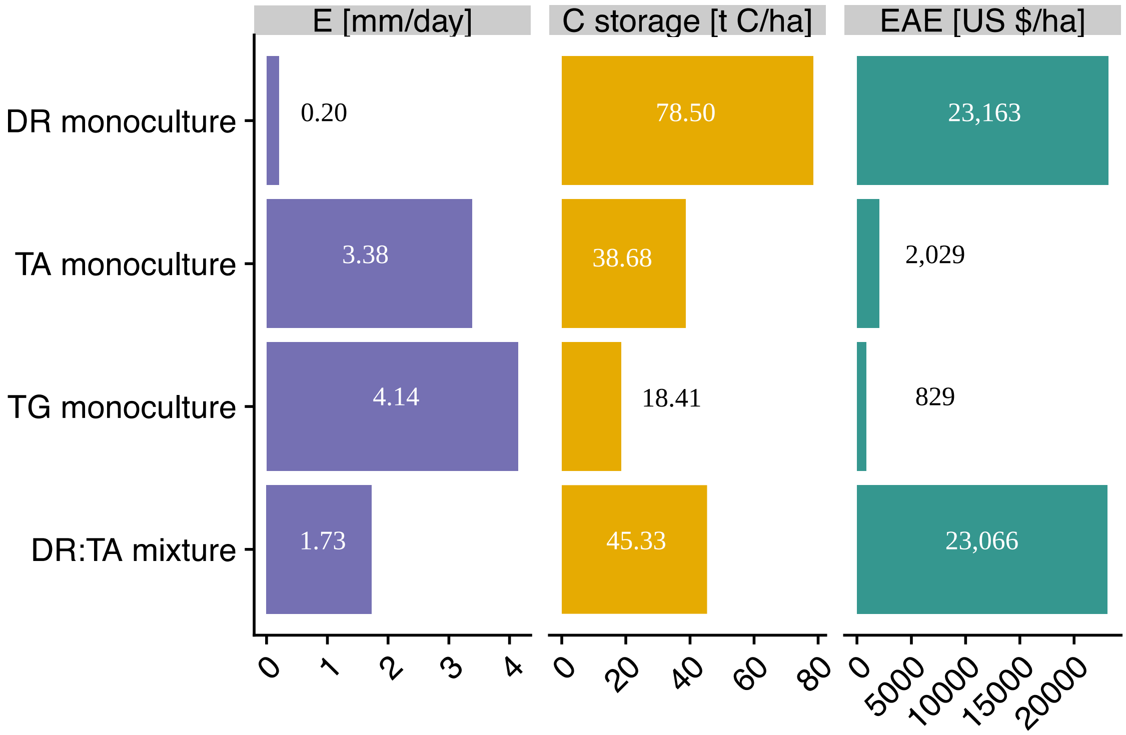

Figure 3-4. Transpiration [*E*; mm/day], carbon storage [C storage; t C/ha], and equal annual equivalent [EAE; US $/ha] by treatment. Transpiration is calculated as the mean daily transpiration. C storage is calculated as the mean C content of the total biomass over the course of the rotation. EAE is calculated as the time corrected NPV of each treatment. DR monoculture: *D. retusa* monocultures; TA monoculture: *T. amazonia* monocultures; TG monocultures: *T. grandis* monocultures; DR:TA mixtures: *D. retusa* and *T. amazonia* two-species mixtures.

3.4 DISCUSSION

3.4.1 Native species can compete financially with Tectona grandis

Based on our assumptions, monocultures and mixtures of *T. amazonia* and *D. retusa* can outcompete *T. grandis* financially. The profitability of *T. grandis* is below that of the native species based on the comparison of NPVs and EAEs. *Dalbergia retusa* monocultures and the two-species mixtures outcompete *T. grandis* considerably from an EAE perspective. At 6% interest, the EAE of *D. retusa* monocultures and mixtures was $23,163 and $23,066, respectively. National and international markets currently sell *D. retusa* at a premium that far exceeds the felling value of either *T. grandis* or *T. amazonia*. While *T. amazonia* has a greater EAE ($2,209 at 6%) than *T. grandis* ($828 at 6%), the difference may not be high enough to persuade landowners to plant *T. amazonia* over *T. grandis*. Although in the baseline case *T. amazonia* had a lower NPV than *D. retusa*, in an optimistic scenario, where felling value of *T. amazonia* increased by 25-50%, the NPV begins to become closer to *D. retusa*. Based on our projections, however, it is unlikely that *T. amazonia* can exceed the NPV of *D. retusa* at the current felling values. *Tectona grandis* on these lands do not grow well and thus do not compete financially well with the native species. Notwithstanding, *T. grandis* is planted throughout Panama, likely a result of optimistic projections and the prices that *T. grandis* can obtain internationally. In Venezuela *T. grandis* can be sold for 220 US $ m^{-3} and 900 US $ m^{-3} in Indonesia (Cubbage et al., 2010), while our price estimate for *T. grandis* was 300 US $ m^{-3}.

Panama has a history of planting *T. grandis* (Griess and Knoke, 2011) and only recently has there been a strong emphasis on selecting native species for plantations (Aguilar and Condit, 2001; Wishnie et al., 2007). However, *T. grandis* on these sites grew particularly poorly in comparison to other sites across Panama where *T. grandis* reached rotation age between 15-20 years (Kraenzel et al., 2003). As such, *T. grandis* may be reasonable to plant on better quality sites across Panama, whereas native species may be better suited for nutrient poor sites. *Terminalia amazonia* has proven to be particularly suited to marginal lands and is the species that had significantly higher growth rates than other native species in the plantation. While *D. retusa* has slower growth rates, the felling value may prove sufficient incentive to landowners, if the 30+ year rotation is not a disincentive. Although monocultures are the most common plantation in Panama, a mixture of the two native species might provide additional benefits to the landowner. Not only do mixtures have the advantage of providing harvestable products at different rotation times, but we found the NPV was higher with the introduction of *D. retusa* in the mixtures. While we present here a conservative estimate of volume for *T. amazonia* in the monocultures, previous work has shown that *T. amazonia* grows better in mixtures than in monocultures (Mayoral et al., 2017), which could shorten rotation age further. Farmers may also prefer to diversify the planting because of uncertainties about the species' survival, performance, or risks from pest damage that have been documented in monoculture plantations (Montagnini et al., 1995). Diversifying is also beneficial to prevent losses when markets for certain species soften. If suddenly landowners begin primarily planting *D. retusa*, the price will eventually decline due to increasing supply relative to demand. If that is the case, other species, such as *T. amazonia*, might become more profitable.

Carbon (C) storage of Dalbergia retusa monocultures exceeds the other treatments

National and international programs promoting reforestation have recognized the importance of placing a value on C sequestration to further promote planting and preserving intact forest.

Markets for C exist and could provide the additional incentive necessary to promote certain species for reforestation. Plantations represent both short-term and long-term C storage. Species that have longer rotation ages generally produce more valuable wood and thus constitute a longer-term storage of fixed carbon when used for construction, furniture, or wood crafts. Alternatively, shorter-term storage, in the form of boxes and poles, are characteristic of species with shorter rotation lengths. *Dalbergia retusa* represents a species with longer-term C storage. Not only does it have the highest C per hectare of all the treatments, but is generally used as craft wood. Both *T. amazonia* and *T. grandis* are used for construction and sometimes veneer for *T. grandis*, but the mean C storage across the rotation is lower than that of *D. retusa*. The C storage for *T. grandis* in these sites was considerably less than that of Panamanian plantations studied in Kraenzel et al., (2003). *Tectona grandis* has been show to grow poorly on clay soils, which make up most the Panama Canal watershed. Additional C storage of *T. amazonia* might make it more valuable than *T. grandis* such that it comes more popular with the added C benefits.

3.4.2 Transpiration as a consideration in plantation design

Though plantations only make up a small portion of the total land area in Panama, they are projected to increase over the next few decades as (1) plantations become more profitable and (2) are promoted as alternatives to cattle ranching by stakeholders hoping to combat rising CO_2 levels (Silver et al., 2000).

In the PCW, research has shown that forested areas can act as sponges, absorbing water during the wet season and providing baseflows during the dry season (Ogden et al., 2013). This is an important finding, especially in an area like the PCW where freshwater resources from the watershed feed both the Panama Canal and serve as a potable water resource for local communities and Panama City. Problems of flooding during the wet season can cause issues in communities and, in extreme cases, potentially shut down the Panama Canal (an event which happened during a strong storm in 2010). Not only is water "lost" via extreme runoff, but the Panama Canal (one of the biggest contributors to Panama's GDP) loses revenue if it must suspend boat transit for short periods of time. Additionally, the Panama Canal Authority has had to place draft restrictions on boats during times of water shortage, limiting potential revenue. Panama also faces issues of water scarcity during the dry season, making shortages of drinking water common in more remote areas.

Indeed, both the Panama Canal Authority (ACP; Spanish acronym) and IDAAN (the potable water supplier) have strong incentives and motivations for being concerned about water quantity (and quality) during both the wet and dry season. Research like Ogden et al., (2013) provides strong incentives for strategic planning around the PCW and promoting regeneration of forests or planted systems to regulate water. Plantations can become problematic when species are used such that transpiration rates are high, particularly in the dry season when soil water content begins to decline. Not only did *D. retusa* have the lowest transpiration rates compared to the other treatments, but since leaf senescence occurs during the dry season, it also transpired very little during the time of the year when water is most rare (Figure 3-4). In contrast, *T. grandis* had the highest transpiration rates, closely followed by *T. amazonia*. One potential positive is that *T. grandis* reduces water use during the dry season even though they still hold on to their leaves. *Terminalia amazonia,* however, has higher transpiration during the dry season than the wet season, except when planted in a mixture during a normal precipitation year (Chapter 2). This provides even greater incentive for planting mixtures of *T. amazonia* and *D. retusa* over monocultures of *T. amazonia* alone.

3.5 CONCLUSION

Plantations have and will continue to serve diverse productive, economic, and ecological functions (Montagnini and Porras, 1998). Tropical plantations have relatively high yields and can provide a significant portion to international markets. Yet estimates of productivity have often overestimated growth of *Tectona grandis*, as estimates are based on a subset of plantations on productive soils. In Panama, opportunities for plantations are often relegated to marginal lands where soils do not support productive *T. grandis*. Native species, such as *T. amazonia* and *D. retusa* are two safe alternatives that have been proven successful on poor quality soils (Mayoral et al., 2017). A major obstacle is often the lack of knowledge in planting and caring for specific native species, but recent advances have reduced this barrier. A book dedicated to reforestation with over 64 native species in Panama details the productive capacity of each species on a variety of soil types and precipitation gradients (Hall and Ashton, 2016).

Despite this, changing landowners' perceptions and transitioning from one species to a lesser known one, is a large risk for the landowner. Despite felling value estimates that can compete and outcompete *T. grandis,* native species may require added incentives. Payment for ecosystem services is one option that may incentivize native species selection. Our work shows that *D. retusa* monocultures and the two-species mixtures not only store the most carbon over the rotation, but they also use the least amount of water. This information provides strong evidence that native species provide greater ecosystem services than *T. grandis* and are a financially viable option.

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APPENDICES

APPENDIX A – Volumetric Water content

APPENDIX B – ANCOVA results and water potential

APPENDIX C – Maps and financial analysis

APPENDIX A

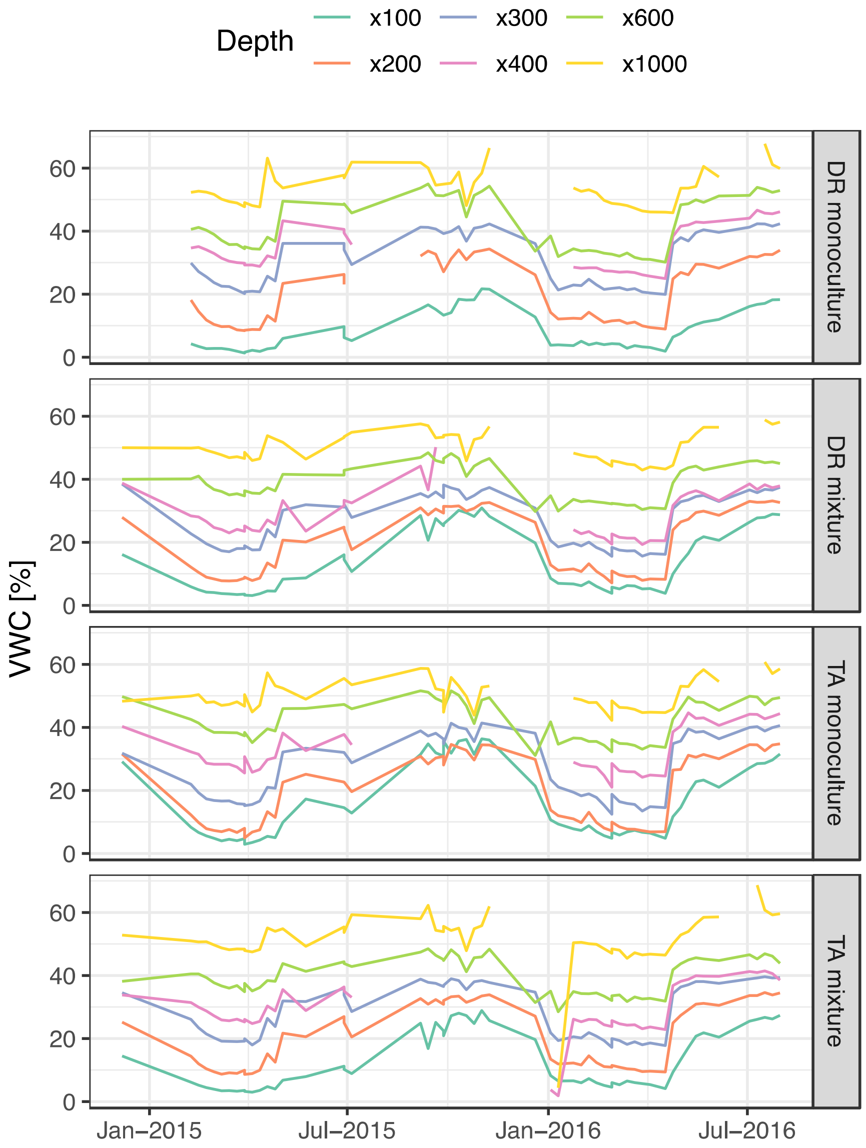


Figure A-1. Volumetric water content [VWC, %] by treatment and depth. VWC measurements included from December 2014 through July 2016. Different soil depths range from 100 mm (x100) to 1000 mm (x1000).

APPENDIX B

Table B-1. ANCOVA table of generalized linear model results of mean normalized sap flux density by mean normalized vapor pressure deficit (VPD). Treatment and Water Year included as factors.

	df	Sum of Squares	Square Mean	F value	P value
VPD	1	0.284	0.284	29.812	< 0.001
Treatment	3	0.427	0.142	14.946	< 0.001
Water Year	3	2.673	0.891	93.617	< 0.001
VPD : Treatment	3	0.071	0.024	2.491	0.0612
VPD : Water Year	3	0.258	0.086	9.036	< 0.001

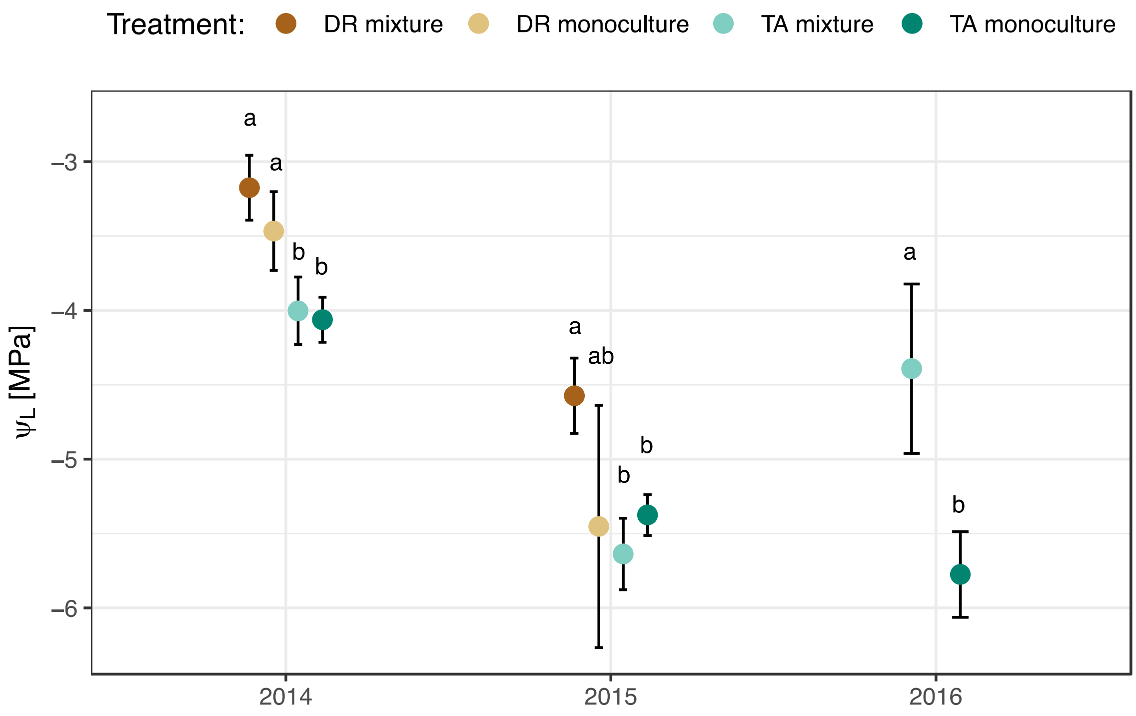


Figure B-1. Midday water potential (Ψ_L) by year and treatment. Letters represent significant differences by treatment within in year. Based on ANOVA and post-hock Tukey test. No data available for *Dalbergia retusa* in 2016 because leaves had not yet flushed during sampling campaign.

APPENDIX C

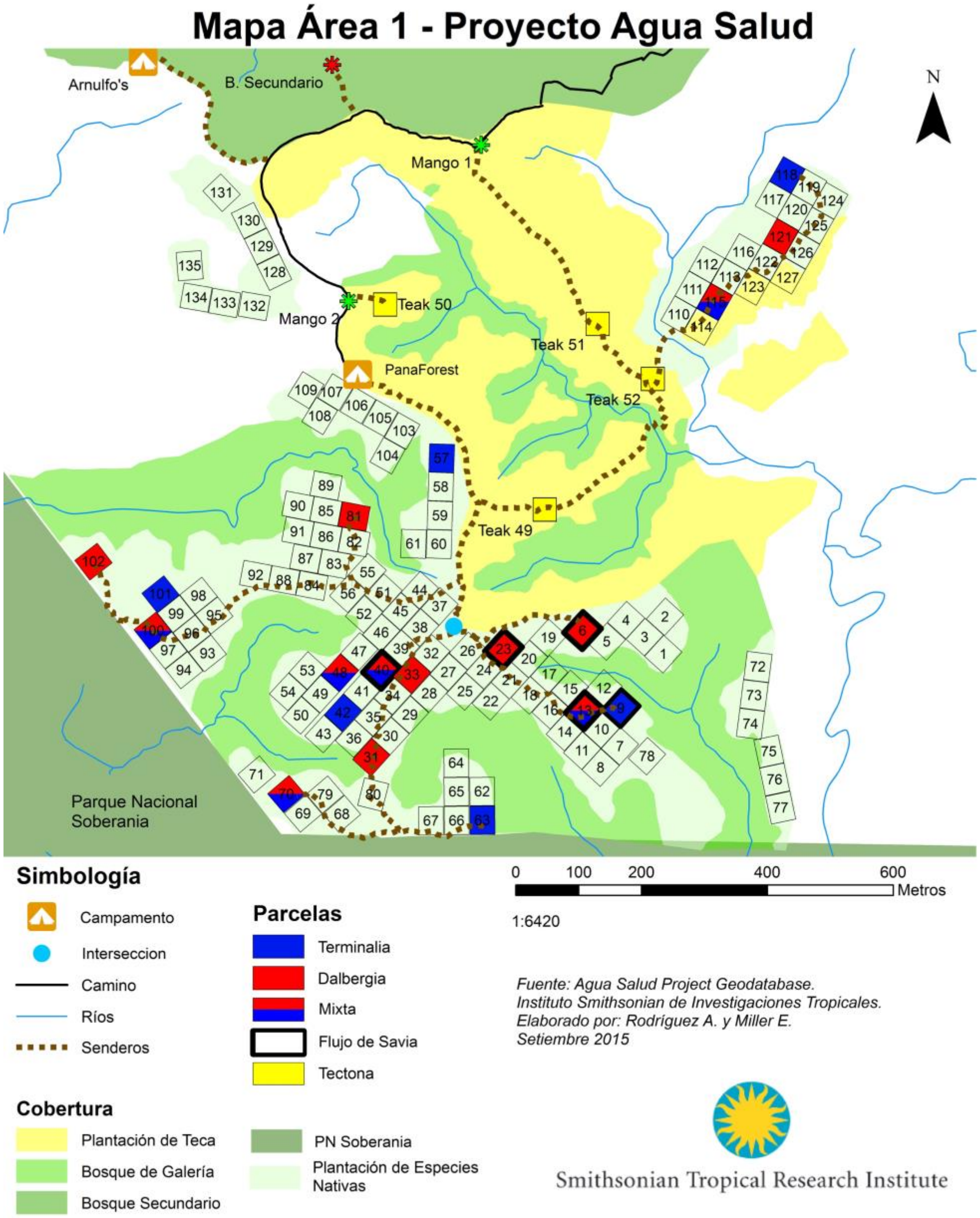
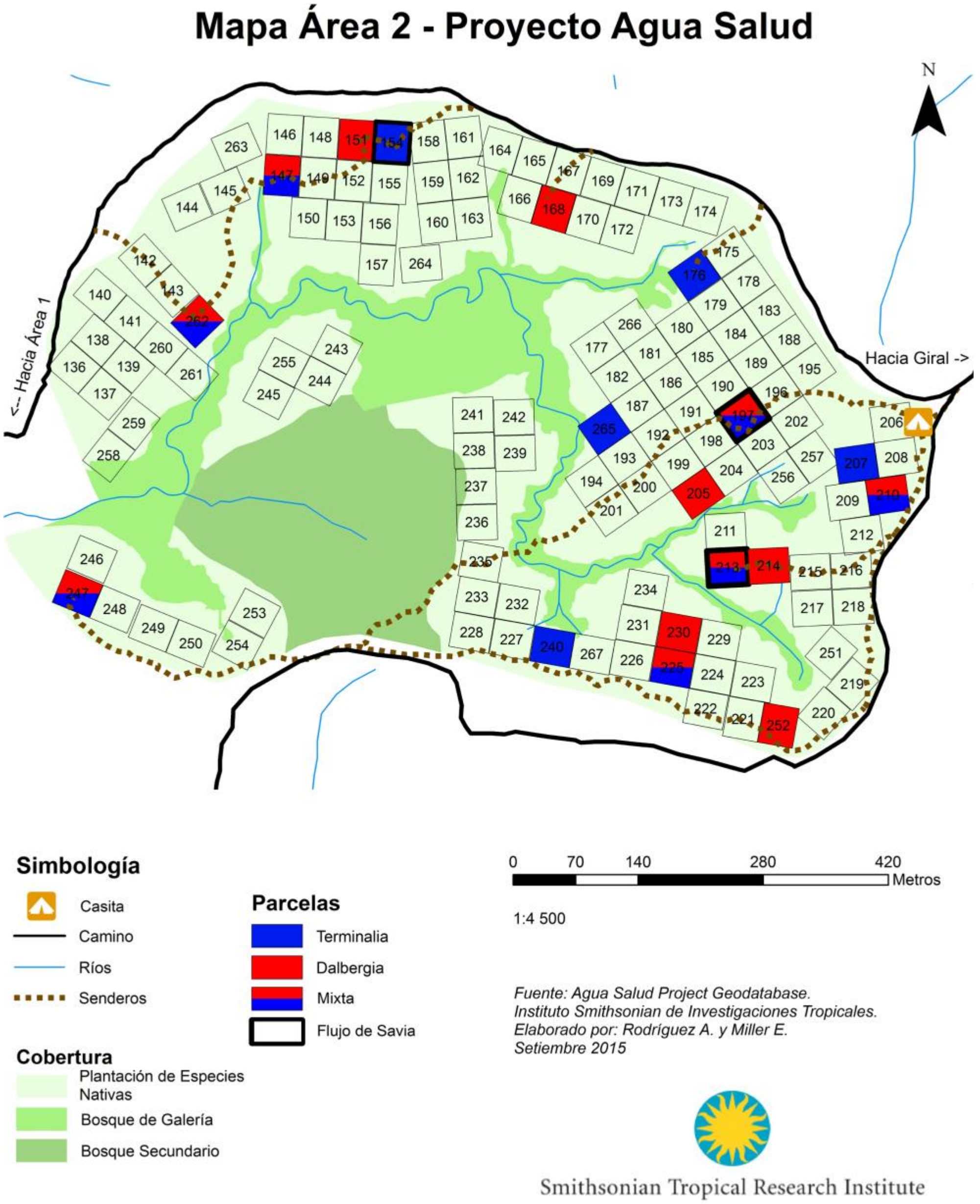


Figure C-1. Map of Area 1 in the Agua Salud Project research site. Red and blue squares with black outlines represent location of *Dalbergia retusa* monocultures and *Terminalia amazonia* monocultures where sap flow was measured, respectively. Square with half red and half blue outlined in black represent locations of two-species mixtures where sap flow was measured. Squares without black outline represent sites included in the full inventory. Yellow squares represent the *Tectona grandis* sites where sap flow was measured.



Fuente: Agua Salud Project Geodatabase.
Instituto Smithsonian de Investigaciones Tropicales.
Elaborado por: Rodríguez A. y Miller E.
Setiembre 2015

Figure C-2. Map of Area 2 in the Agua Salud Project research site. Red and blue squares with black outlines represent location of *Dalbergia retusa* monocultures and *Terminalia amazonia* monocultures where sap flow was measured, respectively. Square with half red and half blue outlined in black represent locations of two-species mixtures where sap flow was measured. Squares without black outline represent sites included in the full inventory. Yellow squares represent the *Tectona grandis* sites where sap flow was measured.

Table C-1. Costs per hectare associated with managing each treatment. Costs are broken down by year and include costs of fire protection, pruning, and manual cleaning when applicable.

	D. retusa monoculture	*T. amazonia* monoculture	*T. grandis* monoculture	*D. retusa & T. amazonia* mixture
Planting costs	3,700	3,700	3,700	3,700
PCT Costs	840	600	600	600
CT Costs	1,200	1,500	1,500	1,350
Harvesting Costs	1,500	1,300	1,300	1,400
Costs Year 1	261	261	261	261
Costs Year 2	301	301	301	301
Costs Year 3	261	203	246	232
Costs Year 4	261	261	203	261
Costs Year 5	203	203	148	203
Costs Year 6	253	253	198	253
Costs Year 7	253	PCT Costs	198	253
Costs Year 8	148	148	PCT Costs	PCT Costs
Costs Year 9	PCT Costs	148	148	148
Costs Year 10	148	148	148	148
Costs Year 11	148	148	148	148
Costs Year 12	148	148	148	148
Costs Year 13	148	148	148	148
Costs Year 14	148	CT Costs	148	148
Costs Year 15	148	148	148	148
Costs Year 16	148	148	148	CT Costs
Costs Year 17	148	148	148	148
Costs Year 18	CT Costs	148	CT Costs	148
Costs Year 19	148	148	148	148
Costs Year 20	148	148	148	148
Costs Year 21	148	148	148	148
Costs Year 22	148	148	148	148
Costs Year 23	148	148	148	148
Costs Year 24	148	148	148	148
Costs Year 25	148	Harvesting Costs	Harvesting Costs	Harvesting Costs
Costs Year 26	148	na	na	148
Costs Year 27	148	na	na	148
Costs Year 28	148	na	na	148
Costs Year 29	148	na	na	148
Costs Year 30	Harvesting Costs	na	na	Harvesting Costs

Table C-2. Actual (gray shading) and modeled (white background) stand development of *Terminalia amazonia* monocultures across projected rotation length (25 years). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

Age	N	N extracted	DBH [cm]	Height [m]	BA tree [m^2]	Tree vol [m^3]	Stand vol [m^3/ha]	Harvest volume [m^3/ha]
1	1111	0						
2	1089	0	0.93	2.07	0.00	0.00	0.08	0
3	1067	0	2.73	3.77	0.00	0.00	1.18	0
4	1046	0	4.53	5.47	0.00	0.00	4.61	0
5	1025	0	6.33	7.17	0.00	0.01	11.56	0
6	1004	0	8.13	8.87	0.01	0.02	23.12	0
7	984	394	9.93	10.57	0.01	0.04	40.28	40.28
8	590	0	11.73	12.27	0.01	0.07	39.13	0
9	578	0	13.53	13.97	0.01	0.10	58.08	0
10	567	0	15.33	15.67	0.02	0.14	81.97	0
11	555	0	17.13	17.37	0.02	0.20	111.18	0
12	544	0	18.93	19.07	0.03	0.27	146.08	0
13	533	0	20.73	20.77	0.03	0.35	186.98	0
14	523	267	22.53	22.47	0.04	0.45	234.16	234.16
15	256	0	24.33	24.17	0.05	0.56	143.72	0
16	251	0	26.13	25.87	0.05	0.69	173.88	0
17	246	0	27.93	27.57	0.06	0.84	207.49	0
18	241	0	29.73	29.27	0.07	1.02	244.60	0
19	236	0	31.53	30.97	0.08	1.21	285.27	0
20	231	0	33.33	32.67	0.09	1.43	329.54	0
21	227	0	35.13	34.37	0.10	1.67	377.44	0
22	222	0	36.93	36.07	0.11	1.93	428.99	0
23	218	0	38.73	37.77	0.12	2.22	484.18	0
24	213	0	40.53	39.47	0.13	2.55	543.02	0
25	209	209	42.33	41.17	0.14	2.90	605.48	605.48

Table C-3. Actual (gray shading) and modeled (white background) stand development of *Dalbergia retusa* monocultures across projected rotation length (30 years). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

Age	N	N extracted	DBH [cm]	Height [m]	BA tree [m^2]	Tree vol [m^3]	Stand vol [m^3/ha]	Harvest volume [m^3/ha]
1	1111	0						
2	1089	0	0.5	0.62	0.00	0.00	0.01	0
3	1067	0	0.5	1.52	0.00	0.00	0.02	0
4	1046	0	0.94	2.42	0.00	0.00	0.09	0
5	1025	0	2.14	3.32	0.00	0.00	0.61	0
6	1004	0	3.34	4.22	0.00	0.00	1.86	0
7	1004	0	4.54	5.12	0.00	0.00	4.16	0
8	984	0	5.74	6.02	0.00	0.01	7.67	0
9	964	300	6.94	6.92	0.00	0.01	12.62	12.62
10	664	0	8.14	7.82	0.01	0.02	13.52	0
11	651	0	9.34	8.72	0.01	0.03	19.45	0
12	638	0	10.54	9.62	0.01	0.04	26.78	0
13	625	0	11.74	10.52	0.01	0.06	35.61	0
14	613	0	12.94	11.42	0.01	0.08	46.02	0
15	601	0	14.14	12.32	0.02	0.10	58.10	0
16	589	0	15.34	13.22	0.02	0.12	71.91	0
17	577	0	16.54	14.12	0.02	0.15	87.51	0
18	565	250	17.74	15.02	0.02	0.19	104.94	104.94
19	315	0	18.94	15.92	0.03	0.22	70.72	0
20	309	0	20.14	16.82	0.03	0.27	82.79	0
21	303	0	21.34	17.72	0.04	0.32	95.97	0
22	297	0	22.54	18.62	0.04	0.37	110.25	0
23	291	0	23.74	19.52	0.04	0.43	125.65	0
24	285	0	24.94	20.42	0.05	0.50	142.17	0
25	279	0	26.14	21.32	0.05	0.57	159.80	0
26	274	0	27.34	22.22	0.06	0.65	178.54	0
27	268	0	28.54	23.12	0.06	0.74	198.39	0
28	263	0	29.74	24.02	0.07	0.83	219.33	0
29	258	0	30.94	24.92	0.08	0.94	241.36	0
30	252	252	32.14	25.82	0.08	1.05	264.45	264.45

Table C-4. Actual (gray shading) and modeled (white background) stand development of *Tectona grandis* across projected rotation length (25 years). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

Age	N	N extracted	DBH [cm]	Height [m]	BA tree [m^2]	Tree vol [m^3]	Stand vol [m^3/ha]	Harvest volume [m^3/h
1	1111	0	4.46	2.41	0.00	0.00	2.09	
2	1089	0	4.46	2.41	0.00	0.00	2.05	0
3	1067	0	5.36	3.61	0.00	0.00	4.35	0
4	1046	0	6.26	4.81	0.00	0.01	7.74	0
5	1025	0	7.16	6.01	0.00	0.01	12.40	0
6	1004	0	8.06	7.21	0.01	0.02	18.47	0
7	984	0	8.96	8.41	0.01	0.03	26.09	0
8	964	300	9.86	9.61	0.01	0.04	35.39	35
9	664	0	10.76	10.81	0.01	0.05	32.66	0
10	651	0	11.66	12.01	0.01	0.06	41.76	0
11	638	0	12.56	13.21	0.01	0.08	52.23	0
12	625	0	13.46	14.41	0.01	0.10	64.12	0
13	613	0	14.36	15.61	0.02	0.13	77.48	0
14	601	0	15.26	16.81	0.02	0.15	92.33	0
15	589	0	16.16	18.01	0.02	0.18	108.72	0
16	577	0	17.06	19.21	0.02	0.22	126.65	0
17	565	0	17.96	20.41	0.03	0.26	146.15	0
18	554	250	18.86	21.61	0.03	0.30	167.23	167
19	304	0	19.76	22.81	0.03	0.35	106.33	0
20	298	0	20.66	24.01	0.03	0.40	119.90	0
21	292	0	21.56	25.21	0.04	0.46	134.36	0
22	286	0	22.46	26.41	0.04	0.52	149.70	0
23	280	0	23.36	27.61	0.04	0.59	165.91	0
24	275	0	24.26	28.81	0.05	0.67	182.98	0
25	269	269	25.16	30.01	0.05	0.75	200.91	200.91

Table C-5. Actual (gray shading) and modeled (white background) stand development of mixed plots of *T. amazonia* and *D. retusa* across projected rotation length (25 years and 30 years, respectively). N: number of trees, N extracted: number of trees extracted, DBH: diameter at breast height, BA tree: basal area of tree, Tree vol: volume of tree, Stand vol: volume of stand.

Age	N_TA	N_DR	N_TA_extracted	N_DR_extracted	DBH_TA [cm]	DBH_DR [cm]	BA tree_TA [m^2	BA tree_DR [m	Height_TA [m]	Height_DR [m]	Tree vol_TA [m^3	Tree vol)DR [m^3	Stand vol_TA [m^3 /h	Stand vol_DR [m^3 /ha]	Harvest volume_TA [m^3 /	Harvest volume_DR [m3/ha]	Combined stand volume [m^3
1	555	556	0	0	0.93	0.5	0.00	0.00	2.07	-0.28	0.00	0.00	0.04	0.00	0	0	0.04
2	544	545	0	0	0.93	0.5	0.00	0.00	2.07	0.62	0.00	0.00	0.04	0.00	0	0	0.04
3	533	534	0	0	2.73	0.5	0.00	0.00	3.77	1.52	0.00	0.00	0.59	0.01	0	0	0.60
4	522	523	0	0	4.53	0.94	0.00	0.00	5.47	2.42	0.00	0.00	2.30	0.04	0	0	2.35
5	512	513	0	0	6.33	2.14	0.00	0.00	7.17	3.32	0.01	0.00	5.78	0.31	0	0	6.08
6	502	503	0	0	8.13	3.34	0.01	0.00	8.87	4.22	0.02	0.00	11.55	0.93	0	0	12.48
7	492	493	0	0	9.93	4.54	0.01	0.00	10.57	5.12	0.04	0.00	20.12	2.04	0	0	22.16
8	482	483	200	0	11.73	5.74	0.01	0.00	12.27	6.02	0.07	0.01	31.94	3.76	32	0	35.70
9	282	473	0	0	13.53	6.94	0.01	0.00	13.97	6.92	0.10	0.01	28.30	6.19	0	0	34.49
10	276	464	0	0	15.33	8.14	0.02	0.01	15.67	7.82	0.14	0.02	39.94	9.43	0	0	49.37
11	271	454	0	0	17.13	9.34	0.02	0.01	17.37	8.72	0.20	0.03	54.17	13.57	0	0	67.74
12	265	445	0	0	18.93	10.54	0.03	0.01	19.07	9.62	0.27	0.04	71.18	18.68	0	0	89.86
13	260	436	0	0	20.73	11.74	0.03	0.01	20.77	10.52	0.35	0.06	91.11	24.84	0	0	115.95
14	255	428	0	0	22.53	12.94	0.04	0.01	22.47	11.42	0.45	0.08	114.10	32.11	0	0	146.20
15	250	419	0	0	24.33	14.14	0.05	0.02	24.17	12.32	0.56	0.10	140.26	40.53	0	0	180.79
16	245	411	100	100	26.13	15.34	0.05	0.02	25.87	13.22	0.69	0.12	169.70	50.17	169.70	50.17	219.86
17	145	311	0	0	27.93	16.54	0.06	0.02	27.57	14.12	0.84	0.15	122.16	47.12	0	0	169.29
18	142	304	0	0	29.73	17.74	0.07	0.02	29.27	15.02	1.02	0.19	144.01	56.51	0	0	200.52
19	139	298	0	0	31.53	18.94	0.08	0.03	30.97	15.92	1.21	0.22	167.96	66.91	0	0	234.87
20	136	292	0	0	33.33	20.14	0.09	0.03	32.67	16.82	1.43	0.27	194.03	78.33	0	0	272.36
21	133	287	0	0	35.13	21.34	0.10	0.04	34.37	17.72	1.67	0.32	222.23	90.80	0	0	313.03
22	131	281	0	0	36.93	22.54	0.11	0.04	36.07	18.62	1.93	0.37	252.58	104.31	0	0	356.90
23	128	275	0	0	38.73	23.74	0.12	0.04	37.77	19.52	2.22	0.43	285.08	118.88	0	0	403.96
24	126	270	0	0	40.53	24.94	0.13	0.05	39.47	20.42	2.55	0.50	319.72	134.51	0	0	454.23
25	123	264	123	0	42.33	26.14	0.14	0.05	41.17	21.32	2.90	0.57	356.50	151.19	356.50	0	507.69
26		259		0		27.34		0.06		22.22		0.65		168.93		0	168.93
27		254		0		28.54		0.06		23.12		0.74		187.71		0	187.71
28		249		0		29.74		0.07		24.02		0.83		207.52		0	207.52
29		244		0		30.94		0.08		24.92		0.94		228.36		0	228.36
30		239		239		32.14		0.08		25.82		1.05		250.21		250.21	250.21