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Survival and growth of five Neotropical timber species in monocultures and mixtures

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ABSTRACT

Conversion of tropical forests to crop lands and pastures has been an on-going issue in the Neotropics for decades. Despite the fact that international agreements and incentives have tried to encourage the reforestation of degraded lands in developing countries, in Panama, the actual area reforested has been limited. One of the reasons is that one of the preferred timber species, *Tectona grandis* (Teak), grows poorly on the infertile and clay soils that dominate much of the country, including the Panama Canal watershed.

Reforestation strategies that optimize both the economic return and the production of ecosystem services in tropical degraded lands could meet the demands of different stakeholders from local to international scales. We evaluated the growth and survival of five valuable native timber species grown in both monocultures and mixtures.

In 2008 a fully replicated design with 267 plots and 21 treatments was set up. A total of 22,267 trees were annually monitored until 2015. Locally developed allometric biomass models were used to determine above-ground biomass (AGB) of each treatment in order to assess growth and productivity in monocultures and mixed plantations from five native species (*Anacardium excelsium, Dalbergia retusa, Pachira quinata, Tabebuia rosea* and *Terminalia amazonia*) that differed in key functional traits.

Biomass accumulation of *Terminalia amazonia* monocultures far exceeded that of all other treatments, with up to 47.1 t/ha of biomass 7 years after planting. Nonetheless, individual tree growth of *T. amazonia* was much higher in mixtures than in monoculture, indicating that intraspecific competition started to limit growth. All target species significantly overyielded in the five-species mixture, indicating a diversity effect. The high Relative Land Output (>4) exhibited by *Pachira quinata* in mixture with the nitrogen fixing *Dalbergia retusa* indicated a facilitation effect from the latter.

1. Introduction

A significant proportion of the agricultural lands and/or cattle grazing farms across the tropics have been obtained by clearing intact forests (Aerts and Honnay, 2011). Once forest cover has been lost, tropical lands can rapidly become eroded and degraded, leading in some cases to declining productivity (Nichols et al., 2001; Maranguit et al., 2017). This unsustainable land use has created large areas of degraded lands across Central America (Kettle, 2012).

In recent years, international agreements such as the Bonn Convention (IUCN 2016) or the United Nations strategic plan for forests, have attempted to encourage the rehabilitation of infertile and degraded tropical lands (Sim et al., 2003; Chazdon et al., 2015) and

raise awareness on the public benefits of forests (Stefanski et al., 2015). Planting trees can reverse the negative effects of deforestation by mitigating the impact of climate change through carbon sequestration (Lamb et al., 2005; Hall et al., 2011a, Plath et al., 2011) and improve forest connectivity in rural landscapes (Harvey et al., 2008; Fagan et al., 2016). Evidence is also emerging that naturally regenerated and planted forests can enhance some water related ecosystem services and processes (Muñoz-Villers and McDonnell 2013; Hassler et al., 2011; Ogden et al., 2013; Zimmerman et al., 2013; Hall et al., 2015). From a socio-economical perspective, timber trees may contribute to the long-term livelihood of livestock farmers (Plath et al., 2011; Hall et al., 2011b) by diversifying their agricultural production beyond pastures and improving their overall productivity and sustainability (Suárez

et al., 2012).

Traditionally, many landowners in the tropics plant monocultures of a few exotic timber species coming from a small number of genera whose silviculture and autoecology is broadly known: *Pinus*, *Eucalyptus*, *Tectona*, *Gmelina* and *Acacia* (Lamprecht 1989; Evans and Turnball 2004; Lamb et al., 2005). For example, the current area of *Tectona grandis* (teak) in Central America is estimated to be 132,780 ha, of which 55,000 ha are in Panama (Kollert and Cherubini 2012). Teak represents 76% of plantations established in Panama between 1992 and 2000 (FAO, 2000). Yet, teak performs poorly on the infertile, acidic and clay soils, which are common in much of the tropics (Stefanski et al., 2015) and have been associated to soil erosion (Calder 2002) and low levels of biodiversity (Pandey and Brown, 2000; Healey and Gara 2003). For these reasons, there is a growing interest in exploring the use and suitability of native timber species for reforestation on the sites that are generally available for reforestation and to which commercial species such as teak are not well adapted (Piotto et al., 2010; van Breugel et al., 2011; Hall and Ashton, 2016; Wheeler et al., 2016).

In tropical plantation forestry, the silviculture of monocultures is much better understood than that of mixed-species stands. Moreover, management, harvest and timber marketing are, in general, relatively simpler in the case of monocultures (Cossalter and Pye-Smith, 2003; Evans and Turnball 2004). However, recent research has shown that for some species, the productivity of mixed stands can exceed that of monocultures, although results are mixed and dependent on the environmental conditions and the species being compared (Piotto et al., 2010; Plath et al., 2011; Ewel et al., 2015; Pretzsch et al., 2015; Forrester and Bauhus, 2016). In addition, mixed plantations may enhance ecosystem functions, services, resilience and resistance better than monocultures (Potvin and Gotelli 2008, Cadotte 2013; Reed et al., 2017). Therefore, there is a growing interest in evaluating the performance of mixtures compared to monocultures (Kelty 2006; Paquette and Messier 2011).

While the terminology in this area can be confusing, the ecological mechanisms that lead to greater productivity of mixtures compared to monocultures can be grouped into two classes: complementarity effect and species identity effect (Loreau and Hector 2001; Fargione et al., 2007; Vanelslander et al., 2009; Roscher et al., 2012; Hantsch et al., 2013; Baeten et al., 2013). In the first group, effects of niche partitioning and/or facilitation (Tobner et al., 2014; Potvin and Gotelli 2008; Baeten et al., 2013) are jointly referred as 'complementarity' since differentiation between both in practice can be quite difficult (Loreau and Hector 2001). If species differ in their resource requirements (niche partitioning), a mixture would result in competitive reduction and a more complete use of available resources, leading to a higher productivity at the stand level (Forrester et al., 2006). While facilitation would be the case of nitrogen fixing trees, which may enhance productivity by providing plant-available nitrogen to non-fixing neighbors through the recycling of leaf litter and fine roots (Vitousek et al., 2002; Forrester et al., 2006; Russell & Raich 2012; Batterman et al., 2013; (Nair and Latt, 2013)). These mechanisms of complementarity imply that higher productivity of mixtures would be related to higher functional diversity, rather than simply species diversity (Lamb et al., 2005; Kunert and Cárdenas 2015; Tobner et al., 2014). The strength of the effects of competitive reduction and facilitation on stand productivity would depend on resource availability and on how traits related to acquisition and utilization of resources vary among the species (Healy et al., 2008; Sterck et al., 2011; Craven et al., 2015). Examples of the underlying mechanisms supporting functional differences among species are related to: light and water use strategies (acquisitive or conservative) (Sterck et al., 2011); ability of root production and root spatial distribution (de Kroon et al., 2012); potential to exploit different soil organic phosphorus compounds of the root symbiotic associates (arbuscular mycorrhizal, ectomycorrhizal or non-mycorrhizal) (Steidinger et al., 2015); ability of the nitrogen fixing species to fix nitrogen over time (Batterman et al., 2013); or timings of different plant phenological activities (leaf expansion, leaf initiation or leaf life span) (Devi and Garkoti, 2013).

The second group of mechanisms are related to the mixture probability of containing a key species with a large impact on productivity (Baeten et al., 2013). The effect of species identity i.e. selecting a highly productive species in the mixture, may bring about that a single species eventually outcompetes all the others for a single resource (i.e. nutrient) reaching the highest biomass -the species that has the highest resource-use intensity-, thus driving down the resource level most (Loreau, 2000; Zeugin et al., 2010). Common metrics used to assess the performance of mixtures vs monocultures are the ratio of yield of the mixture to that of the monoculture (*overyielding*) and the ratio of yield of the mixture to that of the most productive monoculture (the more strict *transgressive overyielding*) (see, e.g., Ewel et al., 2015).

Here we present data on survival and growth of 5 valuable timber species native to Panama and the Neotropics. We selected long-lived pioneer species previously tested in the PRORENA species selection trials (Wishnie et al., 2007; van Breugel et al., 2011). Species selection varied with respect to resource acquisition and use, including crown phenology, N_2-fixation, water use efficiency, rooting morphology and nutrient demand. We hypothesized that mixtures of species with different traits and growth requirements have a greater productivity than single-species stands. To address this hypothesis we established single-species plots, two-species plots with all combinations of the five selected species and plots with the five selected species. First, we assessed biomass accumulation across the whole set of treatments to investigate if stand productivity relates to tree species diversity. Next, we compared mortality and growth of each of the selected species across all treatments to determine differential performance and whether some species consistently perform better or worse in mixtures.

2. Material and methods

2.1. Study site

The study site is located in the Panama Canal watershed in two blocks of experimental plantations that are three km from each other within the Agua Salud project area, in a field site administered by the Smithsonian Tropical Research Institute (9 °13′N, 79 °47′W, 330 m a.s.l). In comparison with most soils of the tropical lowlands, the study-site soils are infertile oxisols (Turner and Englebrecht 2011; Table S1). The average annual rainfall is 2700 mm (Ogden et al., 2013). Initially the area was used as cattle pasture or was covered by very young (< 5 years) secondary forest that was completely cleared before the plantations were installed in 2008 (Weber and Hall, 2009; van Breugel and Hall 2008). Experimental plantations were fertilized only at planting (2 oz of N-P-K, 12-24-12 and organic material mixed with soil and planted with seedling; 2 oz Triple Sulfate several cm from roots) and the grass and competing native vegetation were manually cleared four times a year.

2.2. Experimental design and tree species

A total of 21 treatments with different combinations of five native timber species -*Anacardium excelsium, Dalbergia retusa* (N_2-fixing), *Pachira quinata, Tabebuia rosea* and *Terminalia amazonia* (henceforth 'target species') (Table 1) were established in 267 (42 × 36.5 m) plots. All species are long lived long lived pioneers found in the canopy (Hall and Ashton, 2016), with valuable timber and native to Panama. Our selection was based on previous findings related to nutrient and water cycling (Table 2) believed to potentially enhance complementarity (facilitation or complementary use of resources). The five target species were grown in monocultures, in mixtures of two and five species and in mixtures of one target species with five early successional companion species -*Erythrina fusca, Gliricidia sepium, Inga punctate, Luehea speciose* and *Ochroma pyramidale*-. Companion species were expected to enhance