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# Effect of microsite quality and species composition on tree growth: A semi-empirical modeling approach

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ABSTRACT

Reforestation in the tropics mitigates the negative effects of climate change by sequestering carbon in biomass. However, tree growth is limited by nutrient availability in many tropical regions. A clear understanding of nutrient constraints and topography on growth of native timber species is thus essential to improve both the economic return on reforestation and the ecosystem services in tropical degraded lands. To address this, we use 7-year growth data from a 75-ha reforestation experiment in central Panama to test a modeling approach to predict growth of these species. The experiment includes five valuable timber species in 21 treatments, including monocultures and mixtures. We first fit a non-linear growth model as a function of tree age, then expand the former model parameters as a function of variables related to species mixture and micro-site soil conditions. Finally, we built a final model for each species to predict growth along three axes: nutrient availability, slope and species mixture. The models successfully identified how variation in growth was related to micro-site conditions and the species mixture. Although all species were long-lived pioneers, most were overall more sensitive to nutrient availability and between-trees interactions than to slope. However, the fastest growing species on average was more sensitive to slope than the other species and less sensitive to nutrient availability, showing better performance than the other species even under adverse conditions. Our models aid identification of species with the best growth potential to use in reforestation on infertile soils, leading to a better species selection according to site conditions.

## 1. Introduction

Tropical forests are the most productive biome and are an important terrestrial carbon sink (Asner et al., 2010; Chazdon et al., 2016). However, tropical forests are disappearing at the rate of about 21 to 50 ha per minute (Global Resources Institute, 2014), and may therefore now represent a source, rather than a sink, of $CO_2$ (Baccini et al., 2017). Tropical land clearly represents a vast potential for carbon sequestration through reforestation (Griscom et al., 2017).

The main drivers of tropical deforestation are a combination of multiple causal factors such as agricultural expansion, wood extraction and infrastructure expansion, all varying by geographical and historical contexts (Geist and Lambin, 2002; Dupin et al., 2018). In Panama, policies and laws such as providing the ability to obtain land titles on "productive" land have inadvertently incentivized and accentuated the deforestation process (ANAM, 2003; Oestreicher et al., 2009). Once forest cover is lost, poor management can promote erosion and land degradation, leading to loss of relatively nutrient-rich topsoil, reduced fertility, and decreased productivity (Parrotta, 2002) - processes exacerbated on steep lands or terrain with high topographic variation.

While researchers have been studying reforestation and restoration in Central America for several decades (Butterfield and Fisher, 1994; Montagnini et al., 2004), interest in the potential for reforestation and forest restoration to provide a suite of ecosystem services has intensified in recent years (e.g., Hall et al., 2011a, 2011b). Traditionally, the preferred timber species in Central America has been *Tectona grandis L.f.* (teak) (Kollert and Cherubini, 2012). However, teak performs poorly on the infertile, acidic and clay soils common in much of the

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region (Stefanski et al., 2015), so establishing plantations with native timber species is generating renewed interest (Petit and Montagnini, 2004). Indeed, mixed native species plantations are viewed as a way to combine the restoration of biodiversity, forest cover and vital ecosystem services in human-modified tropical landscapes with long-term economic value (Griscom et al., 2009; Griess and Knoke, 2011; Varela et al., 2017).

Growth and productivity in tree plantations is a function of the supply, capture and efficiency of the use of resources -light, water, nutrients and growing space- and depends on the between-trees interactions (Forrester and Pretzsch, 2015). The species composition of tree plantations influences tree growth and stand productivity (Ewel et al., 2015; Mayoral et al., 2017). Complementary interactions, such as spatial, temporal or chemical stratification in water and nutrient sources and uptake, can lead to reduced competition and/or facilitation, and hence increased productivity (Pretzsch et al. 2015). The outcome of species interactions depends on the ecological traits of the interacting species and on environmental conditions (del Rio et al., 2016).

Soil forming factors (parent material, climate, biota, topography and time) and properties (physical, chemical and biological) will determine plant and soil interactions, and in turn soil resource availability to plants (Toure and Zhou, 2015; Siddique et al., 2008). In many tropical forests, plants typically have to cope with low concentrations of soil nutrients, including phosphorus, potassium and nitrogen (Bare and Ashton, 2016; Cusack et al., 2018), but also excesses of others elements such as aluminum, which in many cases are toxic to plants (Martins et al., 2015). Moreover, topography, including factors such as aspect or slope, is correlated with important environmental variables such as temperature, water, light and nutrients availability (Tsui et al., 2004; Toure and Zhou, 2015). In particular, slope is one of the most important drivers in the universal soil loss equation (Khan et al., 2013). Terrain configuration and topographic geometry, such as slope angle, length and curvature all influence runoff, drainage, soil erosion (Wang et al., 2017), exerting important influences on tree growth (Detto et al., 2013; Pontara et al., 2016; Scholten et al., 2017; Ashton et al., 2018).

Predicting growth of native species under different micro-environmental conditions is currently a key issue for the management of plantings on infertile and degraded tropical lands, where small variations in the abiotic factors may represent significant changes in tree growth. This has led tropical ecologists and foresters to use different modeling approaches for the study of the variability in individual tree growth for tropical species. For example, Le Bec et al. (2015) and Fichtner et al. (2017) modeled tree productivity considering different factors including neighborhood interactions. Nevertheless, research is still needed with respect the sources of variability in native tree growth related to micro-site conditions and their effect on the stand growth dynamics (Scolforo et al., 2017).

In this study, we used a modeling approach in which we modified the Gompertz model (growth-age model), expanding the former model parameters by defining its relationship to microsite-related variables: species mixture, topography and nutrient availability. Our aims were, first, to use this approach to improve knowledge about the sensitivity of five valuable native timber species to variations in nutrient availability and terrain configuration. Second, to disentangle the relative importance of neighboring species and microsite conditions, leading to a more nuanced choice of matching species to sites. This approach allows identification of species with the best growth potential to use in reforestation on infertile soils, improving the knowledge of native timber species to promote the diversification of plantations beyond exotic species on degraded tropical lands (Scolforo et al., 2017). Given the high establishment and management costs of plantations, new approaches are needed to provide better information to help to maximize investment and avoid financial loss. We tested the degree to which differences in growth between selected species were linked to soil nutrient availability and/or slope, and within this framework, how growth would be mediated by neighboring species during the first seven years of stand development. We further hypothesized that there must be specific mixtures of species that maximize growth at low soil nutrient availability. Finally, we tested if a faster growth is necessarily related to a lower sensitivity to negative soil factors.

**Table 1**
Treatments key and functional traits.

| Species mixture | Species % | Replicates | Crown phenology[a] | Nutrient cycling[b] | Root morphology[c] | WUE[d] | Transpiration[e] | Tree form | WSG ($g/cm^3$) |
|---|---|---|---|---|---|---|---|---|---|
| *Terminalia amazonia* (Ta) | 100 | 11 | E | – | LR | | High | Straight stem | 0.43 |
| *Dalbergia retusa* (Dr) | 100 | 12 | D (briefly) | N | TLR | High | | Multiple stems | 0.88 |
| *Anacardium excelsium* (Ae) | 100 | 11 | D | – | TR | Low | | Straight stem | 0.42 |
| *Pachira quinata* (Pq) | 100 | 11 | D | – | TR | | | Straight stem | 0.65 |
| *Tabebuia rosea* (Tr) | 100 | 11 | E | – | TLR | | High | Straight stem | 0.51 |
| Ta + Dr + Ae + Pq + Tr | 20 | 16 | | | | | | | |
| Ae + Dr | 50 | 13 | | | | | | | |
| Ae + Pq | 50 | 13 | | | | | | | |
| Ae + Ta | 50 | 13 | | | | | | | |
| Ae + Tr | 50 | 13 | | | | | | | |
| Dr + Pq | 50 | 13 | | | | | | | |
| Dr + Ta | 50 | 13 | | | | | | | |
| Dr + Tr | 50 | 13 | | | | | | | |
| Pq + Ta | 50 | 13 | | | | | | | |
| Pq + Tr | 50 | 13 | | | | | | | |
| Tr + Ta | 50 | 13 | | | | | | | |
| Ae + X | 50 | 13 | | | | | | | |
| Dr + X | 50 | 13 | | | | | | | |
| Pq + X | 50 | 13 | | | | | | | |
| Ta + X | 50 | 13 | | | | | | | |
| Tr + X | 50 | 13 | | | | | | | |

X: Companion species (*Erythrina fusca, Gliricidia sepium, Inga punctate, Luehea speciose and Ochroma pyramidale*); WUE: Water use efficiency; WSG: Wood specific gravity.

[a] E = evergreen, D = deciduous, SD = semideciduous- partially loses leaves during dry season.

[b] N = N fixing.

[c] TR = tap root, LR = lateral roots, TLR = lateral roots Sinacore et al. (2017).

[d] Cernusak et al. (2007).

[e] Kunert et al. (2010).