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# Local and regional environmental variation influences the growth of tropical trees in selection trials in the Republic of Panama

Andrew Park[a,*], Michiel van Breugel[b], Mark S. Ashton[c], Mark Wishnie[b,1], Emilio Mariscal[b], José Deago[b], Diogenes Ibarra[b], Norma Cedeño[b], Jefferson S. Hall[b]

[a] Department of Biology and Centre for Forest Interdisciplinary Research (CFIR), University of Winnipeg, 515 Portage Avenue, Winnipeg, Manitoba, Canada R3B 2E9
[b] PRORENA, Smithsonian Tropical Research Institute, 401 Ave Roosevelt, Balboa Ancon, Panama
[c] Yale School of Forestry & Environmental Studies, Sage Hall, 205 Prospect Street, New Haven, CT 06511, USA

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ABSTRACT

Native Neotropical trees are being increasingly planted for restoration purposes and timber production, but we lack species-specific data on growth responses to different regional climates and local environmental variation. We used regression trees and variance components to quantify the effects of within- and among-site environmental variation on the basal area (*BA*) of 21 Neotropical and two exotic tree species at three selection trials in the Republic of Panama. Sites represented distinct regional climates in which annual rainfall varied from 1100 to 2226 mm, with dry seasons of 4.1–6.7 months. Local environmental variables included measures of slope steepness and position, soil texture, soil color, and indicators of soil condition, such as subsoil rockiness.

Basal area in 17 species responded primarily to regional differences among sites, and explained between 32% and 72% of species *BA*. Low *BA* plots of most species were located in the driest site, while high *BA* plots were found in the two wetter sites (mean *BA* difference = 117 ± 20.6 cm$^2$). Local variables also influenced the growth of 12 species, with percent slope, soil texture at 5–10 cm, subsoil rockiness and Munsell value from 20 to 50 cm explaining between 0.2% and 24.5% of within-site variance in *BA*. For these variables, *BA* differences across adjacent branches of regression trees ranged from 59 ± 23.4 cm$^2$ (subsoil rockiness) to 176 ± 45.9 cm$^2$ (Munsell value). Our results support the growing evidence that local as well as regional environmental variation influences tree community composition, growth and survival in mature forests. Furthermore, the heterogeneity of responses to local variables among environmentally sensitive species allowed us to make some preliminary site and species-specific silvicultural recommendations. For site generalists, future research should extend the current trials to multiple sites within each regional climate to separate climatic influences from those of the local environment.



## 1. Introduction

In the humid and seasonal tropics, the ongoing conversion of forest to farmland and pasture has left a legacy of over 3.5 million km$^2$ of degraded lands on which natural forest regeneration cannot occur (ITTO, 2002). Deforestation is particularly pervasive in Central America, where it is estimated that seven countries lost from 7% to 37% of their remaining forest cover between 1990 and 2000 alone (FAO, 2001). In response to this challenge, a renewed interest in reforestation and restoration using native tree species is emerging (Butterfield, 1995; Ashton et al., 2001; Leopold et al., 2001; Carpenter et al., 2004). Native tree species are promoted to enhance rural livelihoods (Arnold and Dewees, 1998; Murray and Bannister, 2004), restore biological diversity (Leopold et al., 2001; Lamb and Gilmour, 2003), sequester carbon (Silver et al., 2000), and combat soil erosion (Scott et al., 2005). Renewed attention is also being paid to mixed-species plantations (Kelty, 2006; Nichols et al., 2006), raising the prospect that desirable species traits might be combined in a single forest stand.

Some old world tropical trees are widely used in restoration and reforestation. Both teak (*Tectona grandis*) (Healey and Gara, 2003) and *Acacia mangium* (Norisada et al., 2005) are commonly deployed in afforestation and reforestation projects across Central America and Latin America. Despite widespread interest in planting native species in Central and South America, silvicultural recommendations for Neotropical rainforest trees are, for the most part, qualitative in nature (e.g. Quírico Jimenéz et al., 2002). Unexplained variations in species performance (Butterfield, 1995), inadequate

* Corresponding author. Tel.: +1 204 786 9407.
*E-mail address:* a.park@uwinnipeg.ca (A. Park).
[1] Current address: Equator Environmental, 250 Park Avenue South, New York, NY 10003, USA.

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knowledge of species-site relationships, and a lack of basic silvicultural data (Guariguata and Pinard, 1998; Lamb and Gilmour, 2003) potentially impede the widespread adoption of native species.

Achieving an appropriate match between species and planting sites is a major concern in silviculture (Evans, 1999). Basic site characteristics, such as altitude and slope position (Asner et al., 2009), micro-topography, local soil management practices, and land use history (Kalinganire, 1996; Urich and Reeder, 1999) affect the productivity of secondary forests and tree plantations. Climate and edaphic factors also modify the distribution and growth rates of species in mature tropical forests (Clark et al., 1999; Condit et al., 2002; Baker et al., 2003; Hall et al., 2004; Svenning et al., 2004). Furthermore, significant clone by site (Naik et al., 2009) or environment by genotype interactions have been observed in detailed provenance trials (Butterfield, 1996). Significant topographic effects connected to soil quality and erosion has also been found in a few restoration trials (Carpenter et al., 2004).

The above-cited studies notwithstanding, the influence of local and regional variation in topography, soils and rainfall on the establishment and growth of planted trees in restoration trials remains poorly studied, even though investigations of survival and growth (e.g. Davidson et al., 1998; Leopold et al., 2001; Montagnini et al., 2003) and the influence of trees on soil properties (e.g. Haggar and Ewel, 1997; Stanley and Montagnini, 1999) are common. Studies to relate tree growth to environmental factors in restoration plantations are therefore needed. In this paper, we explore the relative influence of local environmental variables and regionally determined site properties on the growth of 21 native Neotropical and two exotic tree species in three large species selection trials in the Republic of Panama.

We sought to answer two principal questions. First, what is the relative importance of local (within-site) environmental variation versus regional climate (among-site variation) to the growth of a variety of tree species? Secondly, we asked whether intraspecific differences in tree size that were mediated by local environmental variables were any larger than those among tree species in which no local environmental effects were detected? Question 2 was motivated by the need to investigate the practical importance of apparent environmental influences on growth. For example, statistically significant environmental effects may not produce enough variation in growth rates to seriously affect the decision to plant one species over another, or they may, over time, be amplified into major size differences.

## 2. Methods

### 2.1. Study sites

Our research sites were three species selection trials established by PRORENA, the native species reforestation project of the Smithsonian Tropical Research Institute (STRI) and Yale School of Forestry and Environmental Studies. These sites were selected to be representative of regional climates and soils across the Isthmus of Panama (Wishnie et al., 2007). Soberania National Park (hereafter "Soberania") received an average of 2226 mm annual rainfall between 1987 and 2002, with a 4.1-month dry season in which less than 100 mm rain fell in each month. A site at Rio Hato in Panama's "Dry Arc" received 1107 mm of rainfall annually, with a 6.7-month dry season. The third site at Los Santos in the Azuero Peninsula occupied an intermediate regional climate with a 10-year average annual rainfall of 1800 mm (but only 1467 mm from 2000–2004) (Griscom et al., 2009) with a 5.2-month dry season (Craven et al., 2007).

Each site has distinctive topography and edaphic features (Table 1). Soberania and Los Santos are characterized by rolling and hilly terrain punctuated by moist swales, and, in the case of Los Santos, seasonally inundated lowlands. Rio Hato has flat or gently sloping terrain in which substantial patches have suffered from sheet erosion, indicated by erosion pavements covered by small pebbles and a lack of organic matter. Soils at Soberania and Los Santos are primarily clays and silty clay loams, whereas the texture of Rio Hato's mineral soils ranges from loamy sand through to heavy clay. Los Santos soils had relatively high total nitrogen (N), potassium (K) calcium (Ca), magnesium (Mg), and phosphorus (P). The soils at Rio Hato were the least fertile soils among the three sites, with considerably lower cation exchange capacities and concentrations of N, K, Mg, P than at the other two sites (Craven et al., 2007).

All sites were cleared of forest before 1960, and had subsequent histories of grazing or small scale agriculture. At the time of planting, Soberania had not been farmed for at least 10 years, and was dominated by a near-uniform cover of the invasive sugar cane relative *Saccharum spontaneum*. Los Santos continued to experience low intensity cattle grazing of its understory dominated by *Heliconia* sp. and grasses. Rio Hato had been free of livestock for at least 3 years, and vegetation varied from low thorny scrub to pasture grasses.

### 2.2. Species selection and planting

Twenty-one Neotropical and two exotic tree species were planted in 2003. Species selection criteria included restoration potential (e.g. nitrogen fixation, erosion control), timber value, use for fodder, live fencing and fruit production (Wishnie et al., 2007). Seeds of native species were collected by the PRORENA nursery staff, who had an intimate knowledge of the local geography of seed trees of each species. Seed trees were located in mature forest sites across the Isthmus of Panama, and in the wet (Chagres), mesic (Soberiana), semi-dry (Azuero) and dry (Rio Hato) regions between December 2002 and June 2003. Seeds for the exotics (*Acacia mangium* and *Tectona grandis*) were obtained from local suppliers and are the standard provenances used in commercial plantations across Panama. Seedlings were cultivated for 2–8 months (depending on growth rate) in 125 mm root pruning pots. Prior to outplanting, seedlings were acclimated to full sunlight over 3 weeks by being progressively moved into areas of the nursery that enjoyed increasing light levels (Wishnie et al., 2007).

Seedlings were planted in three completely randomized blocks at each site. Provenances collected at different sites were also allocated at random among sites and subplots (three replicates per species per block, 20 seedlings per plot established at 3 m × 3 m spacing; $n = 27$) (José Deago, personal observation). All plots were sprayed biweekly to control insects during the first 2 years of growth. After 2 years of growth, plots were thinned to 50% of their original density (i.e. to 10 stems per plot) to avoid intraspecific competition from crown closure.

### 2.3. Tree measurements

Field technicians measured basal diameter at the root collar, total height, live crown length, and two crown diameters (along the widest axis and perpendicular to it) of all trees on an annual basis from 2004 to 2006. Detailed biomass measurements were also taken from 6 to 12 individuals of each species after 2 years of growth (Bastién Henri et al., submitted). We used linear regression to test basal area (*BA*) derived from basal diameter, height, trunk volume modeled as a cylinder, and a growth index (*GI*) based on the sum of basal area and crown volume as potential predictors of biomass. Of these metrics, $\log_{10} BA$ was consistently the best predictor of $\log_{10}$ transformed biomass, yielding an average $r^2$ of 0.87 ± 0.177 for the 22 species, and was therefore used as our response variable in this study.