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Initial performance and reforestation potential of 24 tropical tree species planted across a precipitation gradient in the Republic of Panama

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Abstract

Decades of deforestation and unsustainable land use have created large expanses of degraded lands across Central America. Reforestation may offer one means of mitigating these processes of degradation while sustaining resident human communities. However, a lack of information regarding tree species performance has been identified as an important limitation on the success and adoption of diversified reforestation strategies. We analyzed the initial growth of 22 native and 2 exotic tree species planted at three sites across a precipitation gradient in the Republic of Panama (1100–2200 mm $year^{-1}$), and identify promising species for use in forest restoration, timber production and on-farm systems.

At all sites, *Acacia mangium*, *Diphysa robinoides*, *Gliricidia sepium*, *Guazuma ulmifolia* and *Ochroma pyramidale* rapidly developed large, dense crowns and attained canopy closure after just 2 years. These species might be used in restoration efforts to rapidly stabilize soils and establish crown cover. As nitrogen-fixing legumes, *D. robinoides* and *G. sepium* may also have the potential to increase soil fertility. Several species valued for their timber performed well at all sites attaining high wood volume indices, these species included *Tectona grandis*, *Pachira quinata* and *Tabebuia rosea*. *Albizia guachapele* and *Samanea saman* were among the best performers at the driest site. The most promising species for use in silvopastoral systems varied among sites; *A. guachapele*, *G. sepium*, *S. saman* and *G. ulmifolia* performed best at the driest site, while *G. sepium*, *G. ulmifolia* and *Spondias mombin* were the top performers at the two wetter sites. It is hoped that the results of this trial will improve the success of reforestation efforts by allowing landholders to select species based upon both local site conditions and their specific reforestation objectives.

Keywords: Central America; Forestry; Rainfall; Restoration; Silvopastoral systems; Timber

1. Introduction

Over the last 50 years the Republic of Panama has lost more than 30% of its forest cover (Romero et al., 1999; FAO, 2000). As in much of the Neotropics, the loss of these forests is due primarily to the conversion of forested land to pasture and agriculture (Heckadon-Moreno, 1984; Toledo, 1992). Once forest cover has been lost, tropical lands can rapidly become eroded and infertile (Nichols et al., 2001; Montagnini and Sancho, 1990), and degraded farmland is regularly abandoned. Woody species can be slow to re-establish in degraded pasture (Gerhardt, 1993; but see Griscom, 2004) and the processes of natural succession can be severely impaired by continued soil degradation (Nepstad et al., 1991), dominance of invasive grasses (Hooper et al., 2004; Jones et al., 2004), lack of seed dispersal (Holl et al., 2000) and poor microsite conditions for seed germination (Aide and Cavelier, 1994). Planting trees in degraded tropical landscapes can have positive effects on soil conditions and the regeneration of woody species (Haggar et al., 1998; Lugo, 1997; Ashton et al., 1997; Montagnini, 2001; Jones et al., 2004), and therefore plantations may offer one means to mitigate or reverse the negative impacts of land degradation in the tropics.

Plantation forestry in Latin America has traditionally concentrated on a few well-known exotic species (Evans and Turnbull, 2004). For example, *Tectona grandis*, *Acacia* sp. and *Eucalyptus* sp. represent more than 51% of all plantations established in the Neotropics (FAO, 2000), and *T. grandis* comprised 76% of plantations established in the Republic of

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Panama between 1992 and 2000 (FAO, 2000; ANAM, 2003). Well-managed monoculture plantations of exotic species may be productive under favorable conditions, but these species have often been selected to produce a very limited set of goods and services, and may do a very poor job of achieving other objectives. For example, there is evidence to suggest that plantations of *T. grandis* support low levels of plant biodiversity (Healy and Gara, 2003) and promote soil erosion (Calder, 2002, 2005), and that some exotic species may negatively impact site conditions by reducing soil quality (Berger, 1993; Lugo, 1997). Perhaps most importantly, such a limited number of species cannot be expected to perform equally well across the broad range of climatic and site conditions encountered in Central America's deforested land base, nor can such a small number of species be expected to provide the full range of goods and services landholders seek from planted forests.

More than 100 species of tree native to Panama are known to be used regularly for their timber, fuel wood, fodder and other products (Haggar et al., 1998; Aguilar and Condit, 2001; Love and Spanner, 2005; Connelly, unpublished data). All of these species have the potential to address a wide range of landholder needs. However, relatively little information exists regarding their performance in reforestation projects. For example, tree size, canopy cover and canopy density have been described as the most important characteristics for encouraging soil stabilization and vegetation recruitment to the understory (Montagnini and Sancho, 1990; Parrotta, 1992; Fisher, 1995; Jones et al., 2004), yet most species used for timber production have been selected in part because they allocate a high proportion of biomass to stem wood and have strong apical control (Evans and Turnbull, 2004), and they may therefore be poor choices for reforestation efforts directed at the restoration of ecological function. Some tree species have very specific uses, such as leguminous fodder species that retain foliage during dry periods, readily coppice, have high leaf nutrient content, and are highly digestible by cattle (Chavarria et al., 1997; Jayasundara et al., 1997; Nygren et al., 2000; Dagang and Nair, 2003), or species that are valued for specific properties of their fruits, resins, or bark. Other species may be used to achieve multiple objectives. Studies in Costa Rica have shown that species such as *Vochysia ferruginea* and *Hyeronima alchorneoides* can aid nutrient cycling and encourage land restoration but also have good growth form and high quality timber (Haggar et al., 1998; Carnevale and Montagnini, 2002).

It is well-established that tropical forests in Panama show clear patterns of spatial organization in relation to precipitation (Pyke et al., 2001). Studies of tree species composition across the Isthmus of Panama have shown that Pacific dry forests are quite distinct from the wetter forests of the Caribbean coast (Condit et al., 2004). However, most studies of native species plantations in Central America have been conducted within relatively small geographic areas (Butterfield, 1995; Montagnini et al., 2000; Carnevale and Montagnini, 2002; Piotto et al., 2004; Jones et al., 2004), and it is therefore difficult to extrapolate the results of many of these studies to areas with different climates or soil conditions (though see CATIE, 1986; Piotto et al., 2003; Stewart and Dunsdon, 1994; for regional and pan-tropical comparisons).

For reforestation strategies to be effective at a national and regional scale, and for reforestation to become a viable, widespread activity, landholders must be able to select tree species based both on their specific restoration objectives and on the climatic and other relevant physical characteristics of their landholdings, and it is therefore critically important that the range of reforestation options available to landholders be increased.

Here we present initial results from a long-term study of the reforestation potential of native Panamanian tree species. In the first phase of this study we planted 24 tropical tree species at three deforested sites in the Republic of Panama that span an annual precipitation gradient of 1100–2200 mm $year^{-1}$. We assess initial species performance across this gradient in relation to three broad use categories:

1. *Restoration potential*: species that rapidly develop wide, dense crowns.
2. *Timber production*: species of known timber value that develop high wood volume indices (VI).
3. *On-farm systems*: fast-growing species useful for silvopastoral or agroforestry systems to increase soil fertility and provide fodder, live fences, and fuel wood.

2. Materials and methods

2.1. Study sites

This study was conducted at three sites in the Republic of Panama: Soberania National Park in the Panama Canal Watershed, Playa Venado in Los Santos Province and Río Hato in Cocle Province (Fig. 1). These sites span an average annual precipitation gradient of 1107–2230 mm, and have varying soil conditions (Table 1). Soberania National Park is the wettest site with mean annual rainfall of 2226 mm and 4.1 dry months annually (defined as months with <100 mm rainfall). Soberania overlies tropical ultisols that are more acidic than those at Los Santos, but have higher concentrations of N and K. Los Santos is the second wettest site with mean annual rainfall of 1946 mm and 5.2 dry months, but has perhaps the richest soils, principally tropical alfisols with the highest concentrations of P, Ca and Mg of the three sites. The soils at both Soberania and Los Santos are

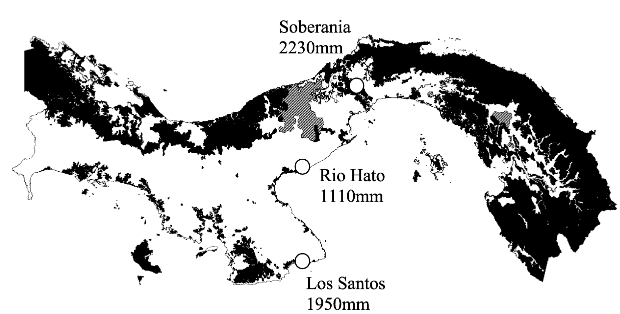

Fig. 1. Map showing forest cover (shaded areas) in Panama in 1992, and the location and rainfall (mm $year^{-1}$) of each of the three experimental sites: Soberania National Park, Los Santos and Rio Hato (ANAM, 1992; map printed from SIG Republic, Eon Systems, all rights reserved).

Table 1
Mean soil chemical properties, annual rainfall and previous land-use of three sites in Panama

Site	Soil properties[a]						Mean annual rainfall[b] (mm year^{-1})	Mean number of drought months[b] (month year^{-1})	Land-use prior to reforestation
	N (%)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	pH			
Rio Hato	0.086 ±0.013	1.86 ±0.15	47.22 ±7.40	599.4 ±52.59	99.82 ±6.38	5.65 ±0.24	1107 ±56	6.7	Degraded, cattle pasture
Los Santos	0.188 ±0.008	7.52 ±0.92	58.07 ±12.79	2373 ±302.2	562.33 ±15.74	6.30 ±0.06	1946 ±65	5.2	Active cattle pasture
Soberania	0.235 ±0.013	4.39 ±0.36	143.04 ±13.91	1246 ±81.32	346.9 ±25.87	5.59 ±0.04	2226 ±67	4.1	Abandoned farmland, dominated by invasive grass

[a] Soil data are mean values per site ± S.E. from samples taken at 0–15 cm depth.
[b] Mean annual rainfall and mean number of drought months per year (months with <100 mm rainfall) were calculated over the period 1987–2002 for the site at Soberania (Panama Canal Authority, unpublished data); 1987–1997 at Los Santos (Achotines Laboratory, Inter American Tropical Tuna Commission, unpublished data); 1987–1997 at Rio Hato (ANAM, unpublished data).

predominantly clay or silty clays (A. Park, unpublished data). Rio Hato is the driest site, with an average annual rainfall of 1107 mm and 6.7 dry months per year. This site has the most nutrient poor soils, which are shallow and, although very variable in texture, soils are generally sandy or silty clays (A. Park, unpublished data).

All sites had been cleared of forest prior to 1960, but remaining forest fragments at each site indicate that natural forest types differed among them. Most of Soberania National Park is covered by secondary tropical seasonal rainforest. Tropical semi-deciduous forest fragments remain in the vicinity of Los Santos, and small fragments of dry deciduous tropical forest are present in the Rio Hato area.

At the time of plantation establishment the site at Soberania National Park had not been farmed for at least 10 years. The Los Santos site was still active cattle pasture, and Rio Hato had not been farmed or grazed for 3 years. Soberania was dominated by the exotic invasive grass *Saccharum spontaneum*. Los Santos and Rio Hato were dominated by mixed grasses and herbs with some scattered trees.

2.2. Species selection, seed collection and seedling production

Twenty-two native and two exotic tree species were selected in relation to three use categories: forest restoration potential, timber production and silvopastoral use (Table 2). Species were selected based on conversations with local landholders, sawmill owners, and timber companies, and on reviews of relevant literature. Species were selected for their restoration potential based on high growth rates in light gaps in natural forest (Condit et al., unpublished data), literature and personal observations suggesting that they produce fruit consumed by a wide variety of animals (Jones et al., 2004, Deago, personal communication), and/or their potential to ameliorate site conditions through nitrogen fixation (CATIE, 1986; Dagang and Nair, 2003). The two exotic species were included for purposes of comparison because they are widely used in plantation forestry and have high timber value (*T. grandis*) or restoration potential (*Acacia mangium*). The species selected encompass a diverse range of ecological attributes and potential growth rates as indicated by the wood density indices which range from 0.15, for *Ochroma pyrimidale*, to 0.99, for *Colubrina glandulosa*.

Seeds were collected between 1 December 2002 and 1 June 2003. Where possible, seeds of each species were collected from three sites within Panama. All seeds were transported to the National Environmental Authority of Panama's (ANAM) nursery in Rio Hato, where they were germinated in sand and transplanted to 45 mm diameter, 120 mm tall root pruning pots containing a well-drained, neutral nursery substrate (pH 6.5, compost formula; 18 parts clay soil:14 rice husk:14 chicken manure:5 charcoal). Immediately after germination seedlings were placed in 75% shade, and then moved into progressively less shaded conditions every 3 weeks for acclimation to full sun conditions prior to transplantation. All seedlings were kept in full sunlight in the nursery for at least 3 weeks prior to

Table 2
Scientific, family, common names, and principal uses of 24 species of tropical tree used in the selection trials

Scientific name	Family	Common name	Species code	Wood density	Uses
Acacia mangium	Fabaceae	Acacia	AM	0.57	Exotic: restoration, timber
Albizia adinocephala	Fabaceae	Frijolillo	AD	0.66	Restoration
Albizia guachapele	Fabaceae	Guachapalí	AG	0.62	Fodder, timber
Astronium graveolens	Anacardiaceae	Zorro	AGr	0.80	High value timber
Calycophyllum candidissimum	Rubiaceae	Madroño, Lluvia de plata	CC	0.82	Restoration
Cedrela odorata	Meliaceae	Spanish cedar	CO	0.44	High value timber
Colubrina glandulosa	Rhamnaceae	Carbonero	CG	0.99	Timber, fuel wood
Copaifera aromatica	Fabaceae	Cabimo	CA		Timber
Cordia alliodora	Boraginaceae	Laurel	CAl	0.46	Timber
Diphysa robinioides	Fabaceae	Macano	DR		Fencing, fuel wood
Dipteryx oleifera	Fabaceae	Almendro de montaña	DP	0.80	Timber
Enterolobium cyclocarpum	Fabaceae	Corotú	EC	0.44	Timber, fodder
Erythrina fusca	Fabaceae	Palo bobo, Palo santo	EF	0.28	Restoration
Gliricidia sepium	Fabaceae	Balo	GS	0.74	Live fencing, fodder
Guazuma ulmifolia	Sterculiaceae	Guácimo	GU	0.55	Fodder, fuel wood
Inga punctata	Fabaceae	Guabita cansaboca	IP	0.58	Fruit, restoration
Luehea seemannii	Tiliaceae	Guacimo Colorado	LS	0.50	Restoration
Ochroma pyramidale	Bombacaceae	Balsa	OP	0.15	Restoration
Pachira quinata	Bombacaceae	Cedro espino	PQ	0.46	Timber
Samanea saman	Fabaceae	Guachapalí	SS	0.57	Fodder, timber
Spondias mombin	Anacardiaceae	Jobo	SM	0.43	Live fencing, fruit, restoration
Tabebuia rosea	Bignoniaceae	Roble	TR	0.84	Timber
Tectona grandis	Verbenaceae	Teak	TG	0.54	Exotic: high value timber
Terminalia amazonia	Combretaceae	Amarillo	TA	0.68	High value timber

transplantation. This process took 2–8 months, depending on species.

2.3. Experimental design

At each of the three sites approimately 4.5 ha were cleared of all vegetation with machetes. Planting sites at Soberania and Rio Hato were also burned to remove brush, although early rains at Los Santos prevented burning. Regenerating vegetation at all sites was treated with glyphosphate herbicide 3 weeks after clearing and at least 3 weeks before seedlings were transplanted. Seedlings were planted in three adjacent blocks, one block on a ridge top, one on the slope and one on a flat area. The site at Rio Hato has little topographic variation, and therefore all blocks were established on flat areas.

Three plots of each species, each containing 20 individuals, were established at randomly assigned locations within each of the three blocks at each site ($20 \times 3 \times 3 = 180$ individuals of each species planted at each site, or 540 individuals of each species in total). Within each plot, seedlings were planted in a $9\ \text{m} \times 12\ \text{m}$ grid with 3 m spacing (equivalent to 1111 seedlings per hectare). Seedlings were transplanted on 5 August 2003 at Soberania, 30 June 2003 and 24 July 2003 at Rio Hato, and 19 June 2003 and 17 July 2003 at Rio Hato. Dead seedlings were replaced 2 weeks after transplanting. The seed collection site of all seedlings was known, and recorded at the time of planting. Where possible, seed source was distributed evenly among sites.

To aid in establishment, fertilizer was applied to each seedling at the time of planting (115 g of 12–72–12 N–P–K granular fertilizer), and again 2 months after planting (115 g of granular phosphate). After planting, competing vegetation in the plots was cleared with machetes when taller than 1 m. The frequency of clearing varied with the growth rates of competing vegetation.

2.4. Soil sampling and analysis

Soils were sampled from 45 and 30 randomly selected locations within the sites at Soberania and Rio Hato respectively, and from nine randomly selected locations within the site at Los Santos. Soils were sampled at least 6 months after burning. Samples were taken from 0 to 15 cm below the soil surface using soil augurs. Samples were air dried for approximately 2 days and then sieved mechanically. Approximately 150–160 g per sample was then placed in sample vials, labeled, and sent to the University of Georgia, College of Agricultural and Environmental Science, Soil, Plant & Water laboratory for analyses.

Soil pH was determined in water using a digital pH meter and electrode. Mehlich 1 extraction (0.05 M HCl + 0.0125 M H_2SO_4) was used to extract P, K, Ca and Mg, and concentrations were determined using inductively coupled plasma spectrography (Thermo Jarrell-Ash model 61E ICP, Thermo Jarrell-Ash Corporation, 27, Forge Parkway, Franklin, MA, USA). Total N (%) was analyzed using a CNS analyzer (LECO CNS 2000, CNS Corp., St. Joseph, WI, USA).

2.5. Seedling measurements

Initial measurements of total height (height from soil surface to the highest living apical bud) and basal diameter (stem diameter at 50 mm above soil surface) were taken between 21 August and 5 September 2003 at Soberania, 11–27 August 2003 at Los Santos, and 4–31 July 2003 at Rio Hato. All seedlings were re-measured approximately 24 months later (22 June–15 August 2005 at Soberania, 26 July–23 September 2005 at Los Santos, and 15 June–12 August 2005 at Rio Hato). At the second census mortality, basal diameter, total height, diameter at breast height (stem diameter at 1.3 m above soil surface; DBH), crown height (height from soil surface to the base of the living crown), and two perpendicular measurements of crown diameter were recorded. Additionally, a qualitative measure of canopy density was estimated as an index from 0 to 4, where 0 indicates no recognizable canopy; 1 indicates that <25% of canopy space was filled with leaves; 2 indicates >25% and <50%; 3 indicates >50% and <75%; and 4 indicates > 75% of canopy space was filled with leaves. Survival and growth rate data from this trial are presented in Dent et al. (in preparation).

Total wood volume per hectare is the standard measure for identifying species with potential for use in commercial forestry. After 2 years, most individuals were too small to have usable wood. However, a wood volume index (VI) was calculated to integrate diameter and height measurements, and to provide a means for comparing total productivity across species. Wood volume index (VI) per tree was calculated as (Newbould, 1967; Montagnini et al., 1995):

$$\mathrm{VI} = \frac{0.5\pi D^2}{4H}$$

where VI represents wood volume index, D basal diameter and H is total height. This calculation was used for all species, and does not allow for a species specific form factor.

2.6. Statistical analyses

Confidence limits were generated for values of height, basal diameter, DBH, crown diameter, crown density, and VI using 1000 bootstrap replicates (Venables and Ripley, 2002). Estimates were assumed to be significantly different when 95% confidence limits did not overlap. VI was scaled up to per-hectare estimates based on a planting system of 1111 trees per hectare. Species were ranked according to VI at each site, and a Spearman's rank correlation was used to test for differences in species rankings between sites (Sokal and Rohlf, 1995). Relationships between crown diameter and crown density, and basal diameter and DBH were correlated. After 2 years of growth, some species were not large enough to yield DBH measurements and so basal diameter was used to compare species. Basal diameter was positively correlated with DBH ($R^2 = 0.463$, $P < 0.001$).

3. Results

3.1. Site effects

All measurements of tree size were significantly lower at Rio Hato than at the two wetter sites (Table 3). Mean tree height was 2.18 m at Rio Hato compared to 3.60 m and 3.68 m at Los Santos and Soberania, respectively. The height, diameter and crown size of trees was not significantly different between Los Santos and Soberania (Table 3), but DBH and VI were slightly greater at Soberania. Comparisons of individual species between sites showed all species except *Albizia guachapele* and *Copaifera aromatica* were significantly shorter and had smaller basal diameters at Rio Hato than at either of the other two sites (Table 4).

Table 3
Means and 95% confidence intervals for tree measurements after 2 years of growth for 24 species planted at three sites across Panama

	Soberania	Los Santos	Rio Hato
Height (m)			
Mean	3.68	3.60	2.18
95% CI	3.62–3.73	3.55–3.65	2.14–2.23
Basal diameter (cm)			
Mean	8.23	8.16	5.17
95% CI	8.11–8.36	8.03–8.30	5.08–5.26
DBH (cm)			
Mean	4.42	4.22	2.56
95% CI	4.34–4.51	4.14–4.30	2.49–2.63
Crown diameter (m)			
Mean	2.76	2.74	1.45
95% CI	2.61–2.89	2.70–2.78	1.41–1.49
Wood volume index (m^3 ha)			
Mean	12.02	10.87	3.19
95% CI	11.55–12.52	10.42–11.32	3.04–3.36

3.2. Tree height and diameter

Across all sites, *A. mangium* and *O. pyramidale* were the tallest trees with mean heights of more than 5 m (Table 5). The six tallest species varied between Rio Hato and the two wetter sites (Table 4). *Albizia guachapele* and *Samanea saman* were among the tallest six species at Rio Hato, but these species were replaced by *Spondias mombin* and *Guazuma ulmifolia* at the wetter sites. The species with the largest basal diameters did not vary greatly between sites (Table 4). The four largest basal diameters were *A. mangium*, *Pachira quinata* and *O. pyramidale* at all sites, with *Gliricidia sepium*, at the wetter sites, and *Enterolobium cyclocarpum* at Rio Hato. The smallest species both in terms of height and diameter were consistent across sites, and included *C. aromatica*, *Dipteryx panamensis* and *Inga punctata* (Table 4).

3.3. Crown diameter and crown density

Crown size and density were positively correlated (Fig. 2) and the species that had the largest crowns did not differ between sites. *A. mangium*, *Diphysa robinoides*, *G. sepium*, *G. ulmifolia* and *O. pyramidale* consistently had the largest and most dense crowns (Table 4; Fig. 3).

3.4. Wood volume index (VI)

The species with the greatest VI per hectare differed between sites (Table 4; Fig. 4). *O. pyramidale*, *A. mangium* and *G. sepium* had the greatest VI at Soberania and Los Santos.

Table 4
Mean basal diameter, height and wood volume index (VI) for 24 species after 2 years of growth at three sites across Panama (S: Soberania; L: Los Santos; R: Rio Hato)

Species	Height (m)			Basal diameter (cm)			VI (m^3 ha)		
	S	L	R	S	L	R	S	L	R
*Acacia mangium**	7.62 a	6.42 b	4.74 c	14.41 a	11.98 b	9.68 c	49.92 a	28.93 b	14.20 c
Albizia adinocephala	3.00 a	2.61 b	2.48 b	3.78 a	3.20 b	2.79 c	1.96 a	1.16 b	0.78 b
Albizia guachapele	2.81 a	3.56 b	3.43 b	5.78 a	7.30 b	6.13 c	3.25 a	6.21 b	4.14 c
Astronium graveolens	1.59 a	2.18 b	1.27 c	3.39 a	4.47 b	3.10 a	0.68 a	1.58 b	0.68 a
Calycophyllum candidissimum	2.55 a	2.52 a	0.86 b	4.67 a	4.59 a	2.08 b	2.05 a	1.93 a	0.17 b
Cedrela odorata	2.44 a	2.88 b	1.33 c	7.63 a	9.34 b	5.64 c	4.47 a	7.66 b	1.78 c
Colubrina glandulosa	4.19 a	3.65 b	2.13 c	8.08 a	7.07 b	3.76 c	9.05 a	6.25 b	1.54 c
Copaifera aromatica	0.79 a	0.74 a	0.49 a	2.12 a	1.96 a	1.31 b	0.14 a	0.12 a	0.05 b
Cordia alliodora	2.07 a	3.20 b	0.86 c	4.74 a	6.52 b	2.17 c	2.63 a	6.16 b	0.50 c
Diphysa robinoides	3.28 a	3.39 a	2.05 b	11.07 a	7.85 b	4.88 c	14.14 a	7.71 b	1.98 c
Dipteryx panamensis	1.85 a	1.75 a	0.76 b	3.12 a	2.95 a	1.63 b	0.74 a	0.60 a	0.08 b
Enterolobium cyclocarpum	3.04 a	2.91 a	1.90 b	7.46 a	7.23 a	5.81 b	5.69 a	5.45 a	3.31 b
Erythrina fusca	3.08 a	2.74 b	1.76 c	10.77 a	11.56 b	7.21 c	12.32 a	17.27 b	2.93 c
Gliricidia sepium	6.01 a	5.99 a	2.73 b	12.05 a	12.28 a	5.92 b	27.31 a	29.29 a	3.52 b
Guazuma ulmifolia	4.86 a	4.23 b	2.41 c	10.23 a	9.08 b	5.55 c	16.09 a	10.92 b	2.80 c
Inga punctata	2.60 a	1.51 b	0.98 c	7.72 a	5.44 b	3.64 c	5.83 a	2.23 b	0.88 c
Luehea seemannii	2.92 a	3.15 b	2.04 c	8.31 a	8.89 a	5.45 b	6.62 a	8.18 b	3.40 c
Ochroma pyramidale	7.02 a	5.98 b	3.55 c	14.91 a	13.46 a	7.76 b	51.02 a	37.69 b	8.94 c
Pachira quinata	2.97 a	3.63 b	2.14 c	11.55 a	13.31 b	8.23 c	13.12 a	21.73 b	5.20 c
Samanea saman	3.16 a	3.64 b	2.70 c	6.03 a	7.55 b	5.25 c	4.03 a	6.69 b	2.51 c
Spondius mombin	4.24 a	4.30 a	1.78 b	10.42 a	10.64 a	5.16 b	15.22 a	17.00 a	1.96 b
Tabebuia rosea	3.78 a	3.55 a	2.37 b	8.31 a	8.35 a	5.54 b	8.41 a	7.77 a	2.48 b
*Tectona grandis**	6.23 a	5.04 b	3.36 c	10.84 a	9.12 b	6.72 c	22.31 a	13.49 b	6.63 c
Terminalia amazonia	3.83 a	2.55 b	1.17 c	5.72 a	4.29 b	2.55 c	4.30 a	1.85 b	0.35 c

Means with the same letters are not significantly different as indicated by 95% confidence limits.
* Species not native to Panama.

Table 5
Means and 95% confidence intervals values for wood volume index (VI), basal diameter, height and crown diameter for 24 tropical tree species of tree after 2 years of growth at three sites across Panama

Species	VI (m^3 ha)		Basal diameter (cm)		Height (m)		Crown diameter (m)	
	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
*Acacia mangium**	30.92	29.07–32.85	12.01	11.74–12.28	6.26	6.13–6.40	3.43	2.86–4.03
Albizia adinocephala	1.30	1.17–1.44	3.26	3.13–3.38	2.72	2.62–2.81	1.36	1.20–1.51
Albizia guachapele	4.56	4.27–4.84	6.41	6.28–6.55	3.27	3.20–3.34	1.66	1.60–1.72
Astronium graveolens	0.98	0.88–1.08	3.65	3.52–3.79	1.68	1.62–1.74	1.19	1.13–1.25
Calycophyllum candidissimum	1.42	1.28–1.56	3.83	3.68–3.98	2.00	1.91–2.09	1.55	1.11–1.97
Cedrela odorata	4.57	4.26–4.88	7.52	7.31–7.72	2.20	2.11–2.29	1.74	1.68–1.81
Colubrina glandulosa	5.82	5.35–6.26	6.41	6.16–6.66	3.45	3.34–3.56	2.97	2.30–3.62
Copaifera aromatica	0.10	0.08–0.12	1.80	1.70–1.90	0.69	0.66–0.72	0.76	0.71–0.81
Cordia alliodora	3.64	2.95–4.34	4.79	4.45–5.14	2.34	2.17–2.51	1.77	1.65–1.90
Diphysa robinoides	7.88	7.06–8.65	7.90	7.54–8.23	2.91	2.83–2.99	3.62	3.51–3.73
Dipteryx panamensis	0.53	0.46–0.60	2.68	2.56–2.81	1.50	1.41–1.59	1.00	0.95–1.05
Enterolobium cyclocarpum	5.02	4.66–5.38	6.97	6.75–7.19	2.78	2.71–2.86	2.68	2.58–2.77
Erythrina fusca	10.57	9.21–11.89	9.77	9.42–10.11	2.54	2.46–2.62	2.49	2.39–2.59
Gliricidia sepium	20.01	18.53–21.49	10.07	9.74–10.40	4.90	4.75–5.05	4.12	4.02–4.22
Guazuma ulmifolia	9.93	9.26–10.60	8.29	8.05–8.52	3.83	3.72–3.94	3.42	3.33–3.51
Inga punctata	3.39	2.95–3.83	5.89	5.59–6.20	1.85	1.75–1.96	2.37	2.24–2.50
Luehea seemannii	5.97	5.48–6.44	7.50	7.24–7.76	2.71	2.62–2.80	2.09	1.98–2.19
Ochroma pyramidale	32.41	29.80–35.06	11.99	11.57–12.42	5.59	5.39–5.79	3.50	3.36–3.64
Pachira quinata	13.34	12.25–14.35	11.02	10.70–11.33	2.91	2.83–2.99	2.57	2.47–2.67
Samanea saman	4.40	4.12–4.70	6.27	6.13–6.43	3.16	3.09–3.24	2.24	1.62–2.82
Spondius mombin	11.33	10.46–12.23	8.72	8.43–9.01	3.44	3.31–3.57	2.56	2.45–2.67
Tabebuia rosea	6.46	6.10–6.84	7.52	7.34–7.70	3.28	3.20–3.36	1.57	1.51–1.64
*Tectona grandis**	14.17	13.30–15.00	8.89	8.68–9.10	4.89	4.73–5.04	2.48	2.40–2.57
Terminalia amazonia	2.39	2.15–2.64	4.33	4.15–4.51	2.66	2.52–2.80	1.81	1.73–1.88

* Species not native to Panama.

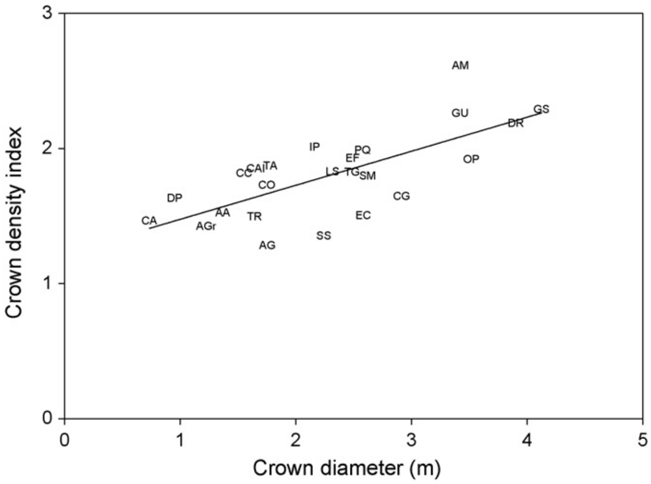

Fig. 2. Mean crown diameter and crown density indices for 24 species of tree across three sites in Panama (Soberania, Los Santos and Rio Hato). Crown diameter and density are positively correlated; $R^2 = 0.481$, $P < 0.001$.

However, at Rio Hato *A. mangium* had the largest VI followed by *O. pyramidale*, *T. grandis* and *P. quinata*. There were shifts in the ranking of species between sites in terms of tree size (Fig. 4). At Los Santos, *P. quinata* had a much higher ranking, and *T. grandis* a much lower ranking, than at the wettest site (Soberania). At the driest site (Rio Hato) *P. quinata* and *A. guachapele* had considerably higher rankings than at Soberania. However, these shifts were not significant because differences in rankings between sites were only evident in the mid-ranking species (Fig. 4; Spearman rank correlations for pair-wise comparisons of species rankings between Rio Hato and Soberania; Rio Hato and Los Santos; and Soberania and Los Santos, respectively, for VI Rho = 0.77, $P < 0.001$; Rho = 0.84, $P < 0.001$; and Rho = 0.92, $P < 0.001$).

Both of the exotic species (*A. mangium* and *T. grandis*) performed well at all sites, and were consistently amongst the top six species in terms of VI. However, at least two native timber species (Table 2) were ranked in the upper half of the 24 species at each site in terms of VI. These included *P. quinata* and *Tabebuia rosea* at all sites as well as *A. guachapele* and *S. saman* at Rio Hato.

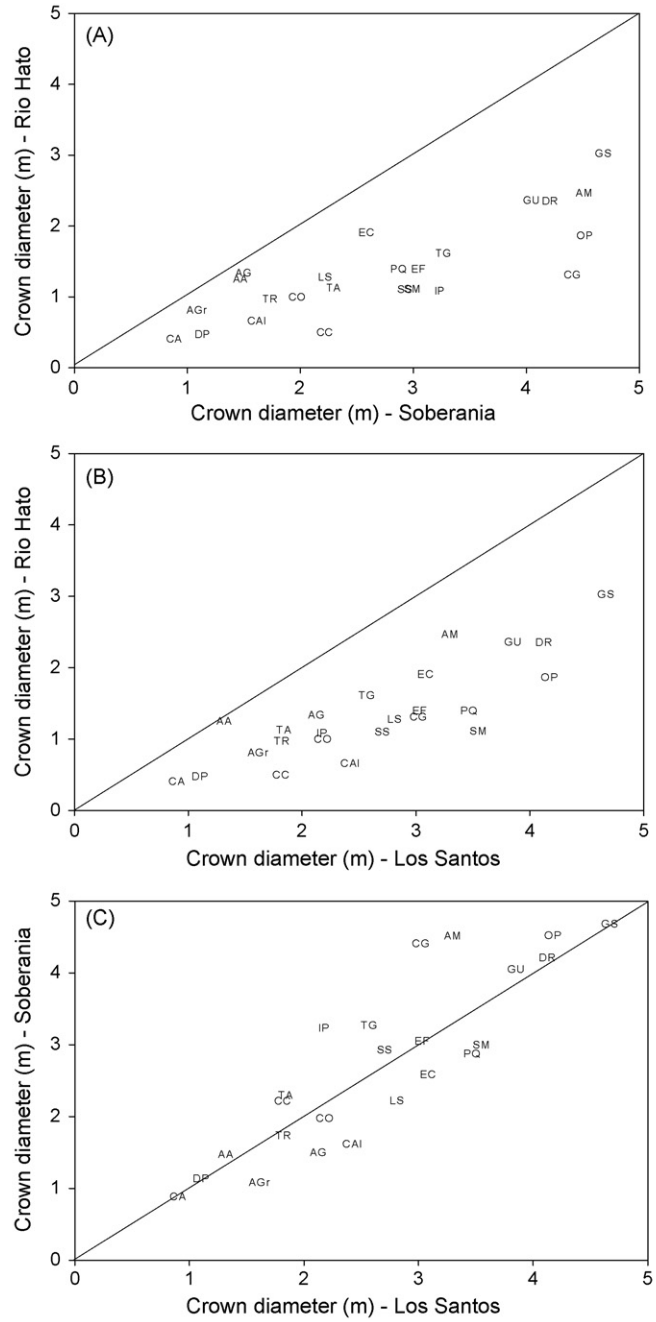

Fig. 3. Mean crown diameter for 24 species after 2 years of growth planted at three sites in Panama (Soberania, Los Santos and Rio Hato). Mean wood volume per species from a site is plotted against the same values from another site as indicated on axes labels. The line indicates a 1:1 relationship; species with points along this line have equivalent volumes at the two sites.

4. Discussion

The conclusions drawn from this study must be treated with caution, as they are based on just the first 24 months of growth. Some slower growing species have been reported to exhibit accelerating growth rates over time, while in comparison, other species with high initial performance have been found to have slower growth with time. For example in a trial in Costa Rica, Butterfield and Espinoza (1995) reported larger diameters and height for *T. rosea* than for *D. panamensis* after 1 year of growth. However, *D. panamensis* exhibited increasing or sustained growth over the subsequent 3 years in comparison with reduced growth rates in *T. rosea* over the same period.

After 2 years, overall patterns in tree size indicate a hierarchy from the wetter, more nutrient rich sites at Soberania and Los Santos to the drier more nutrient poor site at Rio Hato. Overall trees were significantly larger at Soberania and Los Santos than that at Rio Hato. Survival was highest at the wettest site, Soberania, but survival was consistently high, and mean survival was more than 80% at all sites (Dent et al., in preparation), which is consistent with other studies of managed plantations of native trees in Central America (Butterfield, 1995; Haggar et al., 1998; Piotto et al., 2003).

Los Santos had slightly reduced tree size in comparison to Soberania. Average yearly rainfall at Los Santos is only

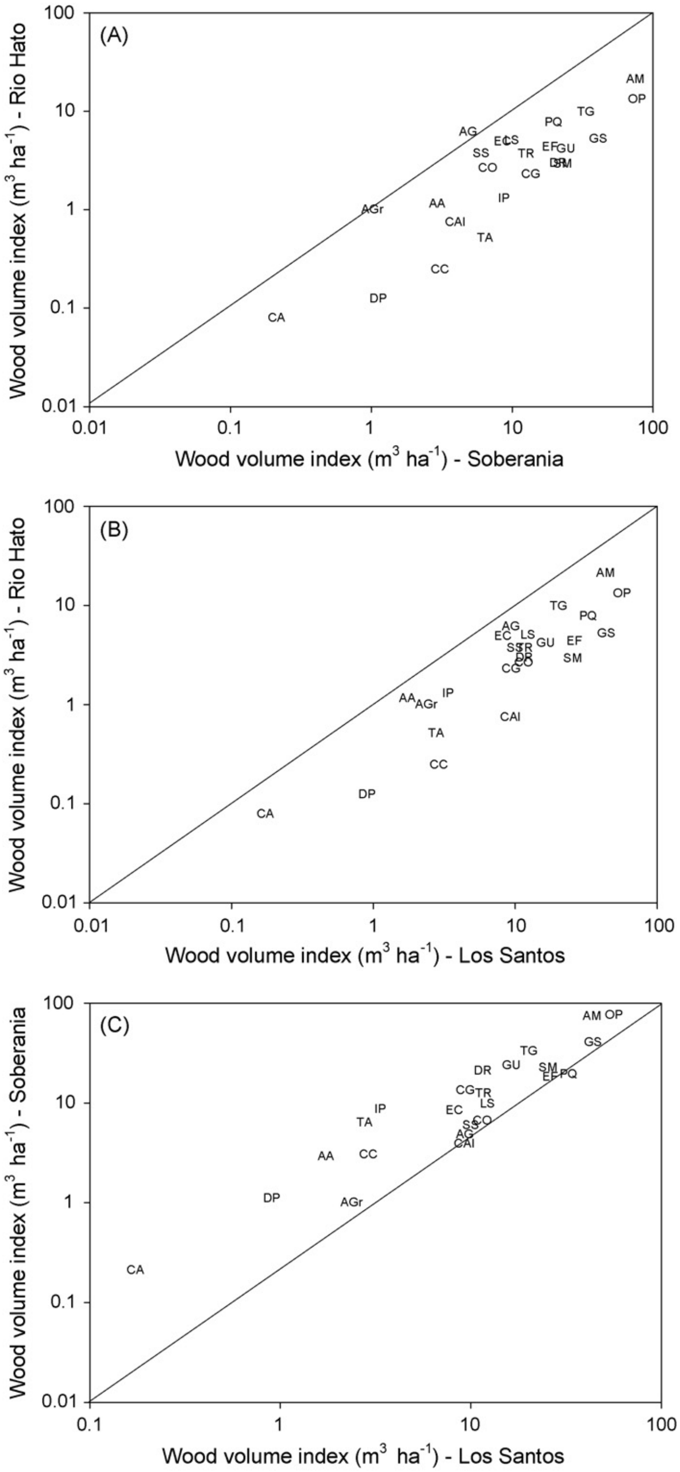

Fig. 4. Mean wood volume indices for 24 species of tree at three sites across a rainfall gradient in Panama. Mean wood volume per species from one site is plotted (log scale) against the same values from a second site, as indicated on axes labels. The line indicates a 1:1 relationship; species with points along this line have equivalent volumes at the two sites.

280 mm less than that at Soberania. However, the dry season is an average of 1.1 months longer at Los Santos, which may explain this pattern. In contrast, average yearly rainfall at Rio Hato is 840 mm less than Los Santos and 1120 mm less than at Soberania, and the dry season is 1.5 and 2.6 months longer, respectively. These differences in water availability, and the relatively poor soil quality at Rio Hato, may partly explain the significantly reduced growth at this site. In contrast, the nutrient rich soils at Los Santos may mitigate the climate related differences between Los Santos and Soberania. It is worth noting that *A. guachapele* and *S. saman*, which are absent from the forests of the moister Panama Canal Watershed

(Condit et al., 2004), but are typical of tropical dry forest in Guanacaste, Costa Rica (Janzen, 1988), shifted up the species ranking from the wettest (Soberania) to the driest site (Rio Hato). This highlights the importance of species adaptations to climate in determining species performance.

A few species had sufficiently poor growth to suggest that they may not be suitable species for planting at some sites. These species were *Cordia alliodora*, *C. aromatica*, and *D. panamensis* at Soberania, *C. aromatica*, *D. panamensis* and *I. punctata* at Los Santos and *C. alliodora*, *C. aromatica*, *D. panamensis* and *I. punctata* at Rio Hato. Although *C. alliodora* is widely used in reforestation in Central America, some studies have reported high mortality of *C. alliodora* in plantations (Butterfield, 1995; Butterfield and Espinoza, 1995). In this study *C. alliodora* had low growth and high mortality at two of the three sites and performed best on the most fertile soils, suggesting that this species could be planted for timber or fire wood but only in areas of high fertility. In contrast, *I. punctata* which is also commonly grown in plantations in Central America, to provide shade for coffee, appeared to be affected more by rainfall than soil fertility with poor performance at the two drier sites. This result indicates that this species could be used for restoration or as a nurse tree in plantation but this would only be economically viable in sites with high annual rainfall and short dry seasons. Two other species that performed poorly at all sites: *C. aromatica*, and *D. panamensis*, have high quality timber and are typical of mature forest and so may perform poorly in high light as young trees. However, a number of studies have grown *D. panamensis* successfully in plantation, and thus it may be the combination of high light, poor soil and/or low soil moisture that contributed to the poor performance of this species, as illustrated by the significantly reduced performance of both *C. aromatica*, and *D. panamensis* at Rio Hato in comparison to the other sites.

Further discussion of species performance is presented in relation to three broad reforestation objectives: forest restoration, timber production, and on-farm use.

4.1. Restoration potential

Planting trees into degraded lands can lead to soil stabilization, including reduced erosion and increased fertility (Montagnini and Sancho, 1990; Fisher, 1995) increased bird visitations and seed deposition (Holl et al., 2000; Jones et al., 2004) and increased understory biodiversity (Parrotta, 1992; Parrotta et al., 1997; Posada et al., 2000). Many of the tree characteristics that relate to these processes are species specific, such as the attractiveness of individual species to seed dispersers (Wunderle, 1997). However, a recent study in the Panama Canal Watershed found that the density of woody species regenerating in the understory of mixed-species plantations was most significantly and positively related to the width and density of the crown of the overstorey tree (Jones et al., 2004). In the present study, species that maintained the largest crowns were consistent across sites. *D. robinoides*, *G. sepium*, *G. ulmifolia*, *A. mangium* and *O. pyramidale* had the largest and densest crowns at all sites after 2 years.

For *G. sepium* and *D. robinoides*, respectively, mean crown diameters were 4.7 m and 4.1 m at Los Santos and 4.7 and 4.2 at Soberania, indicating that these two species had exceeded canopy closure within 2 years. These species, both nitrogen-fixing legumes, may be particularly promising for reforestation in areas dominated by the shade-intolerant invasive grass species *Saccharum spontaneum* (Hammond, 1999; Hooper et al., 2002, 2004). Canopy development was slower at Rio Hato and the largest mean crown diameters were 3.0 and 2.5 m for *G. sepium* and *A. mangium*, respectively, indicating that canopy closure and correlated processes of soil stabilization and understory regeneration may be slower at the driest and most degraded sites.

Further studies are needed before any statements can be made about the direct effects of these tree species on understory conditions and diversity. However, these results are valuable for identifying species that may have potential to aid in the process of succession (Lugo et al., 1993; Lamb, 1998), and provide a starting point for additional studies into understory development.

4.2. Timber production

Several native species demonstrated a high potential for timber production. After just 2 years of growth, a number of native species developed VI as large, or larger, than the two commonly planted exotic timber species (*T. grandis* and *A. mangium*). These exotic species characteristically have high initial rates of growth, which slow over time (Haggar et al., 1998; S.A. Futuro Forestal, unpublished data), and so the comparative VI of native species after such a short period suggest their potential value for timber production. At each site the top eight species in terms of wood volume index included the two exotic species, five or six fast-growing native species with poor wood quality (such as *O. pyramidale* and *G. sepium*) and the native timber tree *P. quinata*, which is valued for its timber quality, and is the only native species planted in significant numbers in plantations in Panama (4.6% of plantations established between 1992 and 2004, ANAM, 2003). *P. quinata* performed particularly well at the two drier sites where it attained mean VI significantly greater than that of teak. A number of other species valued for their high wood quality (Tables 2 and 4) also performed well; *T. rosea* was present in the upper half of species at all sites, and at the driest site (Rio Hato) *A. guachapele* and *S. saman* both ranked highly. These same two species have previously been reported to perform well at a number of very dry (<900 mm rainfall year^{-1}) sites in a pan-tropical species trial of Central American dry zone hardwoods (Stewart and Dunsdon, 1994). These variations in rankings between sites indicate that at drier sites, native dry-site specialists may perform better than species traditionally planted for timber production, such as teak.

Some of the species that were selected for these trials because of their high timber quality and potential for timber production performed badly at all sites. *Astronium graveolens*, *D. panamensis* and *C. aromatica* had low growth and high mortality at all sites, it may be that these species, which are typically found in mature forest (Holdridge and Poveda, 1975; Croat, 1978), are shade-tolerant as young trees and susceptible to photo-inhibition and desiccation in open environments, though it should be noted that *D. panamensis* was found to perform well at trials conducted at a wetter site in Costa Rica (Butterfield and Espinoza, 1995). These species have very high wood value, but wood production would appear not be economically viable in pure plantations. They may be better suited to under-planting systems, where faster-growing, lower-value species could be used in the initial phase of planting, both providing shade and off-setting the costs of the slower growing species (Montagnini et al., 1995).

4.3. On-farm systems

Growth varied between sites for the species recommended for on-farm use causing changes in species rankings. Within this group, *A. guachapele*, *G. sepium*, *S. saman* and *G. ulmifolia* were the tallest species at Rio Hato, while *G. sepium*, *G. ulmifolia* and *S. mombin* were the tallest species at Soberania and Los Santos (Table 4). At each site, all of these species had >95% survival (Dent et al., in preparation). All species, except *G. ulmifolia*, are nitrogen-fixing legumes, and if used in a silvopastoral system might provide fodder and fencing while also improving soil fertility and pasture quality (Jayasundara et al., 1997; Nair et al., 1999; Nygren et al., 2000). This group of species is primarily used by small farmers, a landholder group that may be particularly sensitive to the economic costs of seedling establishment, and which may require that these costs be quickly recouped through high tree survival, growth and productivity (Dagang and Nair, 2003). Site-specific recommendations of high-performing species may be particularly important for this group.

5. Conclusions

Many authors have called for a greater diversity of species to be studied and incorporated into Central American reforestation efforts (Butterfield, 1995; Haggar et al., 1998; Piotto et al., 2003). Increasing the number of tree species reasonably available to landholders should allow for a greater range of forest goods and services to be produced, and by more closely matching species performance to landholder interests, should encourage a greater range of landholders to engage in reforestation activities. The ecological implications of this study in terms of restoration of degraded land are significant in that canopy closure was achieved by many native species after just 24 months. Indicating clear possibilities that these species may be used in the first stages of habitat restoration to alter and stabilize abiotic factors and create an environment in which other woody species can compete and grow. Though based on only the first 24 months of growth, the results of this study allow for initial site-specific recommendations of potentially valuable species for restoration, timber production and silvopastoral uses.

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