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Between and within-site comparisons of structural and physiological characteristics and foliar nutrient content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama

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Abstract

Structural and physiological characteristics and foliar nutrient content of 14 tree species were evaluated at two sites, one being seasonally wet with relatively fertile soils and the other being seasonally dry with relatively infertile soils. Differences in environmental stress between these sites drove the resulting differences in structural and physiological characteristics and leaf nutrient content of the investigated tree species. At the wet site, trees were more productive as site conditions allowed for greater photosynthetic activity to occur. The growth of pioneer tree species such as *Spondias mombin*, *Guazuma ulmifolia*, and *Luehea seemanni*, correlated strongly with high water-use efficiency and large, low-density leaves. Tree species, especially N-fixing species such as *Albizia adinocephala*, *Albizia guachapele*, *Enterolobium cyclocarpum*, and *Gliricidia sepium*, adapted to the greater levels of environmental stress at the dry site with infertile soils by increasing their water-use efficiency. Species differences were also significant, indicating that certain species adapted physiologically and structurally to environmental stress. Tree productivity operated under different structural and physiological constraints at each site. Leaf mass area (LMA), foliar N, and leaf area index (LAI) best predicted mass-based net photosynthetic capacity at the more fertile, wet site while foliar N was the best predictor of mass-based net photosynthetic capacity at the less fertile, dry site. Results from this study suggest the use of pioneer species at wet, fertile sites and N-fixing species at dry, infertile sites for restoration projects.
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1. Introduction

Reforestation has emerged as a strategy to mitigate the ecological and economic costs of past deforestation. Between 1990 and 2000, Panama lost 52,000 ha year^{-1} of forested lands (FAO, 2004). Deforestation has immediate ecological impacts on forest ecosystems, reducing soil fertility and structure, seed availability, and increasing light intensity (Guariguata et al., 1995; Parrotta et al., 1997; Guariguata and Ostertag, 2001). In Panama, 89% of tree plantations in terms of area have been planted with exotic tree genera, such as *Pinus*, *Acacia*, *Tectona*, and *Khaya* (ANAM, 2003). The use of native tree species in plantations potentially obviates certain problems with exotic species, as local populations have extensive experience using them for timber, construction, and live fences (Lamb, 1998). Reforestation projects are needed to rehabilitate degraded areas across a wide variety of edaphic and climatic conditions contained within the landscape matrix, yet their successful establishment depends on selecting appropriate tree species.

In the Neotropics, researchers have evaluated the ability of native tree plantations to ameliorate micro-site conditions of degraded lands in the tropics (Montagnini et al., 1991; Guariguata et al., 1995; Stanley and Montagnini, 1998; Montagnini et al., 2000; Guariguata and Ostertag, 2001; Montagnini et al., 2005). Plantations improve site conditions by reducing soil erosion, increasing soil nutrients, improving soil structure, and promoting recruitment of understory woody plants (Montagnini et al., 1991, 2005; Parrotta, 1992; Guariguata et al., 1995; Stanley and Montagnini, 1998;

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Montagnini et al., 2000; Guariguata and Ostertag, 2001). Established plantations, of both native and exotic species, influence the rate and species diversity of recruitment in the understory (da Silva Junior et al., 1995; Guariguata et al., 1995; Guariguata and Ostertag, 2001).

By affecting photosynthetic rates and patterns of carbon assimilation of plants, drought stress skews species diversity and assemblages in favor of those species that are adapted genetically, structurally, or physiologically to these conditions. Trees proportionally allocate larger amounts of photosynthetic material to maintenance respiration than to competing carbon sinks in response to hostile site conditions (Oliver and Larson, 1996). Stomatal closure, induced by drought stress, modulates photosynthesis by limiting CO_2 diffusion (Lambers et al., 1998). Drought-adapted C_3 species maximize water-use efficiency by lowering their stomatal conductance and water vapor pressure in order to maintain essential biological processes (Lambers et al., 1998; Li et al., 2000; Sack, 2004; Mishra et al., 2006). Aboveground carbon accumulation of non-adapted tree species decreases the longer they experience drought (Larcher, 2003).

Three principal environmental gradients – light, precipitation, soil nutrients – have been studied extensively in tropical forest ecosystems worldwide, elucidating how species interactions with various environmental conditions determine forest composition, diversity, structure, and succession (Ashton and Berlyn, 1992; Wright, 1992; Ashton et al., 1995; Gamage et al., 2003; Hall et al., 2003; Givnish et al., 2004; Ashton et al., 2005). Tree species adjust physiological traits, such as net photosynthetic capacity, transpiration and growth rates, and shoot:root ratios, in response to different light and soil moisture regimes (Bazzaz, 1979). Chazdon and Kaufmann (1993) found that while two species of rain forest shrubs adapted similarly in terms of leaf structure (thicker leaves, higher leaf mass per area) under high light, their physiological response to higher light levels differed. Several genera such as *Shorea*, *Entandrophragma*, *Syzygium*, and *Macaranga* have exhibited different responses to light levels, thereby enabling these species to divide the available light and co-exist within the forest (Ashton and Berlyn, 1992; Ashton et al., 1995; Davies et al., 1998; Gamage et al., 2003; Hall et al., 2003).

Precipitation and soil nutrient gradients impose physical limitations on tropical forest species and determine their distribution and density (Wright, 1992; Swaine, 1996; Santiago et al., 2004). In dry climates, species with high foliar N can photosynthesize at greater rates and take advantage of greater light availability (Mooney et al., 1978; Santiago et al., 2004). Drought stress significantly affects community-wide leaf anatomy and physiology traits (Mooney et al., 1978; Santiago et al., 2004). For example, leaf mass area decreases with ecosystem production efficiency, reflecting the trade-off between maximizing light capture and minimizing water loss (Reich et al., 1997). Rainfall and soil fertility gradients determined forest species composition by physiologically limiting the ability of individual species to establish in Ghana (Swaine, 1996). Each combination of rainfall and soil fertility (wet-fertile, wet-infertile, dry-fertile, dry-infertile) attracted specialist species, with the exception of dry-infertile, which only attracted

site-generalist species (Swaine, 1996). Along a steep rainfall gradient in Panama, foliar nitrogen content and mass-based net photosynthetic capacity decreased with precipitation, due in part to increasing leaf mass area (Santiago et al., 2004).

At two sites in Panama, we studied structural and physiological characteristics and foliar nutrient content of 14 tree species at two sites along a precipitation–soil fertility gradient, wet-fertile and dry-infertile. To analyze how plant stress, created by differing amounts of precipitation and soil nutrient affects tree species, we formulated the following three hypotheses:

(1) Structural and physiological characteristics and foliar nutrient content will be significantly different between sites, as we expect trees to perform better at the wet, fertile site than at the dry, infertile site;
(2) At the seasonally dry site with relatively infertile soil, the variability of integrated tree growth will be significantly higher than at the seasonally wet site with relatively fertile soils, as we expect greater levels of plant stress to accentuate differences in tree performance;
(3) Within and across both sites, leaf mass area and foliar N will significantly predict mass-based net photosynthetic capacity, as we expect these variables to best explain the physical and structural limitations to tree productivity.

2. Methods

2.1. Site description

The research was performed at two locations in Panama: Río Hato and Parque Nacional Soberanía (Fig. 1). The study site at Parque Nacional Soberanía is located in an area of seasonally wet tropical forest along the Panama Canal, approximately 20 km northwest of Panama City. The study site at Río Hato is situated within an area designated by the Ministry of the Environment for forestry-related research, in a region covered by dry tropical forest fragments, pastures, and scrubland along the Pacific Coast, approximately 100 km southwest of Panama City.

P.N. Soberanía received an average of 2127 mm year^{-1} of precipitation from 1966 to 2003, with a 4.1 months year^{-1} dry season, while Río Hato received 1080 mm year^{-1} between 1977 and 1997, with a 6.7 months year^{-1} dry season (ANAM, 2005; Dent et al., in press). Average daily maximum photosynthetic photon flux density was higher at Río Hato (1638 μmol s^{-1} m^{-2}) than at P.N. Soberanía (1441 μmol s^{-1} m^{-2}). Soils at Río Hato are more weathered than at P.N. Soberanía, as levels of phosphorus and sum of bases are significantly lower (Table 1). Soil fertility characteristics are significantly higher at P.N. Soberanía, as levels of base saturation, cation exchange capacity (CEC), pH, and total nitrogen (N) are higher than at Río Hato (Table 1).

2.2. Experimental design

In 2003, species selection trials of 13 native and one exotic tree species were established at the two study sites: *Albizia*

Fig. 1. Map of Panama with site locations (adapted from CIA World Factbook, 2006).

adinocephala, *Albizia guachapele*, *Calycophyllum candidissimun*, *Cedrela odorata*, *Dipteryx panamensis*, *Enterolobium cyclocarpum*, *Erythrina fusca*, *Gliricidia sepium*, *Guazuma ulmifolia*, *Luehea seemannii*, *Ochroma pyramidale*, *Pachira quinata*, *Spondias mombin*, and *Tectona grandis*. Each site was divided into three completely randomized blocks, all of which contain three pure plots for every species and three control plots. All plots initially contained 20 trees with 3 m × 3 m spacing. Since the establishment of the selection trials, all plots have been mowed regularly and controlled for pest infestation with insecticides as needed.

2.3. Field methods

Leaf area index (LAI) was measured for 14 species at two blocks at P.N. Soberanía and at three blocks at Río Hato using two LAI 2000 Canopy Analyzers (Li-Cor, Lincoln, Nebraska, USA) under overcast conditions between 7:00 a.m. and 10:30 a.m. during the rainy season (June–August 2005) (Welles and Norman, 1991). A 90° view cap was placed on both sensors to prevent direct sun light from impinging on the sensors (Welles, 1990). The above-canopy LAI sensor was placed in an open area within the block being sampled facing west and logged measurements every 15 s. To minimize the confounding effects of neighboring plots on LAI measurements, sampling was performed in the two central locations of each plot. Within each central location, measuring 3 m × 3 m, LAI measurements were taken at a uniform height of 1.0 m above the ground at a distance of 0.5 m and 1.0 m from each corner along two transects that bisected each location and at the center of the location while facing west, for a total of 18 measurements per plot.

LAI was estimated on a per-plot basis by interpolating the 18 below-canopy measurements with the above-canopy measurements closest in time and fixing maximum transmittance at 1.00 using LAI-2000 File Viewer 1.01 (Li-Cor Biosciences, Inc., Lincoln, Nebraska, USA).

Gas exchange measurements were taken with a LI-6400 Portable Photosynthesis System (LI-COR Biosciences Inc., Lincoln, NE, USA) between 7:00 a.m. and 12:00 p.m. on 12 mid-canopy, fully sun-exposed leaves per species per site, with each leaf being fully expanded and hardened, and showing minimal signs of scarring, disease, or herbivory (Ashton and Berlyn, 1992). Leaves were sampled from twelve trees divided evenly amongst the three plots per species within each site. Measurements were taken with leaf temperatures of

Table 1

Soil nutrients, sum of exchangeable bases, cation exchange capacity (CEC), and base saturation in soils at P.N. Soberanía and Río Hato

Response variables	P.N. Soberanía	Río Hato	R^2 (%)	Site	*p* value	
					Depth	Site × depth
n	63	80				
Total N (%)[a]	0.182	0.081	50.51	<0.0001	<0.0001	0.0180
pH (in H_2O)	5.570	5.674	2.99	0.0965	0.3653	0.4855
Ca (Cmol kg^{-1})	5.982	3.226	36.97	<0.0001	0.0038	0.0002
K (Cmol kg^{-1})[a]	0.322	0.094	52.98	<0.0001	<0.0001	0.3743
Mg (Cmol kg^{-1})[a]	3.452	0.811	83.44	<0.0001	0.6822	0.4422
Na (Cmol kg^{-1})[a]	0.239	0.343	35.44	<0.0001	<0.0001	0.0050
P (mg kg^{-1})[a]	4.296	1.805	45.14	<0.0001	<0.0001	0.9769
Sum of bases (mg kg^{-1})	9.995	4.473	65.86	<0.0001	0.0037	0.0002
CEC (Cmol kg^{-1})	11.245	5.820	63.70	<0.0001	0.2243	<0.0001
Base saturation (%)	90.325	79.355	14.23	<0.0001	0.1664	0.4247

Differences between sites, depth (0–15 cm and 30–60 cm), and the combination of soil and depth were tested with generalized linear (95% confidence interval, $\alpha = 0.05$, degrees of freedom for site = 1, depth = 1, site × depth = 1) (adapted from J. Goetz, unpublished data).

[a] Values were natural-log transformed for analysis; non-transformed values shown.

$30.9 \pm 1.2\ °C$, relative humidity of the cuvette $70.8 \pm 7.4\%$, and VpdL of $1.4 \pm 0.3\ kPa$. Photon flux density was set to $1800\ \mu mol\ m^{-2}\ s^{-1}$ for net photosynthetic capacity (A_{max}) measurements, and $0\ \mu mol\ m^{-2}\ s^{-1}$ for dark respiration measurements. Stomatal ratio was set to 0 for all measurements, as all species studied were assumed to have abaxial stomates. The leaf area inside the cuvette was $6\ cm^2$ except for those compound leaves in which leaflet area was less and required individual estimation.

Gas exchange measurements were logged when the total coefficient of variation of CO_2 in the sample chamber was $\leq 1\%$. For dark respiration, three data points were taken (at least 30 s apart) and averaged. Instantaneous water-use efficiency (WUEi) was estimated for each measurement as CO_2 assimilation/transpiration. Mass-based A_{max} values were estimated by dividing area-based A_{max} by the leaf mass area of the same leaf (g/m^2).

Following gas exchange measurements, each leaf was removed, clipped at the stem and digitally scanned within 24 h of collection at a resolution of 100 dots per inch. Leaf area estimates were extracted from digitized scans using Adobe Photoshop 6.0 at a tolerance of 70 (Adobe Corporation, San Jose, CA, USA). Pixel counts were converted to m^2. The accuracy of this procedure was verified as >99% using a standard of a known area (LI-COR Biosciences, Inc., Lincoln, NE, USA).

All leaves were dried at $70\ °C$ for at least 7 days, and massed to the nearest 0.0001 g using an ER-182A balance (A&D Company, Limited, Tokyo, Japan). Leaf mass area (LMA), g per m^2, was calculated as dry mass (g)/leaf area (m^2).

Foliar $\delta^{13}C$ for two $1.8 \pm 0.2\ mg$ sub-samples of each pooled plot sample was determined using a continuous flow mass spectrometer (ThermoFinnigan Delta^{Plus} Advantage, Costech Analytical Technologies Inc., Valencia, CA, USA) (Warren et al., 2001; Dawson et al., 2002). We used cocoa powder as a standard reference material (4.185% N, 49.57% C) to generate regression equations that used peak areas to calculate amount percent C and N. Carbon isotope ratios were calculated directly by the instrument. Results were averaged for the two sub-samples from each plot.

The lamina portion of leaf samples were ground using a Cyclotec 1093 Sample Mill (Tecator AB, Hoganas, Sweden) for samples >10 g or a Thomas Scientific mini-mill (Swedesboro, NJ, USA) for samples <10 g. An equal, homogenized sample of each leaf within each plot was then mixed to create a $0.8 \pm 0.1\ g$ pooled sample for each plot. Where leaves lacked sufficient mass to meet this criterion, pooled plot samples were either smaller or unbalanced.

Percents of C and N were measured for two $1.8 \pm 0.2\ mg$ sub-samples of each plot pooled sample either on a continuous flow mass spectrometer or a combustion analyzer (FlashEA 1112 Series NC Soil Analyzer, Thermo Electronic Corporation, Waltham, MA, USA). Cocoa powder (4.185% N, 49.57% C) was used as a standard reference material for the former instrument and rye flour (1.86% N, 44.25% C) for the latter. To ensure the consistency of measurements between machines, standard materials were analyzed on both instruments to cross-reference

their values. Results were averaged for the two sub-samples from each plot. Foliar C:foliar N (C:N) was estimated by dividing amount percent C by amount percent N.

Two $0.30 \pm 0.02\ g$ sub-samples of each pooled plot sample were ashed for 8 h at $500\ °C$ and digested to 50 mL dilution using nitric acid (Likens et al., 1994). Each sub-sample was then analyzed for P, K, Ca, and Mg content using an Optima 3000 Inductively Coupled Plasma Optical Emission Spectrometer (Perkin-Elmer Corporation, Wellesley, MA, USA). Results were converted from parts per million to amount percents [(ppm $\times$ volume $\times$ 10000)/sample mass], and then averaged for the two sub-samples from each plot.

Tree height, crown diameter, height of live crown, and diameter at breast height (DBH) have been measured annually since 2003 (Dent et al., in press). Data used for linear regression models with LAI corresponded directly to the same block and plots sampled for LAI. Soil samples were collected at two depths (0–15 cm and 30–60 cm) across a $20\ m \times 20\ m$ sampling grid at both sites in 2004 (J. Goetz, unpublished data). Samples were analyzed for: pH; total N by dry combustion with a LECO CNS 2000 (LECO Corporation, St. Joseph, MI, USA); and P, K, Ca, Mg, and Na by Mehlich 1 extraction and Thermo Jarrell Ash 61E inductively coupled plasma spectrophotometry (Thermo Jarrell Ash Corporation, Franklin, MA, USA). Sum of exchangeable bases, CEC, and base saturation were calculated based on the results of the soil analysis.

2.4. Data analysis

Prior to analysis, the data sets of foliar nutrient and structural and physiological characteristics were tested for multi-variate normality (SAS 9.1.3, SAS Institute Inc., Cary, NC, USA). Variance stabilizing transformations were performed on certain variables. Of the structural and physiological characteristics, transpiration was natural-log transformed, LAI was cube-root transformed, and conductance was double transformed using the following formula: $((\sin(value - variable\ average) \times (\sqrt{|(value - variable\ average)|}))$. Of the foliar nutrients, Mg was natural-log transformed.

For between-site comparisons of foliar nutrient content and structural and physiological characteristics, a Generalized Linear Model was fitted for each variable to test for the effects of site, species, and the combination of site and species. To test for the overall effects of site, species, and the combination of site and species for foliar nutrient content and structural and physiological characteristics, a MANOVA model was fitted.

For within-site comparisons, a GLM was fitted for transformed LAI values from three blocks at P.N. Soberanía and two blocks at Río Hato and Tukey's Studentized Range (HSD) Test was used to make post-hoc pairwise comparisons between blocks using the PROC GLM statement. Untransformed data for hierarchical cluster analysis were standardized by setting the variance of each variable to one prior to clustering. Euclidean distance and Ward's method were used to determine cluster membership. As two plots at P.N. Soberanía did not contain foliar nutrient data, they were excluded from subsequent analyses (P.

quinata and *T. grandis*). With the group membership from cluster analysis, we used a non-parametric, recursive partitioning algorithm (CART) to find the most significant variable(s) for splitting the untransformed data into the predetermined groups (Evans et al., 2005; R Development Core Team, 2005). The complexity parameter statistic was used to determine how many splits were included in the regression tree.

Data for the linear regression models were pooled by species by site to avoid pseudo-replication. Tree growth data were collected in 2005 at approximately the same time as the physiological and structural data (June–August) (PRORENA, 2005). Linear regression models were fitted using the REG procedure (SAS 9.1.3, SAS Institute Inc., Cary, NC, USA).

Data of soil characteristics were transformed prior to analysis. Total N, K, Mg, Na, and P were natural-log transformed. All soil characteristics were tested for differences between sites, depth, and the combination of site and depth using a GLM (SAS 9.1.3, SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Between-site comparisons

Across all structural and physiological variables (LMA, LAI, $A_{maxmass}$, $A_{maxarea}$, dark respiration, conductance, transpiration, WUE, WUEi, and C:N), the overall effects of site ($p < 0.0001$), species ($p < 0.0001$), and the combination of site and species ($p < 0.0001$) were significant at the 0.05 level (MANOVA, $\alpha = 0.05$, Wilk's Lambda Statistic, degrees of freedom for site = 10, species = 130, site $\times$ species = 130).

The mean value of LMA at P.N. Soberanía was greater than at Río Hato and differed significantly between species and the combination of site and species, but between sites (Table 2). LAI values were almost twice as high at P.N. Soberanía as those at Río Hato and differed significantly by site and by species, but by the combined effect of site and species (Table 2). On an area basis, net photosynthetic capacity differed by site, but not by species nor by the combination of site and species (Table 2). On

a mass-basis, net photosynthetic capacity varied significantly by species and the combination of site and species but by site (Table 2). Both measures of net photosynthetic capacity – mass- and area-based – were higher at P.N. Soberanía than at Río Hato (Table 2). Dark respiration, more negative at P.N. Soberanía than at Río Hato, was significantly different for all effects (Table 2). Although the mean value of conductance at P.N. Soberanía was greater than at Río Hato, differences were not statistically significant by site, species, nor by the combination of site and species (Table 2). Transpiration was greater at P.N. Soberanía than at Río Hato, and differed significantly by site, but NOT by species nor by the combination of site and species (Table 2). Values of instantaneous WUE, greater at Río Hato than at P.N. Soberanía, varied significantly by site but not by species nor by the combination of site and species (Table 2). Intrinsic WUE, less negative at Río Hato than at P.N. Soberanía, differed significantly by species but not by site nor by the combination of site and species (Table 2). C:N, greater at P.N. Soberanía than at Río Hato, differed significantly by site and species, but not by the combination of site and species (Table 2).

Across all variables of foliar nutrient content (C, N, Mg, P, K, and Ca), the overall effects of site ($p < 0.0001$), species ($p < 0.0001$), and the combination of site and species ($p < 0.0001$) were significant (MANOVA, $\alpha = 0.05$, Wilk's Lambda Statistic, d.f. for site = 6, species = 78, site $\times$ species = 78).

Mean values of C were higher at P.N. Soberanía than at Río Hato and differed significantly by species, but not by site nor by the combination of site and species (Table 3). Foliar N, greater at Río Hato than at P.N. Soberanía, was significantly different by site and species, but not by the combination of site and species (Table 3). Mean values of K were greater at P.N. Soberanía than at Río Hato and differed significantly by site and species, but not by the combination of site and species (Table 3). At P.N. Soberanía, mean values of P were greater at Río Hato and were significantly different by site and species, but not by the combination of site and species (Table 3). Foliar

Table 2
Structural and physiological characteristics of 14 tree species at two sites in Panama

Response variables	P.N. Soberanía	Río Hato	R^2 (%)	p value		
				Site	Species	Site $\times$ species
Leaf mass area (g m^{-2})	88.866	83.67	84.57	0.0798	<0.0001	<0.0001
Leaf area index[a]	1.636	0.708	83.18	<0.0001	<0.0001	0.3734
Area-based net photosynethic capacity (μmol m^{-2} s^{-1})	15.581	14.675	65.15	<0.0001	0.187	0.0912
Mass-based net photosynethic capacity (μmol g^{-1} s^{-1})	189.625	181.688	70.46	0.4616	<0.0001	0.0039
Dark respiration (nmol m^{-2} s^{-1})	−2.645	−2.052	73.41	<0.0001	<0.0001	0.0024
Conductance (mol H$_2$O m^{-2} s^{-1})[b]	0.683	0.539	45.11	0.1001	0.072	0.2239
Transpiration (mmol H$_2$O m^{-2} s^{-1})[c]	5.896	4.784	34.60	0.0036	0.748	0.819
Instantaneous water-use efficiency (μmol CO$_2$ mmol H$_2$O^{-1})	2.758	3.858	42.69	0.0269	0.129	0.5028
Intrinsic water-use efficiency (d 13C/12C)	−28.967	−28.813	78.30	0.3982	<0.0001	0.0645
Foliar C/foliar N	23.937	19.238	78.89	0.0002	<0.0001	0.0571

Differences between site, species, and the combination of site and species of structural and physiological characteristics were tested using a GLM (95% confidence interval, $\alpha = 0.05$, degrees of freedom for site = 1, species = 13, species $\times$ site = 13).

[a] Cube-root transformed for analysis; non-transformed values shown

[b] Double transformed (sin value − average) $\times \sqrt{|(value - average)|}$ for analysis; non-transformed values shown.

[c] Natural-log transformed for analysis; non-transformed values shown.

Table 3
Foliar nutrient content of 14 tree species at two sites in Panama

Response variable	P.N. Soberanía	Río Hato	R^2 (%)	Site	Species	Site × species
C (%)	50.257	50.136	65.48	0.6542	<0.0001	0.1436
N (%)	2.433	2.800	92.11	<0.0001	<0.0001	0.3071
K (%)	1.032	0.893	73.65	0.0083	<0.0001	0.1617
P (%)	0.165	0.116	73.29	<0.0001	<0.0001	0.7320
Ca (%)	1.173	1.457	81.14	0.0003	<0.0001	0.0005
Mg (%)[a]	0.478	0.373	93.94	<0.0001	<0.0001	<0.0001

Differences between site, species, and the combination of site and species were tested using a GLM of mass-based (%) foliar nutrient content of 14 tree species at two sites in Panama (95% confidence interval, $\alpha = 0.05$, degrees of freedom for site = 1, species = 13, and site × species = 13)

[a] Data were natural-log transformed for analysis, non-transformed values shown.

Ca levels were greater at Río Hato than at P.N. Soberanía and differed significantly by site, species, and the combination of site and species (Table 3). Magnesium, greater at P.N. Soberanía than at Río Hato, differed significantly by site, species, and the combination of site and species (Table 3).

CART analysis of physiological and structural characteristics, after having assigned group membership by site, yielded dark respiration as the best splitter. Trees at P.N. Soberanía with low dark respiration values had high LAI, while those with high dark respiration values had high LMA. Trees at Río Hato with low dark respiration values, had low LAI, while those with high dark respiration had low LMA. For foliar nutrient content, foliar P was the best splitter when groups were designated by site using CART analysis. All trees at P.N. Soberanía had P values greater than 0.119%. Trees at Río Hato either had low P or high K, in the case that foliar P was high.
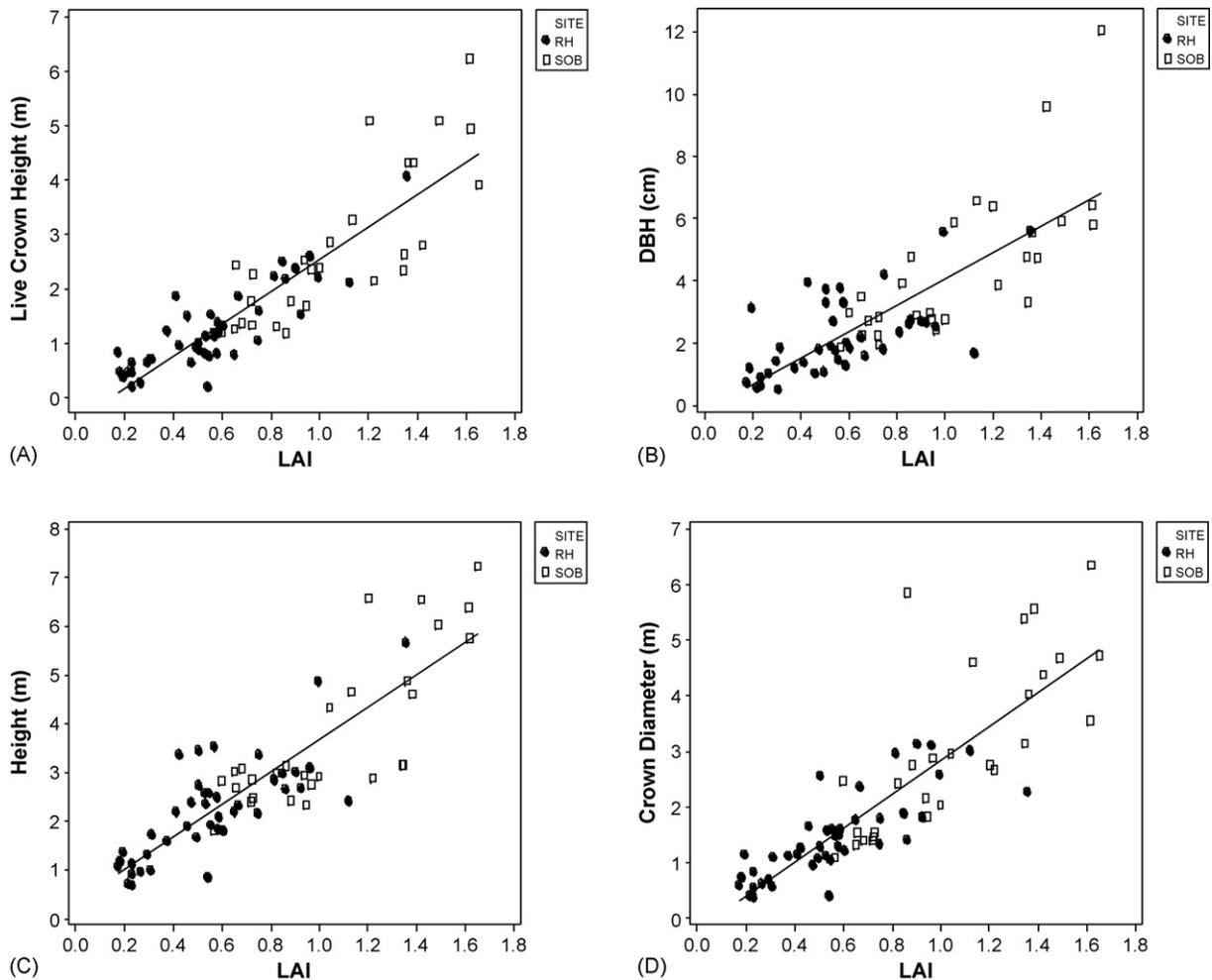

Fig. 2. Linear regression of 14 tree species at two sites in Panama. (A) LAI vs. live crown height ($R^2 = 78.00\%$, $p < 0.0001$). (B) LAI vs. DBH ($R^2 = 61.10\%$, $p < 0.0001$). (C) LAI vs. height ($R^2 = 73.60\%$, $p < 0.0001$). (D) LAI vs. crown diameter ($R^2 = 70.90\%$, $p < 0.0001$). For all regressions, LAI data was cube-root transformed for analysis.

3.2. Within-site comparisons

Linear regression analysis was performed in which LAI values were used to predict integrated measurements of tree growth and performance for all species across both sites. LAI significantly predicted crown diameter values and explained 70.90% of its variability (Fig. 2). Tree height values were predicted at significant levels by LAI, and 73.60% of their variability was explained by LAI (Fig. 2). LAI explained 78.00% of the variability of crown height, and was a significant predictor (Fig. 2). LAI significantly predicted DBH values and explained 61.10% of its variability (Fig. 2).

As a strong predictor of tree growth parameters at both sites, LAI values were analyzed to capture within and between-site variability of tree growth. Mean LAI values were significantly higher at P.N. Soberanía than at Río Hato (GLM and Tukey's HSD, $R^2 = 40.78\%$, $p < 0.0001$). The two blocks at Soberanía were not significantly different from one another (GLM and Tukey's HSD, $R^2 = 40.78\%$, $p < 0.0001$). At Río Hato, the mean LAI value of Block 4 was significantly higher than that of Blocks 5 and 6; the mean LAI value of Block 5 was higher that of Block 6, but not at statistically significant levels (GLM and Tukey's HSD, $R^2 = 40.78\%$, $p < 0.0001$).

Cluster analysis of foliar nutrient content for all tree species was performed at each site to assign group membership for subsequent CART analysis of physiological and structural characteristics. At P.N. Soberanía, species were divided into two principal clusters (Table 4). Group 1 had higher LMA, $A_{maxarea}$, dark respiration, conductance, transpiration, intrinsic WUE, foliar C, foliar N, foliar K, foliar P, and foliar Mg than Group 2 and lower LAI, $A_{maxmass}$, instantaneous WUE, C:N, and Ca than Group 2 (Table 5). In terms of their growth parameters, trees in Group 2 were taller, had taller live crowns, wider crown diameters, and larger DBH than those in Group 1 (Table 5). Species were also divided into two cluster at Río Hato (Table 4), Group 1 had higher LMA, $A_{maxarea}$, conductance, instantaneous WUE, foliar C, foliar N, and foliar Mg than Group 2 and lower LAI, $A_{maxmass}$, dark respiration, transpiration, intrinsic WUE, C:N, foliar K, foliar P and foliar Ca than Group 2 (Table 5). Trees in Group 2 were larger across all growth parameters than those in Group 1 (Table 5).

CART analysis of the physiological and structural characteristics of groups determined by cluster analysis of foliar nutrient content identified LAI as the best splitter at P.N. Soberanía. Trees in Group 1 either had relatively low LAI, or low intrinsic WUE (more negative) if their LAI was high

Table 4
Group membership as determined by hierarchical cluster analysis of foliar nutrient content using Euclidean distance and Ward's method at P.N. Soberanía and Río Hato

Site	Group	Species	# Plots	Life history
P.N. Soberanía	1	A. adinocephala	3	Leguminous
		A. guachapele	3	Leguminous
		C. candidissimun	3	Native timber
		D. panamensis	3	Native timber
		E. cyclocarpum	3	Leguminous
		E. fusca	3	Leguminous
		G. sepium	3	Leguminous
		O. pyramidale	3	Early succession
		P. quinata	1	Native timber
		T. grandis	1	Exotic timber
		C. odorata	1	Native timber
	2	G. ulmifolia	3	Early succession
		L. seemaannii	3	Early succession
		S. mombin	3	Early succession
		C. odorata	2	Native timber
		P. quinata	1	Native timber
		T. grandis	1	Exotic timber
Río Hato	1	A. adinocephala	3	Leguminous
		C. odorata	3	Native timber
		D. panamensis	3	Native timber
		E. cyclocarpum	3	Leguminous
		E. fusca	3	Leguminous
		O. pyramidale	3	Early succession
		C. candidissimun	1	Native timber
		A. guachapele	1	Leguminous
	2	G. sepium	3	Leguminous
		G. ulmifolia	3	Early succession
		L. seemannii	3	Early succession
		P. quinata	3	Native timber
		S. mombin	3	Early succession
		T. grandis	3	Exotic timber
		A. guachapele	2	Leguminous
		C. candidissimun	2	Native timber

Table 5
Physiological, structural, and growth characteristics and foliar nutrient content of groups from hierarchical cluster analysis of foliar nutrient content, using Euclidean distance and Ward's method for P.N. Soberanía and Río Hato

	P.N. Soberanía		Río Hato	
	Group 1	Group 2	Group 1	Group 2
Physiological and structural characteristics				
Leaf mass area (g m^{-2})	92.826	82.89	84.913	82.540
Leaf area index	1.436	1.869	0.359	1.025
$A_{maxarea}$ (µmol m^{-2} s^{-1})	15.732	15.504	14.811	14.551
$A_{maxmass}$ (µmol g^{-1} s^{-1})	185.332	194.811	179.681	183.512
Dark respiration (nmol m^{-2} s^{-1})	−2.718	−2.494	−1.922	−2.171
Conductance (mol H$_2$O m^{-2} s^{-1})	0.73	0.587	0.666	0.424
Transpiration (mmol H$_2$O m^{-2} s^{-1})	6.174	5.353	4.731	4.830
WUEi (µmol CO$_2$ mmol H$_2$O^{-1})	2.631	3.062	4.640	3.146
WUE(d 13C/12C)	−28.663	−29.599	−28.827	−28.800
Foliar C/foliar N	23.741	24.342	18.822	19.617
Foliar nutrient content				
C (%)	51.353	47.983	51.888	48.544
N (%)	2.618	2.049	2.911	2.699
K (%)	1.07	0.953	0.868	0.916
P (%)	0.169	0.1573	0.111	0.120
Ca (%)	1.083	1.361	1.167	1.720
Mg (%)	0.526	0.377	0.402	0.347
Growth characteristics				
Height (m)	3.607	3.97	2.364	2.995
Live crown height (m)	2.348	3.316	1.060	2.043
Crown diameter (m)	3.374	4.11	1.455	2.024
DBH (cm)	4.131	4.661	2.369	2.905

(Table 5). Trees in Group 2 had high LAI and relatively low intrinsic WUE (less negative) (Table 5). At Río Hato, LAI was also the best splitter amongst physiological and structural variables. Trees in Group 1 either had relatively low LAI, or high LMA if their LAI was high (Table 5). In Group 2, trees had relatively low LMA and high LAI (Table 5).

Cluster analysis of physiological and structural characteristics was also performed for both sites prior to CART analysis of foliar nutrient content. At P.N. Soberanía, all species were clustered into two principal groups (Table 6). Group 1 had higher $A_{maxarea}$, $A_{maxmass}$, dark respiration, conductance, transpiration, foliar C, foliar N, foliar K, and foliar P than Group 2, but lower LMA, LAI, instantaneous WUE, intrinsic WUE (more negative), C:N, foliar Ca, and foliar Mg than Group 2 (Table 7). Across all growth

Table 6
Group membership as determined by hierarchical cluster analysis of physiological and structural characteristics using Euclidean distance and Ward's method at P.N. Soberanía and Río Hato

Site	Group	Species	# Plots	Life history
P.N. Soberanía	1	A. adinocephala	3	Leguminous
		E. fusca	3	Leguminous
		G. ulmifolia	2	Early succession
		L. seemannii	1	Early succession
		O. pyramidale	1	Early succession
		S. mombin	1	Early succession
		P. quinata	1	Native timber
		T. grandis	1	Exotic timber
		A. guachapele	1	Leguminous
		C. candidissimun	1	Native timber
		C. odorata	1	Native timber
		E. cyclocarpum	1	Leguminous
	2	D. panamensis	3	Native timber
		G. sepium	3	Leguminous
		A. guachapele	2	Leguminous
		C. candidissimun	2	Native timber
		C. odorata	2	Native timber
		E. cyclocarpum	2	Leguminous
		L. seemannii	2	Early succession
		O. pyramidale	2	Early succession
		S. mombin	2	Early succession
		G. ulmifolia	1	Early succession
		P. quinata	1	Native timber
Río Hato	1	A. adinocephala	3	Leguminous
		A. guachapele	3	Leguminous
		C. odorata	3	Native timber
		E. cyclocarpum	3	Leguminous
		G. sepium	3	Leguminous
		L. seemannii	3	Early succession
		T. grandis	2	Exotic timber
		E. fusca	2	Leguminous
		P. quinata	2	Native timber
		S. mombin	1	Early succession
	2	C. candidissimun	3	Native timber
		D. panamensis	3	Native timber
		G. ulmifoila	3	Early succession
		O. pyramidale	3	Early succession
		L. seemannii	2	Early succession
		S. mombin	2	Early succession
		T. grandis	1	Exotic timber
		E. fusca	1	Leguminous
		P. quinata	1	Native timber

Table 7
Physiological, structural, and growth characteristics and foliar nutrient content of groups from hierarchical cluster analysis of physiological and structural characteristics, using Euclidean distance and Ward's method for P.N. Soberanía and Río Hato

	P.N. Soberanía		Río Hato	
	Group 1	Group 2	Group 1	Group 2
Physiological and structural characteristics				
Leaf mass area (g m^{-2})	83.206	93.902	78.480	89.953
Leaf area index	1.395	1.711	0.894	0.482
$A_{maxarea}$ (μmol m^{-2} s^{-1})	16.853	14.775	17.242	11.567
$A_{maxmass}$ (μmol g^{-1} s^{-1})	206.355	176.064	225.564	128.575
Dark respiration (nmol m^{-2} s^{-1})	−2.715	−2.593	−2.133	−1.955
Conductance (mol H$_2$O m^{-2} s^{-1})	0.778	0.613	0.486	0.604
Transpiration (mmol H$_2$O m^{-2} s^{-1})	6.409	5.536	4.642	4.948
WUEi (μmol CO$_2$ mmol H$_2$O^{-1})	2.752	2.785	4.613	2.943
WUE(d 13C/12C)	−29.178	−28.811	−28.518	−29.170
Foliar C/foliar N	22.524	24.981	16.881	22.092
Foliar nutrient content				
C (%)	50.491	50.085	49.807	50.535
N (%)	2.463	2.410	3.167	2.355
K (%)	1.106	0.978	0.989	0.777
P (%)	0.170	0.162	0.129	0.100
Ca (%)	1.139	1.199	1.324	1.617
Mg (%)	0.420	0.521	0.423	0.313
Growth characteristics				
Height (m)	3.612	3.808	2.903	2.441
Live crown height (m)	2.580	2.724	1.634	1.503
Crown diameter (m)	3.359	3.801	1.904	1.570
DBH (cm)	4.043	4.496	2.716	2.573

parameters, trees in Group 1 were smaller than those in Group 2 (Table 7). At Río Hato, all species were also divided into two clusters (Table 6). Group 1 had higher LAI, $A_{maxarea}$, $A_{maxmass}$, dark respiration, instantaneous WUE, intrinsic WUE (less negative), foliar N, foliar K, foliar P, and foliar Mg than Group 2, but lower LMA, conductance, transpiration, C:N, foliar C, and foliar Mg than Group 2 (Table 7). Trees in Group 1 were larger than those in Group 2 across all growth parameters (Table 7).

Based on the groupings determined by cluster analysis of physiological and structural characteristics, CART analysis of foliar nutrient content identified foliar Mg as the best splitter at P.N. Soberanía. Trees in Group 1 had relatively low foliar Mg, yet high values of foliar P (Table 7). Trees in Group 2 had comparatively high foliar Mg, or low foliar P if foliar Mg was relatively high (Table 7). At Río Hato, foliar N was the best splitter and trees in Group 1 had either high foliar N or high foliar P, if foliar N was relatively low (Table 7). Trees in Group 2 had relatively low amounts of both foliar N and foliar P (Table 7).

3.3. Predictors of tree growth by site and across sites

Linear regressions were performed to select the most significant predictors of $A_{maxarea}$ and $A_{maxmass}$ for both sites

together and separately. For both sites, LMA ($p = 0.0110$) and foliar N ($p = 0.0094$) were significant predictors of A_{maxarea} and explained 32.40% of its variability ($p = 0.0075$). By adding LAI to the linear regression model, the R^2 value increased to 51.45% ($p = 0.0005$); LMA ($p = 0.0015$), leaf N ($p = 0.0008$), and LAI ($p = 0.0053$) were significant predictors. When considering A_{maxmass} values for both sites, LMA ($p = 0.0014$) and leaf N ($p = 0.0031$) were significant predictors and explained 56.98% of the variability in A_{maxmass} values ($p < 0.0001$). The addition of LAI to the linear regression model increased the R^2 value to 71.29% ($p < 0.0001$). Again, LMA ($p = 0.0010$), foliar N ($p = 0.0001$), and LAI ($p = 0.0020$) were significant predictors.

At P.N. Soberanía, LMA and foliar N explained 51.88% of the variability of A_{maxarea} ($p = 0.0179$). LMA ($p = 0.0163$) was a significant predictor of A_{maxarea}, while foliar N ($p = 0.0505$) was not. Adding LAI to the linear regression model increased R^2 to 65.21% ($p = 0.0116$); LMA ($p = 0.0047$) and foliar N ($p = 0.0195$) were significant predictors, while LAI was not ($p = 0.0787$). LMA ($p = 0.0055$) and foliar N ($p = 0.0407$) significantly predicted A_{maxmass} values and explained 63.01% of the variability ($p = 0.0042$). A_{maxmass} was predicted at significant levels by LMA ($p = 0.0102$) and foliar N ($p = 0.0129$), but not LAI ($p = 0.0572$); these variables explained 74.69% of the variability of A_{maxmass} values ($p = 0.0025$).

At Río Hato, foliar N ($p = 0.0240$) was a significant predictor of A_{maxarea}, while LMA ($p = 0.0731$) was not. Although they explained 38.52% of the variability in A_{maxarea} values, they did not do so at significant levels ($p = 0.0689$). While the addition of LAI to the linear regression model improved the R^2 value to 49.10%, the combination of LAI, foliar N, and LMA did not predict A_{maxarea} values at significant levels ($p = 0.0701$). Foliar N ($p = 0.0268$) remained as the only significant predictor of A_{maxarea} at the 0.05 α-level (LMA, $p = 0.0932$; LAI, $p = 0.2673$). Foliar N and LMA explained 65.66% of the variability in A_{maxmass} ($p = 0.0028$). Foliar N ($p = 0.0198$) was a significant predictor, whereas LMA was not ($p = 0.46198$). The addition of LAI to the linear regression increased the R^2 value to 71.09% ($p = 0.0048$), but neither LAI ($p = 0.2004$) nor LMA ($p = 0.3466$) were significant predictors. Foliar N remained as the only significant predictor ($p = 0.0227$). As the lone predictor variable, foliar N was significant ($p = 0.0006$) and explained 63.85% of the variability in A_{maxmass} ($p = 0.0006$).

4. Discussion

4.1. Between-site comparisons

The data of the investigated tree species indicate, as expected, that at the seasonally wet site with relatively fertile soils trees experienced less environmental stress than at the seasonally dry site with relatively infertile soils. Our analysis was aimed at how this was expressed in terms of growth, physiology, morphology, and anatomy. At P.N. Soberanía, area-based net photosynthetic capacity and LAI, measures of

instantaneous and integrated tree productivity, respectively, were significantly higher than at Río Hato. Mass-based net photosynthetic capacity, transpiration, and conductance – metrics commonly associated with greater photosynthetic activity – were also greater at P.N. Soberanía, although not all at statistically significant levels. Increased levels of dark respiration at P.N. Soberanía probably reflected higher ambient temperatures, as dark respiration typically rises linearly with temperature (Larcher, 2003). Also, dark respiration varied significantly by species, indicating a differential tolerance to the same level of environmental stress. Trees at Río Hato adapted to the sub-optimal precipitation levels by increasing water-use efficiency, as evidenced by their significantly higher instantaneous WUE and less negative, although not statistically significant, intrinsic WUE. Intrinsic WUE differed significantly by species, indicating that certain species were better adapted than others to drought conditions. LMA values had a more significant difference between species than by site, demonstrating that species may have a predetermined and differential ability to cope with environmental stress with respect to their leaf thickness, supporting previous studies that have attributed differences in LMA values to successional status (Lambers et al., 1998). C:N ratios, higher at P.N. Soberanía, reflect lower foliar N, as foliar C did not differ between sites.

Foliar leaf content data confirm that trees at P.N. Soberanía had greater amounts of foliar nutrients than those at Río Hato, with the exception of N and Ca. The greater abundance of foliar nutrients at this site reflects the greater abundance and availability of soil nutrients in the rhizosphere. Similarly, higher rates of net photosynthetic capacity, on both a mass and area basis, result in part from the greater availability of macro-nutrients required for photo-chemical processes. Assimilation of foliar C reflected a species-specific trait more so than an adaptation to site conditions. Higher levels of foliar N and Ca at Río Hato reflect a greater retention of macro-nutrients needed for photosynthetic processes. Although foliar N levels decrease considerably with leaf age, leaf sampling controlled for changes in foliar nutrient content related to phenology by sampling at the same functional time at both sites (4–8 weeks after the start of the rainy season) (Grubb, 1977). Foliar nutrient levels also differed significantly by species. This result demonstrates that, despite the similar response of all species to a given set of environmental conditions, their responses are not uniform.

Regression tree analysis showed the nature of physiological and structural adaptations to site conditions at both sites. Species with relatively low rates of dark respiration at P.N. Soberanía had a higher LAI – indicating greater productivity – than those trees at Río Hato with similarly low rates of dark respiration. Trees at Río Hato with higher rates of dark respiration and relatively low LMA values attempted to maintain a positive carbon balance by maximizing light harvest, while perhaps increasing their vulnerability to drought (Reich et al., 1997). Conversely, trees at P.N. Soberanía with relatively higher rates of dark respiration had higher LMA values, as they prioritized minimizing water loss. The results of CART of foliar nutrients reflect how the repeated cutting of an

invasive grass species, *Saccarum spontaneum*, and its subsequent decomposition might have improved soil nutrition and fertility dynamics at P.N. Soberanía.

4.2. Within-site comparisons

LAI was a significant predictor with very high R^2 values for four metrics of integrated plant growth: tree height, crown height, crown diameter, DBH. Using LAI to make community-level comparisons effectively captured the structural complexity and the integrated productivity of the studied species at both sites in terms of tree height, crown height, crown diameter, and DBH (Engelbrecht and Herz, 2001; Jonckheere et al., 2004; Norman and Campbell, 1989). LAI varied significantly between two of the three measured blocks at Río Hato, while there were no significant differences between blocks at P.N. Soberanía. These results validate our hypothesis that integrated tree productivity is more variable where there is lower soil fertility and precipitation.

Cluster and CART analysis were performed to explicitly identify the physiological, structural, and leaf nutritional traits that drove the within-site variability of tree growth at both sites. At P.N. Soberanía, species were clustered by their foliar nutrient content into groups that mostly corresponded to their life history. Species in Group 2, such as *G. ulmifolia*, *S. mombin*, and *L. seemanii*, were mostly early successional, although the other species were native and exotic timber species (*C. odorata*, *T. grandis*, and *P. quinata*) (Condit et al., 1993). Species in Group 1 were either leguminous (*A. adinocephala*, *A. guachapele*, *E. fusca*, *G. sepium*) or native and exotic timber species (*C. candidissimun*, *D. panamensis*, *P. quinata*, *T. grandis*), with the exception of the early successional species *O. pyramidale* (Condit et al., 1993). Species in Group 2 facilitated their greater cumulative growth by using their large, low-density leaves – a product of low foliar C and LMA – to maximize light interception, as seen by their high LAI. These physiological and structural adaptations might explain their ability to colonize rapidly areas with high light availability, such as abandoned pastures, forest gaps, and roadsides.

Regression tree analysis of physiological and structural characteristics, using group membership determined by cluster analysis of foliar nutrient content, further elucidates the relationship between light interception and water-use efficiency at P.N. Soberanía. LAI – the best splitter – was positively correlated with tree growth parameters. Species with relatively high LAI and intrinsic WUE grew well (Group 2); those species (Group 1) with high LAI and low intrinsic WUE did not. These results illustrate that early successional species grow rapidly by virtue of intensive photosynthetic activity, i.e. high $A_{maxmass}$, which is accomplished by maximizing light interception and minimizing water loss.

Life history was not as strong a determinant of cluster membership by foliar nutrient content at Río Hato as at P.N. Soberanía. Group 1 contained a mixture of leguminous species (*A. adinocephala*, *E. fusca*, *E. cyclocarpum*), early successional species (*O. pyramidale*), and native timber species (*D. panamensis*, *C. odorata*,) (Condit et al., 1993). Group 2 was comprised of a similarly varied mixture of early successional species (*S. mombin*, *G. ulmifolia*, *L. seemannii*), leguminous species (*A. guachapele*, *G. sepium)*, and native and exotic timber species (*T. grandis*, *P. quinata*, *C. candidissimun*) (Condit et al., 1993).

Species in Group 1 have evolved a suite of physiological and structural adaptations, such as low LAI and high instantaneous WUE, conductance, and foliar C, that minimize water loss. Results from CART analysis of physiological and structural variables, which identify LAI and LMA as significant splitters, also show how species in Group 1 are better adapted to reduce water loss; species in Group 1 either maintained low amounts of foliage (LAI) or had smaller, thicker leaves (LMA). The growth parameters of Group 1, low as compared to those of Group 2, emphasize how these species have adapted to persist and not to accumulate biomass in dry, infertile sites (Swaine, 1996).

When first clustered by physiological and structural characteristics, life history did not determine cluster membership at P.N. Soberanía. Both groups were comprised of early successional, timber, and leguminous species (Condit et al., 1993). Trees belonging to Group 2 had higher LMA, LAI, and intrinsic WUE and lower mass- and area-based net photosynthetic capacity than those of Group 1. Despite these differences, trees in Groups 1 and 2 were similar in terms of height, live crown height, crown diameter, and DBH. CART analysis of foliar nutrient content differentiated Group 1 from Group 2 by foliar Mg and foliar P. Given the similarity between Groups 1 and 2 in terms of physiological, structural, and allometric characteristics, it would appear unlikely that a differential ability to uptake soil P and soil Mg has conferred a competitive advantage at P.N. Soberanía. The importance of successional status and functional group to tree growth was apparently obviated by the relative abundance of growth factors at P.N. Soberanía; tree growth and productivity was modulated primarily by certain physiological adaptations, such as high LMA, high LAI, low dark respiration, low conductance, low transpiration, and high intrinsic WUE, that did not correlate to a specific functional group or successional status.

At Río Hato, the group membership of species, when clustered by their physiological and structural characteristics, strongly correlated to their life history. The first group was composed mainly of leguminous species (*A. adinocephala*, *E. cyclocarpum*, *G. sepium*, *A. guachapele*, *E. fusca*) and native and exotic timber species (*P. quinata*, *C. odorata*, *T. grandis*), with the exception of *L. seemanni*. The species belonging to the second group were either early successional (*S. mombin*, *O. pyramidale*, *G. ulmifolia*) or native timber species (*C. candidissimun*, *D. panamensis*) (Condit et al., 1993). Species in Group 1 had higher LAI, mass- and area-based net photosynthetic capacity, instantaneous and intrinsic WUE and lower LMA, conductance, transpiration, and C:N than those in Group 2. Growth parameters correlated positively with physiological and structural characteristics, as trees in Group 1 were larger across all growth parameters than Group 2. Results from CART analysis of foliar nutrient content demonstrated a correlation between abundances of foliar N and P with tree growth, as species in Group 1 either had high amounts of foliar

N or P, while those in Group 2 had lower amounts of both. Low precipitation and soil fertility at Río Hato conferred a competitive advantage to those species that could access soil nutrients and water more readily, such as N-fixing species. These results confirm the findings of Mooney and Santiago, who found a positive relationship between foliar N and net photosynthetic capacity (Mooney et al., 1978; Santiago et al., 2004) As it is likely that the species in Group 1 evolved where soil nutrients and precipitation limited growth and survivorship, they also developed physiological and structural characteristics, specifically high intrinsic water-use efficiency and low LMA, that enabled them to maximize their water-use efficiency and minimize their water loss in order to maximize their growth.

4.3. Predictors of tree productivity by site and across sites

Structural and physiological characteristics constrain tree productivity and determine which species are most productive under a given set of environmental conditions. Across both sites, we confirmed Reich's hypothesis that the predictive ability of LMA and foliar N increased when estimating tree productivity using mass-based net photosynthetic capacity (Reich et al., 1997). Scaling net photosynthetic capacity on a mass-basis decreases the site effect and increases that of species. The addition of LAI to the linear regression model further increased its predictive strength to 71.29%, effectively relating a tree's instantaneous productivity to an integrated measure of its productivity. Under the wet, fertile conditions present at P.N. Soberanía, the same relationship between tree productivity and LMA, foliar N, and LAI held. Tree productivity was limited by different constraints at Río Hato, as foliar N was the only significant predictor of mass-based net photosynthetic capacity. The significance of this relationship is two-fold: (1) in nutrient limited soils, species capable of fixing and translocating soil N to their leaves increase their ability to photosynthesize and (2) the successful performance of a tree species in dry, infertile sites should be quantified by its tolerance of adverse environmental conditions and not necessarily by its accumulation of biomass to the accumulation of biomass.

5. Conclusion

The differences in environmental stress present at both sites were catalysts for the investigated tree species to adapt their structural and physiological characteristics and foliar nutrient content to these site conditions. At P.N. Soberanía, trees exhibited higher levels of productivity as a result of higher levels of soil fertility and precipitation which enabled more photosynthetic activity to occur. Pioneer tree species such as *S. mombin*, *G. ulmifolia*, and *L. seemanni*, identified by Condit et al. (1993) for their rapid growth, were notable for the strong correlation of growth parameters to high water-use efficiency and large, low-density leaves. Trees adapted to the less fertile soils and lower precipitation levels at Río Hato by increasing their water-use efficiency and decreasing their net photosyn-

thetic capacity. N-fixing tree species, such as *A. adinocephala*, *A. guachapele*, *E. cyclocarpum*, and *G. sepium*, were especially tolerant of adverse site conditions. The growth-limiting environmental conditions present at Río Hato also increased the variability of integrated tree growth. Tree growth was limited by foliar N at Río Hato, whilst the combination of LMA, foliar N, and LAI best predicted tree productivity at P.N. Soberanía. Our research supports an adaptive management approach to reforestation projects that takes into account environmental conditions by selecting tree species capable of adapting physiologically and structurally to different levels of drought and soil nutrient stress.

Acknowledgements

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