



Biomass distribution among tropical tree species grown under differing regional climates

Sara Bastien-Henri^{a,*}, Andrew Park^b, Mark Ashton^{c,d}, Christian Messier^a

^a Centre d'étude de la Forêt, Département des sciences biologiques, Université du Québec à Montréal, CP 8888, Succursale Centre-Ville, Montréal (Québec), H3C 3P8 Canada

^b University of Winnipeg, Centre for Forest Interdisciplinary Research, Department of Biology, 515 Portage Avenue, Winnipeg, MB, R3B 2E9 Canada

^c Yale University, School of Forestry and Environmental Studies, 195 Prospect Street, New Haven, CT 06511, USA

^d Native Species Reforestation Project (PRORENA), Center for Tropical Forest Science, Smithsonian Tropical Research Institute, Unit 0948, APO, AA 34002, USA

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ABSTRACT

In the Neotropics, there is a growing interest in establishing plantations of native tree species for commerce, local consumption, and to replant on abandoned agricultural lands. Although numerous trial plantations have been established, comparative information on the performance of native trees under different regional environments is generally lacking. In this study, we evaluated the accumulation and partitioning of above-ground biomass in 16 native and two exotic tree species growing in replicated species selection trials in Panama under humid and dry regional environments. Seven of the 18 species accumulated greater total biomass at the humid site than at the dry site over a two-year period. Species-specific biomass partitioning among leaves, branches and trunks was observed. However, a wide range of total biomass found among species (from 1.06 kg for *Dipteryx panamensis* to 29.84 kg for *Acacia mangium* at Soberania) justified the use of an Aitchison log ratio transformation to adjust for size. When biomass partitioning was adjusted for size, a majority of these differences proved to be a result of the ability of the tree to support biomass components rather than the result of differences in the regional environments at the two sites. These findings were confirmed by comparative ANCOVAs on Aitchison-transformed and non-Aitchison-transformed variables. In these comparisons, basal diameter, height and diameter at breast height were robust predictors of biomass for the pooled data from both sites, but Aitchison-transformed variables had little predictive power.

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1. Introduction

Until relatively recently, reforestation in the Neotropics mostly employed exotic species such as teak (*Tectona grandis* Lf.), *Acacia* sp. or *Eucalyptus* sp. Exotic monocultures are thought to provide fewer ecological services relative to native forest (Stier and Siebert, 2002; Craven et al., 2007), and their establishment has even been cited as a driver of deforestation (Butler and Laurance, 2008).

In recent decades, land managers and development organizations in Neotropical countries have become interested in using native tree species in reforestation. Native species are now being planted for commercial (timber and carbon sequestration) purposes, to provide ecological services, and to serve social interests (Lugo, 1997; Carpenter et al., 2004). There is a growing body of information on the growth and survival of some native Neotropical species (Lugo, 1997; Stier and Siebert, 2002; Piotta et al., 2004). Nevertheless, there are still relatively few data on biomass partitioning and habitat preferences for most Neotropical trees. Most

native species plantations have been established on single sites (King, 1991; Menalled and Kelty, 2001; Petit and Montagnini, 2006), which makes it difficult to generalize their growth potential to a variety of sites and regional climates.

Tropical tree species have developed physiological, morphological and phenological plasticity in the face of uncertain water availability. Photosynthesis, intrinsic water use efficiency, dark respiration, and foliar C:N ratios all vary among species and among sites with different rainfall regimes (Mulkey and Wright, 1996; Craven et al., 2007). Precipitation may be the most important climatic variable affecting tree growth in the seasonal tropics. Variable precipitation assumes particular importance in areas such as Central America, where the pronounced dry seasons can last up to eight months. Species distribution (Condit, 1998; Santiago et al., 2004; Santiago and Mulkey, 2005; Engelbrecht et al., 2007) and productivity (Austin and Vitousek, 1998; Coyle and Coleman, 2005) are closely related to rainfall patterns and water availability. Litter quantity and quality, which indirectly affect plant community composition and productivity, are modified by rainfall (Santiago and Mulkey, 2005). Direct nutrient availability to plants may also be affected by the amount of precipitation (Santiago et al., 2004; Coyle and Coleman, 2005).

* Corresponding author. Tel.: +1 514 987 3000x5048; fax: +1 514 987 4647.

E-mail address: sara.bastienhenri@gmail.com (S. Bastien-Henri).

Trees also display year to year phenotypic plasticity (Coomes and Grubb, 1998; King, 2003; Delagrangé et al., 2004; Balandier et al., 2007) in response to seasonal environmental signals, leading to variations in the proportions of biomass allocated to different plant tissues (Coleman et al., 1994). These intraspecific variations allow plants to maximize their functional fitness in response to a changing environment (Coleman et al., 1994; McConnaughay and Coleman, 1999; Lewis and Tanner, 2000). As trees grow, biomass accumulation and partitioning will therefore vary under different site conditions (Ketterings et al., 2001; Zianis and Mencuccini, 2004; Heras et al., 2007). For this reason, the effect of tree size on allometry should be clearly separated from that of the environment, especially when biomass is being compared at different sites among diverse species with highly variable growth patterns.

Site differences are likely to affect the allocation of biomass to leaf, stem and root components that are valued for commercial or subsistence purposes by landowners who plant trees. Differential allocation will also feed back to growth by affecting overall rates of photosynthesis and the ability of plants to absorb sufficient water and mineral nutrients. Our knowledge of biomass accumulation and partitioning under different regional climates must therefore be greatly improved (i) to fine-tune species selection criteria for plantations and agroforestry, and (ii) as a step towards understanding differential growth and survival of multiple species. Comparative studies performed along gradients of site conditions, or in different regional climates are particularly needed (Condit, 1998; Santiago and Mulkey, 2005; Craven et al., 2007; Wishnie et al., 2007).

In this paper, we compare the biomass production and partitioning among 16 Neotropical (hereafter “native”) and two Old World (“exotic”) tree species after two years in plantation. Our primary objectives were (1) to perform intraspecific comparisons of biomass accumulation in species growing on two sites with different regional climates and soils, (2) to compare intraspecific allometric differences among sites after adjusting for species-specific differences in size, and (3) to test the ability of simple biometric variables (such as basal diameter) to predict biomass in a multi-species data set.

2. Methods

2.1. Study sites and species selection

Our research sites were located in two large species selection trials established by PRORENA, the native species reforestation project of the Smithsonian Tropical Research Institute and Yale

School of Forestry and Environmental Studies (PRORENA, 2005). These sites are representative of regional climatic and edaphic extremes that occur across the Isthmus of Panama. Soberania National Park (hereafter “Soberania”) received an average of 2226 mm annual rainfall between 1966 and 2003, with a 4.1-month dry season during which <100 mm of rain fell every month. With a 6.7-month dry season and an average annual rainfall of 1107 mm, Río Hato is part of the driest region of Panama along the Pacific coast in Coclé Province (Wishnie et al., 2007). Soberania is characterized by rolling hills punctuated by moist depressions while Río Hato has flat or gently sloping terrain. Soils at Soberania are primarily clays and silty clay loams, and soil texture at Río Hato ranges from loamy sand to heavy clay (Andrew Park, personal observation). The soils at Río Hato were less fertile than those of Soberania, with considerably lower cation exchange capacities and concentrations of N, K, Mg and P (Craven et al., 2007).

In 2003, 16 native and two exotic tree species (Table 1) were planted at both sites in monoculture plots of 20 trees (initial spacing of 3 m × 3 m) with nine replicates per site (Wishnie et al., 2007). Trees were 2–8-month old when planted, this variation depending on the time needed for the container-germinated seedlings to be ready for planting. On the day of planting and again two months later, 115 g/plant of granular fertilizer (12-72-12 N-P-K) was applied at each planting spot. Competing vegetation was cut with machetes on a regular basis at least three times every year (Wishnie et al., 2007). Species were chosen for their forest restoration potential, timber value, and silvopastoral use (Table 1) (see Wishnie et al., 2007 for further details). After two years of growth in plantation, when some plots had achieved crown closure, all plots were thinned to 50% of their original density by cutting alternate stems in every row.

The planned thinning gave us the opportunity to compare the above-ground partitioning of biomass among species. Between July and September 2005, six two-year old trees per species were selected for biomass measurement from each of the two sites. Sample trees were selected using a stratified random sample of stems from the 1 to 33rd, 34th to 66th, and 67th to 100th percentiles of the basal diameter distributions for each species based on previous measurement.

2.2. Data collection

2.2.1. Pre-harvest biometrics

Prior to cutting the trees, a complete set of crown and stem measurements were taken. These included basal diameter at 5 cm above the soil surface (BD), diameter at the base of the crown below the

Table 1
Scientific name, family, common name, wood density and main uses of the 18 tropical tree species studied (adapted from Wishnie et al., 2007).

| Scientific name | Family | Common name | Species code | Uses |
|--|---------------|-----------------------|--------------|-----------------------------|
| <i>Acacia mangium</i> Willd. | Fabaceae | Acacia | AM | Exotic: restoration, timber |
| <i>Albizia adinocephala</i> (Donn. Sm.) Britton & Rose | Fabaceae | Frijolillo | AA | Restoration |
| <i>Albizia guachapele</i> (Kunth) Dugand | Fabaceae | Guachapalí | AG | Fodder, timber |
| <i>Cedrela odorata</i> L. | Meliaceae | Cedro | CO | High value timber |
| <i>Colubrina glandulosa</i> Perkins | Rhamnaceae | Carbonero | CG | Timber, fuel wood |
| <i>Diphysa robinoides</i> Benth. | Fabaceae | Macano | DR | Fencing, fuel wood |
| <i>Dipteryx panamensis</i> (Pittier) Record & Mell | Fabaceae | Almendro de montaña | DP | Timber |
| <i>Enterolobium cyclocarpum</i> (Jacq.) Griseb. | Fabaceae | Corotú | EC | Timber, fodder |
| <i>Erythrina fusca</i> Lour. | Fabaceae | Palo bobo, Palo santo | EF | Restoration |
| <i>Gilricidia septium</i> (Jacq.) Kunth ex Walp. | Fabaceae | Balo | GS | Live fencing, fodder |
| <i>Guazuma ulmifolia</i> Lamk. | Sterculiaceae | Guácino | GU | Fodder, fuel wood |
| <i>Inga punctata</i> Willd. | Fabaceae | Guabita cansaboca | IP | Fruit, restoration |
| <i>Ochroma pyramidale</i> (Cav. Ex Lam.) Urb. | Bombacaceae | Balsa | OP | Restoration |
| <i>Pachira quinata</i> (Jacq.) W.S. Alverson | Bombacaceae | Cedro espino | PQ | Timber |
| <i>Samanea saman</i> (Jacq.) Merr. | Fabaceae | Guachapalí | SS | Fodder, timber |
| <i>Tabebuia rosea</i> DC. | Bignoniaceae | Roble | TR | Timber |
| <i>Tectona grandis</i> L. | Verbenaceae | Teck | TG | Exotic: high value timber |
| <i>Terminalia amazonia</i> (J.F. Gmel.) Exell | Combretaceae | Amarillo | TA | High value timber |

first live branch, diameter at breast height (DBH, taken on trees whose main stem was ≥ 1.3 m tall), total height (from the ground to the highest leaf or leaflet, H), height of the lowest leaf or leaflet, the length of the live crown (CL, taken from the lowest live branch to the tallest leaf), and crown diameter (CD, mean of two perpendicular measures).

2.2.2. Tree harvest

The biomass measurements were based on the biomass subsampling method outlined by Snowdon et al. (2002), which was adapted, where necessary, to the crown morphologies of our subject species. We first determined fresh weights of main stems, branches and leaves in the field immediately after cutting. These components were weighed on a hanging spring-loaded balance with an accuracy of ± 25 g. An electronic top-loading balance with an accuracy of ± 0.01 g was preferred for tissue fractions weighing < 500 g.

As leaves may differ in area and thickness according to their canopy location, the crown was separated into three parts (bottom, middle and top) to sample the full range of leaf properties (Snowdon et al., 2002). The smallest trees, which were 1.5 m or less in height, and those whose canopies grew as single layers near the apex of the trunk were either not divided or were separated into two parts only. Once removed from the stem, branches were pooled by section (bottom, middle and top of the crown) and weighed. Main stems were weighed separately.

To effectively manage the large amounts of leaves and wood produced by the harvesting, subsamples of each tissue type were taken to calculate wet to dry mass conversion factors (Snowdon et al., 2002). For tree crowns, it was important to choose samples that were representative of the proportion of leaves and branches for the section sampled. Following the recommendations of Snowdon et al. (2002), samples were chosen visually to represent branches from each crown section that were characteristic in terms of the concentration of leaves around branches, numbers of branches and twigs, and the dimensions of the main branch. Leaves were removed from the sampled branches and the wet weight of each component of the sample (leaves and branches) was determined separately.

For monopodial trees, the trunk was defined as the whole length of the stem from soil level to the highest point (including the leader) after removal of the branches. The trunk of monopodial trees was separated into three parts of equal length, and weighed before taking cross-sectional samples to determine oven-dry weight. When a tree had two or more major branches sprouting from the base or close to the base, it was considered a multistemmed tree. In these cases, principal stems could not generally be defined, and all branches identified as “multistem” were weighed together.

Stem subsamples consisted of two cross-sections (cookies) of 3 cm in width that were cut on each side of the center of mass of each stem section to compensate for variations in stem form and wood density. These cookies were weighed immediately after cutting and before drying. Multistem subsamples consisted of two portions of approximately 20 cm from each major stem (one from the upper and one from the lower part of the branch). When large numbers of stems were present in multiple stemmed trees (e.g. *Diphysa robinoides*), we selected a representative subsample of stems based on their length, diameter, and their total number. Two portions of approximately 20 cm from each selected multistem were taken and processed in the same way as monopodial stem cookies.

No field work was done during or immediately after rain to avoid biasing the fresh weight determinations due to tissue wetting. Tissues were processed immediately after being cut to avoid drying of the fresh material (Snowdon et al., 2002). After transport from the field site, samples were initially placed in a low humidity storage room to avoid decomposition or the growth of mould. They were

then dried to constant weight at 65 °C in an industrial wood drying kiln and weighed.

After drying, subsamples were weighed with the electronic balance. Dry to wet mass conversion factors were calculated, and used to extrapolate from wet to dry weights of each tree compartment. From the dry weight/fresh weight ratio of each stem, branch and leaf sample, a proportion was calculated to determine dry biomass of the compartment from the fresh weight using the following formula:

$$DW_c = \left(\frac{DW_s}{FW_s} \right) \times FW_c \quad (1)$$

where DW_c = dry weight of a section of a compartment, FW_c = fresh weight of the same section, DW_s = dry weight of the subsample and FW_s = fresh weight of the same subsample (Snowdon et al., 2002). Section biomasses calculated using Eq. (1) were summed to obtain estimates of the total dry biomass of leaves, branches and trunk for the whole plant.

2.3. Statistical analysis

Based on previous work and experience (e.g. Wishnie et al., 2007), we expected to observe obvious interspecific differences in biomass accumulation in our diverse species pool. We therefore focussed our analysis on intraspecific differences in biomass partitioning between Río Hato (dry regional climate) and Soberania (humid regional climate). We used non-parametric Wilcoxon rank sum tests to analyze intraspecific differences in total biomass between sites. Wilcoxon rank sum tests were also used to analyze site differences in biomass partitioning to leaves, branches and stems. Because some species were represented by relatively low sample sizes at Río Hato, we chose an alpha level of 0.1 as the critical Type I error rate against which to measure statistical significance.

We predicted that the partitioning of biomass to different plant tissues would change with overall plant size to meet physical and mechanical constraints. Size effects on biomass partitioning should therefore be removed from the data if we are to fully understand the effects of environment on the distribution of tissues within a plant. We therefore transformed raw biomass and mensuration data using an Aitchison log ratio transformation (Aitchison, 1986) to control for the effect of tree size on relative biomass partitioning (Eq. (1)):

$$y_{ij} = \log x_{ij} - \frac{1}{p} \sum_i^p \log x_{ij} \quad (2)$$

where y_{ij} is the adjusted value of the j th trait in the i th individual, p is the number of characters included in the analysis, and x_{ij} is the unadjusted value of trait j in the i th individual (Peres-Neto and Magnan, 2004). An Aitchison-transformed variable is therefore standardized with respect to the average value of all (log-transformed) measurements or traits under consideration. The Aitchison transformation has the statistical advantage of maintaining the independence of individual variables while using a composite of several related variables to develop a global measure of size (Peres-Neto and Magnan, 2004).

We performed separate Aitchison transformations on above-ground biomass components: leaves, branches and trunks, and on mensuration data: DBH, BD, H, CL, and CD. Intraspecific differences in Aitchison-transformed biomass components were investigated using Wilcoxon rank sum tests, as described earlier. The transformed mensuration variables were tested against their non-Aitchison-transformed equivalents for their ability to act as simple predictors of total biomass on pooled species data from the two sites. Basal diameter and height were used as simple predictor

variables. Diameter at breast height (DBH) was also used as a predictor for those trees that were taller than 1.5 m. We also tested two ratio variables – the diameter: height ratio and the live crown (crown length:crown height) ratio (LCR) for their predictive power. Raw diameter height ratios and LCRs were arcsin square root transformed. Aitchison-transformed ratio variables were constructed by deducting one from the other because subtraction on logarithms is equivalent to division.

We used exploratory analyses of covariance (ANCOVA) to determine whether each mensuration variable had a similar predictive relationship with biomass at the two sites. In the event that the site by covariate interaction term was significant, we used separate regressions with comparisons of slopes (Zar, 1996) to probe the relationship of mensuration variables to total biomass. As sample size was relatively higher for regression analyses made on pooled species, an alpha of 0.05 was appropriate.

3. Results

3.1. Biomass accumulation and partitioning among species and sites

Overall, trees at Río Hato achieved only 60.8 ± 48.9 percent of the biomass of those growing at Soberania. Seven of the 18 species had significantly greater total biomass at Soberania (Wilcoxon rank sum test, $P \leq 0.1$). These species: *Colubrina glandulosa*, *Diphyssa robinoides*, *Dipteryx panamensis*, *Erythrina fusca*, *Ochroma pyramidale*, *Tabebuia rosea*, and *Terminalia amazonia*, had greater total biomass at Soberania than at Río Hato (Fig. 1). Only three species: *Albizia guachapele*, *Enterolobium cyclocarpum*, and *Samanea saman* had greater average biomass at Río Hato than at Soberania, but these differences were not statistically significant.

Eight species displayed significant differences in at least one of stem, branch, or leaf biomass, and in five species, differences were observed in the biomass of all three compartments (Wilcoxon

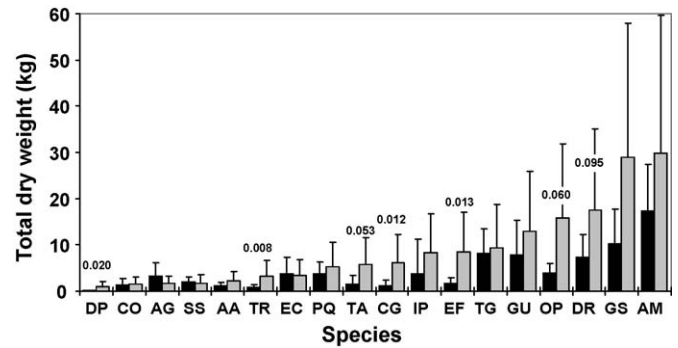


Fig. 1. Comparison of total dry biomass of 18 tree species at Río Hato (black bars) versus Soberania (grey bars). Error bars represent standard deviations of the mean. The numbers above selected error bars are Type I error probabilities returned by Wilcoxon rank sum tests. Species acronyms are as described in Table 1.

rank sum test, $P \leq 0.1$; Fig. 2). *C. glandulosa*, *E. fusca*, *O. pyramidale*, *T. rosea*, and *T. amazonia* had significantly greater biomass in all three compartments at Soberania. *Gliricidia sepium* displayed significant difference in stem biomass alone, while *D. robinoides* and *D. panamensis* had greater stem and leaf biomass at Soberania.

3.2. Effects of size on biomass partitioning

Intraspecific comparisons of Aitchison-transformed biomass demonstrated differing levels of relative investment into tissue compartments at Soberania versus Río Hato. Unlike the untransformed biomass compartments, relative investment in different tissues was sometimes significantly greater at Río Hato than at Soberania (Wilcoxon rank sum tests, $P \leq 0.1$; Fig. 3). For example, *C. glandulosa* invested relatively more resources in leaves at Soberania, but fewer resources in trunks and *D. robinoides* invested more resources into leaves and branches at Río Hato, but fewer resources in trunks.

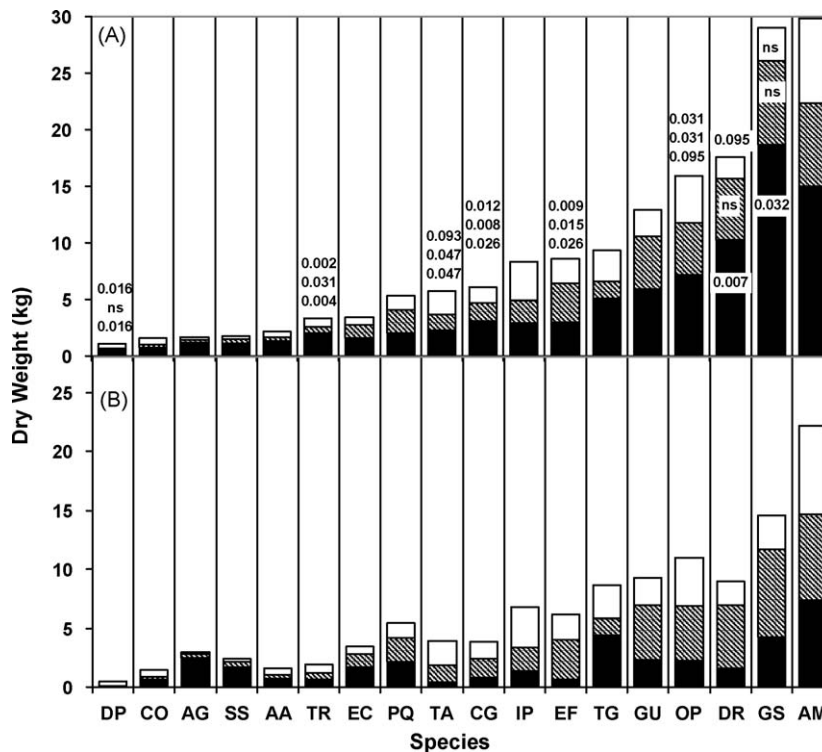


Fig. 2. Comparison of raw biomass allocation to trunks (black), branches (hatched) and leaves (clear) among 18 tree species between (a) Soberania and (b) Río Hato. Significance figures for Wilcoxon rank sum tests follow the same ascending order as the bar plots for tissues. Species acronyms are as described in Table 1.

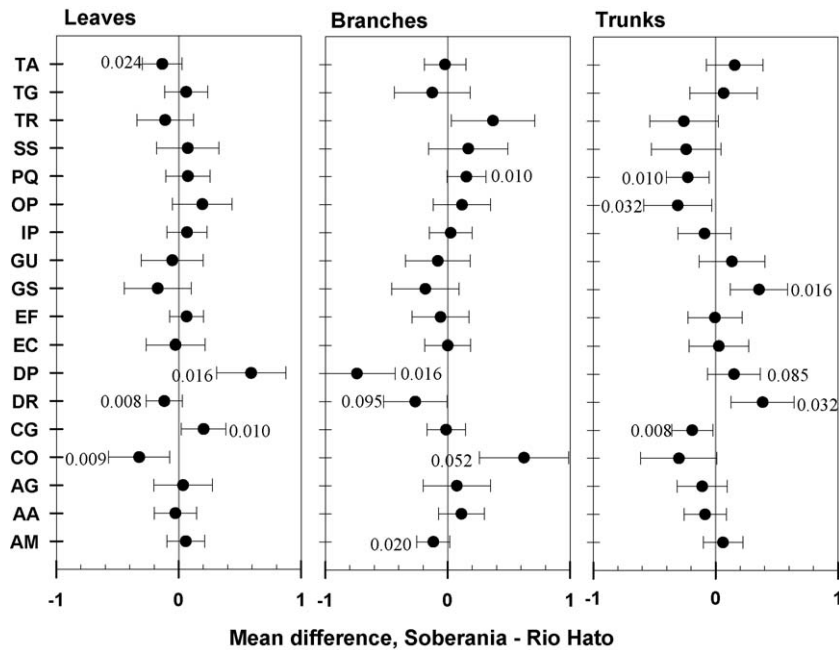


Fig. 3. Mean differences in Aitchison-transformed tissue biomasses for leaves, branches, and trunks. Dark circles are the differences between treatment means (Soberania minus Río Hato), and error bars represent standard errors of the difference between means. Significance figures for each species and tissue tested for intraspecific differences between sites using Wilcoxon rank sum tests. Species acronyms are as described in Table 1.

Although 11 of the differences in untransformed biomass partitioning were eliminated by the Aitchison transformation, seven new differences were recorded (see Figs. 2 and 3). Thus, both *D. robinoides* and *D. panamensis*, species with very different crown architectures, invested relatively more resources in branches at Río Hato than at Soberania. *Acacia mangium* and *Cedrela odorata*, neither of which had significant differences in absolute biomass partitioning between sites, invested relatively more in branches at Río Hato (*A. mangium*), and in leaves at Río Hato and branches at Soberania (*C. odorata*). Similarly, *T. amazonia*, another tree with no site differences in absolute biomass, invested relatively more biomass in leaves at Río Hato compared to Soberania.

3.3. Predicting biomass from biometric traits

The slopes of biometric trait – \log_{10} -transformed total biomass relationships were parallel for both Aitchison-transformed and non-Aitchison-transformed variables (site by covariate interaction, $P > 0.05$ in every case). Subsequent ANCOVAs conformed to the assumptions of parametric analyses (Levene's test for equality of error variance, $P > 0.05$, residuals normally distributed). All of the simple biometric variables, except for arcsine square root-transformed BD:height ratio, had significant positive relationships with \log_{10} transformed total tree biomass (F -test, $P \leq 0.05$; Fig. 4a–e, and Supplemental Tables S1 and S2). Aitchison-transformed BD and height were also significantly related to biomass, but had negative slope coefficients (Fig. 4a and b; Table S2), indicating a greater investment in diameter and height growth (relative to other mensurational traits) among small trees at both sites.

\log_{10} -transformed basal diameter was the most robust predictor of total tree biomass, followed by height and DBH. There was no effect of site for either BD or DBH, which indicated congruence of the regression slopes. Slope coefficients on pooled data from both sites were highly significant for these variables (BD: $F_{1,178} = 478.3$, $P \leq 0.001$, $R^2 = 0.73$; DBH: $F_{1,161} = 177.04$, $P \leq 0.001$, $R^2 = 0.52$). A significant site effect was present in ANCOVAs that included \log_{10} -transformed height, and Aitchison-transformed BD and height

(Fig. 4a and b). \log_{10} -transformed height was a relatively strong predictor of biomass at both Río Hato ($F_{1,83} = 176.7$, $P \leq 0.001$, $R^2 = 0.68$) and Soberania ($F_{1,94} = 238.2$, $P \leq 0.001$, $R^2 = 0.72$). In the case of Aitchison-transformed BD and height, the slopes of the covariate–biomass relationship were negative. Therefore, after subtracting the effect of size, increased relative investment in BD or height growth was associated with lower total tree biomass.

Variables other than BD and height were relatively weak predictors of total biomass. Regressions of Aitchison-transformed DBH and BD:height ratio versus biomass were non-significant, and returned R^2 values of less than 0.02 at both sites (Fig. 4c and e). Non-significant regressions were also recorded for arcsine square root-transformed BD:height ratio versus biomass (Fig. 4e). This variable therefore had no detectable relationship with biomass across a range of species either as a function of size or as a function of relative resource partitioning. Finally, regressions of Aitchison-transformed LCR versus biomass returned slopes with opposite signs for Río Hato ($y = 3.13 - 0.71 \times \text{LCR}$) and Soberania ($y = 3.95 + 1.091 \times \text{LCR}$), although the slope coefficient for Río Hato was not significant ($P = 0.074$). The equivalent relationship of biomass with arcsine square root-transformed LCR was positive at both sites (Río Hato: $F_{1,83} = 42.42$, $P \leq 0.001$, $R^2 = 0.34$; Soberania: $F_{1,94} = 37.53$, $P \leq 0.001$, $R^2 = 0.29$; Fig. 4d).

4. Discussion

4.1. Biomass partitioning

The large differences in total biomass that were observed in this study can be attributed to the divergent regional climates and local characteristics of the sites where the trees were grown (Fig. 1). Factors that could have limited tree growth at Río Hato versus Soberania include an appreciably longer dry season (6.7 months at Río Hato versus 4.1 months at Soberania), rainless periods of up to three weeks at Río Hato during the rainy season (A. Park, personal observation), and localized areas of degraded soils. The long dry season may have affected photosynthetic activity by increasing

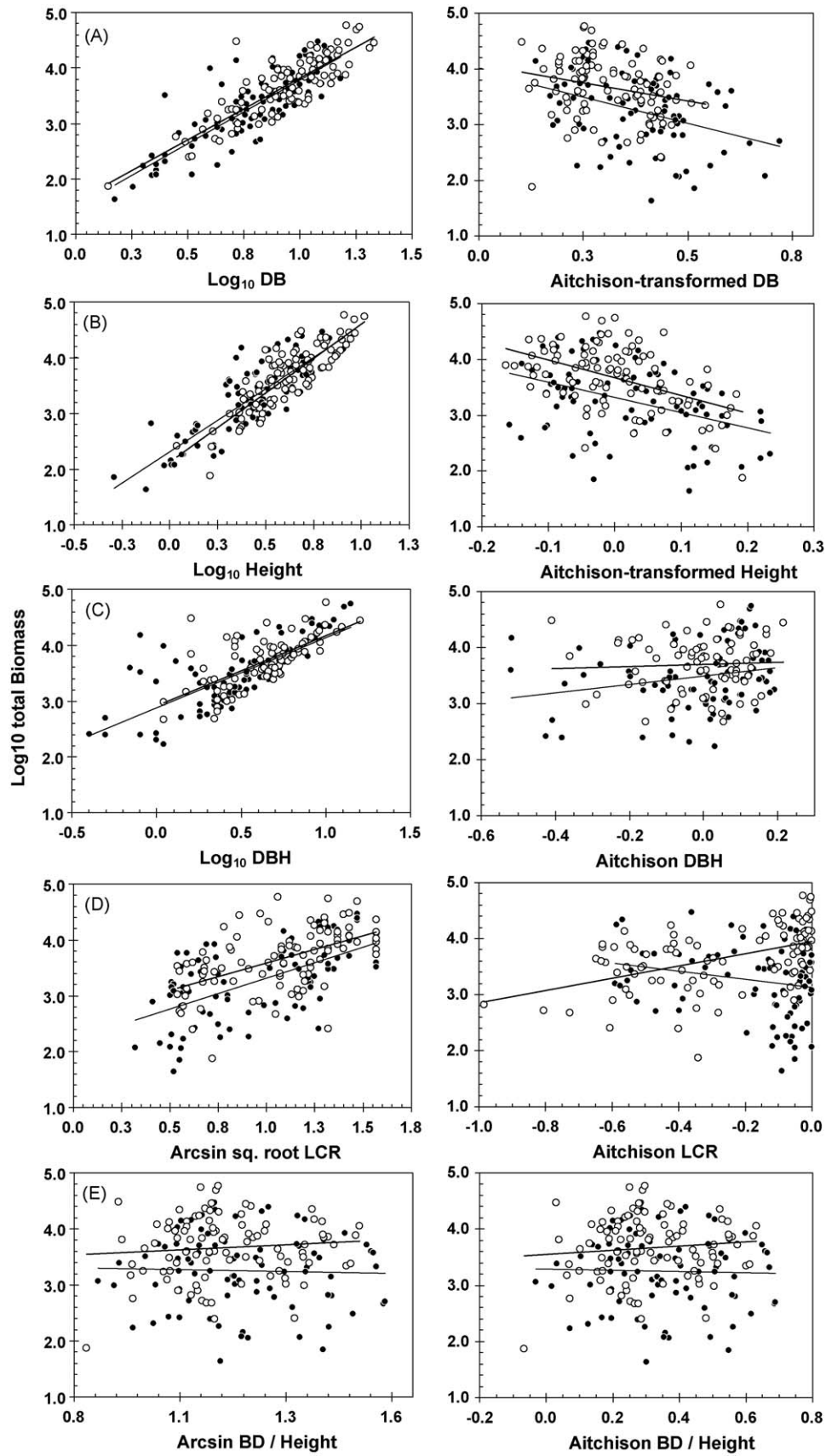


Fig. 4. Comparison of relationships of simple mensuration variables (left hand graphs) with Aitchison-transformed mensuration variables (right hand graphs) at Rio Hato (black circles, thin trend lines) and Soberania (open circles, bold trend lines). (A) Basal diameter, (B) Height, (C) DBH, (D) LCR, and (E) basal diameter: height ratio. Results of linear regression analyses are summarized in [Supplemental Table S2](#). Note that not all tree species had a DBH value.

the duration of the leafless period for deciduous trees at Río Hato (Coyle and Coleman, 2005). Trees exposed to rainless periods within the rainy season may also shut down photosynthesis to conserve water, and may even shed their leaves during these dry spells (Damour et al., 2008). Soils at Río Hato displayed localized evidence of sheet erosion, including patches of plinthite at the surface, erosion pedestals and gullyng (A. Park, personal observation) that may have restricted water and nutrient availability and root growth.

Relatively few intraspecific differences in the relative partitioning of biomass were observed between sites (Fig. 3), and species were as likely to favour greater partitioning of biomass to crown versus stem at Río Hato as at Soberania. In the absence of detailed physiological measurements, explanations for preferential relative partitioning to one compartment or another are necessarily speculative. For example, *D. robinoides*, a leguminous tree that sprouts multiple stems from close to ground level, may have experienced a relative advantage in nitrogen assimilation from the relatively N-poor soils of Río Hato. In other cases, differences in relative biomass partitioning between sites may have been the result of specific autecological factors or singular events. *D. panamensis*, for example, was often observed to be leafless at Río Hato, and may have had poor tolerance for extended dry periods. However, the relatively greater investment in branches by this species in Río Hato indicated, nevertheless, that the “scaffolding” for photosynthesis was well-developed.

Competition within and between plots is another factor that may have affected relative biomass partitioning. Competition may have been especially important at Soberania, where a number of tree species, including *A. mangium*, *D. robinoides* and *G. sepium* had achieved crown closure by their second year of growth. Under these conditions, relatively greater investment in trunks for *D. robinoides* and *G. sepium* may have been a result of the struggle for adequate light. For the majority of trees, however, we could not conclude that regional environment affected significantly either total biomass, or the relative partitioning of biomass to different tissues. Additionally, relatively small sample sizes for each species that included unequal representation at the two sites may have inflated the Type II error rates of our analyses.

4.2. Biometric traits as predictors of total tree biomass

Basal diameter and height were robust predictors of total biomass for the pooled site data of 18 species. This finding confirms that simple variables that are cheap to measure in the field can be used to predict the total biomass of a disparate collection of species in diverse regional environments. The association of Aitchison-transformed DB and height with lower total biomass (right hand panels of Fig. 4a and b) supports the existence of a strong ontogenetic size effect for these variables. Indeed, it appears that the greatest investment in both DB and height relative to other linear and ratio dimensions occurred among species with smaller total biomass at both sites. Given that basal area increases in proportion to diameter squared, we can speculate that smaller trees require relatively more structural support for their frequently top-heavy crowns.

The weak relationships of LCR and BD:height ratio with biomass in our study are not well reflected in the traits literature. Live crown ratio is reported to be a good indicator of both tree relative growth rate (York et al., 2006) and vigour (Ruel et al., 2000), and positive relationships between LCR and tree growth rates have been reported (Scowcroft et al., 2007). It should be noted, however, that much of many detailed analyses of biomass variation with crown traits refer to coniferous trees, in which there is much less variation in crown form than among our heterogeneous collection of tropical hardwoods.

The biomass literature strongly supports the use of diameter to predict biomass. The diameter-biomass relationship is usually expressed as a power function, which is linearized by transforming both biomass and diameter using natural logarithms (Ketterings et al., 2001; Zianis and Mencuccini, 2004). The coefficient of determination in the $\log_{10} \text{BD} - \log_{10} \text{biomass}$ relationship for multiple tree species in our study (0.73) was somewhat lower than reported in a meta-analysis of 13 other studies (~ 0.95 to 0.99 , Zianis and Mencuccini, 2004). The majority of biomass studies have, however, gathered data from only one site (Ketterings et al., 2001), or have been developed separately for each species being analyzed (Saha et al., 2004). Managers in the tropics may not have the luxury of developing species-specific allometric equations for mixed species restoration projects, and therefore, may need to sacrifice a degree of precision to achieve generality. Adding height as a second variable in the allometric equation may add relatively little to the proportion of variance explained, since height and diameter are themselves closely correlated (Ketterings et al., 2001). The addition of height to diameter in the model for our data added only 10% to the original coefficient of determination.

5. Conclusion

The Republic of Panama harbours a number of distinct regional environments in a small geographical space. Significant differences in total biomass and in biomass partitioning to different tissues were recorded in approximately one third of the tree species sampled in two sites representing dry and humid regional environments. In spite of these differences, basal diameter (BD) and height had similar relationships to biomass at both sites, which allowed common regression models to be constructed. Simple measurement, BD or height, can be reasonably successful at predicting biomass in a range of species. Thus a relatively simple metric might be used (at least for 1–3-year-old trees) as a robust predictor of biomass and potentially carbon storage in the tree species that were used. These relationships were largely ontogenetic effects of tree size, and similar regressions of BD and height versus biomass illustrated that relative investment into these variables declined as trees became larger. Relative partitioning of biomass to leaves, branches or trunks also varied between sites, but these differences did not consistently favour greater relative investment at one site or another, which indicates that individual autecological explanations need to be sought for the patterns observed. Future measurements on more mature trees would determine if the effects of site and species would change over time.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2010.04.035.

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