

Linking multiple-level tree traits with biomass accumulation in native tree species used for reforestation in Panama

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Abstract To improve establishment yield and carbon accumulation during reforestation, analyses of species adaptations to local environments are needed. Here we measured, at the individual scale, links between biomass accumulation and multiple-level tree traits: biomass partitioning, crown morphology and leaf physiology. The study was carried out on one- and three-year-old individuals of five tropical tree species assigned to pioneer (P) or non-pioneer (NP) functional groups. Among the species, *Cedrela odorata*, *Luehea seemannii* and *Hura crepitans* showed the greatest biomass accumulation. On our seasonally dry site, species performance during the first year was dependent on a greater investment in above-ground foraging, while performance after three years was mainly related to water relations. However, large biomass accumulations were not simply associated with an efficient

water use but also with contrasting water uses, based on inter-specific relationships. Generally, greater carbon isotope discrimination (Δ_{leaf}) was related to greater allocation to roots. Species with high Δ_{leaf} generally showed high leaf potential nitrogen use efficiency (PNUE), suggesting that lower water use efficiency (WUE) increases the efficiency of photosynthetically active N. Also, PNUE was negatively correlated to leaf mass per area (LMA), implying that photosynthetically active N is diluted as total leaf mass increases. Finally, no distinction in measured traits, including biomass accumulation, was observed between the two functional groups.

Keywords Biomass partitioning · Crown morphology · Functional groups · Nitrogen use efficiency · Water use efficiency

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Introduction

Reforestation is increasingly widespread in the tropics to mitigate heavy harvesting of primary forests and to restore degraded and abandoned lands (e.g., Hartshorn 1989; Lamb 1998; Hagggar et al. 1998; Carpenter et al. 2004a; Carpenter et al. 2004b). Furthermore, in the context of the Kyoto protocol, establishing plantations on land deforested before 1990 is an acceptable way to sequester carbon (Stier and Siebert 2002), especially since tropical plantations of fast-growing species are recognized as important sinks of carbon (Nabuurs and Mohren 1995; Kraenzel et al. 2003). However, in some cases, poor adaptation of exotic species to climate variation, local pests, or edaphic conditions has resulted in surprisingly low yields (Hagggar et al. 1998).

In Panama, as in other tropical regions of Central America, the establishment of mixed- and native-species

plantations is on the rise (Haggar et al. 1998; Carpenter et al. 2004a, b; Piotta et al. 2004), although plantations of exotic and faster growing species tend to be the norm in reforestation efforts. Indeed, based on the inherent adaptation of native species to local climate, such plantations can also help in meeting the critical new concerns for (1) the restoration of local biodiversity and (2) the recovery of the original forest community structure. Nevertheless, given the very large number of native tree species available, analyses of species performance and potential carbon storage are needed to improve and better control the establishment and yield of such plantations.

Biomass estimates can be derived from allometric equations (Nelson et al. 1999; Chave et al. 2001; Ketterings et al. 2001) to evaluate and compare carbon storage capacity of species. Analyses of individual traits, such as biomass partitioning, tree morphology and leaf physiology, are then essential in explaining inter-specific differences in biomass accumulation, since they are responsible for the integrated response of individuals (Givnish 1988). Moreover, the assessment of structural and functional traits generally provides information on species functional groups (cf. Bazzaz 1979; Reich et al. 1998; Ellis et al. 2000; Cornelissen et al. 2003; Poorter and Bongers 2006), an important criterion in species selection for plantations. Species functional groups are commonly defined by patterns of recruitment, growth and mortality that have been observed in the gap dynamics of old-growth forests (Canham et al. 1990; Denslow et al. 1990; Chave et al. 2001). On the one hand, one could expect pioneer species to be well adapted to open environments such as tree plantations. On the other hand, species performance in these environments might be mostly related to the capture and use of below-ground resources (i.e., water and nutrients) rather than light (Casper and Jackson 1997; Coomes and Grubb 2000; Ricard et al. 2003). This latter hypothesis is supported by the fact that soils in the tropics are often highly variable in terms of their nutrient availability, and seasonally water deficient as well (Vitousek and Sanford 1986; Coomes and Grubb 2000; Ricard et al. 2003). Thus, selection of species to be used for large scale reforestation in open landscape needs to be informed by studies of species performance, individual traits, and functional groups.

The objectives of the study were: (1) to link biomass accumulation with multiple-level traits that were related to resource capture and use by a suite of species which were used in reforestation trials, and (2) to analyze species choices, based on their biomass accumulation and functional group classification.

To meet the first objective, biomass partitioning, crown morphology and efficiencies of leaf N and water uses were measured. Both potential photosynthetic nitrogen use

efficiency (PNUE_{max}), which is the ratio of leaf maximal assimilation rate (A_{max} $\mu\text{mol m}^{-2} \text{s}^{-1}$) over leaf nitrogen content expressed on an area basis (N_{a} g N m^{-2}), and leaf carbon isotope discrimination (Δ_{leaf}), which is linearly related to leaf long-term WUE, are traits relating leaf efficiency to use of below-ground resources. Potential nitrogen use efficiency and WUE have been found to be very different among species, age classes and functional groups (e.g., Martinelli et al. 1998; Poorter and Evans 1998; Hikosaka and Hirose 2000; Bonal et al. 2000; Ryan et al. 2000). Thus, we hypothesize that species performance in a young tropical plantation will be related to efficient leaf water and nitrogen use, since leaf physiology is of greater importance than allocational traits in open areas (Valladares et al. 2000).

As a second objective, we analyzed whether performance of various species in a plantation environment is related to their functional groups. With respect to the five studied species, we defined two functional groups (pioneer and non-pioneer) from observed growth in forest gap environments (i.e., from the permanent 50 ha plot of Barro Colorado Island and a literature review). Since light is not a limiting factor in plantations, we expected that pioneer species would be better suited for reforestation than non-pioneer ones.

Materials and methods

Study site and species

The study was carried out in an experimental plantation located in a pasture close to Sardinilla (Colon, Panama, 9°18'22N, 79°38'00W). The site was covered with moist tropical forests similar to those found on Barro Colorado Island (BCI) until the early 1950s, when the forest was slashed (Potvin et al. 2004). The new landowner used the land for subsistence agriculture for a few years before turning the fields into pasture. The topography of the site is one of gently rolling hills with a total elevational change of about 5 m over the 6 ha of the plantation. The bedrock is limestone, overlain by clayey soils that are classed as Typic and Aquic Tropudalfs (Potvin et al. 2004). Mean annual precipitation in Sardinilla is similar to BCI with 2,350 mm concentrated over the wet season (May–November), while mean annual temperature is 25°C (Scherer-Lorensen et al. 2005). The landscape around the plantation is largely pasture with one 15-year-old teak (*Tectona grandis*) plantation and riparian forests along the nearby streams within a radius of 500 m from the plantation.

In 1998, a preliminary reforestation trial was established in Sardinilla using 16 native species selected for their local economic and ecological value. This preliminary trial lies

Table 1 Details on the five selected native tree species used in the Sardinilla plantation (Panama) for the evaluation of growth performance and carbon storage potential

Species	Family	English name	Spanish name	Distribution	Relative growth rate (per year)	Economic uses
<i>Cedrela odorata</i> (Co)	Meliaceae	Spanish cedar	Cedro	On the Pacific coast from Mexico to Argentina	2.3%	High timber value for furniture and housing
<i>Tabebuia rosea</i> (Tr)	Bignoniaceae		Roble savano	From Mexico to tropical South America (Venezuela)	3.4%	High timber value for furniture, Ornamental
<i>Hura crepitans</i> (Hc)	Euphorbiaceae	Sand-box tree	Tornador	From Central America to northern Brazil and Bolivia	4.9%	Medium timber quality (for heavy construction)
<i>Anacardium excelsum</i> (Ae)	Anacardiaceae	Wild cashew	Espavé or Espavel	From Mexico to tropical South America	5.9%	Good timber value for furniture, Canoes
<i>Luehea seemannii</i> (Ls)	Tiliaceae		Guácimo colorado	From Mexico to Argentina	9.1%	High timber value for furniture and flooring

100 m south of the biodiversity plantation. Five of the 16 species were chosen to establish the main Sardinilla experimental plantation in 2001, based on their range of relative growth rates (cf. Table 1). *Cedrela odorata* L. (Co) and *Tabebuia rosea* Bertol. (Tr) were categorized as NP species, while *Hura crepitans* L. (Hc), *Anacardium excelsum* Bert and Balb ex Kunth (Ae), *Luhea seemannii* Tr. and Planch. (Ls) and *Cordia alliodora* (Ruiz and Pavon) Oken (Ca) were classified as pioneers. On this site, Ca showed very high mortality, and therefore, was excluded from the present study. Both Co and Tr have been classified as shade-intolerant and non-pioneer species (Elias and Potvin 2003; Poorter and Bongers 2006). However, these two species (especially Tr) are also known to be capable of tolerating shade (Condit et al. 1996; Hooper et al. 2002). The other three species (Hc, Ae and Ls) have the fastest growth rates (Table 1) and are apparently capable of colonizing relatively large forest gaps (Croat 1978). *Luhea seemannii* is the only species that was already considered as a pioneer species per se (Welden et al. 1991; Ellis et al. 2000; Hooper et al. 2002).

Seedlings were provided by a nursery (Geoforestal S.A., Santa Maria de la Pintada, Panama). Mean individual height at planting was about 30 cm and did not significantly differ among the five species. The plantation was established in two distinct stages. The first plantation was established in July 2001 and consisted of 24 plots with 225 trees per plot. Four plots were randomly assigned to six species, including the five studied species. Planting was done with 3 m spacing between and within rows. The second plantation was established in July 2003 with similar planting density and consisted of eight plots with a mixture of 16 species, including the five being studied. Species location within each plot was randomized. No site

preparation was performed before planting, but the competing vegetation was cut each year to the ground in a 1 m circle around each tree base using a machete.

All measurements were performed in October 2004, during the wet season. After one year of growth in the second plantation (i.e., the 1-year-old plantation), it was assumed that neighbour influence had not yet been established, suggesting that the measured trees were in an environment similar to that of 1-year-old trees in the mono-specific plots. A total of 40 3-year-old saplings ($n = 8$ for each species) and 48 1-year-old seedlings ($n = 10$ for each species, except for Hc and Ls, where $n = 9$) were measured. In order to get a realistic sample, individual selection for morphological and physiological measurements was made according to the actual distribution of tree heights within each species and in both age classes. A posteriori analyses showed that, for each species and age, the mean height of the sample was within the 95% confidence interval of the species population height for any given age (data not shown). Individuals were selected in the field after confirmation of no signs of injury or herbivory.

Growth measurements and biomass estimation

Total height and diameter at 10 cm above the ground were recorded for each of the 88 selected individuals. In order to estimate root, branch and total biomass without disturbing the experimental plots, five individuals of each of the five species were harvested in the buffer area of the experimental plots to calculate allometric relations. For each harvested tree, height and diameter at 10 cm above the ground were measured. The height ranges of harvested trees were 0.95–3.03 m for Co, 0.36–2.07 m for Tr,

Table 2 Parameters for allometric relationships used to estimate total biomass accumulation, allocation to branches (BMR) and allocation to roots (RMR) for *Cedrela odorata*, *Tabebuia rosea*, *Anacardium excelsum*, *Hura crepitans* and *Luehea seemannii*

Species	Linear equation parameters								
	$\log(W_t) = a \log(D) + b$			$\log(1 + W_b) = a \log(D) + b$			$\log(W_r) = a \log(D) + b$		
	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>r</i> ²
<i>Cedrela odorata</i> (Co)	3.24	1.09	0.980	9.33	−5.41	0.855	3.57	0.35	0.958
<i>Tabebuia rosea</i> (Tr)	2.64	1.66	0.992	2.79	−0.13	0.580	2.81	1.00	0.984
<i>Anacardium excelsum</i> (Ae)	2.63	1.25	0.993	4.93	−0.97	0.984	2.55	0.56	0.968
<i>Hura crepitans</i> (Hc)	2.52	1.46	0.997	4.74	−1.80	0.950	2.37	0.95	0.986
<i>Luehea seemannii</i> (Ls)	2.67	1.69	0.949	3.02	0.89	0.905	2.43	1.17	0.859

For each relationship, *r*² of the linear fit is presented

D is tree diameter at 10 cm above the soil surface, *W_t* is total tree, *W_b* total branch, *W_r* total root biomass

0.52–2.99 m for *Ae*, 1.15–4.74 m for *Hc* and 0.80–4.75 m for *Ls*. Leaves, branches, the trunk, and roots with diameters >2 mm (manually excavated) were separated, dried and weighed. Allometric equations that were used for biomass estimation are reported in Table 2. From these data, total tree biomass, root mass ratio (RMR%) and branch mass ratio (BMR%) were computed.

Crown morphology

For each of the 88 selected individuals, crown diameter (mean of the greatest diameter and its perpendicular diameter) and crown height were measured and the crown height over diameter ratio (Crown H/D) was calculated. Crown H/D values <1, =1 and >1 refer to flat horizontal, spherical or vertically expanded crowns, respectively.

Gas exchanges and leaf chemistry

Leaf maximal CO₂ assimilation (*A*_{max} μmol CO₂ m^{−2} s^{−1}), maximal stomatal conductance (*G*_s μmol H₂O m^{−2} s^{−1}), and maximal rate of transpiration (*E* mmol H₂O m^{−2} s^{−1}) were measured simultaneously at the beginning of October between 07h00 and 15h00, using a portable gas analyser (LI-6400, LI-COR, Lincoln, Nebraska, USA). For these measurements, one mature full-sun exposed leaf of the youngest cohort was chosen per individual. While measurements were being taken, light was maintained at 1,800 μmol photon m^{−2} s^{−1} of PPFD, leaf temperature was set at 30°C, air CO₂ concentration at 375 μmol CO₂ mol^{−1}, and relative humidity was maintained between 70 and 80%. Measurements were recorded when gas-exchange reached steady-state (i.e., after an initiation period of at least 5 min). Measured leaves were then harvested and six leaf disks were selected to be dried (at 65°C for

48 h) for estimating leaf mass per area (LMA g m^{−2}). Dried leaf disks were then used to measure (1) nitrogen concentration (*N*_m) using an elemental NCS 2500 analyser (ThermoQuest, Milan, Italy), and (2) leaf carbon isotope ratios (δ_p ¹³CO₂/¹²CO₂) by mass spectrophotometry using a CHN analyser coupled with a isotope ratio mass spectrometer (IRMS) at the Grassland Sciences Laboratory, Swiss Federal Institute of Technology (ETH, Zurich, Switzerland). From these measurements, leaf potential nitrogen use efficiency (PNUE μmol CO₂ gN^{−1} s^{−1}) was computed as the result of *A*_{max} divided by the product of LMA and *N*_m. Finally, leaf carbon isotope discrimination (Δ_{leaf}) was computed using the following equation:

$$\Delta_{\text{leaf}} = (\delta_a - \delta_p) / ((1 + \delta_p) / 1,000) \quad (1)$$

where δ_a was the carbon isotope ratio of the atmosphere (assumed to be −8 ‰) and δ_p was the measured carbon isotope ratio of the leaf tissues. Values of Δ_{leaf} are high-quality predictors of long-term leaf WUE, since both parameters are linearly related (Farquhar et al. 1989; Porté and Loustau 2001). Low values of Δ_{leaf} indicate high values of WUE.

Statistical analyses

Statistical analyses were performed using NCSS software (Hintze 2002). ANOVA was used to analyze diameter, height and total biomass as dependent variables, with functional groups and species nested within functional group as the main factors. Similarly, ANOVA was used to compare physiological, crown morphological and whole individual allocational traits as a function of age, functional groups and species (nested within functional groups). In the analyses, allocation and crown morphology traits were standardized? using individual tree height to account for the effects of height on their variability (cf. Delagrange

et al. 2004). Following ANOVA, means were separated using Tukey–Kramer tests. Pearson’s product-moment correlations were computed between specific traits and total biomass accumulation. Linear regressions were fitted to assess: (1) a predictive model used to estimate biomass partitioning among the contrasting tree compartments from the diameter measurements, and (2) the relationships between specific individual traits (RMR, PNUE, Δ_{leaf} and LMA). These latter linear regressions were performed on species means. Each species mean was incorporated into the regression only if the relationship was significant within the species.

Results

Diameter, height and biomass accumulation

No significant differences were reported in diameter, height or total biomass between pioneer and non-pioneer groups of either age class (Table 3). However, significant differences were observed between species within each functional group (FG), except for height of the 3-year-old saplings (Table 3). In the non-pioneer (NP) group, *Tr* has significantly higher height and total biomass than *Co* for 1-year-old seedlings, while the reverse was true for diameter and total biomass in 3-year-old saplings (Fig. 1a, b and c). In the pioneer (P) group, *Ae* had a significantly smaller diameter, height and total biomass than the other species for the 1-year-old seedlings. For 3-year-old saplings, *Hc* had greater diameters than *Ae* and *Ls*, while *Ae* attained a significantly lower total biomass (Fig. 1a, c). With respect to all species (compared in *a posteriori* tests), only the height ranking for 1-year-old seedlings (Fig. 1b) was consistent with expectation, based on previous growth analyses on this site (cf. Table 1), although *Tr* showed slightly greater height growth than expected.

Table 3 Summary of ANOVA results for stem diameter (cm), height (m) and total biomass (g dry biomass) as a function of functional groups (FG) and species [Sp.(FG)]

Source of variation	df	Diameter		Height		Biomass	
		F	P	F	P	F	P
1-year-old							
FG	1	0.05	0.8366	0.23	0.6635	0.02	0.9046
Sp.(FG)	3	6.01	<0.0001	9.21	0.0016	6.78	0.0008
3-year-old							
FG	1	0.02	0.9081	0.05	0.8442	0.84	0.4280
Sp.(FG)	3	4.61	0.0078	0.74	0.5331	4.38	0.0101

Results are presented for 1- and 3-year-old individuals selected from the Sardinilla experimental plantations

Significant effects ($\alpha = 0.05$) are in *bold*

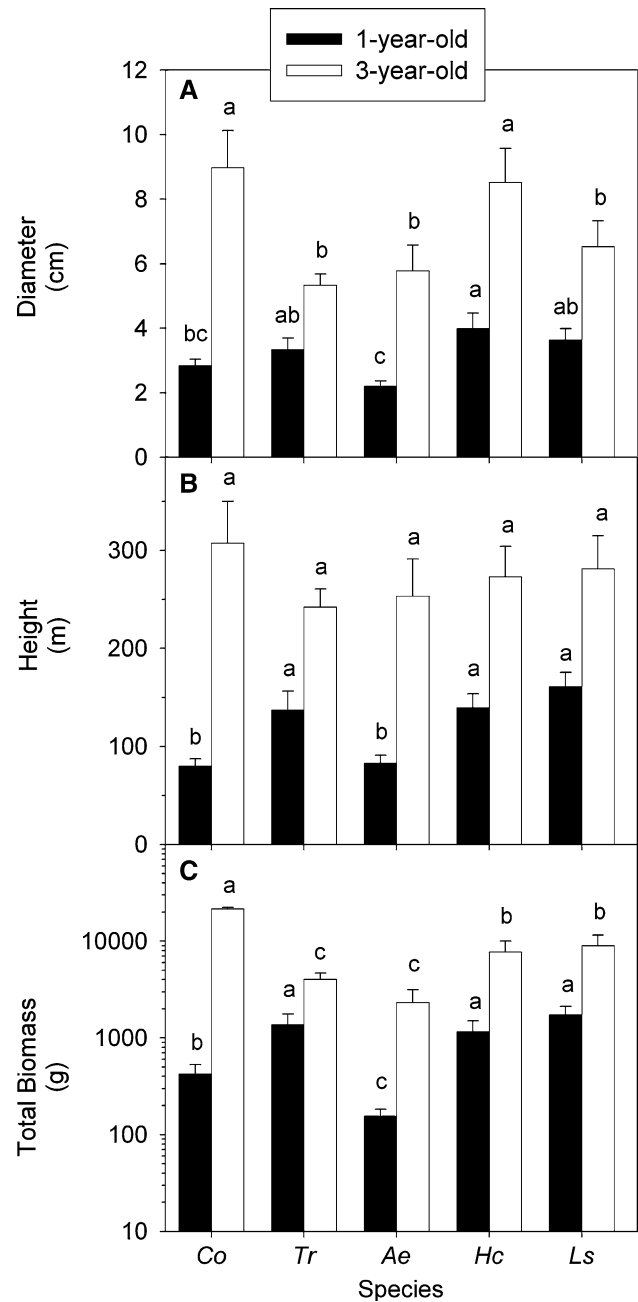


Fig. 1 Means and standard errors for **a** height (cm), **b** diameter (cm) and **c** total biomass (g) in 1-year-old (*open bars*) and 3-year-old (*filled bars*) individuals. Contrasting letters refer to significant differences (at $\alpha = 0.05$) between species for individuals of similar age

Biomass partitioning and crown morphology

As with the growth parameters, no differences were observed when comparing biomass partitioning or crown form between FG, but significant differences were observed between species within each FG, especially after the effect of individual height was taken into account (Table 4). In the NP group, *Tr* allocated more biomass to branches than *Co* and had a more spherical crown

Table 4 Summary of ANOVA results for biomass partitioning (BMR and RMR), crown shape (Crown H/D) and leaf ecophysiology (LMA, NUE and Δ_{leaf}) as a function of functional groups (FG), species [Sp.(FG)], age and their interactions

Source of variation	df	BMR ^a		RMR ^a		Crown H/D ^a		LMA		NUE		Δ_{leaf}	
		F	P	F	P	F	P	F	P	F	P	F	P
FG	1	0.04	0.8461	2.73	0.1972	0.07	0.8120	0.53	0.5199	0.02	0.8998	2.25	0.2305
Sp.(FG)	3	9.18	<0.0001	6.20	0.0008	13.45	<0.0001	24.03	<0.0001	11.64	<0.0001	36.58	<0.0001
Age	1	4.94	0.1127	4.06	0.1374	26.07	0.0145	0.01	0.9967	0.81	0.4345	1.50	0.3077
FG × age	1	0.02	0.8882	1.67	0.2873	0.03	0.8781	0.11	0.7608	1.09	0.3727	0.02	0.9044
SP.(FG) × age	3	5.01	0.0031	8.66	<0.0001	1.15	0.3324	5.43	0.0019	4.91	0.0036	1.66	0.1815

^a Indicates parameters for which a transformation was applied to take into account individual height

Significant effects ($\alpha = 0.05$) are in *bold*

compared to the flat crown of 1-year-old *Co*. After three years, *Co* had a greater proportion of biomass allocated to branches (not significant) and roots than *Tr*, together with a more vertically expanded crown (Fig. 2a–c). In the P group, *Hc* allocated less biomass to branches but more to roots than other species in both 1- and 3-year-old age classes (Fig. 2a, b). *Hc* also had a flatter crown than *Ae* and *Ls*, which had more spherical or slightly vertically expanded crowns (Fig. 2c). Among all species (compared in a posteriori tests) three years after planting, *Ls* showed the greatest allocation to branches and *Co* had the greatest allocation to roots and the most vertically expanded crown.

Leaf structure and ecophysiology

None of the measured leaf traits was significantly different between the two FG (Table 4 and 6). Few differences in leaf traits were observed in the NP group, except for 3-year-old saplings, where *Tr* showed higher leaf nitrogen content (N_{a}), stomatal conductance (G_{s}) and transpiration (E) than *Co* (Table 5). In the P group, *Hc* has the highest maximal assimilation rates (A_{max}), N_{a} , G_{s} and E in 1-year-old seedlings, while those of *Ae* were the lowest (Table 5). For 3-year-old saplings, *Ae* consistently had the lowest values for these four leaf traits, while *Hc* showed similar A_{max} , N_{a} , G_{s} and E than *Ls* (Table 5). In the NP group, leaf mass per area (LMA) and photosynthetic nitrogen use efficiency (PNUE) were lower, and leaf carbon discrimination (Δ_{leaf}) higher, in *Co* versus *Tr* for 1-year-old seedlings (Fig. 3a–c). For 3-year-old saplings, the differences among species were consistent, except where *Tr* had a higher PNUE than *Co*. In the P group, PNUE and Δ_{leaf} were higher in *Ls* than other species in both age classes (Fig. 3b, c). However, *Ae* showed a higher LMA than *Hc* and *Ls* at both ages (Fig. 3a).

Hc had the lowest LMA among species and very low Δ_{leaf} , while *Ls* had the highest PNUE and *Co* the highest Δ_{leaf} among species, and at both ages.

Population trait relationships

For all five species, significant linear relationships (data not shown) were observed between (1) Δ_{leaf} and PNUE, (2) LMA and PNUE, and (3) Δ_{leaf} and RMR (except for *Hc*, which showed no significant relationship between PNUE and LMA). As a result, data were pooled within a given species to draw linear relationships for the five planted species (Fig. 4a, b, c). Among the species under study, (1) when PNUE increased, WUE decreased, (2) when PNUE decreased, LMA increased (*Hc* means were not included since no significant relationships were found between traits for this species, data not shown), and (3) RMR increased with Δ_{leaf} (i.e., with decreasing WUE).

Tree traits, age and biomass accumulation

Pearson's correlation coefficients were computed between individual traits and biomass accumulation as a function of individual age, regardless of species and functional group (Table 7). For 1-year-old seedlings, greater biomass accumulation was related positively and significantly to greater BMR and Crown H/D; for 3-year-old saplings, it was correlated to greater RMR, Crown H/D, NUE and Δ_{leaf} (Table 7). As a result, increases in biomass accumulation for 1-year-old seedlings were associated with a higher above-ground foraging potential, whereas higher biomass accumulations for 3-year-old saplings were more closely related to leaf NUE and water consumption issues (i.e., RMR and WUE) (Table 7).

Discussion

Species growth and resource use efficiency in tropical plantations

Our first objective was to compare species using some of the traits associated with resource capture and use, while trying

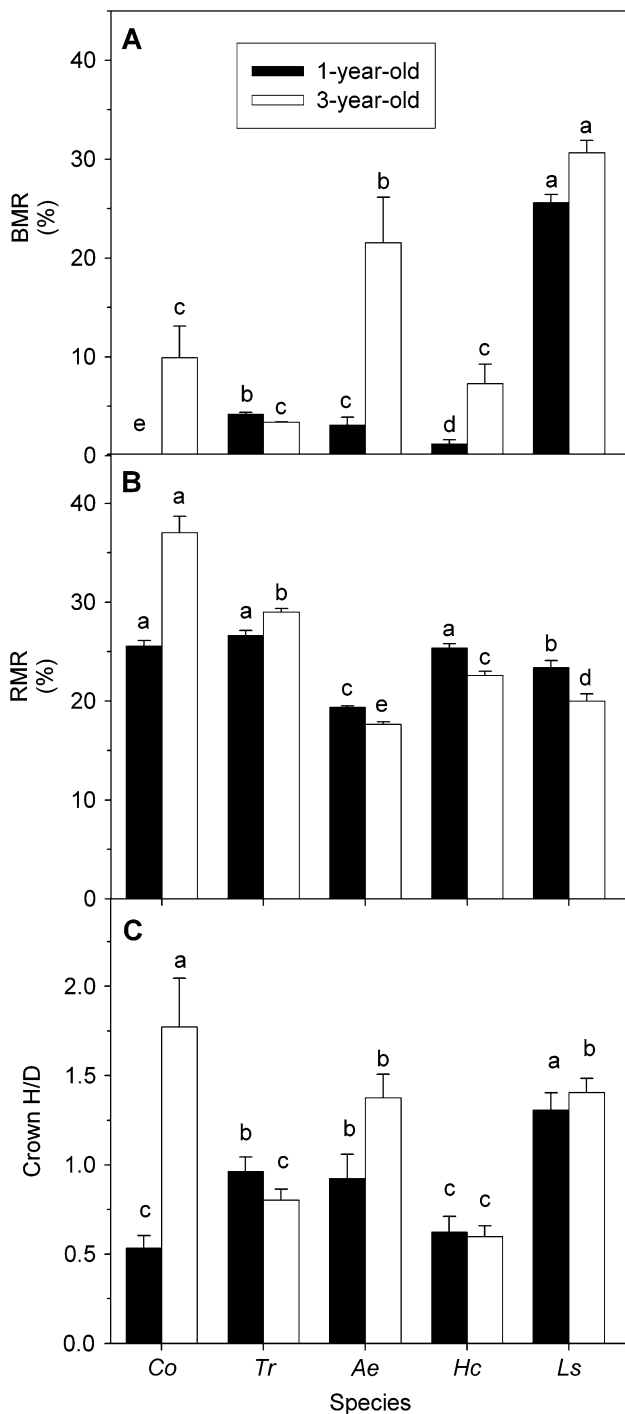


Fig. 2 Means and standard errors for **a** branch mass ratio (BMR), **b** root mass ratio (RMR) and **c** crown height over diameter ratio (Crown H/D) in 1-year-old (*open bars*) and 3-year-old (*filled bars*) individuals. Contrasting letters refer to significant differences (at $\alpha = 0.05$) between species for individuals of similar age

to better understand the relationship between these traits and species performance. Because all individuals were grown in an environment where light was not a limiting factor, particular attention was given to individual

efficiency in the use of below-ground resources. Traits associated with better growth apparently changed with ontogeny. For 1-year-old seedlings, biomass accumulation was significantly related to traits that improved above-ground space exploration and light use by leaves. Conversely, for 3-year-old saplings, growth accumulation was more strongly correlated to traits dealing with water uptake and use. It follows that performance at the establishment stage is critically associated with the interception and use of light by more branches, a wider crown and an efficient use of leaf N for photosynthesis, while longer term performance seems to be related more to patterns of water use. A possible limitation of our experimental design is that the age factor contains contrasting plantation-specific characteristics (e.g., soil or hydrology). Indeed, Healey (2007) reported that environmental variation within the 2001 plantation explained around 50% of tree performance. However, care was taken to establish both plantations in similar terrain, to encompass the same range of topographical variation. Therefore, we are confident that the differences we observed between 1- and 3-year-old individuals are independent of these environmental characteristics.

Dependence of leaf or tree productivity on water use has already been observed in tropical ecosystems, especially when water availability is seasonally restricted (Ares and Fownes 1999; Brodrigg et al. 2002; Santiago et al. 2004; Brien and Zuidema 2005). A recent study (Wüth et al. 2005) concluded that the growth of 17 tropical tree species (including *Ae* and *Ls*) during the dry season was clearly not limited by C availability. Similarly, Casper et al. (2005) reported that, in a dry environment, individual selection based on WUE occurred year by year in a natural population of *Cryptantha flava* because of the pressure of uncertain water availability. Although seasonal drought occurs in Sardinilla, it was not possible to uncover a simple relationship between low Δ_{leaf} (i.e., high WUE) and high growth performance. Indeed, greater growth of some 3-year-old saplings was clearly positively correlated with high Δ_{leaf} , which contradicts Xu et al. (2000). High Δ_{leaf} , however, was achieved on this site through greater biomass allocation to roots. This trend, especially noted for *Co*, allowed this species to maximize photosynthesis to the detriment of water loss. Indeed, higher Δ_{leaf} decreases resistance to CO_2 diffusion into the leaf and thus, increases photosynthetic efficiency of leaf N. Similar relationships have already been reported by Vitousek et al. (1990) and Terwilliger et al. (2001); by facilitating CO_2 entry, photosynthesis per unit of N increases owing to a rise in CO_2 partial pressure at the Rubisco carboxylation site.

Another important trend is that leaf PNUE significantly decreased as LMA increased, with the exception of *Hc*, where the relation was not significant (data not shown).

Table 5 Mean and standard error (SE) for maximal CO₂ assimilation rate (A_{\max}), leaf nitrogen content on an area basis (N_a), stomatal conductance (G_s) and leaf transpiration (E)

Age	Sp. (FG)	A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	N_a (g m^{-2})	G_s ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	E ($\text{mmol m}^{-2} \text{s}^{-1}$)
1-year-old	<i>Co</i> (NP)	11.94 ^c (0.76)	1.62 ^b (0.08)	0.32 ^{bc} (0.02)	4.84 ^{bc} (0.36)
	<i>Tr</i> (NP)	13.81 ^{bc} (0.68)	1.57 ^b (0.14)	0.46 ^b (0.06)	6.42 ^b (0.47)
	<i>Ae</i> (P)	10.68 ^c (0.54)	1.26 ^b (0.06)	0.22 ^c (0.03)	4.01 ^c (0.32)
	<i>Hc</i> (P)	18.69 ^{ab} (1.54)	2.24 ^a (0.21)	0.85 ^a (0.10)	8.43 ^a (0.52)
	<i>Ls</i> (P)	16.50 ^a (0.70)	1.46 ^b (0.09)	0.51 ^b (0.03)	6.37 ^b (0.40)
3-year-old	<i>Co</i> (NP)	13.48 ^{ab} (0.77)	1.44 ^b (0.06)	0.26 ^{bc} (0.05)	3.81 ^{bc} (0.56)
	<i>Tr</i> (NP)	14.16 ^{ab} (1.33)	1.85 ^a (0.12)	0.48 ^a (0.06)	6.21 ^a (0.58)
	<i>Ae</i> (P)	10.69 ^b (0.53)	1.76 ^{ab} (0.06)	0.17 ^c (0.02)	2.67 ^c (0.29)
	<i>Hc</i> (P)	14.99 ^a (0.73)	1.88 ^a (0.09)	0.43 ^{ab} (0.04)	5.61 ^{ab} (0.36)
	<i>Ls</i> (P)	14.97 ^a (0.79)	1.56 ^{ab} (0.06)	0.42 ^{ab} (0.04)	4.52 ^{ab} (0.26)

Means are presented as a function of age and species (Sp.) with reference to their functional group [FG pioneer (P) and non-pioneer (NP)]
Contrasting letters refer to significant differences (at $\alpha = 0.05$) between species within the same age class

This negative relationship has been previously reported for herb, shrub and tree species (Poorter and Evans 1998). Such a dilution of photosynthetically active N as leaf increases its mass per unit area may be related to an increase in C/N ratio, as well as to a higher biomass allocation to cell walls (Onoda et al. 2004). Furthermore, the negative correlation between PNUE and LMA may also explain the lower PNUE reported for leaves that have a lower leaf lifespan (Hiremath 2000). Indeed, leaf lifespan and LMA are closely correlated, so that leaves with a long lifespan allocate more biomass per unit area to improve leaf resistance to external damage (Wright and Westoby 2002). Nonetheless, despite lower PNUE, high CO₂ assimilation rates may be obtained at the leaf or crown level by increasing leaf N content on a mass basis and total leaf area, respectively.

Apparently, species performance in the plantation was associated with differences in combinations of (1) long-term CO₂ diffusion into the leaf (which is highly dependent on root biomass investment) and (2) leaf mass per area (which is associated with leaf lifespan and PNUE). The importance of LMA on species growth in open areas was been reported for numerous late-successional species (Martinez-Garza et al. 2005). Other factors may contribute to the variation in growth performance of these species (Healey 2007). For example, limitation in a given nutrient, or crown shape and leaf organization within the crown volume, were already associated with species performance (e.g., Lewis and Tanner 2000; Valladares et al. 2002; Sterck et al. 2003; Davidson et al. 2004). Here, we observed a positive correlation between crown shape and biomass accumulation. However, considering that plantations in open areas offer an environment where light is not limited, this correlation is more likely to result from the

relationship existing between crown form and (1) crown water conduction potential (Walcroft et al. 1996) or (2) crown self-shading that minimizes evapotranspiration and damage due to excess heat and light (Pearcy et al. 2005). Indeed, crown water relations have already been recognized as a critical factor in limiting tree growth (Ryan and Yoder 1997; Meinzer 2003)

Biomass accumulation and species selection

Growth performance of tropical tree species has been associated with variation in (1) water availability (Condit et al. 1995; Santiago et al. 2004), (2) water use strategies (Casper et al. 2005), and (3) nutrient use efficiency (Hiremath 2000; Hiremath and Ewel 2001; Kitayama et al. 2004). In our experimental plantation site, species performance a few years after establishment seemed to be related to species-specific water use. However, closer examination of the species that accumulated the most biomass (i.e., *Co*, *Ls* and *Hc*), showed that high growth rates were not strictly associated with efficient use of water but with contrasting water uses, which might become an important factor for species co-existence (Drake and Franks 2003).

In our site, *Co* is likely to maximize CO₂ diffusion in order to maintain higher PNUE at the expense of water. However, this was only possible since this species shows a particularly high biomass allocation to roots in order to increase water uptake. It is also noteworthy to mention that this high allocation to roots, typical for shade-tolerant and generally slower growing and non-pioneer species, might explain the delay in its growth observed after one year. A higher allocation to below-ground foraging may indeed reduce primary above-ground growth, but provide better

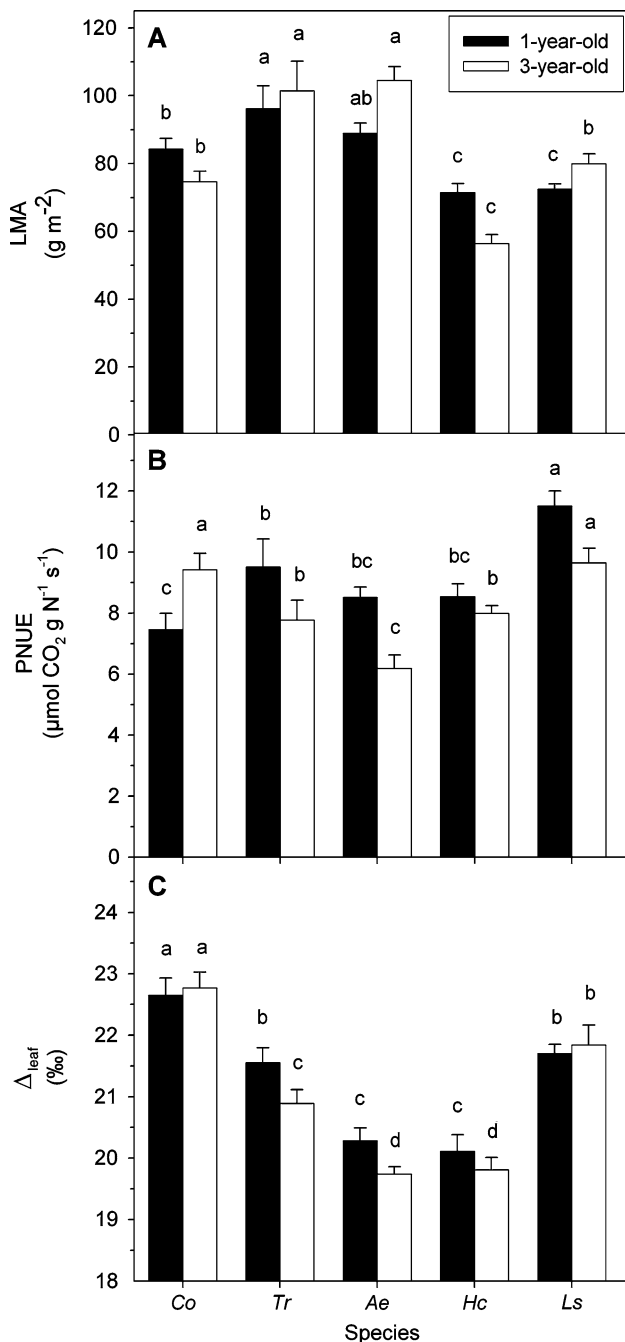


Fig. 3 Means and standard errors for **a** leaf mass per area (LMA), **b** nitrogen use efficiency (NUE) and **c** leaf carbon isotope discrimination values (Δ_{leaf}) in 1-year-old (open bars) and 3-year-old (filled bars) individuals. Results are presented for each species. Contrasting letters refer to significant differences (at $\alpha = 0.05$) between species for individuals of similar age

growth over the longer term. In contrast to *Co* and despite its lower allocation to roots, *Ls* showed a similar low WUE, which was related to a higher PNUe. *Luhea seemannii* surely offset its water requirements through a contrasting root architecture, (i.e., by developing thinner and more ramified roots for very efficient foraging; Ll. Coll,

unpublished data). Furthermore, the high carbon accumulation of *Ls* was obviously also related to its greater allocation to branches and leaves, in that it displayed a very large leaf surface and crown volume for rapid light use. After several years, the particularly dense crown of this species may help in regulating evapotranspiration of a large proportion of its large leaf area through self-shading (Percy et al. 2005). Finally, *Hc* was the most successful species by exhibiting a high WUE but a low PNUE. Compensation for this low efficiency of N was achieved by a high N concentration in leaves, which led to the highest photosynthetic rate on an area basis for species on this site. In addition, *Hc* is possibly able to store large quantities of water in its particularly large trunk, which is shaped like an elephant's foot, buffering periods of limited water availability.

From a carbon accumulation point of view, three species (*Co*, *Ls* and *Hc*) were particularly interesting candidates from which to create plantations with a carbon sink use. From an ecological point of view, using a combination of these contrasting species may also help to maintain (1) a greater diversity of tree species and associated wild life, and (2) a greater diversity of ecological functions. Such diversity has been recognized as critical for greater resilience of ecosystems (Chapin et al. 2000). Furthermore, an additional advantage accrued in using such combinations is the accumulation of biomass in contrasting compartments of the stand; the roots for *Co*, the trunk for *Hc* and branches for *Ls*. In a recent study, Piotto et al. (2004) highlighted the promising contribution of mixed plantations in reforestation since they allowed native species to hold higher growth rates than in pure species plantations and provided a greater range of goods and services. However, it remains difficult to extrapolate and generalize these results to other locations and climates since species leaf traits and efficiencies are highly dependent on other growth-limiting factors (Santiago et al. 2004). More research is thus required to determine the performance of such species (especially in mixed plantations) as a function of a gradient of environmental conditions.

Functional groups

Classification of tree species into functional groups is an approach widely used to simplify and deal with the broad variety of species performances that have been observed in tropical ecosystems (Cornelissen et al. 2003). Among other characteristics, such as seed availability and germination rates, functional groups could be used to select species to be planted in reforestation programs. We hypothesized that, since light is not a limiting factor in plantations, pioneer and shade-intolerant species should be well suited

Fig. 4 Relationships between **a** leaf carbon isotope discrimination ($\Delta_{\text{leaf}} \text{‰}$) and nitrogen use efficiency (PNUE $\mu\text{mol CO}_2 \text{ g N}^{-1} \text{ s}^{-1}$), **b** leaf mass per area (LMA g m^{-2}) and PNUE and **c** Δ_{leaf} and root mass ratio (RMR %). For each relationship, linear regression (dashed line) was performed by pooling all species and ages together. Linear regression for the relationship between LMA and PNUE was performed after removing the *Hc* mean value since the relationship was not significant between these two traits for this species

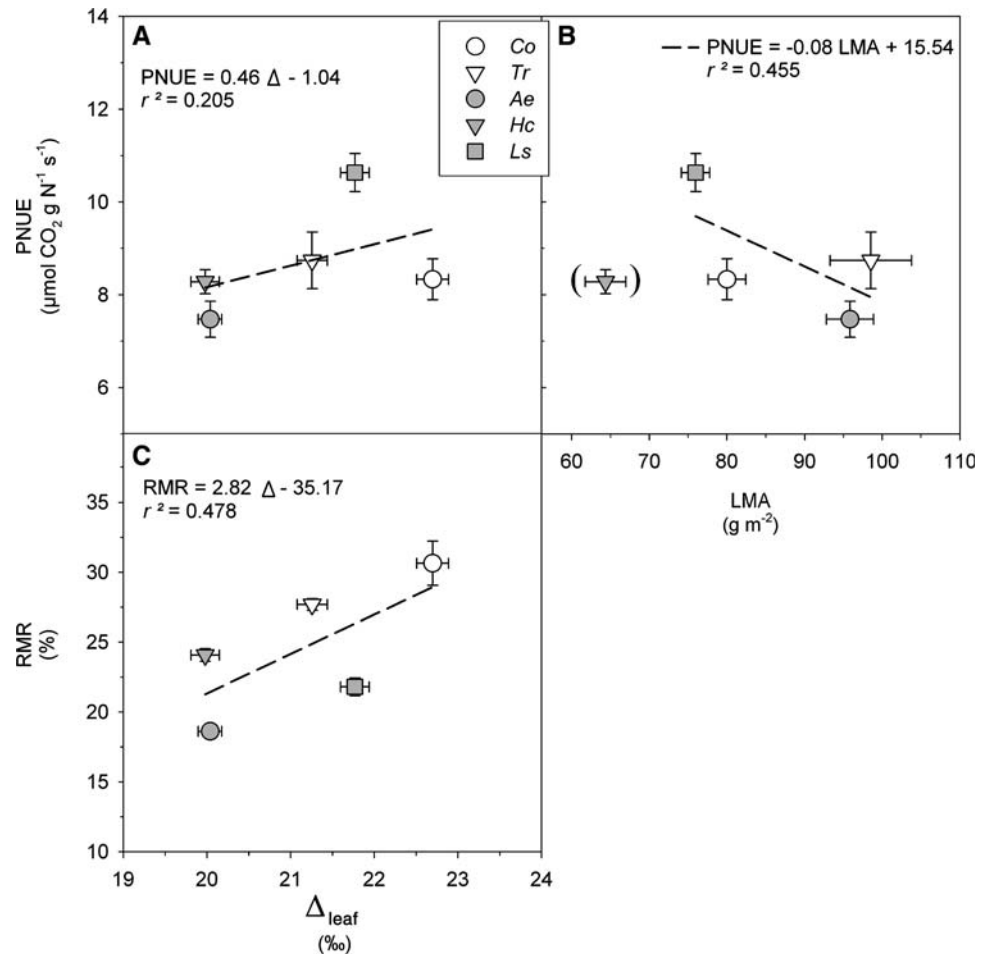


Table 6 Summary of ANOVA results for maximal CO_2 assimilation rate (A_{max}), leaf nitrogen content on an area basis (N_a), stomatal conductance (G_s) and leaf transpiration (E), as a function of functional groups (FG), species [Sp.(FG)], age and their interactions

Source of variation	df	A_{max}		N_a		G_s		E	
		F	P	F	P	F	P	F	P
FG	1	0.15	0.7125	0.07	0.8039	0.06	0.8127	0.01	0.9558
Sp.(FG)	3	19.62	<0.0001	12.05	<0.0001	31.70	<0.0001	32.15	<0.0001
Age	1	0.16	0.7246	0.15	0.7327	1.41	0.3191	10.25	0.0520
FG × age	1	2.57	0.2105	0.02	0.9125	1.02	0.3942	2.62	0.2019
SP.(FG) × age	3	1.58	0.1397	6.13	0.0008	6.27	0.0007	2.08	0.1148

Significant effects ($\alpha = 0.05$) are in *bold*

for such open areas. Nevertheless, no actual differences in growth or biomass accumulation were detected between the P and NP groups on our plantation site. Although only a limited number of species was studied within each group, our results suggest that these NP species may possess individual traits that allow them to be as competitive as P species in open areas. This agrees with one conclusion made by Martinez-Garza et al. (2005), who reported that the absence of late-successional species in open areas may

be related more to the lack of propagules or germination capacity rather than to their inability to grow quickly in open conditions. Together, these results raise some important questions pertaining (1) to the need for comparing species (rather than functional groups) when looking at performance and biomass accumulation potentials in plantation sites, and (2) to limit the use of functional groups as but one criterion for species choices for reforestation.

Table 7 Pearson correlations (r) between total biomass accumulation and biomass partitioning into branch and root compartments (BMR and RMR), crown shape (Crown H/D), and leaf nitrogen and water use efficiency (PNUE, WUE)

	Total biomass			
	1-year-old	3-year-old		
BMR	0.435	**	0.159	ns
RMR	0.205	ns	0.559	***
Crown H/D	0.358	*	0.581	***
NUE	0.043	ns	0.340	*
Δ_{leaf}^a	-0.146	ns	0.490	**

Results are presented for the 1- and 3-year-old populations separately, pooled across species

ns not significant

Levels of significance were $*\alpha = 0.05$; $**\alpha = 0.01$; $***\alpha = 0.001$

^a Δ_{leaf} is inversely related to WUE (Farquhar et al. 1989; Porté and Loustau 2001)

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