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

3

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22 **Key words:** Biomass partitioning, Crown morphology, Functional groups, Nitrogen use  
23 efficiency, Water use efficiency.

24

1 **Abstract:**

2 To improve establishment yield and carbon accumulation during reforestation, analyses  
3 of species adaptation to the local environment are needed. Here we measured, at the  
4 individual scale, links between biomass accumulation and multiple-level tree traits:  
5 biomass partitioning, crown morphology and leaf physiology. The study was carried out  
6 on one- and three-year-old individuals of five tropical tree species belonging to the  
7 pioneer (P) or non-pioneer (NP) functional groups. Among the studied species, *Cedrela*  
8 *odorata*, *Luehea seemannii* and *Hura crepitans* showed the largest biomass  
9 accumulation. On this seasonally dry site, species performance during the first year was  
10 dependent on a greater investment in above-ground foraging while after three years  
11 performance was mainly related to water relations. However, large biomass  
12 accumulations were not simply associated with an efficient water use but also with  
13 contrasting water uses based on inter-specific relationships. Generally, higher carbon  
14 isotope discrimination ( $\Delta_{\text{leaf}}$ ) was related to a high allocation to roots. Species with high  
15  $\Delta_{\text{leaf}}$  generally showed high leaf potential nitrogen use efficiency (PNUE) suggesting that  
16 lower water use efficiency increases the efficiency of photosynthetically active N. Also,  
17 leaf PNUE was negatively correlated to leaf mass per area (LMA), implying that  
18 photosynthetically active N is diluted as total leaf mass increases. Finally, no distinction  
19 in measured traits, including biomass accumulation, was observed between the two  
20 functional groups.

21

1 **Introduction:**

2 Reforestation is increasingly widespread in the tropics to mitigate heavy harvesting of  
3 primary forests and restore degraded and abandoned lands (e.g. Hartshorn 1989, Lamb  
4 1998, Haggar, Briscoe and Butterfield 1998, Carpenter et al. 2004a, Carpenter et al.  
5 2004b). Furthermore, in the context of the Kyoto protocol, establishing plantations on  
6 land deforested before 1990 is an acceptable way to sequester carbon (Stier and Siebert  
7 2002), especially since tropical plantations of fast growing species are recognized as  
8 important sinks of carbon (Nabuurs and Mohren 1995, Kraenzel et al. 2003). However, in  
9 some cases, poor adaptation of exotic species to climate variations, local pests, or edaphic  
10 conditions provides surprisingly low yields (Haggar, Briscoe and Butterfield 1998).

11 In Panama, as in other tropical zones of Central America, although plantations of  
12 exotic and faster growing species tend to be the norm in reforestation efforts,  
13 establishment of mixed- and native-species plantations is on the rise (Haggar, Briscoe and  
14 Butterfield 1998, Carpenter et al. 2004a, Carpenter et al. 2004b, Piotta et al. 2004).  
15 Indeed, based on the inherent adaptation of native species to local climate, such  
16 plantations can also help in meeting the critical new concerns for (i) the restoration of  
17 local biodiversity and (ii) the recovery of the original forest community structure.  
18 Nevertheless, given the very large number of native tree species available, analyses of  
19 species performance and potential carbon storage are needed to improve and better  
20 control the establishment and yield of such plantations.

21 To evaluate and compare carbon storage capacity in species, biomass estimates can be  
22 derived from allometric equations (Nelson et al. 1999, Chave, Riéra and Dubois 2001,  
23 Ketterings et al. 2001). Analyses of individual traits such as biomass partitioning, tree

1 morphology and leaf physiology are then essential, to explain inter-specific differences in  
2 biomass accumulation, since these traits are responsible of the integrated response of  
3 individuals (Givnish 1988). Moreover, the assessment of structural and functional traits  
4 generally provides information on species functional groups (cf. Bazzaz 1979, Reich,  
5 Ellsworth and Walters 1998, Ellis, Hubbell and Potvin 2000, Cornelissen et al. 2003,  
6 Poorter and Bongers 2006), an important criterion for species selection for plantations.  
7 Species functional groups are commonly defined by patterns of recruitment, growth and  
8 mortality observed in the gap dynamics of old-growth forests (Canham et al. 1990,  
9 Denslow et al. 1990, Chave, Riéra and Dubois 2001). On the one hand, one could expect  
10 pioneer species to be well adapted to open environments such as tree plantations. On the  
11 other hand, species performance in these environments might be mostly related to the  
12 capture and use of below-ground resources (i.e., water and nutrients) rather than light  
13 (Casper and Jackson 1997, Coomes and Grubb 2000, Ricard et al. 2003). This latter  
14 hypothesis may be reinforced since in the tropics, soils are often highly heterogeneous in  
15 nutrient availability, and seasonally water deficient (Vitousek and Sanford 1986, Coomes  
16 and Grubb 2000, Ricard et al 2003). Thus, an adapted species selection for large scale  
17 reforestation in open landscape needs to be informed by studies of species performance,  
18 and of the relationship between species performance and individual traits and/or  
19 functional groups.

20 The objectives of the study were: (i) to link biomass accumulation with multiple-level  
21 traits related to resource capture and use for a suite of species used in reforestation trials  
22 and (ii) to analyze species choice based on their biomass accumulation and functional  
23 group classification.

1 To meet the first objective, biomass partitioning, crown morphology and efficiencies  
2 of leaf N and water uses were measured. Both, potential photosynthetic nitrogen use  
3 efficiency (PNUE<sub>max</sub>), which is the ratio of leaf maximal assimilation rate ( $A_{max}$ ;  $\mu\text{mol m}^{-2}$   
4  $\text{s}^{-1}$ ) over leaf nitrogen content on an area basis ( $N_a$ ;  $\text{g N m}^{-2}$ ), and leaf carbon isotope  
5 discrimination ( $\Delta_{leaf}$ ), which is linearly related to leaf long term water use efficiency  
6 (WUE), are traits relating to leaf efficiency to use below-ground resources. PNUE and  
7 WUE have been seen to be very different between species, ages and functional groups  
8 (e.g. Martinelli et al. 1998, Poorter and Evans 1998, Hikosaka and Hirose 2000, Bonal et  
9 al. 2000, Ryan et al. 2000). Thus, since leaf physiology is of greater importance than  
10 allocational traits in open areas (Valladares et al. 2000), we hypothesize that species  
11 performance in a young tropical plantation will be related to efficient leaf water and  
12 nitrogen uses.

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

19

## 20 **Material and Methods**

### 21 *Study site and species*

22 The study was carried out in an experimental plantation located in a pasture close to  
23 Sardinilla (Colon, Panama, 9°18'22N, 79°38'00W). The site was covered with moist

1 tropical forests similar to that of Barro Colorado Island (BCI) until the early 1950 when  
2 the forest was slashed (Potvin et al. 2004). The new land owner used it for subsistence  
3 agriculture for a few years and then turned the fields into pasture. The topography of the  
4 site is one of gently rolling hills with a total change in elevation of around 5 m over the  
5 six-hectares of the plantation. The bedrock is lime and we reported that the soils are  
6 clayey Typic and Aquic Tropudalfs (Potvin et al. 2004). Mean annual precipitation in  
7 Sardinilla is similar to BCI with 2,350mm concentrated over the wet season (May –  
8 November) Scherer-Lorensen et al (2005) while mean annual temperature is 25°C. The  
9 landscape around the plantation is largely pasture with one 15 year-old teak plantation  
10 and riparian forests along the nearby streams within a radius of 500m from the plantation.

11 In 1998, a preliminary reforestation trial was established in Sardinilla using 16 native  
12 species selected for their local economical and/or ecological value. This preliminary trial  
13 lies 100m southward of the biodiversity plantation. Five of these 16 species were chosen  
14 to establish the main Sardinilla experimental plantation in 2001 based on their range of  
15 relative growth rates (cf. Table 1). *Cedrela odorata* L. (*Co*) and *Tabebuia rosea* Bertol.  
16 (*Tr*) were categorized as non pioneer species, while *Hura crepitans* L. (*Hc*), *Anacardium*  
17 *excelsum* Bert & Balb ex Kunth (*Ae*), *Luhea seemannii* Tr. & Planch. (*Ls*) and *Cordia*  
18 *alliodora* (Ruiz and Pavon) Oken (*Ca*) were classified as pioneer. On this site, *Ca*  
19 showed a very high mortality and was therefore excluded from the present study. Both *Co*  
20 and *Tr* have been classified as shade intolerant and non-pioneer species in previous study  
21 (Elias and Potvin 2003, Poorter and Bongers 2006). However, these two species,  
22 especially *Tr*, are also known to be capable of tolerating shade (Condit et al. 1996,  
23 Hooper, Condit and Legendre 2002). The other three species, *Hc*, *Ae* and *Ls* have the

1 fastest growth rates (Table 1) and are apparently capable of colonizing relatively large  
2 forest gaps (Croat 1978). *Ls* is the only species that was already considered as a pioneer  
3 species *per se* (Welden et al 1991, Ellis, Hubbell and Potvin 2000, Hooper, Condit and  
4 Legendre 2002).

5 Seedlings were provided by the nursery, Geoforestal Inc., Panama. Mean individual  
6 height at planting was about 30 cm and was not significantly different among the five  
7 species. The plantation was established in two distinct periods. The first plantation was  
8 established in July 2001 and consists of 24 plots of 225 trees per plot. Four plots were  
9 randomly assigned to six species including the five studied species. Plantation was made  
10 with 3 m spacing between and within rows. The second plantation was established in July  
11 2003 with similar planting density and consists of eight plots with a mix of sixteen  
12 species, including the five studied species. Species location within each plot was  
13 randomized. No site preparation was performed before plantation but the competing  
14 vegetation was cut each year to the ground in a 1 m circle around the tree base using a  
15 "machete".

16 All measurements were performed in October 2004, during the wet season. After one  
17 year of growth in the second plantation (i.e., the 1-year-old plantation), it was assumed  
18 that neighbour influence had not yet established suggesting that measured trees were in a  
19 similar environment to that of a 1-year-old trees in the mono-specific plots. A total of 40  
20 3-year-old saplings (n = 8 for each species) and 48 1-year-old seedlings (n = 10 for each  
21 species, except for *Hc* and *Ls* where n = 9). In order to get a realistic sample, individual  
22 selection for morphological and physiological measurements was made according to the  
23 actual distribution of tree heights within each species and both age classes. A posteriori



1 analyses showed that for each species and age, the mean height of the studied sample was  
2 in the 95% confidence interval of the species population height for any given age (data  
3 not shown). Individuals were selected in the field after confirmation of no signs of injury  
4 or herbivory.

5

#### 6 *Growth measurements and biomass estimation*

7 Total height and diameter at 10 cm from the ground were recorded for each of the 88  
8 selected individuals. In order to estimate root, branches and total biomass without  
9 perturbation of the experimental plots, five individuals of each of the five species were  
10 harvested in the buffer area of the experimental plots to calculate allometric relations. For  
11 each harvested tree, height and diameter at 10 cm from the ground were measured. The  
12 height ranges of harvested trees were 0.95-3.03 m for *Co*, 0.36-2.07 m for *Tr*, 0.52-2.99m  
13 for *Ae*, 1.15-4.74 m for *Hc* and 0.80-4.75 m for *Ls*. Leaves, branches, trunk and roots  
14 with diameter >2mm (manually excavated) were separated, dried and weighed.  
15 Allometric equations use for biomass estimations are reported in Table 2.

16

#### 17 *Crown morphology*

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

22

#### 23 *Gas exchanges and leaf chemistry*

1 Leaf maximal CO<sub>2</sub> assimilation ( $A_{\max}$ ;  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ), maximal stomatal  
2 conductance ( $G_s$ ;  $\mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) and maximal rate of transpiration ( $E$ ;  $\text{mmol H}_2\text{O m}^{-2}$   
3  $\text{s}^{-1}$ ) were measured simultaneously at the beginning of October between 7:00AM and  
4 2:00PM using a portable LI-6400 gas-exchange analyser (LI-COR, Lincoln, Nebraska,  
5 USA). For these measurements, one full sun exposed leaf of the last cohort was chosen  
6 per individual. While measurements were being taken, light was maintained at 1800  $\mu\text{mol}$   
7  $\text{photon m}^{-2} \text{ s}^{-1}$  of PPFD, leaf temperature was set at 30°C, air CO<sub>2</sub> concentration at 375  
8  $\mu\text{molCO}_2 \text{ mol}^{-1}$  and relative humidity was maintained between 70% and 80%.  
9 Measurements were recorded when gas-exchanges reached a steady state (i.e., after an  
10 initiation period of at least 5 minutes). Measured leaves were then harvested and six leaf  
11 disks were selected to be dried at 65°C for 48 hours to estimate the leaf mass per area  
12 (LMA;  $\text{g m}^{-2}$ ). Dried leaf disks were then used to measure (i) nitrogen concentration ( $N_m$ )  
13 using an elemental NCS 2500 analyser (ThermoQuest, Milan, Italia) and (ii) leaf carbon  
14 isotope ratios ( $\delta_p$ ,  $^{13}\text{CO}_2/^{12}\text{CO}_2$ ) by mass spectrophotometry using a CHN analyser  
15 coupled with a IRMS at the Grassland Sciences Laboratory located at the Swiss Federal  
16 Institute of Technology (ETH, Zurich, Switzerland). From these measurements, leaf  
17 potential nitrogen use efficiency (PNUE;  $\mu\text{mol CO}_2 \text{ gN}^{-1} \text{ s}^{-1}$ ) was computed as the result  
18 of  $A_{\max}$  divided by the product of LMA and  $N_m$ . Finally, leaf carbon isotope  
19 discrimination ( $\Delta_{\text{leaf}}$ ) was computed using the following equation:

$$20 \quad \Delta_{\text{leaf}} = (\delta_a - \delta_p)/((1 + \delta_p)/1000) \quad (1)$$

21 where,  $\delta_a$  was the carbon isotope ratio of the atmosphere (assumed to be -8‰) and  $\delta_p$  was  
22 the measured carbon isotope ratio of the leaf tissues. Values of  $\Delta_{\text{leaf}}$  are high-quality  
23 predictors of long-term leaf water use efficiency (WUE) since both parameters are

1 linearly related (Farquhar et al. 1989, Porté and Loustau 2001). Low values of  $\Delta_{\text{leaf}}$   
2 indicate high values of WUE.

3

#### 4 *Statistical analyses*

5 Statistical analyses were performed using NCSS software (Hintze 2002). ANOVA  
6 was used to analyze diameter, height and total biomass as dependent variables and  
7 functional groups and species nested under functional group as main factors. Similarly,  
8 ANOVA was used to compare physiological, crown morphological and whole individual  
9 allocational traits as a function of age, functional groups and species (nested under  
10 functional groups). In the analyses, allocational and crown morphological traits were  
11 normalized using individual tree height to consider the effect of height on the variation of  
12 such parameters (cf. Delagrange et al. 2004). In all ANOVAs, the Tukey-Kramer test was  
13 used to assess multiple comparisons of means.

14 Pearson's (product-moment) correlation coefficients between specific traits and total  
15 biomass accumulation were computed. Linear regressions were fitted to assess (i) a  
16 predictive model to estimate biomass partitioning in the contrasting tree compartment  
17 from diameter measurements and (ii) the relationships between specific individual traits  
18 (RMR, PNUE,  $\Delta_{\text{leaf}}$  and LMA). These latter linear regressions were performed on species  
19 means. Each species mean was incorporated in the regression only if the relationship was  
20 significant within the species.

21

## 22 **Results**

### 23 *Diameter, height and biomass accumulation*

1 No significant differences were reported in diameter, height or total biomass between  
2 pioneer and non-pioneer groups in any ages (Table 3). However, significant differences  
3 were observed between species within each functional group (FG) excepted for height of  
4 the 3-year-old saplings (Table 3). In the non-pioneer (NP) group, *Tr* showed significantly  
5 higher height and total biomass than *Co* for 1-year-old seedlings, while, it was the reverse  
6 for diameter and total biomass for 3-year-old saplings (Figure 1A, B and C). In the  
7 pioneer (P) group, *Ae* showed a significantly smaller diameter, height and total biomass  
8 than the other species for the 1-year-old seedlings. For 3-year-old saplings, *Hc* showed  
9 higher diameter than *Ae* and *Ls*, and *Ae* reached significantly lower total biomass (Figure  
10 1A and C). In regards of all species (compared with the *a posteriori* test), only the ranking  
11 of height for 1-year-old seedlings (Figure 1B) was consistent with expectation based on  
12 previous growth analysis on this site (cf. Table 1), with the exception of *Tr* that showed a  
13 slightly higher height growth than expected.

14

#### 15 *Biomass partitioning and crown morphology*

16 As for growth parameters, no differences were observed when comparing biomass  
17 partitioning or crown form between FG, but significant differences were observed  
18 between species within each FG, especially after effect of individual height was taken  
19 into account (Table 4). In the NP group, *Tr* showed a higher allocation to branches than  
20 *Co* and a more spherical crown compared to the flat crown of *Co* 1-year-old. However,  
21 *Co* had a higher proportion of biomass allocated to branches (not significant) and roots  
22 than *Tr*, as well as, a more vertically expended crown after 3 years (Figure 2A, B and C).  
23 In the P group, *Hc* allocated less biomass to branches but more to roots than other species

1 at 1- and 3-year-old (Figure 2A and B). *Hc* also showed a flatter crown than *Ae* and *Ls*,  
2 which showed more spherical or slightly vertically expended crown (Figure 2C). In  
3 regards of all species (compared with the *a posteriori* test) after 3 years in plantation; *Ls*  
4 showed the greater allocation to branches and *Co* had the greater allocation to roots and  
5 the most vertically expended crown.

6

### 7 *Leaf structure and ecophysiology*

8 None of the measured leaf trait was significantly different between the two FG (Table  
9 4 and 6). Little differences in leaf traits were observed in the NP group excepted for the  
10 3-year-old sapling where *Tr* showed higher leaf nitrogen content ( $N_a$ ), stomatal  
11 conductance ( $G_s$ ) and transpiration ( $E$ ) than *Co* (Table 5). In the P group, *Hc* showed the  
12 highest value for maximal assimilation rates ( $A_{max}$ ),  $N_a$ ,  $G_s$  and  $E$  in 1-year-old seedlings,  
13 while *Ae* showed the lowest values (Table 5). For 3-year-old saplings, *Ae* still reported  
14 the lowest values for these four leaf traits, but *Hc* showed similar  $A_{max}$ ,  $N_a$ ,  $G_s$  and  $E$  than  
15 *Ls* (Table 5). In the NP group, *Co* showed lower leaf mass per area (LMA),  
16 photosynthetically nitrogen use efficiency (PNUE) and higher leaf carbon discrimination  
17 ( $\Delta_{leaf}$ ) than *Tr* for 1-year-old seedlings (Figure 3A, B and C). For 3-year-old saplings,  
18 differences remained similar, excepted for PNUE, where *Tr* showed higher rates than *Co*.  
19 In the P group, *Ls* showed higher PNUE and  $\Delta_{leaf}$  than other species in both ages (Figure  
20 3B and C). However, *Ae* showed a higher LMA than *Hc* and *Ls* in both ages (Figure 3A).

21 *Hc* showed the lowest LMA of all species and very low  $\Delta_{leaf}$ , while *Ls* had the highest  
22 PNUE and *Co* the highest  $\Delta_{leaf}$  of all species, and this at both ages.

23

1 *Population trait relationships*

2 For all five species, significant linear relationships (data not shown) were observed  
3 between (i)  $\Delta_{\text{leaf}}$  and PNUE, (ii) LMA and PNUE, and (iii)  $\Delta_{\text{leaf}}$  and RMR (except for *Hc*  
4 that showed no significant relationship between PNUE and LMA). As a result, data were  
5 pooled within a given species to draw linear relationships for the five planted species  
6 (Figure 4A, B and C). Among the studied species (i) when PNUE increased, WUE  
7 decreased (ii) when PNUE decreased, LMA increased (*Hc* mean was not included since  
8 no significant relationship was found between these traits for this species, data not  
9 shown), and (iii) RMR increased with  $\Delta_{\text{leaf}}$  (i.e., with decreasing WUE).

10

11 *Tree traits, age and biomass accumulation*

12 Pearson's correlation coefficients were computed between individual traits and  
13 biomass accumulation as a function of individual age and regardless of species and  
14 functional group (Table 6). For 1-year-old seedlings, biomass accumulation was related  
15 positively and significantly to higher BMR and Crown H/D while for 3-year-old saplings  
16 it was correlated to higher RMR, Crown H/D, NUE and  $\Delta_{\text{leaf}}$  (Table 6). As a result, for 1-  
17 year-old seedlings, increases in biomass accumulation were associated with a higher  
18 above-ground foraging potential, whereas higher biomass accumulations for 3-year-old  
19 saplings were more related to leaf NUE and water consumption issues (i.e., RMR and  
20 WUE) (Table 6).

21

22 **Discussion**

23 *Species growth and resource use efficiency in tropical plantations*

1        Our first objective was to compare species using some of the traits associated with  
2 resource capture and use and to understand better the relationship between these traits and  
3 species performance. Because all individuals were grown in an environment where light  
4 was not a limiting factor, particular attention was given to individual efficiency in use of  
5 below-ground resources. Traits associated with better growth apparently changed with  
6 ontogeny. For 1-year-old seedlings, biomass accumulation was significantly related to  
7 traits that improved above-ground space exploration and light use by leaves. Conversely,  
8 for 3-year-old saplings, growth accumulation was more correlated to traits dealing with  
9 water uptake and use. It follows that performance at the establishment stage is critically  
10 associated with the interception and use of light by more branches, a wider crown and an  
11 efficient use of leaf N for photosynthesis, while longer term performance seems to be  
12 related more to patterns of water use. A possible limitation of our experimental design is  
13 that the age factor contains contrasting plantation-specific characteristics (e.g. soil or  
14 hydrology). Healey (2007) indeed reported that environmental variation within the 2001  
15 plantation explained around 50% of tree performance. However, care was taken to  
16 establish both plantations in flat and sloppy areas, which are in a close proximity, to  
17 encompass the same range of topographical variations. Therefore, we are confident that  
18 the differences we observed between 1- and 3-year-old individuals are independent from  
19 these environmental characteristics.

20        Dependence of leaf or tree productivity on water use has already been observed in  
21 tropical ecosystems, especially when water availability is seasonally restricted (Ares and  
22 Fownes 1999, Brodribb, Holbrook and Gutiérrez 2002, Santiago et al. 2004, Brien and  
23 Zuidema 2005). A recent study (Würth et al. 2005) concluded that the growth of 17

1 tropical tree species (including *Ae* and *Ls*) during the dry season was clearly not limited  
2 by C availability. Similarly, Casper, Forseth and Wait. (2005) reported that in a dry  
3 environment individual selection based on WUE occurs year by year in a natural  
4 population of *Cryptantha flava* because of the pressure of uncertain water availability. In  
5 Sardinilla, although seasonal drought occurs, it was not possible to uncover a simple  
6 relationship between low  $\Delta_{\text{leaf}}$  (i.e., high WUE) and high growth performance. Indeed,  
7 greater growth of some 3-year-old sapling was clearly positively correlated with high  $\Delta_{\text{leaf}}$   
8 which contradicts Xu et al. (2000). High  $\Delta_{\text{leaf}}$  were however achieved on this site through  
9 a high allocation to roots. This trend, especially marked for *Co*, allowed this species to  
10 maximize photosynthesis to the detriment of water loss. Indeed, higher  $\Delta_{\text{leaf}}$  decreases  
11 resistance to CO<sub>2</sub> diffusion into the leaf and thus increases photosynthetic efficiency of  
12 leaf N. Similar relationship has already been reported by Vitousek, Field and Matson  
13 (1990) and Terwilliger et al. (2001) and it can be explained since by facilitating CO<sub>2</sub>  
14 entrance, photosynthesis per unit of N increases owing to a rise in CO<sub>2</sub> partial pressure at  
15 the Rubisco carboxylation site.

16 Another important trend is that leaf PNUE significantly decreased as LMA increased,  
17 except for *Hc* where the relation was not significant (data not shown). This has already  
18 been reported for herb, shrub and tree species (Poorter and Evans 1998). Such a dilution  
19 of photosynthetically active N as leaf increases its mass per unit area may be related to an  
20 increase in C/N ratio as well as to a higher allocation to cell walls (Onoda, Hikosaka and  
21 Hirose 2004). Furthermore, such a negative relationship between PNUE and LMA may  
22 also explain the lower PNUE reported for leaves that have a lower leaf lifespan  
23 (Hiremath 2000). Indeed, leaf lifespan and LMA are closely correlated so that leaves with



1 a long lifespan allocate more biomass per unit area to improve leaf resistance to external  
2 damages (Wright and Westoby 2002). Nonetheless, despite lower PNUE, high CO<sub>2</sub>  
3 assimilation rates may be obtained at the leaf of crown level by increasing leaf N content  
4 on a mass basis or total leaf area, respectively.

5 Apparently, species performance in the plantation were associated with differences in  
6 the combination of (i) long-term CO<sub>2</sub> diffusion into the leaf (which is highly dependent  
7 on root biomass investment) and (ii) leaf mass per area (which is associated with leaf  
8 lifespan and PNUE). Importance of LMA on species growth in open areas was already  
9 reported in numerous late-successional species (Martinez-Garza et al 2005). Other factors  
10 may contribute to the variation in growth performance on these species (Healey 2007).  
11 For example, limitation in a given nutrient, or crown shape and leaf organization within  
12 the crown volume, were already associated with species performance (e.g. Lewis and  
13 tanner 2000, Valladares, Skillman and Pearcy 2002, Sterck et al. 2003, Davidson et al.  
14 2004). Here, we observed a positive correlation between crown shape and biomass  
15 accumulation. However, considering that plantations in open areas offer an environment  
16 where light is not limited, this correlation is more likely to result from the relationship  
17 existing between crown form and (i) crown water conduction potential (Walcroft et al.  
18 1996) or (ii) crown self-shading to minimize evapotranspiration and damages due to  
19 excess of heat and light (Pearcy et al. 2005). Indeed, crown water relation has already  
20 been recognized as critical factor in limiting tree growth (Ryan and Yoder 1997, Meinzer  
21 2003)

22

23 *Biomass accumulation and species selection*

1 Growth performance of tropical tree species has already been associated with  
2 variations in (i) water availability (Condit et al. 1995, Santiago et al. 2004), (ii) water use  
3 strategies (Casper, Forseth and Wait 2005) and (iii) nutrient use efficiency (Hiremath  
4 2000, Hiremath and Ewel 2001, Kitayama et al. 2004). In our experimental plantation  
5 site, species performance a few years after establishment seemed to be related to species  
6 specific water use. However, closer examination of the species that accumulated the most  
7 biomass (i.e., *Co*, *Ls* and *Hc*), shows that high growth rates was not strictly associated  
8 with an efficient use of water but with contrasting water uses, which might become an  
9 important factor for species co-existence (Drake and Franks 2003).

10 On our site, *Co* is likely to maximize CO<sub>2</sub> diffusion in order to maintain a higher  
11 PNUE at the expense of water. However, this was only possible since this species shows  
12 a particularly high allocation to roots in order to increase water uptake. It is also  
13 noteworthy to mention that this high allocation to roots, typical for shade tolerant and  
14 generally slower growing and non-pioneer species, might explain the delay in growth  
15 observed after one year. A higher allocation to below-ground foraging may indeed reduce  
16 primary above-ground growth, but provide a better growth over the longer-term. On the  
17 other hand, despite a lower allocation to roots than *Co*, *Ls* showed a similar low WUE  
18 which was related to a higher PNUE. *Ls* surely offset its water requirements through a  
19 contrasting root architecture, (i.e., by developing thinner and more ramified roots for very  
20 efficient foraging (Coll L. unpublished data)). Furthermore, the high carbon accumulation  
21 of *Ls* is obviously also related to its greater allocation to branches and leaves, displaying  
22 very large leaf surface and crown volume for a rapid light use. After several years, the  
23 particularly dense crown of this species may help in regulating the evapotranspiration of a

1 large proportion of its large leaf area through self shading (Pearcy et al. 2005). Finally,  
2 *Hc* was the most successful species by exhibiting a high WUE but a low PNUE.  
3 Compensation for this low efficiency of N was achieved by a high N concentration in  
4 leaves which led to the highest photosynthetic rate on an area basis on this site. In  
5 addition, *Hc* is possibly able to store large quantities of water in its particularly large  
6 trunk, shaped like an elephant's foot, buffering periods of limited water availability.

7 From a carbon accumulation point of view, three species (*Co*, *Ls* and *Hc*) seem to be  
8 particularly interesting candidates to select in plantations with a carbon sink use. From an  
9 ecological point of view, using a combination of these contrasting species may also help  
10 to keep (i) a greater diversity of tree species and associated wild life and, (ii) a greater  
11 diversity of ecological functions. Such diversities were recognized to be critical for a  
12 better resilience of the ecosystem (Chapin et al. 2000). Furthermore, an additional  
13 advantage to use such a combination is the accumulation of biomass in contrasting  
14 compartments of the stand, roots for *Co*, the trunk for *Hc* and branches for *Ls*. In a recent  
15 study, Piotta et al. (2004) showed very interesting yields of native tree species planted in  
16 combinations rather than in monocultures, allowing the hypothesis that using these three  
17 species in mixed plantations seems promising. However, it remains difficult to  
18 extrapolate and generalize these conclusions to other locations and climate since species  
19 leaf traits and efficiencies are highly dependant on other growth-limiting factors  
20 (Santiago et al. 2004). More research is thus expected to determine performance of such  
21 species (especially in mixed plantations) as a function of a gradient of environmental  
22 conditions.

23

## 1 *Functional groups*

2        Classification of tree species into functional groups is an approach widely used to  
3 simplify and deal with the broad variety of species performance observed in tropical  
4 ecosystem (Cornelissen et al 2003). Among other characteristics, such as seed availability  
5 and good rates of germination, functional groups could be used to select species to be  
6 planted in reforestation programs. We hypothesized that, since light is not a limiting  
7 factor in plantations, pioneer and shade intolerant species should be well suited for such  
8 open area. Nevertheless, no actual differences in growth or biomass accumulation were  
9 detected between the pioneer (P) and non-pioneer (NP) groups on our plantation site. A  
10 small number of species was studied within each group, however, results clearly suggest  
11 that some NP species may hold individual traits allowing them to be as competitive as P  
12 species. This agrees with one conclusion of Martinez-Garza et al. (2005) which reported  
13 that the absence of late-successional species in open areas may be more related to the lack  
14 of propagules and/or germination capacity rather than to their inability to grow in open  
15 conditions. Furthermore, it might not be surprising that expected differences between  
16 species characterized by contrasting level of shade tolerance are not obtained when  
17 comparing them in an environment where light is not the driving resource. Together,  
18 these results raise some important points pertaining (i) to the need of comparing species  
19 (rather than functional groups) when looking at performance and biomass accumulation  
20 potential in plantation sites and (ii) to limit the use of functional groups as one of the  
21 criteria to choose species for reforestation.

22

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10

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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	Economical 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)	Bignonaceae		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 constructions)
<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 seemanii</i> (Ls)	Tiliaceae		Guácimo colorado	From Mexico to Argentina	9.1%	High timber value for furniture and flooring

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*. For each relationship,  $r^2$  of the linear fit is presented. D is tree diameter at 10cm from the soil surface. Wt, Wb and Wr are total tree, branch and root biomass, respectively.

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>	$r^2$	<i>a</i>	<i>b</i>	$r^2$	<i>a</i>	<i>b</i>	$r^2$
<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



Table 3: Summary of ANOVA results for stem diameter (cm), height (m) and total biomass (g of dry biomass) as a function of functional groups (FG) and species (Sp.(FG)). Results are presented for 1- and 3-year-old individuals selected from the Sardinilla experimental plantations. Significant effects ( $\alpha = 0.05$ ) are in bold.

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

Table 4. Summary of ANOVA results for biomass partitioning (BMR and RMR), crown shape (Crown H/D) and leaf ecophysiology (LMA, NUE and  $\Delta_{\text{leaf}}$ ) as a function of functional groups (FG), species (Sp.(FG)), age and interactions. Significant effects ( $\alpha = 0.05$ ) are in bold. \* indicates parameters for which a transformation was applied to take into account individual height.

Source of variation	df	BMR*		RMR*		Crown H/D*		LMA		NUE		$\Delta_{\text{leaf}}$	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
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	<b>&lt;0.0001</b>	6.20	<b>0.0008</b>	13.45	<b>&lt;0.0001</b>	24.03	<b>&lt;0.0001</b>	11.64	<b>&lt;0.0001</b>	36.58	<b>&lt;0.0001</b>
Age	1	4.94	0.1127	4.06	0.1374	26.07	<b>0.0145</b>	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	<b>0.0031</b>	8.66	<b>&lt;0.0001</b>	1.15	0.3324	5.43	<b>0.0019</b>	4.91	<b>0.0036</b>	1.66	0.1815

Table 5. Mean and standard error (SE) for maximal CO<sub>2</sub> assimilation rate ( $A_{\max}$ ) leaf nitrogen content on an area basis ( $N_a$ ), stomatal conductance ( $G_s$ ) and leaf transpiration (E). 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.

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

Table 6. Summary of ANOVA results for maximal CO<sub>2</sub> 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 interactions. Significant effects ( $\alpha = 0.05$ ) are in bold.

Source of variation	df	$A_{\max}$		$N_a$		$G_s$		E	
		<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
FG	1	0.15	0.7125	0.07	0.8039	0.06	0.8127	0.01	0.9558
Sp.(FG)	3	19.62	<b>&lt;0.0001</b>	12.05	<b>&lt;0.0001</b>	31.70	<b>&lt;0.0001</b>	32.15	<b>&lt;0.0001</b>
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	<b>0.0008</b>	6.27	<b>0.0007</b>	2.08	0.1148

Table 7. Pearson's correlation coefficients 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 efficiency (PNUE, WUE<sup>†</sup>). Results are presented for the 1- and 3-year-old population separately, with all species pooled together.

	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	*
$\Delta_{\text{leaf}}^{\dagger}$	-0.146	ns	0.490	**

<sup>†</sup> :  $\Delta_{\text{leaf}}$  is inversely related to WUE (Farquhar et al. 1989, Porté and Loustau 2001)

## Figure Caption

Figure 1. Mean and standard error values 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 but for individuals of a similar age.

Figure 2. Mean and standard error values 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 but for individuals of a similar age.

Figure 3. Mean and standard error values for (a) Leaf Mass per Area (LMA), (b) Nitrogen Use Efficiency (NUE) and (c) leaf carbon isotope discrimination values ( $\Delta_{\text{leaf}}$ ) 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 but for individuals of a similar age.

Figure 4. Relationships between (A) leaf carbon isotope discrimination ( $\Delta_{\text{leaf}}$ ; ‰) and nitrogen use efficiency (PNUE;  $\mu\text{mol CO}_2 \text{ gN}^{-1} \text{ s}^{-1}$ ), (B) leaf mass per area (LMA;  $\text{g m}^{-2}$ ) and PNUE and (C)  $\Delta_{\text{leaf}}$  and root mass ratio (RMR, %). For each relationship, the linear regression (broken 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.

Figure 1

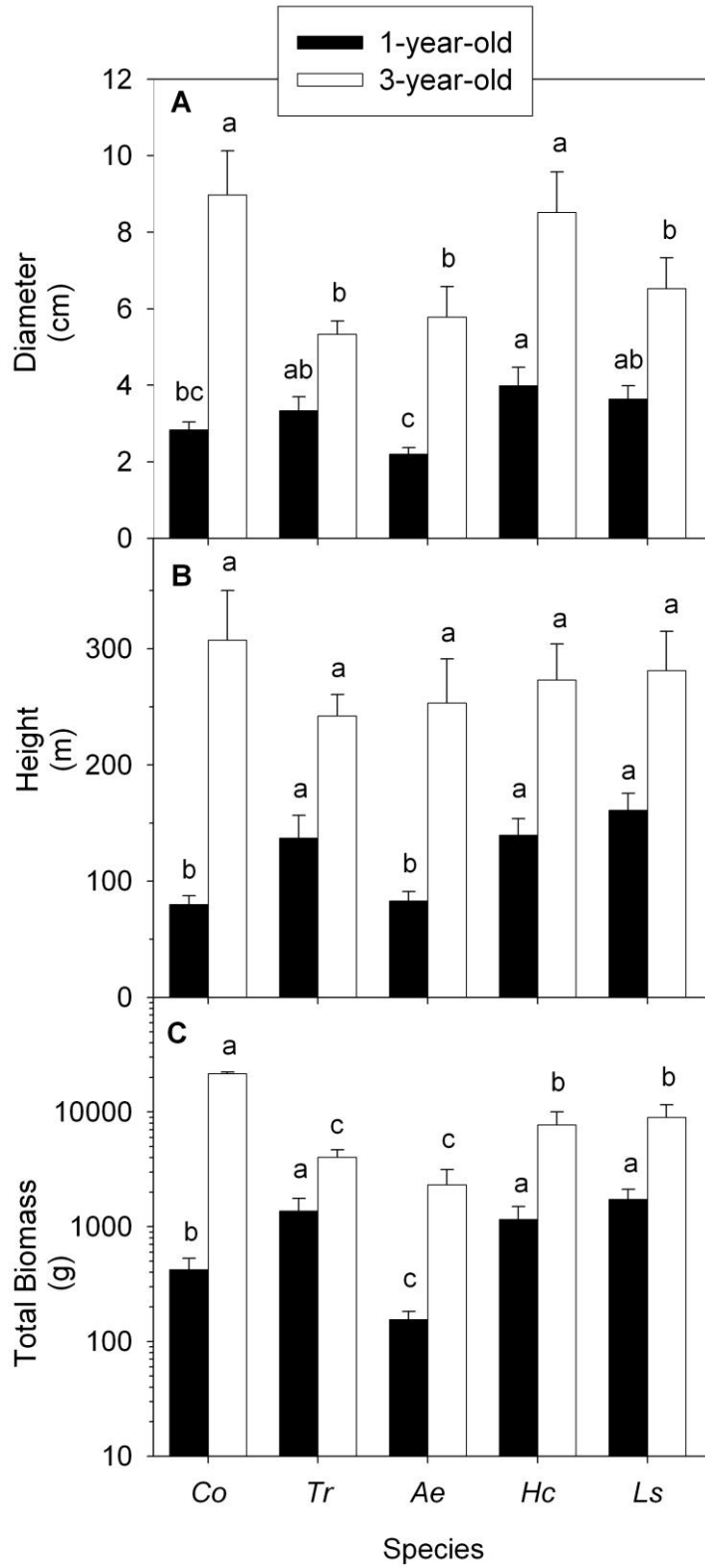


Figure 2

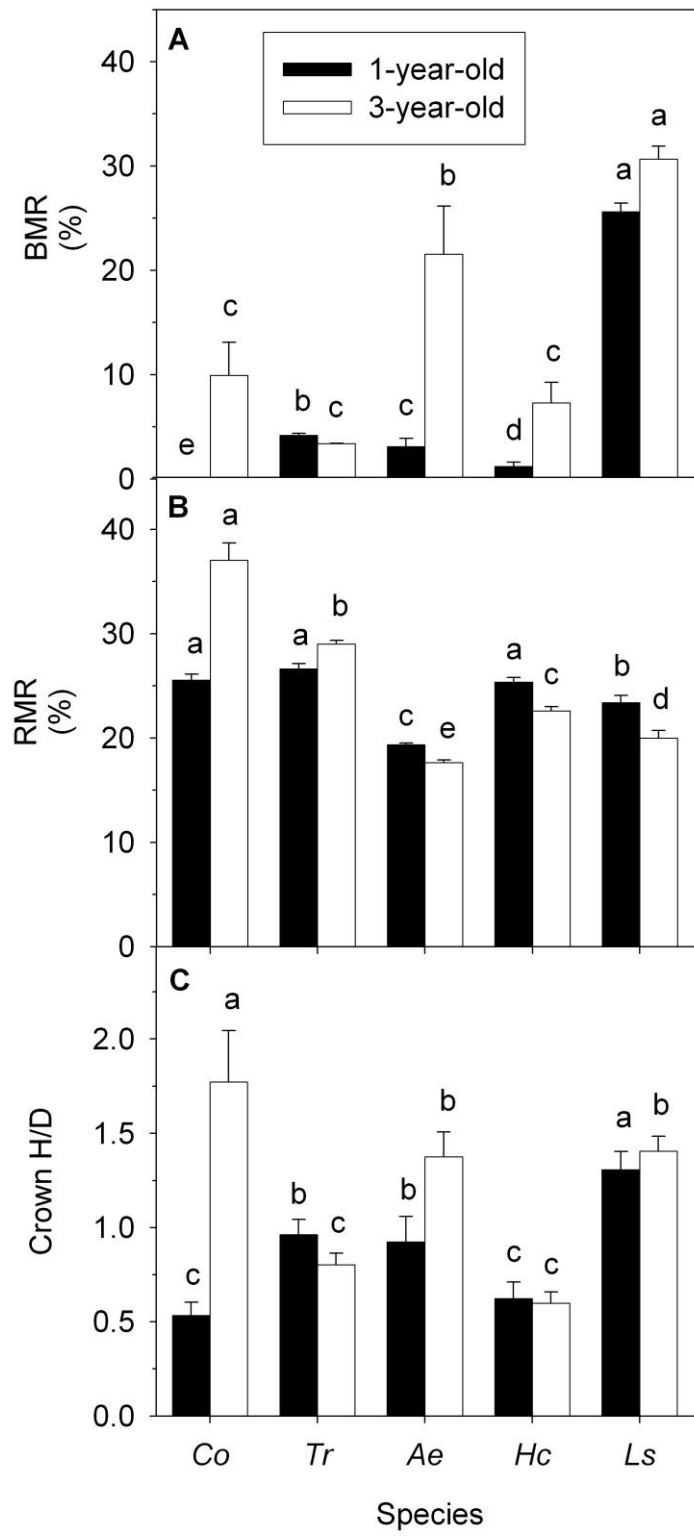




Figure 3

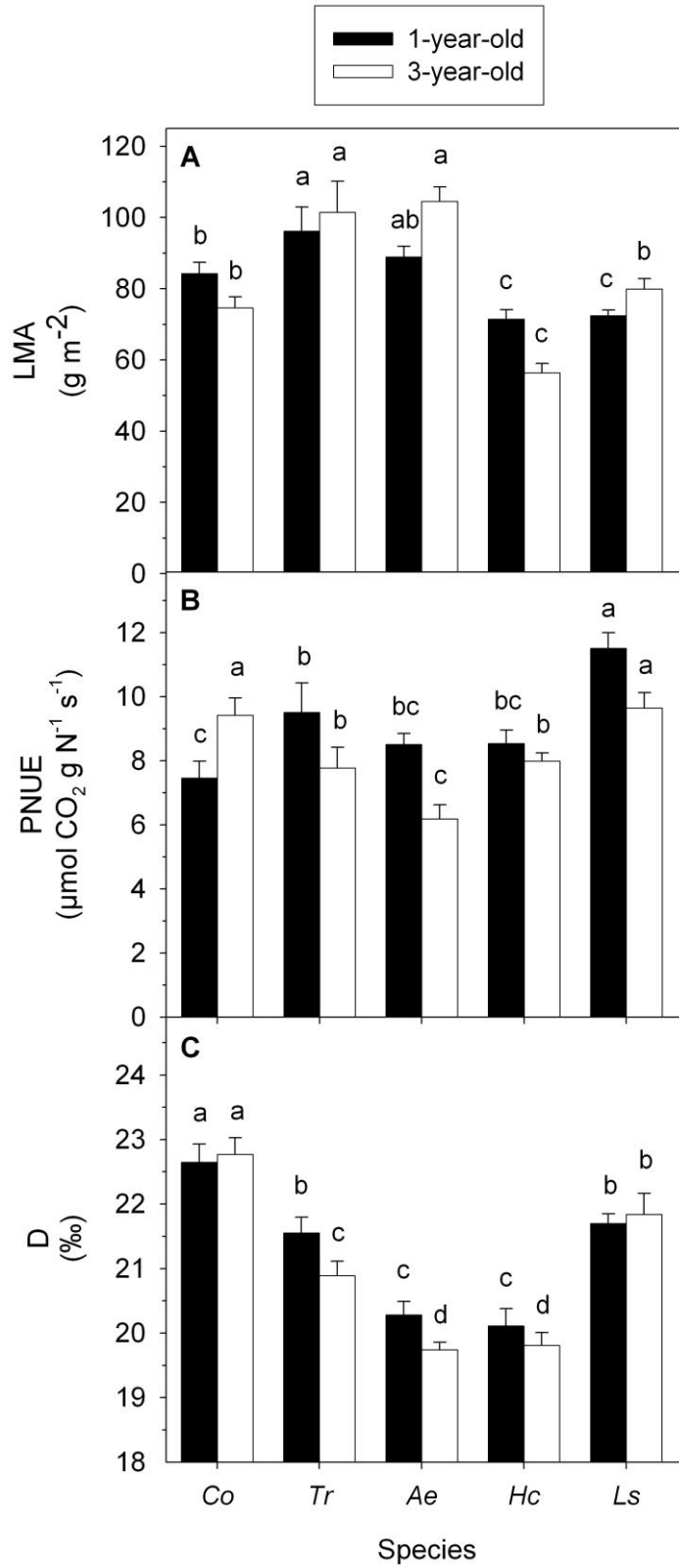


Figure 4

