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5 **Root architecture and allocation patterns of eight native tropical species with**
6 **different successional status used in open-grown mixed plantations in Panama**

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28
29 **Running headline:** Evaluating successional status traits in open-grown conditions

30

31 **Abstract**

32

33 We investigated biomass allocation and root architecture of eight tropical species with
34 different successional status, as classified from the literature, along a size gradient up to 5
35 m. We focused on belowground development, which has received less attention than
36 aboveground traits. A discriminant analysis based upon a combination of allocational and
37 architectural traits clearly distinguished functional types and classified species according
38 to successional status at a 100% success rate. For a given plant diameter, the pioneer
39 species presented similar root biomass compared to the non-pioneer ones but higher
40 cumulative root length and a higher number of root apices. A detailed study on the root
41 system of a sub-sample of three species showed that the most late-successional species
42 (*Tabebuia rosea*) had longer root internodes and a higher proportion of root biomass
43 allocated to the taproot compared to the other two species (*Hura crepitans* and *Luehea*
44 *seemannii*). Most pioneer species showed a higher leaf area ratio due to a higher specific
45 leaf area. We conclude that the functional differences between pioneer and non-pioneer
46 tree species found in natural forests were maintained in open-grown plantation
47 conditions.

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49

50 **Key-words:** allocation, allometry, root architecture, successional status, tropical
51 plantation

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55 Introduction

56

57 Studies done in natural forests suggest that there are hundreds of potentially economically
58 and ecologically interesting native tropical tree species that can be used for reforestation
59 (Condit et al. 1993, Hooper et al. 2002). However, native species are rarely used and only
60 a small number of introduced species (e.g. *Tectona grandis*, *Eucalyptus* spp.) dominate
61 most plantations in degraded lands. The bias is in part due to the lack of existing
62 knowledge about how native trees survive, grow and develop in a plantation setting
63 (Condit et al. 1993, Piotto et al. 2004). Most previous studies analyzing survival,
64 establishment and growth patterns of native tropical species (e.g. Condit et al. 1996a,
65 Welden et al. 1991, Poorter 2006) have been conducted in forest conditions which can
66 differ considerably from the environment characteristic of open-grown plantations.
67 In the tropics, studies on survival, growth strategies and structure of trees under different
68 environmental conditions have mainly concentrated on the aerial parts of the plant (Aiba
69 and Kohyama 1997, King et al. 1997, Sterck 1999, Takahashi et al. 2001, Poorter et al.
70 2003). Noteworthy exceptions are the papers by Kohyama and Grubb (1994) that
71 examined above- and below-ground allocation of 14 warm-temperate rain forest species
72 and that of Paz (2003) for examining an even larger number of tropical species. The first
73 objective of our study was to characterize the development and structure of eight native
74 species of tropical sapling trees (up to 5 m tall) growing in open, mixed plantations.
75 These species are characterized by different abilities to colonize and regenerate in gaps in
76 the nearby forest. We particularly focused on the structure and architecture of the
77 belowground compartment which has received less attention than aboveground structures

78 although it can account for almost a half of total carbon stored by plants (Sanford and
79 Cuevas 1996).

80 The second objective of our study was to examine whether morphological and
81 allocational differences between pioneer and non-pioneer species can be found when
82 plants grow under full sunlight conditions as in a plantation setting. Successional status
83 is usually associated with different physiological and morphological traits (Givnish 1988,
84 Messier et al. 1999, Ellis et al. 2000). For example, it has been shown that late-
85 successional species (which dominate late-successional stages and the understory of
86 closed forest canopies) generally present lower photosynthetic rates and lower leaf area
87 ratios than shade-intolerant pioneer species (Walters et al. 1993, Kitajima 1994). Poorter
88 (1999) demonstrated that under low light, morphological traits rather than physiological
89 traits explained growth differences between species, while under high light, species-
90 specific physiological traits played a more important role. Moreover, since most studies
91 have been conducted with plants at the seedling stage (i.e. Kitajima 1994, Reich et al.
92 1998, Paz 2003), and have shown that allocation patterns and morphology change with
93 plant size (Delagrange et al. 2004, Claveau et al. 2005, Kneeshaw et al. 2006), we
94 sampled a range of tree heights within each species.

95 Finally, our third objective was to compare the root architecture among a sub-sample of
96 three of the eight original species which covered a continuum of successional status.

97 There have been very few studies focusing on the relationship between successional
98 status and root architecture and soil exploitation efficiency (but see Bauhus and Messier
99 1999). Recently, a study by Paz (2003) assessed some root architectural traits for 55
100 species pertaining to different functional types and found that, in general, late -
101 successional species developed thicker roots (lower specific root length (SRL) values)

102 than early-successional ones. Carbon allocation to storage or physical defense in thicker
103 roots has been invoked as a strategy of late-successional species to survive under shade
104 (Kobe 1997).

105 In summary, the basic questions addressed here are: (i) What are the structural and
106 allocational differences found among eight tropical tree species which could potentially
107 be used for land restoration purposes? (ii) Do species with different successional status
108 present structural and allocational functional differences when growing in open-grown
109 plantations? (iii) Do these differences vary along the size gradient investigated? and (iv)
110 Are there differences in root architecture among tropical trees belonging to different
111 successional stages?

112 **Materials and methods**

113

114 *Species selection, plantation establishment and early measurements*

115 The study was conducted in a reforested pasture located in Sardinilla, in the Buena Vista
116 region of Central Panama (9°19'30"N, 79°38'00"W). Eight native species were

117 tentatively classified into two functional types, pioneers (*Luehea seemannii* Triana &

118 Planch. (Tiliaceae), *Cordia alliodora* Ruiz & Pav. (Boraginaceae), and *Antirrhoea*

119 *trichantha* Hemsl. (Rubiaceae)) and non-pioneers (*Enterolobium cyclocarpum* (Jacq.)

120 Griseb. (Leguminosae), *Cedrela odorata* L. (Meliaceae), *Tabebuia rosea* Bertol.

121 (Bignoniaceae), *Sterculia apetala* (Jacq.) Karst. (Sterculiaceae) and *Hura crepitans* L.

122 (Euphorbiaceae)). The species classification was established based on (1) their

123 demographic score (from Condit et al. 1996a), (2) their relative growth rate found at the

124 seedling stage in the Barro Colorado Island permanent plot (BCI) (R. Condit, personal

125 communication) (3) their dry seed mass (J. Wright, personal communication) and (4) a

126 bibliographic analysis. We assume that colonizer species would be those requiring high

127 light levels to germinate, having small seeds, high growth and mortality rates, and a

128 demographic score (d.s.) > 1. *Luehea* and *Cordia* present both a demographic score (d.s.)

129 of 1.8 and 2.5 respectively, high growth rates (at seedling stage), the lowest (with

130 *Antirrhoea*) seed dry masses (< 0.01 g) and have already been described as pioneers in a

131 number of studies (Welden et al. 1991, Condit et al. 1996b, Menalled and Kelty 2001,

132 Dalling et al. 1999, Elias and Potvin 2003). *Antirrhoea* is a rare species in BCI, where it

133 is found mainly on the shore at the northern edge of the Island (Croat 1978) and it has

134 been relatively little studied. However it is decidedly a pioneer species (S. Lao, personal

135 communication), characterized by very small seeds (0.0005 g of dry mass, the lowest

136 value of the eight species studied). Kitajima et al. (2005) and Elias and Potvin (2003) also
137 described *Antirrhoea* as a pioneer species typical of early-successional stages.
138 Four species (*Cedrela*, *Sterculia*, *Tabebuia* and *Hura*) have been described in many
139 studies as long-lived shade-intolerant species but not pioneers (Welden et al. 1991,
140 Poorter and Hayashida-Oliver 2000, Kitajima 2002, Poorter et al. 2006). They are
141 characterized by intermediate growth rates at the seedling stage (see Wright et al. 2003)
142 (with the exception of *Cedrela*, which presents a high growth rate, see Menalled and
143 Kelty 2001) and by seed dry masses above > 0.01 g. From these four species, *Tabebuia* is
144 markedly the most shade tolerant with a d.s. < 0 (Condit et al. 1996, and see also Hooper
145 et al. 2004 and Kitajima 2002). *Enterolobium* on the other hand is a common species in
146 the Panama Canal watershed yet it is characteristic of the dryer forest on the Pacific slope
147 of the isthmus and therefore it is associated with a forest type that is more open than the
148 wet forest of Barro Colorado Island. Seed size of *Enterolobium* would favour its
149 classification in the non-pioneer group.

150 Seedlings were planted in June 1998 in eight 10 m x 25 m plots. One seedling of each
151 pioneer species was randomly interspersed among the non-pioneer seedlings in each plot.
152 It has been argued that native mixed species plantations provide the best opportunity for a
153 range of services such as production, protection or restoration of degraded areas (Piotto et
154 al. 2004). Each plot contained 15 experimental seedlings spaced 3 m apart (about 3-4
155 pioneer trees per plot). Following planting, the only intervention was the removal of grass
156 twice a year around each seedling (circle of 0.5 m diameter). Base-line data were
157 recorded at the onset of the first dry season, in January 1999. Height as well as branch
158 number was recorded for each living seedling. The same data were recorded at the onset
159 of the growing season in July every year thereafter for three years.

160

161 *Allometric and morphological measurements*

162 In August 2001, intensive allometric measurements were initiated. Saplings/trees from
163 each of the eight species were grouped in five size class categories based on their height.
164 The height range for each species in July 2001 was as follows: *Luehea* (0.56-4.42 m.),
165 *Cordia* (1.9-3.32 m.), *Sterculia* (0.58-5.15 m.), *Antirrhoea* (0.57-2.77 m.), *Enterolobium*
166 (1.66-2.48 m.), *Cedrela* (0.56-3.57 m.), *Tabebuia* (0.37-3.18 m.) and *Hura* (0.76-4.85
167 m.). Care was taken to sample a similar height range from all species. Differences in total
168 height among individuals were caused by differences in growth caused by micro-scale
169 variations in topography. All sampled individuals were healthy. Within each size
170 category, we randomly selected one individual per species for allometric and biomass
171 measurements. Sample size was thus five trees per species for a total of forty saplings.
172 Each of the experimental saplings was harvested and the following traits were measured:
173 (1) diameter at 10 cm from the ground; (2) height; (3) number, length and biomass of
174 branches; and (4) trunk biomass. All leaves from the saplings were harvested and dried to
175 provide total leaf biomass. We used specific leaf area (SLA) calculated from another
176 study (Delagrange et al., in press) to scale up biomass of leaves to total leaf area per tree.
177 SLA values were obtained from fifteen to twenty-five leaves per species where the leaf
178 area had been measured with a leaf area meter (Li-Cor 3100) before being dried and
179 weighed. Since *Enterolobium* was not considered in the Delagrange study, SLA and LAR
180 for this species were not available. The root system of the experimental trees was
181 manually excavated and the following measurements were taken: (1) biomass; (2) the
182 number of root apices larger than 2 mm; and (3) the cumulative length of roots larger
183 than 2 mm.

184

185 *Root architecture measurements*

186 Root analysis was conducted on trees that were also three years of age having been
187 planted in 2001 in a field immediately adjacent to the original plantation. The spacing
188 between individual trees was identical to the spacing in the original plantation (3 m).
189 Further details about this second plantation can be found in Scherer-Lorenzen et al.
190 (2005). The root systems of three individuals of *Luehea*, *Hura* and *Tabebuia*, three
191 species representing a range of successional status with *Luehea* being the pioneer species,
192 were carefully excavated by hand for root architecture analysis in November 2004. The
193 manual excavation method in the heavy clay soils of our study site allowed for the
194 removal of roots more than 2 mm in diameter. Although we did not sample fine roots, the
195 distribution of the coarse root system directly affects the extent and location of fine roots
196 and thus it has indeed significant implications for the capacity of the plant to capture
197 resources (Oppelt et al. 2001). The complete root system was then washed and the taproot
198 was separated from other roots. Each proximal root was then topologically described
199 following the protocol used by Ozier-Lafontaine et al. (1999), the topological parameters
200 *altitude* (a , the longest path length from the root base to an external link) and *magnitude*
201 (μ , total number of external links) described in Fitter (1987) were calculated for each
202 intact root. The topological index (TI) was then calculated as the slope of the linear
203 regression between $\log(a)$ and $\log(\mu)$. High TI values (close to 1) are associated with
204 “herringbone” root systems which are more efficient in exploiting soil but more
205 expensive to produce and maintain than dichotomous branching patterns (see Fitter et al.
206 1991). Link length and extreme diameters were measured for each root and order and link
207 number were recorded. Finally, all roots were dried and weighed to calculate biomass.

208

209

210 *Calculations and statistical analysis*

211 Destructive measures of biomass were made only at the end of the third year of growth.

212 Biomass, measured in 2001 (Table 1), was used to calculate the percent allocation to

213 branches (branch weight ratio, BWR = dry mass of branches / total plant dry biomass),

214 stem (stem weight ratio, SWR = stem dry mass / total plant dry biomass), leaves (leaf

215 weight ratio = dry mass of leaves / total plant dry biomass, LWR) and roots (root weight

216 ratio, RWR = dry mass of roots / total plant dry biomass). From the raw data, we

217 calculated the specific leaf area (SLA = leaf area / leaf dry mass) and the ratio between

218 plant leaf area and plant dry biomass (leaf area ratio, LAR).

219 Classification of species within different functional types was verified by a backward

220 discriminant analysis using measured allocational and structural traits. In the discriminant

221 analysis we excluded *Enterolobium* because of the absence of information on leaves.

222 The percent biomass allocation was square-root transformed and analyzed by multivariate

223 analysis of variance (MANOVA) with Functional Group (pioneer vs non-pioneer) and

224 Species nested under each Group as the two main effects. LAR and SLA were analyzed

225 independently by ANOVA testing for the effects of Functional Group and Species nested

226 under each Group. LAR was square-root transformed prior to the analysis to meet the

227 normality criterion. In all these analyses, we used tree height as a covariate to take into

228 account the effect of tree size on allocational ratios and the interaction with functional

229 group.

230 Five allometric relationships were examined by log-log linear regression to understand

231 the architecture of the trees. The first series of regressions came from classical studies of

232 architecture (e.g. Kohyama and Hotta 1990, Takahashi et al. 2001), specifically (1) plant
233 height vs. plant diameter; (2) plant biomass vs. plant diameter; and (3) root biomass vs.
234 plant diameter. The data we collected on root systems allowed estimation of two
235 additional regressions similar to those presented by Kohyama and Grubb (1994): (4) root
236 length vs. plant diameter and (5) number of root apices vs. plant diameter.

237 For each of these relationships, differences in the slope of the linear regression were
238 tested for each functional type (least square method) using Statgraphics Plus v.4.1
239 software. When slopes of the two Functional Types were not significantly different,
240 differences between intercepts were tested.

241 Finally, ANOVA was used to test differences among the three species on root
242 architecture parameters and a Bonferroni corrected t-test was used for the *a posteriori*
243 comparison of treatments means. Significant differences were considered if $p < 0.05$.

244

245 **Results**

246

247 *Biomass allocation*

248 The measured allocational traits calculated from the different biomass measurements
249 (Table 1) were pooled together in a discriminant analysis to determine if the trait
250 differences could distinguish between the two functional types, pioneer and non-pioneer.
251 The discriminant analysis was highly significant (Chi-square = 38.72, $df = 4$, $p < 0.0001$).
252 The traits retained to distinguish the functional types were root, stem and branch weight
253 ratios (RWR, SWR, BWR) and the leaf area ratio. Amongst the 35 observations used to
254 fit the model 100% were correctly classified by the discriminant function. Pioneer species
255 present a positive canonical score (c.s. > 0) and non-pioneers a negative one.
256 Examination of the c.s. revealed that *Antirrhoea* was the species which presented the
257 combination of traits most typical of pioneer species (c.s. = 2.73), while *Tabebuia* was
258 the species presenting the most late-successional specific traits (c.s. = -2.75) (Fig. 1).
259 Biomass partitioning was analysed by MANOVA to test for differences between
260 Functional Group and Species nested under each Group. The effect of the Functional
261 Group was found to be almost statistically different ($p = 0.08$) with Pillai's Trace (Olson
262 1976) equal to 0.8943. The effect of Species nested under each group was statistically
263 different ($p < 0.05$) with Pillai's Trace equal to 1.460. All eight species had different
264 patterns of biomass allocation (Fig. 2). Tree size significantly affected all allocational
265 ratios (SWR, BWR, RWR and LWR), but interactions with functional types were only
266 present for the branch weight ratio and the leaf area ratio (Fig. 3, Table 2). For BWR the
267 differences between the two groups decreased with tree height, while differences between
268 groups for LAR were greater for bigger trees (Fig. 3). Within each functional group,

269 significant variation exists among different species for all the ratios (Fig. 2, Table 2).
270 Pioneer species such as *Antirrhoea* and *Luehea* had the greatest biomass allocation to
271 branches (23 and 29% respectively), while *Cedrela* and *Enterolobium*, both non-pioneer
272 species, were the species which invested the most in roots (34% and 39%).
273 Non-pioneer species had significantly thicker leaves than pioneer species, with mean
274 SLA of 84.1 cm²/g and 130.6 cm²/g, respectively. Across species, SLA ranged from 71
275 cm²/g for *Tabebuia* to 148 cm²/g for *Antirrhoea* (Fig. 2e), but the effect of species within
276 each group was not statistically significant. Both functional types presented similar leaf
277 weight ratios, but LAR was, in general, higher for the pioneer species (Fig. 2f). Thus,
278 across species LAR ranged from 6.4 to 8.8 cm²/g for non-pioneer species and from 8.4 to
279 18.1 cm²/g for pioneer species. However ANOVA did not detect significant differences
280 between functional types once the effect of tree size was removed.

281

282 *Allometric relationships*

283 Within the size gradient studied, tree diameter was a good predictor of species height,
284 belowground biomass and total plant biomass (Fig. 4-5, Table 2). When the species were
285 grouped by their colonizing status, pioneer species showed greater height and biomass for
286 a given diameter ($P < 0.05$, regression intercepts) (Fig. 4a,b). Differences between
287 functional types were more evident when cumulative root length or the number of root
288 apices was related to diameter (Fig. 5b and 5c). Differences in the allometric relationships
289 among groups were mainly due to differences in intercept and not to differences in slope
290 (Table 3).

291

292 *Root architecture*

293 The root topological index (TI) ranged from 0.80 for *Luehea* (a pioneer species) to 0.90
294 for *Tabebuia* but differences were not statistically significant ($p < 0.05$) (Fig. 7a). The
295 diameter at the base of the proximal roots was a good predictor of the total root link
296 number with a correlation coefficient of 0.72, 0.84 and 0.53 for *Luehea*, *Hura* and
297 *Tabebuia*, respectively. For a given root diameter, both *Luehea* and *Hura* presented a
298 higher link number (Fig. 6) and considerably shorter second-order internode length (Fig.
299 7b) than *Tabebuia*, our most shade-tolerant species. Allocation to taproot dramatically
300 changed between species, ranging from 60% of total root weight for *Tabebuia* to 10%
301 and 15% for *Luehea* and *Hura*, respectively (Fig. 7c).

302

303 **Discussion**

304

305 *Structural and allocational differences among tropical tree species in an open-grown*
306 *plantation*

307 Over the last ten years a large number of studies have examined structural and allocation
308 relationships for tropical tree species (e.g. King 1991, Kohyama and Grubb 1994, King et
309 al. 1997, Coomes and Grubb 1998, Sterck 1999, Takahashi et al. 2001, Menalled and
310 Kelty 2001). Efforts have also been made to relate architectural characteristics to
311 ecological characteristics (Kohyama and Hotta 1990, Coomes and Grubb 1998). For
312 example, it is well known that early-successional species tend to increase their allocation
313 to height growth when growing in shade (Takahashi et al. 2001, Sterck 1999, King et al.
314 1997), while late-successional ones tend to reduce or even stop their height growth in
315 order to maintain high LWR and LAR and minimise construction costs in light-limited
316 environments (Takahashi et al. 2001, Sterck 1999, King et al. 1997, Delagrange et al.
317 2004). Biomass allocation in trees thus appears to be relatively plastic. In this study we
318 found that pioneer species were taller than non-pioneer long-lived shade intolerant
319 species for a given diameter. These results agreed with the findings of King (1991) and
320 Poorter et al. (2003) and thus with the hypothesis that pioneer species must give priority
321 to height growth to reach the canopy as soon as possible to avoid competition for light.
322 Bohlman and O'Brien (2006) recently pointed out that the differences in size between
323 functional types were only present in the early stages of plant development (up to 10 cm
324 dbh) which covers the range of dbh of the present study.

325 Tree diameter was a good predictor of both total plant and belowground biomass. It has
326 been suggested that plant biomass is more strongly correlated with secondary (diameter)

327 than primary growth (height) (Chave et al. 2001). Yet we found a very strong correlation
328 between height and biomass at this early life-stage (data not show). Few studies have
329 accounted for belowground development in tropical trees because root sampling is
330 generally difficult and very time consuming (Oppelt et al. 2001). However, in the context
331 of C storage, prediction of biomass allocation belowground must be considered since it
332 can represent between 18% and 46% of total plant biomass (Sanford and Cuevas 1996)
333 (between 22% and 40% in our study, depending on the species). In this study, and
334 elsewhere, aboveground plant traits (i.e. diameter, height) were found to correctly predict
335 belowground biomass and thus C storage in roots (Thies and Cunningham 1996, Curt and
336 Prévosto 2003). Within each allometric relationship, differences among species and
337 groups were mainly found in the intercepts (as in Kohyama and Grubb 1994), probably
338 because the height range investigated was not sufficient to test for differences among
339 slopes (Coomes and Grubb 1998).

340 In our study, LAR varied considerably between trees and species within each functional
341 group, but pioneer tree species tended to present higher LAR values than non-pioneer
342 ones. This was due to species differences in SLA since, as reported above, biomass
343 allocation to leaves varied little (see Fig. 1). This particular difference in leaf morphology
344 between functional types is critical since it provides contrasting nitrogen and water-use
345 efficiencies and different leaf life spans (Terwilliger et al. 2001, Onoda et al. 2004). In a
346 parallel study conducted in the same experimental site we found a positive relationship
347 between SLA and leaf photosynthetic nitrogen use efficiency (PNUE) (Delagrangé et al.
348 in press) and Kitajima (1994) and Walters et al. (1993), among others, have reported
349 higher photosynthetic rates and SLA values for pioneer species than for non-pioneers
350 when growing under high light conditions. SLA is known to well predict photosynthetic

351 capacity under high light conditions and particularly at fertile sites (Craven et al. 2007).
352 In agreement with Veneklaas and Poorter (1998) we believe that in our plantation site
353 physiological differences (e.g. higher photosynthetic rates and PNUE in pioneer species)
354 rather than allocational differences between functional types may predominate. However
355 we found that, when the different allocation traits we measured were combined in a
356 discriminant analysis, species were efficiently separated into two groups based on their
357 successional status.

358 Much research has been recently devoted to functional group classification, and the use
359 of quantitative method has been advocated as an objective way to group species (Ellis et
360 al. 2000, Diaz and Cabido 2001, Lavorel and Garnier 2002, Paz 2003, Poorter et al. 2003,
361 Poorter et al. 2006). In our study, the combination of RWR, SWR, BWR and LAR (rather
362 than a specific trait *per se*) very effectively separated species into two groups. Our data
363 thus support the importance of multiple-trait trade-offs (above- and belowground) to
364 differentiate species strategies.

365

366 Several recent papers have reported that tree size affects aboveground biomass
367 distribution and the need to consider these effects when analysing such traits (Veneklaas
368 and Poorter 1998, Menalled and Kelty 2001, Delagrange et al. 2004). Furthermore, both
369 Delagrange et al. (2004) and Claveau et al. (2005) found that the effects of tree size
370 varied according to the availability of resource, in this case light. In the present study,
371 most allocational ratios were strongly influenced by tree size.

372 Moreover we found that the ontogenetic effects on biomass distribution traits vary among
373 functional types (in agreement with Kneeshaw et al. 2006): pioneer species allocated
374 more to branches when small and increased LAR with size. The assumption of higher

375 allocation to branches in pioneer species during early development needs to be made
376 cautiously because other factors such as leaf size or petiole length can greatly influence
377 branchiness and crown construction (King and Maindonald 1999). In our study, pioneer
378 species were characterized by relatively small leaves while non-pioneers ones have large
379 compound leaves (*Tabebuia*, *Enterolobium*, *Cedrela*) or long petioles (up to 10-13 cm,
380 *Hura*). Differences in leaf size between species could thus also explain why the non-
381 pioneer species start branching at higher size, since first branch height has been found to
382 be positively related to leaf size (and/or petiole length) (King 1998). The interaction
383 between size and functional types for BWR and LAR could alternatively be explained by
384 the presence of an aboveground foraging strategy in pioneer species which would consist
385 in establishing rapidly their branching system to then increase their LAR and maximize
386 light capture and growth. Thus under favourable growing conditions (without seasonal
387 drought periods) pioneer species such as *Luehea* or *Cordia* are probably the most
388 appropriate for rapid land restoration purposes (e.g. Condit et al. 1993). However in sites
389 with restricted water availability or on poor soils the use of more conservative non-
390 pioneer species (with lower LAR and thus lower evaporative demands) or nitrogen-fixing
391 species, such as *Enterolobium*, seems more appropriate (Craven et al. 2007).

392

393 *Variation in root allocation and architecture*

394 A limitation of existing data on tropical tree biomass allocation and morphology is that
395 most studies only consider the aboveground components of trees (but see Kohyama and
396 Grubb 1994). In our study, root biomass was measured and was found to vary widely
397 among species without a clear trend between the two functional types (Fig. 5). However
398 the number of root apices as well as cumulative root length differed significantly between

399 functional types, the pioneer species having, on average, more root apices and root length
400 at a given plant size. In other words, morphological rather than allocational differences
401 were found belowground between functional types, with pioneer species presenting a
402 more branched and thinner root system (higher specific root length) than non-pioneer
403 species. These results agree with those published by other authors (Reich et al. 1998,
404 Huante et al. 1992, Paz 2003), although this study was carried out on a broader plant size
405 gradient and on roots larger than 2 mm. The thicker root system of non-pioneer species
406 supports the hypothesis that allocation to storage or defence is favoured in these species
407 at the expense of soil exploration (Kobe 1997, Canham et al. 1999). Investment in soil
408 exploration would in contrast be needed by pioneer species to compensate higher
409 aboveground development (i.e. SLA, allocation to branches) and hence to balance light
410 interception and belowground acquisition (Reich et al. 1998). Several authors have
411 reported that nutrient uptake potential was more likely related to the number of active
412 apices than to root mass per se (Andrew and Newman 1973, Caldwell and Richards
413 1986).

414 Root architecture was studied in greater detail in a subset of three species. We obtained a
415 topological index (TI) close to 1 for the three species. Such a TI is characteristic of
416 herringbone-like root systems which present high soil exploitation efficiency levels
417 (Fitter 1987). Little is known about how root topology changes among species belonging
418 to different successional stages and more research is needed. Caution is also required
419 when comparing the data from this study with the existing literature since we studied
420 only coarse roots ($d > 2$ mm). Different results might have been obtained if the complete
421 root system had been studied (Oppelt et al. 2001). Unfortunately the soils at the research

422 site have a very high clay content making it impossible to extract fine roots without
423 significant damage.

424 Although we had a small number of replicates per species (sampling was difficult and
425 very time consuming) differences in root architectural traits were found among the three
426 species when roots were examined in greater detail. Firstly, *Tabebuia* presented a less
427 branched root system with longer internode lengths than *Luehea*, a pioneer species, or
428 *Hura*, a species considered as “intermediate” in terms of shade tolerance (Ellis et al.
429 2000, Poorter et al. 2006). Taproot allocation was also dramatically different among the
430 three species, being three times higher in *Tabebuia* than in *Hura* or *Luehea*. Overall, the
431 analyses revealed two different strategies of soil exploration. Species like *Tabebuia* may
432 preferentially invest in storage and would produce few roots with long links to increase
433 their soil exploitation efficiency (Fitter et al. 1991). In contrast *Hura* and *Luehea* present
434 more branched roots and allocate much less to taproot, presumably to increase
435 belowground surface for resource capture. Globally, the results agree with previous
436 studies that have analysed variation of root architecture between species from different
437 successional stages in the tropics (Paz 2003) and in the boreal forest (Bauhus and Messier
438 1999, Gaucher et al. 2005). However, very little is still known about the relationship
439 between species successional status and root development (particularly under natural
440 conditions) and more research would be needed to confirm these results and better
441 understand the interaction between above- and belowground resource capture strategies.

442

443 *Conclusions*

444 We found that pioneer species were taller than non-pioneer ones for a given diameter at
445 the sapling stage. Species and functional types were shown to differ in several

446 belowground (i.e. branchiness, root length, allocation to taproot) and aboveground (SLA,
447 LAR, BWR) traits. Discriminant analysis based on a combination of allocational data
448 confirmed the classification of trees into two groups: pioneers and non-pioneer as
449 suggested from studies done in natural forests. Allocation traits significantly varied with
450 tree size. Pioneer species allocated more to branches than non-pioneer ones when small
451 and increased LAR more dramatically with size. Belowground, the pioneer species
452 presented similar root biomass compared to the non-pioneer species, but higher
453 cumulative root length and a higher number of root apices. Since both groups of species
454 are characterized by different physiologies and growing patterns, the selection of pioneer
455 vs non-pioneer long-lived shade intolerant species for restoration purposes may depend
456 on the environmental conditions (especially the frequency of seasonal drought) at the
457 plantation site.
458

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460

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472

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655
656

657 **Table 1.** Total plant leaf area and dry mass values (mean and sampled range) of the
 658 different plant compartments for the eight studied species. Leaf area was not available
 659 (n.a.) for *Enterolobium cyclocarpum*.

Species	Stem biomass, Kg	Branch biomass, Kg	Leaf biomass, Kg	Root biomass, Kg	Leaf area, m ²
<i>Luehea seemanii</i>	2.47 (0.12-8.49)	4.79 (0.06-20.47)	3.33 (0.02-15.44)	2.65 (0.075-11.34)	39.93 (0.25-185.1)
<i>Cordia alliodora</i>	4.37 (0.81-12.71)	1.76 (0.36-4.81)	1.4 (0.21-4.65)	2.14 (0.52-5.03)	17.19 (2.6-57.2)
<i>Antirrhoea trichantha</i>	0.83 (0.023-1.7)	0.67 (0.004-1.6)	0.41 (0.004-1.02)	0.52 (0.02-1.16)	6.08 (0.06-15.2)
<i>Enterolobium cyclocarpum</i>	0.72 (0.28-1.2)	0.21 (0.05-0.4)	0.15 (0.09-0.26)	0.73 (0.26-1.17)	n.a.
<i>Cedrela odorata</i>	2.35 (0.41-4.17)	1.08 (0-3.41)	0.64 (0.06-1.67)	2.65 (0.19-8.09)	5.52 (0.5-14.4)
<i>Tabebuia rosea</i>	1.08 (0.01-3.73)	0.22 (0-1.02)	0.26 (0.001-1.02)	0.63 (0.004 -2.25)	1.88 (0.007-7.2)
<i>Sterculia apetala</i>	10.3 (0.18-22.43)	3.56 (0-9.89)	1.66 (0.01-5.29)	5.03 (0.16-11.5)	17.83 (0.10-56.9)
<i>Hura crepitans</i>	8.71 (0.27-30.6)	4.33 (0-18.83)	1.7 (0.014 -6.28)	3.97 (0.13-14.9)	14.75 (0.13-54.5)

660

661

662 **Table 2.** Summary of MANOVA results of the stem weight, branch weight, leaf weight
 663 and root weight ratios and ANOVA for LAR. In both analyses tree height was used as
 664 covariable. The main factors included in the analyses were the functional type (pioneer or
 665 non pioneer) and the species nested under these groups.

Source	SS	df	F	<i>P-value</i>
<i>Stem Weight Ratio</i>				
Group	0.000906	1	0.04	0.8516
Species(Group)	0.142541	6	2.26	0.0645
Height	0.098342	1	9.35	0.0047
Height x Group	0.001195	1	0.11	0.7384
Error	0.315528	30		
<i>Branch Weight Ratio</i>				
Group	0.278809	1	15.36	0.0078
Species(Group)	0.108941	6	2.67	0.0338
Height	0.305430	1	44.95	0.0000
Height x Group	0.081025	1	11.92	0.0017
Error	0.203866	30		
<i>Leaf Weight Ratio</i>				
Group	0.001351	1	0.31	0.5981
Species(Group)	0.026200	6	1.22	0.3213
Height	0.064194	1	18.01	0.0002
Height x Group	0.012414	1	3.48	0.0718
Error	0.106945	30		
<i>Root Weight Ratio</i>				
Group	0.000054	1	0.00	0.9525
Species(Group)	0.083525	6	3.52	0.0093
Height	0.021205	1	5.36	0.0276
Height x Group	0.005187	1	1.31	0.2611
Error	0.118634	30		
<i>Leaf Area Ratio</i>				
Group	0.05254	1	0.08	0.7862
Species(Group)	3.20725	5	1.68	0.1743
Height	7.50039	1	19.67	0.0001
Height x Group	1.88254	1	4.94	0.0352
Error	9.91498	26		

666 **Table 3.** F-Ratio and *P*-value of the difference in slope steepness and intercept among the
 667 two functional types (pioneer (P) vs non-pioneer (NP)) for the various allometric
 668 regressions and R-squared value of the regressions for each functional type.

669

670

Relationship	slope		intercept		R ²	
	F-Ratio	<i>P</i> -value	F-Ratio	<i>P</i> -value	P	NP
(1) Height vs. diameter	1.31	0.2598	11.10	0.0020	0.80	0.95
(2) Plant biomass vs. diameter	0.29	0.5967	8.40	0.0063	0.93	0.94
(3) Root biomass vs. diameter	0.01	0.9213	1.19	0.2832	0.91	0.88
(4) Root length vs. diameter	1.07	0.3086	81.25	0.0000	0.95	0.84
(5) Root apices vs. diameter	1.60	0.2141	45.98	0.0000	0.82	0.68

671

672

673

674 **Figure captions**

675

676 **Figure 1.** Average canonical scores estimated by discriminant analysis for the seven of
677 the eight species of saplings studied. Species abbreviations are: Ls (*Luehea seemannii*),
678 Co (*Cordia alliodora*), Sa (*Sterculia apetala*), At (*Antirrhoea trichantha*), Co (*Cedrela*
679 *odorata*), Tr (*Tabebuia rosea*) and Hc (*Hura crepitans*). *Enterolobium cyclocarpum* was
680 excluded from the analysis because of the absence of information on leaves.

681

682 **Figure 2.** Biomass allocation to (A) trunk, (B) branches, (C) leaves and (D) roots,
683 specific leaf area (SLA) (E) and leaf area ratio (LAR) (F) for the eight target species. For
684 each species data is the mean of five individuals and bars indicate standard error. Species
685 are abbreviated as in Figure 1 with the addition of Ec (*Enterolobium cyclocarpum*).

686

687 **Figure 3.** Relationship between tree height, (x-axis) and (A) Branch Weight Ratio
688 (BWR) and (B) Leaf Area Ratio (LAR) (y-axis) between functional types. Solid line
689 indicates non-pioneer species and broken line indicates pioneer ones.

690

691 **Figure 4.** Relationship between diameter (x-axis), height and plant biomass (y-axis) for
692 the eight target species. Variables were log transformed. Solid line indicates non-pioneer
693 species and broken line indicates pioneer ones.

694

695 **Figure 5.** Relationship between diameter (x-axis), root biomass, root length and root
696 apices (y-axis) for the eight target species. Variables were log transformed. Solid line
697 indicates non-pioneer species and broken line indicates pioneer ones.

698 **Figure 6.** Relationship between diameter at the base of primordial roots (x-axis) and link
699 number (y-axis) for *Luehea seemannii* (white squares), *Hura crepitans* (grey squares) and
700 *Tabebuia rosea* (black squares). Regression lines are presented for each species.

701

702 **Figure 7.** (A) Topological index for *L. seemannii*, *H. crepitans* and *T. rosea*. For each
703 species data is the mean of 10 roots and bars indicate standard error. (B) Internode length
704 for first-order (black) and second-order roots (grey). Values represented are means and
705 standard error. The number of sampled roots per species varies between 10 and 70. (C)
706 Percentage of root biomass allocated to taproot. For each species data is the mean of three
707 root systems and bars indicate standard error.

708