

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

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Abstract We investigated biomass allocation and root architecture of eight tropical species with different successional status, as classified from the literature, along a size gradient up to 5 m. We focused on belowground development, which has received less attention than aboveground traits. A discriminant analysis based upon a combination of allocational and architectural traits clearly distinguished functional types and classified species according to successional status at a 100% success rate. For a given plant diameter, the pioneer species presented similar root biomass compared to the non-pioneer ones but higher cumulative root length and a higher number of root apices. A detailed study on the root system of a sub-sample of three species showed that the most late-successional species (*Tabebuia rosea*) had longer root internodes and a higher proportion of root biomass allocated to the taproot

compared to the other two species (*Hura crepitans* and *Luehea seemannii*). Most pioneer species showed a higher leaf area ratio due to a higher specific leaf area (SLA). We conclude that the functional differences between pioneer and non-pioneer tree species found in natural forests were maintained in open-grown plantation conditions.

Keywords Allocation · Allometry · Root architecture · Successional status · Tropical plantation

Introduction

Studies done in natural forests suggest that there are hundreds of potentially economically and ecologically interesting native tropical tree species that can be used for reforestation (Condit et al. 1993; Hooper et al. 2002). However, native species are rarely used and only a small number of introduced species (e.g. *Tectona grandis*, *Eucalyptus* spp.) dominate most plantations in degraded lands. The bias is in part due to the lack of existing knowledge about how native trees survive, grow and develop in a plantation setting (Condit et al. 1993; Piotto et al. 2004). Most previous studies analysing survival, establishment and growth patterns of native tropical species (e.g. Condit et al. 1996a; Welden et al. 1991; Poorter 2006) have been conducted in forest conditions, which can differ considerably from the environment characteristic of open-grown plantations.

In the tropics, studies on survival, growth strategies and structure of trees under different environmental conditions have mainly concentrated on the aerial parts of the plant (Aiba and Kohyama 1997; King et al. 1997; Sterck 1999; Takahashi et al. 2001; Poorter et al. 2003). Noteworthy exceptions are the papers by Kohyama and Grubb (1994)

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that examined above- and below-ground allocation of 14 warm-temperate rain forest species and that of Paz (2003) for examining an even larger number of tropical species. The first objective of our study was to characterise the development and structure of eight native species of tropical sapling trees (up to 5 m tall) growing in open, mixed plantations. These species are characterised by different abilities to colonize and regenerate in gaps in the nearby forest. We particularly focused on the structure and architecture of the belowground compartment, which has received less attention than aboveground structures although it can account for almost a half of total carbon stored by plants (Sanford and Cuevas 1996).

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

Finally, our third objective was to compare the root architecture among a sub-sample of three of the eight original species which covered a continuum of successional status. There have been very few studies focusing on the relationship between successional status and root architecture and soil exploitation efficiency (but see Bauhus and Messier 1999). Recently, a study by Paz (2003) assessed some root architectural traits for 55 species pertaining to different functional types and found that, in general, late-successional species developed thicker roots (lower specific root length (SRL) values) than early-successional ones. Carbon allocation to storage or physical defense in thicker roots has been invoked as a strategy of late-successional species to survive under shade (Kobe 1997).

In summary, the basic questions addressed here are: (1) What are the structural and allocational differences found among eight tropical tree species which could potentially

be used for land restoration purposes? (2) Do species with different successional status present structural and allocational functional differences when growing in open-grown plantations? (3) Do these differences vary along the size gradient investigated? and (4) Are there differences in root architecture among tropical trees belonging to different successional stages?

Materials and methods

Species selection, plantation establishment and early measurements

The study was conducted in a reforested pasture located in Sardinilla, in the Buena Vista region of Central Panama (9°19'30"N, 79°38'00"W). Eight native species were tentatively classified into two functional types, pioneers (*Luehea seemannii* Triana & Planch. (Tiliaceae), *Cordia alliodora* Ruiz & Pav. (Boraginaceae), and *Antirrhoea trichantha* Hemsl. (Rubiaceae)) and non-pioneers (*Enterolobium cyclocarpum* (Jacq.) Griseb. (Leguminosae), *Cedrela odorata* L. (Meliaceae), *Tabebuia rosea* Bertol. (Bignoniaceae), *Sterculia apetala* (Jacq.) Karst. (Sterculiaceae) and *Hura crepitans* L. (Euphorbiaceae)). The species classification was established based on (1) their demographic score (from Condit et al. 1996a), (2) their relative growth rate found at the seedling stage in the Barro Colorado Island permanent plot (BCI) (R. Condit, personal communication) (3) their dry seed mass (J. Wright, personal communication) and (4) a bibliographic analysis. We assume that colonizer species would be those requiring high light levels to germinate, having small seeds, high growth and mortality rates, and a demographic score (d.s.) >1. *Luehea* and *Cordia* present both a demographic score (d.s.) of 1.8 and 2.5, respectively, high growth rates (at seedling stage), the lowest (with *Antirrhoea*) seed dry masses (<0.01 g) and have already been described as pioneers in a number of studies (Welden et al. 1991; Condit et al. 1996b; Menalled and Keltly 2001; Dalling et al. 1999; Elias and Potvin 2003). *Antirrhoea* is a rare species in BCI, where it is found mainly on the shore at the northern edge of the Island (Croat 1978) and it has been relatively little studied. However it is decidedly a pioneer species (S. Lao, personal communication), characterised by very small seeds (0.0005 g of dry mass, the lowest value of the eight species studied). Kitajima et al. (2005) and Elias and Potvin (2003) also described *Antirrhoea* as a pioneer species typical of early-successional stages.

Four species (*Cedrela*, *Sterculia*, *Tabebuia* and *Hura*) have been described in many studies as long-lived shade-intolerant species but not pioneers (Welden et al. 1991; Poorter and Hayashida-Oliver 2000; Kitajima 2002;

Poorter et al. 2006). They are characterised by intermediate growth rates at the seedling stage (see Wright et al. 2003) (with the exception of *Cedrela*, which presents a high growth rate, see Menalled and Kelty 2001) and by seed dry masses above 0.01 g. From these four species, *Tabebuia* is markedly the most shade tolerant with a d.s. <0 (Condit et al. 1996a, b; Hooper et al. 2004; Kitajima 2002). *Enterolobium* on the other hand is a common species in the Panama Canal watershed yet it is characteristic of the dryer forest on the Pacific slope of the isthmus and therefore it is associated with a forest type that is more open than the wet forest of Barro Colorado Island. Seed size of *Enterolobium* would favour its classification in the non-pioneer group.

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

Allometric and morphological measurements

In August 2001, intensive allometric measurements were initiated. Saplings/trees from each of the eight species were grouped in five size class categories based on their height. The height range for each species in July 2001 was as follows: *Luehea* (0.56–4.42 m), *Cordia* (1.9–3.32 m), *Sterculia* (0.58–5.15 m), *Antirrhoea* (0.57–2.77 m), *Enterolobium* (1.66–2.48 m), *Cedrela* (0.56–3.57 m), *Tabebuia* (0.37–3.18 m) and *Hura* (0.76–4.85 m). Care was taken to sample a similar height range from all species. Differences in total height among individuals were caused by differences in growth caused by micro-scale variations in topography. All sampled individuals were healthy. Within each size category, we randomly selected one individual per species for allometric and biomass measurements. Sample size was thus five trees per species for a total of forty saplings. Each of the experimental saplings was harvested and the following traits were measured: (1) diameter at 10 cm from the ground; (2) height; (3) number, length and biomass of branches; and (4) trunk biomass. All leaves from the saplings were harvested and dried to provide total leaf biomass. We used specific leaf area (SLA)

calculated from another study (Delagrange et al. 2008) to scale up biomass of leaves to total leaf area per tree. SLA values were obtained from fifteen to twenty-five leaves per species where the leaf area had been measured with a leaf area meter (Li-Cor 3100) before being dried and weighed. Since *Enterolobium* was not considered in the Delagrange study, SLA and LAR for this species were not available. The root system of the experimental trees was manually excavated and the following measurements were taken: (1) biomass; (2) the number of root apices larger than 2 mm; and (3) the cumulative length of roots larger than 2 mm.

Root architecture measurements

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

Calculations and statistical analysis

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

Biomass, measured in 2001 (Table 1), was used to calculate the percent allocation to branches (branch weight ratio, BWR = dry mass of branches/total plant dry biomass), stem (stem weight ratio, LWR = stem dry mass/total plant dry biomass), leaves (leaf weight ratio, LWR = dry mass of leaves/total plant dry biomass) and roots (root weight ratio, RWR = dry mass of roots/total plant dry biomass). From the raw data, we calculated the specific leaf area (SLA = leaf area/leaf dry mass) and the ratio between plant leaf area and plant dry biomass (leaf area ratio, LAR).

Classification of species within different functional types was verified by a backward discriminant analysis using measured allocational and structural traits. In the discriminant analysis we excluded *Enterolobium* because of the absence of information on leaves.

The percent biomass allocation was square-root transformed and analysed by multivariate analysis of variance (MANOVA) with Functional Group (pioneer vs. non-pioneer) and Species nested under each Group as the two main effects. LAR and SLA were analysed independently by ANOVA testing for the effects of functional group and species nested under each group. LAR was square-root transformed prior to the analysis to meet the normality criterion. In all these analyses, we used tree height as a covariate to take into account the effect of tree size on allocational ratios and the interaction with functional group.

Five allometric relationships were examined by log-log linear regression to understand the architecture of the trees. The first series of regressions came from classical studies of architecture (e.g. Kohyama and Hotta 1990; Takahashi et al. 2001), specifically (1) plant height vs. plant diameter; (2) plant biomass vs. plant diameter; and (3) root biomass vs. plant diameter. The data we collected on root systems allowed estimation of two additional regressions similar to those presented by Kohyama and Grubb (1994): (4) root length vs. plant diameter and (5) number of root apices vs. plant diameter.

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

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

Results

Biomass allocation

The measured allocational traits calculated from the different biomass measurements (Table 1) were pooled together in a discriminant analysis to determine if the trait differences could distinguish between the two functional types, pioneer and non-pioneer. The discriminant analysis was highly significant (Chi-square = 38.72, $df = 4$, $P < 0.0001$). The traits retained to distinguish the functional types were root, stem and branch weight ratios (RWR, SWR, BWR) and the leaf area ratio. Amongst the 35 observations used to fit the model 100% were correctly classified by the discriminant function. Pioneer species present a positive canonical score (c.s. > 0) and non-pioneers a negative one. Examination of the c.s. revealed that *Antirrhoea* was the species which presented the combination of traits most typical of pioneer species (c.s. = 2.73), while *Tabebuia* was the species presenting the most late-successional specific traits (c.s. = -2.75) (Fig. 1).

Biomass partitioning was analysed by MANOVA to test for differences between Functional Group and Species nested under each Group. The effect of the Functional Group was found to be almost statistically different

Table 1 Total plant leaf area and dry mass values (mean and sampled range) of the different plant compartments for the eight studied species

Species	Stem biomass (Kg)	Branch biomass (Kg)	Leaf biomass (Kg)	Root biomass (Kg)	Leaf area (m ²)
<i>Luehea seemannii</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)	NA
<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)

Leaf area was not available (NA) for *Enterolobium cyclocarpum*

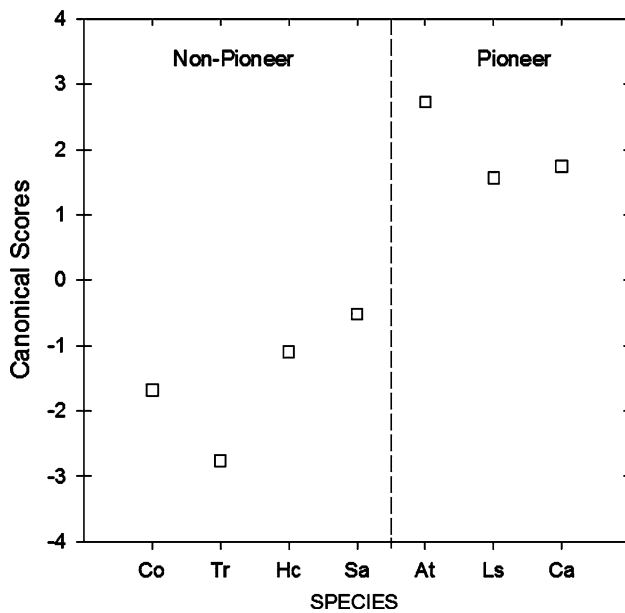


Fig. 1 Average canonical scores estimated by discriminant analysis for the seven of the eight species of saplings studied. Species abbreviations are: Ls (*Luehea seemannii*), Co (*Cordia alliodora*), Sa (*Sterculia apetala*), At (*Antirrhoea trichantha*), Co (*Cedrela odorata*), Tr (*Tabebuia rosea*)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

($P = 0.08$) with Pillai's Trace (Olson 1976) equal to 0.8943. The effect of Species nested under each group was statistically different ($P < 0.05$) with Pillai's Trace equal to 1.460. All eight species had different patterns of biomass allocation (Fig. 2). Tree size significantly affected all allocational ratios (SWR, BWR, RWR and LWR), but interactions with functional types were only present for the branch weight ratio and the leaf area ratio (Fig. 3; Table 2). For BWR the differences between the two groups decreased with tree height, while differences between groups for LAR were greater for bigger trees (Fig. 3). Within each functional group, significant variation exists among different species for all the ratios (Fig. 2; Table 2). Pioneer species such as *Antirrhoea* and *Luehea* had the greatest biomass allocation to branches (23 and 29%, respectively), while *Cedrela* and *Enterolobium*, both non-pioneer species, were the species which invested the most in roots (34 and 39%).

Non-pioneer species had significantly thicker leaves than pioneer species, with mean SLA of 84.1 and 130.6 cm^2/g , respectively. Across species, SLA ranged from 71 cm^2/g for *Tabebuia* to 148 cm^2/g for *Antirrhoea* (Fig. 2e), but the effect of species within each group was not statistically significant. Both functional types presented similar leaf weight ratios, but LAR was, in general, higher for the pioneer species (Fig. 2f). Thus, across species LAR ranged from 6.4 to 8.8 cm^2/g for non-pioneer species and

from 8.4 to 18.1 cm^2/g for pioneer species. However ANOVA did not detect significant differences between functional types once the effect of tree size was removed.

Allometric relationships

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

Root architecture

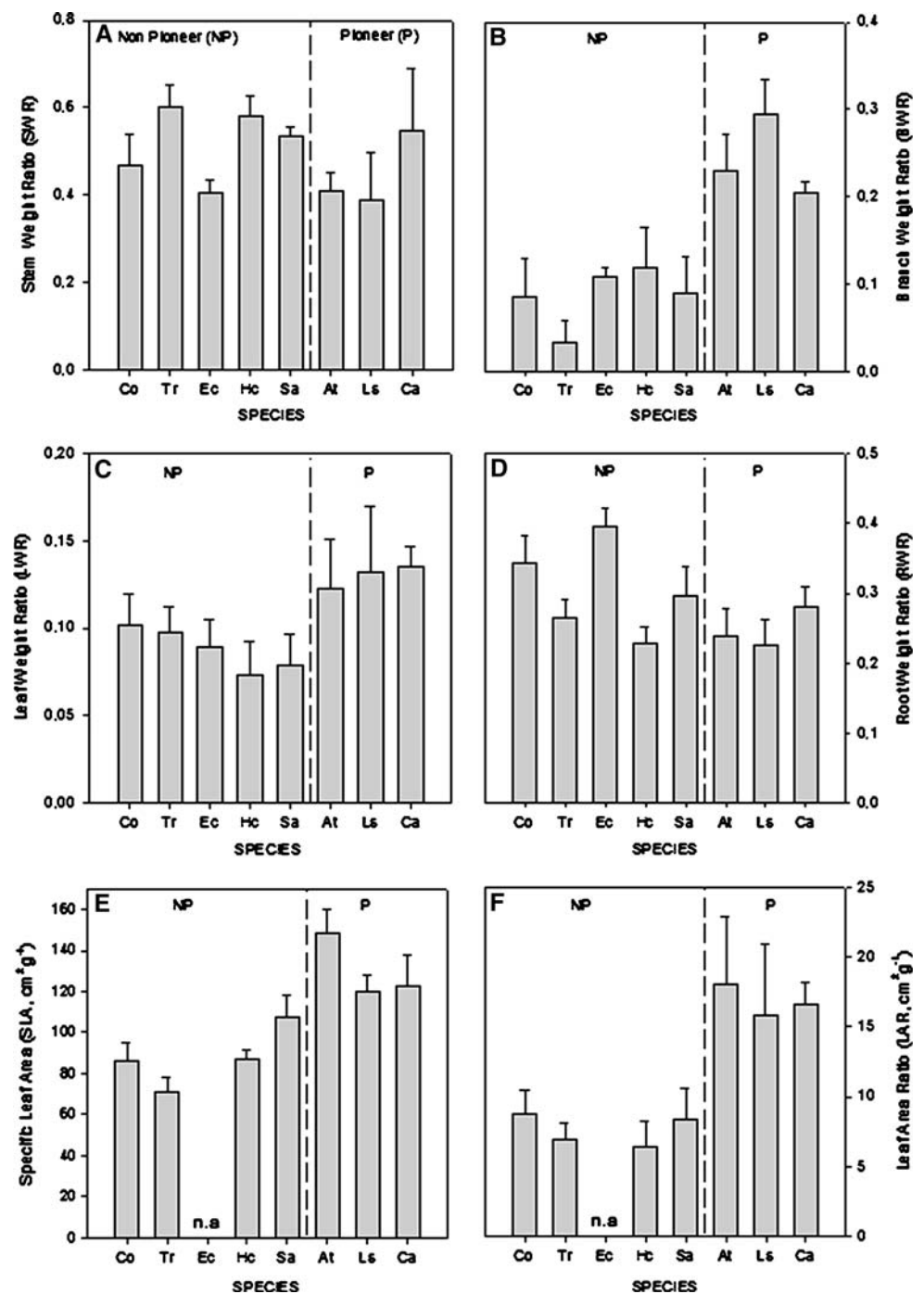
The root TI ranged from 0.80 for *Luehea* (a pioneer species) to 0.90 for *Tabebuia* but differences were not statistically significant ($P < 0.05$) (Fig. 7a). The diameter at the base of the proximal roots was a good predictor of the total root link number with a correlation coefficient of 0.72, 0.84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

Discussion

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

Over the last ten years a large number of studies have examined structural and allocation relationships for tropical tree species (e.g. King 1991; Kohyama and Grubb 1994; King et al. 1997; Coomes and Grubb 1998; Sterck 1999; Takahashi et al. 2001; Menalled and Keltly 2001). Efforts have also been made to relate architectural characteristics to ecological characteristics (Kohyama and Hotta 1990; Coomes and Grubb 1998). For example, it is well known that early-successional species tend to increase their allocation to height growth when growing in shade (Takahashi et al. 2001; Sterck 1999; King et al. 1997), while late-successional ones tend to reduce or even stop their height growth in order to maintain high LWR and

Fig. 2 Biomass allocation to (a) trunk, (b) branches, (c) leaves and (d) roots, specific leaf area (SLA) (e) and leaf area ratio (LAR) (f) for the eight target species. For each species data is the mean of five individuals and bars indicate standard error. Species are abbreviated as in Fig. 1 with the addition of Ec (*Enterolobium cyclocarpum*)



LAR and minimise construction costs in light-limited environments (Takahashi et al. 2001; Sterck 1999; King et al. 1997; Delagrangé et al. 2004). Biomass allocation in trees thus appears to be relatively plastic. In this study we found that pioneer species were taller than non-pioneer long-lived shade intolerant species for a given diameter. These results agreed with the findings of King (1991) and Poorter et al. (2003) and thus with the hypothesis that pioneer species must give priority to height growth to reach the canopy as soon as possible to avoid competition for

light. Bohlman and O'Brien (2006) recently pointed out that the differences in size between functional types were only present in the early stages of plant development (up to 10 cm dbh) which covers the range of dbh of the present study.

Tree diameter was a good predictor of both total plant and belowground biomass. It has been suggested that plant biomass is more strongly correlated with secondary (diameter) than primary growth (height) (Chave et al. 2001). Yet we found a very strong correlation between

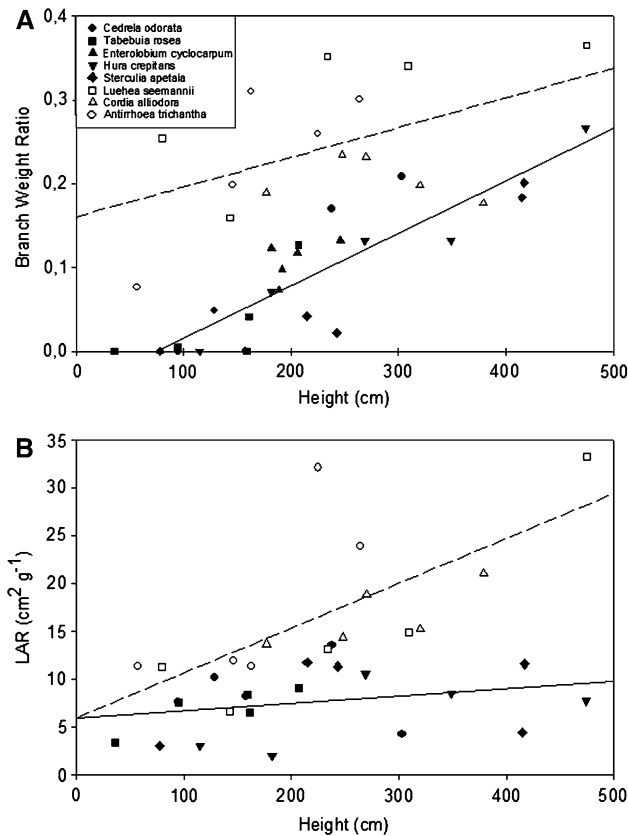


Fig. 3 Relationship between tree height, (x-axis) and (a) Branch Weight Ratio (BWR) and (b) Leaf Area Ratio (LAR) (y-axis) between functional types. *Solid line* indicates non-pioneer species and *broken line* indicates pioneer ones

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

In our study, LAR varied considerably between trees and species within each functional group, but pioneer tree species tended to present higher LAR values than non-pioneer ones. This was due to species differences in SLA

Table 2 Summary of MANOVA results of the stem weight, branch weight, leaf weight and root weight ratios and ANOVA for LAR. In both analyses tree height was used as covariable

Source	SS	df	F	P value
Stem weight ratio				
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 × Group	0.001195	1	0.11	0.7384
Error	0.315528	30		
Branch weight ratio				
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 × Group	0.081025	1	11.92	0.0017
Error	0.203866	30		
Leaf weight ratio				
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 × Group	0.012414	1	3.48	0.0718
Error	0.106945	30		
Root Weight Ratio				
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 × Group	0.005187	1	1.31	0.2611
Error	0.118634	30		
Leaf Area Ratio				
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 × Group	1.88254	1	4.94	0.0352
Error	9.91498	26		

The main factors included in the analyses were the functional type (pioneer or non pioneer) and the species nested under these groups

since, as reported above, biomass allocation to leaves varied little (see Fig. 1). This particular difference in leaf morphology between functional types is critical since it provides contrasting nitrogen and water-use efficiencies and different leaf life spans (Terwilliger et al. 2001; Onoda et al. 2004). In a parallel study conducted in the same experimental site we found a positive relationship between SLA and leaf photosynthetic nitrogen use efficiency (PNUE) (Delgrange et al. 2008) and Kitajima (1994) and Walters et al. (1993), among others, have reported higher photosynthetic rates and SLA values for pioneer species than for non-pioneers when growing under high light conditions. SLA is known to well predict photosynthetic capacity under high light conditions and particularly at

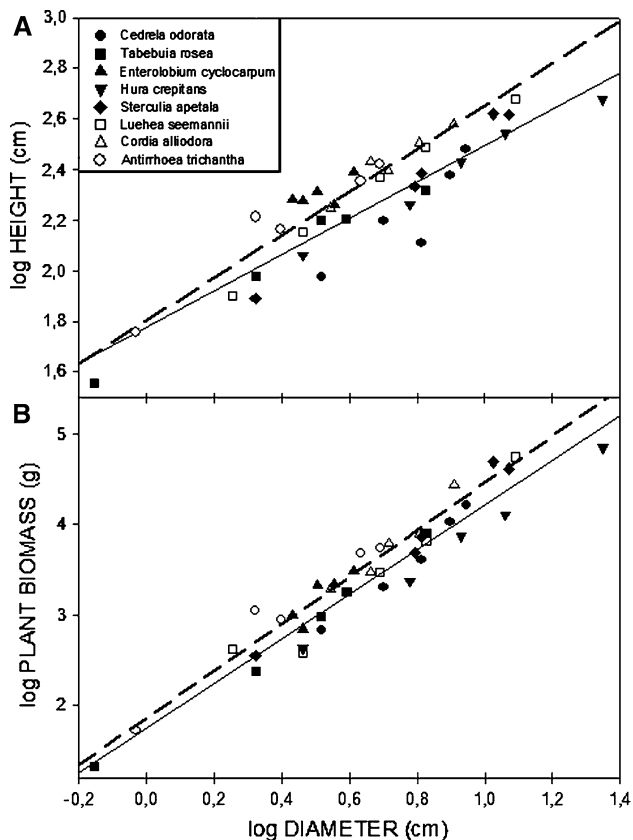


Fig. 4 Relationship between diameter (x -axis), height and plant biomass (y -axis) for the eight target species. Variables were log transformed. *Solid line* indicates non-pioneer species and *broken line* indicates pioneer ones

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

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

Several recent papers have reported that tree size affects aboveground biomass distribution and the need to consider these effects when analysing such traits (Veneklaas and

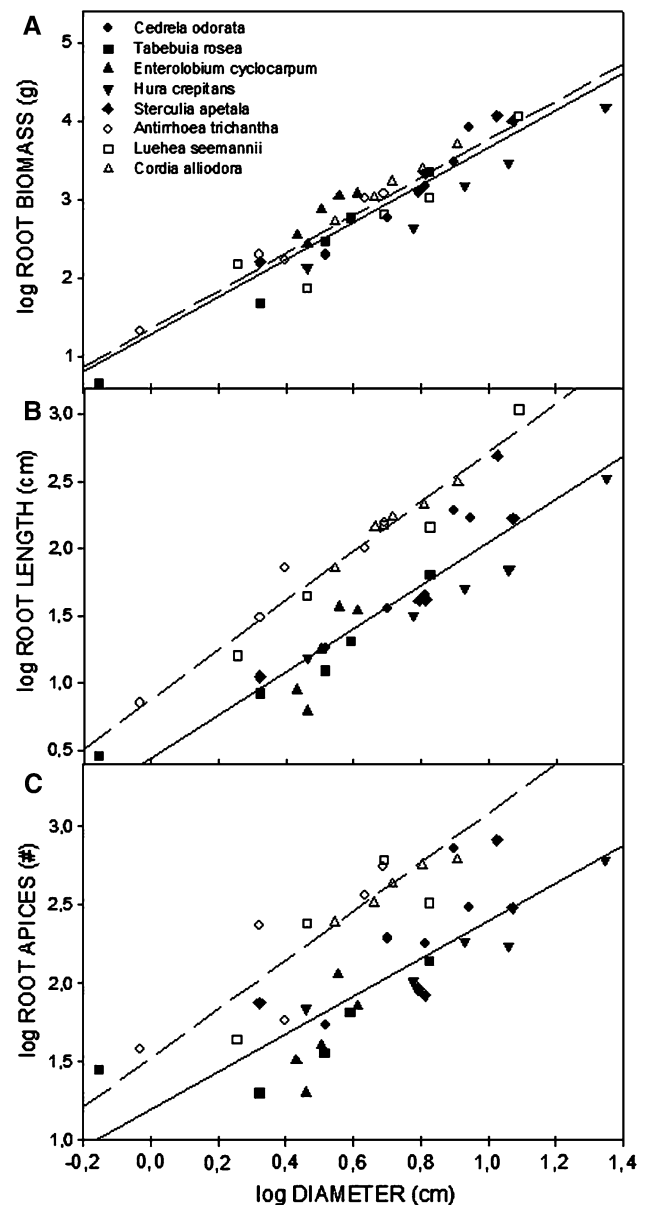


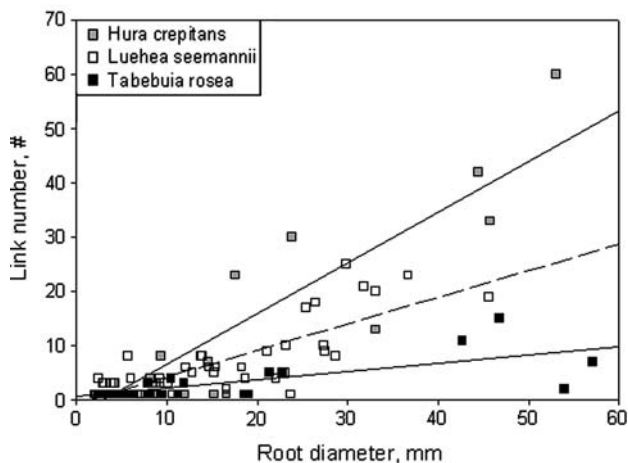
Fig. 5 Relationship between diameter (x -axis), root biomass, root length and root apices (y -axis) for the eight target species. Variables were log transformed. *Solid line* indicates non-pioneer species and *broken line* indicates pioneer ones

Poorter 1998; Menalled and Kelty 2001; Delagrange et al. 2004). Furthermore, both Delagrange et al. (2004) and Claveau et al. (2005) found that the effects of tree size varied according to the availability of resource, in this case light. In the present study, most allocational ratios were strongly influenced by tree size.

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

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

Relationship	Slope		Intercept		<i>R</i> ²	
	<i>F</i> -Ratio	<i>P</i> -value	<i>F</i> -Ratio	<i>P</i> -value	P	NP
Height versus diameter	1.31	0.2598	11.10	0.0020	0.80	0.95
Plant biomass versus diameter	0.29	0.5967	8.40	0.0063	0.93	0.94
Root biomass versus diameter	0.01	0.9213	1.19	0.2832	0.91	0.88
Root length versus diameter	1.07	0.3086	81.25	0.0000	0.95	0.84
Root apices versus diameter	1.60	0.2141	45.98	0.0000	0.82	0.68

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

in pioneer species during early development needs to be made cautiously because other factors such as leaf size or petiole length can greatly influence branchiness and crown construction (King and Maindonald 1999). In our study, pioneer species were characterised by relatively small leaves while non-pioneers ones have large compound leaves (*Tabebuia*, *Enterolobium*, *Cedrela*) or long petioles (up to 10–13 cm, *Hura*). Differences in leaf size between species could thus also explain why the non-pioneer species start branching at higher size, since first branch height has been found to be positively related to leaf size (and/or petiole length) (King 1998). The interaction between size and functional types for BWR and LAR could alternatively be explained by the presence of an aboveground foraging strategy in pioneer species which would consist in establishing rapidly their branching system to then increase their LAR and maximize light capture and growth. Thus under favourable growing conditions (without seasonal drought periods) pioneer species such as *Luehea* or *Cordia* are probably the most appropriate for rapid land restoration purposes (e.g. Condit et al. 1993). However in sites with

restricted water availability or on poor soils the use of more conservative non-pioneer species (with lower LAR and thus lower evaporative demands) or nitrogen-fixing species, such as *Enterolobium*, seems more appropriate (Craven et al. 2007).

Variation in root allocation and architecture

A limitation of existing data on tropical tree biomass allocation and morphology is that most studies only consider the aboveground components of trees (but see Kohyama and Grubb 1994). In our study, root biomass was measured and was found to vary widely among species without a clear trend between the two functional types (Fig. 5). However the number of root apices as well as cumulative root length differed significantly between functional types, the pioneer species having, on average, more root apices and root length at a given plant size. In other words, morphological rather than allocational differences were found belowground between functional types, with pioneer species presenting a more branched and thinner root system (higher specific root length) than non-pioneer species. These results agree with those published by other authors (Reich et al. 1998; Huante et al. 1992; Paz 2003), although this study was carried out on a broader plant size gradient and on roots larger than 2 mm. The thicker root system of non-pioneer species supports the hypothesis that allocation to storage or defence is favoured in these species at the expense of soil exploration (Kobe 1997; Canham et al. 1999). Investment in soil exploration would in contrast be needed by pioneer species to compensate higher aboveground development (i.e. SLA, allocation to branches) and hence to balance light interception and belowground acquisition (Reich et al. 1998). Several authors have reported that nutrient uptake potential was more likely related to the number of active apices than to root mass per se (Andrew and Newman 1973; Caldwell and Richards 1986).

Root architecture was studied in greater detail in a subset of three species. We obtained a TI close to 1 for the three species. Such a TI is characteristic of herringbone-like root

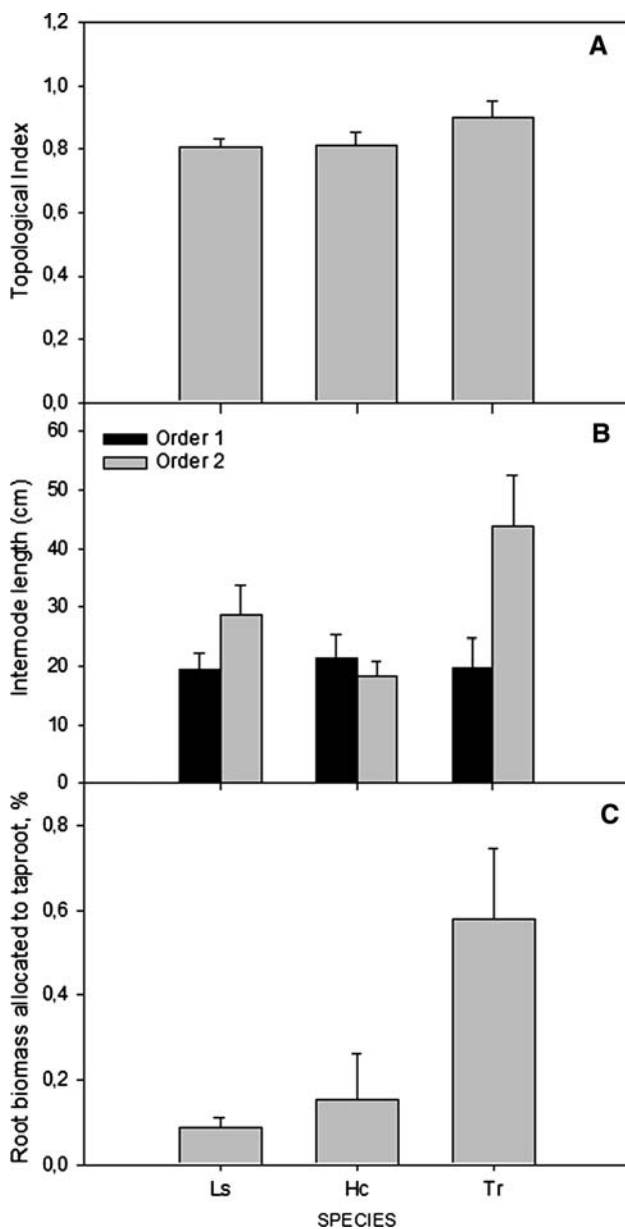


Fig. 7 **a** Topological index for *L. seemannii*, *H. crepitans* and *T. rosea*. For each species data is the mean of ten roots and bars indicate standard error. **b** Internode length for first-order (black) and second-order roots (grey). Values represented are means and standard error. The number of sampled roots per species varies between 10 and 70. **c** Percentage of root biomass allocated to taproot. For each species data is the mean of three root systems and bars indicate standard error

systems which present high soil exploitation efficiency levels (Fitter 1987). Little is known about how root topology changes among species belonging to different successional stages and more research is needed. Caution is also required when comparing the data from this study with the existing literature since we studied only coarse roots ($d > 2$ mm). Different results might have been obtained if the complete root system had been studied (Oppelt et al.

2001). Unfortunately the soils at the research site have a very high clay content making it impossible to extract fine roots without significant damage.

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

Conclusions

We found that pioneer species were taller than non-pioneer ones for a given diameter at the sapling stage. Species and functional types were shown to differ in several belowground (i.e. branchiness, root length, allocation to taproot) and aboveground (SLA, LAR, BWR) traits. Discriminant analysis based on a combination of allocational data confirmed the classification of trees into two groups: pioneers and non-pioneer as suggested from studies done in natural forests. Allocation traits significantly varied with tree size. Pioneer species allocated more to branches than non-pioneer ones when small and increased LAR more dramatically with size. Belowground, the pioneer species presented similar root biomass compared to the non-pioneer species, but higher cumulative root length and a higher number of root apices. Since both groups of species are characterised by different physiologies and growing patterns, the selection of pioneer versus non-pioneer long-lived shade intolerant species for restoration purposes may

depend on the environmental conditions (especially the frequency of seasonal drought) at the plantation site.

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References

- Aiba S-I, Kohyama T (1997) Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. *J Ecol* 85:611–624
- Andrew RE, Newman EI (1973) Root density and competition for nutrients. *Oecol Plant* 5:319–334
- Bauhus J, Messier C (1999) Soil exploitation strategies of fine roots in different tree species of the southern boreal forest of eastern Canada. *Can J For Res* 29:260–273
- Bohlman S, O'Brien S (2006) Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island, Panama. *J Trop Ecol* 22:123–136
- Caldwell MM, Richards JH (1986) Competing root systems: morphology and models of absorption. In: Givnish TJ (ed) *On the economy of plant form and function*. Cambridge University Press, Cambridge, pp 251–273
- Canham CD, Kobe RK, Latty ER, Chazdon RL (1999) Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. *Oecologia* 121:1–11
- Chave J, Riera B, Dubois M-A (2001) Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *J Trop Ecol* 17:79–96
- Claveau Y, Messier C, Comeau PG (2005) Interacting influence of light and size on aboveground biomass distribution in sub-boreal conifer saplings with contrasting shade tolerance. *Tree Physiol* 25:373–384
- Condit RG, Hubbell SP, Foster RB (1993) Identifying fast-growing native trees from the neotropics using data from a large, permanent census plot. *For Ecol Manag* 62:123–143
- Condit RG, Hubbell SP, Foster RB (1996a) Assessing the response of plant functional types to climatic change in tropical forests. *J Veg Sci* 7:405–416
- Condit RG, Hubbell SP, Foster RB (1996b) Changes in tree species abundance in a Neotropical forest: impact of climate change. *J Trop Ecol* 12:231–256
- Coomes DA, Grubb PJ (1998) A comparison of 12 species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Funct Ecol* 12:426–435
- Craven D, Braden D, Ashton MS, Berlyn GP, Wishnie M, Dent D (2007) Between and within-site comparisons of structural and physiological characteristics and foliar nutrient content of 14 tree species at a wet, fertile site and a dry, infertile site in Panama. *For Ecol Manag* 238:335–346
- Croat TB (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford, p 943
- Curt T, Prévosto B (2003) Root biomass and rooting profile of naturally regenerated beech in mid-elevation Scots pine woodlands. *Plant Ecol* 167:269–282
- Dalling JW, Lovelock CE, Hubbell SP (1999) Growth responses of seedlings of two neotropical pioneer species to simulated forest gap environments. *J Trop Ecol* 15:827–839
- Delagrange S, Messier C, Lechowicz MJ, Dizengremel P (2004) Physiological, morphological and allocational plasticity in understory deciduous trees: importance of plant size and light availability. *Tree Physiol* 24:775–784
- Delagrange S, Potvin C, Messier C, Coll L (2008) Linking multiple-level tree traits with biomass accumulation in native tree species used for reforestation in Panama. *Trees*. doi:10.1007/s00468-007-0189-0
- Diaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:464–655
- Elias M, Potvin C (2003) Assessing inter- and intra-specific variation in trunk carbon concentration for 32 neotropical tree species. *Can J For Res* 33:1039–1045
- Ellis AR, Hubbell SP, Potvin C (2000) In situ photosynthetic measurements of photosynthetic rates of tropical tree species: a test of the functional group hypothesis. *Can J Bot* 78:1336–1347
- Fearnside P (2000) Global warming and tropical land use change: Greenhouse gas emissions from biomass burning, decomposition and soil in forest conversion, shifting cultivation and secondary vegetation. *Clim Change* 46:115–158
- Fitter AH (1987) An architectural approach to the comparative ecology of plant root systems. *New Phytol* 106:61–77
- Fitter AH, Strickland TR, Harvey ML, Wilson GW (1991) Architectural analysis of plant root systems. I. Architectural correlates of exploitation efficiency. *New Phytol* 118:375–382
- Gaucher G, Gougéan S, Mauffette Y, Messier C (2005) Seasonal variation in biomass and carbohydrate partitioning of understory sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) seedlings. *Tree Physiol* 25:93–100
- Givnish TJ (1988) Adaptation to sun and shade: a whole-plant perspective. *Aust J Plant Physiol* 15:63–92
- Hooper ER, Condit R, Legendre P (2002) Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. *Ecol Appl* 12:1626–1641
- Hooper ER, Legendre P, Condit R (2004) Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology* 85:3313–3326
- Huante P, Rincon E, Gavito M (1992) Root system analysis of seedlings of seven tree species from a tropical dry forest in Mexico. *Trees* 6:77–82
- King DA (1991) Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Funct Ecol* 5:485–492
- King DA (1998) Influence of leaf size on tree architecture: first branch height and crown dimensions in tropical rain forest trees. *Trees* 12:438–445
- King DA, Maindonald JH (1999) Tree architecture in relation to leaf dimensions and tree stature in temperate and tropical rain forests. *J Ecol* 87:1012–1024
- King DA, Leigh EG Jr, Condit R, Foster RB, Hubbell SP (1997) Relationship between branch spacing, growth rate and light in tropical forest saplings. *Funct Ecol* 11:627–635
- Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428
- Kitajima K (2002) Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. *Funct Ecol* 16:433–444

- Kitajima K, Mulkey SS, Wright J (2005) Variation in crown light utilization characteristics among tropical canopy trees. *Ann Bot* 95:535–547
- Kneeshaw D, Kobe RK, Coates KD, Messier C (2006) Sapling size influences shade tolerance ranking among southern boreal tree species. *J Ecol* 94:471–480
- Kobe RK (1997) Carbohydrate allocation as a basis of interspecific variation in sapling survivorship and growth. *Oikos* 80:226–233
- Kohyama T, Hotta M (1990) Significance of allometry in tropical saplings. *Funct Ecol* 4:515–521
- Kohyama T, Grubb PJ (1994) Below- and above-ground allometries of shade-tolerant seedlings in a Japanese warm-temperature rain forest. *Funct Ecol* 8:229–236
- Lavorel S, Garnier E (2002) Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy grail. *Funct Ecol* 16:545–556
- Menalled FD, Kelty MJ (2001) Crown structure and biomass allocation strategies of three juvenile tropical tree species. *Plant Ecol* 152:1–11
- Messier C, Doucet R, Ruel J-C, Claveau Y, Kelly C, Lechowicz MJ (1999) Functional ecology of advance regeneration in relation to light in boreal forests. *Can J For Res* 29:812–823
- Olson CL (1976) On choosing a test statistic in multivariate analysis of variance. *Psychol Bull* 83:579–586
- Onoda Y, Hikosaka K, Hirose T (2004) Allocation to cell walls decreases photosynthetic nitrogen-use efficiency. *Funct Ecol* 18:419–425
- Oppelt AL, Kurth W, Godbold DL (2001) Topology, scaling relations and Leonardo's rule in root systems from African tree species. *Tree Physiol* 21:117–128
- Ozier-Lafontaine H, Lecompte F, Sillon J-F (1999) Fractal analysis of the root architecture of *Gliricidia sepium* for the spatial prediction of root branching, size and mass: model development and evaluation in agroforestry. *Plant Soil* 209:167–180
- Paz H (2003) Root/shoot allocation and root architecture in seedlings: variation among forest sites, microhabitats, and ecological groups. *Biotropica* 35:318–332
- Piotto D, Viquez E, Montagnini F, Kanninen M (2004) Pure and mixed forest plantations with native species of the dry tropics of Costa Rica: a comparison of growth and productivity. *For Ecol Manag* 190:359–372
- Poorter L (1999) Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. *Funct Ecol* 13:396–410
- Poorter L, Hayashida-Oliver Y (2000) Effects of seasonal drought on gap and understorey seedlings in a Bolivian moist forest. *J Trop Ecol* 16:481–498
- Poorter L, Bongers F, Sterck FJ, Wöll H (2003) Architecture of 53 rain forest tree species differing in adult stature and shade tolerance. *Ecology* 84:602–608
- Poorter L, Bongers L, Bongers F (2006) Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. *Ecology* 87:1289–1301
- Reich PB, Tjoelker MG, Walters MB, Vanderklein DW, Buschena C (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Funct Ecol* 12:327–338
- Sanford RL, Cuevas E (1996) Root growth and rhizosphere interactions in tropical forests. In: Mulkey S, Chazdon RL, Smith AP (eds) *Tropical Forest plant ecophysiology*. Chapman and Hall, New York, pp 268–300
- Scherer-Lorenzen M, Potvin C, Koricheva J, Schmid B, Hector A, Bornik Z, Reynolds G, Schulze ED (2005) The design of experimental tree plantations for functional biodiversity research. In: Scherer-Lorenzen M, Korner Ch, Schulze ED (eds) *Forest diversity and function: temperate and Boreal systems*. Ecological Studies 176. Springer, Berlin, pp 347–376
- Sterck FJ (1999) Crown development in tropical rain forest trees in gaps and understorey. *Plant Ecol* 143:89–98
- Takahashi K, Seino T, Kohyama T (2001) Responses to canopy openings in architectural development of saplings in eight deciduous broad-leaved tree species. *Can J For Res* 31:1336–1347
- Terwilliger VJ, Kitajima K, Le Roux-Swarthout DJ, Mulkey S, Wright SJ (2001) Intrinsic water-use efficiency and heterotrophic investment in tropical leaf growth of two Neotropical pioneer tree species as estimated from $\delta^{13}\text{C}$ values. *New Phytol* 152:267–281
- Thies WG, Cunningham PG (1996) Estimating large-root biomass from stump and breast-height diameters for Douglas-fir in western Oregon. *Can J For Res* 26:237–243
- Veneklaas EJ, Poorter L (1998) Carbon partitioning strategies of tropical tree seedlings in contrasting light environments. In: Lambers H, Poorter H, Van Vuuren MMI (eds) *Inherent variation in plant growth. Physiological mechanisms and ecological consequences*. Backhuys Publishers, Leiden, pp 337–361
- Walters MB, Kruger EL, Reich PB (1993) Growth, biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. *Oecologia* 94:7–16
- Welden CW, Hewett SW, Hubbell SP, Foster RB (1991) Sapling survival, growth, and recruitment: relationship to canopy height in a neotropical forest. *Ecology* 72:35–50
- Wright SJ, Muller-Landau H, Condit R, Hubbell SP (2003) Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. *Ecology* 84:3174–3185