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Diameter increment patterns among 106 tree species in a logged and silviculturally treated Costa Rican rain forest

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1. Introduction

Interspecific variations in tree growth rates play a pivotal role in the determination of the structure, composition and timber yield of forests (Whitmore, 1984; Hubbell and Foster, 1990; Alder, 1995). In apparent recognition of this fact, Alder and Synnott (1992, p. 66) recommend the correct botanical identification of every measured tree in permanent sample plot (PSP) studies of stand dynamics, growth and yield in mixed tropical forest. Many factors may play a role in determining whether or not this recommendation is implemented. Data based on local or industrial taxonomy may be adequate for many purposes, including those directly linked to management. Vanclay (1991), for example, used standard trade names for tree species in the development of increment functions for the prediction of timber yields of north Queensland rain forests. Considerable understanding of forest stand dynamics and productivity has been gained from the major research initiative at Paracou, French Guiana (e.g. Schmitt and Bariteau, 1990), even though the complete botanical identification of species in PSPs was only being completed during 1998 (A. Franc, personal communication). Similarly, Silva et al. (1995) were able to give a clear description of growth and yield of a heavily logged forest at Tapajos National Forest in the Brazilian Amazon, another well-known neotropical research site, without giving information on growth rates of individual species. It must also be taken into account that the presence of 100–200 tree species or more, $\geq$10 cm DBH in a typical 1.0 ha PSP in neotropical lowland rain forest (Gentry, 1988), represents a formidable logistical barrier to the identification of all individuals in the PSP. Nevertheless, if greater insight regarding the biological and ecological factors that determine forest dynamics and productivity is required, the identification of botanical species is needed. Now that forest managers are required not only to sustain production, but also to conserve biodiversity (Sayer and Wegge, 1992; ITTO, 1992; Stork et al., 1997), this need has arguably become urgent.

The present study was carried out in a lowland rain forest of northeastern Costa Rica, under management for timber production since 1988. This forest is situated in the Central American Atlantic Moist Forest ecoregion (Dinerstein et al., 1995) a forest region which is poorly known from the standpoint of biophysical aspects of forest management (Finegan and Camacho, in press). Forest responses to different silvicultural approaches are under investigation at the site using standard permanent sample plot techniques (Alder and Synnott, 1992), with botanical identification to species level of all individuals present in the plots. Full details of stand dynamic responses to timber harvesting and silvicultural interventions in this forest are given by Finegan and Camacho (in press). Our overall objective for the present paper was to identify trends and patterns of stem diameter growth rates in relation to taxonomic identity and functional criteria, such as adult size and putative light requirements for successful regeneration. We also wished to determined the effects of silvicultural treatments and tree attributes such as crown illumination on these trends and patterns.

2. Methods

2.1. Study site

A full site description is given by Finegan and Camacho (in press). The study site was La Tirimbina Farm (now Tirimbina Rain Forest Centre), near La Virgen, Sarapiquí Canton, Heredia Province, Costa Rica (10° 24′N, 84° 06′W) at an altitude of 180–200 m asl. The life zone is tropical wet forest (Holdridge's system; Tosi, 1969) with mean annual precipitation of 3864 mm and mean annual temperature 24.5°C, and the site is situated in the Central American Atlantic Moist Forest ecoregion (Dinerstein et al., 1995). La Tirimbina lies on highly weathered old lava flows in which the dominant materials is andesitic basalt (Mata, 1997). Topography is of low hills dissected by streams, some of which rise within the property, and soils are Ultisols (Mata, 1997).

2.2. Silvicultural experiment

The silvicultural experiment is fully described by Finegan and Camacho (in press). The originally old-growth forest, dominated by *Pentaclethra macroloba* (Fabaceae/Mim.) was lightly logged at irregular intervals over the period 1960–1989 (J.R. Hunter, personal communication). The experiment is under way in a

540 m × 540 m (29.16 ha) area which was placed under management for the sustainable production of timber in 1989. Timber was harvested at low intensity (10.1 m^3 ha^{-1}) from the whole area in 1989 and 1990. The area was then divided into nine 180 m × 180 m (3.24 ha) plots for the application of post-harvest silvicultural treatments. Three different treatment regimes were contemplated under a complete randomised block design (three replicate plots per silvicultural regime; hereafter, silvicultural regimes are referred to as 'treatments' and individual 3.24 ha plots as 'treatment plots'). The first treatment was the timber harvest with no subsequent intervention, referred to hereafter as the 'control' treatment. The second treatment was applied in 1991 and involved a refinement and subsequent liberation of individuals determined to be potential crop trees. Potential crop trees were identified by criteria of species (current market value), crown form and stem form. This treatment is hereafter referred to as the 'liberation/refinement' treatment. The third treatment was applied in 1992 and consisted of the formation of a shelterwood (see Baur, 1968) by felling of the middle stories of the forest for industrial firewood and posts. This treatment is hereafter referred to as the 'shelterwood'.

Stem diameter increments of all individuals ≥10 cm DBH (DBH: 1.3 m) were monitored in a square 1.0 ha permanent sample plot (PSP) in the centre of each 3.24 ha treatment plot. As silvicultural treatments were applied to each complete 3.24 ha plot, the PSPs were separated from neighbouring treatment plots, as well as adjacent unmanaged forest, by 40-m wide buffer strips. Measurement began in 1988 in three PSPs with the intention of obtaining information on pre-intervention growth rates; these were PSPs 3 (liberation/refinement treatment), 4 and 8 (both control plots). Enumeration of the complete set of nine PSPs was implemented in 1990; the six additional PSPs set up in this latter year were all enumerated before the timber harvest. The control and liberation treatments were subsequently measured annually to 1994 and again in 1996, while the shelterwood treatment was measured in 1990, 1991, 1993, 1994 and 1996.

At each enumeration, DBH of all live individuals ≥10 cm DBH was measured to the nearest mm with a fibreglass diameter tape. The point of measurement was permanently marked on each tree with paint, as was a code identifying each individual. Crown illumination and crown form were estimated at the first enumeration, and again in 1992, 1994 and 1996 using Dawkins's five-point scales (see Alder and Synnott, 1992). For crown illumination, the categories were: 5 – emergent crown; 4 – crown fully illuminated from above; 3 – crown partially illuminated from above; 2 – crown with lateral illumination only; and 1 – crown with no significant direct illumination. The crown form categories were: 5 – 'perfect' crown; 4 – good form (irregular circle); 3 – tolerable crown (distinctly asymmetrical and thin); 2 – poor crown, strong asymmetry with few main branches; and 1 – very poor crown, one or few branches only. The degree of competition from lianas was estimated in the same years as crown illumination and form, using the following scale (Hutchinson, 1987): 1 – no lianas visible on tree; 2 – lianas visible on tree but recently severed; 3 – lianas on trunk only; 4 – lianas on crown only; and 5 – lianas on both trunk and crown. All these variables have shown significant correlations with tree DBH increments in tropical rain forests (Alder and Synnott, 1992).

Unless the individual was of a common species, a voucher specimen was taken from each one. Species identifications were carried out by NZ on field visits or by examination of voucher specimens. Each species identified was classified according to the height range normally occupied by the adult tree, as follows: 2 – understory: adult <5 m total height: 3 – middle story, adult >5 m and <25 m total height; 4 – subcanopy/canopy, adult >25 m and <35 m total height; and 5 – canopy/emergent: adults reaching >35 m total height. This classification is hereafter referred to as 'adult size'.

2.3. Analysis of data

Species were grouped on the basis of two criteria (Alder, 1995): similarity of their observed diameter increments, and adult size. Cluster analysis was used as the primary method for grouping species, being carried out on diameter increment data only and employing procedures provided by the Statistical Analysis System (Statistical Analysis System Institute Inc., 1985). All species for which increments were available for at least one individual per hectare in at least one of the three treatments were included in the analysis; 106 species met this criterion, 45 of them meeting it in each experimental treatment. The first quartile, median and third quartile of the increment distribution were used to characterise each species. The silvicultural treatments showed a highly significant effect on diameter increments for the period 1993–1996 at La Tirimbina (Finegan and Camacho, in press) and preliminary analyses comparing the 1990–1993 and 1993–1996 periods showed that such an effect was also evident in the results of the cluster analysis. Given the objectives of the present paper, we present the results of analysis for the latter period of the study. A single cluster analysis was finally carried out, classifying the raw data by species and experimental treatment. As the abundances of some species were ≥ 1 individual ha^{-1} in two or three treatments, they therefore appeared two or three times in the raw data matrix and the resulting classification. This approach permitted the evaluation of the effects of silvicultural treatment on the classification. For clustering, Ward's method was used on a similarity matrix containing the squares of the Euclidean distances between species; Pseudo-*F* and Tukey tests ($\alpha = 0.05$) were applied to select a definitive number of groups from the alternatives possible. Discriminant analyses were subsequently applied to test the robustness of the groups generated by the cluster analysis and determine whether any species should be relocated. Canonical Correlation Analysis was used to assess the relationships between the descriptor variables and the species groups, and for visual interpretation of the groups. The species groups finally established on the basis of diameter increments were then subdivided on the basis of adult size to form the final grouping.

After the establishment of the species grouping, a preliminary exploration of the factors affecting the diameter growth of individual trees within each group was made using correlation analysis (the non-parametric Spearman correlation coefficient r_s was used). The tree characteristics whose relationships to diameter growth rates were thus investigated were initial DBH, crown illumination, crown form and presence of lianas.

3. Results

Cluster analysis indicated that the optimum number of groups for this dataset was 3–6. The value of the third quartile (Q3) was the single parameter of the increment distributions with greatest influence on the classifications. Tukey tests indicated that the greatest differences between groups were manifest when five groups were considered, so that five species groups based on diameter increments are presented here as the first step in the development of the species grouping. These groups are subsequently referred to as those of very slow growth, slow growth, moderate growth, fast growth and very fast growth, respectively. Not all the diameter increment groups contained species in all the adult size categories, so that their subdivision on the basis of this latter criterion produced a final classification comprising seventeen groups out of a possible 20 (five increment groups × four adult size categories) (see Appendix A). The relationship between diameter growth rates and adult size categories is considered below.

Although the species grouping was derived from a single analysis, the results are presented by treatment in order to highlight treatment effects on diameter increments. It is emphasised that in characteristics such as the proportions of species in different increment groups and the increment groups to which certain individual species belong, treatment effects on the grouping were clearly very strong.

The mean values of each of the three parameters of the increment distribution used in the cluster analysis, are shown for each of the five diameter increment groups in Table 1 (the diameter increment groups are shown alongside the final classification incorporating adult height in Appendix A, where the individual species assigned to each group, with their respective adult category and values of the increment distributions, are also presented). During the study period, the interspecific variability of diameter increments in this forest, ≥ 10 DBH, was clearly enormous: the mean value of the median annual diameter increment was ca. 15 times greater in the group of very fast diameter increments, at 15.7 mm, than in that of very slow increments at ca. 1 mm (Table 1). Part of this enormous variability was related to adult height. All adult height categories were represented in the very slow increment group, but under each of the three experimental treatments, more than half the species in this group occupy the under- and middle stories of the forest as adults (groups 1 and 2 of the final classification – very slow-growing understory species and very

Table 1
Mean group values per experimental treatment of diameter increment parameters (first quartile, median and third quartile, in mm year^{-1}) used in formation of groups, under three regimes of silvicultural treatment in a managed lowland rain forest at La Tirimbina, northeastern Costa Rica. Figures in parentheses are the total numbers of species ≥10 cm DBH in each group. See text for details of assignment of species to groups

Treatment	Diameter increment group	Diameter increment parameter		
		first quartile	median	third quartile
Control	very slow (38)	0.1	0.8	1.8
	slow (21)	1.4	3.3	5.9
	moderate (12)	2.5	5.4	11.8
	fast (–)	—	—	—
	very fast (3)	7.2	15.7	21.2
Liberation	very slow (22)	0.4	1.1	2.1
	slow (24)	1.4	3.7	6.5
	moderate (13)	1.8	6.0	10.5
	fast (8)	6.3	9.3	14.7
	very fast (3)	9.7	15.3	18.2
Shelterwood	very slow (32)	0.4	1.1	2.2
	slow (23)	1.7	3.5	5.9
	moderate (6)	3.2	6.1	10.8
	fast (7)	6.1	9.9	14.2
	very fast (3)	10.3	15.7	18.3

slow-growing midcanopy species, respectively; see Fig. 1(a)). Canopy and emergent species, on the other hand, dominated in the groups of fast and very fast growth (groups 14 and 17 of the final classification – fast-growing and very fast-growing canopy and emergent species, respectively; see Fig. 1(a)). An interesting corollary of these latter results is that the greater the diameter increments, the lower the variety of adult height categories represented and the fewer the groups of the final classification.

The strong effect of silvicultural treatment on stand dynamic patterns in this forest (Finegan and Camacho, in revision) may also be noted in the species grouping (Fig. 1(b)). The total numbers of species included in the analysis were similar for each treatment, but the proportions of species in each diameter increment group varied markedly between treatments: 51% of species in the control plots were assigned to the very slow diameter increment group, for example, but only 31% of the species under the liberation/refinement treatment. Similarly, while the sum of the proportions of species in moderate, fast or very fast increment groups was only 20% for control plots, 34% of species in the liberation/refinement plots were assigned to one or other of these categories. These between-treatment differences are partly artefactual – the numbers of slow-growing species meeting the criteria for inclusion in the analysis were reduced by silvicultural treatment – and partly due to growth responses. It is notable that the fast diameter increment group, and the corresponding groups of the final classification, was represented exclusively in the silviculturally treated plots; all the species found in this diameter increment group, when present in other experimental treatments, were assigned by the analysis to other groups. This point may be illustrated with respect to species of the canopy/emergent category of adult height. Examination of Appendix A and Table 2 indicates that for the liberation/refinement plots, the fast diameter increment group was made up, with one exception (*Simarouba amara*) of species found in the slow or moderate growth groups in the control plots. Four of these were commercially important and may be cited as examples. *Pterocarpus hayesii* switched from species group 8 of the final classification (slow-growing canopy/emergent species) in the control plots to group 14 (fast-growing canopy/emergent species) in the liberation/refinement plots. *Pentaclethra macroloba*, *Qua-*

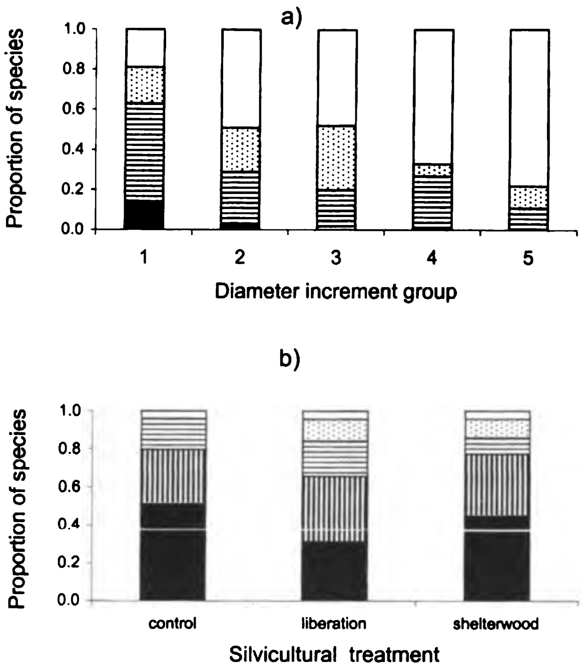

Fig. 1. (a) The proportions of species in each diameter increment group belonging to different categories of adult size. Closed bars, understorey species; cross hatched bars, middle storey, dotted bars, subcanopy species, open bars, canopy emergent species. Diameter increment group codes: (1) very slow growth; (2) slow growth; (3) moderate growth; (4) fast growth; and (5) very fast growth. (b) The proportions of species belonging to each diameter increment group under each of the three silvicultural regimes. Closed bars, very slow growth, vertically hatched bars, slow growth, cross-hatched bars, moderate growth, dotted bars, fast growth, open bars, very fast growth. Managed lowland rain forest at La Tirimbina, northeastern Costa Rica.

lea paraense and *Virola koschnyii* all switched from species group 11 (canopy/emergent species of moderate growth) in the control plots to the same species group 14 under the liberation/refinement treatment.

Although the proportions of species in different diameter increment groups differed between treatments, treatments were similar in the size and composition of the very fast increments group. This group was made up of three species under each treatment and similar numbers of individuals (Table 1, Appendix A), and the Canonical Correlation Analysis showed it to be the best-differentiated group of all (unpublished data). *Vochysia ferruginea* was part of this group under each treatment (Table 2, Appendix A), being accompanied by a total of five other species of long-lived pioneer (*Inga alba*, *Jacaranda copaia*, *Balizia elegans* (better known by its former name, *Pithecellobium elegans*), *Simarouba amara* and *Stryphnodendron microstachyum*) and one short-lived pioneer, *Croton smithianus* (Appendix A). The functional diversity within commercial species groupings is illustrated by the canopy and emergent species of relatively high value in this forest. Some of these species – *Carapa guianensis*, *Minquartia guianensis*, *Terminalia amazonia* and *Virola sebifera* – appear to be of slow or very slow growth, maintaining modest productivity even though apparently capable of responding positively to silvicultural treatment, as switches from the very slow to the slow increment group in the silviculturally treated plots indicate (Table 2). High value species such as *Qualea paraense* and *Virola koschnyii*, on the other hand, are clearly capable of fast growth. The small group of non-commercial canopy and emergent species – those of Chrysobalanaceae (the genera *Couepia*, *Hirtella* and *Maranthes*) and Sapotaceae (*Pouteria*) was notably concentrated in the slow and very slow increment groups (Table 2).

The independent variables correlated with within-increment group diameter growth rates are shown in Table 3. Across treatments, crown form was the independent variable most frequently associated with increments, significant correlations being shown under all three experimental treatments. Significant correlations between increments and crown illumination were also found, though not in the liberation/refinement plots, while correlations with presence of lianas were limited to the silviculturally treated plots. Adult height showed little relationship to increments within groups, probably because much of the variance associated with this factor had been accounted for in the separation of the increment groups by the cluster analysis.

In order to further investigate the factors underlying the grouping of species by diameter increments, we characterised each group in terms of tree attributes (crown illumination, crown form and diameter distributions) for canopy and emergent species only. Differences among diameter increment groups were very highly significant for each of the three attributes (Kruskal–Wallis test, $p < 0.0001$). The taxonomic component of these trends is emphasised: these are effectively trends is the characteristics of different

Table 2
Species groups to which commercial (C) or ecologically important (E) canopy and emergent tree species were assigned (see text for details of grouping strategy). For species which were present in more than one treatment, individuals were grouped by treatment and analysed separately. Figures in parentheses represent the number of individuals per treatment

Species	Guild [a]	Treatment and species group [b]					
		control		liberation		shelterwood	
		final	inc.	final	inc.	final	inc.
Hirtella triandra (E)	ST	3	1 (11)	7	2 (11)	7	2 (9)
Carapa guianensis (C)	ST	4	1 (9)	8	2 (16)	8	2 (12)
Maranthes panamensis (E)	ST	—	—	4	1 (6)	4	1 (3)
Minquartia guianensis (C)	ST	4	1 (27)	8	2 (21)	8	2 (24)
Pouteria campechiana (E)	ST	4	1 (13)	4	1 (11)	4	1 (6)
Terminalia amazonia (C)	I	4	1 (4)	8	2 (8)	8	2 (5)
Couepia polyandra (E)	ST	8	2 (3)	4	1 (3)	8	2 (4)
Laetia procera (C)	LLP	8	2 (22)	8	2 (6)	8	2 (21)
Pterocarpus hayesii (C)	I	8	2 (8)	14	4 (5)	8	2 (8)
Sterculia recordiana (C)	LLP	8	2 (11)	8	2 (3)	8	2 (4)
Stryphnodendron microstachyum (C)	LLP	8	2 (3)	17	5 (4)	14	4 (8)
Virola sebifera (C)	ST	8	2 (8)	8	2 (5)	8	2 (8)
Humiriastrum diguense (C)	I	—	—	8	2 (10)	14	4 (5)
Otoba novogranatensis (C)	I	11	3 (3)	11	3 (31)	11	3 (6)
Pentaclethra macroloba (C)	ST	11	3 (200)	14	4 (145)	14	4 (166)
Qualea paraense (C)	I	11	3 (10)	14	4 (8)	14	4 (13)
Tapirira guianensis (C)	ST	11	3 (19)	11	3 (17)	11	3 (17)
Virola koschnyii (C)	ST	11	3 (6)	14	4 (6)	8	2 (6)
Simarouba amara (C)	LLP	17	5 (4)	14	4 (6)	14	4 (9)
Vochysia ferruginea (C)	LLP	17	5 (11)	17	5 (14)	17	5 (17)

[a] Codes for guilds: LLP – long-lived pioneer; I – intermediate; ST – shade tolerant.
[b] Explanation of numeric codes: Inc., diameter increment groups: (1) very slow growth; (2) slow growth; (3) moderate growth; (4) fast growth; (5) very fast growth; Final, final groups obtained by subdividing diameter increment groups on the basis of adult height.

species populations. Notable trends were, on passing from the very slow growth group to that of very fast growth, the increase in the proportions of trees with fully illuminated or emergent crowns, and with good or perfect crown form (Fig. 2(a)–(e)). The very fast diameter increment group stands out particularly with respect to its crown characteristics, having almost 70% of all individuals with emergent crowns or crowns fully illuminated from above, and a similar proportion with good or 'perfect' crown form (Fig. 2(e)). None of the other diameter increment groups exceeded 40% of all individuals in these categories of crown illumination and form. This latter diameter increment group was also unique with respect to the diameter distribution for canopy and emergent species, which was irregular in form, with more trees in the 30–39.9-cm DBH class than in the 20–29.9-cm class (Fig. 2(e)). The other diameter increment groups, in contrast, tended to exhibit typical 'reverse-J' distributions (straight lines on semilog plots) for canopy and emergent species.

4. Discussion

4.1. The strategy for grouping species

We followed Vanclay (1994) and Alder (1995) in seeking a non-subjective classification of species on the basis of observed diameter increments and some measure of adult size – in this case, the height range attained by adults (see Section 4.2.2 for further discussion of this point). The adult height classification was used instead of maximum observed DBH as suggested by Alder (1995) for two main reasons: firstly, because for many species, the largest DBH

Table 3
Within-diameter increment group correlations (Spearman's *r*) of diameter increments with tree attributes for the 1993–1996 period in a lowland rain forest managed for timber production, La Tirimbina, northeastern Costa Rica. See text for details of assignment of species to diameter increment groups

Treatment and tree attribute in 1993		Diameter increment group				
		very slow	slow	moderate	fast	very fast
Control						
DBH	*r*	0.04	0.17 [a]	0.07	—	0.09
adult size	*r*	0.06	0.04	0.03	—	0.37 [a]
crown illumination	*r*	0.22 [c]	0.17	0.13	—	0.36 [a]
crown form	*r*	0.27 [c]	0.29 [c]	0.06	—	0.45 [b]
lianas	*r*	0.08	0.06	0.04	—	0.23
	N	516	197	263	—	27
Liberation						
DBH	*r*	0.12	0.20 [b]	0.17	0.27 [b]	0.16
adult size	*r*	0.07	0.05	0.03	0.00	—
crown illumination	*r*	0.06	0.11	0.03	0.03	0.40
crown form	*r*	0.25 [b]	0.37 [c]	0.39 [b]	0.25 [b]	0.52 [a]
lianas	*r*	0.07	−0.15 [a]	−0.30 [a]	−0.38 [c]	0.21
	N	177	191	85	185	22
Shelterwood						
DBH	*r*	0.02	0.03	0.24 [b]	0.13	0.47 [a]
adult size	*r*	0.03	0.02	0.04	0.12	0.26
crown illumination	*r*	0.11	0.23 [b]	0.09	0.47 [b]	0.34
crown form	*r*	0.20 [b]	0.37 [c]	0.20 [b]	0.41 [b]	0.18
lianas	*r*	−0.20 [b]	−0.20 [b]	−0.24 [c]	0.10	0.29
	N	235	223	218	47	25

[a] $p < 0.05$.
[b] $p < 0.01$.
[c] $p < 0.001$.

observed in the PSPs did not correspond to the known adult size, and secondly, because the vertical space occupied by the adult may be considered ecologically more meaningful than maximum DBH. However, maximum DBH may be required for model development.

The species grouping presented in this paper must be considered preliminary, because of the short length of the study (three years), and the relatively small sample sizes for many species, both of which may reduce the precision and accuracy of the characterizations of the growth rates of species. Tree diameter increments may vary widely between measurement periods over the short term, thus biasing estimates of species-specific growth rates (Clark and Clark, 1994). In addition, growth rates in managed forests are expected to vary in relation to time since disturbance (logging or silvicultural treatment) (Alder, 1995), so that in the framework of a felling cycle, our results are specific to the years immediately following the application of silvicultural treatment. With respect to the relative positions of species in the diameter increment groups, however, the strong autocorrelation of growth rates over successive time periods (Mervart, 1972; Swaine et al., 1987a) suggests that although absolute increments may vary over time, changes in species rankings are unlikely.

Small sample sizes for some species are difficult to avoid using standard PSP techniques. A large proportion of the species ≥10 cm DBH in a 1.0 ha PSP are represented by few or single individuals, so that larger plots (Condit, 1995), or more of them, or plotless censuses of large areas (Clark and Clark, 1992) are required to obtain large samples for species other than the most common ones. The species grouping developed in the present paper is nevertheless valuable, as it reveals ecologically and silviculturally interpretable trends and patterns in diameter increments; in addition, this paper contains the only published information on growth rates for the majority of the species included in our analyses (see Section 4.2).

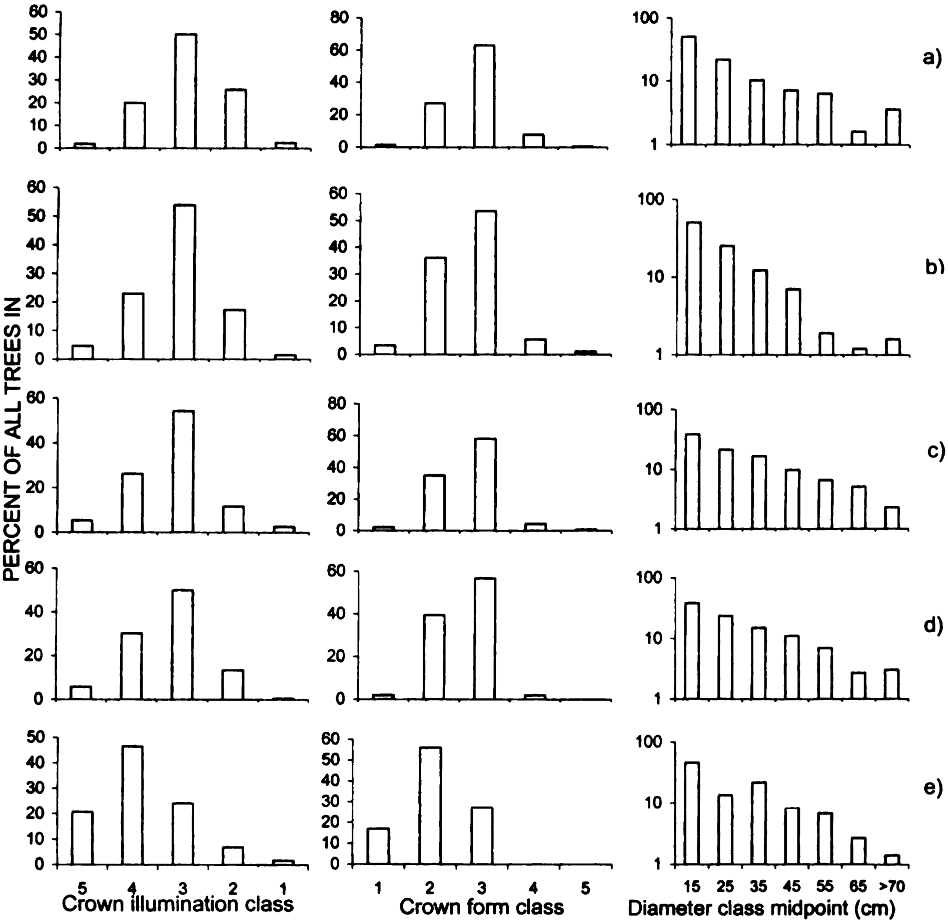

Fig. 2. Distributions of the number of trees in each diameter increment group belonging to different categories of crown illumination, crown form and diameter at breast height; canopy and emergent species only. Diameter increment groups: (a) very slow growth; (b) slow growth; (c) moderate growth; (d) fast growth; and (e) very fast growth. See text for explanation of formation of diameter increment groups.

There appears to be no consensus on the best diameter increment parameters to be used for the grouping of species. Parameters of regression equations relating tree size to growth have been suggested (Vanclay, 1994) and mean diameter increments are a practical and widely-used option (Alder, 1995). By the use of median and quartiles of the increment distributions, we wished to recognise and take account of the wide ranges and typically positively-skewed distributions of diameter increments in dense forest stands (Mervart, 1972; Kohyama and Hara, 1989). Maximum and minimum increments were not used because their determination is much more susceptible to measurement error than that of the median and quartiles, while minimum increments were in any case 0, −1 or −2 mm in a large number of species and so have a low power to discriminate between them. The fact that the third quartile (Q3) was the single parameter with greatest influence on the final grouping, means that the location of a species in the grouping is greatly dependent on the growth rates of the fastest growing trees of the population. A comparison of cluster analyses is beyond the scope of this paper, but it may be observed that clustering on the basis of the median only locates a greater proportion of species in the slow and very slow diameter increment groups (Marlen Camacho and Bryan Finegan, unpublished data). Whether or not a clustering strategy may be considered satisfactory will depend greatly on the objectives of a particular study. For the present study, it was taken into account that patterns of growth and mortality in tropical forests are consistent with the view that assemblages of adult trees are largely composed of individuals which have grown rapidly throughout their lives (Swaine et al., 1987b). The tendency towards a combination of faster growth and lower mortality (Finegan and Camacho, in press) in individuals with well-illuminated, well-formed crowns at La Tirimbina (Section 4.2.1), and the autocorrelation of diameter increments over successive time periods (see above), both support this view. If this scenario is correct, then it may be argued that a clustering strategy such as that used here, which gives greater weight to faster growing individuals, provides a more realistic framework for the analysis, interpretation and modelling of stand dynamic processes than one based on median or mean increments.

4.2. Causes of variation in diameter growth rates

4.2.1. Crown characteristics and silvicultural treatment

Diameter increments of La Tirimbina trees tend to be greater in individuals with better-formed, better-illuminated crowns, little liana foliage in their crowns (this paper) and more growing space conferred by silvicultural treatment (Finegan and Camacho, in press). Many studies have given emphasis to the importance of crown illumination in the determination of increments in tropical moist forests (Clark and Clark, 1992; Silva et al., 1995), but the importance of crown form has not previously been addressed (Alder and Synnott, 1992). Taken together, these crown characteristics may be interpreted in terms of both the availability of light (illumination, presence of lianas) and the capacity of the tree to utilize that light (crown form). Differences between experimental treatments in the strength of correlations of the different tree characteristics with increments may be interpreted in ecological and silvicultural terms. Crown illumination was only correlated with increments in control and shelterwood plots, perhaps because the combined refinement and liberation treatment to a large extent reduces effects on growth of individuals ≥ 10 cm DBH caused by light limitation, while the upper canopy remains relatively undisturbed under the other two treatments. Correlations of growth with presence of lianas were only found in silviculturally treated plots, probably due to increases in liana abundance in these plots, a forest response which is currently under investigation; increases of the abundance and growth rates of lianas are a common, though by no means universal, response of tropical forests to silvicultural treatment (Baur, 1968).

In spite of the between-treatment differences in patterns of correlation, and lack of attention to the importance of crown form in previous studies, however, it may be concluded that our results verify the applicability, in the La Tirimbina rain forest as in forests of other wet tropical sites (Dawkins, 1958; Baur, 1968; Alder and Synnott, 1992) of basic and probably ancient silviculturalist's precepts. The location of the La Tirimbina forest in an ecoregion little-known in the context of tropical forestry, however, makes necessary further discussion with respect to one of the site's most distinctive characteristics: its species complement.

4.2.2. The taxonomic and functional component

One of the most obvious trends across the final species grouping is that of the proportions of species belonging to different adult height categories within the different diameter increment groups: under- and middle story species characterise the slow-growing end of the spectrum, and subcanopy, canopy and emergent species the fast-growing end (though present in the group of very slow growth). Lieberman and Lieberman (1987) found a similar trend related to adult size among individuals ≥ 10 cm DBH in forest at La Selva Biological Station. This trend is undoubtedly related at least partially to the fact that for under- and middle story species, many individuals ≥ 10 cm DBH are mature or approaching that state (sampling individuals ≥ 10 cm DBH, for example, of a species whose maximum DBH is 15 cm, may be considered roughly equivalent to sampling only individuals ≥ 60 cm DBH of a species whose maximum is 90 cm). As sampling individuals ≥ 10 cm DBH excludes most life history stages of species which are small as adults, characterisations of growth rates such as that presented here should be understood to apply only to the diameter range sampled. We speculate, however, that characteristic under- and middle story species of the La Tirimbina forest, such as *Capparis pittieri*, *Ardisia palmana*, *Macrolobium costaricense*, *Dystovomita* *paniculata* and *Protium* spp. (Appendix A), maintain relatively slow growth rates across all life-history stages. Further work on such species, which form a large part of the woody species biodiversity of the forest, would contribute considerably to understanding of the sustainability of forest management at the site.

It is widely assumed that the putative light requirements and regeneration strategies of tropical forest tree species are related to potential growth rates (e.g. Whitmore, 1984, chapter 7). As observed in Section 4.1, however, such relationships are not always clear in PSP datasets, including that from La Tirimbina. The cluster analysis indeed indicated that during the period of study, pioneer *Cecropia* and light-demanding taxa such as *Apeiba membranacea*, *Inga* spp. and *Laetia procera* (see Finegan, 1992, 1996; Clark and Clark, 1992) had diameter increment patterns similar to those of more shade-tolerant species such as *Couepia polyandra*, *Lecythis ampla* and *Pentaclethra macroloba*. This may be due to fundamental defects in current guild concepts for tropical trees, or at least inadequate testing of those concepts (Clark and Clark, 1992), or small sample sizes for some species; it may also be that for ontogenetic reasons, differences between species are most evident for individuals <10 cm DBH. One point in which our results correspond to expectations derived from guild concepts is, however, with respect to the species which form the group with very fast diameter increments. This group was always made up of pioneers, whether short or long-lived. It was also distinctive with respect to tree crown characteristics, as well as the group diameter distribution. These points may now be discussed.

Vochysia ferruginea, *Jacaranda copaia* and *Simarouba amara* are widely-distributed species which although present in old-growth forests, may become much more common in landscapes heavily disturbed by human activity (Finegan, 1992) or natural phenomena such as hurricanes (Boucher and Mallona, 1997) and are here considered long-lived pioneers. These three species were among the 28 fastest-growing tree species in undisturbed moist forest on Barro Colorado Island, Panama (Condit et al., 1993), where median annual diameter increments during 1982–1985 were similar to those at La Tirimbina for *Vochysia* and *Jacaranda*: 14 mm as against 15–19 mm at La Tirimbina for the former species and 11 mm as against 14 mm for the latter. *Simarouba*, however, seems to grow significantly more slowly at Barro Colorado Island than at La Tirimbina.

Although the formation of a group of very fast diameter increments by short and long-lived pioneer tree species is not surprising, it is less obvious that the trees in this group should be distinctive in terms of their crown characteristics and group diameter distribution. It should be noted that as about two-thirds of the individual trees in this group came from the control and shelterwood plots, the predominance of well-illuminated and well-formed crowns among the trees in the group is not a consequence of silvicultural treatment. Rather, we believe that the very fast increment group is composed of trees recruited in large canopy gaps associated with the unplanned logging of the forest carried out over almost 30 years prior to the implementation of experimental management. It is reasonable to assume that these trees are able to maintain well-illuminated, well-formed crowns and rapid growth rates in such conditions.

Tentative generalisations regarding growth rates at the species level are possible for a small number of species other than the pioneers (it is emphasised that for the great majority of the species shown in Appendix A which are not mentioned in this Discussion, the data presented represent the only published information on growth rates). The shade-tolerant *Minquartia guianensis* is also very widely distributed in the neotropics and is consistently one of the slower-growing species where found, though interestingly, its growth in the control plots at La Tirimbina appears faster than at sites on poorer soils in French Guiana and near Manaus, Brasil, where Favrichon et al. (in press) recorded mean annual increments of 0.16 cm $year^{-1}$. The non-commercial canopy and emergent species of Chrysobalanaceae and Sapotaceae also clearly belong, like *Minquartia guianensis*, to the group of slower-growing species at La Tirimbina. The abundances of these species were markedly reduced by the refinement stage of the silvicultural treatment (unpublished data). Non-commercial status and slow growth may make species such as these especially vulnerable to population decline when silvicultural treatments are applied, especially if combined with limited dispersal and infrequent recruitment (cf. Martini et al., 1994). Population declines of non-commercial species may not be important from the point of view of commercial productivity, but their effects with respect to long-term ecosystem sustainability remain unknown.

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Appendix A

Species assigned to the different groups of the final classification ('Group' in the table) formed by subdividing the five diameter increment groups ('Growth' in the table) on the basis of adult height, under the three different silvicultural regimes.

Group	Growth [a]	Adult size [b]	CG [c]	Species	N/3.0 ha	Increments (mm year^{-1}) Q1	Median	Q3
Control								
1	1	2	N	*Capparis pittieri*	7	0.0	0.0	0.0
1	1	2	N	*Faramea occidentalis*	4	0.0	0.5	1.0
1	1	2	N	*Colubrina spinosa*	5	0.0	1.0	1.0
1	1	2	N	*Vismia macrophylla*	4	1.0	1.5	3.5
2	1	3	N	*Theobroma angustifolium*	4	−0.5	0.0	0.0
2	1	3	N	*Warszewiczia coccinea*	19	0.0	0.0	0.0
2	1	3	N	*Ocotea cenura*	4	0.0	0.0	0.5
2	1	3	N	*Posoqueria latifolia*	8	0.0	0.0	0.5
2	1	3	N	*Macrolobium costaricensis*	37	0.0	0.0	1.0
2	1	3	N	*Naucleopsis naga*	15	0.0	0.0	1.0
2	1	3	N	*Quararibea bracteolosa*	5	0.0	0.0	1.0
2	1	3	N	*Unonopsis pittieri*	8	0.0	0.0	1.5
2	1	3	N	*Ocotea laetevirens*	4	0.0	0.5	1.0
2	1	3	N	*Dystovomita paniculata*	23	0.0	1.0	1.0
2	1	3	N	*Lacunaria panamensis*	3	0.0	1.0	1.0
2	1	3	N	*Saurauria sp.*	6	0.0	1.0	1.0
2	1	3	N	*Protium pittieri*	10	0.0	1.0	1.0
2	1	3	N	*Marila laxiflora*	19	0.0	1.0	2.0
2	1	3	N	*Lonchocarpus oliganthus*	9	1.0	1.0	2.0
2	1	3	N	*Protium ravenii*	34	0.0	1.0	3.0
2	1	3	N	*Protium schippii*	8	0.5	1.0	3.0
2	1	3	N	*Eugenia glandulosa-punctata*	3	0.0	1.0	5.0
2	1	3	N	*Ardisia palmana*	23	0.0	2.0	2.0
2	1	3	N	*Cupania glabra*	3	1.0	2.0	3.0
2	1	3	N	*Ferdinandusa panamensis*	112	0.0	2.0	3.5
2	1	3	N	*Cordia dwyeri*	3	1.0	2.0	4.0
3	1	4	N	*Pseudolmedia spuria*	3	0.0	0.0	2.0
3	1	4	N	*Brosimum guianense*	4	0.0	0.5	1.5

3	1	4	C	*Dendropanax arboreus*	34	0.0	0.5	2.0
3	1	4	N	*Conceveiba pleiostemona*	7	0.0	1.0	2.0
3	1	4	N	*Hirtella triandra*	11	0.0	2.0	4.0
4	1	5	C	*Aspidosperma spruceanum*	4	0.0	0.0	0.0
4	1	5	C	*Carapa guianensis*	9	0.0	0.0	2.0
4	1	5	N	*Brosimum lactescens*	14	0.0	0.5	1.0
4	1	5	N	*Ocotea mollifolia*	6	0.0	0.5	1.0
4	1	5	N	*Pouteria campechiana*	13	0.0	1.0	4.0
4	1	5	C	*Terminalia amazonia*	4	0.5	1.5	3.0
4	1	5	C	*Minquartia guianensis*	27	1.0	2.0	4.0
6	2	3	N	*Miconia punctata* * d	7	1.0	3.0	4.0
6	2	3	N	*Hyeronima oblonga*	6	1.0	3.0	7.0
6	2	3	N	*Protium panamensis*	13	2.0	4.0	5.0
6	2	3	N	*Casearia arborea*	27	2.0	4.0	6.0
6	2	3	N	*Guarea kunthiana*	3	4.0	4.0	7.0
7	2	4	N	*Guatteria aeruginosa* * d	4	0.0	2.0	5.0
7	2	4	N	*Pourouma bicolor*	20	1.0	2.5	5.0
7	2	4	N	*Pourouma minor*	10	2.0	3.0	7.0
7	2	4	N	*Inga pezizifera*	5	1.0	6.0	6.0
8	2	5	N	*Apeiba membranacea* * d	7	0.0	1.0	6.0
8	2	5	C	*Cespedesia macrophylla*	3	0.0	1.0	7.0
8	2	5	C	*Sterculia recordiana*	11	0.0	2.0	5.0
8	2	5	C	*Stryphnodendron microstachyum*	3	1.0	2.0	5.0
8	2	5	C	*Tetragastris panamensis*	18	2.0	2.5	5.0
8	2	5	C	*Virola sebifera*	8	1.5	3.0	5.0
8	2	5	N	*Spachea correa*	3	1.0	3.0	6.0
8	2	5	N	*Maranthes panamensis*	7	2.0	3.0	6.0
8	2	5	C	*Pterocarpus hayesii*	8	2.0	3.5	5.5
8	2	5	N	*Nectandra salicifolia*	9	2.0	5.0	6.0
8	2	5	C	*Laetia procera*	22	2.0	5.0	8.0
8	2	5	N	*Couepia polyandra*	3	2.0	6.0	8.0
9	3	3	N	*Ocotea insularis*	3	2.0	3.0	12.0
9	3	3	N	*Cecropia insignis*	3	1.0	3.0	14.0
10	3	4	C	*Ormosia velutina*	3	0.0	2.0	11.0
10	3	4	N	*Ampelocera macrocarpa*	6	3.0	5.5	13.0
10	3	4	N	*Ocotea puberula*	3	5.0	7.0	12.0
10	3	4	N	*Inga thibaudiana*	3	5.0	8.0	9.0
10	3	4	N	*Inga punctata*	4	3.5	8.0	13.0
11	3	5	C	*Tapirira guianensis* * d	19	2.0	4.0	9.0
11	3	5	C	*Virola koschnyii*	6	1.0	5.0	12.0
11	3	5	C	*Otoba novogranatensis*	3	0.0	5.0	15.0
11	3	5	C	*Pentaclethra macroloba*	200	3.0	6.0	9.0
11	3	5	C	*Qualea paraense*	10	4.0	8.0	12.0
15	5	3	N	*Croton smithianus*	12	7.0	16.5	24.5
17	5	5	C	*Vochysia ferruginea*	11	8.0	15.0	18.0
17	5	5	C	*Simarouba amara*	4	6.5	15.5	21.0

Group	Growth [a]	Adult size [b]	CG [c]	Species	*N*/3.0 ha	Increments ($mm\ year^{-1}$) Q1	Median	Q3
Liberation								
1	1	2	N	*Colubrina spinosa*	5	0.0	0.0	1.0
1	1	2	N	*Parathesis sp.*	4	0.0	0.5	2.0
1	1	2	N	*Capparis pittieri*	7	0.0	1.0	2.0
1	1	2	N	*Neea sp.*	3	0.0	1.0	2.0
1	1	2	N	*Faramea occidentalis*	4	2.0	2.5	2.0
2	1	3	N	*Borojoa panamensis*	12	0.0	0.5	1.0
2	1	3	N	*Posoqueria latifolia*	4	0.0	0.5	2.0
2	1	3	N	*Warszewiczia coccinea*	24	0.0	1.0	1.0
2	1	3	N	*Naucleopsis naga*	7	0.0	1.0	2.0
2	1	3	N	*Dystovomita paniculata*	23	0.0	1.0	2.5
2	1	3	N	*Cupania glabra*	3	0.0	1.0	3.0
2	1	3	N	*Ardisia palmana*	12	1.0	2.0	1.0
2	1	3	N	*Macrolobium costaricensis*	5	1.0	2.0	1.0
2	1	3	N	*Lonchocarpus oliganthus*	6	1.0	2.0	1.5
2	1	3	N	*Marila laxiflora*	23	1.0	2.0	4.0
3	1	4	N	*Pachira aquatica*	3	0.0	0.0	1.5
3	1	4	N	*Guarea bullata*	4	0.5	1.0	4.0
3	1	4	N	*Sapium sp.*	4	0.5	1.0	4.0
4	1	5	N	*Brosimum lactescens*	4	0.0	0.0	3.0
4	1	5	N	*Couepia polyandra*	3	1.0	1.0	2.0
4	1	5	N	*Maranthes panamensis*	6	0.0	1.5	3.0
4	1	5	N	*Pouteria campechiana*	11	1.0	2.0	1.5
5	2	2	N	*Henriettella tuberculata*	3	1.0	4.0	6.0
6	2	3	N	*Licaria sarapiquensis** [d]	7	0.0	1.0	6.0
6	2	3	N	*Ocotea laetevirens*	3	0.0	1.0	9.0
6	2	3	N	*Protium schippii** [d]	4	1.5	3.0	7.0
6	2	3	N	*Saurauria sp.*	4	0.5	3.5	6.0
6	2	3	N	*Miconia punctata*	11	4.0	5.0	4.0
6	2	3	N	*Protium pittieri*	13	1.0	5.0	5.0
6	2	3	N	*Protium ravenii*	32	3.5	5.0	6.5
6	2	3	N	*Lacunaria panamensis*	5	4.0	6.0	8.0
7	2	4	N	*Hirtella triandra*	11	1.0	4.0	6.0
7	2	4	C	*Ormosia velutina*	3	2.0	4.0	8.0
7	2	4	C	*Dendropanax arboreus*	7	0.0	5.0	6.0
7	2	4	N	*Pourouma minor*	4	2.5	5.5	5.0
8	2	5	C	*Calophyllum brasiliense*	3	1.0	1.0	5.5
8	2	5	C	*Virola sebifera*	5	0.0	2.0	8.0
8	2	5	N	*Ilex skutchii*	3	0.0	3.0	5.0
8	2	5	C	*Terminalia amazonia*	8	1.0	3.0	6.0
8	2	5	C	*Carapa guianensis*	16	1.0	3.0	7.0
8	2	5	C	*Laetia procera*	6	2.0	3.0	8.0
8	2	5	N	*Nectandra salicifolia*	4	3.0	3.5	5.0
8	2	5	C	*Minquartia guianensis*	21	2.0	4.0	7.0
8	2	5	C	*Sterculia recordiana*	3	0.0	4.0	8.0

8	2	5	C	*Humiriastrum diguense*	10	1.0	4.5	8.0
8	2	5	C	*Cespedesia macrophylla*	5	1.0	6.0	5.0
9	3	3	N	*Inga umbellifera*	4	0.5	4.5	9.0
9	3	3	N	*Ferdinandusa panamensis* * [d]	6	2.0	6.0	12.0
9	3	3	N	*Casearia arborea*	19	5.0	7.0	9.0
9	3	3	N	*Inga heterophylla*	3	3.0	7.0	11.0
10	3	4	N	*Inga thibaudiana*	3	2.0	5.0	13.0
10	3	4	N	*Pourouma bicolor*	9	4.0	7.0	8.0
11	3	5	C	*Chimarrhis parviflora*	3	0.0	4.0	8.0
11	3	5	C	*Tetragastris panamensis*	3	0.0	4.0	12.5
11	3	5	C	*Terminalia bucidiodes*	3	1.0	5.0	9.0
11	3	5	C	*Lecythis ampla* * [d]	4	2.0	5.5	14.0
11	3	5	N	*Apeiba membranacea*	8	1.5	6.5	9.5
11	3	5	C	*Tapirira guianensis*	17	3.0	8.0	10.0
11	3	5	C	*Otoba novogranatensis*	3	0.0	8.0	11.0
12	4	3	N	*Protium panamensis*	6	7.0	10.5	16.0
12	4	3	C	*Cordia bicolor*	3	4.0	11.0	11.5
13	4	4	N	*Inga pezizifera*	6	5.0	6.0	11.0
14	4	5	C	*Pterocarpus hayesii*	5	7.0	7.0	17.0
14	4	5	C	*Qualea paraense*	8	7.5	9.0	14.0
14	4	5	C	*Pentaclethra macroloba*	145	6.0	9.0	17.0
14	4	5	C	*Virola koschnyii*	6	8.0	10.0	15.0
14	4	5	C	*Simarouba amara*	6	6.0	11.5	16.0
17	5	5	C	*Stryphnodendron microstachyum*	4	7.0	13.5	14.0
17	5	5	C	*Vochysia ferruginea*	14	10.0	15.5	21.5
17	5	5	C	*Balizia elegans*	4	12.0	17.0	19.0
Shelterwood								
1	1	2	N	*Faramea occidentalis*	4	0.0	0.0	1.5
1	1	2	N	*Rinorea sp.*	3	0.0	0.0	1.0
1	1	2	N	*Capparis pittieri*	3	0.0	0.0	2.0
2	1	3	N	*Borojoa panamensis*	3	0.0	0.0	1.0
2	1	3	N	*Macrolobium costaricensis*	3	0.0	0.0	1.0
2	1	3	N	*Lonchocarpus oliganthus*	14	0.0	0.5	1.0
2	1	3	N	*Quararibea bracteolosa*	4	0.0	0.5	1.0
2	1	3	N	*Warszewiczia coccinea*	23	0.0	1.0	1.0
2	1	3	N	*Ardisia palmana*	9	0.0	1.0	2.0
2	1	3	N	*Dystovomita paniculata*	12	0.5	1.0	2.0
2	1	3	N	*Naucleopsis naga*	20	0.0	1.0	2.5
2	1	3	N	*Ocotea insularis*	3	1.0	1.0	3.0
2	1	3	N	*Ferdinandusa panamensis*	6	0.0	1.5	2.0
2	1	3	N	*Licaria sarapiquensis*	4	0.5	1.5	2.0
2	1	3	N	*Marila laxiflora*	14	1.0	1.5	2.0
2	1	3	N	*Cinnamomum chavarrianum*	4	1.0	1.5	2.5
2	1	3	N	*Protium ravenii*	37	1.0	3.0	3.0
2	1	3	N	*Cordia lucidula*	4	2.0	3.0	3.0
3	1	4	N	*Pachira aquatica*	4	0.0	0.0	0.5

Group	Growth [a]	Adult size [b]	CG [c]	Species	N/3.0 ha	Increments (mm year^{-1}) Q1	Median	Q3
3	1	4	N	*Pseudolmedia spurea*	3	0.0	0.0	3.0
3	1	4	N	*Sloanea sp.*	4	0.0	0.5	1.5
3	1	4	N	*Guarea bullata*	5	0.0	1.0	2.0
3	1	4	N	*Brosimum guianense*	3	0.0	2.0	3.0
3	1	4	N	*Guatteria aeruginosa*	4	0.0	2.0	4.0
3	1	4	N	*Inga thibaudiana*	9	1.0	3.0	3.0
4	1	5	N	*Pouteria campechiana*	6	0.0	0.0	1.0
4	1	5	C	*Dussia macroprophyllata*	5	0.0	0.0	3.0
4	1	5	C	*Vitex cooperi*	4	0.5	1.0	3.5
4	1	5	N	*Brosimum lactescens*	5	1.0	2.0	2.0
4	1	5	N	*Maranthes panamensis*	3	2.0	2.0	4.0
4	1	5	C	*Tetragastris panamensis*	4	0.0	2.0	4.5
4	1	5	N	*Nectandra salicifolia*	6	0.0	2.5	4.0
6	2	3	N	*Protium pittieri*	11	2.0	2.0	5.0
6	2	3	N	*Casearia arborea*	22	2.0	3.0	5.0
6	2	3	N	*Miconia punctata*	7	1.0	3.0	6.0
6	2	3	N	*Protium panamensis*	18	1.0	3.5	5.0
6	2	3	N	*Protium schippii*	4	1.0	3.5	6.5
6	2	3	N	*Cecropia insignis*	3	2.0	6.0	6.0
7	2	4	N	*Pourouma minor* * [d]	10	1.0	3.0	4.0
7	2	4	C	*Dendropanax arboreus*	15	1.0	3.0	5.0
7	2	4	N	*Hirtella triandra*	9	4.0	5.0	5.0
7	2	4	N	*Byrsonima crispa*	3	1.0	5.0	6.0
8	2	5	N	*Apeiba membranacea*	11	0.0	1.0	8.0
8	2	5	C	*Carapa guianensis* * [d]	12	0.5	2.0	6.0
8	2	5	C	*Abarema macradenia*	3	2.0	2.0	8.0
8	2	5	C	*Pterocarpus hayesii*	8	0.0	2.5	7.0
8	2	5	C	*Minquartia guianensis*	24	2.0	3.0	5.5
8	2	5	C	*Laetia procera*	21	1.0	3.0	7.0
8	2	5	N	*Couepia polyandra*	4	1.0	3.5	6.0
8	2	5	C	*Cespedesia macrophylla*	10	3.0	3.5	6.0
8	2	5	C	*Sterculia recordiana*	4	4.0	4.5	5.0
8	2	5	C	*Virola sebifera*	8	1.0	4.5	7.0
8	2	5	C	*Rollinia pittieri*	5	2.0	5.0	5.0
8	2	5	C	*Terminalia amazonia*	5	2.0	5.0	6.0
8	2	5	C	*Virola koschnyii*	6	4.0	5.0	6.0
10	3	4	N	*Conceveiba pleiostemona*	6	1.0	4.5	11.0
10	3	4	N	*Inga pezizifera*	8	4.0	5.5	10.5
10	3	4	N	*Pourouma bicolor*	15	3.0	8.0	11.0
11	3	5	C	*Tapirira guianensis*	17	4.0	5.5	10.0
11	3	5	C	*Otoba novogranatensis*	6	3.0	6.0	10.0
11	3	5	C	*Pentaclethra macroloba*	166	4.0	7.0	12.0
12	4	3	N	*Hampea appendiculata*	5	9.0	10.0	12.0
12	4	3	N	*Croton smithianus*	4	5.5	11.5	16.0

14	4	5	N	*Vouarana guianensis*	3	3.0	7.0	16.0
14	4	5	C	*Humiriastrum diguense*	5	7.0	9.0	11.0
14	4	5	C	*Qualea paraense*	13	5.0	10.0	15.0
14	4	5	C	*Simarouba amara*	9	7.0	11.0	13.0
14	4	5	C	*Stryphnodendron microstachyum*	8	6.5	11.0	16.5
16	5	4	C	*Jacaranda copaia*	5	8.0	14.0	16.0
17	5	5	N	*Inga alba*	3	7.0	14.0	19.0
17	5	5	C	*Vochysia ferruginea*	17	16.0	19.0	20.0

[a] Growth = diameter increment group: (1) very slow; (2) slow; (3) moderate; (4) fast; (5) very fast.
[b] Adult size: (2) understory (<5 m height); (3) middle story (5–25 m); (4) subcanopy/canopy (25–35 m); (5) canopy/emergent (>35 m).
[c] CG Commercial group: C – commercial species; N – non-commercial.
[d] R relocation: * = species relocated within the classification by the discriminant analysis.

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