Relationships between branch spacing, growth rate and light in tropical forest saplings

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Summary

1. The spacing of branches along central stems was related to growth rate and light level in forest saplings and trees in tropical moist forest on Barro Colorado Island (BCI), Panama. The study included 14 species with tiers of plagiotropic branches (having planar leaf arrangements) and four species with continuous distributions of plagiotropic branches.

2. All species showed increases in branch spacing with increasing light and growth rate of diameter, similar to the patterns in leaf spacing noted previously in species which initially bear large leaves on unbranched stems.

3. Non-tiered species had shorter internodes than tiered species but because the latter bear more branches per node, both groups had similar numbers of branches per unit stem length, when compared at similar growth rates.

4. Differences in the relationship between internode length and growth rate among tiered species were related to demographic characteristics, suggesting that tree architecture may influence forest composition.

5. The strong correlation observed between branch spacing and growth rate suggests that branch spacing may be used to estimate past growth histories of forest tree species with plagiotropic branches.

Key-words: Internode length, tree architecture, tropical tree

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Introduction

The spacing and arrangement of tree branches influences light interception and the structural costs of foliage support. Patterns of branching vary widely among tree species (Hallé, Oldeman & Tomlinson 1978) and variation in branching within species may also occur. For example, Kohyama (1980) found that the spacing of branches along the trunk in *Abies* saplings was much greater in sun- than in shade-grown individuals. Such shifts in branch spacing may be important in allowing individuals to grow and compete across the range of light environments that forest trees are likely to encounter. Consider the case where lateral branches are borne on a vertical trunk. Widely spaced branches reduce self shading and may increase the rate of height growth in productive environments, while closely spaced branches require smaller increments of trunk growth for each new branch and may be favoured in shaded sites where little photosynthate

remains for wood production after leaf and root construction costs have been met (King 1991).

Although branch spacing may affect growth and competition between trees, there have been no comprehensive studies of how this character varies among the different species of a given forest. Other studies of tree growth suggest that many species are 'generalists' that are able to survive under a wide range of light conditions, once established, while a smaller group of 'specialists', including pioneers (*sensu* Swaine & Whitmore 1988), have more restricted growth requirements (Welden *et al.* 1991). Thus, a question of interest is 'do all species exhibit similar shifts in branch spacing in relation to light level or do they vary in this character?'. This question was addressed by a study of branch spacing or internode length in a lowland tropical forest in Panama. The study was restricted to a subset of the observed tree architectures for logistical reasons.

Materials and methods

The study was conducted on Barro Colorado Island (BCI), Republic of Panama (9 ° 10 'N, 79 ° 51 'W). BCI

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supports lowland tropical moist forest receiving about 2·6 m of rain per year with a pronounced dry season from January through April (Leigh, Rand & Windsor 1982). The project examined the branch spacing and growth of small, temporarily marked saplings and larger permanently marked individuals on the 50 ha forest dynamics plot established on BCI in 1980 (Hubbell & Foster 1990). The 18 species chosen for study included a subset of the architectural models defined by Hallé *et al.* (1978), all of which bear nearly horizontal branches on vertical mainstems when shaded. The typical number of branches per node ranged from one to five, with species with three to five branches per node having a whorled or pseudo-whorled arrangement (with slight offsets between the branches of a node). Species with tiers of branches were emphasized, as preliminary observations suggested substantial variation in branch spacing among this group. The selected species are more or less shade tolerant (Coley 1983; Welden *et al.* 1991), except for *Cordia alliodora*, which is considered light demanding. Other species attributes are listed in Table 1.

The temporary growth study examined the growth of 1 to 3 m tall saplings over a period of 8 to 9 months, beginning in October 1990. Ten to 26 saplings per species were chosen to include individuals from both tree-fall gaps and shaded understorey. Most of the chosen saplings were in old forest on the central plateau of the island near the permanent plot. Three rings were painted on each stem at about a third, a half and two thirds of total height. The following data were then recorded at the beginning and end of the study

period: stem diameter at each ring (measured to the nearest 0·05 mm in two perpendicular directions with a dial caliper) and the distances between the upper branches along the stem, including branches initiated during the study. Light environments were characterized from hemispherical fisheye lens photographs taken from the apex of each sapling in November 1990. The fraction of total diffuse light reaching each sapling was then computed with the video image analysis system of Becker, Erhart & Smith (1989).

The permanent plot study included individuals ranging from 3 to 28 m tall, with the maximum height dependent on the maximum size of each species and the degree of retention of the initial branching pattern in larger trees (Table 1). Individuals of each study species were located from lists of their coordinates on the gridded plot. Trees were rejected if they exhibited forked main stems or noticeable discontinuities in stem diameter, indicating past breakage. Trees of common species were examined preferentially near trails, to reduce plot disturbance, while most individuals were checked in the case of rarer species. The following measurements were taken on accepted trees: trunk diameter at 1·3 m, total tree height and the branch height at several nodes within the crown, including the top node. Heights above 4 m were determined by first measuring the eye-to-branch distance with a range finder, multiplying that distance by the sine of the sighting angle to the horizontal (determined by clinometer) and then adding on the eye-to-tree base height. Diameter growth over the past 5 to 6 years was determined for each tree by subtracting diameters recorded by the permanent plot survey team

Table 1. Characteristics of tree species studied at BCI, Panama. Architectural models are as defined by Hallé *et al.* (1978) and apply to understorey saplings; adult stature categories are: T, canopy tree; M, mid-sized tree; U, understorey tree; S, shrub-sized treelet; abundance refers to individuals ≥1 cm in stem diameter at 1·3 m height on the BCI forest dynamics plot in 1990 (Condit, Hubbell & Foster 1996). Species are as given by Croat (1978) and updated by Condit *et al.* (1996) for *Garcinia intermedia, Ocotea whitei, Trichilia tuberculata* and *Virola* sp. nov.

	Species	Family	Architectural model	Branches per node	Adult stature	Abundance (no./ha)	Sample height range on plot (m)
Asp	*Aspidosperma cruenta*	Apocynaceae	Massart	3	T	9·7	5–17
Cora	*Cordia alliodora*	Boraginaceae	Fagerlind	3	T	2·4	4–22
Corb	*Cordia bicolor*	Boraginaceae	Nozeran	3	M	21	4–16
Corl	*Cordia lasiocalyx*	Boraginaceae	Nozeran	3	M	34	5–13
Des	*Desmopsis panamensis*	Annonaceae	Roux	1	U	243	
Dios	*Diospyros artanthifolia*	Ebenaceae	Massart	3–5	M	1·4	
Far	*Faramea occidentalis*	Rubiaceae	Roux	2	U	538	3·5–10
Gar	*Garcinia intermedia*	Guttiferae	Roux	2	M	86	
Lac	*Lacmellea panamensis*	Apocynaceae	Massart	4–5	M	2·0	5–13
Mour	*Mouriri myrtilloides*	Melastomaceae	Massart	2–6	S	152	
Oco	*Ocotea oblonga*	Lauraceae	Massart	4–5	T	3·8	3–22
Ocw	*Ocotea whitei*	Lauraceae	Massart	4–5	T	15	3–16
Quar	*Quararibea asterolepis*	Bombacaceae	Massart	5	T	47	3–15
Term	*Terminalia oblonga*	Combretaceae	Aubreville	3–6	T	2·0	3–12
Vse	*Virola sebifera*	Myristicaceae	Massart	4–5	M	42	3·5–23
Vsp	*Virola sp. nov*	Myristicaceae	Massart	4–5	T	1·1	5–28
Vsu	*Virola surinamensis*	Myristicaceae	Massart	4–5	T	4·8	8–22
Xyl	*Xylopia macrantha*	Annonaceae	Roux	1	M	21	

in 1985 from current diameters measured January through June 1991. In 1985, small trees <5·5 cm in diameter were measured to the nearest 0·5 cm (rounding down) with a plastic plate. In 1991, small tree diameter was taken as the average of diameters measured in two perpendicular directions with a caliper and included only a small portion of the 240 000 trees measured in 1985. Because diameters were measured with differing precision and techniques at the two times, trees with calculated growth rates of <0·05 cm year^{-1} were excluded. Large errors would have otherwise occurred in the analyses of logarithmically transformed variates, where the error is equal to error/actual value, before transformation. This approach differs from that of Condit, Hubbell & Foster (1993) who rounded down more precise 1990 whole plot diameters to determine average growth rates within size classes.

An approximate estimate of height growth over the past 5 to 6 years was inferred from the diameter growth increment for each tree using height *vs* diameter relationships derived from the sampled trees of each species. This height-growth estimate was used to select the measured nodal position nearest the tree top in 1985. The distance between this node and the topmost node divided by the number of internodes between these two points then provides an estimate of the internode length for branches produced during the same 5 to 6 year interval that diameter growth was measured.

Results

The spacing of branches along the stem was quite variable, ranging from 2·6 to 96 cm among the temporarily marked saplings and 8 to 225 cm among the individuals of the permanent plot. This variation

was associated with variation in the light level and growth rate of individuals and interspecific differences in internode length. Diameter growth rate was significantly correlated with the fraction of diffuse light reaching the individual for all but one of the species of the temporary study and internode length was significantly correlated with the diffuse light fraction for almost half of these species (two-tailed $P < 0·05$, Table 2). Note that the sample size is generally larger for the correlations involving growth rate than for internode length, as not all individuals produced new branches during the 9-month interval of study. The number of new branch nodes produced over the study interval (including individuals with no new nodes) was also positively correlated with diameter growth rate for 12/13 species, significantly so for five. However, the study period was too short to determine accurate relationships between branch production rates and growth rates, as less than half the study saplings produced new branches in the case of *Mouriri myrtilloides* and *Quararibea asterolepis*.

Ln(internode length) was highly correlated with ln(diameter growth) for most of the temporary study species (Table 2). This ln–ln correlation was stronger than the correlation between untransformed variates for internode length *vs* diameter growth, but not for the relationships involving the diffuse light fraction. The plots of internode length *vs* diameter growth rate shown in Figs 1 and 2 indicate that the relationship between the logarithmically transformed variates was linear, or nearly so, for both the permanent plot trees and the temporarily marked saplings. Thus, internode length is better expressed as a power function of diameter growth rate (determined by back transformation of the log variates), than as a linear relationship.

The temporary study showed somewhat different patterns than the permanent plot study. Internode

Table 2. Correlations among growth rate, branch internode length and fraction of diffuse light reaching the sapling apex for the small, temporarily marked saplings. Correlations denoted by *, ** and *** differ from zero at the two-tailed levels of $P < 0·05$, $P < 0·01$ and $P < 0·001$, respectively. Sample sizes given in parentheses

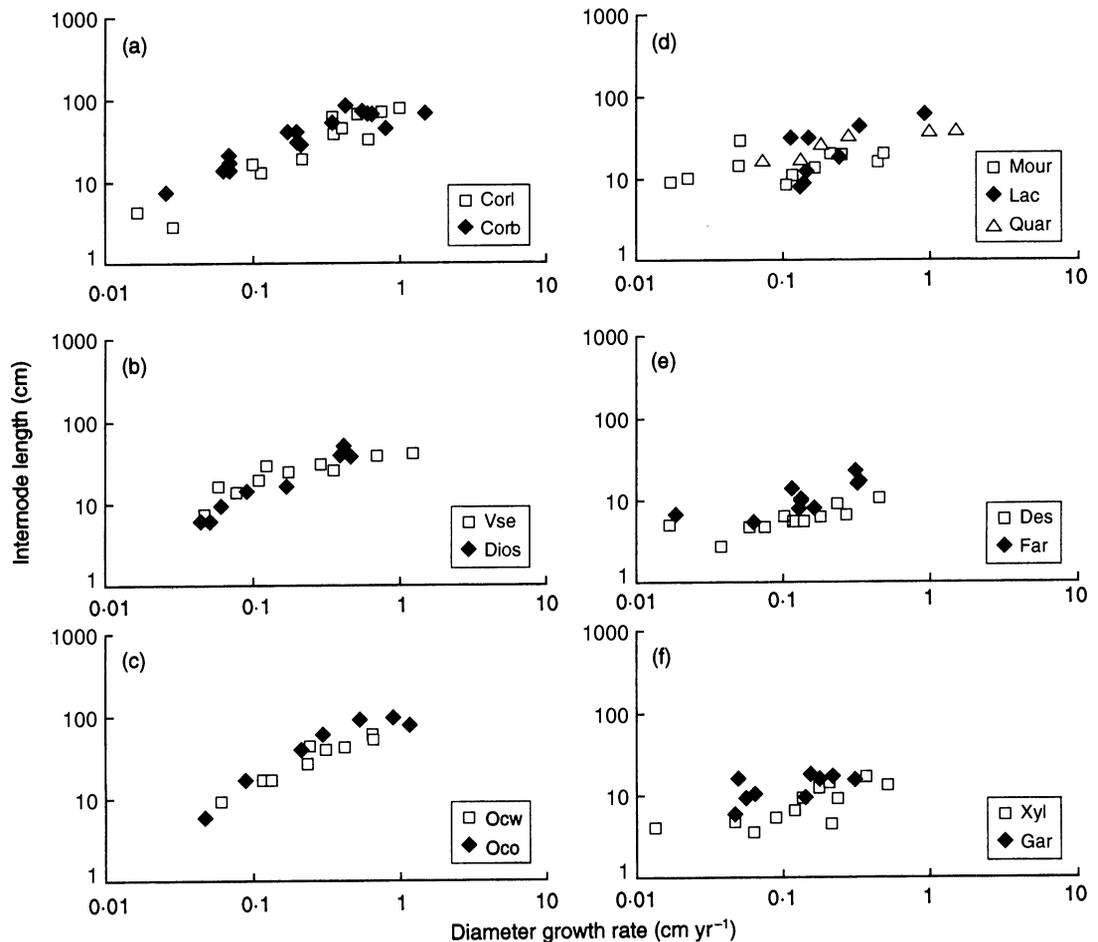| Species	Growth rate *vs* light	Internode length *vs* light	Log (internode length) *vs* log (growth rate)
	r	r	r
Cordia bicolor	0·86*** (17)	0·71*** (16)	0·92*** (16)
Cordia lasiocalyx	0·76** (12)	0·57 (11)	0·95*** (12)
Desmopsis panamensis	0·57* (14)	0·73** (13)	0·77** (13)
Diospyros artanthifolia	0·81* (9)	0·71 (7)	0·98** (8)
Faramea occidentalis	0·78** (13)	0·57 (10)	0·77** (10)
Garcinia intermedia	0·68** (14)	0·71 (8)	0·58 (9)
Lacmellea panamensis	0·97*** (10)	0·81* (8)	0·68 (8)
Mouriri myrtilloides	0·89*** (26)	0·30 (11)	0·44 (11)
Ocotea oblonga	0·75* (10)	0·81 (6)	0·94** (7)
Ocotea whitei	0·86*** (19)	0·78* (9)	0·97*** (9)
Quararibea asterolepis	0·93*** (10)	0·89* (5)	0·90* (6)
Virola sebifera	0·90*** (13)	0·65 (6)	0·88*** (10)
Xylopia macrantha	0·44 (14)	0·51 (12)	0·78** (13)
Mean r	0·78	0·67	0·81

Fig. 1. Internode length *vs* stem diameter growth rate for branches or branch tiers produced on 1 to 3 m tall saplings over a 9-month interval, plotted on a log–log scale. Species abbreviations given in Table 1. Non-tiered species shown in panels (e) and (f).

length was a higher power of growth rate for the temporary study for each of the eight species included in both studies, while the internode length associated with the intermediate diameter growth rate of 0·2 cm year^{-1} was smaller for the temporary study (Table 3). These differences may reflect the averaging of growth over 5 years for the permanent plot study and possible differences in branch spacing between small saplings and larger individuals. However, the values for the co-occurring species (shown in Fig. 3) were significantly correlated between the two study groups (two-tailed $P < 0.02$), for both the power function exponent and the internode length associated with a 0·2 cm year^{-1} diameter growth rate. Thus, the following general patterns apply to saplings and trees of a range of sizes, so long as the initial branching pattern is still apparent.

The internode length was related to the number of branches per node. Species with paired branches had nearly twice the internode length of species with one branch per node and species with three or more branches per node had greater internode lengths than those with paired branches (Table 3, Figs 4 and 5). However, when branch spacing is expressed as inter-

node length/(number of branches per node) the above differences in spacing disappear. Significant differences in internode length were observed among tiered species (Table 3), with fast growing *Cordia bicolor* and *Ocotea oblonga* trees spacing their tiers more than 1 m apart, in contrast to a spacing of less than 0·5 m in *Virola sebifera* and *Quararibea asterolepis* (Figs 4 and 5). The latter pattern may be related to the greater degree of ramification within the branches of the first two species as compared with the last two species which produce branches that are much longer than wide (defining branch dimensions in terms of foliage display). Individuals with widely spaced tiers appeared to bear greater leaf area per tier than closely branched individuals, although this pattern was not quantified.

Sapling crown dimensions were also related to their branching patterns and growth rates. Relative crown length (vertical distance from the bottommost to topmost leaf divided by sapling height) increased with diameter growth rate for all 13 species of the temporary study, significantly so for eight of them. Relative crown length tended to be greater for the species with one or two branches per node than for the tiered
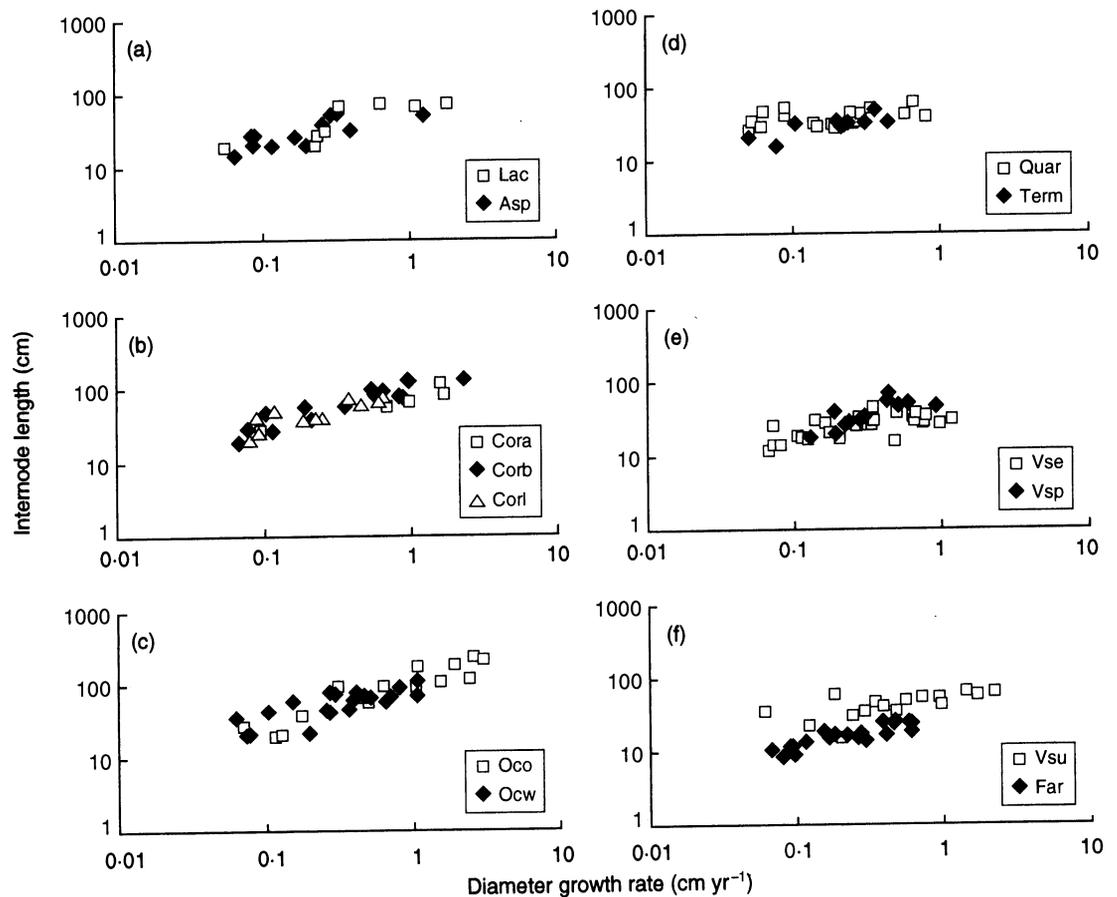
Fig. 2. Internode length of upper branches or branch tiers *vs* stem diameter growth rate over a 5- to 6-year interval for saplings and trees on the permanent plot, plotted on a log–log scale. Species abbreviations given in Table 1.

species, as shown in Fig. 6. Relative crown width (crown width/sapling height) showed no significant correlation with diameter growth rate, except for a positive correlation for *C. bicolor* and *Q. asterolepis*, significant at $P < 0.05$, but not at $P < 0.01$.

For tiered species, the exponent in the power function relationship between internode length and growth rate was highly correlated with the projected internode length for the rapid diameter growth rate of 1 cm year^{-1} (Table 4). The power function exponent (equal to the regression slope of log internode length *vs* log growth rate) also appeared to be related to certain demographic characteristics, as shown in Table 4. The exponent was negatively correlated with the abundance of each tiered species on the 50 ha plot, as some of the rarer species showed a greater shift in branch spacing with changes in growth rate than the common species. The significant positive correlation between the exponent and growth rate in areas of the permanent plot with a canopy height <10 m, for the eight species where the latter was determined by Welden *et al.* (1991), suggests that those tiered species which space their tiers widely in gaps also grow faster in them. The exponent was negatively correlated with the relative crown length of the temporary study species,

although this relationship was only marginally significant (Table 4).

Significant correlations were also noted between the mean log growth rate per species of the sample trees and the above demographic parameters, with the faster growing species tending to have greater low canopy recruitment and growth rates, and lower abundances and high canopy survival rates. These correlations introduce some uncertainty into the previously noted relations between the power function exponents and demographic parameters, depending on the degree to which the actual relationships between internode length and growth rate depart from the log–log relations fit to the data. This departure is negligible for most species, but noticeable for a few (Figs 1 and 2).

Discussion

The observed increase in branch spacing with increasing light and growth rate within all study species and reports of similar trends in temperate conifers (Koyhama 1980; Tucker *et al.* 1987) suggest a general occurrence of this pattern, at least in species bearing plagiotropic branches (having planar leaf arrangements) on vertical stems. A

Table 3. Branch spacing–diameter growth relationships for small, temporarily marked saplings and larger individuals on the forest dynamics plot at BCI, Panama, designated as small saplings and trees, respectively. The superscripts > and < indicate that a value is significantly greater than or less than the mean value for tiered species in the respective column, with single, double and triple symbols indicating significance at the $P<0.05$, $P<0.01$ and $P<0.001$ levels, respectively. Sample sizes given in parentheses

	Log (internode length) *vs* log (growth rate) regression slope for		Internode length (cm) for diameter growth rate of $0.2 \, cm \, year^{-1}$ for	
	Small saplings	Trees	Small saplings	Trees
Species with tiers of branches				
Aspidosperma cruenta		0·39 (12)		29
Cordia alliodora		0·44 (6)		37
Cordia bicolor	0·58 (16)	0·51 (15)	32$^{\gg}$	47$^{\gg}$
Cordia lasiocalyx	0·83 (12)	0·44 (13)	23	47$^{\gg}$
Diospyros artanthifolia	0·86$^{>}$ (8)		23	
Lacmellea panamensis	0·72 (8)	0·47 (8)	21	30
Mouriri myrtilloides	0·15$^{\ll}$ (11)		16$^{<}$	
Ocotea oblonga	0·83 (7)	0·61$^{>}$ (15)	30	38
Ocotea whitei	0·76 (9)	0·44 (22)	25	43$^{>}$
Quararibea asterolepis	0·29$^{<}$ (6)	0·13$^{\ll}$ (21)	24	37
Terminalia oblonga		0·34 (9)		31
Virola sebifera	0·43 (10)	0·26 (33)	23	24$^{\lll}$
Virola sp. nov.		0·54 (12)		29
Virola suranimensis		0·25 (16)		33
Mean for tiered species	0·61	0·40	24	35
Species with two branches per node				
Faramea occidentalis	0·42 (10)	0·39 (21)	13$^{\lll}$	15$^{\lll}$
Garcinia intermedia	0·31 (9)		14$^{<}$	
Species with one branch per node				
Desmopsis panamensis	0·30$^{<}$ (13)		7·0$^{\lll}$	
Xylopia macrantha	0·40 (13)		9·0$^{\lll}$	

similar relationship between leaf internode length and light and growth rate has been noted in unbranched tropical forest saplings (Alexandre 1977; King 1993, 1994). This relationship involved species with large leaves, most of which initiated ascending, orthotropic branches at a height of 1 to 5 m, and does not apply to the spacing of leaves along plagiotropic branches, which does not appear to change. The relationship between internode length and growth rate was quite similar for leaves on stems and plagiotropic branches on stems, with a mean power function exponent of 0·53 relating branch internode length to diameter growth rate of the 13 temporarily marked species of this study and a mean exponent of 0·50 relating leaf internode length to height growth rate for the 10 Panamanian species studied by King (1994), over a similar time interval. In both cases, the production rate of leaves or branches also increased with increasing growth rate, as would be expected when internode length is proportional to growth rate raised to a power of less than one. However, these relationships apply to juvenile trees in forest understories or gaps and not to mature or open-grown trees. The occurrence of some curvilinearity in the internode length–growth relations for several species (Figs 1 and 2) suggests that open grown individuals may depart from the relations established here, which involved saplings receiving from 1 to 25% of above-canopy diffuse light, in the case of the short-term study.

The increase in internode length with growth rate may be related to shifts in the allocation of new biomass between the foliage and stem. King (1991, 1994) found that saplings growing rapidly in gaps produced more new stem and branch biomass than
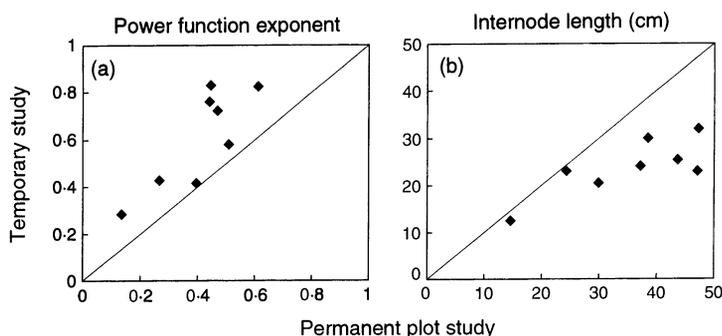

Fig. 3. Relationships between internode length parameters for temporary *vs* permanent plot individuals for the eight species common to both studies. The power function exponent in panel (a) is the slope of the regression relationship between log (internode length) and log (diameter growth rate). The internode length in panel b is that derived from the regressions for a stem diameter growth rate of 0·2 cm year⁻¹.

leaf biomass, while suppressed understorey saplings allocated most of their new tissue production to leaves, resulting in a slow turnover of existing foliage, with little accompanying height growth. This shift in growth allocation directs the minimal production of suppressed plants to replacing senescing tissues, while increasing the height growth rate of gap
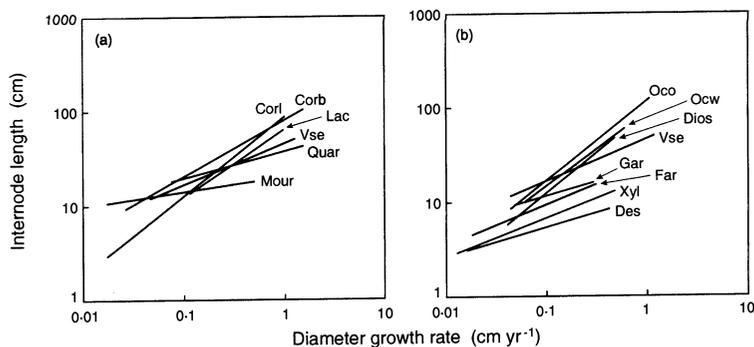

Fig. 4. Regression-derived relationships between internode length and diameter growth rate plotted on a log–log scale for the temporary study saplings. Species abbreviations given in Table 1. *Virola sebifera* is included in both panels for comparison.
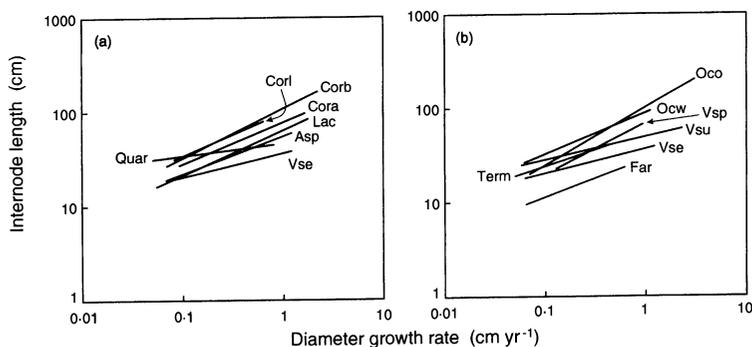

Fig. 5. Regression-derived relationships between internode length and diameter growth rate plotted on a log–log scale for the permanent plot individuals. Species abbreviations given in Table 1. *Virola sebifera* is included in both panels for comparison.
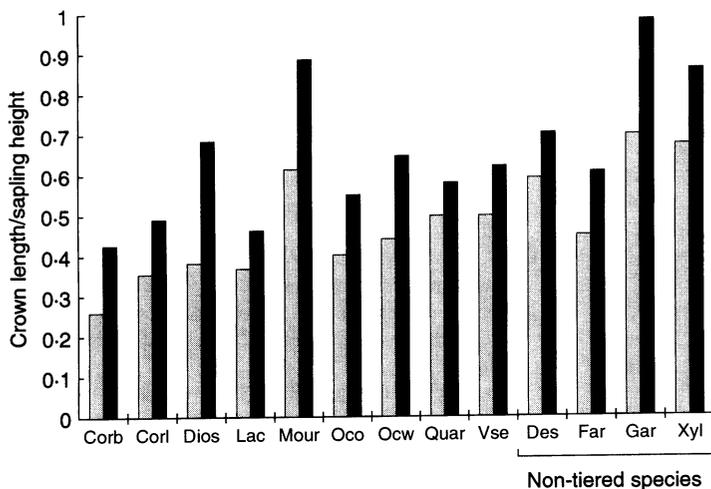

Fig. 6. Relative crown length (crown length/sapling height) associated with diameter growth rates of 0·1 cm year^{-1} (grey bars) and 0·4 cm year^{-1} (black bars), derived from regressions to non-transformed variates for the temporary study saplings. Crown length is vertical distance from the lowest to the highest leaf. Species abbreviations given in Table 1.

plants, where such growth is critical in keeping abreast of competitors. The close branch spacing of suppressed saplings may thus be an expression of low allocation to stem growth in these energetically constrained plants.

The observation that tiered species showing large increases in internode length with increasing growth rate tend to be rare, grow fast in gaps and have shallow crowns in shade (Table 4, Fig. 6) suggests a possible relation between tree architecture and demography. Saplings can achieve rapid height growth by producing new tiers at a rapid rate or by producing widely spaced tiers at less frequent intervals. A sapling in a gap which produces widely spaced tiers at infrequent intervals can extend a given tier to cover a large area with foliage before that tier is shaded by the next tier. This strategy may allow an individual to expand laterally and co-opt much of the gap space so long as it has no overlapping neighbours. On the other hand, a sapling producing tiers at a faster rate suffers more self shading of lower tiers by upper tiers, but has the advantage of continuously raising its upper crown, thereby lessening its chances of being overtopped by competitors. Thus, species that produce widely spaced tiers in gaps may be rare because the situation in which they excel, uncrowded gaps, may occur rarely in tropical forests. Such architecture–density relationships are speculative, because of the small species sample size and lack of replication between forests, but they do suggest a mechanistic basis for some differentiation in regeneration patters among non-pioneer species. However, the fact that rarer species tend to have lower survival rates and often grow faster in gaps than common species on the BCI plot (Welden 1991) makes it difficult to separate morphological influences on growth from other factors, such as degree of shade tolerance, which may be correlated with abundance (Hubbell & Foster 1990). Note also the tendency of wide-tiered, plagiotropic species to grow faster in gaps applies only to non-pioneer species at BCI, where most pioneers are either orthotropic or non-tiered, if plagiotropic.

Although a variety of tropical species bear tiers of plagiotropic branches, this form is less common on the forest dynamics plot at BCI than either orthotropic forms or non-tiered plagiotropic forms, including both vertical stemmed and arching forms (Table 5). Species producing widely spaced plagiotropic tiers in gaps comprise only a small subset of the species and individuals on the plot, comparable in importance to pioneer species of large gaps. Demographic differences may also exist between tiered species in general and non-tiered plagiotropic species. The non-tiered species of the study had higher survival rates ($P = 0·02$) and lower growth rates in low canopy areas ($P = 0·11$) than the tiered species, as derived from the survival and growth rates reported by Welden *et al.* (1991). However, the non-

tiered species were generally more common than the tiered species (Table 1), again making it difficult to separate out other factors which may be associated with abundance. Other characters, such as height of first branching and leaf life span, vary between species (Coley 1988; Reich *et al.* 1991) and in the case of leaf life span, may produce differences in growth rate among shade-tolerant species (King 1994). Thus, the study documents substantial inter-specific variation in branch spacing within a given forest, but the effect this variation on forest dynamics remains uncertain. On the other hand, larger scale architectural patterns, such as the decrease in frequency of plagiotropy in canopy trees *vs* under-storey saplings, are more easily explained in terms of the costs and benefits of different forms across broad environmental gradients (Leigh 1990).

The high correlations between branch spacing and growth rate (Table 2) suggest that branch spacing could be used to infer the growth histories of tropi-cal trees, which do not produce dependable annual rings. Such an approach would not be as accurate as long-term studies, particularly in assessing individ-uals with past breakage or dieback. However, the resulting estimates of growth histories may be of use in the study of species not occurring within long-term study plots and to assess past forest disturbances, as recorded in the branch spacing of common species, such as *Faramea occidentalis*, the second most common tree species on the permanent plot on BCI.

Table 4. Relationships between the regression slope of log(internode length) *vs* log(diameter growth rate) of tiered species and their demographic characteristics on the forest dynamics plot at BCI, Panama. The regression slopes included the species of both the temporary and the permanent plot study groups, with average values used for each of the seven-tiered species common to both groups. Low canopy growth rate refers to the diameter growth rate of 1–4 cm d.b.h. saplings in areas with a canopy height <10 m, low canopy recruitment is the proportion of total new recruits in low canopy areas and high canopy survival is the survival rate of 1–4 cm d.b.h. saplings in areas with a canopy height >10 m, as reported by Welden *et al.* (1991). The relative crown length of small saplings refers to the ratio of crown length to sapling height estimated for a diameter growth rate of 0.2 cm year^{-1}

Relationship between regression slope for tiered species and	r	P	n
Projected internode length for diameter growth rate of 1 cm year^{-1}	0.87	0.00005	14
Abundance on permanent plot	−0.54	0.048	14
Low canopy growth rate	0.76	0.029	8
Low canopy recruitment	0.03	0.93	10
High canopy survival rate	−0.63	0.070	9
Relative crown length, small saplings	−0.64	0.065	9

Table 5. Frequency of occurrence of different general architectural forms among species with 50 or more individuals ≥1 cm d.b.h. on the 50 ha forest dynamics plot on BCI in 1990 (D.A. King, unpublished data). The plagiotropic forms have branches with planar leaf arrangements, because of either a two-ranked leaf arrangement along each branch axis or a collection of upturned twigs with leaf clusters making an over-all plane of foliage. The orthotropic forms have more radially symmetric arrange-ments of leaves about the branch axes, which are generally angled upward. The 188 tabulated species comprise 62% of the species and 99.4% of all individuals ≥1 cm d.b.h. on the plot. Note that some of the species considered plagiotropic here become orthotropic under high light

Architectural form	No. of species	Individuals ≥1 cm d.b.h.
Tiers of plagiotropic branches on a vertical stem	21	9%
Plagiotropic branches (not in tiers) on a vertical stem	33	25%
Plagiotropic branches on an arching stem	40	30%
Orthotropic forms	80	33%
Intermediate forms	12	3%
Unexamined	2	0.05%

Acknowledgements

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