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Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia

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Summary

1. The development of simple predictors of tree growth is important in understanding forest dynamics. For this purpose, tree height, crown width in two perpendicular directions, trunk diameter at 1·3 m height (d.b.h.) and crown illumination index (CI) were determined for 727 pole-sized trees (8–20 cm d.b.h.) of 21 species, on forest dynamics plots at Pasoh Forest Reserve, Peninsular Malaysia and Lambir Hills National Park, Sarawak, Malaysia. A light-interception index (LI = $A_{cr}CI^2$, where A_{cr} is crown area) was calculated for each tree, and wood density (stem wood dry mass/fresh volume) was estimated for each species from reported values.
2. Diameter growth rates were linearly correlated with LI (mean per species $r^2 = 0{\cdot}45$, excluding substantially damaged and vine-covered trees).
3. Among trees of all species, diameter growth rate was highly correlated with LI/wood density.
4. Mean growth rate per species varied 10-fold among the study species, but increased linearly with mean LI/wood density ratio ($r^2 = 0{\cdot}78$), consistent with the previous pattern.
5. Thus much of the variability in tree growth rates, both within and among species, can be accounted for by the simple mechanistic assumption that, within a given size class, growth is proportional to light interception/wood density.

Key-words: crown area, tree architecture, tropical forest

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Introduction

The dynamics and abundance of forest tree species are determined in part by the relationships between tree growth, crown dimensions and light. Trees of wet tropical forests show much variation in growth rate, with many slow-growing individuals, particularly in the smallest size classes (Condit, Hubbell & Foster 1993; Clark & Clark 1999). Among saplings this variation in growth has been associated with variation in leaf area and light level (Sterck *et al*. 1999, 2003; Poorter 2001). Such factors have been incorporated into spatially explicit forest simulation models, which calculate growth rates as empirical functions of neighboring tree positions, or as functions of light as estimated from neighbor position and size (Lorimer 1983; Shugart 1984; Pacala *et al*. 1996). However, the individual tree growth rates predicted by such models are rather weakly correlated with observed growth rates on mapped plots, particularly in tropical forests (Vanclay 1995; Gourlet-Fleury & Houllier 2000; Uriarte *et al*. 2004). The models perform better for structurally simpler temperate forests, particularly when measures of the effects of neighbors on crown dimensions are included (Monserud 1975; Cole & Lorimer 1994). Likely reasons for the inability of spatial models to reproduce observed growth rates in diverse tropical forests include unexplained variation in light interception due to irregularities in tree height, crown size and vine loads.

We hypothesize that much of the observed variation in growth, both within and among species, can be related to two central factors: the amount of light intercepted by a tree; and the density of its wood. More specifically, we expect an inverse relationship between growth rate and wood density, given that the thickness of the shell of stem wood associated with a given biomass increment is inversely proportional to its density. To test this hypothesis, we estimated crown dimensions and exposure to light among 727 pole-sized trees (8–20 cm d.b.h.) of 21 species of contrasting wood density in long-term forest dynamics plots at Pasoh, Peninsular Malaysia and Lambir Hills National Park, Sarawak, Malaysia (north-west Borneo). This size range was chosen to include a more equitable distribution of crown light exposure than would be encountered among trees of

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smaller or larger size classes. From these measurements we developed a composite predictor of growth, which is indicative of whole-tree light interception. As all trees ≥1 cm in diameter have been tagged and mapped on the plots, we were also able to compute neighborhood-related competition indices and compare their predictive capacity with the derived predictor.

Materials and methods

SITES, SPECIES AND TREE SELECTION

The study was carried out in lowland forests dominated by Dipterocarpaceae on forest dynamics plots at Pasoh Forest Reserve, Peninsular Malaysia (2°59′ N, 102°18′ E) and Lambir Hills National Park, Sarawak, Malaysia (north-west Borneo) (4°12′ N, 114°01′ E). The 50 ha plot at Pasoh was established in 1986 (Manokoran *et al.* 1990); the 52 ha Lambir plot in 1991 (Lee *et al.* 2002). In both plots all trees ≥1 cm diameter at 1·3 m height (d.b.h.) (excluding lianas and palms) were tagged, mapped to ±10 cm, and identified. Tree diameters were measured repeatedly to ±1 mm in 5-year censuses, and new recruits mapped and tagged (Condit 1998). Both sites receive relatively equitable rainfall, averaging 1810 and ≥3000 mm year^{-1} at Pasoh and Lambir, respectively (Yamakura *et al.* 1996; Noguchi, Nik & Tani 2003). Most of the Pasoh plot is on a level alluvial plain ≈100 m above sea level, but includes a small hill and some differentiation in soils (Davies *et al.* 2003). The Lambir plot is on more rugged terrain, ranging from 109 to 240 m above sea level (Yamakura *et al.* 1995), with soils ranging from sandy loams on sandstone ridges and uplands to shale-derived clays on some of the lower slopes and hollows (Davies *et al.* 2005).

The chosen species were mostly common, large-stature trees that were still juvenile in the study size range, and thus likely to allocate substantial biomass to stem growth rather than reproduction. The study included both light and heavy wooded members of the Dipterocarpaceae. At Pasoh, *Dyera costulata* was chosen as a light-wooded non-dipterocarp emergent species, along with the pioneer species *Macaranga hypoleuca*, and another of the fastest-growing species, *Lithocarpus rassa*. The fast-growing species *Adinandra dumosa*, which is strongly associated with landslips, was included at Lambir. Most of the species chosen at Lambir had a widespread distribution over the sandstone substrates comprising about three-quarters of the plot area (Davies *et al.* 2005), with several also occurring on shale and mixed shale/sandstone substrates.

The study trees had trunk diameters ranging from 9 to 20 cm (Pasoh 2000–01 census) and 8 to 20 cm d.b.h. (Lambir 1997 census), with a slightly lower minimum diameter chosen for Lambir to account for growth in the longer interval until this study. One tree was omitted at Lambir, which had attained 31 cm d.b.h. and was anomalously thick for its height, as the purpose of the study was to relate growth to light and crown proportions within a limited size range. Current diameters of the rest of the study trees ranged from 8 to 25 cm d.b.h.

Variable-length line transects of 20 × 20 m quadrats were selected along the width of each plot. Quadrats were chosen over the whole length of each plot, but slopes exceeding ≈30° were mostly excluded at Lambir (18% of the plot area). From 31 January–15 March 2004 all currently live study trees per selected quadrat were measured, except for the more common species, which were discontinued after attaining a sample size of 40. About 4% of the trees encountered were not measured, primarily due to difficulties in seeing the crown. At Pasoh, trees measured in the 27th line of quadrats (13 trees comprising 3·7% of those measured at Pasoh) were omitted, as three of four trees with improbable diameter decreases of ≥4 mm in ≈3·4 years were in this line. In total, 340 and 387 trees were measured at Pasoh and Lambir, respectively,

MEASUREMENTS

For each tree selected, we measured current diameter and the vertically projected crown width in two perpendicular directions, including that of greatest width. Vertical tree heights were calculated from optical or laser rangefinder measurements of distance to the tree top and clinometer-measured sighting angles. Each tree was inspected for breakage and crown dieback, and the ratio of the stem diameter above *vs* below any breaks was estimated. The fraction of the crown ellipse covered by vines *vs* tree foliage was also estimated.

Crown illumination indices were estimated using the protocol of Clark & Clark (1992) which assigns values as follows:

1. shaded crowns exposed to neither overhead nor side gaps;
2. crowns exposed to intermediate amounts of lateral, but no vertical light;
3. crowns with 10–90% of their area exposed to vertical light;
4. crowns >90% exposed to vertical light;
5. emergent crowns where an upward-facing cone enclosing the crown with sides angled 45° to the horizontal would include no foliage from other trees.

Among trees shaded from above, a value of 1·5 was assigned to crowns exposed to small amounts of lateral light (a small side gap) and 2·5 to crowns receiving substantial side light from several gaps or a quite large opening (Clark & Clark 1992). Inadvertent repeated measurements of six trees assigned identical illumination indices to four trees and values differing by 0·5 to the other two.

Diameter growth rates were calculated as $\mathrm{d}D/\mathrm{d}t = (D_f - D_i)/(T_f - T_i)$, where D_f and D_i and T_f and T_i are, respectively, the diameters and times of measurements during the current study and the last currently available census. The interval between diameter measurements ranged from 2·6 to 4 (mean = 3·4 year) for the Pasoh study trees, and 6·4 to 6·8 (mean = 6·6 year) for Lambir.

For each species, stem-wood density, including bark (ρ = dry mass/fresh volume), was estimated from reported air-dry wood densities without bark (ρ_a = air-dry mass/air-dry volume), using the following relationship determined by Suzuki (1999) for 5 cm d.b.h. forest-grown trees of West Kalimantan, Indonesian Borneo (≈500 km south-west of Lambir):

$$\rho = 0{\cdot}67807\rho_a + 0{\cdot}042901 \qquad \text{eqn 1}$$

($n = 284$ species, $r^2 = 0{\cdot}949$). For this purpose, averages of ρ_a values given by Desch (1941, 1941 and 1954) for Peninsular Malaysia, and by the World Agroforestry Centre (2004) for Indonesia and Malaysia, were used for the Pasoh species. Values from the Forest Industries Development Project (1973) for Sarawak, Malaysia and from the World Agroforestry Centre (2004) were averaged for the Lambir species. The value for *Alseodaphne insignis* is the midpoint of the range reported for this genus in South-East Asia (Sosef, Hong & Prawirohatmodijo 1998), as no values were found for this species. For each of the six study species for which ρ had been determined by Suzuki (1999), an average was taken of this value and that calculated from equation 1 from the reported air-dry densities.

LIGHT-INTERCEPTION INDEX

Perhaps the simplest assumption regarding the relation between growth, crown status and light is that diameter growth is directly proportional to intercepted light for trees of a given size class and species. For saplings, Davies *et al*. (1998) found a curvilinear–concave relationship between incident light and crown illumination index (CI), as assessed by hemispherical photographs. We thus assumed incident light to be proportional to CI^2 – that pole-sized trees fully exposed to overhead light (CI = 4) would, on average, receive four times the light of trees with no overhead exposure, but an intermediate exposure to lateral light (CI = 2). In support of this assumption, we found a stronger correlation between growth rate and the resultant estimates of light interception than if incident light was assumed to be directly proportional to CI. We thus defined the light-interception index (LI) as:

$$\text{LI} = A_c\text{CI}^2 \qquad \text{eqn 2}$$

where A_c is the area of the ellipse encompassing the crown, as projected onto a horizontal plane.

COMPETITION INDEX

Competition indices are convenient predictors of growth on forest dynamics plots, where they can be derived from available stem maps and trunk diameters. Hence the predictive capacity of the above measures were compared with a competition index derived from the spacing and size of neighboring trees, as follows: for study tree *i*, the competition index was defined as:

$$\text{comp}_i = \Sigma\, w_{ij}(\text{dist}_{ij}, D_j) \qquad \text{eqn 3}$$

where dist = distance between tree i and its jth neighbor (of trunk diameter D_j), for all trees with diameters exceeding that of the ith tree for which $\text{dist}_{ij} < 60D_j$. The weighting factor was then defined as

$$w_{ij} = 1 \quad \text{for} \quad \text{dist}_{ij} \le 30D_j$$

and

$$w_{ij} = (60D_j - \text{dist}_{ij})/(30D_j) \quad \text{for } 30D_j < \text{dist}_{ij} < 60D_j \qquad \text{eqn 4}$$

This variant of traditional competition indices (Lorimer 1983) was chosen because it produced stronger correlations with growth rate than alternative formulations with increased or decreased areas of neighbor influence, or which simply counted all larger neighbors within a fixed distance of the target tree. The competition index was computed for all study trees >20 m from a plot boundary (beyond which out-of-plot trees have little effect on the index) based on 1997 and 2000 census data for Lambir and Pasoh, respectively.

ANALYSIS

Analyses of untransformed data were used to assess the strength and nature of the relationships between individual trees, given the expectation of a linear relation between growth rate and LI, and the fact that some estimated growth rates were slightly negative, precluding simple logarithmic transforms. As mean growth rate per species was always positive, analyses of interspecific patterns were performed on logarithmically transformed species means. Standardized major axis regression (SMA) slopes were compared using (S)MATR ver. 1 (Falster, Warton & Wright 2003). The SMA slope = ordinary regression slope/r minimizes the variance perpendicular to the fit line after transformation so that var y = var x (Ricker 1984; Warton & Weber 2002). This approach incorporates errors in x, as well as y, as is appropriate here, given that LI is more uncertain than diameter growth rate. In these analyses, trees were omitted which had any of the following: an old stem break where the above break diameter was $<0{\cdot}75 \times$ the below-break diameter; an estimated vine cover ≥ tree leaf cover; apparent dieback of ≥1/2 of the crown; or damage at the point of diameter measurement. The trees omitted comprised 16% of the total measured.

Results

Diameter growth rate varied greatly among individuals (Fig. 1) and substantially among the study species at

Table 1. Coefficients of determination (r^2) for diameter growth rate *vs* listed variates for study trees (excluding substantially damaged or vine-covered trees) at each site

	Coefficients of determination (r^2) for diameter growth rate *vs*:								
Site	A_{cr}	CI	CI^2	A_{cr}CI	LI = A_{cr}CI^2	LI/ρ	LI + sp.	LI + sp. + int.	*N*
Pasoh	0·22	0·33	0·34	0·40	0·48	0·56	0·57	0·69	274
Lambir	0·21	0·38	0·37	0·41	0·49	0·52	0·63	0·64	339

Variates: crown ellipse area as projected onto a horizontal plane (A_{cr}); crown illumination index (CI); light-interception index (LI); and LI/ρ, where wood density ρ is dry mass/fresh stem volume, as determined for each species from reported values (see Materials and methods).
Values of r^2 are also shown for multiple regressions of growth rate *vs* LI + species (considered as a factor) and growth rate *vs* LI + species + interaction.

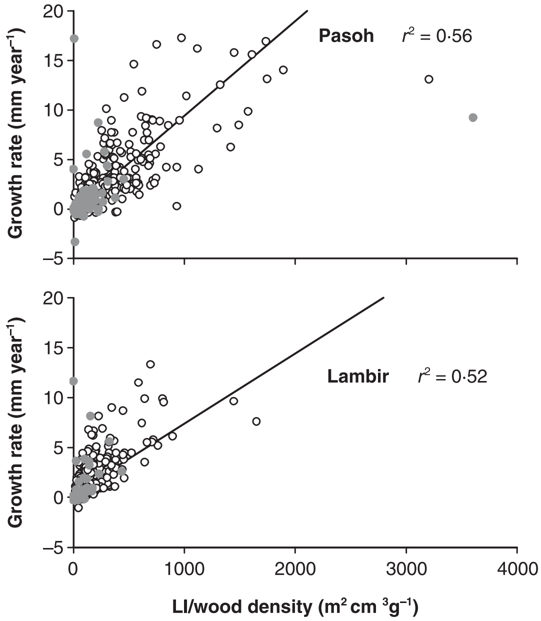

Fig. 1. Measured growth rate over the study interval of all trees in relation to light-interception index/wood density. Shaded points indicate substantially damaged or vine-laden trees excluded from analysis. The SMA regression lines derived from the non-excluded trees are growth rate (mm year^{-1}) = −0·155 + 0·00956 LI(m^2)/ρ(g cm^{-3}) for Pasoh; and growth rate = 0·380 + 0·00702 LI/ρ for Lambir.

both Pasoh and Lambir. Growth rate was successively more strongly correlated with crown area (A_{cr}), crown illumination index (CI), and light-interception index (LI = A_{cr}CI^2) (Table 1). At each site, interspecific differences in growth were, in part, associated with interspecific differences in wood density (ρ), as the correlations with LI/ρ were greater than those with LI alone (Table 1). This pattern is expected, given that the diameter increment per unit of biomass added to the stem is proportional to 1/ρ. The standard major axis slope of growth rate *vs* LI/ρ was significantly higher for Pasoh than for Lambir (0·00956 *vs* 0·00702 mm year^{-1} m^{-2} g cm^{-3}, $P < 0{\cdot}001$). The species growth rates for the sample trees (without exclusions) did not differ significantly from the corresponding species means for all plot trees of similar size, as determined from previous census data: there was no obvious bias in the selection of sample trees.

Table 2. Coefficients of determination (r^2) between listed variates and competition index for study trees ≥20 m from a plot border (omitting substantially damaged or vine-covered trees)

Site	Diameter growth rate	A_{cr}	CI	LI = A_{cr}/CI^2	*N*
Pasoh	0·19	0·07	0·23	0·21	259
Lambir	0·27	0·11	0·15	0·18	315

A_{cr} = crown area; CI = crown illumination index; LI = light-interception index.
All correlations are negative, indicating lower growth rates for crown area and light-related indices with greater crowding by larger trees.

Three of the four most notable outliers of Fig. 1 were excluded trees, including a fast-growing *Shorea leprosula* at Pasoh and a fast-growing *Shorea parvifolia* at Lambir, both of which had recently been broken (but still had live bark) and hence had LI = A_{cr} = 0. The two right-most points for Pasoh correspond to wide, fully exposed crowns of *M. hypoleuca*, the species with lowest wood density, the excluded tree being mostly covered by vines. However, most trees with incompletely repaired breakage or substantial vine loads had small crowns and thus low LI values, and were slow-growing (Fig. 1). Within species, the growth rate of non-excluded trees was significantly correlated with LI in 20 of 22 cases (19 of 21 species) considered (mean per species r^2 = 0·57/0·34 at Pasoh/Lambir).

Diameter growth rate was negatively correlated with the competition index derived from neighboring tree sizes and distances, but this correlation was weaker than that with either CI or LI (Tables 1 and 2). CI and diameter growth rate showed rather similar correlations with competition index, but crown area was only weakly related to competition index (Table 2).

INTERSPECIFIC PATTERNS

There were substantial differences among species in CI, A_{cr}, LI and growth rate, with five- to sixfold ranges in species means of A_{cr} and LI, and a 10-fold range among species in growth rate, as assessed for non-excluded trees (Table 3). *Dyera costulata* had the lowest mean

Table 3. Characteristics and mean values of the measured variates of the study species

Species	Family	Large adult diameter (cm)	Abundance (number ha^{-1})	ρ (g cm^{-3})	CI	A_{cr} (m^2)	LI (m^2)	comp	Growth rate (mm year^{-1})	SMA slope (mm year^{-1} m^{-2})	N
Pasoh, Peninsular Malaysia											
Dipterocarpus cornutus Dyer	Dipterocarpaceae	92	63·0	0·59	2·92	13·3	136	20·0	2·13	0·0166***	24
Dyera costulata (Miq.) Hook. f.	Apocynaceae	99	5·1	0·30	2·32	6·6	49	22·3	2·27	0·0664***	20
Koompassia malaccensis Benth.	Fabaceae	81	12·7	0·66	2·81	23·2	202	20·6	2·52	0·0102***	28
Lithocarpus rassa (Miq.) Rhed.	Fagaceae	28	9·9	0·67	2·98	33·0	311	18·8	6·07	0·0170***	17
Macaranga hypoleuca (Reichb. f. & Zoll.) Muell. Arg.	Euphorbiaceae	17	2·1	0·28	3·54	19·0	256	20·1	5·43	0·0172***	14
Neobalanocarpus heimii (King) Ashton	Dipterocarpaceae	135	63·0	0·68	2·75	19·1	153	21·4	2·43	0·0199***	29
Santiria laevigata Bl.	Burseraceae	72	10·4	0·52	2·68	18·0	140	21·2	3·02	0·0239***	17
Shorea leprosula Miq.	Dipterocarpaceae	78	30·1	0·36	3·33	15·8	189	19·7	5·31	0·0308***	32
Shorea maxwelliana King	Dipterocarpaceae	79	116·8	0·73	2·63	19·1	141	20·5	1·38	0·0163***	34
Shorea parvifolia Dyer	Dipterocarpaceae	68	15·8	0·31	2·78	18·6	155	20·9	4·21	0·0369***	36
Sindora coriacea (Baker) Prain	Fabaceae	86	23·1	0·50	2·85	19·3	165	19·6	2·62	0·0237^{NS}	23
Lambir, Sarawak, Malaysia											
Adinandra dumosa Jack	Theaceae	33	10·0	0·50	3·17	13·9	163	26·6	3·67	0·0172***	27
Alseodaphne insignis Gamble	Lauraceae	82	9·2	0·51	2·42	10·7	69	32·3	1·40	0·0170*	25
Dialium indum L.	Fabaceae	42	5·3	0·71	2·57	19·0	136	31·2	2·27	0·0174***	27
Dipterocarpus globosus Vesque	Dipterocarpaceae	99	63·8	0·62	2·39	9·0	59	37·2	0·71	0·0129***	37
Dryobalanops aromatica Gaertn. f.	Dipterocarpaceae	103	202·6	0·64	2·74	15·4	125	35·0	2·45	0·0181***	36
Scaphium borneensis (Merrill) Kosterm.	Malvaceae	31	26·7	0·46	3·07	9·3	93	35·3	1·67	0·0276*	28
Shorea havilandii Brandis	Dipterocarpaceae	58	15·5	0·79	2·23	22·7	119	32·8	1·02	0·0093^{NS}	33
Shorea macroptera Dyer ssp. *baillonii* (Heim) Ashton	Dipterocarpaceae	44	14·9	0·43	2·33	16·8	99	28·9	1·60	0·0207**	29
Shorea parvifolia Dyer	Dipterocarpaceae	97	10·5	0·31	3·22	25·5	287	26·8	6·08	0·0153**	21
Swintonia schwenkii Hook. f.	Anacardiaceae	62	19·4	0·54	2·62	10·0	75	35·8	1·49	0·0199***	39
Whiteodendron moultonianum (W.W. Sm.) *vs* Steen.	Myrtaceae	41	65·3	0·67	2·34	9·8	62	36·6	0·63	0·0125**	37
Pasoh species means				0·51	2·87	18·6	172	20·5	3·40	0·0254	
Lambir species means				0·56	2·65	14·7	117	32·6	2·09	0·0171	

Characteristics include large adult trunk diameter (95% quantile of all diameters ≥0·1 × maximum diameter); abundance of trees ≥1 cm d.b.h. and stem-wood density (ρ).
Measured variates include mean crown illumination index (CI); crown area (A_{cr}); light-interception index (LI = A_{cr}CI^2); competition index (comp); diameter growth rate; and SMA regression slope of growth rate *vs* LI for sample size (N), excluding substantially damaged and vine-laden trees.
Stem-wood densities (air-dry mass/fresh volume) were determined from reported stem densities and air-dry wood densities (see Materials and methods).
*, **, *** indicate $P < 0·05$, $P < 0·01$ and $P < 0·001$, respectively, for the correlations between growth rate and LI, associated with the SMA slopes.
For each of the six measured variates at each site there were significant differences among species ($P < 0·001$), except for comp at Pasoh ($P = 0·34$), as determined by ANOVA of logarithmically transformed data, except for the SMA slopes.

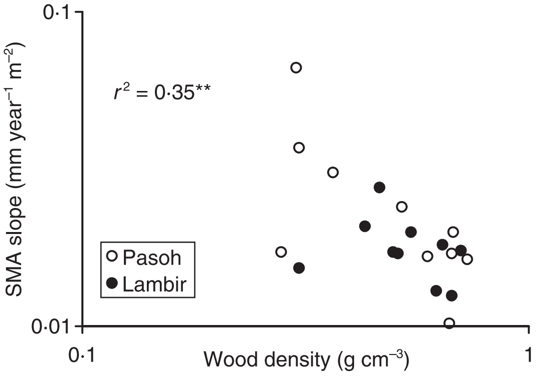

Fig. 2. Standard major axis regression slope of growth rate *vs* light-interception index (LI) for each species plotted against wood density (oven-dry stem mass/fresh volume). Two species (*Sindora coriacea* of Pasoh and *Shorea havilandii* of Lambir), for which growth rate was not significantly correlated with LI, were omitted. The coefficient of determination (r^2) is for log slope *vs* log wood density; ** indicates significance at $P < 0{\cdot}01$.

A_{cr}, second-lowest CI, and hence the lowest LI. The mean growth rate of this species was among the lowest at Pasoh, in contrast to the other light-wooded species measured there (*M. hypoleuca*, *S. leprosula* and *S. parvifolia*), which had high growth rates, and LI values that were three to five times that of *Dyera* (Table 3). This soft-wooded species also had a relatively high fraction of damaged or vine-laden trees (9/29) and was unusually short statured in the pole stage considered here (unpublished data).

The mean values of the competition index for the Lambir species varied widely (26·6–37·2) and were higher than at Pasoh (18·8–22·3) (Table 3). *Adinandra dumosa*, which is strongly associated with landslips, had the lowest competition index at Lambir, but there was much variation among the remaining species on this topographically and edaphically heterogeneous plot. Tree basal area was substantially higher at Lambir than at Pasoh (43·6 *vs* 32·1 m^2 ha^{-1}), consistent with the differences in competition index.

The species differed in the SMA slope of the relation between growth rate and light interception ($P < 0{\cdot}001$). This slope was inversely related to wood density (Fig. 2).

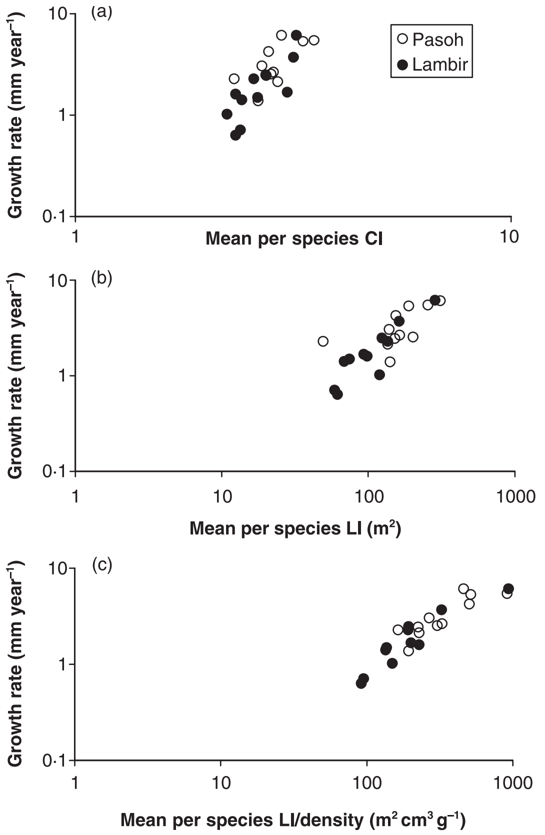

Fig. 3. Mean growth rate per species *vs* species means of (a) crown illumination index (CI); (b) light illumination index (LI); (c) LI/wood density.

There were no significant differences between sites in the slopes or elevations of the SMA relationships involving species means, so the sites were combined in these analyses. Mean growth rate per species (again excluding substantially damaged or vine-covered trees) was highly correlated with mean LI/ρ (Fig. 3; Table 4). Of the three variates comprising this predictor (A_{cr}, CI and ρ), growth was most strongly correlated with CI, but the SMA regression slope of log(growth rate) *vs* log(CI) was quite high, suggesting that growth rate ∝ CI^5. As A_{cr}/ρ also increased with CI (Table 4), this high exponent is due to the combined effects of light and correlated differences in crown area/wood density among

Table 4. Standard major axis (SMA) regressions and coefficients of determination (r^2) derived from species means of diameter growth rate; crown area (A_{cr}); crown illumination index (CI); light-interception index (LI); and stem-wood density (ρ) for both study sites combined

Interspecific relationship	SMA intercept	SMA slope	r^2
Log growth rate *vs* log A_{cr}	−1·58	1·63	0·30**
Log growth rate *vs* log CI	−1·85	5·06	0·62***
Log growth rate *vs* log LI	−2·32	1·27	0·65***
Log growth rate *vs* log ρ	−0·22	−2·00	0·30**
Log growth rate *vs* log LI/ρ	−2·08	1·02	0·85***
Growth rate *vs* LI/ρ	0·51 mm year^{-1}	0·0072 mm year^{-1} m^{-2} g cm^{-3}	0·78***
Log A_{cr}/ρ vs log CI	0·13	3·69	0·35**

Intercepts for log–log relationships derived from growth rates given in mm year^{-1}; A_{cr} and LI in m^2; ρ in g cm^{-3}.
*, **, ***, $P < 0{\cdot}05$, $P < 0{\cdot}01$ and $P < 0{\cdot}001$, respectively.

species. Ordinary multiple regression of the species means yielded log (growth rate) = 1·75 ± 0·25 + 0·75 ± 0·18 log(A_{cr}) + 2·23 ± 0·61 log(CI) – 0·85 ± 0·23 log(ρ) (r^2 = 0·83). These coefficients are all within 1·5 standard errors of the relationship log(growth rate) = a + log(A_{cr}) + 2log(CI) – log(ρ) which, when back-transformed, yields growth rate ∝ A_{cr}CI^2/ρ, that is, growth rate ∝ LI/ρ.

Discussion

Our results support the premise that variation in light interception and interspecific differences in wood density are major determinants of the variation in growth among trees of a given forest. Within species, growth rate increased linearly with light interception, although there was substantial unexplained variation in growth. Likely causes for this variation include inaccuracies in the assessment of light interception, variation in allocation of growth between the lower stem and other tree parts, and variation in soil resources and pest and pathogen loads.

Light, leaf area and growth vary from year to year in forest trees (Sterck *et al*. 1999), resulting in weak correlations between growth in different years among tropical saplings (Clark & Clark 1992). Between-year growth correlations reported by Clark & Clark (1992) were considerably higher for 10–30 cm diameter trees, which may vary more slowly in leaf area and crown position. Nonetheless, the coupling of single estimates of light interception at the end of the study with growth rates measured over mean intervals of 3·4 and 6·6 years, respectively, at Pasoh and Lambir, is a likely source of error. Among temperate trees, there are large shifts in the balance between height and diameter growth over decade-long periods, possibly due to temporal variation in light gradients (Sumida, Ito & Isagi 1997). This variation in allocation to stem thickening, coupled with intraspecific variation in soils, pest and pathogen loads, and photosynthetic responses, would also produce unexplained variation in growth.

On the other hand, the emphasis on large-stature species may have produced stronger correlations between growth rate and light interception than would have been the case for small-stature, shade-tolerant species. Gourlet-Fleury & Houllier (2000) reported greater responses to crowding by neighbors among fast-growing, large-stature species than among species of lesser stature with slow mean growth rates. Limited photosynthetic capacities among small-stature, shade-tolerant species (Thomas & Bazzaz 1999) and/or increased allocation to reproduction in response to light in understorey adults (Levey 1988) may result in weaker relations between diameter growth rate and light interception in this species group.

The moderate correlations between growth rate and CI observed here are within the range reported for other tropical forest species (Clark & Clark 1992; Davies *et al*. 1998), but were weaker than those involving LI (Table 2). While CI alone is a useful estimator of growth, the inclusion of crown area improves the prediction of growth (Table 1) and makes more sense from a mechanistic view.

The correlations between growth rate and competition index were weaker than those between growth rate and either CI or LI (Tables 1 and 2). These correlations would have been even weaker had smaller saplings been studied (D.A.K., unpublished results; Uriarte *et al*. 2004). Similarly weak correlations were observed between CI and competition index (Table 2). Apparently, variation in tree dimensions, erectness and symmetry limit the degree to which light levels can be predicted from the positions and sizes of tree bases (Moravie, Durand & Houllier 1999). The even weaker correlation between crown area and competition index (Table 2) suggests that the positions of the larger trees that determine this index and mostly overtop the target tree have little effect on its crown area.

Our results link observed interspecific differences in growth rate to interspecific differences in wood density and light interception. Because the biomass increment associated with a given diameter increment is directly proportional to wood density, diameter growth rate should be inversely proportional to wood density, all else being equal. Such inverse relationships between mean growth rate per species and wood density have been reported for a dry (Enquist *et al*. 1999) and a seasonally wet tropical forest (Muller-Landau 2004). In the latter case, the correlation between sapling relative growth rate and wood density was rather weak (r = –0·5), comparable with the correlation between log (growth rate) and log (wood density) reported here for pole-sized trees of $r = -0·55$. (Table 4). Intraspecific variation in wood density (Djoen Seng 1990), and any biases in the estimated species values used here, would also affect the resulting correlations.

However, all else is not equal regarding the central process of light interception, as the study species differed substantially in mean LI due to differences in crown exposure to light and crown size (Table 4). Interspecific differences in crown size and illumination among pole-sized trees were also reported by Poorter *et al*. (2003) and Kohyama *et al*. (2003), who found that crown dimensions and tree height were, in part, correlated with adult stature. As expected from a mechanistic viewpoint, the relationship between growth rate per species and LI/wood density was stronger than the relations involving either of these variates alone.

The importance of considering both LI and wood density is illustrated by *D. costulata*, which has quite light wood, but a low mean growth rate among pole-sized trees of the old-growth forest at Pasoh. This species is considered light-demanding as a seedling, but can persist in a stunted state as a shaded sapling, responding with accelerated growth when the canopy is opened (Aminuddin 1982; Appanah & Weinland 1993). In the current study, slow-growing *Dyera* trees had small, poorly illuminated crowns, with frequent past breakage and/or vine infestation. However, for given light interception, *Dyera* showed efficient growth due to its low-density, low-cost wood.

In conclusion, wood density, crown size and light environment are major determinants of tree growth. Variations in crown size and exposure to light give rise to much variation in tree growth rates, while differences among species in wood density and light interception explained most of the observed interspecific variation in growth rate. Species also vary in photosynthetic characteristics, in association with leaf lifespan (Reich *et al*. 1997) and adult size (Thomas & Bazzaz 1999). Photosynthetic capacity tends to be greater among light-demanding species, which often have low-density wood (Swaine & Whitmore 1988), and both these traits may contribute to interspecific differences in crown illumination by influencing the invasion of new growing space.

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