

Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest

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Abstract

Tree stature is an important ecological and silvicultural characteristic and the high diversity of many tropical forests is associated with a broad range in species stature. A measure of adult size, the 95th percentile of trunk diameter of all diameters $\geq 0.1 \times$ maximum observed diameter ($D95_{0.1}$) was found to be independent of species abundance and highly correlated with maximum height. $D95_{0.1}$ was determined for 573 species with at least 20 trees with diameters $\geq 0.1 \times$ maximum observed diameter in old-growth, lowland evergreen forest on the 50-ha forest dynamics plot at Pasoh Forest Reserve, Malaysia. These species, comprising 98.3% of all trees ≥ 1 cm diameter in the plot, were then divided into five life forms of differing stature; shrubs ($D95_{0.1} < 5$ cm), treelets ($5 \text{ cm} \leq D95_{0.1} < 12$ cm), understory trees ($12 \text{ cm} \leq D95_{0.1} < 25$ cm), canopy trees ($25 \text{ cm} \leq D95_{0.1} < 60$ cm) and emergents ($D95_{0.1} \geq 60$ cm). Each life form showed a distinctive pattern of mortality versus trunk diameter, but all showed higher mortality in the largest diameter class per life form. Mean growth rates increased with trunk diameter within each life form, consistent with reported increases in irradiance with height at Pasoh. Among trees of similar diameter, growth rates increased across life forms from the smallest to largest. These differences in growth rate among life forms may be due to associated differences in allometry, photosynthetic capacity and reproductive allocation.

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1. Introduction

A challenge in managing and conserving tropical forests is that most of their constituent species are rare and hence poorly known (Thomas, 2003). This challenge is particularly evident for the diverse, timber-rich, lowland mixed dipterocarp forests of Southeast Asia, most of which have been converted to oil palm plantations or degraded forest over the past several decades (Whitmore, 1998; Curran et al., 2004). Forest ecologists have dealt with this high diversity by classifying species into functional groups, based on adult size and shade tolerance or other growth characteristics (Vanclay, 1991; Gourlet-Fleury and Houllier, 2000; Kohler et al., 2000). While shade tolerance has traditionally been viewed as both an indicator of regeneration requirements and an axis of ecological differentiation (Whitmore, 1998; Turner, 2001), adult stature

has received increasing attention as a basic species attribute and mechanism for species coexistence (Kohyama, 1993; Kohyama et al., 2003; Thomas, 2003; Poorter et al., 2005).

Tropical trees typically show a broad and continuous range in adult size, with maximum heights of co-occurring species ranging from 1 to 70 m (Kohyama et al., 2003; Thomas, 2003; King et al., 2005b). This range in stature results in a tradeoff between size at first reproduction and life-long reproductive output, where the latter is enhanced by prolonged vegetative growth to construct large, elevated crowns that intercept much light and produce large seed crops (Turner, 2001). Trees also show tradeoffs in adaptations to overstorey versus understorey light conditions with canopy trees having greater photosynthetic capacity than understory trees, even when compared among similar-sized saplings in similar light environments (Thomas and Bazzaz, 1999). Large-statured species typically have higher growth rates than small species (Vanclay, 1991; Gourlet-Fleury and Houllier, 2000) and higher growth rates have been reported for canopy tree juveniles than for understory trees (Thomas, 1996a; Sterck et al., 2001), although the latter observations are restricted to a few genera or families of trees.

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However, it can be difficult to assess the adult size of many tropical species, due to their rarity. Typically, maximum or near maximum height has been used to characterize adult stature (Thomas, 1996a; Poorter et al., 2003). As these methods require extensive height measurements they are not directly applicable to the trunk diameter data available for most forest plots. Here, we evaluate a new method of characterizing maximum adult tree diameter, which is shown to be unbiased with respect to sample size, insensitive to occasional errors in tree identification and highly correlated with the asymptotic maximum heights derived by Thomas (1996a). We use the method to estimate maximum diameters for 573 species comprising 98.3% of the 339,000 stems ≥ 1 cm dbh on the 50-ha forest dynamics plot at Pasoh Forest Reserve, Malaysia. We group these species into five stature classes, which are then shown to have distinctive patterns of growth and mortality that are obscured when all species are combined. By including all individuals ≥ 1 cm dbh, we are able to determine the proportions of small stems that are saplings of canopy and emergent species and therefore important in the regeneration of timber trees.

2. Methods

2.1. Study site

The study was based on census data from the 50-ha forest dynamics plot at Pasoh Forest Reserve, peninsular Malaysia (2°59'N, 102°18'E), in lowland forest dominated by the Dipterocarpaceae (Manokaran et al., 1990). Most of the plot is on a level alluvial plain ca. 100 m above sea level, but includes a small hill and some differentiation in soils (Davies et al., 2003). The site receives relatively equitable rainfall, averaging 1810 mm year⁻¹ (Noguchi et al., 2003). All trees ≥ 1 cm diameter at 1.3 m height (dbh) (excluding lianas and palms) were tagged, mapped to ± 10 cm, and identified. Tree diameters were measured repeatedly to ± 1 mm and new recruits mapped and tagged in 5-year censuses (Condit, 1998). As 1–5 cm dbh trees were measured to ± 5 mm in the first, 1987 census, our analysis is based on the more accurate censuses of 1990 and 1995. Most trees were measured at 1.3 m height, but larger buttressed trees were measured at a marked height above the highest buttress. Among the 339,000 tagged trees in 1995, 818 species were identified (Davies et al., 2003).

2.2. Adult size

The adult size of species has been characterized in a number of ways, including asymptotic maximum height (Thomas, 1996a), an average of the one to three tallest trees encountered (King et al., 2005b) and the 95th percentile of height values of either all trees per species > 10 cm dbh (Poorter et al., 2003) or of trees > 15 cm in girth (Kohyama et al., 2003). However, the latter measures omit species that never or rarely attain the respective minimum diameter. Kochummen et al. (1990) classified all species on the Pasoh plot into five stature classes or life forms (shrubs, treelets, understorey trees, canopy trees

and emergents) based on approximate estimates of maximum tree height and trunk diameter. Note that in this case “shrub” refers to the smallest size category, whose members are commonly single stemmed, rather than the spreading, multi-stemmed habit of many temperate shrubs.

We tested three methods of characterizing adult size, all based on plot diameter distributions and chose the method that showed the least dependence on sample size and provided reasonable estimates for both small and large species. These characterizations included (1) the mean diameter of the three thickest trees per species on the plot ($D_{\max 3}$), (2) the 95th percentile of diameter of all trees ≥ 1 cm dbh ($D95$) and (3) the 95th percentile of diameter of all trees $\geq 0.1 \times D_{\max}$ ($D95_{0.1}$), where D_{\max} is the diameter of the thickest tree. In the case where $D_{\max} < 10$ cm, all trees ≥ 1 cm dbh were included in the sample used to compute $D95_{0.1}$, as trees < 1 cm dbh were not measured. The first two approaches are adaptations of previous methods used to estimate maximum height (Kohyama et al., 2003; Poorter et al., 2003; King et al., 2005b).

To compare the robustness of these approaches, we calculated adult size as a function of sample size by randomly sampling (10,000 replicates with replacement) the diameters of the most common large emergent species and the most common small treelet. Here and elsewhere, the maximum diameter used to select the trees $\geq 0.1 \times D_{\max}$ in the calculation of $D95_{0.1}$ was determined from the trees of each sample. As $D95_{0.1}$ provided the most reasonable estimates of adult size, we computed this measure for all species having 20 or more tagged individuals $\geq 0.1 \times D_{\max}$. For subsequent analyses, these species were divided into five life forms approximating the five stature classes of Kochummen et al. (1990), where $D95_{0.1} < 5$ cm for shrubs, $5 \text{ cm} \leq D95_{0.1} < 12$ cm for treelets, $12 \text{ cm} \leq D95_{0.1} < 25$ cm for understorey species, $25 \text{ cm} \leq D95_{0.1} < 60$ cm for canopy species and $D95_{0.1} \geq 60$ cm for emergent species. As $D95_{0.1}$ ranged from 1.7 to 149 cm for the Pasoh species, the above divisions are proportionately nearly equal.

2.3. Growth and mortality

Growth was calculated for each live tree measured in the 1990 and 1995 censuses as $G = (D_1 - D_0)/T$, where D_1 and D_0 are trunk diameter at the point of measurement in the 1995 and 1990 censuses, respectively, and T is the time interval between measurements for the tree. The small fraction of trees where the point of measurement (POM) had been moved to a new stem, usually due to breakage and resprouting below the POM, were excluded from subsequent calculations of average growth rates, as were a few extreme outliers with calculated growth rates > 60 or < -20 mm year⁻¹.

Mortality was calculated for a given population of trees as $m = (\ln n_0 - \ln S_1)/t$, where n_0 is the number of trees in the population in 1990, S_1 is the number of those trees which survived till the subsequent census and t is the mean census interval for the population. Confidence intervals for mortality were calculated assuming a binomial variance (Condit et al., 1995). Confidence intervals for growth rate were based on bootstrapped distributions of mean growth rate.

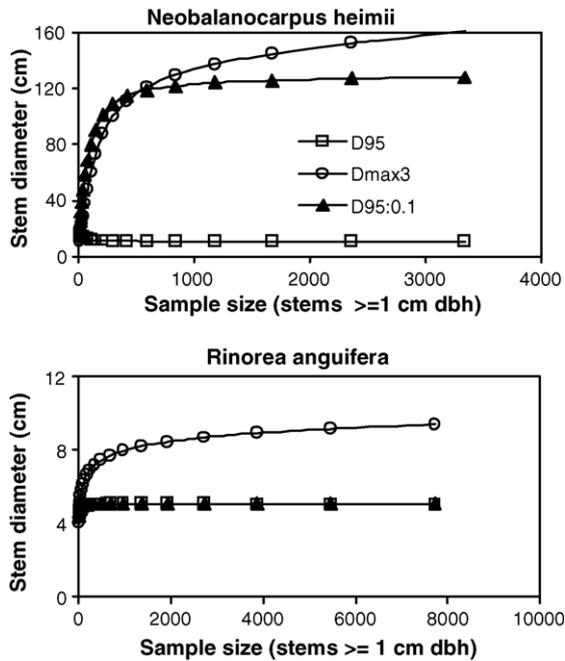


Fig. 1. Estimated adult trunk diameter vs. sample size (trees ≥ 1 cm dbh) for two common species of contrasting stature at Pasoh Forest Reserve, Malaysia. D_{95} is the 95th percentile of trunk diameter of all sample trees ≥ 1 cm dbh, $D_{\max 3}$ is the mean trunk diameter of the three thickest sample trees and $D_{95:0.1}$ ($=D_{95_{0.1}}$) is the 95th percentile diameter of all sample trees $\geq 0.1 \times$ maximum sample diameter. Note that the latter subsample is much smaller than the total sample shown on the x-axis for the large species, while the two are nearly identical for the small species.

3. Results

The relationship between estimated adult trunk diameter and sample size for two common species of contrasting stature is shown in Fig. 1. As expected, the mean diameter of the three thickest trees ($D_{\max 3}$) increased with sample size, while the 95th percentile diameters showed little change over a wide range of sample sizes. However, the 95th percentile of all stems ≥ 1 cm dbh was only 10.5 cm for the emergent *Neobalanocarpus heimii*, due the large proportions of small stems for this (and many other) species. In contrast, $D_{95_{0.1}}$, the 95th percentile diameter of all trees $\geq 0.1 \times D_{\max}$ (i.e. ≥ 19.7 cm for *N. heimii*) was 129 cm for this species. In the case of the small species, *Rinorea anguifera*, the largest tree was 10.8 cm dbh, so $D_{95_{0.1}}$ was virtually identical to the 95th percentile of all trees ≥ 1 cm dbh (Fig. 1). For this species, omission of the largest tree in the original data set (17 cm dbh), which was found to be misidentified, caused a reduction of 23% in the mean diameter of the three largest trees, but only a 6% reduction in $D_{95_{0.1}}$.

$D_{\max 3}$ was substantially affected by outliers and sample size because these features directly affect the trees included in this average. In the case of $D_{95_{0.1}}$, these features affect the diameter threshold used to select the trees included in the 95th percentile calculation, but have little or no effect on the probability distribution of diameter itself. Changing the diameter threshold from $0.1 \times D_{\max}$ to $0.2 \times D_{\max}$ or $0.05 \times D_{\max}$ changed the

Table 1

Log–log relationships between $D_{95_{0.1}}$ (the 95th percentile of diameter of all trees $\geq 0.1 \times D_{\max}$, as defined for each species) and other measures of size for the 573 species with 20 or more trees $\geq 0.1 \times D_{\max}$ on the 50 ha Pasoh plot

Diameter measure	Log–log regression slope	Log–log SMA slope	r
$D_{\max 3}$	0.865	0.896	0.965
D_{95}	0.787	0.840	0.936
$D_{95_{0.2}}$	0.958	0.981	0.977
$D_{95_{0.05}}$	0.948	0.958	0.989
$D_{90_{0.1}}$	0.994	0.1001	0.993
$D_{97.5_{0.1}}$	0.978	0.986	0.992

Here, $D_{\max 3}$ is the mean diameter of the three thickest trees, D_{95} is the 95th percentile of diameter of all trees ≥ 1 cm dbh, $D_{95_{0.2}}$ and $D_{95_{0.05}}$ are the 95th percentile of diameter of all trees $\geq 0.2 \times D_{\max}$ and $\geq 0.05 \times D_{\max}$, respectively, and $D_{90_{0.1}}$ and $D_{97.5_{0.1}}$ are the 90th and 97.5th percentile of diameter of all trees $\geq 0.1 \times D_{\max}$, respectively. The standardized major axis regression slope, defined as SMA slope = ordinary regression slope/ $|r|$, describes the relation between two variables where neither may be considered the dependent variable (Ricker, 1984). A log–log SMA slope of one indicates that the two variables are directly proportional to each other.

predicted diameters by an average of +19% or –11%, respectively, for the species of the Pasoh plot. However, the resulting estimates of $D_{95_{0.2}}$ and $D_{95_{0.05}}$ were quite closely related to $D_{95_{0.1}}$, as were $D_{90_{0.1}}$ and $D_{97.5_{0.1}}$ (Table 1), i.e. minor changes in the diameter threshold or percentile used to define tree size had little effect on the resulting species size distributions.

$D_{95_{0.1}}$ was highly correlated with the asymptotic maximum height determined by Thomas (1993) for shrub- to canopy-sized species of *Aporosa*, *Baccaurea*, *Diospyros*, *Garcinia* and *Ixora* on the Pasoh plot ($r^2 = 0.77$ for $\log(D_{95_{0.1}})$ versus $\log(\text{asymptotic height})$, $n = 34$ species). As $D_{95_{0.1}}$ was little affected by sample size, so long as at least 20 trees were included in the subsample used to calculate it, this measure was used for the 573 species having at least 20 trees with trunk diameters $\geq 0.1 \times D_{\max}$. (For *N. hemeii*, a random sample of 500 trees ≥ 1 cm dbh had on average 20.7 trees with trunk diameters $\geq 0.1 \times D_{\max}$. Thus, the fact that $D_{95_{0.1}}$ showed little dependence on sample size for total $N > 500$ for this species supports use of the above criterion.) The resulting selected species included 98.3%, 97.4% and 93.3%, respectively, of all trees with trunk diameters of 1–9.9, 10–99.9 and ≥ 100 cm. $D_{95_{0.1}}$ is hereafter referred to as adult size, recognizing that this measure applies to large adults, which may be closer to their maximum size than to their size of first reproduction. Many Pasoh species begin reproducing at less than half their maximum height (Thomas, 1996b).

The species showed a broad distribution of adult size, as plotted over half octave size classes in Fig. 2. Two-thirds of all species had adult diameters of 10–50 cm, while the distribution of stem basal area was shifted towards the larger species, with species with adult diameters of 16–128 cm comprising 82% of the total basal area. The relative abundances of the five life forms based on $D_{95_{0.1}}$ are plotted as a function of octave stem diameter class in Fig. 3. Each of the three intermediate life forms (treelet, understory and canopy trees) showed a peak in relative abundance corresponding to its adult size, where it

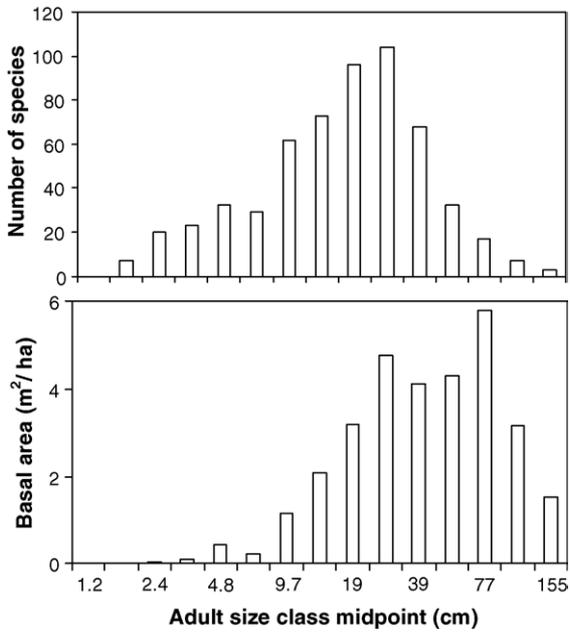


Fig. 2. Adult size distribution of 573 Pasoh species among half octave-wide ($2^{0.5}$) trunk diameter classes (top panel). Adult size is $D_{95_{0.1}}$, the 95th percentile diameter of all trees $\geq 0.1 \times$ maximum diameter. The stem basal area of trees of the species of each adult size class is shown in the bottom panel.

comprised 25–60% of all stems. The shrubs and emergent trees reached their greatest relative abundances in the smallest and largest size classes, respectively (Fig. 3).

Mean growth rate increased substantially with life form stature, particularly among larger trees (Fig. 4). All five life forms showed increasing growth rates with increasing diameter, a pattern that was more pronounced in canopy and emergent species, except for the largest emergent diameter class (Fig. 4). For the 21 most common species considered individually, growth rates were higher for the largest versus next largest diameter size class for nearly all of the smaller species, but generally not for the canopy and emergent species.

All life forms showed an increase in mortality with size at the upper end of their diameter distributions, which was significant for all but the emergent species (Fig. 4). The 95%

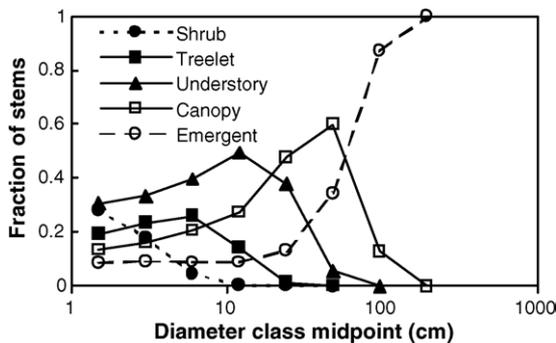


Fig. 3. Proportion of trees belonging to each of five life forms in each octave (two-fold) wide stem diameter class. Life forms are shrubs ($D_{95_{0.1}} < 5$ cm), treelets ($5 \text{ cm} \leq D_{95_{0.1}} < 12$ cm), understorey trees ($12 \text{ cm} \leq D_{95_{0.1}} < 25$ cm), canopy trees ($25 \text{ cm} \leq D_{95_{0.1}} < 60$ cm) and emergents ($D_{95_{0.1}} \geq 60$ cm).

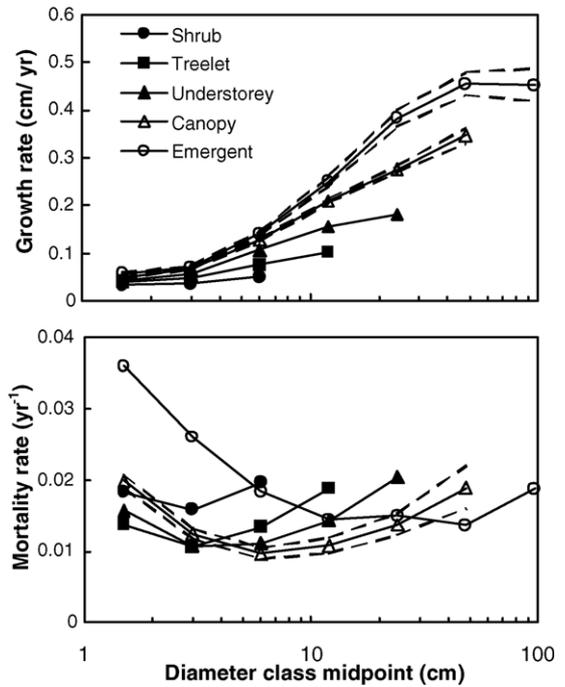


Fig. 4. Mean diameter growth and mortality rates vs. octave-wide diameter class for trees of each life form, as defined in Fig. 3. Confidence limits (95%) shown for growth for the life forms for which these limits exceeded the width of the points. Confidence limits for mortalities of shrubs, treelets and understorey species are similar to the illustrated 95% limits for canopy species; those for emergent species were $\sim 1.5 \times$ as large. Growth and mortality rates shown for diameter classes with >400 trees per respective life form.

confidence limits were proportionately larger for mortality than growth because relatively few trees died over the 5-year census interval. However, each of the five life forms had a mortality curve which differed significantly from any given other life form over at least one diameter class, as indicated by non-overlapping 95% confidence intervals. The high mortality rates among sapling emergents were associated with even higher mortality rates among light-wooded emergent dipterocarps of the light red meranti timber group (*Shorea acuminata*, *S. leprosula*, *S. lepidota*, *S. ovalis* and *S. parvifolia*) (Fig. 5). This group also showed two-fold higher growth rates than the other emergents over all but the largest diameter classes (Fig. 5).

Table 2

Correlations between $\log(\text{mean growth rate})$ and $\log(D_{95_{0.1}})$ for trees of the designated diameter class of those species with ≥ 10 surviving trees per designated diameter class

Diameter class (cm)	<i>r</i>	No. of species
1–1.9	0.42****	509
2–4.9	0.45****	532
5–9.9	0.36****	443
10–19.9	0.50****	339
20–39.9	0.52****	156
Wood density	-0.07 ns	179

Correlation between $\log(D_{95_{0.1}})$ and $\log(\text{wood density})$, based on wood densities given by Desch (1941a,b, 1954) for Peninsular Malaysia, is given in the bottom row.

**** $P < 10^{-9}$.

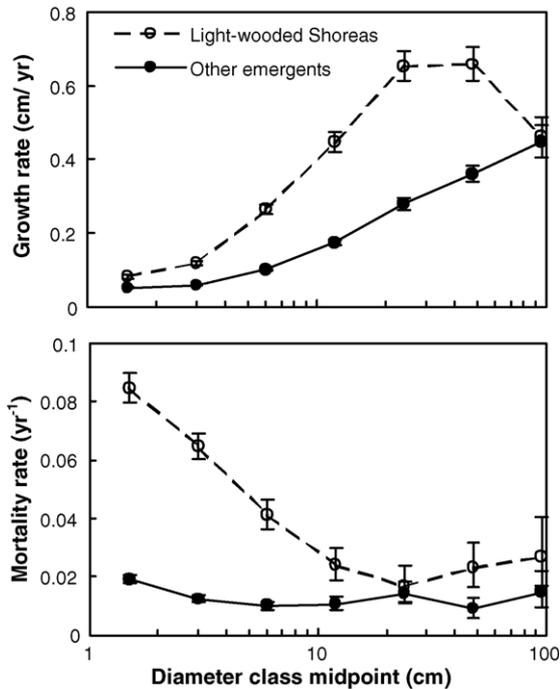


Fig. 5. Mean diameter growth and mortality rates with 95% confidence limits for five light-wooded emergent *Shorea* species and for all other emergent species.

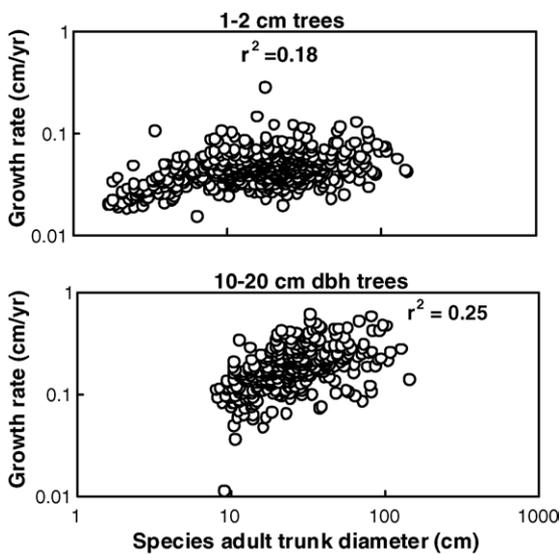


Fig. 6. Mean diameter growth rate vs. adult size ($D_{95_{0.1}}$) for those species for which growth could be determined for at least 10 trees in the indicated diameter class.

Mean growth rate per species and stem diameter class varied up to 10-fold within each life form. Nonetheless, these growth rates were substantially correlated with adult size (Table 2; Fig. 6), consistent with the comparisons across life forms. Among smaller diameter trees, this increase was relatively greater across shrub- and treelet-sized species, as illustrated for 1–2 cm dbh trees in Fig. 6.

4. Discussion and conclusion

The 95th percentile of diameter of all trees per species $\geq 0.1 D_{\max}$ ($D_{95_{0.1}}$), where D_{\max} is the largest measured diameter per species, should be of broad use for characterizing adult tree size. Our results indicate that only 20 trees $\geq 0.1 D_{\max}$ are needed for unbiased estimates of $D_{95_{0.1}}$, provided that the study forest contains old-growth trees that are approaching maximum size. However, once derived from such forests, these estimates could easily be used to assess the proportions of different stature classes in regenerating forests. While the exact method used to estimate adult size may be varied somewhat with little effect (Table 1), the practice of relating the diameter threshold to an approximation of maximum diameter is a large improvement over using the same threshold for all species (Fig. 1).

Forest-wide patterns of growth can be related to the variation in growth with species stature reported here. Wet tropical forests typically exhibit a 10-fold or greater increase in mean stem diameter growth rate across the 100-fold range in trunk diameter from 1-cm dbh saplings and shrubs to emergent trees (Condit et al., 1999; Newbery et al., 1999). This increase is associated with species-specific increases in growth rate with size (Vanclay, 1991; Clark and Clark, 1992; Condit et al., 1993) that are augmented by shifts in the proportions of slower growing small species versus faster growing large species (Fig. 3). These species-specific growth patterns in turn reflect the strong increase in light levels with height in tropical forests (Turner, 2001). At Pasoh, Kira (1978) reported an exponential increase in mean irradiance from 1% of above-canopy levels at 5 m to 20% at a height of 30 m (the approximate height of 30 cm dbh trees at this site). As growth is strongly limited by light over this range (e.g. King, 1994; Poorter, 2001), the above pattern would explain the large size-related increase in growth rate among species of similar adult size (Fig. 4).

On the other hand, the intrinsic diameter growth rates of mature trees often decrease with increasing stem diameter, as estimated for fixed competitive effects (Vanclay, 1991). In accordance with this pattern, diameter growth rates often plateau or decline across the largest size classes for individual canopy and emergent species (Condit et al., 1993; Clark and Clark, 1999), for which light is less limiting. However, the strong increase in mean irradiance with crown height among smaller-statured species may more than offset any declines in intrinsic growth rate after maturity, producing the observed increase in growth rate across the whole size range in all but the emergent life form (Fig. 4). The fact that the largest trees of each life form are mostly comprised of the larger (and hence somewhat faster growing) species of that life form may also contribute to the increase in growth rate across the largest diameter classes.

Possible reasons for the tendency of growth rates to increase with species size include stature-dependent shifts in allometry and photosynthetic capacity. Within a given diameter class, tree height tends to increase with increasing adult stature, particularly when adult understorey trees are contrasted with juveniles of canopy species (King, 1996; Kohyama et al., 2003;

Poorter et al., 2003). This pattern may lead to corresponding increases in mean crown illumination. Within selected species genera, Davies (1998) and Thomas and Bazzaz (1999) found that saplings of large-statured species had greater photosynthetic capacity and lower density wood. The latter feature should increase diameter growth rates by increasing the diameter increment per increment of stem biomass and per species growth rates typically show a negative correlation with wood density (ter Steege et al., 2003; Verburg and van Eijk-Bos, 2003; Muller-Landau, 2004; King et al., 2005b). On the other hand, we found no correlation between wood density and adult stature for the Pasoh plot species for which Desch (1941a,b, 1954) had reported adult wood densities (Table 1). As these wood densities are mostly restricted to economically useful species, further measurements of wood density are needed, emphasizing the underrepresented small-statured species. Finally, allocation to reproduction in adults of small-statured species should also lower their diameter growth rates relative to that of juveniles of larger species.

The segregation of trees by adult size reveals patterns of mortality that are obscured when all trees are combined. Forest-wide mortality rates typically decline from high levels for seedlings to lower levels that show little dependence on size for trees >5 cm dbh (Harcombe, 1987; Lieberman and Lieberman, 1987; Condit et al., 1999; Leigh, 1999; Turner, 2001). Lower mortality for 2–3.9 cm versus 1–1.9 cm dbh trees was observed for each of the five stature classes or life forms, consistent with these forest-wide patterns. However, each life form also showed increased death rates in the largest size class, consistent with at least some of the constituent species having finite, size-dependent lifespans (Fig. 4). Davies (2001) reported higher mortality rates in the largest size classes for three out of 11 species of *Macaranga* in northwestern Borneo, but long-term studies or very large sample sizes are needed to assess mortality patterns for species with low death rates (Clark and Clark, 1996).

A striking pattern of high sapling mortality and rapid mean growth rates for all but the largest trees was noted for emergent light-wooded *Shorea* species of the Dipterocarpaceae (*Shorea* sections *Mutica* and *Ovalis*) (Fig. 5), a group of high commercial value (Appanah and Weinland, 1993). The five species of this group all have relatively low wood densities (0.48–0.58 g cm⁻³ air dry mass/air dry volume for heartwood) (Desch, 1941a). These species appear to be less shade tolerant than heavier wooded *Shorea* species (Still, 1996; Whitmore, 1998), but are most abundant in the smallest size classes, as are other shade tolerant species (Wright et al., 2003) and are not considered pioneers.

Thus, adult size is an important ecological and silvicultural characteristic, both in its own right and as a correlate of other traits that also influence growth and mortality. The trees of Pasoh show substantial differentiation in stature, though more species lie near the middle of the stature distribution than at the extremes (Fig. 2; Thomas, 2003). There is some evidence that shade tolerance declines, on average, with increasing adult stature (Thomas and Bazzaz, 1999; Davies et al., 1998; Poorter et al., 2003). However, the stature gradient seems mostly

independent of the traditional gradient in shade tolerance, with species with contrasting mortality rates in shade occurring among all stature classes (Welden et al., 1991). The classification of species into functional groups is a standard procedure in modeling the growth and yield of diverse tropical forests (Vanclay, 1995). Our results support the use of adult size as one of the axes of this classification, possibly in combination with wood density or shade tolerance (Chave, 1999; King et al., 2005a). Knowledge of the demographic patterns of the less studied, small-statured species reported here should be of particular interest to conservation biologists.

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