

A comparison of species growth rates from four moist tropical forest regions using increment-size ordination

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SUMMARY

Growth rates and typical size are compared for 204 species from permanent sample plots in Brazil, Costa Rica, Guyana and Papua New Guinea. Growth rates were expressed as mean dbh increment, and typical size as 95% point of cumulative diameter distribution (D_{95}). An ordination of species was analysed by a weighted cluster analysis method to form 16 species groups for the data from the 4 regions. Only trees 20 cm and above were included, and species with 50 or more sample trees. Results are tabulated for mean group increments, mortality rates and D_{95} . Common species in each group and PSP locality are listed and their ecology discussed. Ecology and wood density are consistent between localities in their position on the increment-size graph. Mortality estimated by formula from the increment-size graph correlates with observed mortalities (R^2 69.9%), although there is systematic overestimation. The methodology presented may be useful for estimating probable growth rates from forest inventory data where PSP data is lacking, for purposes of simple stand projection. A website (www.myrlin.org) provides worksheets, software and further documentation.

INTRODUCTION

Certification of forest management to internationally accepted standards, such as those of the Forestry Stewardship Council (FSC), is increasingly being seen as a necessary requirement in the forestry sector in the tropics (eg. Focus on Finance, 2002). This implies that the forest manager must among other things undertake growth projections for the forest in question in order to demonstrate that harvesting is sustainable in the long run (FSC, 2001, §5.6). Although growth projection models can vary greatly in complexity, at a minimum they require estimates of diameter increment and mortality by species in order to make simple stand projections over a number of felling cycles (Alder, 2002). The problem facing the forest manager in many localities in the tropics is that they have no locally available growth data with which to prepare such a simple model, and no standard to indicate how reliably they may borrow data from elsewhere (Wright, 2000).

To address this issue, a study has been undertaken of growth rates and species group patterns from Brazil, Costa Rica, Guyana and Papua New Guinea, which combined with a simple stand projection model, is designed to assist in planning sustainable forest management in natural tropical forest. The objectives and directions of this study were summarised in Wright & Alder (2000). A website detailing the methodology and providing a user's guide and download point for the projection model can be found at <http://www.myrlin.org> (Alder *et al*, 2002). The present paper reports some findings from this study concerning the typical growth and mortality rates and species groupings for the data from these four countries. It also reviews the relationship between these species groups and their ecological attributes.

SOURCES OF DATA

The data used in this study derive from four sets of PSPs located respectively in the northern zone of Costa Rica, in the eastern Amazon region of Brazil, in central Guyana, and in the lowland forests of Papua New Guinea. Table 1 summarises some comparative statistics regarding the plot designs. The BR1, BR2 and BR3 plots are located in eastern Amazonia (Pará state) and are managed by EMBRAPA, the federal Brazilian agricultural and forestry research agency. At Tapajos, there are two sites known as km-67 and km-114 respectively. The km-67 plots are described and analysed in some detail in Silva (1989), and with the inclusion of more recent growth data, in Silva *et al* (1995). Some preliminary results from the km-114 plots are further discussed in Silva *et al* (1996). Alder (1995) gives some results relating to a growth model based on the BR1 and BR2 plots, whilst Alder & Silva (2000) describe a more evolved version of this model and a comparison of its projections with

actual growth data over 17 years. As Table 1 indicates, all the BR1 and BR2 plots are of ¼-ha design, with all trees down to 5 cm dbh measured. The BR3 plots at Jari employ a 1-ha square design, with measurement to 20 cm dbh on the whole plot, and a 10% sub-sample to 5 cm dbh using randomly selected quadrats. In total there are 136 PSPs covering 64 ha of natural forest, with 52,320 trees from 224 genera sampled for increment and mortality rates.

In Costa Rica, five groups of PSPs contributed to the present study. Features of the CODEFORSA and Portico plots (CR1-3) have been described in Alder (1997) in the context of the development of the SIRENA growth model. The CR1 and CR2 plots were established by CODEFORSA from 1991 onwards, and comprise 1-ha (100 x 100 m) and ¼-ha (50 x 50 m) designs respectively, both measured down to 10-cm minimum dbh according to standards specified by Synnott (1979). Plot locations, and floristic descriptions are given in Zamora (1997). These were passive monitoring plots, established in selection-managed forests characterised by the predominance of *Pentaclethra macroloba* and with *Vochysia ferruginea* commonly occurring. They are similar to the La Tirimbina plots described in detail by Finegan & Camacho (1999). The CR3 plots were established by Portico SA as experimental plots, and include controls and two or three levels of silvicultural treatment. These plots occur in forests dominated by *Carapa guianensis*, with *Pentaclethra macroloba* remaining a common stand component and *Vochysia ferruginea* rare or absent. The CR4 plots were established by ITCR and are 70 m square plots (0.49 ha), but otherwise of similar measurement standard and occurring in the same forest types as CR1 and CR2. The CR5 plots were 20 x 25 m plots (0.05 ha) established to monitor regrowth in abandoned pastures. They are described in detail in Fedlmeier (1996).

The Papua New Guinea PSP locations and measurement standards are described by Oavika (1999), and the data processing systems by Yosi (1999), both in Gideon & Oavika (1999). Alder *et al* (1998) also describes the plots in some detail. Briefly, these plots were established under an ITTO project in 1992, and re-measured between 2 and 3 times biannually up until 1998. One or two older Forest Research Institute plots were also adopted by the project, giving a total measurement span from 1990-1998. There were 72 plots established, all of 1-ha square design, measured for all species down to 10 cm dbh, of which 70 were re-measured. With two exceptions, the plots were in lowland tropical forests, placed in pairs at randomly selected locations in strata throughout PNG. Two plots were located in sub-montane forest. All plots were established immediately after logging, with a view to monitoring forest recovery. The data from the plots has been analysed in several reports, including Alder (1998a, 1998b) and Alder *et al.* (1998), and used to develop a growth model for lowland tropical forests in PNG called PINFORM.

The Guyana data comprise two sets of plot dispositions. The Tropenbos plots have been described by van der Hout (1999, 2000) and briefly in Zagt (1997). They comprise plots of 140 x 140 m (1.96ha) arranged in a randomised block experiment at Pibiri in central Guyana. All species down to 20 cm were measured on the main plots, with smaller trees down to 5 cm being sub-sampled. The 1-ha Barama plots were established and managed by the Edinburgh Centre for Tropical Forestry (ECTF) under contract; details have not hitherto been published, but the plot designs and results from analysis of trees down to 20 cm are described in Alder (2000).

All the PSPs in these four regional data sets came from lowland moist tropical forest. The large majority of the plots were logged either before first measurement, or during the course of their measurement period. Only a small number of the plots from the BR2 and BR3, and the GY1 plots were from unlogged 'virgin' forest. Because of the irregularities of harvesting, the intensity of disturbance on the logged plots varied from a near total removal of overwood to an almost undisturbed state.

This data was pooled into a common database, with the varying formats of the individual datasets transformed as necessary to a common basis. For each tree, the database includes its origin (origin code, as per Table 1, original plot and tree number), a standardised species code, flags to indicate whether the tree had indications of natural defect or logging damage, whether the tree appeared to be a recruit or to have died or been logged during the period, the first and last dates observed, and the initial and final diameters.

| origin code | source | plot size m ² | no. of plots | no. of trees | years measured | no. of genera |
|--------------|-------------------------|--------------------------|--------------|---------------|----------------|---------------|
| BR1 | EMBRAPA Tapajos km-67 | 2500 | 36 | 13946 | 1981-97 | 138 |
| BR2 | EMBRAPA Tapajos km-114 | 2500 | 60 | 24876 | 1981-95 | 152 |
| BR3 | EMBRAPA Jari | 10000 | 40 | 13498 | 1984-94 | 172 |
| CR1 | CODEFORSA 1-ha | 10000 | 9 | 4857 | 1991-98 | 227 |
| CR2 | CODEFORSA ¼-ha | 2500 | 27 | 3963 | 1992-98 | 159 |
| CR3 | Portico SA | 10000 | 17 | 8811 | 1989-96 | 125 |
| CR4 | ITCR/DFID Project | 4900 | 41 | 9958 | 1994-97 | 178 |
| CR5 | COSAFORMA/GTZ Project | 600 | 34 | 2712 | 1991-96 | 113 |
| PG1 | PNG/ITTO Project | 10000 | 70 | 26549 | 1990-98 | 274 |
| GY1 | Tropenbos Guyana | 19600 | 15 | 6018 | 1993-97 | 94 |
| GY2 | Barama Co. Ltd., Guyana | 10000 | 62 | 17153 | 1993-99 | 84 |
| Total | | | 411 | 132341 | | |

Table 1 : Location and basic statistics for permanent sample plot dispositions used in the study.

PAN-TROPICAL SPECIES GROUPS

Some system of species grouping may be regarded as essential in developing management plans and growth projections for natural tropical forest. This is because there are too many species to be listed or modelled individually, with many less common species being represented by only a few individuals in any given sample. In practical forest management, grouping may be based on commercial or trade categories, but these alone are not very suitable for growth studies, because the economic classes do not correlate well with growth or ecological behaviour of species (Vanclay, 1994, p127). In growth and yield studies in the tropics various statistical methods have often been employed to form groups. For example, Vanclay (1991) used pairwise F-tests to group growth functions with non-significant differences. More commonly, cluster analysis in some form has been used based on diameter increment linked with some other parameters to achieve an ordination in at least two dimensions. The other parameters have included maximum diameter (Alder, 1995, p.165), mean diameter (Eba'a Atyi, 1997, 2000), height (Finegan *et al* (1999), increment at successive measurements (Atta-Boateng & Moser, 1998), mortality, size and commercial status (Alder & Silva, 2000). Favrichon (1994) used diameter, diameter increment and recruitment rates. Purely statistical techniques are however less than ideal. There are subjective choices that must be made about the spatial scaling and weighting of points, and the possible clustering algorithm, that will influence results. The many rarer species represented by one or two observations reduce the effectiveness and functional clarity of the grouping. To avoid these problems, functional groups based on ecological characteristics have been used in some significant studies. Bossel *et al* (1994) classified species as understorey, treelets (*sic*), canopy trees, emergents and pioneers. Gourlet-Fleury & Houllier (2000) described Favrichon's (1994) statistical classes in terms of similar ecological groups, but with shade tolerant and light demanding canopy trees also distinguished. In the functional category, we must also mention the Plant Functional Attributes (PFA) approach evaluated by Vanclay *et al.* (1997). These attributes are primarily morphological, and include leaf size, inclination, chlorotype, and habit, the general life form, and rooting habit.

For the present study, the approach of Alder (1998a, 2000) was adopted. This involves an ordination of species mean increment (I_d) on the 95% percentile of the diameter distribution (D_{95}), with a cluster analysis based on Euclidean distance between points. After some trial and error, I_d was scaled by a factor of 100 to calculate distance in the ordination space, with D_{95} being unscaled; this gives equal weight to the increment range of 0-1 cm yr⁻¹ and diameter range of 0-100 cm). Groups were initiated by subjectively located seed points. The species closer to a given seed point than any other were added to that group as a provisional value. The centroid of the group was then calculated, weighted by the number of observations for each species. The process was then repeated, using the calculated centroids as new seed points, until species group allocations and group centroids

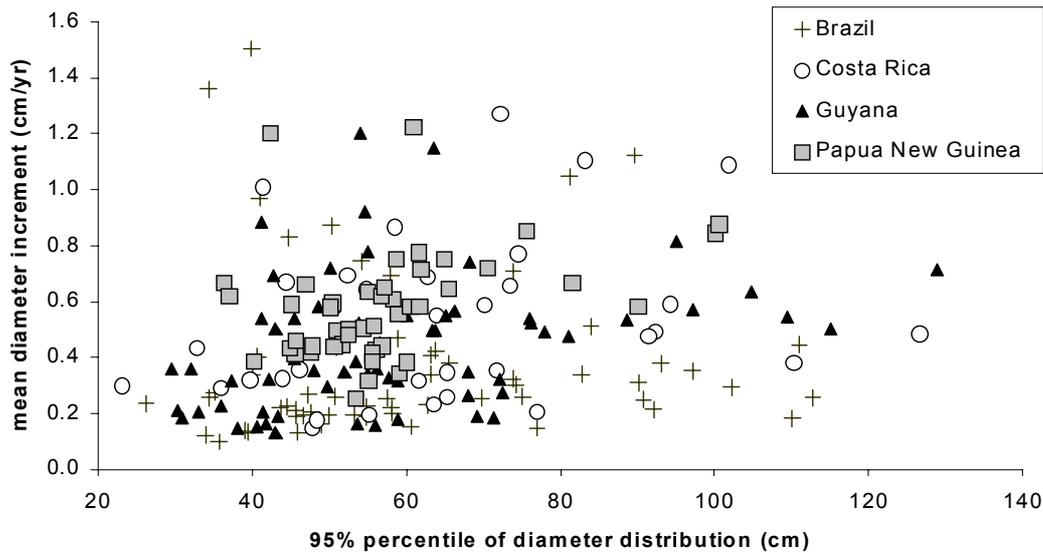


Figure 1 : Ordination of species increment and size for 204 species from PSPs in four countries. *All species shown are represented by at least 50 increment trees. The smallest tree size included was 20 cm dbh*

stabilised. This typically took 5-6 iterations. The algorithm for this process was coded in Visual Basic, and performed within Microsoft Excel. A copy of this program can be obtained at <http://www.myrlin.org>. The method is similar to that reported by Eba'a Atyi (1997, 2000), who gives relevant formulae. Pielou (1977, Ch. 20) also describes ordination methods and algorithms and was the basic text used in developing the method. The method is essentially the k-means algorithm embodied in many statistical packages, but has the advantage that the scaling, weighting and seeding techniques (all of which influence the outcome of k-means clustering – see Hartigan, 1975) are more efficiently and transparently controlled.

The data used to calculate species mean increment and D_{95} was extracted from the database summarised in Table 1. Only trees with initial diameters of 20 cm or above were used, to avoid any confusion due to different lower measurement limits on some of the PSPs. Trees with doubtful increment measurements, or recorded as dead were not used to estimate I_d , although they contributed to the D_{95} estimate. For the ordination, only species with 50 or more observations were included. This left a total of 204 species, comprising 61 from Brazil, 33 from Costa Rica, 48 from Papua New Guinea, and 62 from Guyana. 'Species' in this context indicates the best available identification for a tree, which in some cases was to the generic level only.

The 95% percentile diameter was estimated for each species by sorting the available data from smallest to largest diameter, censored to include only trees above 20 cm. Then the method recommended by NIST (2002, §7.2.5.2) was applied. The largest integer k is calculated such that $k \leq 0.95N$, and a decimal part d as $0.95N - k$. If the ordered diameters are $D_1, D_2 \dots D_N$, then 95% diameter is given as $D_k + d(D_{k+1} - D_k)$.

The initial seed points were located after examining the data graphically, as shown in Figure 1. Four size categories were considered: 40, 60, 80 and 100 cm, and four increment levels, which were adjusted at each size category to span the distribution of the data from slowest to fastest growing. After application of the clustering algorithm this resulted in the groups and centroids shown in Figure 2. The 16 groups were designated by the letters A-S, omitting I, O and Q for clarity on graphs. Table 2 gives group statistics for number of species, number of trees, and centroid I_d and D_{95} . This table also gives the weighted average annual mortality rate (AMR), as discussed below, and an estimate of typical age as the time of passage from 20 cm to D_{95} , conventionally calculated as $(D_{95} - 20)/I_d$. Table 3 gives the three most common species in each group from each regional data set. If there are less than three species in the sample data, only those available are listed.

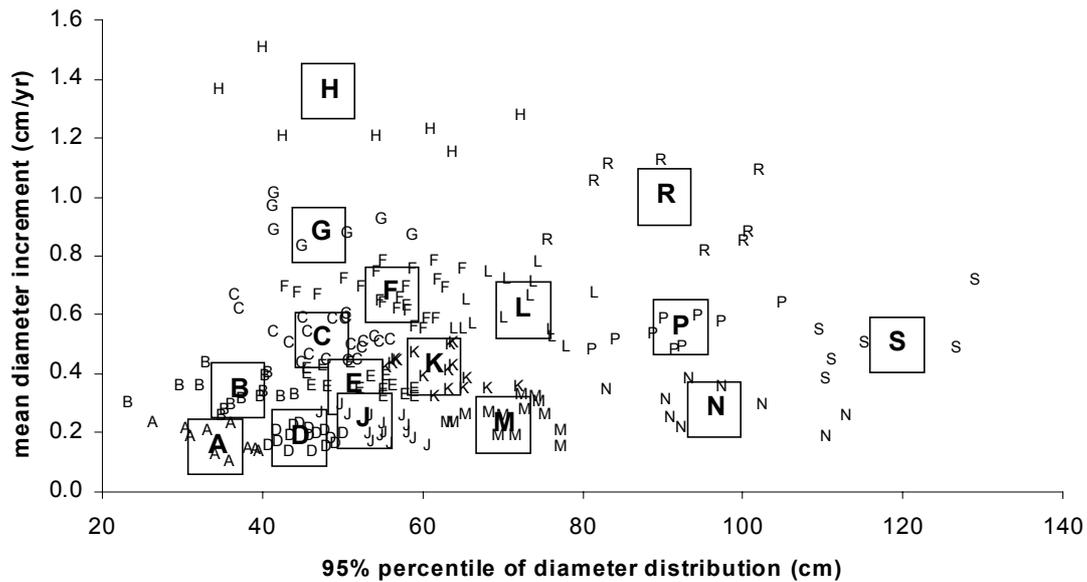


Figure 2 : Results of cluster analysis to form 16 species groups from species ordination. The cluster centroids is shown by square symbols. Small letters indicate location of individual species within each cluster.

| Group | Number of species | Number of trees | D_{95} cm | I_d cm yr ⁻¹ | AMR % yr ⁻¹ | Est. Age to D_{95} , yrs |
|-------|-------------------|-----------------|-------------|---------------------------|------------------------|----------------------------|
| A | 10 | 1337 | 34.1 | 0.15 | 2.45 | 93 |
| B | 14 | 1536 | 36.9 | 0.34 | 2.70 | 49 |
| C | 21 | 3863 | 47.4 | 0.52 | 2.20 | 53 |
| D | 16 | 1951 | 44.6 | 0.19 | 2.10 | 133 |
| E | 15 | 6144 | 51.5 | 0.36 | 2.38 | 88 |
| F | 23 | 5437 | 56.1 | 0.67 | 3.56 | 54 |
| G | 7 | 994 | 47.0 | 0.87 | 3.65 | 31 |
| H | 7 | 1041 | 48.2 | 1.36 | 1.70 | 21 |
| J | 15 | 4950 | 52.8 | 0.24 | 2.33 | 135 |
| K | 16 | 2679 | 61.3 | 0.43 | 1.91 | 97 |
| L | 14 | 5621 | 72.5 | 0.62 | 2.59 | 85 |
| M | 14 | 3137 | 70.0 | 0.23 | 1.49 | 219 |
| N | 9 | 1127 | 96.4 | 0.28 | 1.12 | 271 |
| P | 9 | 1753 | 92.2 | 0.56 | 1.54 | 129 |
| R | 8 | 880 | 90.2 | 1.00 | 2.23 | 70 |
| S | 6 | 490 | 119.2 | 0.50 | 1.85 | 199 |

Table 2 : Statistics of 16 species groups established by cluster analysis

MORTALITY RATES

In stand projection, mortality is an important and sensitive parameter. It typically varies between average rates of 1-3% for undisturbed stands, with higher rates for some years following logging, fire or storm damage (see Alder, 1995, p 136 for citations). Mortality in forestry is usually quoted as an Annual Mortality Rate (AMR), whereas in ecological literature it may be indicated by the exponential mortality coefficient. The two can be very similar in value as annual rates, but lead to very different long-term estimates (Sheil *et al.*, 1995). An AMR of 1% rate implies 60.5% survival after 50 years, whereas 2% and 3% mortality give 36.4% and 21% survival respectively. AMR is difficult to determine accurately on PSPs as it may involve the accurate registration of 1 or 2 trees dying, amongst some 5-6 trees for a given species which disappear, lose their numbers, 'move' outside a plot, are harvested without any record., are missed during measurement etc. Only a careful and rigorously supervised PSP programme is likely to give useful mortality estimates.

In the present study mortality was estimated for each species using the methods described in Alder (1995, p.137), excluding trees which had died directly as result of logging, silvicultural treatment, or had been harvested. Mortality rates for the groups were estimated as the weighted mean of the species mortalities, using number of trees observed for each species as the weighting parameter. Table 2 shows the AMR mean values estimated for each group.

The ordination of increment on 95% diameter provides for an alternative way of estimating mortality, based on some theoretical assumptions. If mortality rate and increment are assumed to be approximately constant for a species between 20 cm dbh and the D_{95} diameter, and the diameter distribution itself is assumed to represent an equilibrium distribution, then AMR can be estimated from I_d and D_{95} . By definition, the D_{95} size limit represents the point at which a cohort of trees has been reduced in numbers by 95% from its value at 20 cm dbh. This is because, given the assumptions of constant increment and mortality rates, one is dealing with an idealised exponential distribution (Meyer, 1952). The time it takes a tree to grow from 20 cm to D_{95} , assuming uniform increment, will be $(D_{95} - 20)/I_d$. Given that the general formula for AMR and survival after a period t is:

$$S = (1 - \text{AMR})^t \quad \text{\{eq.1\}}$$

then in this case, $S = 0.05$ (5% of the population surviving), and $t = (D_{95} - 20)/I_d$ as noted above. Thus, with a little algebra AMR is given by:

$$\text{AMR} = 1 - 0.05^{I_d / (D_{95} - 20)} \quad \text{\{eq.2\}}$$

Using this formula, an expected AMR has been calculated for each group using its mean I_d and D_{95} value. This is shown graphically in Figure 3, with the expected value from equation {2} above on the y-axis, and the observed group mean mortality on the x-axis. If group H (small, very fast growing trees) are omitted, the regression has an R^2 of 69.9%, which is significant at better than 99% with 15 data points (13 d.f.). However, the regression indicates a bias in this method of estimating mortality: it consistently overestimates by a factor of about 2 (an unbiased method would be close to the 1:1 line on the graph). This bias is due to deviations in reality from the assumptions, of which the weakest is likely to be that concerning the equilibrium nature of the diameter distribution, given that most of the PSPs in the study are more or less disturbed. The outlying H group contains typical pioneer species (*Cecropia*, *Anthocephalus*), and its occurrence will indicate a young stand in which maximum size may not be fully expressed. Thus the D_{95} value should represent not 5% of the original 20 cm cohort, but rather a higher survival fraction; around 25% survival to D_{95} for group H would give consistency with the observed mortality rate.

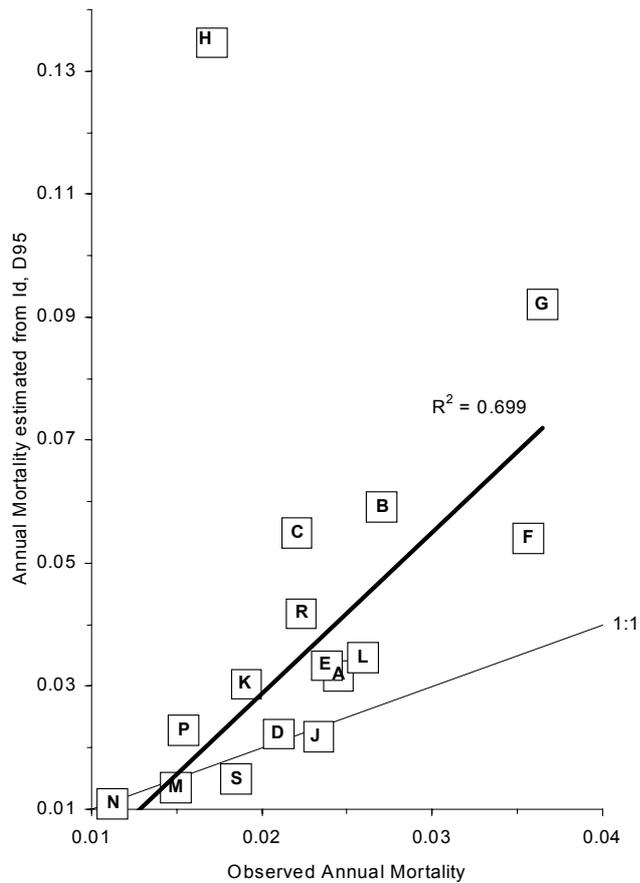


Figure 3 : Mean mortality rates for species groups as observed and estimated from mean increment and 95% diameter

The regression excludes group H, which is treated as an outlier.

The existence of a moderately close relationship (*ie.* an R^2 of 69%) between theoretical mortality rates and the empirical values for species groups indicates that the grouping of species by ordination of I_d on D_{95} also provides appropriate groups for mortality rate estimation. This is important as many species grouping studies do not consider this aspect, and simply assume that groups derived statistically or based on functional characteristics will be internally consistent for mortality rates, without demonstrating any direct evidence.

ECOLOGICAL CHARACTERISTICS

The species groups shown on Figure 2 and exemplified by typical species in Table 3 seem to be consistent with the broad functional groups proposed by Favrichon (1994) and Bossel *et al* (1994), among others. These include understory trees, sub-canopy species, canopy light-demanding species (gap opportunists and long-lived pioneers), canopy shade tolerant species, emergents, and pioneer species. However, the increment-size diagram (Figures 2,3) gives an indication of the continuum of ecological strategies. The sixteen groups used in the present analysis map onto these broader groups in a generally clear and consistent way, as evidenced by the common species characteristic of each group in Table 3. This is shown visually in Figure 4.

The discussion which follows also includes basic species-specific wood density as a factor linked to the ecological category and related to growth rate. Enquist *et al.* (1999) discuss a theoretical model for this relationship, and present data from 29 Amazonian tree species indicating a correlation of -0.47 between growth rate and basic density. Data on tropical tree wood densities will be found in Richter & Dallwitz (2000), and for Brazilian species, Fearnside (1997), among other sources.

Low growth rates (2-3 mm yr⁻¹), associated with the groups A, D, J, M, N are indicators of shade tolerance, and also result in higher wood densities. Average lower growth rates are a result of the species typically occurring in a lower canopy or understory position. The larger diameter groups in this category (M, N) are likely to be very long lived; Table 2 gives age estimates of 220-270 years. These groups include some important timber trees known for their heavy, durable wood, such as *Chlorocardium rodiei* (Greenheart, Guyana) and *Miquartia guianensis* (Acariquara, Brazil).

Figure 4 : Species groups related to broader ecological categories
Letters in circle are group centroids.

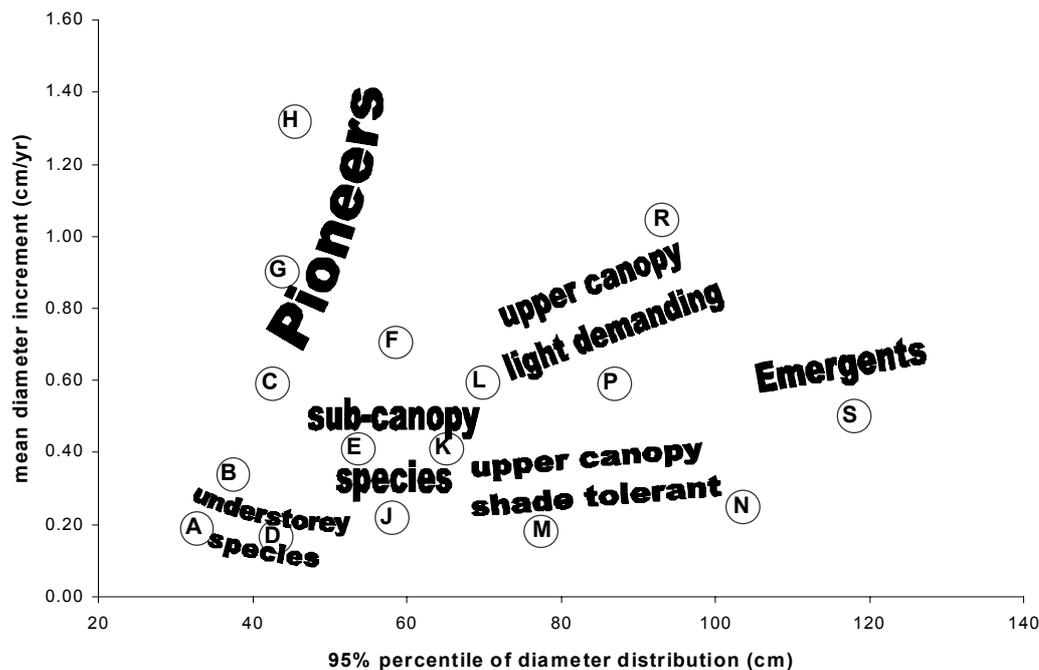


Table 3 : Most common species in species groups, by region
Species group letter is shown at left. The three most common species are shown. If there are fewer than three species, only those are shown. Some groups are not represented in some regions, so no species are shown.

| | Brazil | Costa Rica | Guyana | Papua New Guinea |
|----------|--|---|---|---|
| A | <i>Rinorea guianensis</i> (Viol.) <i>Maytenus floribunda</i> (Celastr.) <i>Anaxagorea dolichocarpa</i> (Annon.) | | <i>Licania canescens</i> (Chrysobalan.) <i>Chaetocarpus schomburgkianus</i> (Euphorbi.) <i>Guatteria</i> (Annon.) | |
| B | <i>Protium apiculatum</i> (Burser.) <i>Drypetes variabilis</i> (Euphorbi.) <i>Protium opacum</i> (Burser.) | <i>Dendropanax arboreus</i> (Icacin.) <i>Protium spp</i> (Burser.) <i>Simira maxoni</i> (Rubi.) | <i>Mabea sp</i> (Euphorbi.) <i>Tovomita</i> (Guttifer.) <i>Inga spp</i> (Mimos.) | <i>Myristica</i> (Myristic.) |
| C | | | <i>Pentaclethra macroloba</i> (Mimos.) <i>Ocotea spp</i> (Laur.) <i>Clathrotropis</i> (Papilion.) | <i>Canarium</i> (Burser.) <i>Cryptocarya</i> (Laur.) <i>Planchonella</i> (Sapot.) |
| D | <i>Protium sagatianum</i> (Burser.) <i>Dendrobanhia boliviana</i> (Icacin.) <i>Eschweilera blanchetiana</i> (Lecythid.) | <i>Brosimum guianensis</i> (Mor.) <i>Grias cauliflora</i> (Lecythid.) | <i>Catostemma fragrans</i> (Bomb.) <i>Licania alba</i> (Chrysobalan.) <i>Vouacapoua macropetala</i> (Caesalpini.) | |
| E | <i>Guatteria poeppigiana</i> (Annon.) | <i>Virola sebifera</i> (Myristic.) | <i>Eschweilera spp</i> (Lecythid.) <i>Licania heteromorpha</i> (Chrysobalan.) <i>Pouteria guianensis</i> (Sapot.) | <i>Pimeleodendron amboinicum</i> (Euphorbi.) <i>Horsfieldia</i> (Myristic.) <i>Vatica rassak</i> (Dipterocarp.) |
| F | <i>Jacaranda copaia</i> (Caric.) <i>Tapirira guianensis</i> (Anacardi.) | <i>Pourouma bicolor</i> (Cecropi.) <i>Couma macrocarpa</i> (Apocyn.) <i>Cordia alliodora</i> (Boragin.) | <i>Alexa sp.</i> (Fab.) <i>Protium decandrum</i> (Burser.) <i>Inga rubiginosa</i> (Mimos.) | <i>Calophyllum</i> (Clusi.) <i>Litsea</i> (Laur.) <i>Terminalia spp</i> (Combret.) |
| G | <i>Inga spp</i> (Mimos.) <i>Bixa arborea</i> (Bix.) <i>Porouma longipendula</i> (Mor.) | <i>Hampea appendiculata</i> (Malv.) <i>Goethalsia meiantha</i> (Tili.) | <i>Tapirira marchandii</i> (Anacardi.) <i>Byrsonima spicata</i> (Malpighi.) | |
| H | <i>Cecropia sciadophylla</i> (Mor.) <i>Cecropia leucoma</i> (Mor.) | <i>Qualea paraensis</i> (Vochysi.) | <i>Cecropia angulata</i> (Mor.) <i>Pterocarpus officinalis</i> (Papilion.) | <i>Elaeocarpus</i> (Elaeocarp.) <i>Anthocephalus chinensis</i> (Rubi.) |
| J | <i>Geissospermum sericeum</i> (Apocyn.) <i>Eschweilera jurunensis</i> (Lecythid.) <i>Eschweilera amazonica</i> (Lecythid.) | <i>Licania affinis</i> (Chrysobalan.) | <i>Licania guianensis</i> (Chrysobalan.) <i>Lecythis confertiflora</i> (Lecythid.) <i>Swartzia leiocalycina</i> (Caesalpini.) | <i>Diospyros spp</i> (Eben.) |
| K | <i>Carapa guianensis</i> (Meli.) <i>Virola michelli</i> (Myristic.) <i>Ocotea douradensis</i> (Laur.) | <i>Elaeoluma glabrescens</i> (Sapot.) <i>Tetragastris paname</i> (Burser.) <i>Otoba novogranatensis</i> (Myristic.) | <i>Carapa guianensis</i> (Meli.) <i>Ecclinusa guianensis</i> (Sapot.) <i>Apeiba echinata</i> (Tili.) | <i>Syzygium</i> (Myrt.) <i>Dysoxylum</i> (Meli.) <i>Garcinia</i> (Clusi.) |
| L | <i>Sclerolobium tinctorium</i> (Caesalpini.) | <i>Pentaclethra macroloba</i> (Mimos.) <i>Hernandia didymantha</i> (Hernandi.) <i>Virola koschnyi</i> (Myristic.) | <i>Catostemma commune</i> (Bomb.) <i>Sterculia pruriens</i> (Sterculi.) <i>Pouteria sp</i> (Sapot.) | <i>Pometia pinnata</i> (Sapind.) <i>Pterocarpus indicus</i> (Fab.) <i>Homalium sp</i> (Flacourtii.) |
| M | <i>Pouteria sp</i> (Sapot.) <i>Minuartia guianensis</i> (Olac.) <i>Corytophora ramosa</i> (Lecythid.) | <i>Pouteria sp</i> (Sapot.) <i>Brosimum lactescens</i> (Mor.) <i>Guarea sp</i> (Meli.) | <i>Chlorocardium rodiei</i> (Laur.) <i>Mora gongrijpii</i> (Caesalpini.) <i>Eschweilera coriacea</i> (Lecythid.) | |
| N | <i>Manilkara huberi</i> (Sapot.) <i>Goupia glabra</i> (Celastr.) <i>Couratari oblongifolia</i> (Rubi.) | | | |
| P | <i>Endopleura uchi</i> (Humiri.) | <i>Carapa guianensis</i> (Meli.) <i>Dialium guianense</i> (Caesalpini.) <i>Apeiba membranacea</i> (Tili.) | <i>Aspidosperma cruentum</i> (Apocyn.) <i>Parinari campestris</i> (Chrysobalan.) <i>Pithecelobium jupunba</i> (Mimos.) | <i>Ficus sp</i> (Mor.) |
| R | <i>Sclerolobium chrysophyllum</i> (Caesalpini.) <i>Tachigalia myrmecophylla</i> (Caesalpini.) | <i>Vochysia allenii</i> (Vochysi.) <i>Vochysia ferruginea</i> (Vochysi.) | <i>Goupia glabra</i> (Celastr.) | <i>Vitex</i> (Verben.) <i>Euodia</i> (Rut.) <i>Alstonia</i> (Apocyn.) |
| S | <i>Aspidosperma desmanthum</i> (Apocyn.) | <i>Pterocarpus officinalis</i> (Papilion.) <i>Dipteryx panamensis</i> (Papilion.) | <i>Manilkara bidentada</i> (Sapot.) <i>Peltogyne</i> (Caesalpini.) <i>Swartzia jenmanii</i> (Caesalpini.) | |

The groups B, E, K, P and S, in increasing order of typical size (D_{95}) show somewhat higher growth rates, in the range 3-5 mm yr⁻¹. The larger K, P and S groups have typically mid-range wood densities and durability, and include important utility timbers such as *Carapa guianensis* (Andiroba, Crabwood, Royal Mahogany). These species appear to be still relatively shade tolerant. The S group comprises the large canopy emergents of the climax forest, many of which are important timber trees (eg.. *Dipteryx panamensis*, *Pterocarpus officinalis*, *Aspidosperma desmanthum*, *Manilkara bidentata*).

The C, F, L, and R groups, with increments in the range 5-10 mm yr⁻¹, appear to be light demanding species with lower density timbers. The C and F groups include smaller trees of the lower canopy. *Jacaranda copaia*, for example, is a common member of this group from the Brazilian data, and is characteristic of disturbed forest after logging. It is also a significant timber tree, in spite of its relatively small size. In Costa Rica, *Cordia alliodora* occurs in group F, and is also a typical secondary forest species of medium size and significance as a timber tree (Francis & Lowe, 2000). Groups L and R include important fast-growing, large, long lived trees. *Vochysia ferruginea* for example is noted by Finegan *et al.* (1999) to be strongly light demanding; *Goupia glabra* is similarly described by Rose (2000). In the L group from Papua New Guinea are the important timber trees *Pometia pinnata* and *Pterocarpus indicus*. In Guyana, the L group includes the *Catostemma commune* (Baromalli). In Costa Rica, the ubiquitous and dominant species of the northern lowland forests, *Pentaclethra maculosa* (Gavilan) is in this group.

The G and H groups are trees of fast growth rate (10-20 mm yr⁻¹), relatively short life spans (20-50 years), low density timber, of strongly pioneer characteristics, occurring after heavy disturbance. The common species noted in table 3 include *Cecropia* species and *Anthocephalus chinensis*. Other rarer species, not shown in the table, include *Acacia mangium* (Papua New Guinea) and *Ochroma lagopus* (Balsa, Costa Rica). *Qualea paraensis* is described by Weissenhofer (1996) as a long-lived pioneer, but occurs in this group as a fast-growing tree with mean increment of 1.27 cm yr⁻¹ and D_{95} of 74.5 cm. This places it to the extreme right of the H cluster (Figure 2) and adjacent to the R group, to which it should more properly belong.

Some widely distributed species occur in different groups in different regions. For example, *Pterocarpus officinalis* occurs in group H in Guyana (I_d 1.1 cm yr⁻¹, D_{95} 63.5 cm, 65 trees sampled) which would suggest a fast-growing pioneer, whilst it is seen in group S in Costa Rica (I_d 0.49 cm yr⁻¹, D_{95} 126.6 cm, 192 trees sampled). *Carapa guianensis* occurs in group K in Brazil (I_d 0.424 cm yr⁻¹, D_{95} 63.8 cm, 239 trees sampled), and in group P in Costa Rica (I_d 0.593 cm yr⁻¹, D_{95} 94.2 cm, 730 trees sampled). *Pentaclethra maculosa* occurs in Guyana in group C (I_d 0.20 cm yr⁻¹, D_{95} 33.1 cm, 72 trees sampled), and in Costa Rica, where it is a very common species, in group L (I_d 0.66 cm yr⁻¹, D_{95} 73.5 cm, 2568 trees sampled). In some cases species identified only to the generic level occur in different groups, but little can be said about this, as they may well represent different species in the different localities.

These different classifications are unlikely to be due to sampling effects alone, although this would be a factor if small numbers of trees were involved. In all cases, these are relatively common, ubiquitous trees. The most likely explanation is a combination of genetic drift, leading to subtle changes in species ecology and growth patterns across a wide distribution, and site differences which favour the growth of a species in one locale and reduce it in another. Further research on the behaviour of these common species across their range is needed to fully explore these issues.

DISCUSSION AND CONCLUSIONS

Ordination of permanent sample plot data from four distinct tropical regions on mean increment and typical size shows consistent patterns and clusters of species that coincide with the major functional groups: understorey trees, mid-, upper-canopy and emergent shade tolerant species, short and long-lived pioneers, medium and large light demanding species. These patterns are also consistent with wood density information, with heavy hardwoods tending to be in slow growing groups, and light, low density timbers in faster growing groups. The range of growth rates is between 2 mm yr⁻¹ and 8 mm yr⁻¹ for the majority of species, with those of recognisably pioneer characteristics having maximum growth rates up to 15 mm yr⁻¹ for smaller sized species, and up to 11 mm yr⁻¹ for the larger, long-lived pioneers. These are average growth rates for the species, including in this data all size class from 20 cm and above.

It is of course true, as many authors have observed, that diameter increment for a given tree varies considerably over its lifespan, both due competitive, biotic, and geometric factors. Average increment for populations of a species similarly show changes with size and competitive classes (see Alder, 1995, for some examples). This should not be regarded as invalidating the use of species mean increment I_d , as a robust descriptive statistic, or of implying that increment for a species needs to be constant over size for the methods presented here to be valid.

There is a general tendency for mean growth rate to increase with typical species size. This is probably an effect of both the canopy position of the species and its ecological strategy. On the other hand, the limits to growth rate decline as size increases for the fastest growing species. For smaller pioneers, mean growth rates around 15 mm yr⁻¹ occur. For larger long-lived species considered to be of pioneer habit (such as *Vochysia ferruginea*, *Goupia glabra*), maximum species-average growth rates are around 11 mm yr⁻¹, whilst for the largest emergents, this figure falls to 6-7 mm yr⁻¹.

For forest managers and planners in the tropics who need to make a provisional estimate of commercial volume increment, and hence sustainable yield, this information can be of assistance where direct permanent sample plot data is absent. It is necessary to estimate the 95% cumulative diameter (D_{95}), neglecting trees below 20 cm dbh, from conventional forest inventories, and to have some idea of the ecology and/or wood density of the species. Then from Figure 2, a reasonable estimate of likely increment can be made. This is clearly a very provisional method, that does not replace the need for permanent sample plots, but it is a means of providing a rational estimate that is unlikely to be far wrong unless the ecological behaviour or wood density of the species have been incorrectly defined. This approach has been worked up into a series of spreadsheets with accompanying macros and documentation at the website <http://www.myrlin.org>.

When analysing existing permanent sample plot data, the increment-size diagram is a useful aid to developing a method of species grouping, or of visualising or testing existing species grouping strategies. It has the advantage over more abstract ordinations of being relatively robust with weak data, and easily visualised and presented; and over functional methods of not requiring *a priori* knowledge of species ecology or morphology.

It may be argued that both I_d and D_{95} are modified by stand treatment. Logging will remove mainly the larger trees, and therefore presumably curtail the diameter distribution. Likewise, increments tend to be higher in disturbed stand than in virgin forest. In practice, with real-world operations, these factors do not seem to be strong enough to invalidate the analysis. At the MYRLIN website noted above, a method is presented for adjusting the D_{95} scale according to a mean D_{95} value to compensate for effects of treatment or site. However, further work is required into the statistical behaviour of D_{95} , so that confidence limits relative to sample size can be calculated, and its sensitivity to logging and disturbance evaluated. It would be very interesting to prepare graphs using the methodology described here for the other major moist tropical forest regions that have not been covered: West and Central Africa, and South-East Asia. The Dipterocarps, with their high growth rate and light-demanding habits, would most probably fall into the R group of Figure 2. In West Africa, light-demanding, fast growing species such as *Triplochiton scleroxylon* (Obeche) or *Piptadeniastrum africanum* (Dahoma) might similarly fall into the R group, whilst the slower growing but light demanding *Khaya ivorensis* (African Mahogany) might fall into the P group. These ideas can easily be tested from available information, and the authors suggest this idea to research workers in these countries as a useful line of study.

In conclusion, the authors would wish to emphasise the main points of this research. The increment-size diagram, based on PSP data from four different forest regions, shows consistent patterns that coincide with the known ecology of species. This is useful in placing limits to expected growth rates, given a knowledge of species size (95% diameter) and ecology, and could be used to provide first-order estimates of growth rates where PSP data is lacking (as shown at www.myrlin.org). It also shows that in spite of their great species diversity, the aggregate growth characteristics of moist tropical forest in different regions appears quite similar. The increment-size diagram is also a useful research tool for reporting and describing PSP data sets, whatever method of species grouping or ordination may ultimately be preferred.

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