Two-year tree growth patterns investigated from monthly girth records using dendrometer bands in a wet evergreen forest in India

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(Accepted 19th December 1999)

ABSTRACT. With the aim of characterizing tree growth patterns, this paper re-examines the growth data of 100 selected trees belonging to 24 species that were recorded monthly in a 0.2-ha plot of a wet evergreen forest in the Western Ghats of India during the period 1980–82 using dendrometer bands. The mean growth profile, combining all of the selected trees, showed: (a) a significantly lower annual growth rate during the second year of survey which seemed to be negatively related to monsoon precipitation; (b) significant intra-annual growth variation clearly related to the regular alternation between a period of heavy rain and a quite long dry season of the monsoon climatic regime. Analysis of the variability of the individual smoothed growth profiles representing the 2-y trend of the growth data showed that: (a) the mean growth rate depended on a combination of an intrinsic endogenous variable (the structural class grouping species according to their maximum size), a tree size variable (tree diameter at breast height, dbh) and a neighbourhood variable (the number of taller neighbours in a 10-m radius); (b) the sudden change in growth rate from one year to the other was not predictable using these variables. The amplitude of the seasonal variations, investigated from the detrended growth profiles, appeared to be dependent on a combination of tree dbh and the number of taller neighbours in a 10-m radius. A co-inertia analysis of the smoothed and the detrended growth profiles indicated that the trees with fast growth also exhibited high seasonal variation. It is suggested that fast growing trees are those with favourable crown positions, which are consequently subject to high transpiration rates due to radiation and wind exposure.

KEY WORDS: dendrometer bands, detrended growth profiles, seasonal growth variations, smoothed growth profiles, tropical wet evergreen forest, 2-y growth trend, Western Ghats of India
INTRODUCTION

Tree growth is of central interest for ecologists and foresters because of its usefulness in assessing and predicting forest yield (e.g. Vanclay 1994), as well as its implication in understanding tree population demography and stand dynamics (e.g. Swaine & Lieberman 1987). Unfortunately, many tropical trees do not form annual growth rings in the xylem, precluding dendrochronological analyses (Bullock 1997, Clark & Clark 1994). Many studies have therefore dealt with individual or species growth rates, which were evaluated from diameter increments recorded at successive inventories, in natural or treated forests (e.g. Devineau 1991, Felfili 1995, Hladik 1982, Lang & Knight 1983; Lieberman & Lieberman 1985, 1987; Loffeier 1989, Manokaran & Kochummen 1987, Ng & Tang 1974, Okali & Ola-Adams 1987, Pélissier et al. 1998, Swaine et al. 1987a).

Most of these studies have shown strong inter-individual (i.e. inter- and intra-specific) variability of growth in space and time – that is among neighbouring trees and among consecutive time intervals. On the one hand, life-form, species autecology and genetics are endogenous factors that render individual tree growth to be a fairly conservative process over many years (Swaine et al. 1987b), even if changes in growth patterns are sometimes observed through ontogeny (Clark & Clark 1992). On the other hand, exogenous biotic (e.g. disease, competition; Lieberman & Lieberman 1987, Lieberman et al. 1985) or abiotic factors (e.g. climate, season; Bullock 1997, Clark & Clark 1994, Lieberman 1982, Sheil 1995), are able to produce, even for adult trees, more or less delayed growth variations. Such diversity remains to a large extent responsible for the lack of reliable, but vital, understanding of tree growth patterns in tropical forests.

Since the early 1980s, the French Institute of Pondicherry has conducted collaborative research programmes with the Kerala and the Karnataka Forest Departments, on the structure and dynamics of the wet evergreen forests of the Western Ghats of India (Elouard et al. 1997, Loffeier 1989; Pascal 1982, 1986, 1988; Pascal & Pélissier 1996; Pélissier 1997, 1998; Pélissier et al. 1998). A 0.2-ha plot was installed in Attapadi forest (Kerala State) in 1979–80 and regularly surveyed for several years (Loffeier 1989, Pascal 1988). In this paper we propose a re-examination of the tree growth data recorded monthly in this plot during the period 1980–1982 using dendrometer bands. The objective was to investigate factors that may explain inter-individual variability of the 2-y tree growth profiles.

MATERIALS AND METHODS

Study site

The wet evergreen forest of Attapadi (Kerala State; 11°05' N, 76°27' W) is situated at medium elevation (c. 900 m asl) on the hillside to the south-west
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of the Nilgiri hills. It has a monsoon climate (average rainfall > 4000 mm y⁻¹) with a south-westerly onset of rains in summer and a marked dry season, lasting 3–3.5 mo, in winter (Figure 1).

Attapadi forest was classified under the Cullenia exarillata – Mesua ferrea – Palaquium ellipticum type of medium elevation wet evergreen forests (Pascal 1982, 1988; the authority for the names of species cited in the text is given in Table 1). It is a dense and diverse unlogged forest dominated by an emergent Bombacaceae species, Cullenia exarillata, followed by an understorey Meliaceae species, Reinwardtiodendron anamallayana and an emergent Sapotaceae species, Palaquium ellipticum, which together represent about 50% of the relative density and 65% of the relative basal area of trees with girth at breast height (gbh) ≥ 10 cm. Simpson’s floristic diversity, estimated as 1–λ, was 0.90 (Pascal 1988).

Stand density for trees ≥ 3.18, 10, 30 and 50 cm dbh (diameter at breast height) was 1470, 690, 164 and 63 trees ha⁻¹, respectively, for a mean basal area of 59.6 m² ha⁻¹. The canopy cover was estimated at 91.5% (Pascal 1988).

Sampling and data

In 1979–80, 147 trees with gbh ≥ 10 cm and belonging to the commonest species were fitted with home-made stainless steel dendrometer bands (Murphy 1970). The dendrometer bands were placed at breast height (1.30 m above ground level or above buttresses if any), on a smooth bark surface. The trees were selected according to a stratified sampling system taking into account species diameter distribution and density: to obtain a good representation of the size classes of each of the studied species, the sampling intensity was lower for frequent species and small trees than for rarer species and larger
Table 1. List of the tree species included in the stratified sampling system in Attapadi wet evergreen forest, Western Ghats, India. Grouping of species in the different structural classes is based on tables from Pascal (1988): 1 = emergent and upper canopy species; 2 = lower canopy species; 3 = understorey species.

<table>
<thead>
<tr>
<th>Species name</th>
<th>Structural class</th>
<th>dbh (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>≥ 3.18</td>
</tr>
<tr>
<td>Reinwardtiiodendron anamallayanan (Bedd.) Saldanha</td>
<td>2</td>
<td>16</td>
</tr>
<tr>
<td>Cullenia exarillata A. Robyns</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>Agrostisacteys meboldii Pax &amp; K. Hoffm.</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>Gonpandra tetrandra (Wall.) Sleumer</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Hydnocarpus alpinus Wt.</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Palagurium ellipticum (Dalz.) Baillon</td>
<td>1</td>
<td>7</td>
</tr>
<tr>
<td>Mallotus beddomei J. Hk.</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Mesua ferrea L.</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Turpinia malabarica Gamble</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Holigarna arnottiana J. Hk.</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Myristica dactyloidea Gaertn.</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Garancia morella (Gaertn.) Desr.</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Actinodaphne sp.</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Cassine glauca (Rottb.) Kuntze</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Drypetes elata (Bedd.) Pax &amp; Hoffm.</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Kneea attenuata (J. Hk. &amp; Thw.) Warb.</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Polyalthia fragans (Dalz.) Bedd.</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Schleichera oleosa (Lour.) Oken</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Artocarpus heterophyllus Lam.</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Galophyllum polyanthum Willd.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Jambosa muconii Walp.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Litsa oleoides J. Hk.</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Persa macrantha (Nees) Kosterm.</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Syzygium laetum (Haw.) Gandhi</td>
<td>3</td>
<td>1</td>
</tr>
</tbody>
</table>

Trees. Among these fitted trees, 100 were retained on the basis of the quality of the 2-y growth data (see Table 1) after elimination of some doubtful series of measurement because of disturbed or damaged dendrometers.

The girths were recorded monthly with an accuracy of ±0.2 mm. Since newly installed bands often underestimate actual girth (Keeland & Sharitz 1993, Murphy 1970), the first readings were discarded and series of 25 records were considered for analyses, from April 1980 to April 1982. Because the number of days between consecutive measurements varied (from 17 to 40), diameter increments were adjusted by \((729 \times \Delta \text{dbh})/(24 \times \Delta t)\), where \(\Delta \text{dbh}\) corresponds to the measured diameter increment during \(\Delta t\) in days; 729 and 24 are the total number of days and months covering the 2-y monitoring period (Clark & Clark 1994). The tree growth profiles presented correspond to the adjusted series of diameter increments as a function of time in months.

For some analyses, the species were grouped according to their maximum size (Aiba & Kohyama 1997) into three structural classes which represented the different layers in the vertical structure of the stand that trees are able to occupy on reaching adult status. From the tables given in Pascal (1988), we considered: emergent and upper canopy species with maximum height \(\geq 25\) m (SC1), lower canopy species with maximum height between 15 and 25 m (SC2) and understorey species with maximum height \(< 15\) m (SC3). SC1 was composed of 10 species representing 37.6% of the total number of the sampled
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Statistical analysis

The study focused on adjusted (see above) tree growth profiles. To analyse both characteristics of these profiles, namely the seasonal variations and the 2-y trend, the growth data were smoothed using the locally weighted regression-scatterplot smoothing method described by Cleveland (1979). It is a robust moving-average approach using the \( v \) nearest neighbours of each point (date) weighted by a cubic function (details on the regression procedure can be found in Cleveland 1993). The parameter \( v \) was determined after the examination of the variations of the smoothing error as a function of the number of nearest neighbours taken into account in the regression. This error is computed as the squared difference between the values observed and predicted by the regression (Cleveland & Devlin 1988). Two new data sets were then obtained. The first one corresponded to the smoothed growth profiles, i.e. the monthly values predicted by the locally weighted regression and related to the first predicted value (so that all the curves started from zero in April 1980). The second one corresponded to the detrended growth profiles computed as residuals of the locally weighted regression, i.e. as the differences between the observed and predicted values. The smoothed profiles express the 2-y trend of the growth data and the detrended profiles express the seasonal variations.

Keeping in mind that the stratified sample was not representative of the whole population, we considered in a first section the mean growth profile resulting from the combination of all individuals of all species. Serial dependence within the detrended mean growth profile was investigated using an autocorrelation function (ACF; Diggle 1990). Stationarity of the data was assumed by the use of the detrended profile. The ACF estimate is easy to interpret: a positive autocorrelation at lag \( k \) indicates that the observed values distant from \( k \) time intervals are similar, while a negative autocorrelation at lag \( k \) indicates that they differ. When \( k \ll n \) (where \( n \) is the number of points (dates) of the series), an approximated confidence interval for the ACF estimate for a stationary random sequence (white noise) is given by \( \pm z_{\alpha}/\sqrt{n} \), where \( z_{\alpha} \) is the standard normal deviate for a given significant level \( \alpha \) (Diggle 1990).

To study the variability of the individual tree growth patterns, principal component analyses were conducted on the covariance matrix (centred-PCAs) of both the individual detrended and smoothed growth profiles. The effects of independent variables on scores on the principal components were then tested through analyses of variance. Three groups of independent variables were considered in these analyses: (a) intrinsic endogenous characteristics (species and structural class); (b) individual tree size characteristics (tree dbh and tree height); and (c) individual neighbouring characteristics (local density). The local density was computed in circles of 5, 10 and 15-m radius, centred on each individual and took into account: (a) the total number of neighbours within...
the corresponding circle (N); or (b) the number of neighbours taller than the central tree within the corresponding circle ($N_{sup}$). The former parameter reflects the two-sided competition (e.g. for water and nutrients), while the later reflects the one-sided competition (e.g. for light) between the central tree and its neighbours (Moravie et al. 1997). The computation involved all the trees with gbh $\geq 10$ cm in April 1980 (not only those fitted with a dendrometer) and used Ripley’s (1977) edge effect correction for the trees near the plot boundary (for more detail about edge-corrections, see e.g. Goreaud & Pélissier 1999).

Locally weighted regressions and PCAs were computed using ADE-4 software (Thioulouse et al. 1997) and ACFs and general linear models using SYSTAT 5.1 (Wilkinson 1990).

RESULTS

Mean growth profile

Characteristics of the mean growth profile, resulting from the combination of all individuals of all species, are summarized in Figure 2. As the raw data exhibited growth variations with phases of fast increment and phases of stagnation or even regression, they were smoothed using the locally weighted regression technique (Figure 2a). An optimal smoothing was obtained by taking into account the 20 nearest neighbours of each point (date) value from which the regression error plateau-ed (Figure 2b). As would be expected from the smoothed profile, the mean growth rate slowed down significantly during the second year of survey (Mann-Whitney U-test: $P = 0.007$). This could be linked to year-to-year climatic variations, but we did not have rainfall records at the study site corresponding to the period of study.

The ACF estimated from residuals of the regression showed significant seasonal variations ($P < 0.05$) with a negative autocorrelation at lag 6 mo and a positive autocorrelation at lag 12 mo (Figure 2d). Obviously these growth variations can be related to alternation between the dry and rainy seasons, which are apparent in the climatic diagram in Figure 1, but with a time-lag between rainfall and growth peaks of c. 1–2 mo: the main peak of rainfall is in July while growth is maximum in August–September; the main trough of dryness is in January while growth is minimal in April–May.

Smoothed tree growth profiles

The first principal component (PC1) of the smoothed growth profiles accounted for 99.5% of the total variance of the scatterplot indicating that a single factor explained the structure of the data set. In fact, scores on PC1 were proportional to the last value of the growth profiles ($r = -0.99$, df = 98, $P < 0.001$), thus reflecting simply the total diameter increment. We then transformed the data into growth rates by calculating in each series the differences
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Figure 2. Mean tree growth profile in the wet evergreen forest of Attapadi, Western Ghats, India. (a) Raw data and the 2-y growth trend approach by locally weighted smoothing. (b) Mean smoothing error as a function of the number of measurement dates taken into account. (c) Detrended mean growth profile corresponding to residuals of the locally weighted smoothing. (d) Autocorrelation function (ACF) estimate with 95% confidence interval of a random sequence (white noise).

between all successive increments. This data-transformation prior to PCA computing was done to give prominence to changes in the trend of the profiles (Tomassone et al. 1993). In this second analysis, PC1 accounted for 97.5% of the total variance and PC2 for 2.2%. Scores on PC1 were highly correlated with the mean annual growth rate \( r = 0.99, P < 0.001 \) and scores on PC2 were highly correlated with the difference between growth rate of the second and the first year \( r = -0.99, P < 0.001 \).

The position of the measurement dates in the PC1–2 plane showed an arch effect, which opposed on PC2, growth rates of the beginning and of the end of the time series (Figure 3a). The PC1–2 plane displayed the trees according to the shape of their growth curves, taking into account the mean growth rate.
Figure 3. Centred-PCA of the smoothed tree growth profiles in the wet evergreen forest of Attapadi, Western Ghats, India. (a) Projection of the measurement dates onto the PC1–2 plane. (b) Projection of the trees onto the PC1–2 plane. (c) Examples of smoothed growth profiles corresponding to the numbered trees in (b).

and the major changes in the trend of the profile, i.e. sudden increases or decreases in growth rate (Figures 3b and 3c).

We then conducted an analysis of variance to test the effects of independent tree characteristics on the trend of the growth profiles, taking the scores of the trees on PC1 and PC2 as dependent variables. Only those trees belonging to
Table 2. F-values for the analysis of variance of scores on PC1 and PC2 of the centred-PCAs performed on the tree growth profiles of Attapadi wet evergreen forest, Western Ghats, India. Only trees belonging to species represented by more than three individuals have been considered (n = 73). The independent variables were: species (Sp: nine classes) and structural class (SC: three classes); tree log-transformed dbh (log(dbh)) and height (H); overall local density (n) and local density of the taller neighbours (Nsup) in circles of 5, 10 and 15 m radius, respectively.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Smoothed profiles</th>
<th>Detrended profiles</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>PC1</td>
<td>PC2 ns</td>
</tr>
<tr>
<td></td>
<td>PC1</td>
<td>PC2 ns</td>
</tr>
<tr>
<td>Sp</td>
<td>2.620*</td>
<td>0.183 ns</td>
</tr>
<tr>
<td>SC</td>
<td>5.239**</td>
<td>0.036 ns</td>
</tr>
<tr>
<td>log(dbh)</td>
<td>35.767***</td>
<td>1.494 ns</td>
</tr>
<tr>
<td>H</td>
<td>65.636***</td>
<td>1.811 ns</td>
</tr>
<tr>
<td>N(5)</td>
<td>0.026 ns</td>
<td>0.294 ns</td>
</tr>
<tr>
<td>N(10)</td>
<td>0.222 ns</td>
<td>0.001 ns</td>
</tr>
<tr>
<td>N(15)</td>
<td>0.006 ns</td>
<td>0.219 ns</td>
</tr>
<tr>
<td>Nsup(5)</td>
<td>17.626***</td>
<td>2.895 ns</td>
</tr>
<tr>
<td>Nsup(10)</td>
<td>23.155***</td>
<td>2.611 ns</td>
</tr>
<tr>
<td>Nsup(15)</td>
<td>22.900***</td>
<td>1.712 ns</td>
</tr>
<tr>
<td></td>
<td>2.456*</td>
<td>1.660 ns</td>
</tr>
<tr>
<td></td>
<td>2.082 ns</td>
<td>2.132 ns</td>
</tr>
<tr>
<td></td>
<td>66.109***</td>
<td>0.001 ns</td>
</tr>
<tr>
<td></td>
<td>85.004***</td>
<td>0.071 ns</td>
</tr>
<tr>
<td></td>
<td>1.621 ns</td>
<td>0.685 ns</td>
</tr>
<tr>
<td></td>
<td>0.099 ns</td>
<td>0.146 ns</td>
</tr>
<tr>
<td></td>
<td>0.433 ns</td>
<td>0.869 ns</td>
</tr>
<tr>
<td></td>
<td>18.797***</td>
<td>0.369 ns</td>
</tr>
<tr>
<td></td>
<td>27.415***</td>
<td>0.573 ns</td>
</tr>
<tr>
<td></td>
<td>26.057***</td>
<td>0.533 ns</td>
</tr>
</tbody>
</table>

* P < 0.05; ** P < 0.01; *** P < 0.001

species represented by more than three individuals were considered in this analysis. We first performed separate one-way ANOVAs for each variable (Table 2). This showed the dominant effect on PC1 of the size variables (log(dbh) and H) and the local density of the taller neighbours (Nsup), but a less significant effect of the specific variables, the species (Sp) and the structural class (SC). None of the variables tested appeared significant on scores on PC2.

In a second step, we selected from the one-way ANOVAs the most significant effect in each group of variables and used them in a general linear model taking into account the selected factors plus all interaction terms with P < 0.05. The additive model retained for predicting scores on PC1 included SC (P = 0.014), log(dbh) (P < 0.852), Nsup(10) (P < 0.023) and the interaction term SC × log(dbh) (P < 0.001) with r² = 0.594. (Though having a lower F-value than H in the one-way ANOVA, we retained log(dbh) in the model, because it is a more commonly used and a much more precisely measured tree size variable; moreover, this choice did not modify the other terms in the final model.) The model indicates that the mean diameter increment mainly varied as a function of the structural class, the number of taller neighbours within a 10-m radius and the tree size within the structural class. The emergent and upper canopy species (SC1) grew faster than the lower canopy species (SC2), which grew faster than understorey species (SC3); trees with fewer neighbours grew faster than trees with many neighbours; and, within the structural classes, large trees grew faster than small ones (Figure 4). The examination of Figure 4 shows, moreover, that in Attapadi, most small trees exhibited a very slow growth while most big trees had a largely positive increment. Though none of the tested variables was significant in the one-way ANOVAs, we checked that no interaction between the variables was significant on scores on PC2: the
Figure 4. Distribution of the mean tree diameter increment as a function of (a) tree size (log(dbh)) and 
(b) the number of taller neighbours in a 10-m radius ($N_{sup}(10)$) in the wet evergreen forest of Attapadi, 
Western Ghats, India.
tested variables were not able to predict changes in the trend of the 2-y growth profiles.

**Detrended tree growth profiles**

A second centred-PCA was performed on the detrended growth profiles. The two first principal components accounted for 64% of the total variance of the scatterplot (50.7% for PC1 and 13.3% for PC2). Scores on PC1 were positively correlated with the sum of the residuals of the first half-year (January – June; \( r = 0.946, \text{df} = 98, P < 0.001 \)) and negatively correlated with the sum of the residuals of the second half-year (July – December; \( r = -0.922, P < 0.001 \)). Scores on PC2 were negatively correlated with the sum of the summer residuals (April – September; \( r = -0.819, P < 0.001 \)) and positively correlated with the sum of the winter residuals (October – March; \( r = 0.821, P < 0.001 \)).

The projection of the measurement dates on the PC1–2 plane showed the correlation of the residuals at a lag of 12 mo, which highlighted the seasonal variations of the growth data (Figure 5a). Trees growing without seasonal variations were located near the axes' origin while those exhibiting important fluctuations were in the periphery of the scatterplot. Trees with a seasonal profile in phase with the mean pattern of the forest (cf. Figure 2c) were displayed along PC1; those exhibiting shifted peaks in comparison with this pattern were displayed along PC2 (Figures 5b & 5c).

To test the effects of some tree characteristics on the seasonal variations of the growth profiles, we first conducted separate one-way ANOVAs for each variable, taking PC1 and PC2 as dependent variables and the same independent variables as in the previous section (Table 2). The variables most significantly related to scores on PC1 were the size variables (log(dbh) and H) and the local density of the taller neighbours (\( N_{\text{sup}} \)), the species (Sp) being much less significant than the former. Again, none of the tested variables appeared to be significantly related to the scores on PC2.

As in the previous section, we used the most significant variables with \( P < 0.05 \) in a general linear model. The additive model retained for predicting scores on PC1 included log(dbh) (\( P < 0.001 \)), \( N_{\text{sup}}(10) \) (\( P < 0.001 \)) and the interaction term log(dbh) \( \times N_{\text{sup}}(10) \) (\( P < 0.001 \)) with \( r^2 = 0.620 \). This indicated that, in this forest, the intensity of the seasonal variations, represented by the sum of the absolute values of the monthly residuals, mainly varied as a function of the size of the trees and the number of taller neighbours in a 10-m radius: large trees with few neighbours had greater seasonal variations than small trees with many neighbours (Figure 6). There was no significant interaction between the tested variables for predicting scores on PC2 in Attapadi.

**Co-inertia of the two data sets**

Comparison of Figures 4 and 6 suggested a link between the structure of the smoothed and detrended data sets. To test this hypothesis we performed a co-inertia analysis maximizing the covariance of the two data sets (Chessel &
Figure 5. Centred-PCA of the detrended tree growth profiles in the wet evergreen forest of Attapadi, Western Ghats, India. (a) Projection of the measurement dates onto the PC1–2 plane. (b) Projection of the trees onto the PC1–2 plane. (c) Examples of detrended growth profiles corresponding to the numbered trees in (b).

Table 3. Co-inertia analysis of the smoothed (1) and detrended (2) growth profiles in Attapadi wet evergreen forest, Western Ghats, India. CoVar = covariance projected in the co-inertia analysis; Var1 and Var2 = variance of the two data sets projected in the co-inertia analysis; Iner1 and Iner2 = variance of the two data sets projected in the separate analyses, respectively; r = Pearson’s correlation coefficient between the individual scores of the two data sets in the co-inertia analysis.

<table>
<thead>
<tr>
<th>Axis</th>
<th>CoVar</th>
<th>Var1</th>
<th>Var2</th>
<th>Iner1</th>
<th>Iner2</th>
<th>r</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.0228</td>
<td>0.0255</td>
<td>0.0284</td>
<td>0.0255</td>
<td>0.0300</td>
<td>0.8469</td>
</tr>
<tr>
<td>2</td>
<td>0.0011</td>
<td>0.0006</td>
<td>0.0037</td>
<td>0.006</td>
<td>0.0079</td>
<td>0.7916</td>
</tr>
</tbody>
</table>
Figure 6. Distribution of the sum of the absolute values of the residuals of the locally weighted smoothing of the tree growth profiles as a function of (a) tree size (log(dbh)) and (b) the number of taller neighbours in a 10-m radius ($N_{sup}(10)$) in the wet evergreen forest of Attapadi, Western Ghats, India.
The results indicated that more than 80% of the variance projected on the PC1-2 planes of the two separate centred-PCAs, respectively, was projected on the first plane of the co-inertia analysis (Table 3). Moreover, tree scores from the two data sets were linked by strong correlations in the co-inertia analysis ($r = 0.85$ and 0.79, respectively, for axes 1 and 2 of the co-inertia analysis). This suggested in particular, that the trees that had fast growth, also exhibited high seasonal fluctuations and vice versa.

DISCUSSION

Two-year growth trend

In spite of the distortion due to the stratified sampling, our results suggest that the mean annual growth rate of the forest slowed down significantly during the second year of survey, probably due to climatic variations. Although we did not have rainfall records in Attapadi corresponding to the period of study, the monsoon precipitation recorded at Palghat (97 m asl), the nearest meteorological station with data available for this period, was higher in 1981 than in 1980 (2606 mm with 119 rainy days vs. 2418 mm with 113 rainy days; data from the Survey of India). This suggests a possible negative correlation between annual growth rate and annual precipitation, as has already been observed in other wet tropical forests (Clark & Clark 1994, Sheil 1995). One hypothesis that has been proposed to explain this negative correlation is a reduction of the photosynthetically active radiation (PAR) due to substantial cloud cover during the years of high rainfall, which could limit tree productivity (Clark & Clark 1994, Murphy 1970). To test this hypothesis, long-term simultaneous records of rainfall, tree growth and PAR are required.

The interpretation of the first axis of the centred-PCA indicates that the mean growth rates summarize almost all of the inter-individual variability of the smoothed growth profiles. A relatively simple model for predicting $c.60\%$ of the variance of the scores on PC1 can be derived. This model suggests that the mean diameter increment varied significantly with: (a) the structural class of the species (emergent and upper canopy species grew faster than lower canopy species which grew faster than understorey species); (b) the number of taller neighbours in a radius of 10-m (trees with few neighbours grew faster than trees with many neighbours); and (c) tree-size within each structural class (large trees grew faster than small ones). Growth rate has often been found to be correlated with species, tree size or crown position in tropical wet forests (e.g. Gourlet-Fleury 1998; Lieberman & Lieberman 1985, 1987; Pélissier et al. 1998, Swaine & Lieberman 1987). But it has to be underlined that each variable may explain a complementary part of the variability in growth rate. The species (or the group of species, like structural class) reflects the intrinsic ecological characteristics, while tree size and neighbourhood reflect, through crown exposure, the inter-individual competition for light. However, the interaction between structural class and tree-size raises the question of species long-term
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growth patterns. Indeed, the growth performance of emergent and canopy species can vary during their lifetime, not only because of micro-environmental modifications, but also because of ontogenetic changes (Clark & Clark 1992).

Scores on PC2 were highly correlated with sudden changes in the trend of the growth profiles, but most of the trees had a low regular diameter increment over the period of study, which explains why PC2 summarized only a low proportion of the inter-individual variability of the smoothed growth profiles. This is also why researchers generally consider successive individual diameter increments to be autocorrelated (Sheil 1995, Swaine & Lieberman 1987). The ontogenetic shifts in growth rate are probably continuous processes with low significant effects on the short-term growth trend, which moreover vary in an unpredictable fashion among the species (Clark & Clark 1992). But the trees reaching suddenly better growth conditions are able to respond opportunistically with an accelerated growth rate, changing suddenly the trend of the growth profile. The phenomenon is well known in wet evergreen forests, where juveniles of shade-tolerant species can show important growth release in canopy openings (e.g. Canham 1988, King 1993; Oberbauer et al. 1988, 1989). In our study in Attapadi, none of the tested variables appeared to be significantly related to scores on PC2, but most of the trees exhibiting sudden growth rate reduction did die within a few years of the end of our study. Decreasing, and sometimes negative, growth rates for several years prior to death have already been reported in tropical forests (e.g. Durrieu de Madron 1993, Swaine & Lieberman 1987) and are generally interpreted as old, suppressed or diseased tree decline.

Seasonal growth rhythms

Significant seasonal variations in tree growth have been demonstrated from the detrended profiles in Attapadi wet evergreen forest. These variations appear to be cyclic on an annual basis and are in phase with the mean rainfall pattern with a time-lag of c.1–2 mo. This cyclic pattern confirms the annual flushing pattern already observed in the wet evergreen forests of the Western Ghats (Aravajy 1995). These seasonal variations are related to the features of the monsoon climatic regime with a unique peak of heavy rainfall and a quite long dry season. This may open the way to finding relatively distinct growth rings in the xylem of some evergreen species in these forests.

The seasonal growth variations originate from hydrostatic stem flexibility, which depends on rainfall through the soil moisture status and the degree of turgidity or water stress of the tree (Sheil 1995). As a consequence, intra-annual variations are sometimes greater than inter-annual variations, rendering the calculation and comparison of tree growth rates problematic in wet forests (Phillips & Gentry 1994, Sheil 1995). Shrinkage, which depends on drought intensity, is probably more variable than dilatation and we suggest that in these forests, annual diameter measurements would be preferable at the end of the rainy season when turgidity is maximal.
The centred-PCA shows that the intensity of the seasonal fluctuations is the principal factor of variability of the individual detrended growth profiles. The trees in phase with the mean growth pattern are displayed along PC1. Those having shifted seasonal patterns are displayed along PC2. A simple linear model involving tree dbh and the number of taller neighbours within a radius of 10 m predicted more than 60% of the variance of the scores along PC1. This model suggests that large trees with a few neighbours have greater seasonal variations than small trees with many neighbours. The intensity of the seasonal fluctuations of tree growth appears to be more dependent on individual than on specific characteristics, which has been already noted in other tropical forests (Murphy 1970). Moreover, none of the tested variables were significant in predicting the individual tree scores along PC2.

The co-inertia analysis revealed that the trees having the fastest growth also exhibited the greatest seasonal fluctuations. Since trees having fast growth rates are those with favourable crown positions, we can hypothesize that they are subject to high transpiration rates due to high radiation and wind exposure. Consequently, these trees may show greater amplitude in girth fluctuation.

CONCLUSION

On the basis of 2-y growth records, our results confirm those obtained in other studies in tropical rain forests: in spite of year-to-year growth variations, individual mean growth rates depend upon a combination of tree size, specific ecological characteristics and neighbourhood. Moreover, tree growth can exhibit significant seasonal variations on an annual basis due to the regular alternation between dry and rainy seasons. The fast growing trees are those exhibiting the greatest amplitude of seasonal variations. This could have an important methodological consequence when calculating and comparing tropical tree growth rates, and the seasonal growth rhythms should always be taken into account in long-term growth studies. That is why it is recommended that annual diameter increments be measured at the end of the rainy season.

ACKNOWLEDGEMENTS

We thank the Kerala Forest Department for permitting the plot survey and monitoring. We are also grateful to the staff of the French Institute of Pondicherry who collaborated with this work and to the colleagues and the reviewers who commented on the manuscript.

LITERATURE CITED


