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# Structure and floristic composition of a tropical evergreen forest in south-west India

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ABSTRACT. A permanent plot of 28 ha was established in a dense wet evergreen forest in the Western Ghats of India to study the functioning of the ecosystem. Since April 1990, 1981 trees of ≥30 cm gbh have been enumerated in a systematic sampling of five strips totalling 3.12 ha. This paper describes the main structural and floristic characteristics of the plot.

The density (635 trees ≥30 cm gbh per hectare) and basal area (39.7 $m^2$ $ha^{-1}$) are high. Despite the high diversity (Simpson's D = 0.92 and Shannon's H′ = 4.56), four species are distinctly dominant in terms of an importance value index (relative density + relative basal area). Each of these four species occupies a different layer in the ecosystem: *Humboldtia brunonis* Wall. (Fabaceae) dominates the undergrowth, *Myristica dactyloïdes* Gaertn. (Myristicaceae) the intermediate strata, *Vateria indica* L. (Dipterocarpaceae) the higher canopy level and *Dipterocarpus indicus* Bedd. (Dipterocarpaceae) the emergents. This pronounced species hierarchy is one of the most important characteristics of the evergreen forests of the Western Ghats. The two dipterocarps account for 20.1% of the total number of trees and contribute 40.9% to the total basal area. This formation can, therefore, be considered as the westernmost lowland dipterocarp forest of Asia.

Analysis of the spatial variations in the floristic composition and in the structure of the main species populations shows that two kinds of mature phases can be identified: where the topography is raised and gently sloping, the vertical structure of the stand is discontinuous, with *Dipterocarpus indicus* and *Vateria indica* forming an emergent layer above a dense undergrowth; on slopes, the stand is lower, vertically continuous and saturated with *Vateria indica* and *Myristica dactyloïdes*. The link between the structure of the stand and dynamic processes is discussed.

KEY WORDS: floristic composition, India, population structure, spatial structure, tropical evergreen forest, Western Ghats.

## INTRODUCTION

In order to understand the complexity and heterogeneity of tropical forest ecosystems, a number of large permanent plots were established for long-term studies: Barro Colorado in Panama (Leigh *et al.* 1982), La Selva in Costa Rica (Hartshorn 1983), Paracou in French Guiana (Schmitt 1984), Pasoh in Malaysia (Manokaran *et al.* 1990). These plots are generally big enough to take into account the heterogeneity of the stand. They have often led to the establishment of a computer database from which it would be possible to distinguish homogeneous units in the stand, as well as to prepare models of the forest dynamics.

Most authors consider openings (gaps, chablis) as the starting point, the main spring, of the dynamic process (Bossel & Krieger 1991, Hallé *et al.* 1978, Shugart 1984, Wissel 1991). The forest is thus considered as a mosaic of ecounits (Oldeman 1983) which are different stages of unsynchronized sylvigenetic cycles. However, openings vary in size (Riéra 1983) and frequency (Putz & Milton 1982, Riéra & Alexandre 1988). Hence, all openings should not be considered as equivalents in the process of forest dynamics as they act at different scales both in time and space.

Moreover, field observations show that some parts of the forest are relatively less affected by openings (chablis). Very often the trees die standing. This phenomenon is more widespread than is generally believed (Durrieu de Madron 1993).

It was with the intention of analysing the spatial variations in the dominant mechanisms of forest dynamics that the French Institute of Pondicherry set up a permanent plot in a primary forest in southern India. This paper presents the main structural and floristic parameters of the stand and provides some examples of the structural variations within the forest. The next step will be the recognition of the different homogeneous units in the stand in relation to the functioning of the dynamics.

## STUDY SITE

### *Location*

In southern India, the evergreen forests are now confined to the hills of the Western Ghats. This narrow mountainous strip, with its highest point at Anaimudi (2695 m) in the Anamalai hills, extends over a length of 1600 km (8° to 21° N) along the western coast. The dense wet evergreen forests are found on the western side, up to the crest of the Ghats. Pascal (1984/1988) has distinguished 12 forest types according to two main climatic gradients: lowering of the temperature with altitude, and lengthening of the dry season with latitude.

The Uppangala forest is situated in the Kadamakal Reserve Forest (Kodagu district) in the foothills of the Ghats (12° 30′ N, 75° 39′ W; 500–600 m alt.). Floristically, it belongs to the low elevation *Dipterocarpus indicus–Kingiodendron pinnatum–Humboldtia brunonis* type of wet evergreen forests (Pascal 1982a).

### *Climate*

The rainfall regime is characterized by a period of heavy rainfall alternating with a dry season. The rains are brought by the south-west monsoon winds which strike against the natural barrier of the Western Ghats.

The climate of the study area is illustrated by Sampaji (Figure 1). Because of its higher elevation, Uppangala receives slightly more rainfall than Sampaji (5100 mm per year). The rainfall peak, in June or July, coincides with the

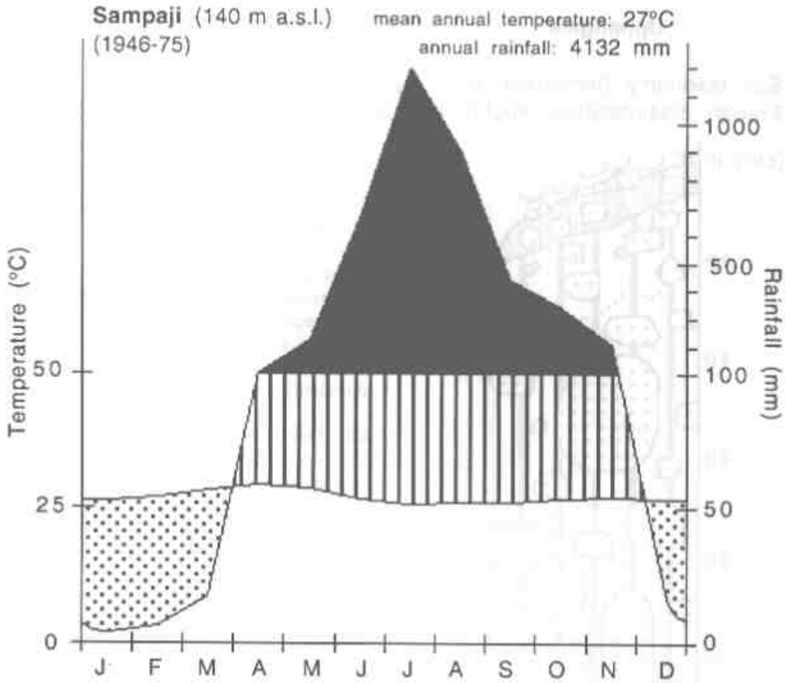


Figure 1. Ombrothermic diagram for Sampaji, Western Ghats, India.

minimum mean temperature, about 25°C (Alleppey–Mangalore regime, Pascal 1982b). The dry season ($R < 2T$ where R is the monthly rainfall in mm and T the monthly mean temperature in °C) lasts about 4.5 months, the maximum mean temperature occurring in April (*c.* 29°C).

*Geomorphology and pedology*

South of 16° N, the Western Ghats are made up of archean rocks of the Precambrian shield. These formations are classified, according to their degree of metamorphism, into granite, gneiss or schist. Peninsular gneisses are dominant between 11° and 14° N.

Heavy rainfall favours a ferrallitic pedogenesis. Ferry (1992) has classified the soils of Uppangala forest as highly desaturated, impoverished ferrallitic soils (Figure 2). They are acidic, on thick and very old alterites (kaolinitic types of clay); the cation exchange capacity is mainly due to the organic matter of the upper horizon. On steep scree-covered slopes, however, illite or chlorite in the profiles provide evidence of less evolved soils (Bourgeon 1989).

In neighbouring Bhagamandala, Peterschmitt (1993) has shown that available water capacity (AWC) at the end of the rainy season is about 81 mm per metre of soil, which is sufficient to avoid physiological drought up to the end of the dry season. The depth of the soil seems to be the determining factor for AWC; the deep alterites (3 m at Bhagamandala) are favourable to the formation

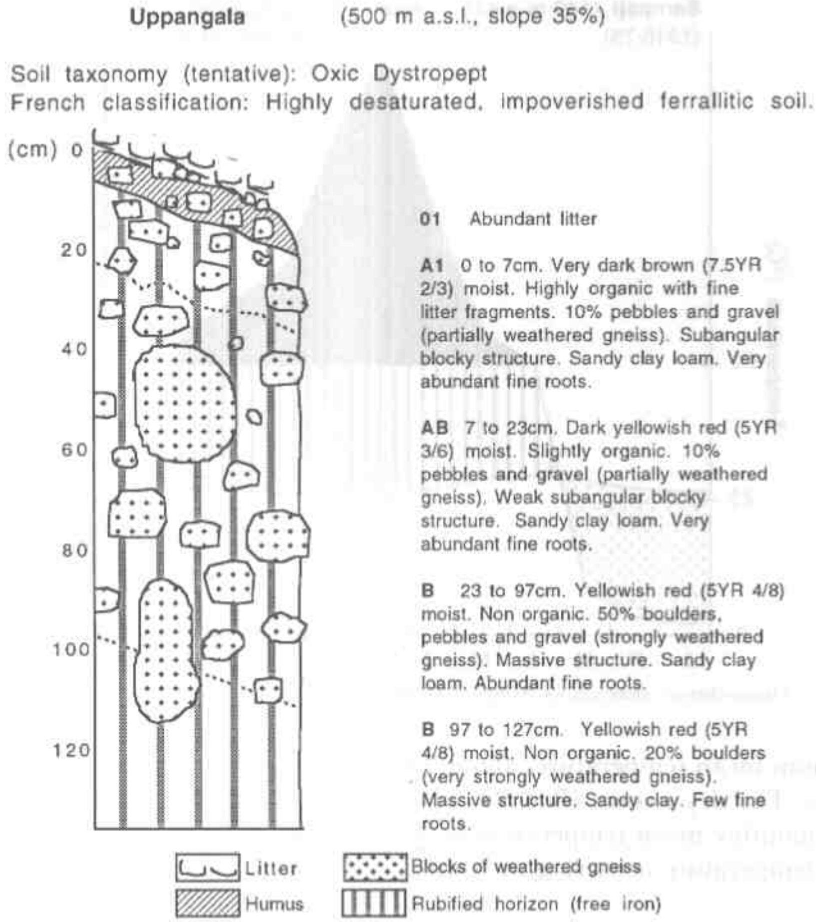


Figure 2. Soil profile of Uppangala forest, Western Ghats, India (from Ferry 1992).

of a large water reserve. But, sometimes, soils can be less than 1 m deep (Peterschmitt 1993), full of rocky boulders and continuously rejuvenated by strong superficial erosion.

*Features and representativeness of the Uppangala site*

The dense wet evergreen forests, although controlled by the Forest Department, have been greatly exploited in the past (Buchy 1990). Despite the numerous reserves created, anthropic pressure remains high throughout the Ghats (Garrigues *et al.* 1988). In Karnataka state, the authorities have introduced a ban on felling rainforests since 1988, which has left a few rare and well-preserved sites, such as the Uppangala forest.

The Uppangala forest was subdivided into logging plots of about 30 ha each. These have all been selectively exploited in rotation between 1974 and 1988 (Loffeier 1988) with the exception of the study site. The topography

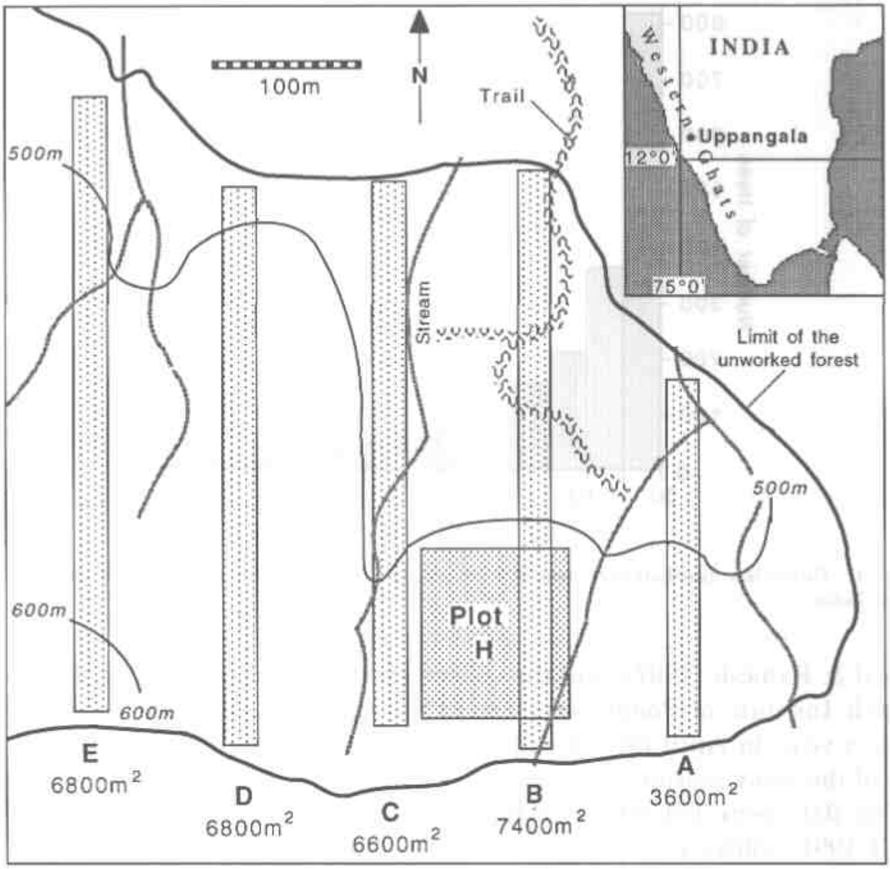


Figure 3. Location map of Uppangala forest, Western Ghats, India, and sampling in five strips (A to E) and added plot (H).

is steep but forest trails allow access during the dry season. Surrounded by logged plots, the study site is therefore protected from anthropic pressure and represents one of the rare, natural dense wet evergreen forests of southern India.

## METHODS

The area studied is a plot of 28 ha. Five north–south oriented strips (A to E) were established in 1990: 100 m apart, 20 m wide and 180 to 370 m long. They formed a systematic sample of 3.12 ha (Figure 3).

All the data were collected in 10 m × 10 m quadrats. The contiguous grid of quadrats enabled the constitution of quadrats of varying sizes according to the analytical needs (20 m × 20 m, 20 m × 30 m).

All trees of girth ≥30 cm measured at breast height (gbh: 130 cm from the ground or above the buttresses) were numbered, plotted on a map and fitted with a permanent dendrometric belt. They were identified with the field key of

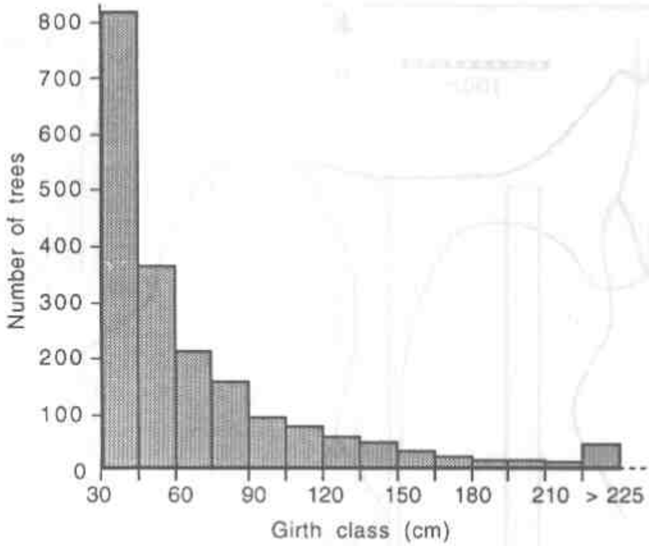


Figure 4. Girth class distribution of trees ≥30 cm gbh in 3.12 ha sampled in Uppangala forest, Western Ghats, India.

Pascal & Ramesh (1987), and the collections deposited in the herbarium of the French Institute of Pondicherry (HIFP). From 1990, the girth was recorded twice a year: in April (at the end of the dry season) and in November (at the end of the rainy season).

The data were fed into a relational database using 4th Dimension® 4.2.2 (ACI 1991) software.

The floristic and structural characteristics described in this paper are based on the data collected during the first survey (April 1990) in the five strips. In order to establish the height–diameter relationships, all the trees in the five strips were measured for the less common species, while for the most common, only the trees in 20 m × 20 m quadrats (systematically distributed at 60 m intervals along the strips) were considered. These height–diameter relationships were compared with those obtained from a 100 m × 110 m plot (H in Figure 3) located on a wide and slightly sloping plateau. Schematic depictions of the structural profiles of two 20 m × 20 m quadrats were generated by computer using the total heights of the trees, heights of the base of the crown and the crown projections in the four cardinal directions.

## RESULTS

### *Density, basal area and girth class distribution*

In the 3.12 ha studied, 1981 trees of girth size ≥30 cm were counted. The mean density was 635 trees per ha and the basal area 123.8 $m^2$, i.e. 39.7 $m^2$ $ha^{-1}$. The cumulative curves showed that the means settled down after 1 ha; hence,

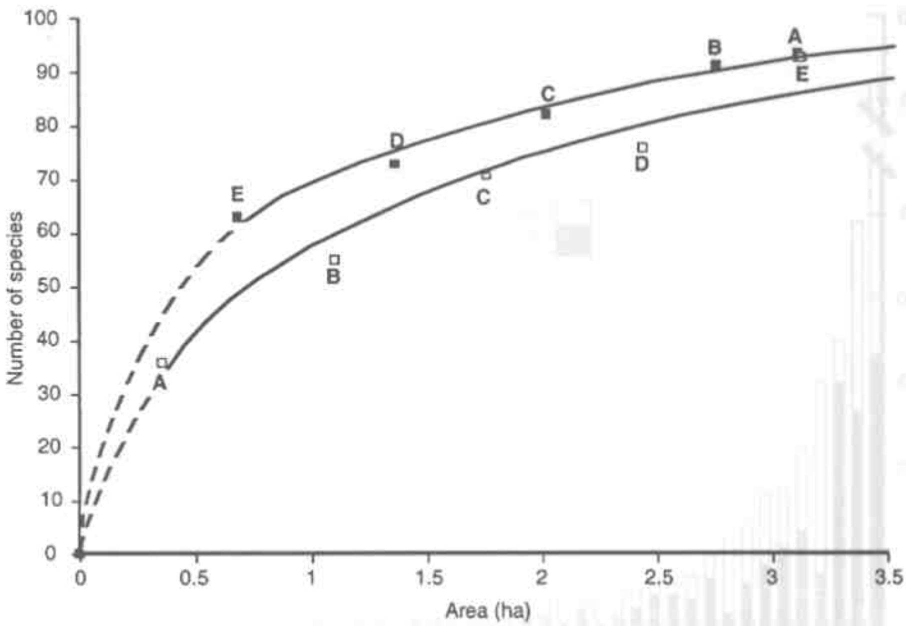


Figure 5. Species–area curves. —■— West–east direction (E towards A). —□— East–west direction (A towards E). – – – – Extrapolated to zero.

3 ha are largely sufficient to represent the mean density and mean basal area values. The distribution of girth classes follows the classic negative exponential pattern commonly found in undisturbed rainforests (Figure 4).

### *Floristic data*

*Floristic composition and richness.* Ninety-one species belonging to 31 families were identified in the five strips. However, 12 species found in this forest were not observed in the sample (a complete list is given in the Appendix). In terms of the number of species, the best represented families are Euphorbiaceae (20 species), Anacardiaceae (7), Lauraceae, Ebenaceae and Meliaceae (6 each), Annonaceae, Clusiaceae and Dipterocarpaceae (5 each). Dipterocarpaceae constitute 21.1% of the stand in terms of relative density of trees. Myristicaceae is next with 19.4% represented by three species, followed by Fabaceae with 16.0% and two species. Half the species (47) are endemic to the Western Ghats (cf. Appendix) and about 80% of the trees belong to these endemic species.

Species–area curves were obtained for the discontinuous sampling (Figure 5). In the west–east direction (E towards A), the curve stabilizes faster than the opposite direction (A towards E); the E strip contains 63 species, of which 17 were not found in the others. However, the equations for both regression curves give very similar estimates of the species richness when extrapolated to 28 ha (137 and 140).

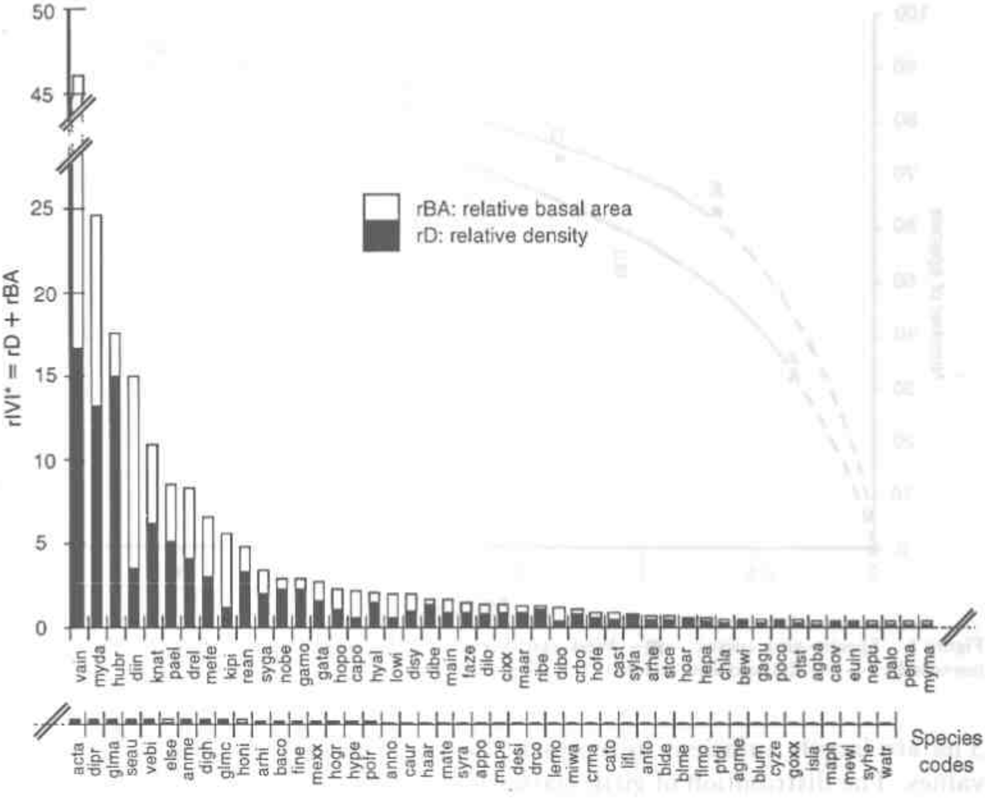


Figure 6. Importance Value Indices (IVI*) of the 91 species identified in 3.12 ha sampled in Uppangala forest, Western Ghats, India. Species codes are given in the Appendix.

*Floristic diversity*. Simpson's diversity index D is equal to 0.92, indicating that 92 pairs out of 100 taken at random are composed of different species. Shannon's index H′ is 4.56, maximum diversity ($H_{max}$) 6.54 and equitability (E) 0.7.

The floristic structure was studied by using an index derived from Curtis & McIntosh's (1950) Importance Value Index. This index (IVI) is generally calculated as the sum of the relative density (rD), relative basal area (rBA) and relative occurrence in the quadrats (rF) for each species. In this study, we took only the relative density and relative basal area into consideration: IVI* = rD + rBA. Therefore, the total value for all the species is 200. The IVI* of each species is given in the Appendix.

The IVI* decreases rapidly in steps (Figure 6); values below 25 are obtained from the second species onwards, less than 15 at the fifth and less than 5 after the tenth. The rare species (less than three individuals per hectare) comprise nearly two-thirds of the species enumerated (58). The most common families are also those which have the highest IVI*: Dipterocarpaceae (IVI* = 63.3), Myristicaceae (35.9) and Fabaceae (23.2). The dominant species are *Vateria indica* (IVI* = 46.0), *Myristica dactyloïdes* (24.6), *Humboldtia brunonis* (17.6) and

*Dipterocarpus indicus* (15.0). The first three species represent nearly 45% of the trees, accounting for 16.7, 14.9 and 13.2%, respectively. The basal area of *Vateria indica* is very high (29.3%), followed by *Dipterocarpus indicus* (11.6%) and *Myristica dactyloïdes* (11.5%), these three species together contributing more than half of the total basal area.

*Species populations*

*Girth class distributions.* A correspondence analysis was carried out to group the species according to their girth distribution patterns, using ADE 3.4 software (Chessel & Dolédec 1993). The data matrix was a table of 35 species, represented by more than two individuals per hectare (rows), and 26 girth classes 15 cm wide (columns). Axes I and II account for 32.4 and 19.7%, respectively, of the total variance of the scatterplot. Axis I separates a group of small-sized species from other medium and large-sized species. Axis II distinguishes three patterns of girth distributions. Thus, four groups of species can be recognized (Figure 7): (i) group 1 contains species with a flat girth distribution, showing a relatively high proportion of large trees. From the dynamic point of view, the mortality rate of young trees (girth <45 cm) seems to be very high and the survivors have a better chance of growing into large trees. *Dipterocarpus indicus*, *Lophopetalum wightianum* and *Kingiodendron pinnatum*, i.e. the big emergents, are in this group. *Calophyllum polyanthum* should also have a place in this group, but out of 11 individuals in the sample only two have a girth >135 cm. (ii) Group 2 comprises species with a negative exponential distribution and capable of attaining large girths, such as *Vateria indica*, the third dipterocarp *Hopea ponga*, *Mesua ferrea*, *Cinnamomum* sp., *Diospyros sylvatica* and *Palaquium ellipticum*. (iii) Species of group 3 also show a negative exponential girth distribution pattern. They are species of the understorey with small girth classes such as *Humboldtia brunonis*, *Syzygium laetum*, *Rinorea bengalensis* and *Dimorphocalyx beddomei*. (iv) The distribution pattern in group 4 is characterized by a large number of medium and small girth classes. The characteristic species are the two most common Myristicaceae, *Myristica dactyloïdes* and *Knema attenuata*, and the Euphorbiaceae *Drypetes elata*. We should also include in that group *Garcinia morella* but it is represented only by small trees in the sample.

*Height–diameter relationships.* According to Oldeman (1974), these relationships reflect the different growth phases of a tree. Young trees growing in conformity with their initial model are found along the line H = 100 D and constitute the set of the future. Trees are considered as adults when they begin to reiterate their initial model spontaneously (set of the present). Their growth continues in girth rather than in height and, hence, are found to the right of the line.

Cusset (1980) has shown that this straight line is a practical smoothing of a more complex curve retracing the height–diameter relationships in a natural dense forest where the trees grow competing for light. According to him, the

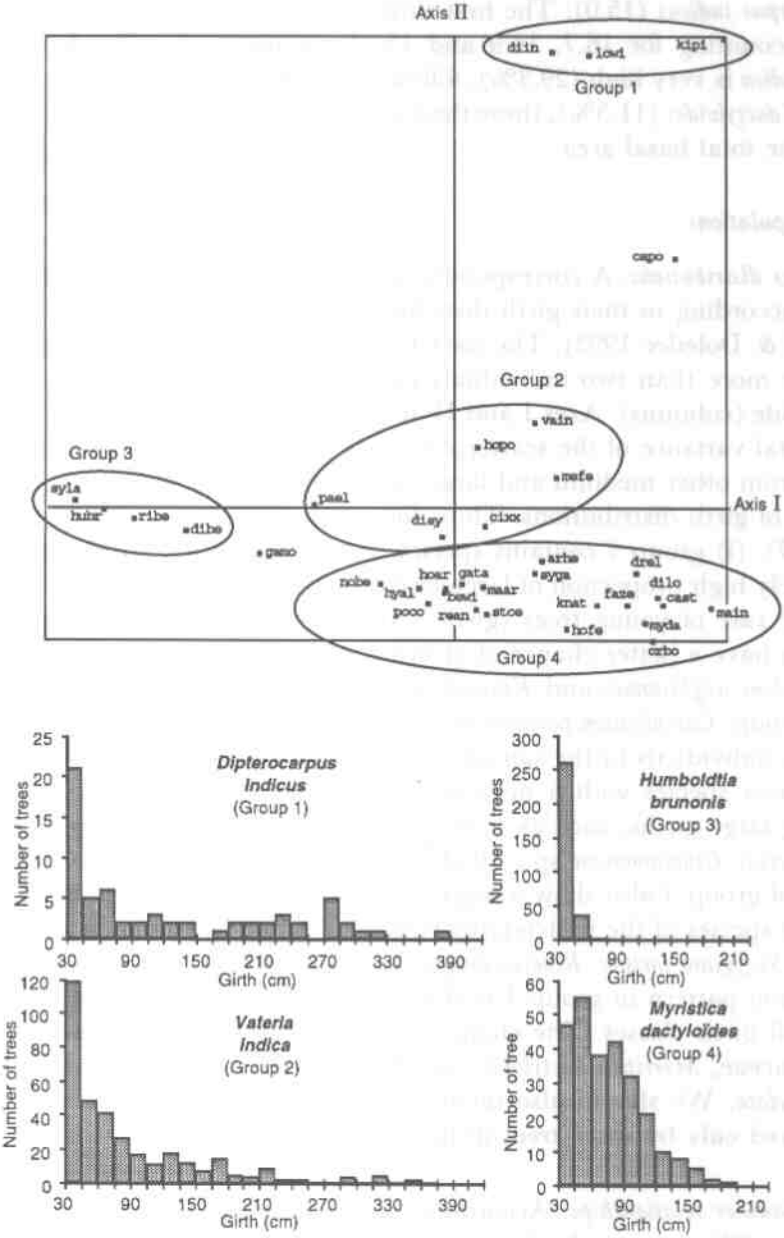


Figure 7. Correspondence analysis performed on the girth class distributions of 35 species (frequency >2 trees per ha) of Uppangala forest, Western Ghats, India, and examples of distributions corresponding to the four identified groups. arhe: *Artocarpus heterophyllus*, bewi: *Beilschmiedia wightii*, capo: *Calophyllum polyanthum*, cast: *Canarium strictum*, cixx: *Cinnamomum* sp., crbo: *Cryptocarya bourdillonii*, dibe: *Dimorphocalyx beddomei*, diin: *Dipterocarpus indicus*, dilo: *Dimocarpus longan*, disy: *Diospyros sylvatica*, drel: *Drypetes elata*, faze: *Fahrenheitia zeylanica*, gamo: *Gardinia morella*, gata: *Gardinia talbotii*, hoar: *Holigarna arnottiana*, hofe: *Holigarna ferruginea*, hopo: *Hopea ponga*, hubr: *Humboldtia brunonis*, hyal: *Hydnocarpus alpina*, kipi: *Kingiodendron pinnatum*, knat: *Knema attenuata*, lowi: *Lophopetalum wightianum*, maar: *Mastixia arborea*, main: *Mangifera indica*, mefe: *Mesua ferrea*, myda: *Myristica dactyloïdes*, nobe: *Nothopegia beddomei*, pael: *Palaquium ellipticum*, poco: *Polyalthia coffeoïdes*, rean: *Reinwardtiodendron anaimalaiense*, ribe: *Rinorea bengalensis*, stce: *Strombosia ceylanica*, syga: *Syzygium gardneri*, syla: *Syzygium laetum*, vain: *Vateria indica*.

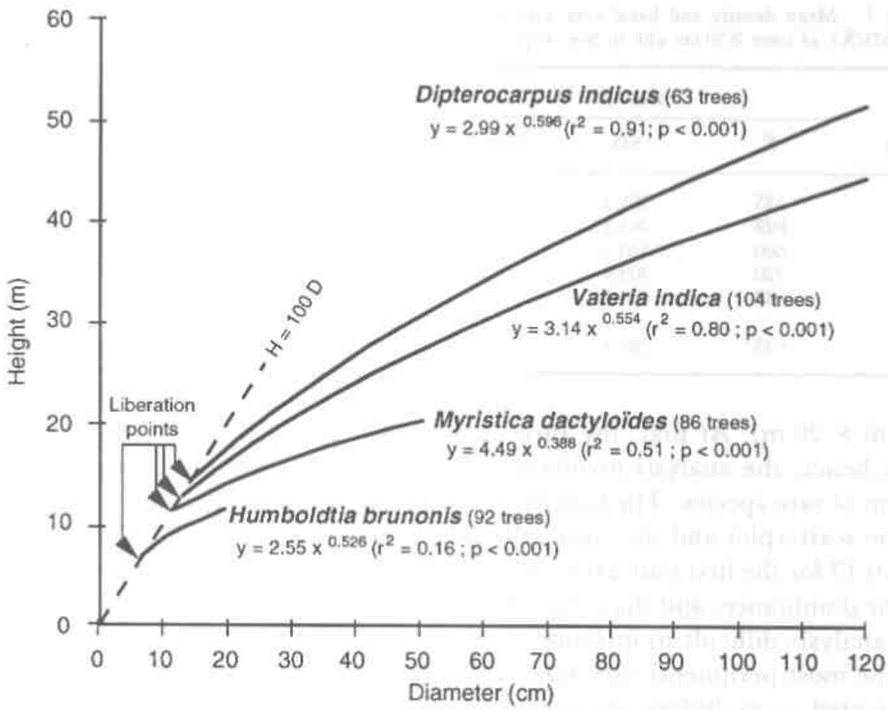


Figure 8. Height–diameter relationships of the four dominant species in 3.12 ha sampled in Uppangala forest, Western Ghats, India.

inflexion of the curve towards the right of the line is, in fact, a 'liberation point' which corresponds to overtopping a stratum in the stand.

In both cases, the point at which the curve leaves the H = 100 D line is a good indicator of the role of a species in the vertical structuring of the stand.

Regression curves for the four main species, *Dipterocarpus indicus*, *Vateria indica*, *Myristica dactyloïdes* and *Humboldtia brunonis* (Figure 8), show that each of them is established at a different layer in the vertical structure of the forest. Broken trees (H much lower than 100 D) have been excluded.

### *Structural variations*

*Spatial structure.* Spatial variation in the density and basal area was studied in elementary quadrats of 100 $m^2$. It was impossible to establish any correlation between these parameters and the slope of the quadrats, in spite of their variations. The coefficient of variation (Scherrer 1984) for the density and basal area for all the quadrats together is 45 and 87%, respectively (Table 1). Nevertheless, it may be stated that the most important variations were observed in the A and C strips which traverse deep valleys.

*Floristic structure.* Variations in the floristic structure was studied by a correspondence analysis of the species IVI* calculated in each of the 76 quadrats

Table 1. Mean density and basal area with standard deviation (SD) and coefficient of variation (CV = 100 SD/$\bar{X}$), of trees ≥30 cm gbh in five strips sampled in Uppangala forest, Western Ghats, India.

| Strips | Density ($ha^{-1}$) | | | Basal area ($m^2\ ha^{-1}$) | | |
|---|---|---|---|---|---|---|
| | $\bar{X}$ | SD | CV (%) | $\bar{X}$ | SD | CV (%) |
| A | 525 | 301.3 | 57.4 | 42.6 | 40.7 | 95.5 |
| B | 628 | 261.2 | 41.6 | 39.1 | 30.3 | 77.5 |
| C | 600 | 350.5 | 58.4 | 35.0 | 37.5 | 107.1 |
| D | 720 | 309.8 | 43.0 | 44.7 | 30.5 | 68.2 |
| E | 648 | 270.4 | 41.7 | 39.4 | 37.3 | 94.7 |
| All | 635 | 285.5 | 44.9 | 39.7 | 34.7 | 86.7 |

(20 m × 20 m). At first, the rare species were grouped into a single category and, hence, the analysis involved 35 species which are more common plus the group of rare species. The first axis accounts for only 9.2% of the total variance of the scatterplot and the eigenvalues decrease very gradually (0.20, 0.19, 0.15, and 0.13 for the first four axes). This suggests that there is no clear demarcation in the dominance, and that several species could be locally dominant, rendering the analysis difficult to interpret.

The most peripheral variables of the first plane were then eliminated, which amounted to excluding the species present in only a few quadrats. The data matrix was thus reduced to 25 species and 76 quadrats. The variance of the scatterplot accounted for by the first two axes was still quite low (11.5% and 9.3% for axes I and II, respectively, but it became possible to interpret the CA plot. The relative contribution of *Dipterocarpus indicus* to axis I formation, i.e. the species variance on axis I divided by the variance of all species on that axis, is 70.3%. This species is in opposition to a group of smaller-sized species (*Drypetes elata*, *Humboldtia brunonis* and *Myristica dactyloïdes*). *Vateria indica* contributes 43.5% to the axis II formation and is opposite to *Reinwardtiodendron anaimalaiense* and *Drypetes elata*. However, it was impossible to identify distinct groups but, when projecting the IVI* values of the main species on the first CA plot (following the approach of Dolédec & Chessel 1992), three sectors could be distinguished (Figure 9). These sectors do not correspond to the location of the quadrats in the strips, but to a heterogeneity in the species dominance at the scale of the quadrats. In Sector 1, quadrats are dominated by both *Dipterocarpus indicus* and *Vateria indica*. Small-sized species importance is thus very low. *Vateria indica* is dominant in Sector 2 in association with *Myristica dactyloïdes* and/or *Humboldtia brunonis*. In Sector 3, the importance of the two dipterocarps is low and quadrats are dominated by small-sized species.

*Vateria indica*, *Myristica dactyloïdes* and *Humboldtia brunonis* are widely distributed. Only 5, 2 and 2%, respectively, of the quadrats do not contain these species. On the other hand, *Dipterocarpus indicus* is absent in 47% of the quadrats.

*Growth potential of species.* Local variations in the expression of the growth potential of species have been observed and seem to be related to the topography.

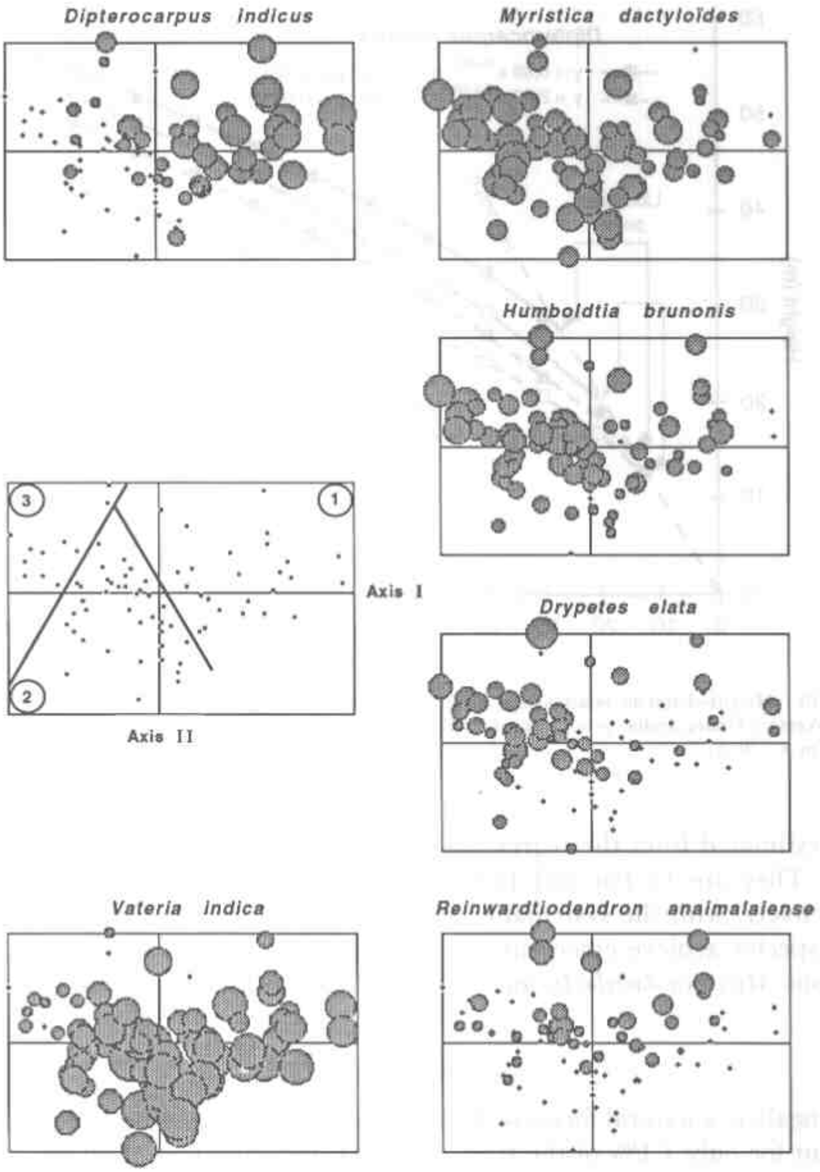


Figure 9. Correspondence analysis performed on the Importance Value Indices (IVI*) of species in 76 20 m × 20 m quadrats in Uppangala forest, Western Ghats, India, and projections on axes I/II CA plot, of the species IVI* values in each quadrat. Circle area is proportional to species IVI*, crosses corresponding to the absence of the species.

Figure 10 shows two series of adjustments in the height–diameter relationships of *Vateria indica* and *Dipterocarpus indicus*. One is obtained from the systematic sampling (the five strips) and gives the average for the whole population. The other is from plot H only. This plot was, in fact, selected because of its location on a wide and slightly sloping plateau with a tall and well-structured stand. The 'liberation point' of these two species is higher in plot H. Their heights

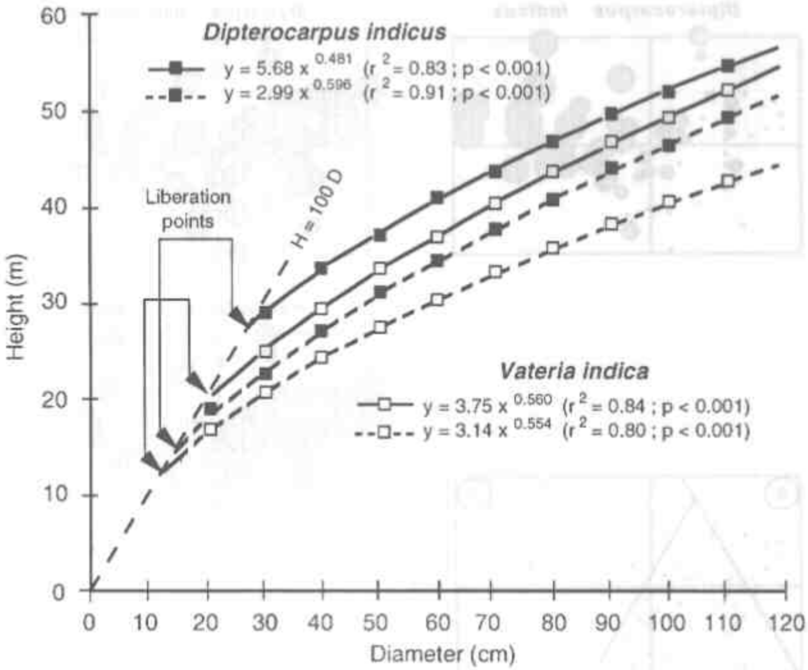


Figure 10. Height–diameter relationships for *Dipterocarpus indicus* (■) and *Vateria indica* (□) in Uppangala forest, Western Ghats, India. (– – – –) in the whole 3.12 ha systematic sampling (five strips). (——) in plot H (100 m × 110 m).

were estimated from the regression equations of the height–diameter relationships. They are 12.9 m and 14.9 m for *Vateria indica* and *Dipterocarpus indicus*, respectively, with the systematic sampling; and 20.1 m and 28.6 m on plot H. Both species achieve emergent status in plot H, whereas *Vateria indica* hardly overtops *Myristica dactyloïdes* and *Drypetes elata* in other areas of the forest.

## DISCUSSION

Uppangala is a natural forest without major disturbances where pioneer species account for only 1.1% of the trees. A systematic sampling of about 3 ha gives a fairly good representation of the density, basal area and floristic composition.

This forest is characterized by high density and high basal area, placing it among the best forests in Asia and above those of Africa and South America (Table 2). The floristic richness is not very high (91 species in 3.12 ha) compared to data for trees ≥*c.* 30 cm in Asia (198 species in 1.81 ha in Sabah (Nicholson 1965), 214 species in 1 ha in Sarawak (Proctor *et al.* 1983) and 244 species in 2 ha in Malaysia (Manokaran & Kochummen 1987)), but closer to the values obtained in Africa (50 species in 4.05 ha in Nigeria (Okali & Ola-Adams 1987) and 120 species in 2 ha in Ghana (Swaine *et al.* 1987)). The diversity is quite high because of numerous rare species, although lesser than

Table 2. Mean density and basal area of trees ≥c. 30 cm gbh in the present study at Uppangala forest, Western Ghats of India, compared with others in tropical forests.

| Location | Minimum gbh (cm) | Plot area (ha) | Mean density ($ha^{-1}$) | Mean basal area ($m^2 ha^{-1}$) | Source |
|---|---|---|---|---|---|
| *SOUTH-EAST ASIA* | | | | | |
| Sepilok, Sabah | 30.5 | 1.81 | 660 | 42.1 | (1) |
| Mulu, Sarawak | 31.4 | 1 | 739 | 57.0 | (2) |
| Sungei-Menyala, Malaysia | 31.4 | 2 | 493 | 32.4 | (3) |
| Pasoh, Malaysia | 31.4 | 50 | 530 | 25.2 | (4, 5) |
| Danum Valley, Sabah | 30 | 8 | 470 | 26.6 | (6) |
| Uppangala, India (present study) | 30 | 3.12 | 625 | 39.7 | |
| *SOUTH AMERICA* | | | | | |
| El Verde, Puerto Rico | 31.4 | 0.7 | 593 | 35.7 | (7) |
| La Selva, Costa Rica | 31.4 | 12.4 | 446 | 27.8 | (8) |
| Central Amazon, Brazil | 31.4 | 5 | 625 | — | (9) |
| Ste. Elie, French Guiana | 31.4 | 1.78 | 609 | 34.8 | (10) |
| *AFRICA* | | | | | |
| Makokou,Gabon | 31.4 | 0.4 | 450 | 34.8 | (11) |
| Omo, Nigeria | 31.4 | 4.05 | 562 | 29.6 | (12) |
| Kade, Ghana | 31.4 | 2 | 552 | 30.8 | (13) |

References: (1) Nicholson 1965, (2) Proctor *et al.* 1983, (3) Manokaran & Kochummen 1987, (4) Kochummen *et al.* 1990, (5) Manokaran & La Frankie 1990, (6) Newbery *et al.* 1992, (7) Crow 1980, (8) Lieberman & Lieberman 1987, (9) Rankin-de-Merona *et al.* 1990, (10) Pélissier & Riéra 1993, (11) Hladik 1982, (12) Okali & Ola-Adams 1987, (13) Swaine *et al.* 1987.

in Amazonia (H′ between 4.8 and 5.4 for trees ≥10 cm dbh, Ulh & Murphy 1981) or Sabah (H′ = 4.78 for trees ≥30 cm gbh, Newbery *et al.* 1992) or Malaysia (Manokaran & Kochummen 1987). In Uppangala, endemics represent 48% (47 species) of the total number of tree species, placing this forest in an intermediate position in the endemism pattern of southern Western Ghats, where endemism could be as high as 63% (for trees ≥10 cm dbh, Ramesh & Pascal 1991).

Legris & Meher-Homji (1968) considered the evergreen and semi-evergreen series of the Malabar coast (south-west India) as one of the two concentration zones of the Indo-Malayan floristic element in India (comprising species of the Indian and Malaysian peninsulas). They estimated the proportion of Indo-Malayan elements in the wet evergreen series at 26% (59 species) and that of species confined to the Malabar province (Malabarian element) at 38% (88 species). When only the family Dipterocarpaceae is considered, the Western Ghats evergreen forests are much poorer than, for example, those of Malaysia. In Sungei Menyala Forest Reserve (peninsular Malaysia), Manokaran & Kochummen (1987) enumerated 14 dipterocarp species among the emergent group, while there are only five Dipterocarpaceae members in Uppangala. However, as the dense wet evergreen forests of southern India are dominated by dipterocarps, they can be considered as the westernmost lowland dipterocarp forests of Asia. The importance of Dipterocarpaceae diminishes from south to north, corresponding to the lengthening of the dry season (*Hopea ponga* is the only dipterocarp found in these evergreen forests when the dry period exceeds five months).

*Species dominance*

Pronounced species hierarchy is one of the most striking characteristics of the evergreen forests throughout the Western Ghats (Pascal 1984/1988). In Uppangala, the four main species (in terms of IVI*) represent more than 48% of the trees and 55% of the basal area and constitute the framework of the forest. As each of them occupies a different layer, they practically determine the vertical structure of the local stand: (i) *Dipterocarpus indicus* is an emergent and its importance is due to trees of large girth established in the top canopy. (ii) *Vateria indica* is the most common species, well represented in all girth classes. Its plasticity enables it to get established from the intermediate strata to the emergents. (iii) *Myristica dactyloïdes* fills the intermediate layer. Its limited capacity to grow in height, as well as in diameter, hinders its access to the upper storey. It is only in the absence of the emergents that this species forms the canopy. (iv) *Humboldtia brunonis* is the main species of the understorey.

*Stand structure*

Two structural patterns can be identified in the forest except in regions where the canopy is disturbed, or dominated by small-sized trees, or constituted by pioneer species. They represent two distinct forms of old homeostatic (biostatic) phases forming a continuous closed canopy, composed of mature trees (Hallé *et al.* 1978). (i) A type with an emergent layer, between 30 and 50 m, composed of *Dipterocarpus indicus*, *Vateria indica*, *Kingiodendron pinnatum* and other tall species (Figure 11a). The intermediate stratum, comprising species such as *Myristica dactyloïdes*, *Knema attenuata*, *Drypetes elata*, is not well represented. The undergrowth is dense. Hence, there is a vertical discontinuity with an empty level between the undergrowth and the emergents. (ii) A type where the canopy is lower, saturated between 10 and 30 m with *Vateria indica*, *Myristica dactyloïdes* and others (Figure 11b). There are no emergents nor any vertical discontinuity.

Such structural types have already been described in tropical forests, particularly in *Shorea albida* Sym. (Dipterocarpaceae) formations in Brunei and Sarawak (Ashton & Hall 1992). The structural variations were mainly attributed to differences in the available water capacity of the soil. Soils experiencing frequent water deficits would bear a mixed-species forest with a low canopy. Whatever the nutritional value of the soil, the growth of emergents is limited; they hardly exceed the main canopy or are absent.

In Uppangala, tall and low structures can be recognized within the same forest related to the topography. Low structures are found on slopes and tall structures on raised and gently sloping areas or along the streams. Peterschmitt (1993) found local variations in the depth of the soil affecting the available water capacity. Fine roots are present down to the alterite. Hence, these two

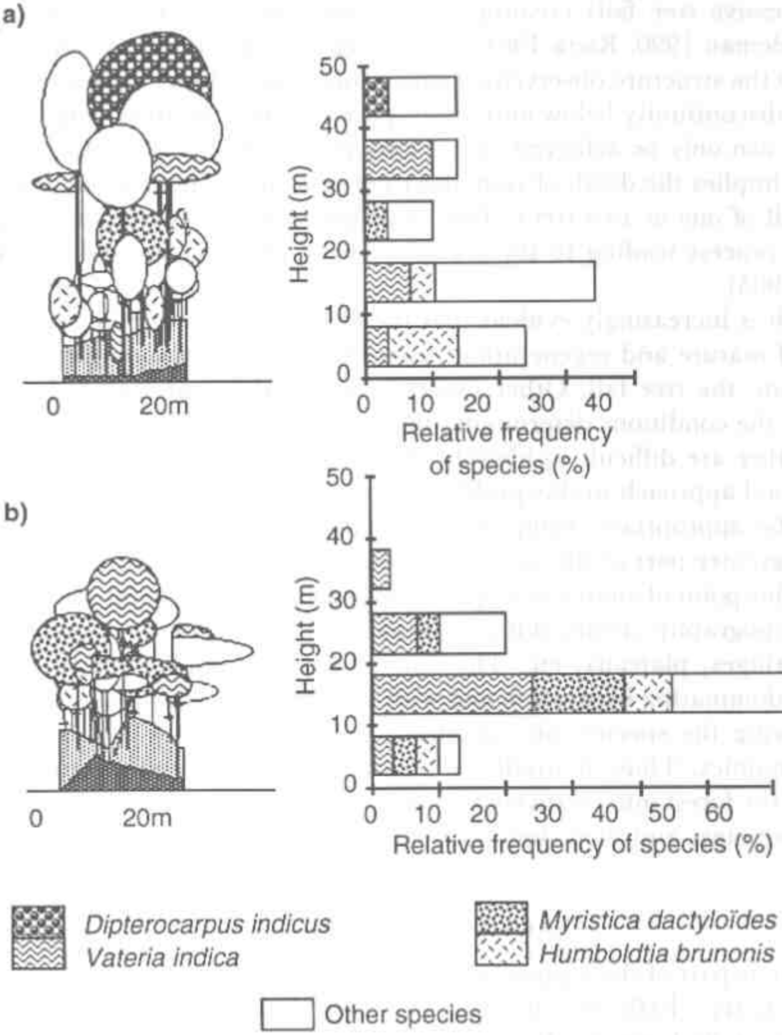


Figure 11. Profiles of 20 m × 20 m quadrats in Uppangala forest, Western Ghats, India, and corresponding height class distributions.

forms of the old mature stages in the same forest may be dependent on the water availability. The presence of *Dipterocarpus indicus*, an exclusively emergent species, could be related to deep well-watered soils. By contrast, *Vateria indica*, which is a plastic species, gets established among the emergents when the water availability is good and in the intermediate stratum when it is not so good. Local conditions of water availability may thus be the determining factor for its growth capacity.

One of the objectives of studying the Uppangala plot was to establish relationships between the structural variations of the stand and the dynamic processes in order to model the forest dynamics. Steep slopes are favourable to frequent and successive tree falls creating large-sized openings (Ashton 1992, Basnet 1992, Oldeman 1990, Riéra 1983). These big openings do not seem to be compatible to the structure observed on raised and gentle slope: higher canopy with a foliage discontinuity below and more space between the trees (Fig. 11a). This structure can only be achieved over a long period of time without disturbance. It rather implies the death of standing trees or a small opening like that caused by the fall of one or two trees. This structure seems to correspond to another dynamic process leading to the organization of the trees around an emergent (Pascal 1995).

Thus, it is increasingly evident that the forest can no more be regarded as a mosaic of mature and regeneration phases resulting from a single disturbance mechanism, the tree fall. Other processes act at different scales of space and time, but the conditions determining the predominance of one dynamic process over another are difficult to identify. Study of the structural variations seems to be a good approach to this problem. However, systematic sampling does not seem to be appropriate. Sampling of specific conditions, selected in order to isolate a greater part of the variation, would be preferable.

From this point of view, the Uppangala forest presents several advantages. Its uneven topography creates different situations: deep valleys, slopes of varying degrees, ridges, plateaux, etc. The dominance of a small number of species, each one dominating its stratum and with a different population structure, helps in classifying the species into functional groups, necessary for modelling the forest dynamics. Thus, it would be possible, in the not-too-distant future, to delineate the forest into relatively homogeneous units based on their main structural parameters and their dominant dynamic processes.

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APPENDIX

List of tree species found in the 3.12 ha sampled in Uppangala forest, Western Ghats, India (+: not found in the sample but seen in the area). Relative density (rD), relative basal area (rBA) and Importance Value Index (IVI*). † Endemic species of the Western Ghats.

| | Species code | rD (%) | rBA (%) | IVI* (rD + rBA) |
|---|---|---|---|---|
| ANACARDIACEAE | | | | |
| *Holigarna arnottiana* J. Hk.† | hoar | 0.40 | 0.22 | 0.62 |
| *Holigarna ferruginea* March.† | hofe | 0.56 | 0.36 | 0.92 |
| *Holigarna grahamii* (Wt.) Kurz† | hogr | 0.15 | 0.05 | 0.20 |
| *Holigarna nigra* Bourd.† | honi | 0.10 | 0.23 | 0.33 |
| *Mangifera indica* L. | main | 0.76 | 0.85 | 1.61 |
| *Nothopegia beddomei* Gamble† | nobe | 2.17 | 0.74 | 2.91 |
| *Semecarpus auriculata* Bedd.† | seau | 0.20 | 0.09 | 0.29 |
| | | 4.34 | 2.54 | 6.88 |
| ANNONACEAE | | | | |
| *Cyathocalyx zeylanicus* Champ ex J. Hk. & Th. | cyze | 0.05 | 0.01 | 0.06 |
| *Goniothalamus* sp. Bl. | goxx | 0.05 | 0.01 | 0.06 |
| *Polyalthia coffeoïdes* J. Hk. & Th. | poco | 0.35 | 0.11 | 0.46 |
| *Polyalthia fragrans* (Dalz.) Bedd. | pofr | 0.05 | 0.14 | 0.19 |
| Undetermined Annonaceae | anno | 0.10 | 0.06 | 0.16 |
| | | 0.60 | 033 | 0.93 |
| ARECACEAE | | | | |
| *Caryota urens* L. | caur | 0.10 | 0.06 | 0.16 |
| BIGNONIACEAE | | | | |
| *Pajanelia longifolia* (Willd.) Schum. | palo | 0.10 | 0.27 | 0.37 |
| BURSERACEAE | | | | |
| *Canarium strictum* Roxb. | cast | 0.40 | 0.43 | 0.83 |
| CELASTRACEAE | | | | |
| *Euonymus indicus* Heyne ex Wall. | euin | 0.30 | 0.08 | 0.38 |
| *Lophopetalum wightianum* Arn. | lowi | 0.50 | 1.49 | 1.99 |
| *Microtropis wallichiana* Wt. | miwa | 0.10 | 0.02 | 0.12 |
| | | 0.90 | 1.59 | 2.49 |
| CLUSIACEAE | | | | |
| *Calophyllum polyanthum* Wall. ex Choisy | capo | 0.50 | 1.73 | 2.23 |
| *Garcinia gummi-gutta* (L.) Robson | gagu | 0.25 | 0.23 | 0.48 |
| *Garcinia morella* (Gaertn.) Desr. | gamo | 2.22 | 0.65 | 2.87 |
| *Garcinia talbotii* Raiz. & Sant.† | gata | 1.51 | 1.18 | 2.69 |
| *Mesua ferrea* L. | mefe | 2.88 | 3.71 | 6.59 |
| | | 7.36 | 7.50 | 14.86 |
| CORNACEAE | | | | |
| *Mastixia arborea* (Wt.) Bedd. | maar | 0.76 | 0.50 | 1.26 |

APPENDIX (*cont.*)

| | Species code | rD (%) | rBA (%) | IVI* (rD + rBA) |
|---|---|---|---|---|
| DIPTEROCARPACEAE | | | | |
| + *Dipterocarpus bourdilloni* Brandis† | | | | |
| *Dipterocarpus indicus* Bedd.† | diin | 3.38 | 11.62 | 15.00 |
| + *Hopea parviflora* Bedd.† | | | | |
| *Hopea ponga* (Dennst.) Mabberly† | hopo | 1.01 | 1.28 | 2.29 |
| *Vateria indica* L.† | vain | 16.71 | 29.29 | 46.00 |
| | | 21.10 | 42.19 | 63.2 |
| EBENACEAE | | | | |
| + *Diospyros assimilis* Bedd.† | | | | |
| *Diospyros bourdillonii* Brandis† | dibo | 0.30 | 0.90 | 1.20 |
| + *Diospyros buxifolia* (Bl.) Hiern | dibu | | | |
| *Diospyros ghatensis* B.R. Ramesh & D. De Franceschi† | digh | 0.20 | 0.06 | 0.26 |
| *Diospyros pruriens*Dalz.† | dipr | 0.25 | 0.06 | 0.31 |
| *Diospyros sylvatica*Roxb. | disy | 0.96 | 0.97 | 1.93 |
| | | 7.71 | 1.99 | 3.70 |
| ELAEOCARPACEAE | | | | |
| *Elaeocarpus serratus* L. | else | 0.05 | 0.23 | 0.28 |
| EUPHORBIACEAE | | | | |
| *Agrostistachys meeboldii* Pax & K. Hoffm. | agme | 0.05 | 0.01 | 0.06 |
| *Antidesma menasu* Miq. ex Tul. | anme | 0.20 | 0.06 | 0.26 |
| *Baccaurea courtalensis* M. Arg.† | baco | 0.20 | 0.03 | 0.23 |
| *Blachia denudata* Benth.† | blde | 0.05 | 0.02 | 0.07 |
| *Blachia umbellata* Baill.† | blum | 0.05 | 0.01 | 0.06 |
| *Croton malabaricus* Bedd.† | crma | 0.05 | 0.05 | 0.10 |
| *Dimorphocalyx beddomei* (Benth.) A. Shaw† | dibe | 1.36 | 0.32 | 1.68 |
| *Drypetes elata* (Bedd.) Pax & Hoffm.† | drel | 3.99 | 4.35 | 8.34 |
| + *Drypetes oblongifolia* (Bedd.) A. Shaw | drob | | | |
| *Fahrenheitia zeylanica* (Thw.) A. Shaw | faze | 0.76 | 0.74 | 1.50 |
| *Glochidion malabaricum* Bedd.† | glma | 0.25 | 0.06 | 0.31 |
| *Macaranga peltata* (Roxb.) Mueller | mape | 0.10 | 0.04 | 0.14 |
| *Mallotus philippensis* (Lam.) Mueller | maph | 0.05 | 0.01 | 0.06 |
| + *Mallotus stenanthus* M. Arg. | mast | | | |
| *Mallotus tetracoccus* (Roxb.) Kurz | mate | 0.10 | 0.06 | 0.16 |
| + *Margaritaria indica* (Dalz.) A. Shaw | mrin | | | |
| | | 7.31 | 5.78 | 13.09 |
| FABACEAE | | | | |
| *Humboldtia brunosis* Wall.† | hubr | 14.89 | 2.75 | 17.64 |
| *Kingiodendron pinnatum* (Roxb. ex DC) Harms† | kipi | 1.06 | 4.52 | 5.58 |
| | | 15.95 | 7.27 | 23.22 |
| FLACOURTIACEAE | | | | |
| *Casearia ovata* (Lam.) Willd. | caov | 0.30 | 0.08 | 0.38 |
| *Flacourtia montana* Graham† | flmo | 0.05 | 0.02 | 0.07 |
| *Hydnocarpus alpina* Wt. | hyal | 1.41 | 0.72 | 2.13 |
| *Hydnocarpus pentandra* (Buch.-Ham.) Oken† | hype | 0.05 | 0.15 | 0.20 |
| | | 1.81 | 0.97 | 2.78 |

| | Species code | rD (%) | rBA (%) | IVI* (rD + rBA) |
|---|---|---|---|---|
| ICACINACEAE | | | | |
| + *Gomphandra tetrandra* (Wall.) Sleumer | gote | | | |
| LAURACEAE | | | | |
| *Actinodaphne tadulingami* Gamble† | acta | 0.20 | 0.11 | 0.31 |
| *Beilschmiedia wightii* Benth. ex J. Hk.† | bewi | 0.40 | 0.16 | 0.56 |
| *Cinnamomum* sp. Schaeff. | cixx | 0.76 | 0.64 | 1.40 |
| *Cryptocarya bourdillonii* Gamble† | crbo | 0.66 | 0.41 | 1.07 |
| *Litsea floribunda* (Bl.) Gamble | lifl | 0.05 | 0.03 | 0.08 |
| *Persea macrantha* (Nees) Kosterm. | pema | 0.10 | 0.27 | 0.37 |
| | | 2.17 | 1.62 | 3.79 |
| MELASTOMATACEAE | | | | |
| *Memecylon wightii* Thw. | mewi | 0.05 | 0.01 | 0.06 |
| *Memecylon* sp. | mexx | 0.15 | 0.06 | 0.21 |
| | | 0.20 | 0.07 | 0.27 |
| MELIACEAE | | | | |
| *Aglaia barberi* Gamble† | agba | 0.10 | 0.28 | 0.38 |
| + *Aglaia jainii* Viswa. & Ramachan.† | agja | | | |
| + *Aglaia simplicifolia* (Bedd.) Harms† | | | | |
| *Aphanamixis polystachya* (Wall.) Parker | appo | 0.10 | 0.05 | 0.15 |
| *Reinwardtiodendron anaimalaiense* (Bedd.) Mabb.† | rean | 3.18 | 1.53 | 4.71 |
| *Walsura trifolia* A. Juss. | watr | 0.05 | 0.01 | 0.06 |
| | | 3.43 | 1.87 | 5.30 |
| MORACEAE | | | | |
| *Antiaris toxicaria* Lesch. | anto | 0.05 | 0.02 | 0.07 |
| *Artocarpus heterophyllus* Lam. | arhe | 0.35 | 0.36 | 0.71 |
| *Artocarpus hirsutus* Lam.† | arhi | 0.15 | 0.10 | 0.25 |
| *Ficus nervosa* Roth | fine | 0.10 | 0.13 | 0.23 |
| | | 0.65 | 0.61 | 1.26 |
| MYRISTICACEAE | | | | |
| *Knema attenuata* (J. Hk. & Thw.) Warb.† | knat | 6.11 | 4.86 | 10.97 |
| *Myristica dactyloïdes* Gaertn.† | myda | 13.18 | 11.45 | 24.63 |
| *Myristica malabarica*Lam.† | myma | 0.15 | 0.19 | 0.34 |
| | | 19.44 | 16.5 | 35.94 |
| MYRTACEAE | | | | |
| *Syzygium gardneri* Thw. | syga | 1.92 | 1.47 | 3.39 |
| *Syzygium hemisphericum* (Walp.) Alston | syhe | 0.05 | 0.01 | 0.06 |
| *Syzygium laetum* (Buch.-Ham.) Gandhi† | syla | 0.66 | 0.11 | 0.77 |
| | | 2.63 | 1.59 | 4.22 |
| OLACACEAE | | | | |
| *Strombosia ceylanica* Gardn. | stce | 0.45 | 0.25 | 0.70 |
| OLEACEAE | | | | |
| + *Olea dioica* Roxb. | oldi | | | |

APPENDIX (*cont.*)

| | Species code | rD (%) | rBA (%) | IVI* (rD + rBA) |
|---|---|---|---|---|
| RHIZOPHORACEAE | | | | |
| *Blepharistemma membranifolia* (Miq.) Ding Hou† | blme | 0.05 | 0.02 | 0.07 |
| RUBIACEAE | | | | |
| *Neonauclea purpurea* (Roxb.) Merr. | nepu | 0.10 | 0.27 | 0.37 |
| RUTACEAE | | | | |
| *Glycosmis macrocarpa* Wt.† | glmc | 0.20 | 0.06 | 0.26 |
| *Vepris bilocularis* (Wt. & Arn.) Engler† | vebi | 0.10 | 0.19 | 0.29 |
| | | 0.30 | 0.25 | 0.55 |
| SAPINDACEAE | | | | |
| *Dimocarpus longan* Lour. | dilo | 0.71 | 0.72 | 1.43 |
| *Harpullia arborea* (Blanco) Radlk. | haar | 0.10 | 0.06 | 0.16 |
| *Otonephelium stipulaceum* (Bedd.) Radlk.† | otst | 0.25 | 0.18 | 0.43 |
| | | 1.06 | 0.96 | 2.02 |
| SAPOTACEAE | | | | |
| *Chrysophyllum lanceolatum* (Bl.) DC. | chla | 0.25 | 0.32 | 0.57 |
| *Isonandra lanceolata* Wt. | isla | 0.05 | 0.01 | 0.06 |
| + *Mimusops elengi* L. | | | | |
| *Palaquium ellipticum* (Dalz.) Baillon† | pael | 4.95 | 3.59 | 8.54 |
| | | 5.25 | 3.92 | 9.17 |
| STERCULIACEAE | | | | |
| *Heritiera papilio* Bedd.† | hepa | 0.30 | 0.28 | 0.58 |
| *Leptonychia moacurroides* Bedd.† | lemo | 0.10 | 0.02 | 0.12 |
| *Pterospermum diversifolium* Bl. | ptdi | 0.05 | 0.02 | 0.07 |
| | | 0.45 | 0.32 | 0.77 |
| SYMPLOCACEAE | | | | |
| *Symplocos racemosa* Roxb. | syra | 0.10 | 0.06 | 0.16 |
| URTICACEAE | | | | |
| *Dendrocnide sinuata* (Bl.) Chew. | desi | 0.10 | 0.03 | 0.13 |
| VERBENACEAE | | | | |
| *Callicarpa tomentosa* (L.) Murray | cato | 0.05 | 0.03 | 0.08 |
| VIOLACEAE | | | | |
| *Rinorea bengalensis* (Wall.) O. Kuntze | ribe | 1.01 | 0.20 | 1.21 |