
Patterns of tree growth in relation to environmental variability in the tropical dry deciduous forest at Mudumalai, southern India

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Tree diameter growth is sensitive to environmental fluctuations and tropical dry forests experience high seasonal and inter-annual environmental variation. Tree growth rates in a large permanent plot at Mudumalai, southern India, were examined for the influences of rainfall and three intrinsic factors (size, species and growth form) during three 4-year intervals over the period 1988–2000.

Most trees had lowest growth during the second interval when rainfall was lowest, and skewness and kurtosis of growth distributions were reduced during this interval. Tree diameter generally explained <10% of growth variation and had less influence on growth than species identity or time interval. Intraspecific variation was high, yet species identity accounted for up to 16% of growth variation in the community. There were no consistent differences between canopy and understory tree growth rates; however, a few subgroups of species may potentially represent canopy and understory growth guilds. Environmentally-induced temporal variations in growth generally did not reduce the odds of subsequent survival.

Growth rates appear to be strongly influenced by species identity and environmental variability in the Mudumalai dry forest. Understanding and predicting vegetation dynamics in the dry tropics thus also requires information on temporal variability in local climate.

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1. Introduction

Stem diameter is among the most sensitive character traits in trees likely to be affected by local environmental stresses (Dobbertin 2005). Dry tropical forests are excellent locations to study functional plasticity in tree diameter growth as they are characterized by large weather variations that include severe annual dry periods lasting from three to eight months (Murphy and Lugo 1986; Gerhardt and Hytteborn 1992). Here we examine tree diameter growth variations in relation to environmental, taxonomic and ontogenetic variations over 12 years in a tropical dry forest.

We have been studying the long-term dynamics of a tropical dry deciduous forest in Mudumalai, southern India, within a 50-hectare permanent forest plot (Sukumar *et al* 1992, 2004) that is part of an international network of

large-scale and long-term Forest Dynamics Plots (Losos and Leigh 2004). Several features of the Mudumalai dry forest environment differ from those of other paleotropical or neotropical forests in the network. In particular, floristic diversity is relatively low (Losos and Leigh 2004), the canopy is relatively open and stochastic environmental fluctuations such as high intra and inter-annual rainfall variability, dry season ground fires and intensive browsing by large herbivores are common (Sukumar *et al* 1992, 2005). We would expect these environmental variations to be reflected in species' demographic traits, and the low floristic diversity to be associated with the way in which resources are partitioned in the community. Although tropical rainforests have been relatively well studied and characterized, similar studies on tropical dry forests are generally lacking (Murphy and Lugo 1986; Swaine *et al* 1990; Gerhardt and Hytteborn

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1992). Thus, comparisons of the Mudumalai dry forest with wetter tropical forests are important for understanding the range of growth responses by tropical trees to environmental variation.

Previous studies using dendrometers to obtain daily, weekly or monthly measurements for up to two years in a range of forest types including dry lowland deciduous (Reich and Borchert 1984), moist semideciduous (Daubenmire 1972; Baker *et al* 2002, 2003a), and wet evergreen forests (Breitsprecher and Bethel 1990; Pelissier and Pascal 2000) have demonstrated that intra-annual or seasonal diameter variations are generally positively associated with rainfall and soil water. However, longer term studies (without dendrometers) have suggested that on an annual basis the relationship between rainfall and growth might become negative as the average annual rainfall increases. Thus, a four year study in a dry evergreen rainforest of Ghana (Swaine *et al* 1990; annual rainfall: 570–910 mm, at least eight months with less than 100 mm) found that faster growth occurred during higher rainfall years as expected based on seasonal patterns, whereas studies lasting up to eight years in moist forest sites of Panama (Condit *et al* 1993a, 2004; annual rainfall: 2030–2892 mm, 3.5 to 4.5 months with less rainfall than potential evapotranspiration) found higher growth rates in saplings and several large trees during a drought year, and similarly a six-year study in a wet forest of Costa Rica (Clark and Clark 1992; annual rainfall: 3859 mm, no months with less than 100 mm) found highest median annual growth rates in the smallest and largest size classes during the lowest rainfall years and lowest growth during the highest rainfall years in most of the species studied. Similarly, a short two-year dendrometer study in a wet evergreen forest of India (Pelissier and Pascal 2000; annual rainfall >4000 mm, five months with less than 100 mm) also showed higher average annual growth during the relatively drier year. It has been hypothesized for moist forests that increased growth during relatively dry years may be due to reduced cloud cover resulting in increased photosynthetically active radiation (Clark and Clark 1992, 1994; Wright *et al* 1999; Condit *et al* 2004) or due to increased atmospheric temperatures during droughts (Condit *et al* 2004). In this context it is interesting to examine the long term relationship between rainfall and tree growth in the comparatively dry forest of Mudumalai.

With regard to intrinsic influences on tree growth, studies in tropical semi-deciduous and moist forests have reported that growth is strongly positively related to tree diameter (Swaine *et al* 1987; Condit *et al* 1993b; King *et al* 2006), that growth rates are species-specific (Lang and Knight 1983; Lieberman and Lieberman 1987; Clark and Clark 1992, 1999), and that different species may have specialized growth strategies relating to their demographic or functional guilds in the community (reviewed in Turner 2001). Although grouping species into separate guilds sometimes

appears arbitrary (Turner 2001), growth-related continuums from the ‘pioneer’ strategy characterized by high growth and shade-intolerance, to the “mature canopy” or “understory shade-tolerant” strategy characterized by progressively lower growth rates (Lieberman *et al* 1985; Welden *et al* 1991; Condit *et al* 1996; Clark and Clark 1999; Nascimento *et al* 2005) have been described. These classifications in tropical moist forests generally have been associated with species’ partitioning of the light gradient, either horizontally or vertically (Baker *et al* 2003b). It is not clear if similar evolutionary pressures have produced similar patterns of growth in relation to size and species identity in tropical dry forests, or if similar growth guilds can be identified here, as dry forests generally are open-canopied, species poor and floristically simple (Murphy and Lugo 1986; Gentry 1995).

In this study we examine the plasticity of Mudumalai dry forest tree diameter growth rates in relation to the external environmental factor of rainfall and the intrinsic factors of tree size, species identity and growth form. The following null hypotheses were tested:

- (i) There is no significant variation in growth rates of trees during different census intervals.
- (ii) Growth rates are not related to the extrinsic factor, rainfall.
- (iii) Growth rates are not related to the intrinsic factors of stem diameter, species identity and growth form classification.
- (iv) Growth rate variations across time intervals do not reduce survival.

2. Methods

2.1 Study site

During 1988–89 a 50-ha permanent vegetation monitoring plot was set up in the Mudumalai Wildlife Sanctuary (Tamilnadu, southern India), located between 11°35′ 41” and 11°35′ 57” N latitudes, and 76°31′ 50” and 76°32′ 22” E longitudes (Sukumar *et al* 1992, 2004) to complement similar-sized plots established in the wetter tropical forest sites of Barro Colorado Island (BCI), Panama (Hubbell and Foster 1992) and Pasoh, Malaysia (Manokaran *et al* 2004). This paper presents analyses of data collected during the first twelve years of the plot, between 1988 and 2000. Vegetation in the plot is mainly tropical dry deciduous forest, and the average annual rainfall is approximately 1200–1250 mm, received mainly between May and November. There is a pronounced 5-month dry season (less than 100 mm average rainfall per month), from around December to April. Extensive ground fires occurred in the plot during five of the twelve years: 1989, 1991, 1992, 1994 and 1996. Fairly abundant populations of large herbivores such as elephants

(*Elephas maximus*), gaur (*Bos gaurus*), sambar deer (*Cervus unicolor*) and axis deer (*Axis Axis*), as well as smaller mammal species such as Hanuman langur (*Semnopithecus entellus*), wild pig (*Sus scrofa*), barking deer (*Muntiacus muntjak*), porcupine (*Hystrix indica*) and other rodents occur in the sanctuary and impact the vegetation by browsing, debarking, breaking or uprooting plants (Sukumar *et al* 2004).

2.2 Data collection and growth rate calculations

All woody species stems with a dbh of at least 10 mm (i.e., diameter at breast height, measured at 1.3 m or slightly higher if stem joints, buttresses or natural deformities occur at this height) were initially identified, tagged, mapped and measured in 1988–1989. Subsequently the plot has been enumerated annually to record deaths and recruits, while stem diameters or girths are measured every four years. This study used diameter or girth measurements from three 4-year intervals: 1988–1992, 1992–1996, and 1996–2000. Censuses were usually carried out during the wet season, between June and December, by which time most plants had flushed leaves and it was easier to differentiate dead from living stems.

The annual diameter growth per individual for each four-year interval was calculated as the following linear measure: $(D_2 - D_1) / t$, where D_1 = diameter at the start of the interval, D_2 = diameter at the end of the interval and t = time interval between the two measurement dates, in terms of years. Individuals with injuries or joints at the point of measure (between 1% and 4% of stems that survived each census) were excluded. Positive growth increments up to 75 mm.yr⁻¹ and negative diameter changes up to 75% of starting diameter per census interval (i.e. allowing shrinkage up to 7% per year) were considered as acceptable values, and this cut-off range excluded a further 1% to 2% of stems, thus leaving between 13221 and 14964 valid growth rates per interval for analyses. As Mudumalai is a disturbed and dynamic dry forest, we considered it possible that net annual shrinkage might occur in otherwise healthy stems during intervals of prolonged drought; however, these growth limits are wider than some previously used cutoffs (Condit *et al* 1993a, 1993b; Sheil 1995). Hence analyses were repeated using a narrower cutoff range (Sheil 1995) in addition to the above, which excluded an additional 1% from the first and third intervals and 5% from the second interval. Results were generally similar regardless of the growth range used, and only the relatively important variations obtained with conservative growth cutoffs are reported.

Twelve size classes were used for most analyses, with the following limits (mm): 10, 20, 50, 100, 200, 300, 400, 500, 600, 700, 800, 900 and 1500 (in some cases fewer classes were used), with minimum sample size (N) of five per class.

2.3 Time intervals and rainfall

Community level variations across time intervals were examined using 95% confidence intervals for median growth rates. Growth and diameter distributions were checked for skewness and kurtosis, with probability values obtained from t -statistics (Sokal and Rohlf 1998) and by bootstrapping with 1000 iterations. Species' variations across time intervals were examined with paired t -tests and Wilcoxon matched pairs signed ranks tests with P -values generated using 1,000 bootstrap iterations. The value of alpha (type I error) was set at 0.05, and Bonferroni correction was applied for the number of groups tested.

Rainfall data were available from Kargudi (located three km south of the plot) for 90% of the days between March 1990 and December 2000, and from Gamehut (located four km west of the plot) on a semi-monthly basis between January 1998 and December 2000. Missing rainfall data for Kargudi were estimated from Gamehut data as these two datasets were significantly correlated (Pearson $r = 0.74$, $P < 0.001$). Missing Kargudi data were filled in the following three ways, generating three slightly differing datasets for Kargudi: (i) 'annual', using a linear regression equation between all the overlapping data of Kargudi and Gamehut, (ii) 'seasonal', using a separate linear regression equation for each of four seasons and (iii) 'monthly', using a linear or non-linear predictive equation for each of the twelve

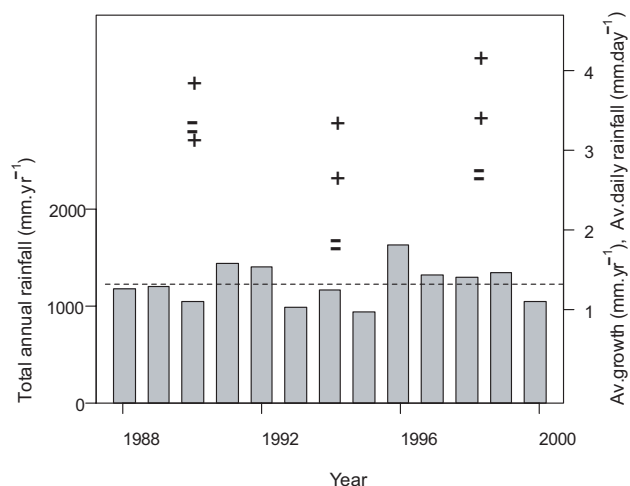


Figure 1. Bar chart of total annual rainfall (mm.yr⁻¹) between 1988 and 2000 in the Mudumalai dry deciduous forest, averaged from Kargudi and Gamehut datasets. Mean annual rainfall, 1237 mm.yr⁻¹, is indicated by a dashed line [median rainfall (not shown) = 1207 mm.yr⁻¹]. Plotted above the bars are the upper and lower 95% confidence intervals of average annual growth [“Av.growth (mm.yr⁻¹)”] of the three growth intervals (1988–1992, 1992–1996, 1996–2000), indicated by “-”, and the corresponding confidence intervals of average *daily* rainfall [“Av.daily rainfall (mm.day⁻¹)”], indicated by “+”.

months (see Appendix 1 for details). Annual rainfall values averaged across the four datasets (i.e. three Kargudi and one Gamehut dataset) are shown in figure 1. Average daily rainfall was calculated at the community level by using mean dates of consecutive censuses to delineate average census intervals, and at the individual level by using exact dates of girth measurement to delineate the rainfall interval per individual.

Consistency of the growth-rainfall relationship was examined using a sign test across pairs of intervals for species in different size classes (hereafter "species-size groups"). First, a measure of homogeneity was obtained between growth and rainfall changes across each pair of intervals for all species-size groups. For this, the sign of association (positive or negative) between the mean or median difference in growth and the corresponding mean or median difference in rainfall, per interval pair, was obtained for each species-size group. Consistency of these growth-rainfall associations across different sets of interval pairs was then checked for by comparing each interval pair with another to obtain the proportion of groups with matching signs in both pairs of intervals. This gave a simple estimate of predictability of the growth-rainfall relationship for species in different size classes.

2.4 *Intrinsic factors*

The influence of stem diameter on growth rates of common species was examined using linear regressions to predict growth from the diameter, the natural log (ln) of diameter or the squared radius. Interspecific variations were tested with single factor ANOVA per interval. Maximum potential growth rate per species was the average of the fastest growing 5% of stems.

All species were classified *a priori*, on the basis of field estimations of maximum height at maturity, into three growth form categories: canopy, understory and shrub (see Appendix 2). Principal components analysis (PCA, similarity matrix standardized with correlation) and cluster analyses (growth values converted to z-scores) were carried out using four growth parameters for juveniles (juveniles were trees <100 mm dbh, except for *Helicteres isora*, the only shrub species used, <40 mm dbh) and adults (non-juveniles) per interval, to try and obtain growth form-related groups or a continuum. The following four parameters were used: average growth, high and low growth (highest and lowest 25% of growth rates, respectively) and relative growth (average growth rate divided by starting diameter). Seven to 12 species per interval could be tested for juveniles (minimum $N = 20$) and 23 to 24 species per interval could be tested for adults (minimum $N = 30$). Cluster analyses also were carried out on PCA scores, using Euclidean or Manhattan distances and single linkage, complete linkage,

Ward's and unweighted centroid algorithms (Ludwig and Reynolds 1988).

PCA and cluster analysis were carried out again after including deterministically calculated lifetime growth information (cf. Lieberman *et al* 1985). For this analysis data from all three intervals were used together for 16 species (with at least 150 individuals across the three intervals), to obtain seven parameters: the above four growth parameters, plus the additional variables of maximum dbh, average number of years to achieve maximum dbh, and minimum number of years to achieve maximum dbh. The average and minimum number of years to achieve maximum dbh were obtained from species' expected lifetime growth trajectories that were created using the average and maximum growth values per size class (size classes ranged from 10 to 80 mm per species), respectively. For size classes without individuals, a cubic spline was applied to estimate growth rates.

2.5 *Individual and interactive effects*

In order to assess the relative importance of different factors on growth and to highlight any important interactions between them, 2- and 3-way ANOVAs were carried out using the factors: species, growth form, time interval and dbh size class. Minimum sample size for unbalanced factorial models was 100 individuals per species or growth form per interval, and allowed individuals to be repeated across intervals. Balanced models with individuals selected randomly without replacement (to ensure independence within and across groups) also were run, with sample sizes of 20 or 30 per group for 2-way models and five per group for 3-way models. Balanced models were run 1000 times each and results are reported as proportions of iterations in which each factor or interaction term was significant at $P < 0.05$.

2.6 *Growth variations and survival*

For all trees that survived the first two intervals, differences in relative growth rates of third interval survivors versus non-survivors were tested with *t*-tests and Wilcoxon signed ranks tests. Minimum sample size for survivors and non-survivors was five, and seven size classes were used (class limits: 10, 50, 100, 200, 300, 400, 600, and 1500 mm). Growth distributions were trimmed by 5% of the range to eliminate outliers. Logistic regression analysis also was carried out to assess the effect of the difference in relative growth rates (trimmed by 5% of the range) between the first and second intervals on survival from natural causes other than fire and elephants, during each year between 1997 and 2000. All analyses were carried out using R, version 2.2.1.

3. Results

3.1 Variations across time intervals in relation to rainfall

Average growth rates of all stems together during the three consecutive time intervals were 3.32 ± 3.36 mm.yr⁻¹ (i.e. \pm SD), 1.84 ± 3.03 mm.yr⁻¹ and 2.71 ± 3.11 mm.yr⁻¹, respectively, with 95% confidence intervals (CI) of ± 0.05 mm.yr⁻¹ in all cases (figure 1). Growth rates were significantly different for all pairs of intervals. The corresponding average daily rainfall values experienced by individuals in the plot, averaged across the four datasets (i.e. three Kargudi datasets and one Gamehut dataset), were 3.49 mm.day⁻¹ ± 6.86 (CI = 0.36), 3.0 mm.day⁻¹ ± 6.70 (CI = 0.35) and 3.79 mm.day⁻¹ ± 7.38 (CI = 0.37), respectively. The overall pattern of high versus low rainfall across three intervals appears similar to the corresponding pattern in growth rates (figure 1).

At the community level all size classes, except the smallest size class, had highest growth in the first interval and lowest growth in the second interval (table 1, figure 2). Median growth in the second interval was significantly different ($P < 0.05$) from that of the first and third intervals in eleven and nine size classes, respectively, while growth rates of the first and third intervals were significantly different from each other in eight classes. There also was significant positive skewness and kurtosis of growth rates ($P < 0.05$ with Bonferroni correction for number of size classes tested) in many small and medium size classes and in some large size classes during all intervals, which generally declined in value during the second interval, probably due to increased proportions of low and negative growth rates during this interval (table 1). Conservative growth cutoffs increased skewness of growth distributions as most size classes were significantly skewed, which did not generally reduce in the second interval as a result of excluding many negative values. Diameter distributions were rarely significantly skewed and were generally negatively kurtotic (table 1) indicating that growth rate skewness and kurtosis were not influenced by diameter distributions.

Over half of the species tested individually, including the four most dominant canopy species (*Lagerstroemia microcarpa*, *Terminalia crenulata*, *Anogeissus latifolia* and *Tectona grandis*), had significantly lower growth during the second interval compared to the first or third intervals in at least 50% of their size classes ($P < 0.05$ with Bonferroni correction for number of size classes tested per species). Approximately 73% of species had significantly lower growth during the second interval in at least one size class, which collectively accounted for over half of all individuals tested. No species in any size class had significantly higher growth during the second interval except for 10–20 mm dbh stems of *Cassia fistula*, a common understorey tree, which grew faster in the second interval compared to the first.

The direction of association between growth and rainfall differences across interval pair 1–2 (1988–92 and 1992–96) was the same as that across interval pair 2–3 (1992–96 and 1996–2000) in 85% to 90% of 105 species-size groups tested (using mean or median growth and rainfall, with four different rainfall datasets), indicating a possible strong positive relationship between rainfall and growth for different species and size classes. However, evidence for this relationship was not so strong when the interval pair 1–3 (1988–92 and 1996–2000) was used. In this case fewer groups had matching growth-rainfall relationships with interval pair 1–2 (31% to 35% of 103 groups tested) or with interval pair 2–3 (40% to 43% of 103 groups tested).

3.2 Variations with size

There was high variation in average growth across size classes per interval (table 1). Within size classes also there was large variation in growth, with standard deviations generally close to or greater than 100% of the means. During the first and third time intervals, growth rates generally increased with stem size; however, during the second interval the pattern was substantially different, with growth rates decreasing as tree size increased (figure 2). Among the common species this negative effect was most pronounced in very large stems of the canopy species *T. crenulata* and *T. grandis*, and to a lesser extent in the understorey species *Phyllanthus emblica*. A window of generally high growth also was observed in the smallest stems (10–20 mm dbh) and of low growth in medium-sized stems (approximately 50–300 mm dbh), respectively (figure 2).

In most of the common species dbh was not a significant predictor of growth. Linear regressions of growth on dbh for 17 to 20 common species (i.e. species with at least 50 valid growth rates per interval) showed that only five to eight species had significant regression slopes per interval ($P < 0.05$, with Bonferroni correction for number of species tested), the magnitudes of which were low and explained 1% to 18% of growth variation. When using conservative growth cutoffs nine to ten species had significant slopes explaining less than 1% to 20% of the variation, although with both cutoffs most regressions explained $< 10\%$ of variation. Significant negative regression slopes occurred in two intervals for *C. fistula* and *Helicteres isora*, and the number of species with significant negative slopes increased in the second interval. In the four most abundant canopy species dbh explained only 1% to 7% of growth variation.

The predictive value of stem diameter improved only marginally or declined when using \ln (dbh) or squared radius (to represent cross-sectional area per stem). The only exception was the understorey species, *Cordia wallichii*, in which \ln (dbh) predicted 32% of growth rate variation in the third interval. Thus, for most of the common species growth

Table 1. Average growth, percent low growth, and significant skewness and kurtosis of growth rate distributions and dbh distributions in different size classes per interval.

Size class (mm)	N	Av. growth \pm SD (mm.yr ⁻¹)	Low growth (%)	Growth		Dbh	
				Skewness	Kurtosis	Skewness	Kurtosis
1998 - 1992							
10 - 20	485	3.19 \pm 3.07	27	1.25	2.32	[0.17]	-1.95
20 - 50	730	3.87 \pm 3.41	19	0.99	[3.08]	[0.17]	-1.28
50 - 100	1436	3.95 \pm 3.82	22	1.86	8.14	[-0.19]	-1.16
100 - 200	4396	2.67 \pm 2.98	28	2.70	17.40	[-0.03]	-1.15
200 - 300	3560	3.13 \pm 3.18	21	2.51	19.34	0.22	-1.12
300 - 400	1978	3.54 \pm 3.16	16	2.04	10.28	[0.17]	-1.17
400 - 500	1243	3.80 \pm 3.40	15	[0.73]	7.77	[0.15]	-1.08
500 - 600	662	3.99 \pm 4.01	16	[0.69]	18.47	[0.24]	-1.10
600 - 700	289	4.59 \pm 3.78	12	1.24	4.19	[0.22]	-1.10
700 - 800	109	4.88 \pm 4.70	8	2.22	6.46	[0.23]	[-0.72]
800 - 900	42	5.21 \pm 4.34	10	1.29	[1.54]	[0.40]	[-1.15]
900 - 1500	34	8.39 \pm 8.29	6	1.71	[2.37]	[1.03]	[0.61]
1992 - 1996							
10 - 20	186	4.61 \pm 3.33	16	[0.26]	-0.94	[-0.03]	[-1.06]
20 - 50	433	3.19 \pm 3.11	25	0.83	[1.08]	[0.03]	-1.14
50 - 100	819	2.36 \pm 2.80	36	0.86	1.75	[-0.23]	-1.19
100 - 200	3914	1.51 \pm 2.50	45	1.36	8.96	[-0.08]	-1.13
200 - 300	3448	1.91 \pm 2.81	38	0.72	3.84	0.17	-1.12
300 - 400	2050	2.04 \pm 3.18	38	0.95	6.21	[0.15]	-1.15
400 - 500	1297	1.76 \pm 3.39	42	0.87	5.59	[0.10]	-1.17
500 - 600	692	1.48 \pm 3.86	46	[5.13]	75.31	[0.20]	-1.09
600 - 700	334	1.29 \pm 3.56	46	[0.03]	3.17	[0.16]	-1.14
700 - 800	131	0.71 \pm 3.68	52	[0.09]	2.07	[0.05]	[-1.25]
800 - 900	46	0.17 \pm 4.63	52	[-1.56]	6.42	[0.54]	[-0.77]
900 - 1500	39	0.35 \pm 7.18	59	[0.68]	[2.02]	[0.69]	[-0.77]
1996 - 2000							
10 - 20	206	4.33 \pm 3.24	17	0.69	[0.34]	[-0.08]	[-0.59]
20 - 50	504	3.64 \pm 3.28	23	0.81	[0.40]	[0.25]	-1.10
50 - 100	714	2.88 \pm 2.99	29	2.40	11.73	[-0.19]	-1.27
100 - 200	3558	1.95 \pm 2.64	40	7.02	126.8	-0.14	-1.11
200 - 300	3394	2.56 \pm 2.55	27	1.78	12.99	[0.12]	-1.14
300 - 400	2184	3.09 \pm 3.71	25	6.14	78.23	[0.13]	-1.17
400 - 500	1328	3.19 \pm 3.48	24	3.99	54.52	[0.11]	-1.17
500 - 600	750	3.22 \pm 3.36	21	[1.52]	18.77	[0.16]	-1.16
600 - 700	357	3.57 \pm 3.42	17	3.07	19.64	[0.07]	-1.25
700 - 800	136	3.30 \pm 3.48	23	[1.13]	4.38	[-0.11]	[-1.10]
800 - 900	49	3.54 \pm 4.89	22	[4.03]	[22.37]	[0.51]	[-0.67]
900 - 1500	41	4.73 \pm 4.44	20	[0.74]	[0.36]	[1.00]	[0.58]

Skewness and kurtosis statistics were considered significant if the *P*-value obtained by *t*-statistics method and by bootstrap method (1000 iterations) were both <0.05 (with Bonferroni correction for number of size classes per interval). Non-significant skewness and kurtosis values are in square brackets. N, total number of stems; Av.growth \pm SD, average annual growth rate \pm standard deviation; Low Growth %, percent of stems with less than 1 mm growth per year.

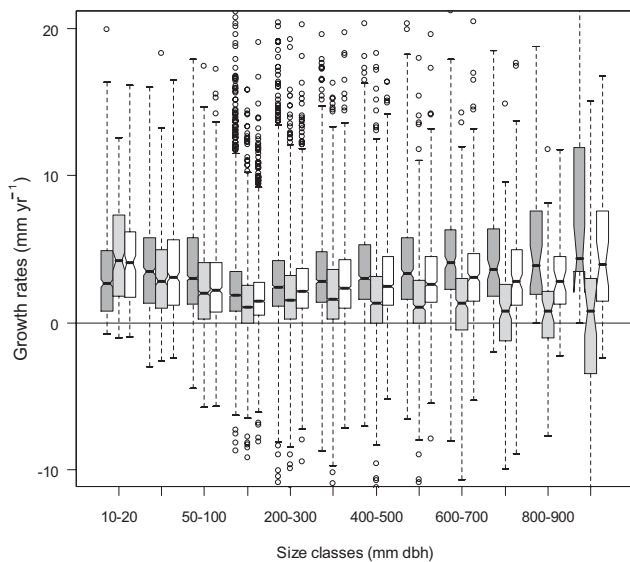


Figure 2. Boxplots of growth rate distributions in twelve size class during three time intervals. Whiskers are indicated with dotted lines, with a range of thrice the interquartile range. Notches signify 95% confidence limits for medians. Dark grey boxes = 1988–1992; light grey boxes = 1992–1996; White boxes = 1996–2000.

rate variations were only weakly related to stem diameter and in some cases the direction of the relationship changed with time.

3.3 Variations across species

Growth rates were examined in three size categories per species: small (10–50 mm dbh), medium (50–500 mm dbh), and large (at least 500 mm dbh). Average growth in these categories varied widely across species, the highest being 7.9 mm.yr⁻¹ for medium stems of *Hymenodictyon orixense* in 1988–1992 and the lowest being -1.7 mm.yr⁻¹ for large stems of *Terminalia bellirica* in 1992–1996 (table 2). Conservative growth cutoffs eliminated many negative growth rates especially from large stems during the second interval, and consequently the lowest average growth rate obtained was relatively higher, at -0.3 mm.yr⁻¹, for medium stems of *Schrebera swietenoides* in 1992–1996. Standard deviations of species' growth rates per size class were generally high (usually larger than 50% of the means).

There was high variability in growth rates among species across time intervals. For example, *T. bellirica* in the large size category changed from being first-ranked in 1988–1992 with an average growth rate of 7.7 mm.yr⁻¹, to being last-ranked in 1992–1996, with an average growth rate of -1.7 mm.yr⁻¹ (table 2). On the other hand, *Cordia obliqua* in the small stems category and *C. fistula* in the medium size

category showed relatively stable growth. A few species had generally high growth rates (for e.g. *L. microcarpa*, *Kydia calycina*, *G. arborea*, *Grewia tiliaefolia* and *C. fistula*), or generally low growth (for e.g. *H. isora*, *T. crenulata*, *A. latifolia* and *Terminalia chebula*).

Despite the generally high intraspecific growth variation, single-factor ANOVA of species' growth rates per interval was significant ($P < 0.0001$) with species identity explaining 15% to 16% of growth variation in the community (16% to 20% when using conservative growth rate cutoffs). Tukey's HSD tests (for species with at least 50 valid growth rates) revealed that 56% to 68% of species pairs had significantly different growth rates per interval.

3.4 Growth forms and growth strategy groupings

Principal components analysis of species using four growth-related parameters failed to consistently separate species on the basis of growth form. There were no significant differences between canopy and understory species (inclusive or exclusive of the only shrub with sufficient sample size to be used, *H. isora*), except for adults along the second PCA axis during the first and third intervals (one-way ANOVA and Wilcoxon signed ranks tests, $P < 0.05$ with Bonferroni correction for three interval pairs tested). PCA biplots of juveniles and adults also showed no consistent groupings, nor any continuum of growth, that was associated with growth form. However, species scores of adults along the first axis were significantly correlated across interval pairs 1–3 and 2–3, while second axis scores were significantly correlated across the interval pair 1–3 (Pearson and Spearman correlations, $P < 0.05$ with Bonferroni correction for number of interval pairs tested). PCA biplots of juveniles and adults also showed no consistent groupings, nor any continuum of growth, that was associated with growth form. However, species scores of adults along the first axis were significantly correlated across interval pairs 1–3 and 2–3, while second axis scores were significantly correlated across the interval pair 1–3 (Pearson and Spearman correlations, $P < 0.05$ with Bonferroni correction for number of interval pairs tested). For juveniles first axis scores were significantly correlated only across interval pair 2–3 (figure 3).

For adults the first axis scores were significantly negatively correlated with average, high and low growth in all three intervals, and also with relative growth in the second interval, while second axis scores were significantly positively correlated with relative growth in the first and third intervals (Pearson and Spearman correlations, $P < 0.05$ with Bonferroni correction for number parameters tested). For juveniles the first axis scores similarly showed negative correlations for average, high and low growth in all three intervals, except for lack of significant correlation with low growth in the third interval, and second axis scores were significantly negatively correlated with relative growth in the first interval (Pearson and Spearman correlations, $P < 0.05$ with Bonferroni correction for number parameters tested). Across intervals and size categories the first two

Table 2. Growth rates per species in three size categories during three time intervals. Growth rates are ordered from highest to lowest mean growth rate in each size category per interval.

1988–1992					1992–1996					1996–2000				
Sps	N	Av. gr.	SD	Top 5%	Sps	N	Av. Gr.	SD	Top 5%	Sps	N	Av. Gr.	SD	Top 5%
10 – 50 mm dbh														
allc	9	5.29	4.29	13.63	casf	255	4.96	3.40	11.95	corw	12	5.82	5.66	14.76
lagl	140	5.23	3.82	14.93	lagl	85	4.15	3.25	11.19	casf	432	4.45	3.22	11.65
coro	23	4.30	2.80	9.66	coro	11	4.13	4.02	9.75	coro	11	3.96	4.05	10.09
casf	454	4.24	3.62	11.98	rand	76	2.84	2.14	7.32	lagl	66	3.55	3.74	12.52
stet	7	3.88	4.46	9.06	step	6	2.33	1.88	4.94	allc	5	2.91	2.41	5.50
corw	11	3.86	1.75	6.46	corw	8	2.19	1.43	4.19	rand	56	2.71	2.37	7.94
dall	10	3.83	3.76	11.79	antd	5	1.72	1.94	4.68	heli	94	2.32	2.32	7.62
antd	7	3.39	2.05	5.74	heli	139	1.35	2.04	6.08	tecg	9	0.67	1.69	3.53
kydc	31	3.37	2.78	8.73										
elag	8	3.16	2.19	7.13										
rand	92	3.16	1.97	7.39										
indc	9	2.50	2.23	5.99										
malp	9	2.50	1.54	4.65										
heli	317	2.46	2.55	8.67										
writ	9	2.41	2.49	7.53										
step	8	2.31	2.38	5.29										
tecg	35	1.56	1.82	5.85										
shor	7	1.40	1.26	3.24										
50 – 500 mm dbh														
hymo	7	7.85	7.09	22.90	ptem	6	6.36	9.47	25.19	syzc	336	5.91	5.01	18.06
kydc	634	6.39	4.66	18.80	gmea	12	4.87	9.16	21.40	diom	108	5.38	3.53	13.48
lanc	6	6.37	3.41	11.77	kydc	186	3.69	3.41	11.68	gret	169	5.01	3.45	12.76
gmea	17	5.24	4.29	12.94	gret	204	3.46	3.73	11.86	gmea	9	4.62	4.38	12.98
malp	12	5.14	4.11	11.14	scho	19	3.45	5.53	16.37	step	67	4.07	4.76	19.02
terb	8	4.99	6.44	20.38	casf	459	3.38	2.84	10.28	dall	25	3.98	4.03	13.02
bomm	17	4.58	2.83	10.23	diom	105	3.24	3.27	10.62	zizr	8	3.91	1.75	7.58
gret	254	4.57	3.40	13.18	syzc	319	3.17	3.00	10.40	kydc	80	3.72	3.66	13.32
lagl	3229	4.40	3.62	14.49	lagl	3124	3.05	3.26	11.02	lagl	3050	3.54	3.19	12.15
coro	32	4.38	3.34	10.47	bomm	14	2.92	2.95	8.66	casf	466	3.48	2.55	9.85
cand	16	4.38	2.93	9.66	allc	6	2.56	2.12	5.76	coro	34	3.47	2.79	9.55
step	72	4.22	2.72	10.78	coro	32	2.47	2.63	7.60	scho	15	3.13	2.15	6.78
scho	21	4.10	3.70	12.41	dall	24	2.47	3.79	9.39	terb	6	3.11	3.26	7.46
syzc	331	3.83	3.09	12.21	corw	38	2.13	3.90	10.99	cand	13	2.87	2.34	7.09
casf	396	3.77	2.63	10.19	lanc	5	2.05	2.78	5.82	case	37	2.75	2.01	7.56
elag	5	3.75	1.63	6.23	step	65	2.01	3.43	9.95	rand	386	2.73	3.08	10.42
butm	29	3.69	3.01	11.17	hymo	7	1.97	3.22	7.32	mitp	11	2.61	2.34	5.87
diom	108	3.68	2.68	9.45	rand	437	1.84	3.19	9.58	ougo	45	2.59	2.85	10.45
tecg	1118	3.45	2.59	10.69	baur	7	1.84	2.96	7.33	bomm	14	2.58	1.97	6.81

Table 2 (continued)

mitp	11	3.41	1.52	5.45	case	38	1.24	1.86	5.05	hymo	7	2.40	2.05	6.17
dall	31	3.39	2.49	7.05	tecg	1051	1.24	2.14	5.88	tecg	1041	2.34	2.73	8.39
corw	41	3.16	3.72	10.45	mitp	11	1.11	3.69	4.53	baum	20	2.23	1.96	6.07
ougo	77	3.12	2.52	9.56	anol	2118	1.05	1.76	4.84	brir	16	2.22	2.24	6.57
zizr	6	3.10	2.38	6.70	ougo	67	1.03	2.57	6.02	corw	40	2.00	2.49	7.82
flai	7	3.06	1.39	5.23	stet	274	0.99	2.30	6.27	phye	367	1.98	3.78	10.66
stet	288	2.90	2.52	9.91	cand	14	0.98	1.90	3.70	cara	17	1.97	1.31	4.26
ptem	10	2.87	4.65	12.75	phye	414	0.89	2.03	6.57	malp	5	1.85	2.96	6.88
garp	8	2.77	2.00	6.04	cara	19	0.77	3.29	7.57	anol	2107	1.77	2.19	6.37
sema	11	2.64	2.51	7.03	malp	7	0.74	3.02	5.74	heli	21	1.76	2.61	6.90
zizx	11	2.53	2.09	5.72	zizx	5	0.68	3.90	4.88	stet	264	1.68	2.07	7.58
brir	23	2.51	2.84	10.23	butm	27	0.62	3.48	6.95	eriq	10	1.30	2.15	6.46
rand	524	2.40	2.78	9.40	tert	2113	0.61	1.91	4.96	lagp	60	1.22	1.89	6.16
lagp	68	2.32	2.21	9.09	baum	21	0.54	2.40	4.11	tert	2175	1.21	1.71	5.39
baum	22	2.28	2.60	9.34	brir	20	0.44	2.50	4.91	garp	5	1.15	1.39	2.87
anol	2156	2.27	2.25	8.09	lagp	65	0.26	2.00	3.20	lanc	5	1.14	1.15	2.83
case	41	2.19	2.75	5.70	terc	39	0.18	1.02	1.89	terc	40	0.98	1.43	4.51
phye	443	1.78	2.04	7.71	garp	6	-0.21	1.58	1.56	schs	29	0.77	1.53	4.78
cara	20	1.69	2.37	6.73	sema	9	-0.25	3.10	3.86	sema	7	0.65	0.81	2.15
oled	5	1.67	1.23	3.35	heli	41	-0.25	1.75	3.57	butm	27	0.35	3.19	8.15
tert	2184	1.54	2.19	7.61	schs	32	-0.59	1.23	1.28	baur	6	0.01	3.50	2.82
schs	41	1.51	1.58	5.69	zizr	7	-0.82	4.45	4.96					
eriq	123	1.42	2.65	8.16	terb	6	-0.93	3.22	4.96					
baur	7	1.40	0.62	2.52	eriq	27	-1.47	2.52	1.80					
heli	73	1.33	2.66	8.28										
terc	44	0.90	1.49	3.01										
>500 mm dbh														
terb	25	7.70	8.29	25.84	gret	111	4.34	4.22	14.27	syzc	26	7.25	3.38	14.87
bomm	18	7.41	7.12	24.95	lagl	63	3.97	3.65	11.76	gret	121	7.06	4.70	18.68
lagl	47	6.74	3.82	16.79	syzc	23	3.72	5.51	16.74	gmea	15	5.31	8.05	20.68
gmea	19	6.34	6.79	20.64	lanc	7	3.35	3.66	10.99	lagl	93	4.88	3.21	11.04
gret	86	5.46	5.12	16.07	scho	48	3.14	9.53	30.05	garp	13	4.35	4.10	9.99
ptem	6	5.36	3.03	11.08	garp	14	2.16	4.28	8.82	scho	51	4.20	5.32	11.13
garp	16	5.33	4.59	14.37	gmea	13	1.95	4.93	7.06	bomm	19	3.68	2.28	8.05
lanc	6	5.32	3.33	10.47	anol	16	1.70	3.43	6.68	lanc	8	3.41	3.76	12.04
step	20	5.00	2.73	10.45	ptem	7	1.42	3.81	8.26	step	22	3.13	1.71	7.02
tecg	514	4.72	3.59	14.62	tecg	556	1.00	2.87	6.57	ptem	7	3.13	3.46	10.32
scho	45	4.48	3.75	14.54	step	22	0.13	3.37	4.72	tecg	590	3.07	2.80	9.84
anol	13	4.12	2.36	7.86	tert	295	-0.20	2.31	4.28	anol	13	2.62	2.26	6.04
syzc	21	3.73	9.12	16.63	bomm	19	-0.22	5.46	4.60	terb	25	2.48	3.20	10.04
dall	5	2.48	2.04	6.01	terb	26	-1.71	5.60	8.37	dall	8	1.69	1.83	5.71
tert	279	2.37	3.12	11.64						tert	301	1.55	1.76	5.96

Sps, species code (corresponding species' names are given in Appendix 2); *N*, sample size (minimum = 5); Av. gr., average annual growth rate; SD, standard deviation; Top 5% - mean of highest 5% of growth rates (all growth measurements are in mm.yr⁻¹).

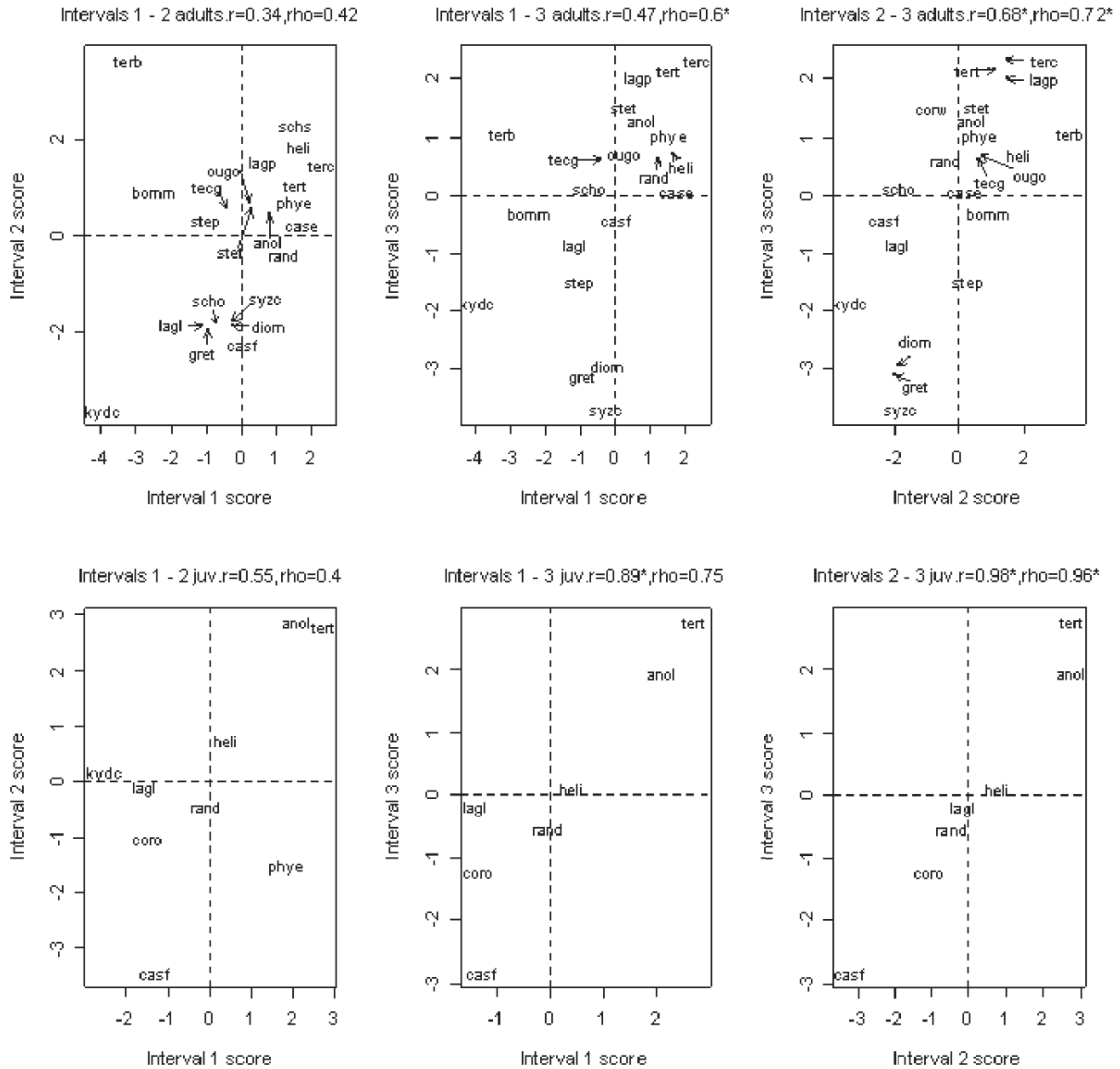


Figure 3. Correlation plots of PCA Axis 1 species scores across paired time intervals, using adults and juveniles of seven to 24 species. There was no clear separation of canopy and understorey trees. Species' scientific names associated with the four-letter codes are given in Appendix 2. juv., Juveniles; r, Pearson correlation coefficient; rho, Spearman rank correlation coefficient. Significant correlation coefficients ($P<0.05$) are indicated by “*”.

components accounted for 89% to 96% of variation, with the first axis explaining 69% to 90% of variation and the second axis explaining 6% to 21% of variation.

A few species appeared to form smaller groupings independent of other species, such as *T. crenulata* and *A. latifolia* (both canopy species) juveniles, which occurred close together in PCA biplots on account of their significantly

lower values for average, high and relative growth rates (one-way ANOVA, $P<0.05$ with Bonferroni correction for number of growth parameters tested, inconsistent across three intervals; non-significant with Wilcoxon signed ranks test). Among adults, a group of nine canopy species, *T. bellirica*, *Bombax ceiba*, *S. oleosa*, *G. tiliaefolia*, *S. colais*, *T. grandis*, *L. microcarpa*, *Diospyros montana* and *S. cumini* generally

had relatively large values for average, high and low growth rates (one-way ANOVA and Wilcoxon signed ranks test, $P < 0.05$ with Bonferroni correction for number of growth parameters tested). Interestingly, the understory species *K. calycina* and *C. fistula* also had large values for average, high and low growth rates, and strengthened the significant differences obtained when added to the canopy species group above. *K. calycina* and *C. fistula* adults occurred in proximity of each other during all three intervals due to their generally high relative growth rates, as also in the case of *H. isora* (one-way ANOVA and Wilcoxon signed ranks test, $P < 0.05$ with Bonferroni correction for number of growth parameters tested, inconsistent across three intervals). Cluster analyses using the four growth-related parameters (non-standardized or standardized) or PCA scores together generally placed canopy species in the same clusters as understory species, showing that there was no overall difference between the growth rates of understory and canopy species (shrubs were represented by only one species, *H. isora*). The only species that consistently clustered together when using standardized growth parameters or PCA scores were *T. crenulata* and *A. latifolia* juveniles.

The addition of lifetime growth trajectory data also failed to produce clear growth form-based groupings. There were no significant differences between canopy and understory species (inclusive or exclusive of *H. isora*) when using broad growth rate cutoffs, but with conservative growth cutoffs there were significant differences of second axis species scores between the two growth form categories (one-way ANOVA and Wilcoxon signed ranks tests, $P < 0.05$). The first two principal components explained 80% of variation. The first axis (explaining 47% of variation) was significantly negatively correlated with average, high and low growth rates and significantly positively correlated with the average number of years to attain maximum diameter, however, when using conservative growth rate cutoffs the average number of years to attain maximum diameter was not correlated with the first axis. The second axis was significantly negatively correlated with maximum dbh (Pearson and Spearman correlations, $P < 0.05$ with Bonferroni correction for number parameters tested) when using wider cutoffs, and also with mean number and minimum number of years to maximum diameter, as well as correlated in the opposite direction with relative growth rates when using conservative growth cutoffs. Cluster analysis using the seven standardized parameters or all PCA scores together revealed a group of five canopy species, *L. microcarpa*, *Diospyros montana*, *G. tiliifolia*, *S. cumini* and *S. colais*, that generally occurred together. Another generally consistent cluster was a mixed group of four canopy species, *A. latifolia*, *Lagerstroemia parviflora*, *Radermachera xylocarpa* and *Desmodium oojeinense*, along with two understory species, *P. emblica* and *C. spinosa*.

3.5 Relative importance of individual and interactive effects on growth

In unbalanced ANOVA models, all independent terms and two-way interaction terms were significant ($P < 0.05$), whereas three-way interactions were generally not significant when less than five size classes were used. In balanced models, among the individual factor effects species identity always had the highest proportions of iterations with significant effects on growth rates ($\geq 99\%$), while growth form usually showed the lowest proportion of significant iterations (generally $< 50\%$, table 3). Time interval often was significant in $\geq 90\%$ of iterations, and generally showed higher proportions than dbh. The use of conservative growth cutoffs generally reduced proportions of significant iterations for the time intervals factor and slightly increased the proportions for growth forms and dbh classes. Despite this, time intervals were significant more often than dbh and growth form.

In balanced models the interaction terms generally were significant less often than independent factors. Two-way interactions usually were significant in $< 30\%$ of iterations, while three-way interactions between factors were significant in $< 10\%$ of iterations. Relatively common significant interactions occurred between species and time intervals, between growth form and dbh size classes, and between time intervals and large numbers of size classes (table 3).

These results suggest that among the factors tested species identity was most closely related to growth variations, and the next most important factor was time interval. Dbh size class was significant slightly less often, while growth form was least often significantly associated with growth variations.

3.6 Growth rate variations and survival

For the majority of species and size classes tested (totaling 50 groups) across four years of mortalities, relative growth during the first two intervals was not related to survivorship in the third interval. Only *L. microcarpa* sapling (100–200 mm dbh) survivors of 1998 and 2000 had significantly higher relative growth than non-survivors ($P < 0.05$, with Bonferroni correction for species-size groups per year), when considering mortalities due to natural agents other than fire and elephants. However, *K. calycina* sapling survivors of elephant-caused mortality in the same size class in 1998 and in the 50–100 mm dbh size class in 1997 had significantly lower relative growth than non-survivors.

Almost all of the 23 species-size groups showed no significant relationship between survival in the third interval and the difference in relative growth rates of the first two intervals. Only medium-sized saplings (100–200 mm dbh)

Table 3. Proportions per 1000 iterations, of significant results (at $P < 0.05$) per explanatory factor or interaction term in balanced factorial 2- and 3-way ANOVA models, using individual growth rates as the dependent factor.

Model	sp	grf	int	dbh	sp*int	grf*int	sp*dbh	grf*dbh	int*dbh	sp*int*dbh	grf*int*dbh
2-way ANOVA											
13 sp, 3 int, $N=30$	1.00		1.00		0.89						
16 sp, 3 int, $N=20$	1.00		1.00		0.70						
3 grf, 3 int, $N=30$		0.67	0.78			0.06					
2 grf ² , 3 int, $N=30$		0.31	0.71			0.06					
3 grf, 3 int, $N=20$		0.47	0.62			0.06					
5sp, 5 dbh, $N=20$	1.00			0.82			0.26				
8 sp, 3 dbh, $N=20$	1.00			0.52			0.27				
2 grf, 5 dbh, $N=30$		0.08		0.51				0.41			
2 grf, 3 dbh, $N=30$		0.08		0.15				0.44			
2 grf, 2 dbh, $N=30$		0.22		0.42				0.27			
3 int, 7 dbh, $N=30$			1.00	0.80					0.61		
3 int, 5 dbh, $N=30$			0.97	0.65					0.20		
3 int, 3 dbh, $N=30$			0.90	0.16					0.16		
3-way ANOVA, $N=5$											
3 sps, 3 int, 5 dbh	1.00		0.88	0.59	0.09		0.27		0.10	0.08	
6 sps, 3 int, 3 dbh	1.00		0.96	0.48	0.36		0.25		0.16	0.05	
7 sps, 3 int, 2 dbh	0.99		0.42	0.13	0.10		0.37		0.07	0.08	
2 grf, 3 int, 5 dbh		0.07	0.51	0.27		0.07		0.24	0.07		0.05
2 grf, 3 int, 3 dbh		0.07	0.36	0.10		0.05		0.24	0.07		0.03
2 grf, 3 int, 2 dbh		0.16	0.15	0.22		0.05		0.17	0.05		0.05

[#]shrubs excluded

Factors used in the models are as follows: sp, species identity; grf, growth form identity; int, time intervals; dbh, diameter size categories. First and second order interaction terms per model are indicated with “*”. N , Sample size per group.

of *L. microcarpa* showed a significant negative relationship between the odds of survival in 1998 and relative growth rate difference of the preceding intervals ($P < 0.05$, with Bonferroni correction for species-size groups per year).

4. Discussion

4.1 Growth variations in relation to external environmental factors

Large variations in growth rates reflect the dynamic nature of species' growth during the period of the study, and indicate plasticity in growth responses of Mudumalai dry forest trees to their environment. Community and species growth rates appear to show high sensitivity to large-scale environmental variations across time, with a pronounced effect during the second interval (1992–1996). The widespread nature of relatively reduced growth in the second interval across the plot community indicates that one or more common environmental factors strongly influenced diameter growth rates during this period.

Extreme shrinkage in large trees was excluded from analyses by conservative growth cutoffs; however, previous studies with dendrometers have shown that large trees, especially those with few neighbours, may experience greater seasonal drought stress and consequently shrink more than smaller trees (Pelissier and Pascal 2000; Baker et al 2002). Also, for some large trees in this forest with fire-adapted thick and fissured bark, measurement error may be up to 5 mm over the four-year interval. Hence, a lower growth limit of -2 mm.yr^{-1} may not be appropriate for the Mudumalai dry forest. Interactions between time intervals and species or size classes suggests variations in the sensitivity of different species and size classes to different levels of environmental stress, which may promote species coexistence or reveal specific adaptations. Further study of these interactions is required.

Growth rates of most small and medium-sized stems were significantly positively skewed, and kurtotic suggesting that most trees in small and medium-size classes had highly similar growth rates, perhaps due to suppression by neighbours. Harper (1977) described such plant populations as being largely composed of “suppressed weaklings”,

implying that only a few individuals exhibited much greater than average growth while most individuals tended to cluster around low growth values, especially under density stress. Similar effects were found in a Costa Rican rain forest (Clark and Clark 1992), and in Sarawak, Malaysia (Primack *et al* 1985). Interestingly, in 1992–1996 skewness and kurtosis values were reduced, suggesting less competitive interactions under unfavourable growth conditions (although this effect was not obvious with conservative cutoffs).

Lower than average rainfall during the second time interval was associated with significantly lower growth in several size classes of common species in the plot. Although the growth-rainfall relationship was not predictable when comparing the first with the third interval, this is not surprising as the magnitude of change in growth across these two intervals was less than that between the second interval and either of these intervals and, in addition, the rainfall ranges of the first and third intervals overlapped more with each other than with that of the second interval. Confounding individual variations (for e.g. initial size of individuals) or environmental variations (such as elevated temperatures or differences in fire occurrences) also may have been greater between the first and third intervals due to the longer time gap than when either of these intervals was paired with the second.

The large rainfall reduction during the second interval is likely to have had the strongest influence on growth rates. Other environmental factors such as temperature, insolation, humidity and fires also may have influenced growth during the first and third intervals, when the rainfall difference was low. For instance, three ground fires occurred in the plot during the first interval (during early 1989, 1991 and 1992) and two fires occurred in the second interval (early 1994 and 1996), while none occurred in the third interval. Fires may influence growth via damage to tissue, reduction of competition (for light and resources) by causing mortalities, destruction of pests at or near ground-level and changes of soil fertility by ash deposition. In addition, the interactions between rainfall and other environmental variables such as temperature, humidity, sunlight, fire, topography, soils and neighbour identity or density, and their combined influences on tree growth require further study. A separate analysis carried out by us (C D Nath, H S Suresh, H S Dattaraja, N V Joshi and R Sukumar, manuscript in review) of the influence of spatial environmental variation have indicated that topographic factors and neighbouring trees also influence growth rates in a few common species; however, this effect appears limited in comparison to that of temporal environmental variations. Thus, we believe that the dominating environmental influences in the Mudumalai dry forest are likely to be rainfall and fire, and our results indicate that deficit rainfall may limit growth in most species of the Mudumalai dry forest.

The association of low rainfall with high growth in small stems of the understory species *C. fistula* during the second interval may be due to widespread mortalities, mainly due to fire and elephants (Sukumar *et al* 2005), that occurred in the first and second intervals, reducing the population by 33% and 40% in the second and third intervals, respectively. This suggests that while rainfall may limit growth of most trees in this dry deciduous forest, light availability also may limit growth for some understory species, especially in the juvenile classes.

4.2 Intrinsic factors affecting growth

In a few common species of Mudumalai growth was related to stem size; however, the relationships were generally weak. This is in contrast to many tropical moist forest studies that found strong positive relationships between tree diameter and growth (Swaine *et al* 1987; Condit *et al* 1993b; King *et al* 2006). The relationship between stem diameter and growth usually has been associated with crown illumination (Clark and Clark 1999; Turner 2001; King *et al* 2005, 2006). However, in Mudumalai the generally weak, and sometimes negative, diameter-growth relationship indicates that factors other than stem size (and therefore crown position or leaf-area/biomass ratios) may have equal or more important influences on growth.

Low growth was generally observed among medium sized saplings (approximately 50–300 mm dbh) that may be due to increased competition. We infer increased competition among stems of these size classes from their generally high frequencies in the plot (table 1). In particular, 100–200 mm stems constituted the modal frequency class with highest skewness values in all three intervals, lowest average growth rates in the first and third intervals, and highest kurtosis in the third interval (table 1), suggesting that competition affects growth most strongly in these saplings. The largest size classes in some common species appeared most sensitive to environmental stresses in the second interval, supporting earlier findings in other seasonal forests (Pelissier and Pascal 2000; Baker *et al* 2002).

Species-specific effects on growth were generally stronger than size-specific effects in the Mudumalai dry forest. Several common species had generally high or low growth, although most species' growth rates fluctuated across time intervals due to temporal environmental variation, and also possibly due to developmental plasticity. The consistent differentiation between species growth rates may be important for maintaining diversity in this forest and interactions with time or size classes suggests that certain environmental conditions or size classes may favour greater differentiation between species' growth rates. This requires further investigation.

Canopy and understory trees did not differentiate into separate groups or along a continuum of growth rates. A large proportion of canopy and understory species occurred together showing no clear canopy-understory growth dichotomy, suggesting that there is flexibility of growth strategies for canopy and understory trees in different size classes and time intervals. However, a few small groups of species may represent strategies similar to those described in rainforests. For example, juveniles of the canopy species *T. crenulata* and *A. latifolia* may represent a strategy similar to that of slow-growing shade-tolerant species in wetter forests (Lieberman *et al* 1985; Nascimento *et al* 2005), although the same strategy was not evident in the adults. At the other growth extreme, *C. fistula*, *K. calycina* and *H. isora* adults suggested an “understory species” growth strategy of high relative growth rates. Also, a “canopy species” growth strategy might be generally represented by some or all of the canopy species *L. microcarpa*, *D. montana*, *G. tiliaefolia*, *S. cumini*, *S. colais*, *T. bellirica*, *B. ceiba*, *S. oleosa* and *T. grandis*. However, lack of consistency of these groupings across time or size classes, and the general similarity in many canopy and understory species’ growth parameters suggest that variable climatic regimes and other disturbances might limit growth guild specialization in the Mudumalai dry forest. Further investigations are required that include recruitment, mortality and other demographic parameters, in order to see if the growth-based groupings detected here constitute demographic guilds.

Perhaps the most important limiting resource gradient for growth in tropical moist and aseasonal forests is light availability, along which species may specialize or differentiate into growth or demographic guilds (Turner 2001; King *et al* 2005, 2006), whereas in the relatively open-canopied dry tropical forests trees may not experience similarly high levels of light limitation and, thus, may not show the “gap phase dynamics” commonly described from tropical moist forests (Swaine *et al* 1990; Sukumar *et al* 1992). However, an equally or more important resource gradient in the dry forests may be soil water availability, especially during seasonal droughts, and species may specialize or differentiate into guilds based on strategies to deal with seasonal drought stress (Baker *et al* 2002, 2003b). Hence, future attempts to separate dry tropical forest species into growth guilds might benefit from additional information on phenology, seasonal storage organs (including underground storage) and root growth strategies (Meinzer *et al* 1999; Enquist and Leffler 2001; Baker *et al* 2002, 2003a), as well as factors associated with fire tolerance, such as root and stem coppicing, wood density and bark thickness (Gignoux *et al* 1997; Sukumar *et al* 2005).

4.3 Relationship between growth variations and survival

Relative growth variations during the first two intervals generally did not affect mortality during subsequent years,

suggesting that Mudumalai dry forest trees are tolerant of a broad range of growth variations, including stem shrinkage, that may be caused by climatic variations. Unpredictable environments can select for traits that show short-term physiological or functional plasticity during the lifetime of an organism (Schlichting 1986; Sultan 2000), and for plants functional plasticity is important due to their lack of mobility (Bradshaw 1972; Schlichting 1986; Huey *et al* 2002). Previous studies have demonstrated that root growth, branch growth and biomass allocation can show highly plastic responses to stress, spatial heterogeneity and temporal variability of resources in the environment (Nicotra *et al* 1997; Sultan *et al* 1998; Vretare *et al* 2001). Our results suggest that temporal variation of stem diameters in response to environmental variations such as seasonal drought, as well as its tolerance, can be considered as functionally plastic traits of tropical dry forest species. This may be mediated by seasonal expansion or shrinkage of elastic storage and transport tissues in the stem (Sheil 1995; Baker *et al* 2002) that may facilitate rapid mobilization of water and nutrients between above- and below-ground organs of the plant

Less commonly, in 100–200 mm dbh saplings of *L. microcarpa* increased densities may make this size class more vulnerable to unfavourable growth variations so that faster and less variable relative growth rates may be required to survive. Paradoxically, faster growth in medium saplings of *K. calycina* was associated with higher mortality due to elephants. Being one of the fastest growing in the sapling classes, *K. calycina* saplings may have fewer anti-herbivore defences, making them more attractive to elephants.

4.4 Comparison of Mudumalai seasonally dry forest with other tropical forests

Previously it has been suggested that tropical dry forests are likely to have lower annual growth rates and net primary productivity than moist forests due to the shorter growing period of the former (Murphy and Lugo 1986). However, the range of growth rates reported for Mudumalai dry forest species appears broadly comparable to those reported for other dry and moist tropical forests around the world. In addition, a comparison of growth rates across four large and two small tropical forest plots around the world (table 4), all of which used standardized protocols for data collection and analysis (Losos and Leigh 2004), revealed that Mudumalai trees clearly had the fastest average growth rates in the smallest size class. It is possible that trees in wetter forests are limited by other factors such as low light or poor soils (Baker *et al* 2003a, b), resulting in realized annual growth rates that are similar to those of the deciduous water-stressed trees of Mudumalai. On the other hand, Mudumalai dry forest trees experience a short growing interval coupled with severe environmental disturbances in the form of

Table 4. Comparison of Mudumalai tree growth rates in three different dbh size classes, with those of other plots in the Centre for Tropical Forest Science Forest Dynamics Plots (CTFS FDP) network.

Plot location, Date, Size	Rf (mm)	Dry Mo.	Temp (°C)	Vegetation type	Interval	Mean growth (mm.yr ⁻¹)		
						Dbh size class (cm)		
						1–9.9	10–29.9	≥30
Nanjenshan, Taiwan 1989, 3 ha.	3582	0	20.3, 26.8	Evergreen rainforest (montane)	1991–97	1.14	1.62	2.74
Lambir, Malaysia 1991, 52 ha.	2725	0	22.9, 30.3	Mature lowland mixed dipterocarp, evergreen	1992–97	0.52	1.63	2.7
BCI, Panama 1980, 50 ha.	2551	5–6	23.2, 31.1	Semideciduous lowland moist forest	1982–85 1985–90 1990–95	1.02 0.82 0.58	3.26 2.32 2.14	6.47 6.07 3.88
Bukit Timah, Singapore 1993, 2 ha.	2473	0	23.1, 30.7	Coastal hill forest evergreen/ everwet	1993–95 1995–2003	0.94 0.5	2.8 2.35	4.19 3.79
Pasoh, Malaysia 1986, 50 ha.	1571	1	22.7, 33.2	Lowland mixed dipterocarp	1986–90 1990–95 1995–2000	1.36 0.63 0.42	2.33 2.13 1.38	3.37 3.79 2.45
Huai Kha Khaeng, Thailand 1992, 50 ha.	1476	6	17.7, 30.4	Seasonal dry evergreen	1993–99	1.84	2.5	3.13
Mudumalai, India, 1988, 50 ha	1200	5–6	17.3, 28.2	Dry (and partly moist) deciduous	1988–92 1992–96 1996–2000	3.69 2.9 3.29	2.77 1.67 2.2	3.74 1.82 3.22

Plots are arranged in order of decreasing mean annual rainfall. Date, Year of initiation; Size, plot size in hectares; Rf., Mean annual rainfall; Dry Mo., number of dry months (<100 mm rainfall) per year; Temp. (°C), Mean daily minimum and maximum temperature, in degrees Celsius. (All data from Losos and Leigh 2004).

unpredictable and frequent ground fires, and damage by large mammalian herbivores. Also, on account of frequent fires in Mudumalai a large proportion of recruits in the plot (87% to 99.8% annually) were root and stem sprouts, which may rely more on underground storage organs than on light for their relatively fast growth (Sukumar *et al* 2005). These factors together may have resulted in the extremely fast juvenile growth rates observed indicating that high environmental variability promotes growth plasticity in this forest.

Another difference between Mudumalai growth rates and those of the other plots is that all the other plots showed average growth rates increasing with size class, whereas Mudumalai had highest growth rates in the smallest size class in two out of three time intervals (table 4). Also, the coefficients of variation (CV) of growth rates across size classes per measurement interval was generally lowest for Mudumalai, which reflected the lack of relationship between size and growth rates, compared to the strong positive relationship evident in all the other (generally wetter) sites. Finally, growth rates across multiple census intervals for the smallest stems in Mudumalai generally had the lowest CV and the largest stems had the highest CV, whereas in the other three plots with multiple censuses growth rates of the smallest stems had the highest CV while the largest stems

had relatively low CV. This supports our earlier conclusion that environmental factors in Mudumalai may have selected for species with invariably fast growth in small stems.

The substantial variation in growth rates across different time intervals highlights the need for long term monitoring of tropical forests (Hubbell and Foster 1992; Clark and Clark 1999; Losos and Leigh 2004). Our current results suggest that in order to understand and predict vegetation dynamics in the dry tropics, local monitoring of short and long term climatic variations may be of equal importance.

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Appendix 1

Details of three different methods used to fill gaps in the daily rainfall data of Kargudi weather station, located three km south of the plot, using semi-monthly data available from Gamehut weather station, located four km west of the plot. Gamehut data were first converted to daily values and the missing Kargudi data were then estimated with the help of predictive equations between Kargudi (the dependent variable, y , in all equations below) and Gamehut daily values (the independent variable, x , in all equations below). Numbers given below, per season or month, represent parameter values for the predictive linear and non-linear equations used.

Method 1: 'Annual' method used a common linear equation, $y = a + (b*x)$, to fill all gaps in Kargudi data between 1988 and 2000.

Intercept (a) = 1.09, slope (b) = 0.978.

Method 2: 'Seasonal' method used separate linear equations, $y = a + (b*x)$, per season:

Cool dry season (January–March): 1.333, 1.948.

Hot dry season (April–May): 6.491, 0.973.

Monsoon1 season (June–September): 5.542, 0.974.

Monsoon2 season (October–December): -7.431, 1.080.

Method 3: 'Monthly' method used a different linear or non-linear equation per month (months 1–12 are in order from January to December), as follows:

*Months 1 to 5: Linear regression, $y = a + (b*x)$.*

Month 1: 0.715, -0.409.

Month 2: 0.204, 0.643.

Month 3: 1.463, 3.088.

Month 4: 4.273, 1.138.

Month 5: 1.853, 0.939.

*Months 6, 7, 11 and 12: Quadratic regression, $y = a + (b*x) + (c*x*x)$.*

Month 6: 18.734, 0.526, 0.003.

Month 7: 6.288, 0.866, 0.001.

Month 11: 0.061, 0.768, 0.002.

Month 12: 0.360, 0.277, 0.013.

Month 8: Exponential association, $y = a(1 - exp(-b*x))$*

Month 8: 206.442, 0.009.

*Months 9 and 10: Logistic equation, $y = a/(1 + (b*exp(-c*x)))$.*

Month 9: 106.429, 12.752, 0.051.

Month 10: 327.217, 42.485, 0.024.

The top ten best-fitting curves for each month were obtained using CurveExpert (trial ver. 1.34) and final curve selection was based on the variance explained, number of parameters and curve shape.

Appendix 2.

Scientific names of tree species in the Mudumalai 50 ha plot corresponding to the codes used in tables and figures, along with growth form and family classifications. Nomenclature follows Gamble (1935), as updated by Mabberley (2005).

Code	Scientific name	Family	Code	Scientific name	Family
<u>CANOPY SPECIES</u>			<u>UNDERSTORY SPECIES</u>		
albo	<i>Albizia odoratissima</i>	Leguminosae	baur	<i>Bauhinia racemosa</i>	Leguminosae
anol	<i>Anogeissus latifolia</i>	Combretaceae	butm	<i>Butea monosperma</i>	Leguminosae
artg	<i>Artocarpus gomezianus</i>	Moraceae	cand	<i>Canthium dicocum</i>	Rubiaceae
baum	<i>Bauhinia malabarica</i>	Leguminosae	cara	<i>Careya arborea</i>	Lecythidaceae
bisj	<i>Bischofia javanica</i>	Euphorbiaceae	casf	<i>Cassia fistula</i>	Leguminosae
bomm	<i>Bombax ceiba</i>	Bombacaceae	corw	<i>Cordia wallichii</i>	Boraginaceae
brir	<i>Bridelia retusa</i>	Euphorbiaceae	daln	<i>Dalbergia lanceolaria</i>	Leguminosae
case	<i>Casearia esculenta</i>	Flacourtiaceae	eriq	<i>Eriolaena quinquelocularis</i>	Sterculiaceae
chut	<i>Chukrasia tabularis</i>	Meliaceae	flai	<i>Flacourtia indica</i>	Flacourtiaceae
coro	<i>Cordia obliqua</i>	Boraginaceae	kydc	<i>Kydia calycina</i>	Malvaceae
dall	<i>Dalbergia latifolia</i>	Leguminosae	phye	<i>Phyllanthus emblica</i>	Euphorbiaceae
diom	<i>Diospyros montana</i>	Ebenaceae	rand	<i>Catunaregam spinosa</i>	Rubiaceae
elag	<i>Cassine glauca</i>	Celastraceae	vita	<i>Vitex altissima</i>	Labiatae

eryi	<i>Erythrina variegata</i>	Leguminosae	writ	<i>Wrightia tinctoria</i>	Apocynaceae
garp	<i>Garuga pinnata</i>	Burseraceae	zizr	<i>Ziziphus rugosa</i>	Rhamnaceae
gmea	<i>Gmelina arborea</i>	Labiatae	zizx	<i>Ziziphus xylopyrus</i>	Rhamnaceae
gret	<i>Grewia tiliaefolia</i>	Tiliaceae			
hymo	<i>Hymenodictyon orixense</i>	Rubiaceae			
lagl	<i>Lagerstroemia microcarpa</i>	Lythraceae			
lagp	<i>Lagerstroemia parviflora</i>	Lythraceae			
lanc	<i>Lannea coromandelica</i>	Anacardiaceae	allc	<i>Allophylus cobbe</i>	Sapindaceae
madn	<i>Madhuca nilifolia</i>	Sapotaceae	antd	<i>Antidesma diandrum</i>	Euphorbiaceae
mani	<i>Mangifera indica</i>	Anacardiaceae	greh	<i>Grewia hirsuta</i>	Tiliaceae
mitp	<i>Mitragyna parvifolia</i>	Rubiaceae	heli	<i>Helicteres isora</i>	Sterculiaceae
oled	<i>Olea dioica</i>	Oleaceae	indc	<i>Indigofera cassioides</i>	Leguminosae
ougo	<i>Desmodium oojeinense</i>	Leguminosae	malp	<i>Mallotus philippensis</i>	Euphorbiaceae
pret	<i>Premna tomentosa</i>	Labiatae			
ptem	<i>Pterocarpus marsupium</i>	Leguminosae			
scho	<i>Schleichera oleosa</i>	Sapindaceae			
schs	<i>Schrebera swietenoides</i>	Oleaceae			
sema	<i>Semecarpus anacardium</i>	Anacardiaceae			
shor	<i>Shorea roxburghii</i>	Dipterocarpaceae			
step	<i>Stereospermum colais</i>	Bignoniaceae			
stet	<i>Radermachera xylocarpa</i>	Bignoniaceae			
syzc	<i>Syzygium cumini</i>	Myrtaceae			
tecg	<i>Tectona grandis</i>	Labiatae			
terb	<i>Terminalia bellirica</i>	Combretaceae			
terc	<i>Terminalia chebula</i>	Combretaceae			
tert	<i>Terminalia crenulata</i>	Combretaceae			

SHRUB SPECIES

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