

# Biotic Interactions in the Tropics

## Their Role in the Maintenance of Species Diversity

Edited by

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## CHAPTER TWENTY ONE

# The dynamics of a tropical dry forest in India: climate, fire, elephants and the evolution of life-history strategies

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### Introduction

Tropical dry forests constitute over 40% of all tropical forests (Murphy & Lugo 1986), yet their dynamics have been poorly studied relative to tropical moist forests (Bullock *et al.* 1995). Major ecological factors influencing the dynamics of tropical dry forests include high variability in climate, herbivory by wild mammals and domestic livestock (Skarpe 1991; Sukumar *et al.* 1998), natural and human-induced fires (Swain 1992; Goldammer 1993) and human extraction of a variety of products (Chopra 1993; Narendran *et al.* 2001). There has been much thinking on the issue of stability of tropical forests; some of this follows from or is related to the broader issue of the stability–diversity debate (e.g. Connell 1978; Pimm 1984; Lawton 1994; Johnson *et al.* 1996) or that of the turnover rate of tropical forests (Philips *et al.* 1994; Sheil 1995). These have been discussed mostly in the context of tropical moist forests.

It is being increasingly recognized that environmental variability is a major influence in shaping the structure, functioning and evolution of communities. In particular, we can expect that environmental variability would influence the evolution of life-history traits of species that constitute a particular community (e.g. Murphy 1968; Gadgil & Bossert 1970; Stearns 1977, 1992; Boyce & Daley 1980). Interannual variation in climate (e.g. precipitation) is usually taken as the most important measure of environmental variability that shapes life-history traits in a species. At the same time, the role of disturbances (e.g. hurricanes, fire) in eliciting short-term ecological responses should also be considered. In principle, a recurring disturbance that operates over longer time scales could be a source of environmental variability; for instance, fires (both natural and anthropogenic) are known to have occurred in tropical regions during the Pleistocene and the Holocene (see review by Schule 1990) and would have introduced

ecological stress into systems already subject to climate-related stress such as drought. It could be expected that plant species associated with such communities would show life-history adaptations to these factors.

From this perspective we think it would be extremely useful to compare the structure, life-history traits and the dynamics of tropical forests along environmental and disturbance gradients; ideally this should span the entire range of 'forest types' from the seemingly simple woodland-savanna vegetation through dry forest and seasonal moist forest to the complex aseasonal rain forest. Are there predictable patterns of life-history traits such as the nature of sapling recruitment, growth rates of juvenile versus adult stems, mortality rates in relation to stem size, and reproductive structures across an environmental gradient? How are these traits eventually reflected in the structure of forests across the gradient?

We have been studying the structure and dynamics of a tropical dry forest in southern India since 1988 (Sukumar *et al.* 1992, 1998, 2004; John *et al.* 2002). This is part of an international network of large-scale (50-ha) plots coordinated by the Center for Tropical Forest Science (see Condit 1995) that provides an opportunity for comparisons across forests. One such comparison between two tropical moist forests, one in Panama (Hubbell & Foster 1983) and the other in Malaysia (Manokaran *et al.* 1992), was reported by Condit *et al.* (1999). In this chapter, we first describe the observed patterns in the structure and dynamics of the tropical dry-forest plot in southern India, and then go on to make some comparisons with the Panamanian and Malaysian plots from published information (Condit *et al.* 1999) to make possible inferences about the role of environmental variability and disturbance from fire in shaping life-history traits of tropical tree species. Rather than describe in detail the population structure and changes of individual species, we have chosen to characterize the dry-forest community in terms of overall species population, size distribution of stems, and the guild of canopy versus understorey species before making comparisons with the other forest sites. More details of forest structure and the short-term dynamics of individual species are either available (Sukumar *et al.* 1992, 1998; John *et al.* 2002) or will be presented elsewhere.

## Material and methods

### The study area

Our tropical dry-forest plot was set up during 1988–89 in the Mudumalai Wildlife Sanctuary of Tamilnadu State in southern India. Mudumalai is located to the east of the Nilgiri hills, which are part of the Western Ghats chain of mountains in peninsular India. The natural vegetation of Mudumalai varies along a rainfall gradient from tropical dry thorn forest in the east (c. 800 mm annual precipitation), through dry deciduous forest over much of the reserve to moist deciduous forest in the southwest (c. 1800 mm annual precipitation). Small patches of

semi-evergreen forest are also seen in the reserve, as are swampy grasslands within the tract of moist forests. The dry season extends for a period of about 5 months (December–April) during which little or no rain occurs.

The 50-ha permanent plot (11° 35' 41" to 11° 35' 57" N, 76° 31' 50" to 76° 32' 22" E) is centrally located at Mudumalai, within Compartment 17, close to the transition between the dry and moist deciduous forests (Sukumar *et al.* 1992, 2004). *Lagerstroemia microcarpa* is at present the most abundant tree in the plot, followed by *Terminalia crenulata*, *Anogeissus latifolia* and *Tectona grandis*. The main understorey trees are *Cassia fistula*, *Xeromphis spinosa* and *Kydia calycina* (the most abundant woody plant at the time the plot was set up), while the most common shrub is *Helicteres isora*. The reserve has sizeable populations of the larger mammals characteristic of peninsular India, including the Asian elephant (*Elephas maximus*), which makes a major impact on the vegetation. Densities of the larger herbivorous mammals are about 2 individuals km<sup>-2</sup> for elephant, 25 km<sup>-2</sup> for axis deer (*Axis axis*), 7 km<sup>-2</sup> for sambar (*Cervus unicolor*) and 6 km<sup>-2</sup> for gaur (*Bos gaurus*) (Varman & Sukumar 1995, and unpublished data for 1996–2000). The reserve is bordered by human settlements to the south and the east. In addition, several swampy grasslands in the western sector are under cultivation. To the north and the west the reserve is bordered by other protected areas. Direct human influences include some fuel-wood removal by villagers and grazing of livestock, particularly in the eastern part of the reserve; however, there is practically no direct human impact on the 50-ha plot. Human-induced ground fires are also common during the dry months of January–April. The 50-ha plot is generally free from direct human disturbances with the exception of fires that may spread here from other parts of the reserve. The forests of Mudumalai have a history of logging going back to at least the early part of the nineteenth century (Ranganathan 1939). Selective logging of Compartment 17, where the plot is located, was last carried out during 1968.

### Field methods

The basic field methods used in the study have been described in an earlier publication (Sukumar *et al.* 1992). These will be briefly recapitulated here. The plot was surveyed with a theodolite and grid into quadrats of 20 m × 20 m after making appropriate corrections for slope. All woody plants >1 cm diameter at breast height (dbh) were tagged with numbers during the period May 1988 to May 1989. The plants were identified, measured for dbh, tagged and mapped to the nearest 0.5 m. Each 20 m × 20 m quadrat was further divided into sub-quadrats of 10 m × 10 m with the aid of ropes before mapping stem locations.

As most of the stems shed their leaves during January–April, the censuses during subsequent years began in June by which time they had flushed leaf, enabling greater accuracy in identification of species. The annual censuses recorded mortality of stems and new recruits (stems growing to >1 cm dbh). In practice, a

stem was considered dead if the above-ground portion was burnt and no coppices had reached 1 cm dbh. However, a stem was considered as living if it had been merely broken below 1.3 m but was still alive. A recruit was considered as the appearance of a new stem >1 cm dbh; while these included previously tagged stems that might have burnt completely but coppiced subsequently and grown to 1 cm dbh, they excluded broken stems that had been recorded as alive in the previous census. For every recruit an attempt was made to determine whether it had originated from a seed (sexual reproduction) or through vegetative means (clonal propagation or coppicing from the root stock of a 'dead' stem).

At the end of the dry season the extent of burning, if any, was mapped at a 10 m × 10 m resolution. During the study period fires occurred during the dry seasons of 1989, 1991, 1992, 1994 and 1996. Every four years the stems were also measured for calculating growth rates. Stem sizes were measured again during 1992, 1996 and 2000.

### Analyses

Because the Mudumalai plot is censused annually, the recruitment rates and size-dependent mortality rates are expressed as arithmetic means of the yearly rates. The annual size-based mortality rates are accurate only for the years 1989, 1993 and 1997 for which all stems had been measured during the previous year (1988, 1992 and 1996, respectively, when complete censuses were carried out). During other years, a certain proportion of stems would have moved into a higher size class at the time of death because of growth. Growth rates of stems in various size classes are expressed as mean annual increments (in mm yr<sup>-1</sup>) computed from the 4-yr census intervals.

Using the observed rates of recruitment, growth and mortality in various size classes, we used a deterministic, matrix-projection model (Caswell 1989) to simulate the trends in population size and basal area of the four major canopy trees, *Lagerstroemia microcarpa*, *Tectona grandis*, *Anogeissus latifolia* and *Terminalia crenulata*, that constituted 44% of all individuals (woody species >1 cm dbh) and 67% of basal area in the plot during the 1988–89 census. Details of the model and the results are being published elsewhere but its basic features are described here.

For each of the four species, individuals were categorized into size classes for analysis of growth and mortality, and for population projections. For each of the approximately 4-yr intervals of stem measurement (1988–92, 1992–1996, 1996–2000) the annual growth rates were computed for individuals in each of the size classes. Up to 2% of outliers showing extremely fast growth or shrinkage were removed from the data in order to minimize possible errors in field recording of measurements. The mean size-class specific growth rates calculated across the various size classes were smoothed and best-fit functions used for incorporating growth into the model. Annual mortality rates were likewise calculated for



various size classes of a species and the rates smoothed before fitting suitable functions. Average mortality rates were calculated for the 12 years of the study as well as for years with fire (1989, 1991, 1992, 1994 and 1996) and without fire. Recruitment was incorporated as the number of stems of size 1–3 cm dbh (growth from <1 cm to >3 cm dbh was considered unlikely to occur within a year) of a species appearing each year on average for the period 1988–2000 as well as during years with fire and without fire. Because most of the recruits were vegetative sprouts, we did not relate these to the adult population size of the species.

Beginning with the population recorded in 1988, the model projected the number of individuals in each of the size classes surviving and moving into one of the higher size classes (through growth), remaining in the same size class or moving into a lower size class (through shrinkage of stem). For the projections we used a 0.5-cm dbh class interval for the faster-growing *L. microcarpa* and *T. grandis*, but a 0.25-cm class interval for the relatively slow-growing *A. latifolia* and *T. crenulata*. Apart from an 'average scenario' incorporating the mean growth, mortality and recruitment rates observed during 1988–2000, we also ran other scenarios including lower and higher fire frequencies; one of these was a 'worst case' scenario that used the lowest recruitment and stem growth rates and the highest mortality rates observed during the study period. Only the projected basal areas are reported here.

### Comparison with two moist-forest plots

We compare the Mudumalai dry forest plot with the moist-forest plots at Barro Colorado Island (BCI) and Pasoh Reserve, basing the comparison entirely on the published work of Condit *et al.* (1999) for the latter two plots. These three Forest Dynamics Plots represent a gradient of environmental variability. For our purposes we use interannual climatic variability as a simple measure of environmental variability. The rainfall data for the period 1990–2002 indicate that Mudumalai has the highest rainfall variability (annual mean = 1118 mm; coefficient of variation [CV] = 26.1%) and strong seasonality (dry season of five months; a dry month defined as one with <100 mm rainfall), BCI moderate variability (mean = 2642 mm; CV = 18.8%) and seasonality (four-month dry season), and Pasoh the lowest variability (mean = 1788 mm; CV = c. 15%) and relative lack of seasonality (no dry month). In addition, the Mudumalai forest is subject to dry-season fire, a stress factor absent at the other two sites.

## Results

### Changes in population size, species richness and size distributions

The total population (all stems >1.0 cm dbh) of individuals in the Mudumalai plot declined noticeably over the period 1988–1996 and then increased between 1996 and 2000. The first census (in 1988–89) of the plot recorded 25 554

individuals from 72 species (excluding the one species of bamboo – a 'tree grass'). The numbers fell steeply to 17 654 individuals from 70 species by 1992 and at a lower rate to 15 346 individuals (65 species) by the 1996 census. During this period the years 1993 and 1995 recorded small increases in population size over the previous years whereas all other annual censuses registered declines. After 1996 the population increased steadily to 18 177 individuals (75 species) by the year 2000. Of the original number of species recorded during 1988–89, two species have been lost, while three new species have appeared and persisted until the year 2000. Five species have been ephemeral during this period. Four species have disappeared during at least one of the yearly censuses but have later appeared. Correspondingly, the population sizes of most species also declined overall during the period 1988–1996 (62 of the 72 species recorded in 1988 declined by 1996), but many of them then increased during 1996–2000 (29 of the 65 species recorded in 1996 increased by 2000, while 25 species still declined).

Declines have been disproportionately higher in the smaller size classes for practically all species. Thus, the total change between 1988 and 1996 was –13.1% for stems >10 cm dbh as compared with –79.0% for stems 1–10 cm dbh. The increase in population during 1996–2000 is also characterized by a disproportionate increase in the smaller stems, as can be expected because of recruitment of seedlings and young saplings into >1 cm dbh size and their subsequent growth (147% increase in stems 1–10 cm dbh and –3.9% decline in stems >10 cm dbh).

Population change has varied considerably among the common canopy trees, understorey trees and shrubs (Table 21.1). *Kydia calycina* (understorey tree), the most abundant species in the plot during 1988 (5175 individuals), underwent a precipitous decline through to 1996 (247 individuals); its population size was 190 individuals in the year 2000. The shrub *Helicteres isora* also declined steeply from a population of 2569 individuals in 1988 to 307 individuals by 1996, but then increased to 548 individuals in 2000, mainly through a doubling during the last year. The decline of both these species could be largely attributed to herbivory by elephant, though fire also played a role in the death of smaller stems. *Lagerstroemia microcarpa* (canopy tree), the second most abundant species in 1988 (and at present the most abundant), maintained an almost identical population size in 2000 in spite of registering a decline of about 10% during the intermediate period. The canopy tree *Tectona grandis* declined by 16.7% between 1988 and 1996, but since then increased by 5.7% by 2000. Two other abundant canopy species, *Terminalia crenulata* (–8.5%) and *Anogeissus latifolia* (–5.8%) registered modest overall declines between 1988 and 2000. The population of *Cassia fistula* (understorey) in the plot showed the highest interannual fluctuations amongst the commoner species, registering an annual increase as high as 50% (1992–93) and decreases up to –37% (1995–96).

**Table 21.1** Population changes in 10 most abundant species (1988 census) during the period 1988–2000

Species (life form)	Population size during full census year			
	1988	1992	1996	2000
<i>Kydia calycina</i> (U)	5175	1096	247	172
<i>Lagerstroemia microcarpa</i> (C)	3982	3817	3567	3981
<i>Terminalia crenulata</i> (C)	2771	2678	2604	2536
<i>Helicteres isora</i> (S)	2569	808	307	548
<i>Anogeissus latifolia</i> (C)	2281	2232	2187	2149
<i>Tectona grandis</i> (C)	2139	1857	1782	1884
<i>Cassia fistula</i> (U)	1884	1092	1214	3200
<i>Xeromphis spinosa</i> (U)	770	725	589	519
<i>Emblica officinalis</i> (U)	577	500	456	422
<i>Grewia tiliifolia</i> (C)	540	459	396	375

C = canopy tree, U = understorey tree, S = shrub

### Recruitment rates and patterns

The overall rate of recruitment defined as appearance of stems >1.0 cm dbh during a census, averaged 4.4% over the 12-yr period of the study. Mean recruitment rates were significantly higher during years without dry-season fire (6.0%) than during years with dry-season fire (2.2%). In particular, the recruitment rate was highest during the census interval 1999–2000, when the plot registered a 12.6% rate of recruitment, twice as high as the next highest rate recorded (6.1% in each of the periods 1996–97 and 1997–98). During the three full census periods, the recruitment rates were lowest during 1988–92 and highest during 1996–2000. However, the average rate obscures the fact that only a few species showed strong recruitment, while at the other extreme several moderately abundant and abundant species did not show any recruitment over the 12-year period. In particular, the abundant understorey tree *Cassia fistula*, with a mean recruitment rate of 25% per annum, contributed over 50% of all recruits recorded during the study period.

Recruitment was almost exclusively (>99%) through vegetative means. Very often stems that had died above ground in previous years through fire coppiced from the root; likewise stems broken to <1.3 m in height also coppiced. In one sense, the disappearance of a young stem through burning does not necessarily imply death, but rather survival as a root or stem at ground level. An examination of seedlings showed that these too sprouted from roots or rhizomes. It is of course possible that a certain proportion of these may have originally sprouted from seeds (i.e. sexually)-but repeatedly burnt to ground level. Because of the need to avoid disturbance to the soil and young plants in the plot, it was not



possible to distinguish clonal propagation from vegetative coppicing; the former could be occurring in some species but has to be studied out of the plot.

### Growth rates and patterns

We examined growth rates for two full census intervals, 1988–92 and 1992–96, across stem sizes for all canopy trees and all understorey trees (plus the few shrubs in the plot). Among canopy tree species the annual growth increments were highest in the smallest stems (1–5 cm dbh) and in the large trees (>60 cm dbh) during the period 1988–92 (Fig. 21.1a). The smallest stems similarly increased in diameter at the highest rate during the subsequent period (1992–96) but growth of the large trees came to a virtual halt; in fact, the largest stems (over about 80 cm dbh) in the plot shrank slightly on average. Overall, the growth rates across all stem sizes of canopy species were also higher during the first census interval than the second interval. Among understorey species the smallest stems actually grew at higher rates during the second census interval, although a depression in growth could be seen among stems >5 cm dbh (Fig. 21.1b).

### Mortality rates and patterns

The average annual mortality rate of all individuals >1.0 cm dbh during 1988–2000 was 7.0% (range 1.9–13.1%). Mortality rates varied substantially across size classes with the average rates being progressively lower in the larger size classes (Fig. 21.2). Thus, the average mortality rate of 23.5% in the 1–5 cm size class decreases to about 4% in the 10–20 cm size class and thereafter to under 0.6% in stems >30 cm dbh. During 1990, however, there was little difference in mortality rates between the 1–5 cm and 5–10 cm size classes, and during 1993 the mortality rate was highest in the 5–10 cm dbh class. These were years without dry-season fires, which would have killed a high proportion of smaller stems. Therefore mortality rates were relatively high in medium-sized stems, largely because of elephant utilization of *Kydia calycina*. Interannual variability in mortality rates was generally higher in smaller individuals and decreased with size, except for the very large trees (demographic rates of very large trees are not reliable because of small sample sizes). In general, there was a declining trend in mortality rates of most size classes from the first full census interval (1988–92) to the subsequent two full census intervals (1992–96 and 1996–2000).

Causes of mortality were broadly classified as due to fire, elephant herbivory or other causes. For 'other' causes, it was possible to identify the agent in only a few cases, as in tree fall due to strong wind or a storm. Dry-season fires occurred in the plot during five (1989, 1991, 1992, 1994 and 1996) of the 12 years of the study reported here. Of these the fires were widespread (>80% area burnt) across the plot during the years 1991, 1992 and 1996. Fire-related mortality rates were obviously higher during these years. During the non-fire years a small proportion

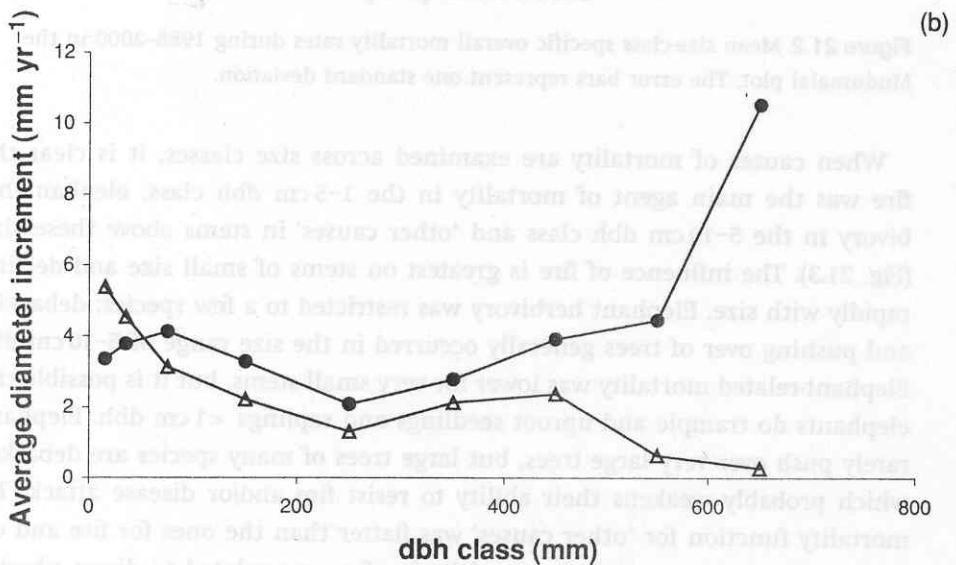
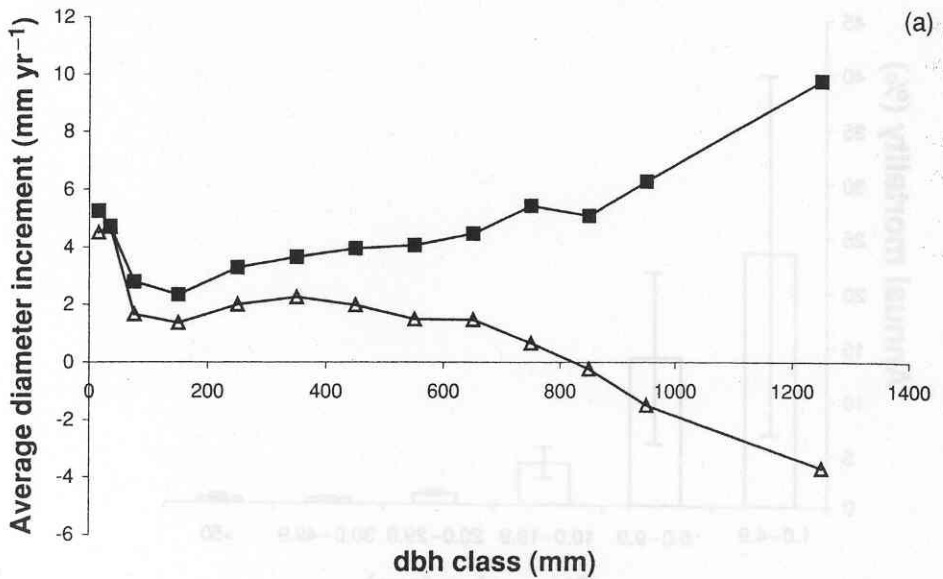


Figure 21.1 Growth rates (mean increment in stem diameter in mm yr<sup>-1</sup>) of (a) canopy species during the period 1988-92 (solid square) and 1992-96 (open triangle), and (b) understorey species during 1988-92 (solid circle) and 1992-96 (open triangle) in the Mudumalai Forest Dynamics Plot.

of deaths was attributed to weakening of stems from fire during the preceding year. Over the 12 years of the study, fire was the leading agent of mortality during four years, while elephant browsing was the leading cause in five years (of these the mortality rates due to fire and to elephants were identical during 1988-89). In later years, the mortality due to elephants declined because of sharp reductions in the population of their favoured food-plant species.

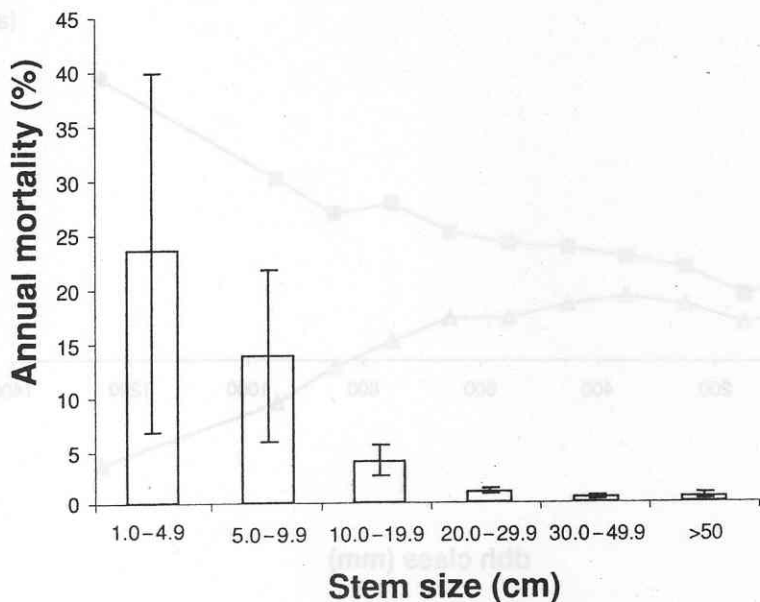


Figure 21.2 Mean size-class specific overall mortality rates during 1988–2000 in the Mudumalai plot. The error bars represent one standard deviation.

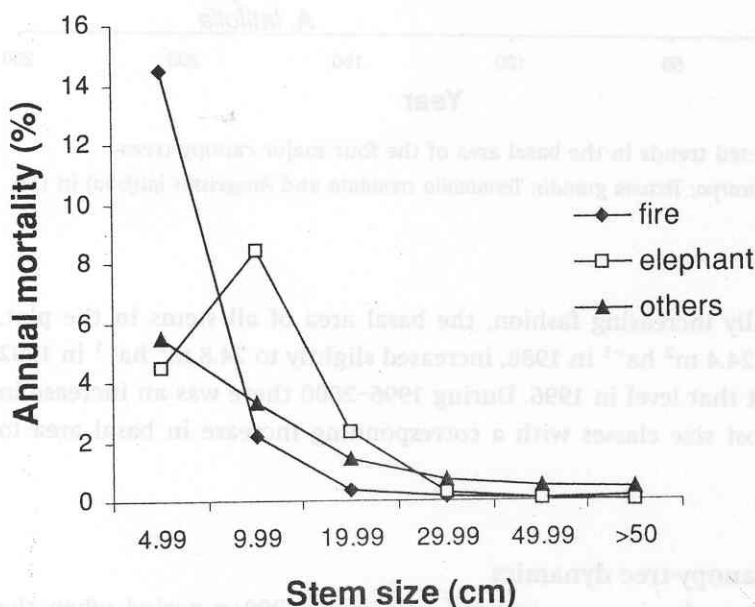
When causes of mortality are examined across size classes, it is clear that fire was the main agent of mortality in the 1–5 cm dbh class, elephant herbivory in the 5–10 cm dbh class and 'other causes' in stems above these sizes (Fig. 21.3). The influence of fire is greatest on stems of small size and declines rapidly with size. Elephant herbivory was restricted to a few species; debarking and pushing over of trees generally occurred in the size range of 5–10 cm dbh. Elephant-related mortality was lower for very small stems, but it is possible that elephants do trample and uproot seedlings and saplings <1 cm dbh. Elephants rarely push over very large trees, but large trees of many species are debarked, which probably weakens their ability to resist fire and/or disease attack. The mortality function for 'other causes' was flatter than the ones for fire and elephant. This category captures a multitude of causes related to direct physical damage by treefalls or windstorms, and attacks by termites, diseases and pests, which are more likely to attack stems weakened by physiological and ecological stress. Mortality rates due to these causes were lower than those due to fire and elephant for small- and medium-sized stems respectively, but they accounted for most of the mortality in large trees.

#### Changes in size-class distributions and basal area

When changes in basal area of the different species are considered, a very different picture emerges. Thirty-one of the 72 species recorded in the first census actually increased in basal area by 1996 even though most of them declined in

**Table 21.2** Number of individuals in various size classes during the full census years in the Mudumalai plot

Size class (cm)	Number of individuals			
	1988	1992	1996	2000
1.0–4.9	5039	1891	1247	4594
5.0–9.9	5478	1720	1017	991
10.0–19.9	6162	5065	4166	3549
20.0–29.9	3986	3868	3662	3528
30.0–49.9	3576	3701	3774	3895
>50	1313	1408	1487	1613
Total	25 554	17 653	15 353	18 170



**Figure 21.3** Mortality rate of stems of different sizes due to various causes during 1988–2000 in the Mudumalai plot.

absolute numbers (all stems > 1 cm dbh). During 1996–2000, 38 of the 65 species recorded in 1996 increased in basal area.

Even though the total number of stems declined in the plot during 1988–96, this decline was not uniform across size classes (Table 21.2). Stems over 30 cm dbh actually increased during this period. Thus, stems in the 30–50 cm size class registered a 4.5% increase and those over 50 cm a 12% increase during this 8-yr period. In the absence of fire during 1996–2000, saplings < 5 cm dbh also increased in total numbers. As the larger stems also contribute to basal area

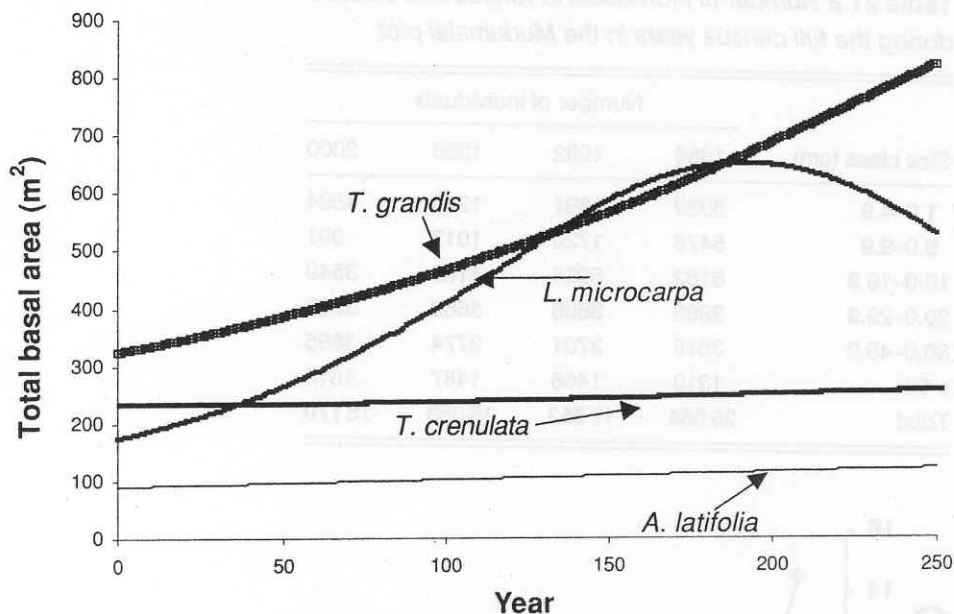


Figure 21.4 Projected trends in the basal area of the four major canopy trees (*Lagerstroemia microcarpa*; *Tectona grandis*; *Terminalia crenulata* and *Anogeissus latifolia*) in the Mudumalai plot.

in a geometrically increasing fashion, the basal area of all stems in the plot, which averaged  $24.4 \text{ m}^2 \text{ ha}^{-1}$  in 1988, increased slightly to  $24.8 \text{ m}^2 \text{ ha}^{-1}$  in 1992 and remained at that level in 1996. During 1996–2000 there was an increase in stems across most size classes with a corresponding increase in basal area to  $25.9 \text{ m}^2 \text{ ha}^{-1}$ .

### Projection of canopy-tree dynamics

All four canopy species increase in basal area over a 200-yr period when the mean rates of recruitment, growth and mortality during the period 1988–2000 are used in the model (Fig. 21.4). These demographic variables incorporate fire during five of the twelve years of observation. The increase in basal area is modest for the slow-growing species *Terminalia crenulata* and *Anogeissus latifolia* and much higher for the other two canopy trees. Even if one were to discount the steep increase in basal area of *Lagerstroemia microcarpa*, the total basal area of the four major canopy trees in the plot is still projected to increase overall during the next two centuries. The results are broadly similar even when fire frequencies are increased from the observed frequencies. Only under the worst-case scenario with sharply enhanced mortality and lowered recruitment and growth do the basal areas of three species (*Tectona grandis*, *T. crenulata* and *A. latifolia*) decline while that of *L. microcarpa* still continues to increase.



## Discussion

### Dynamics and life-history patterns of a tropical dry forest

The 50-ha forest plot at Mudumalai, typical of the tropical dry deciduous forests of the Western Ghats of southern India, shows considerable short-term instability in the face of interannual variation in climate, occurrence of fire and herbivory by large mammals such as elephants. The main features of structure and dynamics of this forest type can be summarized as follows:

- (a) The species richness of woody plants is very low compared with tropical moist forests and perhaps even lower than other tropical dry forests such as the dry dipterocarp forests of Thailand (Rundel & Boonpragob 1995). Indeed, our larger data set from Mudumalai itself indicates that the (alpha) plant diversity of the dry deciduous forest is lower than that of dry thorn forests which have even lower rainfall; this is the consequence of higher fuel loads in the dry deciduous forest resulting in more intense dry-season fires (unpublished data). However, the dry deciduous forest plot has shown a remarkable ability to maintain species numbers in spite of the dynamic nature of the forest.
- (b) Recruitment in the dry deciduous forest is almost entirely through resprouting from below-ground organs or from broken stems and not directly from germination of seeds. Rates of recruitment vary enormously amongst species, with only a few species showing strong recruitment during the decadal time scale of the study. At the other extreme, certain common canopy species showed virtually no recruitment during this period. Overall rates of recruitment were, however, comparable to other tropical forests, even though the absolute number of recruits was low.
- (c) The growth rates across stem size showed a distinct pattern of high growth during the young sapling stage followed by a decrease. In stems of canopy species >20 cm dbh there was considerable variation between two time periods (1988–92 and 1992–96) for which growth rates have been calculated; in the first census period these stems increased in growth rate with size whereas in the second census period they remained relatively steady or declined in growth. The understorey species showed relative constancy in growth rates with size, although the growth rate of larger stems was higher during the first census interval whereas that of the smaller stems was higher during the second.
- (d) Mortality rates are highly variable across stem sizes with very high rates being recorded in the smaller stems and a general decline with increase in stem size. Fire and elephant are the two most important agents of mortality, the former killing the smaller stems of a wide range of species and the latter destroying medium-sized stems of a few favoured forage species. Mortality rates of large trees (>30 cm dbh) were well below 1% per annum, one of the lowest rates recorded in tropical forests globally.

- (e) The Mudumalai forest shows high turnover and high instability in the sub-canopy strata of small understorey trees and shrubs but remarkable stability in the canopy layer. The results from the matrix-projection model indicate that the most common canopy trees would continue to survive and grow over the time scale of several decades or even a couple of centuries in the face of environmental stresses such as observed climate variability and frequent fire. We recognize that it is unlikely that basal area of the canopy trees would continue to increase in the projected manner over a period of two centuries; this would mean a doubling of the basal area of these four species during this period. There are obviously factors, not well understood at present, that could regulate the dynamics of such forests over time scales longer than the decadal time period of our observations. These could include deterministic factors such as density-dependent regulation (John *et al.* 2002) or stochastic factors such as severe climatic events (e.g. prolonged drought, which could reduce growth and increase mortality across stems of all sizes, or windstorms that could sharply increase mortality of the large trees). However, it is reasonable to assume on the basis of the existing observations and model inferences that the basal area and standing biomass of this forest type would be maintained or even increase in the coming decades.

Dry tropical forests subject to periodic disturbances from fire and other factors may have adapted through a regime of strong, episodic (vegetative) reproduction, high juvenile growth rates and very low adult mortality, enabling populations to persist for long periods of time. Such a system may exemplify the 'storage effect' and the 'lottery competitive system' (Chesson & Warner 1981; Warner & Chesson 1985). The frequency and intensity of ground fires are therefore key determinants of the dynamics of tropical dry deciduous forests such as those in south and Southeast Asia (Goldammer 1993; Stott 1986; Puyravaud *et al.* 1995).

### Comparison of the dynamics of a dry forest with two moist forests

We can compare the Mudumalai dry forest plot (high environmental variability and stress) with the plots at Barro Colorado Island (seasonal moist forest with moderate environmental variability) and Pasoh Reserve (aseasonal rain forest with low environmental variability).

- (a) The dry-forest plot at Mudumalai has far fewer species and individuals >1 cm dbh (72 species, 25 500 individuals in 1988–89) than the moist-forest plots at BCI (305 species, 235 000 individuals in 1982) and Pasoh (815 species, 335 000 individuals in 1987). In spite of this tremendous difference in species and population density the Mudumalai plot had a greater number of large trees (5042 individuals >30 cm dbh in 1996; only the main stem measured in multiple-stem individuals) than BCI (4113 individuals during 1995) and Pasoh (3738 individuals during 1995) (Table 21.3). The basal area

**Table 21.3** Size-class distribution of trees (only main stems of multiple-stem individuals) in the Mudumalai, BCI and Pasoh plots

Size (dbh cm)	Number of individuals		
	Mudumalai (1996)	BCI (1995)	Pasoh (1995)
1-4.9	1247	177 850	244 834
5-9.9	1017	29 751	44 805
10-19.9	4166	13 635	20 092
20-29.9	3662	3687	5047
30-39.9	2348	1777	1889
40-49.9	1426	941	808
50-99.9	1457	1232	985
100+	30	163	56

Data for BCI and Pasoh based on Condit *et al.* (1999).

of all woody stems  $>1$  cm dbh is lower at Mudumalai ( $25.8 \text{ m}^2 \text{ ha}^{-1}$ ), but the difference with BCI ( $31.8 \text{ m}^2 \text{ ha}^{-1}$ ) and Pasoh ( $30.3 \text{ m}^2 \text{ ha}^{-1}$ ) is much less than would be indicated by the differences in population size. When the basal area of only stems  $>10$  cm dbh is considered, there is much less difference between Mudumalai ( $24.6 \text{ m}^2 \text{ ha}^{-1}$ ) and BCI ( $27.8 \text{ m}^2 \text{ ha}^{-1}$ ) and practically no difference with Pasoh ( $24.4 \text{ m}^2 \text{ ha}^{-1}$ ). At this time we cannot convert the stem-size distribution or basal area to standing biomass because the regression functions used for calculating biomass may vary from one forest type to another (for instance, the trees at Pasoh have relatively greater ratios of height to stem diameter than BCI).

- (b) In terms of absolute number of recruits the Mudumalai plot had few recruits relative to BCI and Pasoh, but the rate of recruitment was higher than at either of the other sites (Table 21.4). Recruitment at Mudumalai was highly variable (range 1.2–12.6% annually). Pasoh had the lowest rate of recruitment (although the number of recruits during 1990 is an underestimate; Condit *et al.* 1999).
- (c) The growth rate of small saplings (1–2 cm dbh) of both canopy species and understorey species at Mudumalai is 5–10-fold greater than those observed at BCI and Pasoh (see Condit *et al.* 1999). Whereas saplings grew at only  $0.64 \text{ mm yr}^{-1}$  at BCI and at  $0.59 \text{ mm yr}^{-1}$  at Pasoh on average during all the census periods, those at Mudumalai grew at  $>3 \text{ mm yr}^{-1}$  and up to  $5.3 \text{ mm yr}^{-1}$  during the two census periods for which we calculated the rates. This difference between the dry and moist forest sites also seems to be true for larger saplings up to c. 5 cm dbh. However, stems greater than c. 5 cm dbh at BCI and Pasoh grew as fast as or faster than those at Mudumalai.

**Table 21.4** Comparison of mean recruitment rates (stems >1 cm dbh) at Mudumalai, BCI and Pasoh

Location	Interval	Recruitment rate ( $\pm$ SE)
Mudumalai	1988–1992	2.09 $\pm$ 0.51
	1992–1996	3.80 $\pm$ 0.78
	1996–2000	7.35 $\pm$ 2.06
BCI	1982–1985	4.43 $\pm$ 0.05
	1985–1990	3.34 $\pm$ 0.03
	1990–1995	2.09 $\pm$ 0.03
Pasoh	1987–1990	0.60 $\pm$ 0.02
	1990–1995	2.37 $\pm$ 0.02

Data of BCI and Pasoh based on Condit *et al.* (1999). The recruitment rate for Pasoh is an underestimate because recruits were undercounted during 1990.

**Table 21.5** Comparison of mortality rates of woody plants at Mudumalai, BCI and Pasoh

Location	Period	Stem-size class (cm)	Mortality rate (mean)
Mudumalai	1988–2000	>1 cm	6.98
		>10 cm	2.80
		>30 cm	0.58
BCI	1982–1995	>1 cm	2.64
		>10 cm	2.26
		>30 cm	*
Pasoh	1987–1995	>1 cm	1.46
		>10 cm	1.48
		>30 cm	*

\* Actual mortality rates could not be obtained, but as interpreted from Condit *et al.* (1999) the rates were considerably higher (>1%) than at Mudumalai.

- (d) There are striking differences between the dry- and the moist-forest sites in their mortality rates as a function of stem size (Table 21.5). Mortality rates of canopy trees at BCI and Pasoh decline slightly from 1 cm to 5 cm dbh and are relatively constant thereafter through to larger size classes, or rise marginally (see Condit *et al.* 1999). One exception was during a drought period at BCI (1982–85), when mortality rates rose sharply in larger trees. In the understorey trees at both sites, the mortality rates were relatively constant across size classes. In contrast, at Mudumalai there was a sharp

decline in mortality rates with stem size in all species. While the mortality rates of smaller-sized stems (1–20 cm dbh) at Mudumalai were higher than corresponding stems at BCI and Pasoh, the mortality rates of larger trees (>20 cm dbh) were significantly lower at Mudumalai than at the wet sites. Indeed the mortality rates of large trees (>30 cm dbh) are consistently in the range of 0.5% to 1.0% per annum, i.e. less than half the rates recorded at the moist sites.

### **Life-history variation in relation to environmental variability and stress**

The patterns of life-history variation in woody plants across these three sites, experiencing considerable differences in the magnitude of environmental variability and stress, can be summarized as follows:

- (a) The trade-off between regenerating through resprouting (vegetative) and seeding (sexual) clearly favours the former in habitats subject to environmental stress through rainfall seasonality and fire (Bellingham & Sparrow 2000). Recruitment in the dry-forest plot is almost entirely through vegetative sprouts from roots or coppices from stems burnt to ground level; thus a burnt stem survives below ground. An examination of seedlings showed that these too sprout from roots or rhizomes. While these may be root suckers (a stem originating from a root bud at some distance from the parent stem, as defined by Hoffman 1998), it is possible that some may have originally sprouted from seeds (i.e. sexually) but repeatedly burnt to ground level. Seedlings may require favourable periods (absence of fires, release from competition by grasses etc.) of several years before they are able to emerge to a size at which they can escape from ground fires. In such plants the strategy may be to store the small quantity of photosynthetic products of seedlings in underground organs rather than attempting to use them in above-ground vegetative growth immediately. The resources stored below ground could then be mobilized during favourable periods for rapid growth. In the relatively open dry forests the relative lack of light limitation would favour rapid growth, while in a rain forest such rapid growth would be possible only in canopy gaps. On the other hand, reproduction through seeding would be the favoured strategy in the more stable, moist tropical habitats. Genetic recombination through sexual reproduction would also be a necessity for plants in their co-evolutionary battle with the high diversity of pests and pathogens characteristic of the moist tropical forests.
- (b) Overall recruitment rates can be expected to be higher in habitats subject to frequent disturbance, if recruitment has to compensate for high mortality of small individuals. At the same time, recruitment may also be highly variable depending on favourable conditions not just across the population of woody stems but also across species within the community.



- (c) Where frequent fires kill the saplings of woody plants, we can expect that recruitment opportunities would be limited to perhaps a few 'windows' of several years without fire. Saplings should thus be in a position to grow rapidly and establish themselves in the fire-immune size class during a short favourable period. The observed growth rates in the three plots support this expectation, with the saplings at Mudumalai showing much higher growth rates than the other two plots, and saplings at BCI showing higher growth rate than at Pasoh.
- (d) Perhaps the most striking aspect of life-history evolution is that of very low adult-mortality rates in the highly seasonal habitat subject to various stresses such as fire and herbivory. The mortality rates of the large stems at Mudumalai are among the lowest recorded for large trees in tropical forests globally. The low death rates of large trees permit the persistence of the population over time scales of several centuries. Thus, it is possible that the long-lived trees could have higher lifetime reproductive success irrespective of short-term recruitment rates.
- (e) Although the turnover of stems in the understorey of a tropical dry forest is very high, the canopy layer may be remarkably stable. This is exemplified by the constancy or increase in basal area projected for the four common canopy trees at Mudumalai. In contrast, both canopy and understorey species in a moist tropical forest show relative stability. In this respect the Pasoh forest seems more stable than BCI (Condit *et al.* 1999) as can be perhaps expected from the greater climatic stability in the former site.

Management strategies for tropical forests have to take into account differences in life-history traits that represent evolutionary and ecological adaptations to regional environmental variability. This would include the management of fire, logging and the harvest of various non-timber forest products.

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