MaB

MAN AND THE BIOSPHERE SERIES

Series Editor J.N.R. Jeffers

VOLUME 20

FOREST BIODIVERSITY RESEARCH, MONITORING AND MODELING

Conceptual Background and Old World Case Studies

Edited by

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and

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Smithsonian Institution
Washington DC, USA

PUBLISHED BY

UNESCO

PARIS

AND

The Parthenon Publishing Group

International Publishers in Science, Technology & Education

CHAPTER 28

DYNAMICS OF A TROPICAL DECIDUOUS FOREST: POPULATION CHANGES (1988 THROUGH 1993) IN A 50-HA PLOT AT MUDUMALAI, SOUTHERN INDIA

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INTRODUCTION

There has been increasing interest in long-term dynamics of tropical forests over relatively large spatial scales (Hubbell and Foster, 1983; Condit, 1995). One result should be a better understanding of how very high levels of diversity are maintained in tropical forests, knowledge that can contribute to conservation and management of these forests. An international network of large-scale plots is being established in tropical forests, an effort coordinated by the Center for Tropical Forest Science at the Smithsonian Tropical Research Institute (Condit, 1995; Ashton, Chapter 3).

During 1988 and 1989, a 50-ha vegetation plot was set up in the tropical deciduous forests of Mudumalai in southern India by the Indian Institute of Science as part of that country's biosphere reserve program (Sukumar *et al.*, 1992). The Mudumalai plot complements two plots of similar size in Panama and Malaysia that represent semi-evergreen and evergreen forests, respectively (Hubbell and Foster, 1983; Manokaran *et al.*, 1992). The aspects of forest dynamics under investigation at Mudumalai differ to some extent from those in Panama and Malaysia. For example, the Mudumalai plot is significantly influenced by fire and large mammals such as elephants, factors that are not relevant to the evergreen sites (exception Pasoh, Malaysia, where elephants were once part of the ecosystem).

In this paper, we provide a basic description of recruitment and mortality at the Mudumalai plot from 1988 to 1993 and draw inferences for the management of this forest. As with other researchers manipulating large data sets (Condit *et al.*, In press), we are still in the process of assessing our data; thus, some of the numbers reported here are tentative and subject to corrections. We anticipate that any corrections will be minor and will not change the overall conclusions of this paper. More detailed analyses of these data and of growth-rate data for individuals and species populations will enable us to test various hypotheses of tropical forest community ecology and to model future trends in forest structure and diversity.

STUDY AREA

The plot is centrally located (11°35'41" to 11°35'57"N, 76°31'50" to 76°32'22"E) in Mudumalai Sanctuary at an altitude of 980 to 1,120 m. The vegetation of the plot is tropical dry deciduous forest, with *Lagerstoemia microcarpa*, *Terminalia crenulata*, *Anogeissus latifolia*, and *Tectona grandis* the dominant canopy species (for more details of vegetation types and species composition, see Sukumar *et al.*, 1992).

FIELD METHODS

The plot was divided into 20-m² quadrats, using a theodolite, and all woody plants >1 cm in diameter at breast height were identified, measured (for dbh), and numbered with aluminum tags; their spatial locations were mapped. The first enumeration began in May 1988 and was completed in May 1989. During subsequent years, the plot was enumerated annually to record recruitment (our operating definition of recruitment is the growth of a stem into the >1-cm dbh class, not necessarily to a reproductively mature size) and mortality of stems. Censuses began each year in June and were usually completed in three to four months. The first re-census began in June 1989. A detailed map of the extent of fire in the plot is prepared every year in April at the end of the dry season, enabling us to determine whether any individual stem has been subjected to fire. All stems are remeasured every four years to calculate growth rates; the first such re-enumeration took place in 1992.

ANALYSES

Causes of mortality, size class-specific mortality rates, and annual mortality rates of species populations are expressed as percentage of stems living at time N_t and dying by time N_{t+1}. Annual recruitment rates were calculated in percentages as $(r \times 100)/N$, where r is the number of stems recruited to >1 cm dbh during a given year, and N is the total population size during the previous year.

Changes in species populations between 1988 and 1993 are expressed as the overall percentage change during this time interval and also as annualized rates of change calculated as $(\ln N_t - \ln N_0)/t$, where N_t is the population at time t, and N_0 is the population at time 0. This was done to facilitate comparisons with other studies that report changes in this manner (Condit *et al.*, In press). The time interval t was five years in our calculation, even though the mean interval between 1988 and 1993 censuses for a species population may not have been exactly five years.

RESULTS

Changes in species populations

The initial enumeration of the plot totaled 25,929 individuals >1 cm dbh from 72 species (multiple stems were considered as one individual). The 1992 census indicated that the number of individuals declined to 17,458, followed by a slight increase to 17,651 individuals (71 species) in 1993 for a net change in population size of −32%.

Three species (*Cassia montana*, *Crotalaria* sp., and *Buchanania axillaris*) disappeared from the plot, two (*Jatropha curcas* and *Grewia orbiculata*) were ephemerals, and two (*Holarrhena antidysenterica* and an unidentified species) were added.

With few exceptions, most species declined in population size (Table 28.1). While changes in species with small initial population sizes could be attributed to stochastic fluctuations, we postulated that population changes in species with large population sizes at the outset could be more meaningful. For example, *Kydia calycina*, an understory tree that was the most abundant in 1988, suffered the steepest population-size decline – from 5,175 to 712 individuals – in 1993; currently, *K. calycina* is the seventh most abundant species. The shrub *Helicteres isora* went from the fourth most abundant species (2,571 individuals) in 1988 to sixth most abundant (716 individuals) in 1993. The sharply decreasing trend for *Cassia fistula* was reversed from 1992 to 1993, although the population remained below its 1988 size. Changes in other abundant species such as *Lagerstroemia microcarpa* (−4.3%), *Terminalia crenulata* (−4.3%), *Anogeissus latifolia* (−2.6%), and *Tectona grandis* (−10.8%) were less spectacular, but certainly noticeable.

Mortality rates and patterns

Overall mortality rates averaged 9.6%/year from 1988 to 1992 (range 7.6% to 14.3%), dropping to 3.4% from 1992 to 1993. Figure 28.1 shows the annual mortality rates and causes (classified as fire, elephants, and other causes) for this period. Rates of mortality caused by elephants increased from 1988 through 1991 and decreased during subsequent years as the populations of their favored food plants, *K. calycina* and *H. isora*, declined steeply. Mortality from fire fluctuated to a greater degree, depending on the absence or presence of fire and its extent during a given year. Fires occurred at the plot during the dry months (January through March) of 1989, 1991, and 1992 when the overall mortality rates were 10.5%, 14.3%, and 12.1%, respectively. During 1990 and 1993, there were no fires. However, the death of some individuals in these years were attributed to their weakening during the fires of the preceding years.

Mortality rates generally were substantially higher in the smaller size classes than in the larger size classes (Figure 28.2) during all years. The rates for 1990, 1991, and 1992 are not precise because a certain proportion of stems that were

Table 28.1 Species population changes (percent and annual rate) from 1988 to 1993

Species	Population		% change 1988–1993	Annual rate of change
	1988	1993		
Kydia calycina	5,175	712	−86.24	−0.397
Lagerstroemia microcarpa	3,980	3,810	−4.27	−0.009
Terminalia crenulata	2,775	2,656	−4.29	−0.008
Helicteres isora	2,571	716	−72.15	−0.256
Anogeissus latifolia	2,280	2,221	−2.59	−0.005
Tectona grandis	2,143	1,912	−10.78	−0.023
Cassia fistula	1,881	1,604	−14.73	−0.032
Xeromphis spinosa	770	706	−8.31	−0.017
Emblica officinalis	577	496	−14.04	−0.030
Grewia tiliifolia	539	444	−17.63	−0.039
Syzygium cumini	415	401	−3.37	−0.007
Bambusa arundinacea	381	4	−98.95	−0.911
Radermachera xylocarpa	357	336	−5.88	−0.012
Eriolaena quinquelocularis	251	160	−36.25	−0.090
Cordia obliqua	197	107	−45.69	−0.122
Diospyros montana	130	116	−10.77	−0.023
Stereospermum colias	123	124	0.81	0.002
Ougeinia oojeinensis	111	92	−17.12	−0.038
Lagerstroemia parviflora	92	80	−13.04	−0.028
Shorea roxburghii	79	35	−55.70	−0.163
Cordia wallichii	78	77	−1.28	−0.003
Dalbergia latifolia	76	57	−25.00	−0.058
Schleichera oleosa	75	69	−8.00	−0.017
Schrebera swietenioides	69	54	−21.74	−0.049
Terminalia chebula	61	49	−19.67	−0.044
Gmelina arborea	60	51	−15.00	−0.033
Casearia esculenta	47	43	−8.51	−0.018
Bridelia retusa	40	30	−25.00	−0.058
Bombax ceiba	38	35	−7.89	−0.016
Terminalia bellirica	34	33	−2.94	−0.006
Careya arborea	34	33	−2.94	−0.006
Butea monosperma	34	26	−23.53	−0.054
Garuga pinnata	32	30	−6.25	−0.013
Ziziphus xylopyrus	31	17	−45.16	−0.120
Cassine glauca	31	21	−32.26	−0.078
Bauhinia malabarica	30	25	−16.67	−0.036
Mallotus philippensis	28	21	−25.00	−0.058
Pterocarpus marsupium	22	17	−22.73	−0.052
Indigofera cassioides	22	11	−50.00	−0.139
Cassia montana	21	1	−95.24	−0.609
Mitragyna parvifolia	20	18	−10.00	−0.021
Canthium dicoccum	20	18	−10.00	−0.021
Allophyllus cobbe	19	24	26.32	0.047
Hymenodictyon orixense	14	14	0.00	0.000
Semecarpus anacardium	14	12	−14.29	−0.031
Antidesma diandrum	13	10	−23.08	−0.052
Ficus virens	12	16	33.33	0.058

Table 28.1 Continued

Species	Population		% change 1988–1993	Annual rate of change
	1988	1993		
Lannea coromandelica	12	12	0.00	0.000
Ficus tsjahela	11	13	18.18	0.033
Bauhinia racemosa	11	11	0.00	0.000
Dalbergia lanceolaria	9	4	−55.56	−0.162
Albizzia odorotissima	9	4	−55.56	−0.162
Ziziphus rugosa	8	7	−12.50	−0.027
Flacourtia indica	8	7	−12.50	−0.027
Wrightia tinctoria	8	8	0.00	0.000
Olea dioica	7	6	−14.29	−0.031
Ficus religiosa	7	7	0.00	0.000
Erythrina indica	6	5	−16.67	−0.036
Grewia hirsuta	5	2	−60.00	−0.183
Pavetta indica	5	1	−80.00	−0.322
Ficus drupacea	4	3	−25.00	−0.058
Mangifera indica	4	4	0.00	0.000
Ficus benghalensis	3	3	0.00	0.000
Premna tomentosa	2	2	0.00	0.000
Chukrasia tabularis	1	1	0.00	0.000
Artocarpus gomezianus	1	1	0.00	0.000
Unidentified sp.	1	1	0.00	0.000
Buchanania axillaris	1	0	−100.00	0.000
Crotalaria sp.	1	0	−100.00	0.000
Bischofia javanica	1	1	0.00	0.000
Vitex altissima	1	1	0.00	0.000
Madhuca neriifolia	1	1	0.00	0.000
Grewia orbiculata	0	0	0.00	0.000
Unidentified sp.	0	1	0.00	0.000
Jatropa curcus	0	0	0.00	0.000
Holarrena antidysenterica	0	1	0.00	0.000
Total	25,929	17,651	−31.96	−0.077

not measured would have grown into higher size classes. However, mortality rates for 1989 and 1993 accurately reflected specific size-class rates. While mortality averaged 33.8% in stems 1 to 2 cm dbh, they were only 0.6 to 1.2% in size classes >16 cm dbh. The higher rates in the smaller size classes could be attributed to fire and elephant-induced mortality, the former affecting plants mainly in the 1- to 2-cm dbh class and the latter mainly the 4- to 8-cm dbh class.

Among the 20 most abundant species in 1988, mortality rates averaged >10%/ year for *K. calycina* (34.4%), *H. isora* (23.3%), *Cassia fistula* (17.7%), *Cordia obliqua* (19.4%), and *Shorea roxburghii* (37.7%). *Bambusa arundinacea*, a monocarpic species of 'tree-grass', flowered gregariously from 1989 through 1990, and almost the entire population (except for four individuals) died out by 1991.
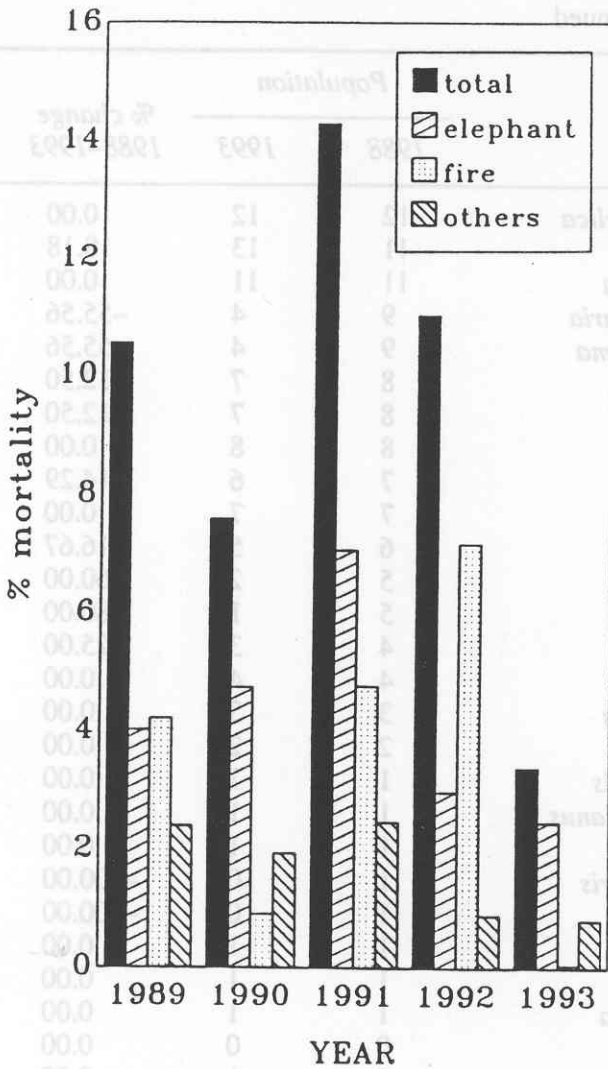
Figure 28.1 Mortality rates (expressed as a percentage during different years) because of fire, elephants, and other causes. The total mortality rate is also shown

Recruitment rates and patterns

Rates of recruitment (i.e. saplings growing to >1 cm dbh) averaged 2.6% from 1988 to 1993, with the highest rate (4.4%) recorded from 1992 to 1993. In most species, the recruitment rates into the >1-cm dbh class were much lower than the overall mortality rates (Figure 28.3). This was most obvious for species such as *K. calycina* (about 100 recruits and > 4,500 deaths), *H. isora* (about 250 recruits and > 2,000 deaths), and *Emblica officinalis* (7 recruits and 88 deaths). Certain species had no recruitment; among the 20 most abundant species, these included *Terminalia crenulata*, *Anogeissus latifolia*, and *Eriolaena quinquelocularis*.

Notable exceptions to the general lack of recruitment included *Lagerstroemia microcarpa* from 1989 through 1990 and 1992 through 1993, *Tectona grandis* from 1992 through 1993, and *Cassia fistula* from 1989 through 1990 and 1992
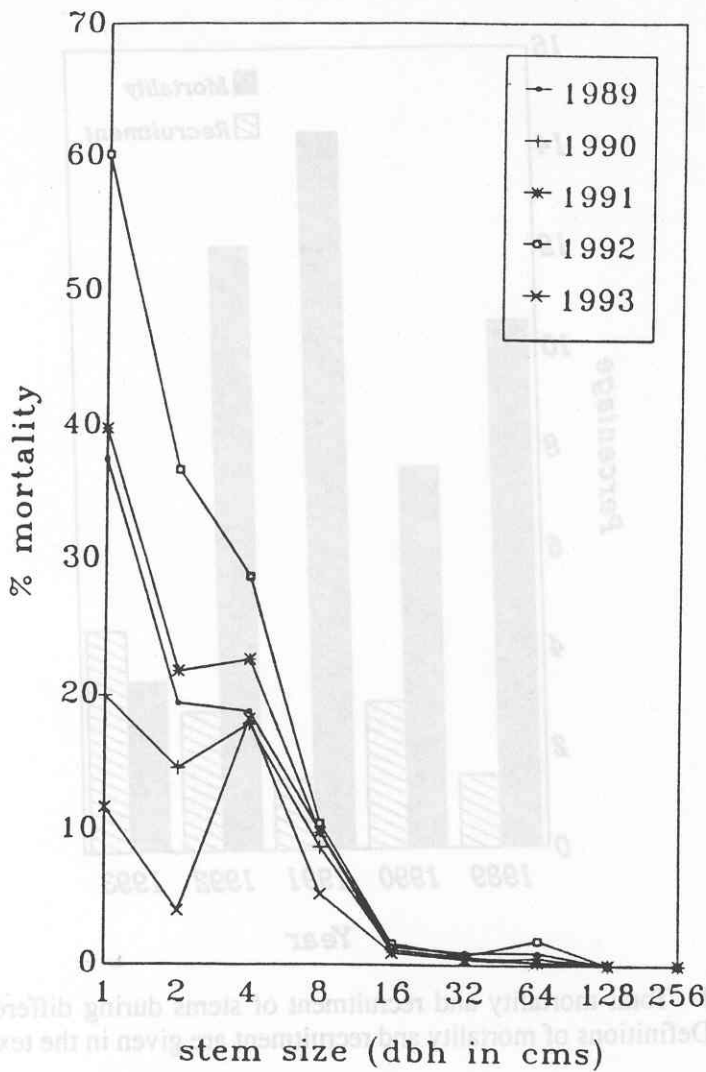
Figure 28.2 Mortality rates of stems in different size classes from 1988 to 1993. These rates are accurately represented only for the 1989 and 1993 censuses, but not for other years because a certain proportion of stems would have grown and moved into a higher size class. Stem sizes were measured only during 1988 and 1992 (see text for explanation)

through 1993. *C. fistula*, in particular, showed strong recruitment (561 individuals) as opposed to marginal mortality (20 individuals) from 1992 through 1993. *Stereospermum colias* also showed higher recruitment than mortality.

Basal area changes

The basal area of stems >1 cm dbh was 24.7 m²/ha (± 3.55, 1 SD) during 1988. Basal area increased slightly to 25.0 m²/ha (± 3.81) by 1992, when all stems were measured. The increase occurred in spite of an overall decline in the total number of stems because growth of persisting stems compensated for the reduced overall population. Stem growth was most notable for individuals >32 cm dbh, the classes in which the number of stems increased because of stem growth from smaller size classes (Table 28.2).
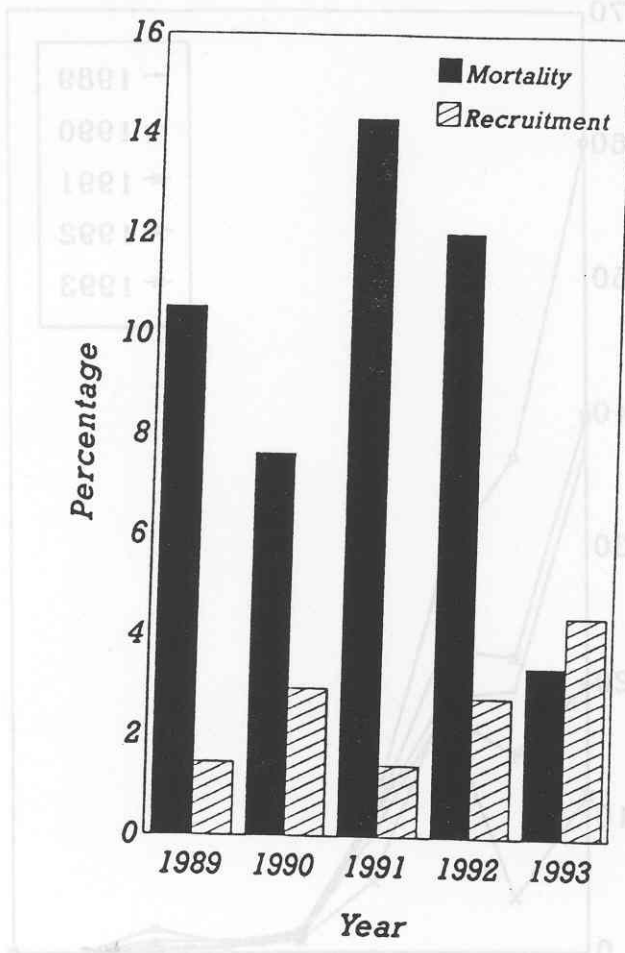
Figure 28.3 Total mortality and recruitment of stems during different years in the 50-ha plot. Definitions of mortality and recruitment are given in the text

Table 28.2 Changes in number of stems in different size classes between 1988 and 1992 (*Bambusa* not included)

Size class dbh (cm)	Number of stems	
	1988	1992
1–2	2,094	551
2–4	1,926	892
4–8	4,535	1,283
8–16	6,091	3,848
16–32	6,576	6,317
32–64	3,938	4,090
64–128	385	459
128–256	3	7
> 256	0	0

DISCUSSION

The degree of stability of tropical forests may have important implications for maintaining biodiversity (Phillips and Gentry, 1994). Although moderate levels of disturbance may enhance levels of forest diversity (Connell, 1978), the same may not be true when disturbances are severe. It is well recognized that semi-arid savanna ecosystems such as those in East Africa are highly unstable, but possibly resilient ecosystems (Norton-Griffiths, 1979). Such systems may have tremendous capacity to absorb disturbances and recuperate to their 'original state' rapidly when conditions are favorable.

The deciduous forest of Mudumalai is an example of relative instability in the face of disturbance by fire, elephants, and other herbivores. Short-term data from the 50-ha Mudumalai plot clearly indicate that most species are declining in absolute numbers and that there has been a shift in the overall population to larger stems, accompanied by a steep decline in smaller stems. The shift in size class distribution cannot be attributed merely to stem growth and successional process – high mortality rates for smaller stems must also be considered an important factor. At this stage, it is not clear if the decline of stems in the smaller size classes will result in a decline in the population of larger stems in the future (over at least the next few decades). A modeling approach using data on recruitment and size-class specific growth and mortality rates, may provide some answers. We plan to develop a stage-projection matrix model based on Lefkovitch (1965) and Caswell (1989).

It is interesting to note that the basal area of stems remained constant, indicating that the much-talked-about equilibrating forces may be operating in the community. At Mudumalai, there certainly seems to be strong equilibration for basal area of the forest, perhaps through compensatory growth of surviving stems when the stem density is reduced. Only future censuses will reveal whether there is any equilibration for species composition of the forest.

Inter-annual variation in life-history events is an important consideration in understanding the dynamics of a community. The burst of recruitment from 1992 through and 1993 for *Cassia fistula* is a good example of how a sharply declining trend in a species population can be reversed within a year or so. Given the high environmental variability, the forest community at Mudumalai may have adapted through low adult mortality rates and strong, episodic reproduction (the 'storage effect' of Warner and Chesson, 1985) that could result in population persistence over long time periods. Data from five years may be inadequate to understand long-term processes influencing seasonal tropical forest dynamics.

Fire and elephants are two factors responsible for most mortalities. In absolute numbers, elephants caused slightly more mortalities than fire. However, elephant-caused mortality explained declines in just a few species, particularly *K. calycina* and *H. isora* (among the most abundant species), while fire-caused mortality affected a range of species, including several abundant and the majority of rarer species. In addition, fire-caused mortality may have been slightly underestimated

because stems weakened by fire could have died from other causes (fallen over in a storm or attacked by pathogens or herbivores) that the stems might have survived if not for the impacts of fire. It should also be remembered that fire influences the dynamics of woody plant populations not only by causing the deaths of standing stems >1 cm dbh, but also by preventing recruitment of stems <1 cm dbh into the census population. This was clear from the relatively high rates of recruitment during 1990 and 1993 when there were no fires in the plot.

Although we have yet to examine in detail the relative role of fire and elephants in species population dynamics, it seems entirely possible that in the absence of fire, most species could have maintained stable population sizes – with recruitment balancing mortality.

Tropical dry forests such as those of Mudumalai have been subjected to fire over several centuries. Wild fires can – and do – occur. Thus, fire is an integral part of the ecosystem, and most species have adapted to a periodic fire regime. The majority of fires today, however, are caused by people for a variety of reasons (Goldammer, 1993). What changed during recent years was probably the frequency and timing of fires. During our study, fires usually occurred at the peak or latter part of the dry seasons, periods of low atmospheric humidity and low moisture of grass and ground litter. Under such conditions, fires sweeping through the undergrowth can be very intense, killing all seedlings, a large proportion of saplings up to 5 cm dbh, and even some mature trees. For most species, however, below-ground perennating organs have the ability to coppice.

During the study period, rainfall was normal or even above normal, unlike during the previous six years when drought associated with El Niño anomalies occurred in 1982 and 1987. At Barro Colorado Island, Panama, the drought of 1982 and 1983 resulted in significantly higher mortalities for trees in a 50-ha plot (Condit *et al.*, In press). It is possible that in Mudumalai, the two droughts could have killed a number of trees, opened up the canopy, and stimulated grass growth, thereby fueling intense fires in later years (during our study). The medium-term effects of the droughts on tree survival could also have persisted into our study period. Logging of these forests prior to 1968 could also have opened up the canopy and increased the fuel load (grass) for fires.

Managers of protected areas usually cannot wait for long-term research data to initiate management actions. Based on our short-term observations, it is not clear whether larger trees would decline given the current rates of recruitment and mortality. However, the drastic change in population sizes and size-class distribution seem to indicate that it may be wise to take actions to reverse these trends.

In this respect, there is clearly a need for a pragmatic fire-management strategy for the Mudumalai forests (and probably similar forests in southern India). It is beyond the scope of this discussion to present the details of such a strategy, but, in general, the plan should recognize the impossibility of eliminating all human-

caused fires. Rather, the aim should be to reduce the destructive impacts of uncontrolled dry-season fires. This may be possible through controlled burning – the so-called 'cool burn' – early in the dry season when the fuel load has a higher moisture content that reduces the intensity of fires. Such burning may be carried out in forest blocks on a rotational basis, perhaps every two or three years. Low-intensity fires will reduce seedling and sapling mortality rates, thus increasing recruitment rates, and also reduce the fuel load, thus rendering an area less prone to high-intensity fires during a particularly dry spell. Clearly, experiments along these lines are needed before specific details of fire management can be decided.

ACKNOWLEDGMENTS

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