

DYNAMICS OF A TROPICAL DECIDUOUS FOREST : POPULATION CHANGES
DURING 1988-93 IN A 50 HA PLOT AT MUDUMALAI, SOUTHERN INDIA

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ABSTRACT :

A 50 ha permanent plot was set up during 1988-89 in the tropical deciduous forests of Mudumalai, southern India, and is being monitored annually to understand long-term changes in vegetation. From an initial population of 25,929 woody plants (72 species) >1 cm dbh during 1988, the population declined to 17,651 individuals (71 species) during 1993. Three species disappeared from the plot, two species were ephemerals, and two species were added to the plot during this period. Overall mortality rates averaged 9.6% per annum and exceeded recruitment rates (2.6%) during all years except in 1993. The major causes of mortality are fire and elephants. The former affected the plants mainly in the 1-4 cm dbh size class and the latter mainly the 4-16 cm dbh class. The 20 most abundant species have almost all declined, especially those species palatable to elephants, such as Kydia calycina (-86.2%), once the most abundant species (currently in seventh position), and Helicteres isora (-72.2%). The exceptions are Cassia fistula, in which a declining trend was reversed by strong recruitment during 1993, and Stereospermum colias. During 1988-92, the basal area remained constant, because growth of persisting stems compensated for the declining population. Implications of the observed short-term dynamics for the management of deciduous forests are discussed.

INTRODUCTION :

There has been increasing interest in studying the long-term dynamics of tropical forests over relatively large spatial scales (Hubbell and Foster 1983, Condit et al. 1995). Such studies will promote a better understanding of how very high levels of diversity are maintained in tropical forests and contribute to their conservation and management. An international network of large-scale plots is being set up in tropical forests. This effort is being coordinated by the Center for Tropical Forest Science at the Smithsonian Tropical Research Institute (Condit et al. 1995).

During 1988-89, a 50 hectare vegetation plot was set up in the tropical deciduous forests of Mudumalai, southern India, by the Indian Institute of Science as part of the country's biosphere reserve programme (Sukumar et al. 1992). The Mudumalai plot, set up in a deciduous forest, is intended to complement two earlier plots of similar size, in Panama and Malaysia representing semi-evergreen and evergreen forests respectively (Hubbell and Foster 1983, Manokaran et al. 1992). The aspects of forest dynamics to be investigated also differed to some extent in the Mudumalai plot. For instance, the dynamics of this forest are significantly influenced by fire and large mammals such as elephants, factors which are not relevant to the evergreen sites (with the exception of Pasoh, Malaysia, where elephants were once a part of the system).

This paper provides a basic description of the changes, in terms of recruitment and mortality, that have occurred in the

Mudumalai plot during the period 1988-93, and draws inferences for the management of this forest. As with other large data sets (Condit et al. ms in review), we are still in the process of "cleaning up" our data sets, and the figures presented here are preliminary and subject to corrections. Such numerical corrections would however be minor and will not change the overall conclusions of this paper. More detailed analyses of these data along with analyses of growth rates of individuals and species populations will enable us to test various hypotheses of community ecology of tropical forests and to model future trends in forest structure and diversity.

MATERIALS AND METHODS :

The study area :

The plot is centrally located (11°35'41" to 11°35'57" N, 76°31'50" to 76°32'22" E) at an altitude of 980-1120 m in Mudumalai Sanctuary (11°32' to 11°43' N, 76°22' to 76°45' E) of southern India. The vegetation of the plot is tropical dry deciduous forest (mean annual rainfall is about 1200 mm), with Lagerstroemia microcarpa, Terminalia crenulata, Anogeissus latifolia and Tectona grandis as the dominant canopy species (for more details of vegetation types in the sanctuary and species composition of the plot, see Sukumar et al. 1992).

Field methods :

The plot was gridded into quadrats of 20m x 20m using a theodolite, and all woody plants >1 cm dbh were identified,

measured (for dbh), numbered with aluminium tags and their spatial locations 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 and mortality of stems. Our operational definition of recruitment is the growth of a stem to >1 cm dbh size and not necessarily to a reproductively mature size. A stem was considered as dead if it had disappeared (usually due to fire), dried completely (with no trace of living tissue when a small cut was made on the stem) or had been burnt or uprooted and dead (even though root coppices below 1.3 m height may be present). Causes of mortality have been recorded as fire, elephants or other causes (including uprooting by wind, insect attack, natural death, etc.).

From 1989 onwards the enumeration began every year in June and was usually completed in 4-6 months' time. A detailed map of the extent of fire in the plot is prepared every year at the end of the dry season (April). This record enables us to determine whether any individual stem has been subject to fire. All stems are re-measured every four years in order to calculate growth rates. The first such complete re-enumeration of the plot was carried out during 1992.

Analyses :

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

given year and N the total population size during the previous year.

Changes in species populations between 1988 and 1993 have been 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 the population at time 0. This has been done to facilitate comparisons with other studies which report change in this manner (Condit et al. in press). The time interval t has been taken as 5 years in our calculation, even though the mean interval between the 1988 and 1993 censuses for a species population may not be exactly 5 years.

RESULTS :

1. Changes in species populations :

The initial population size of all individuals (>1 cm dbh) (including 72 species) during the 1988-89 enumeration was 25,929 individuals (multiple stems were counted as one individual). The total population declined during the subsequent years to 17,458 individuals by 1992. This decline was followed by a slight increase to 17,651 individuals (71 species) during 1993. The net change in population size was therefore - 32 % during 1988-93.

During this period three species (Cassia montana, Crotalaria sp. and Buchanania axillaris) disappeared from the plot, two species (Jatropha curcas and Grewia orbiculata) were ephemerals,

and two species (Holarrhena antidysenterica and an unidentified species) were added to the plot.

With few exceptions most species have declined in population size (Table 1). While changes in species with small population sizes could be attributed to stochastic fluctuations, it is more meaningful to consider population changes in species with large initial sizes.

Kydia calycina, an understorey tree, which was the most abundant species in the plot during 1988 has also suffered the steepest decline from 5175 to 712 individuals by 1993 (currently in seventh position). The shrub Helicteres isora also declined from 2571 in 1988 (fourth position) to 716 in 1993 (sixth position). A sharply declining trend in Cassia fistula was reversed during 1992-93, although the population still remained well below the 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%) have been less spectacular, but noticeable during 1988-93.

2. Mortality rates and patterns :

Overall mortality rates averaged 9.6% per annum during 1988-92 (range 7.6 - 14.3%), and came down to 3.4% during 1992-93. Fig. 1 shows the annual mortality rates and causes (classified as fire, elephant and other causes) for this period. Rates of mortality due to elephants increased between 1988 and 1991 and decreased during subsequent years as the populations of their favored food plants, Kydia calycina and Helicteres isora,

declined steeply. Mortality due to fire has fluctuated to a greater degree, depending on the absence or presence of fire and its extent during a given year. Fires occurred in the plot during the dry months (January-March) of 1989, 1991 and 1992; during these years the overall mortality rates were 10.5%, 14.3% and 12.1% respectively. During 1990 and 1993 there were no fires in the plot; the death of a few stems during these years were however attributed to their weakening during the previous years' fires.

Mortality rates have been, in general, substantially higher in the smaller size classes as compared to the larger size classes (Fig. 2) during all years. For 1990, 1991 and 1992 these rates are not accurate because a certain proportion of stems would have grown into higher size classes, which we have not measured. However, the mortality rates for 1989 and 1993 accurately reflect the size-class specific rates. While rates have averaged 33.8% in stems 1-2 cm dbh, they have been only 0.6-1.2% in the >16 cm dbh classes. The higher rates in the smaller size classes may be attributed to fire and elephant-induced mortality, the former affecting plants mainly in the 1-4 cm dbh class and the latter mainly the 4-16 cm dbh class.

Among the 20 most abundant species (during 1988) in the plot, mortality rates have averaged over 10% per annum in Kydia calycina (34.4%), Helicteres 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 during 1989-90 and almost the entire population (except for 4 individuals) died out by 1991.

3. Recruitment rates and patterns :

Rates of recruitment (that is, saplings growing to >1 cm dbh) have averaged 2.6% during 1988-93, the highest rate (4.4%) being recorded during 1992-93. In most species the rates of recruitment into the >1 cm dbh size class were much lower than the overall rates of mortality (Fig. 3). This is most obvious in species such as Kydia calycina (about 100 recruits versus over 4500 deaths), Helicteres isora (about 250 recruits, over 2000 deaths) and Embluca officinalis (7 recruits, 88 deaths). Certain species showed no recruitment at all during this period; among the 20 most abundant ones, these include Terminalia crenulata, Anogeissus latifolia and Eriolaena quinquelocularis.

Notable exceptions to the general lack of recruitment include Lagerstroemia microcarpa during 1989-90 and 1992-93, Tectona grandis during 1992-93 and Cassia fistula during 1989-90 and 1992-93. Cassia fistula in particular showed strong recruitment (561 individuals) as opposed to marginal mortality (20 individuals) during 1992-93. Stereospermum colias also showed higher recruitment than mortality.

4. Change in basal area :

The basal area of stems >1 cm dbh was 24.7 m² (± 3.55 , 1 SD) per hectare during 1988. This increased marginally to 25.0 m² (± 3.81) by 1992, when all stems were measured. This increase in

basal area occurred in spite of an overall decline in the total number of stems, because growth of persisting stems compensated for the reduced population. This was most noticeable in stems greater than 32 cm dbh, in which the number of stems actually increased due to growth of stems from smaller size classes (Table 2).

DISCUSSION :

The deciduous forest of Mudumalai is an example of relative instability, in the face of disturbance by fire, elephants and other herbivores. The short-term data from the 50 hectare plot at Mudumalai clearly indicate that most species are declining in absolute numbers and that there has been a shift in the overall population to larger sized stems, with a steep decline in the smaller sized stems. The shift in size class distribution cannot be attributed merely to stem growth and the successional process, but is due to the high mortality rates of the smaller stems. 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 sized stems in the future (over a time-scale of a few decades). A modelling approach using data on recruitment, and size-class specific growth and mortality rates may provide some answers. We do 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 has remained constant, indicating that the much-talked about equilibrating forces may be operating in the community. In this

case, 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 during 1992-93 (when there was no dry season fire) in 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 here may have adapted through low adult mortality rates and strong, episodic reproduction ("the storage effect" of Warner and Chesson 1985) that could potentially result in population persistence over long time periods. Five years' data may be very inadequate to understand long-term processes influencing tropical seasonal forest dynamics.

Fire and elephants are the two factors responsible for the highest mortalities. In absolute numbers, elephants were responsible for slightly higher mortality of stems than was fire. However, elephant-caused mortality could explain the decline of only a few species, in particular Kydia calycina and Helicteres isora among the abundant ones. On the other hand, fire-caused mortality affected a range of species, including several of the abundant ones and the majority of the rarer ones. Mortality due to fire was also slightly underestimated because stems weakened

by fire could have died due to other causes (fallen over in a storm, attacked by pathogens or herbivores). It is also important to remember that fire influences the dynamics of woody plant populations not only by causing the death of standing stems >1 cm dbh but also by preventing stems <1 cm from being recruited 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 the population dynamics of individual species, it seems entirely possible that in the absence of fire most species (the exceptions being those favored by elephants) could have maintained stable population sizes with recruitment balancing mortality.

Tropical dry forests such as those of Mudumalai have been subject to fire over several centuries. Natural fires can and do probably occur. Fire is thus an integral part of the system and most species are adapted to a periodic fire regime. The majority of fires today are, however, caused by people for a variety of reasons (Goldammer 1993). In recent years it is possible that the frequency and/or timing of fires has changed. During the study period fires usually occurred at the peak or the latter part of the dry season, a period of low atmospheric humidity and low moisture of grass and ground litter. Fires which sweep through the undergrowth can be very intense and kill all seedlings, a large proportion of saplings up to 5 cm dbh and even a few mature

trees. In most species, however, the below-ground perennating organs have the ability to coppice.

During the study period (1988-93) the rainfall was normal or even above normal, unlike during the previous six years, when two years (1982 and 1987) were periods of drought associated with El Nino anomalies. In Barro Colorado Island, Panama, the drought of 1982-83 resulted in significantly higher mortalities in trees in a 50 ha plot (Condit et al. in press, in review). It is possible that in Mudumalai the two droughts could have killed a number of trees, opened up the canopy, stimulated grass growth and in turn fuelled more intense fires in later years (during our study). The medium-term effects of the drought on natural survival of trees could also have persisted into our study period. Logging of these forests prior to 1968 would have also opened up the canopy and increased the fuel load (grass) for fires.

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

In this respect, there is clearly a need for a pragmatic fire management scheme for the Mudumalai forests (and other such deciduous forests in southern India). It is beyond the scope of

this discussion to go into detail about such a management scheme. This should recognize that a complete elimination of human-caused fires is virtually impossible and aim at controlling the destructive effects of uncontrolled, dry season fires. It may be possible to achieve this through controlled burning, early in the dry season (the so-called "cool burn") so that the intensity of fire is lower (because of higher moisture content of the fuel load). Such burning may be carried out in forest blocks on a rotational basis, perhaps every two or three years. Low intensity fires will reduce the mortality rates of seedlings and saplings (thus increasing the recruitment rate) and also reduce the fuel load (thus rendering an area less prone to high intensity fire during a particularly dry spell). Clearly experiments along these lines have to be carried out before specific details of fire management can be worked out.

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

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LEGENDS TO FIGURES

Figure 1. Mortality rates expressed as a percentage during different years due to fire, elephant and other causes. The total mortality rate is also shown.

Figure 2. Mortality rates in stems of different size classes during 1988-93. These rates are accurately represented only for the 1989 and 1993 census, but not for other years because a certain proportion of stems would have grown and moved into a higher size class. Stem sizes have been measured only during 1988 and 1992 (see text for explanation).

Figure 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.

Sl. No	Species	Population changes		Percentage change 1988-93	Annual rate of population change
		1988	1993		
1	<i>Kydia calycina</i>	5175	712	-86.24	-0.397
2	<i>Lagerstroemia microcarpa</i>	3980	3810	-4.27	-0.009
3	<i>Terminalia crenulata</i>	2775	2656	-4.29	-0.008
4	<i>Helicteres isora</i>	2571	716	-72.15	-0.256
5	<i>Anogeissus latifolia</i>	2280	2221	-2.59	-0.005
6	<i>Tectona grandis</i>	2143	1912	-10.78	-0.023
7	<i>Cassia fistula</i>	1881	1604	-14.73	-0.032
8	<i>Xeromphis spinosa</i>	770	706	-8.31	-0.017
9	<i>Emblica officinalis</i>	577	496	-14.04	-0.030
10	<i>Grewia tiliifolia</i>	539	444	-17.63	-0.039
11	<i>Syzygium cumini</i>	415	401	-3.37	-0.007
12	<i>Bambusa arundinacea</i>	381	4	-98.95	-0.911
13	<i>Radermachera xylocarpa</i>	357	336	-5.88	-0.012
14	<i>Eriolaena quinquelocularis</i>	251	160	-36.25	-0.090
15	<i>Cordia obliqua</i>	197	107	-45.69	-0.122
16	<i>Diospyros montana</i>	130	116	-10.77	-0.023
17	<i>Stereospermum colias</i>	123	124	0.81	0.002
18	<i>Ougeinia oojeinensis</i>	111	92	-17.12	-0.038
19	<i>Lagerstroemia parviflora</i>	92	80	-13.04	-0.028
20	<i>Shorea roxburghii</i>	79	35	-55.70	-0.163
21	<i>Cordia wallichii</i>	78	77	-1.28	-0.003
22	<i>Dalbergia latifolia</i>	76	57	-25.00	-0.058
23	<i>Schleichera oleosa</i>	75	69	-8.00	-0.017
24	<i>Schrebera swietenioides</i>	69	54	-21.74	-0.049
25	<i>Terminalia chebula</i>	61	49	-19.67	-0.044
26	<i>Gmelina arborea</i>	60	51	-15.00	-0.033
27	<i>Casearia esculenta</i>	47	43	-8.51	-0.018

28	<i>Bridelia retusa</i>	40	30	-25.00	-0.058
29	<i>Bombax ceiba</i>	38	35	-7.89	-0.016
30	<i>Terminalia bellirica</i>	34	33	-2.94	-0.006
31	<i>Careya arborea</i>	34	33	-2.94	-0.006
32	<i>Butea monosperma</i>	34	26	-23.53	-0.054
33	<i>Garuga pinnata</i>	32	30	-6.25	-0.013
34	<i>Ziziphus xylopyrus</i>	31	17	-45.16	-0.120
35	<i>Cassine glauca</i>	31	21	-32.26	-0.078
36	<i>Bauhinia malabarica</i>	30	25	-16.67	-0.036
37	<i>Mallotus philippensis</i>	28	21	-25.00	-0.058
38	<i>Pterocarpus marsupium</i>	22	17	-22.73	-0.052
39	<i>Indigofera cassioides</i>	22	11	-50.00	-0.139
40	<i>Cassia montana</i>	21	1	-95.24	-0.609
41	<i>Mitragyna parvifolia</i>	20	18	-10.00	-0.021
42	<i>Canthium dicoccum</i>	20	18	-10.00	-0.021
43	<i>Allophyllus cobbe</i>	19	24	26.32	0.047
44	<i>Hymenodictyon orixense</i>	14	14	0.00	0.000
45	<i>Semecarpus anacardium</i>	14	12	-14.29	-0.031
46	<i>Antidesma diandrum</i>	13	10	-23.08	-0.052
47	<i>Ficus virens</i>	12	16	33.33	0.058
48	<i>Lannea coromandelica</i>	12	12	0.00	0.000
49	<i>Ficus tsjahela</i>	11	13	18.18	0.033
50	<i>Bauhinia racemosa</i>	11	11	0.00	0.000
51	<i>Dalbergia lanceolaria</i>	9	4	-55.56	-0.162
52	<i>Albizzia odorotissima</i>	9	4	-55.56	-0.162
53	<i>Ziziphus rugosa</i>	8	7	-12.50	-0.027
54	<i>Flacourtia indica</i>	8	7	-12.50	-0.027
55	<i>Wrightia tinctoria</i>	8	8	0.00	0.000
56	<i>Olea dioica</i>	7	6	-14.29	-0.031
57	<i>Ficus religiosa</i>	7	7	0.00	0.000
58	<i>Erythrina indica</i>	6	5	-16.67	-0.036

59	<i>Grewia hirsuta</i>	5	2	-60.00	-0.183
60	<i>Pavetta indica</i>	5	1	-80.00	-0.322
61	<i>Ficus drupacea</i>	4	3	-25.00	-0.058
62	<i>Mangifera indica</i>	4	4	0.00	0.000
63	<i>Ficus benghalensis</i>	3	3	0.00	0.000
64	<i>Premna tomentosa</i>	2	2	0.00	0.000
65	<i>Chukrasia tabularis</i>	1	1	0.00	0.000
66	<i>Artocarpus gomezianus</i>	1	1	0.00	0.000
67	Unidentified sp	1	1	0.00	0.000
68	<i>Buchanania axillaris</i>	1	0	-100.00	0.000
69	<i>Crotalaria</i> sp.	1	0	-100.00	0.000
70	<i>Bischofia javanica</i>	1	1	0.00	0.000
71	<i>Vitex altissima</i>	1	1	0.00	0.000
72	<i>Madhuca neriifolia</i>	1	1	0.00	0.00
73	<i>Grewia orbiculata</i>	0	0	0.00	0.000
74	Unidentified sp	0	1	-	-
75	<i>Jatropha curcus</i>	0	0	0.00	0.000
76	<i>Holarrena antidysenterica</i>	0	1	-	-
	TOTAL	25929	17651	-31.96	-0.077

Table 2: Changes in number of stems in different size classes between 1988 and 1992 (Bambusa is omitted in these figures).

Size class dbh (cm)	Number of stems	
	1988	1992
1-2	2094	551
2-4	1926	892
4-8	4535	1283
8-16	6091	3848
16-32	6576	6317
32-64	3938	4090
64-128	385	459
128-256	3	7
> 256	0	0

% mortality

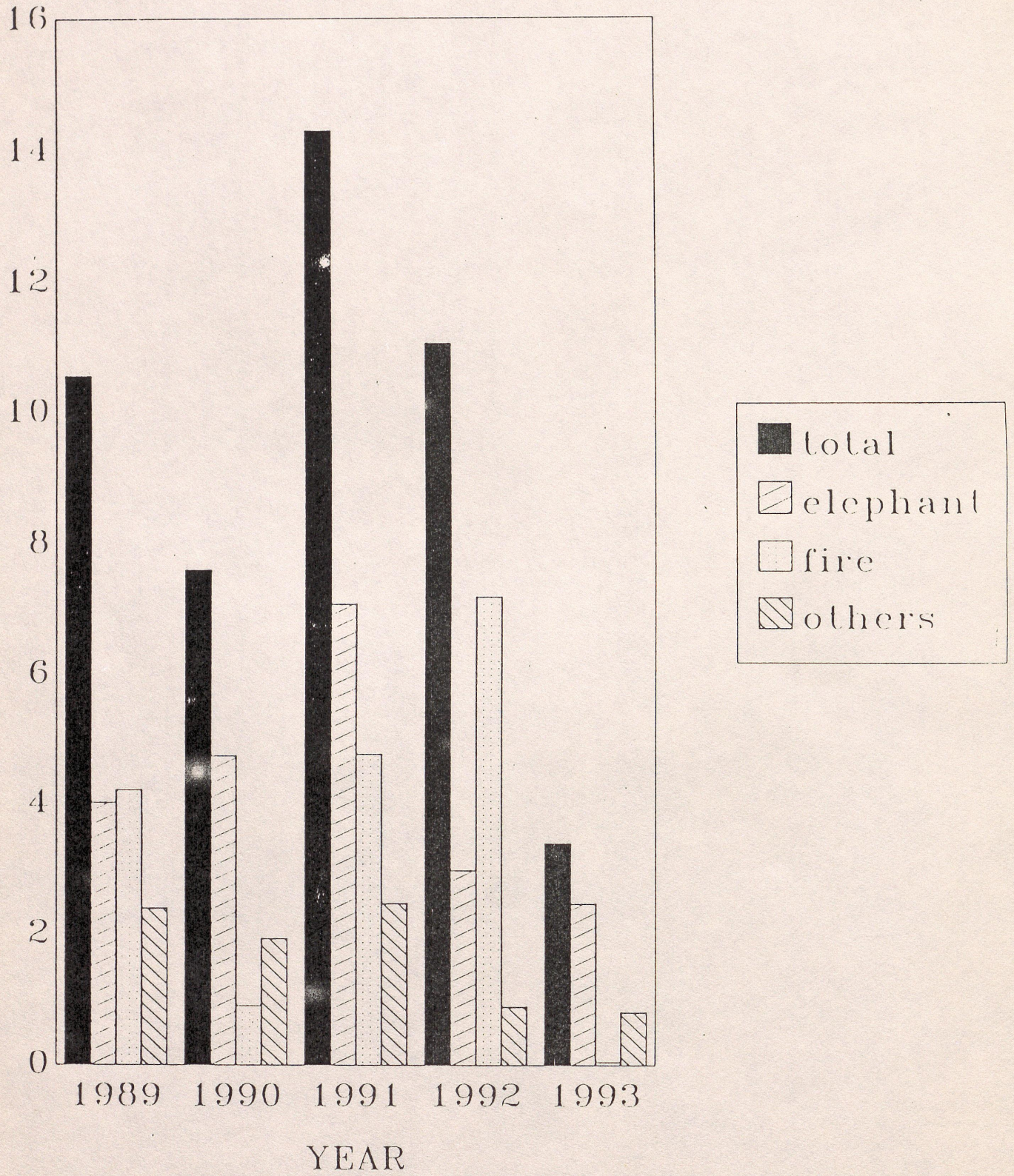


fig: 1

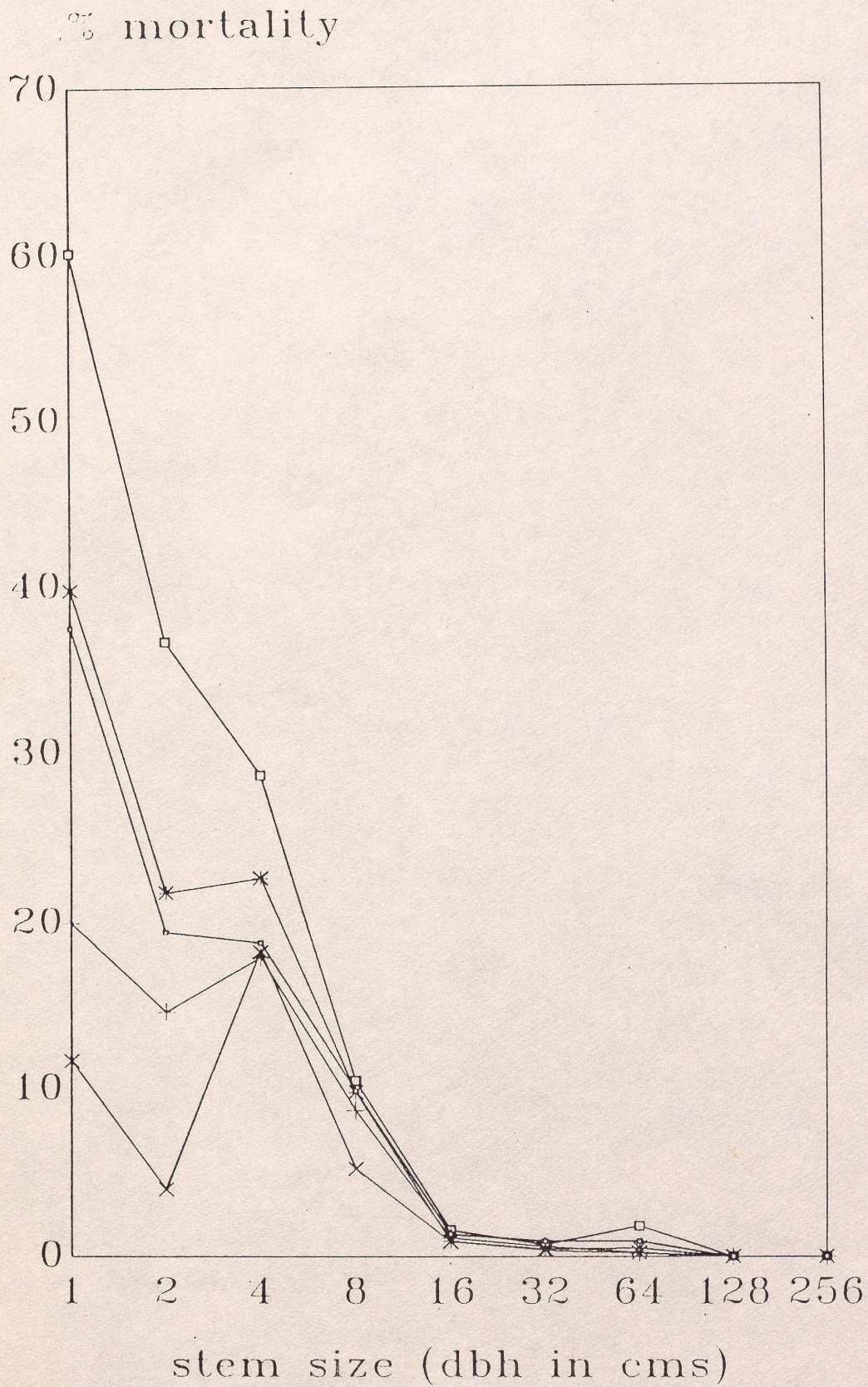


fig: 2

Percentage

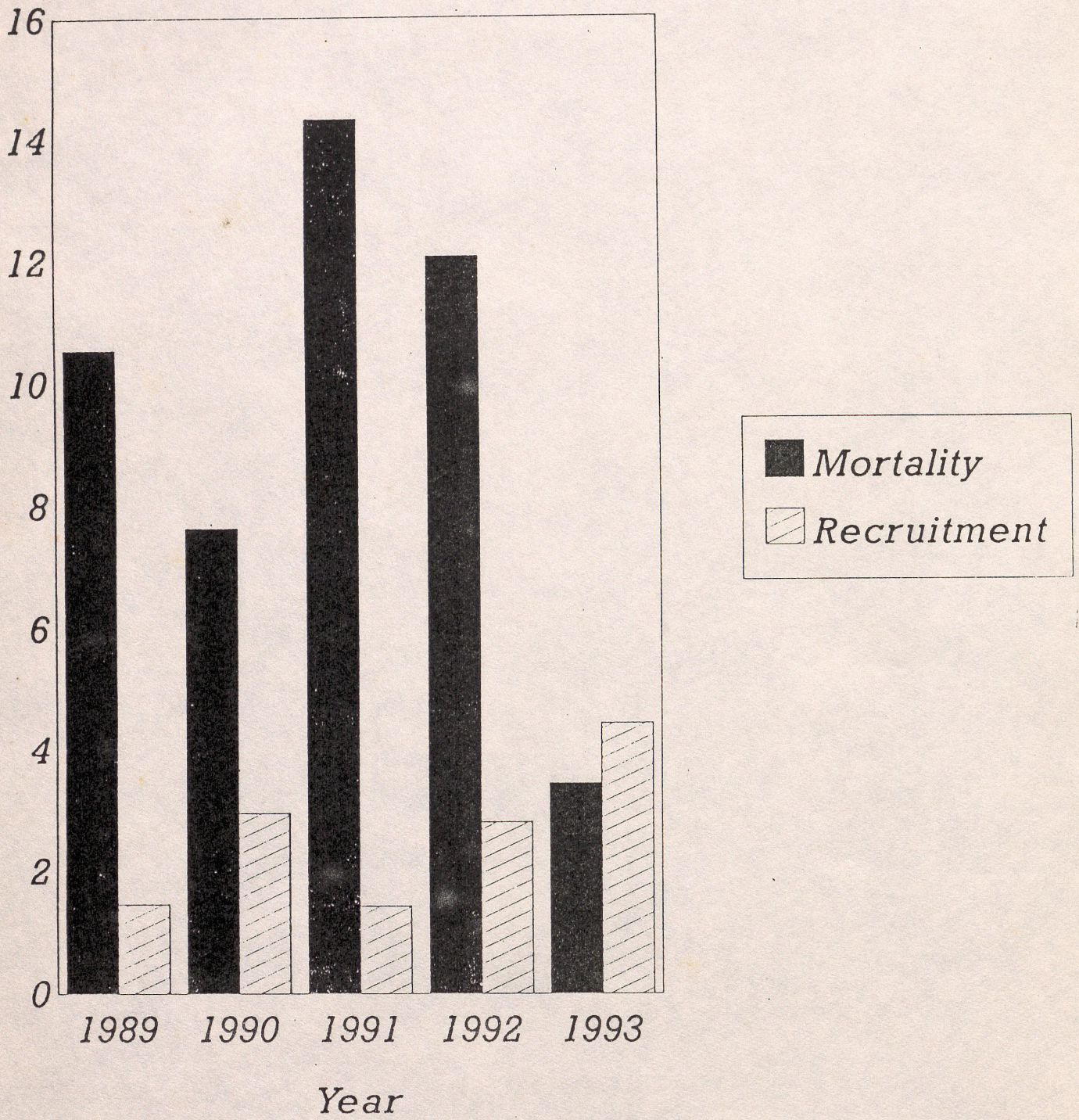


Fig. 3