Journal of Vegetation Science 13: 45-56, 2002

Density-dependence in common tree species in a tropical dry forest in Mudumalai, southern India

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Abstract. Density-dependence in tree population dynamics has seldom been examined in dry tropical forests. Using long-term data from a large permanent plot, this study examined 16 common species in a dry tropical forest in southern India for density-dependence. Employing quadrat-based analyses, correlations of mortality, recruitment and population change with tree densities were examined. Mortality in 1-10 cm diameter trees was largely negatively correlated with conspecific density, whereas mortality in > 10 cm diameter trees was positively correlated. Mortality was, however, largely unaffected by the basal area and abundance of heterospecific trees. Recruitment was poor in most species, but in *Lagerstroemia microcarpa* (*Lythraceae*), *Tectona grandis* (*Verbenaceae*) and *Cassia fistula* (*Fabaceae*), species that recruited well, strong negative correlations of recruitment with conspecific basal area and abundance were found. In a few other species that could be tested, recruitment was again negatively correlated with conspecific density. In *Lagerstroemia*, recruitment was positively correlated with the basal area and abundance of heterospecific trees, but these correlations were non-significant in other species. Similarly, although the rates of population change were negatively correlated with conspecific density they were positive when dry-season ground fires occurred in the plot. Thus, the observed positive density-dependence in large-tree mortality and the negative density-dependence in recruitment in many species were such that could potentially regulate tree populations. However, repeated fires influenced density-dependence in the rates of population change in a way that could promote a few common species in the tree community.

Keywords: Ground fire; Long-term data; Mudumalai; Permanent plot; Population dynamics; Species coexistence.

Introduction

The regulation of plant populations, especially in species-rich tropical forests, is poorly understood. Among the many hypotheses that have been proposed to explain the regulation of tree populations and the maintenance of diversity, density-dependence has long been an important paradigm (Yoda et al. 1963; Harper 1977; Watkinson & Harper 1978; Reynolds 1984; Weiner 1984; Fowler 1988; see Antonovics & Levin 1980; Pacala 1989; Roughgarden 1989 for reviews). The density of any species is, of course, ultimately limited by the self-thinning densities obtained in monospecific stands by direct competition for resources (Yoda et al. 1963). However, tree species seldom attain such high densities in mixed-species communities, particularly in species-rich communities such as tropical forests, where most tree species are infrequent or rare. Are such species also regulated by density-dependent effects? It has been argued further that plants, being rooted organisms, probably compete mainly with their nearest neighbours and not with the population as a whole, illustrated by the use of the phrase ‘neighbourhood effect’ to describe intraspecific competition (Mack & Harper 1977; Antonovics & Levin 1980; Pacala & Silander 1990; Kenkel 1988). This seems to suggest that population density may not be the most appropriate variable to consider in understanding plant performance, and that the immediate neighbourhood of an individual plant is the scale over which plants interact. However, with so few studies and data that have addressed these questions in detail, it is far from clear as to what constitutes a plant’s ecological neighbourhood, and over what spatial scales individual plants interact.

Field studies, particularly in neotropical moist forests, have demonstrated neighbourhood effects of varying extents in different species (Wright 1983; Clark & Clark 1984; Schupp 1988; Hubbell et al. 1990; Condit et al. 1992), neighbourhood effects extending well beyond immediate neighbours have also been shown (Augspurger 1983, 1984; Howe et al. 1985). However, most studies have considered only the effects of proximity to the nearest adult or the interactions of individuals at a local scale. Only a few studies have examined the influence of density at the scale of many adult trees or even the regional density of conspecific trees (Connell et al. 1984; Hubbell et al. 1990; Schupp 1992; Wills et al. 1997; Wills & Condit 1999). The importance of spatial scale in understanding plant neighbourhood effects was emphasized by Schupp (1992) following an experimental study conducted in Barro Colorado Island, Panama. He examined distance- and density-dependent effects on the survival of seeds of an understorey tree (*Faramea occidentalis*) and found that although survival beneath adults was significantly less than survival 5 m away, the density of adult trees in a 1-ha area surrounding the experimental trees did not influence seed survival beyond 5 m from adult crowns. Survival beneath adults and survival of all seeds (beneath and away) was positively, rather than negatively density-dependent, at the population level. This led him to suggest that density- and distance-dependent survival on the scale of a few metres need not translate into density-dependent survival on the scale of a population and need not be evidence for a force stabilizing the population.

Taking up this suggestion, Wills et al. (1997) employed a quadrat-based analysis to examine density-dependence at the scale of multiple adult trees in a 50-ha permanent vegetation plot in BCI, Panama. Using quadrat sizes ranging from 20 m × 20 m to 100 m × 100 m, they found strong, intra-specific density-dependent effects on survival and recruitment of the kind that could regulate populations and maintain diversity in this forest. These effects were much stronger and more pervasive than had been previously detected using focal adult analyses in the same forest (Condit et al. 1992). Later, using similar quadrat-based analyses, Wills & Condit (1999) examined 100 common species, matched for abundance, from plots in Panama and Pasoh Forest Reserve, Peninsular Malaysia. Although these forests differ considerably in seasonality, diversity, floristics and turnover rates similar density-dependent effects were found to operate in both forests.

While density-dependence has been examined in moist tropical (Connell et al. 1984; Condit et al. 1992, 1994; Wills et al. 1997; Dalling et al. 1998; Wills & Condit 1999; Harms et al. 2000) and temperate forests (Ford 1975; Yeaton 1978; Weiner 1984; Peet & Christensen 1987; Kenkel 1988; Duncan 1991; Newton & Jolliffe 1998; He & Duncan 2000) there are very few studies from dry tropical forests. In such forests, it has been argued, large-scale natural disturbance caused by droughts and fires are more important in structuring the plant community (Blasco 1983; Sukumar et al. 1992; van Groenendael et al. 1996) and density-dependence is expected to play only a limited role. However, to our knowledge, no study has examined tree species in dry tropical forests for density-dependence in life history parameters in any detail.

Our study was carried out in a 50-ha permanent vegetation plot in a dry tropical forest in Mudumalai, southern India (Sukumar et al. 1992). The study design and methodology were similar to the earlier 50-ha plots established in Barro Colorado Island, Panama (Hubbell & Foster 1992) and Pasoh Reserve Forest, Malaysia (Manokaran et al. 1990). However, the Mudumalai forest has fewer species than the moist forests of Panama and Malaysia. Thus, for all individuals ≥ 1 cm DBH, the Mudumalai 50-ha plot had 70 species of trees and shrubs, whereas the plots in Panama and Malaysia had 314 and 807 species respectively (Ashton 1998). The canopy is also relatively open and the ground layer is covered by grass. Further, unlike BCI and Pasoh, Mudumalai supports a high density of large mammalian herbivores (Varman & Sukumar 1995), and is moderately disturbed by human-induced dry-season grass fires (Sukumar et al. 1998).

In this paper, we examine density-dependence in recruitment at the scale of many adult trees employing the quadrat-based analysis suggested by Wills et al. (1997). Density-dependent effects could operate at various plant life history stages. Therefore, in addition to recruitment, we examined density-dependence in mortality rates as well as in population growth rate.

Methods

Study area

The 50-ha permanent vegetation plot is located in Mudumalai Wildlife Sanctuary in the state of Tamil Nadu, southern India, near the borders with the Kerala and Karnataka states. The sanctuary (11° 32' to 11° 43' N, 76° 22' to 76° 45' E) is situated to the north of the Nilgiri plateau with an altitudinal range of 900 - 1200 m a.s.l. and has an area of 321 km^2. The climate is monsoonal, with warm wet summers and cool dry winters. The major part of the sanctuary constitutes dry deciduous forest, with smaller areas of scrub forest in the east and moist deciduous forest in the west (Puri et al. 1989). The most common trees in the dry deciduous forest include *Tectona grandis*, *Lagerstroemia microcarpa*, *Terminalia crenulata*, *Anogeissus latifolia*, and *Kydia calycina* (Table 1). The plot is located in dry deciduous forest and receives annual rainfall of ca. 1230 mm, with a 6-month dry season that extends from November to April, during which the monthly rainfall is < 100 mm (there could be no rain at all during certain months) (von Lengerke 1977). The vegetative and reproductive phenology of several tree species in the dry deciduous forest has been studied in detail (Murali & Sukumar 1993, 1994). Phenological events are strongly coupled with seasons in this highly seasonal forest. Leaf-fall occurs during the beginning of the dry season and leaf flush begins later in the dry season, attaining a peak just before the onset of rains (Murali & Sukumar 1993).

The flora of Mudumalai Wildlife Sanctuary is well documented (Sharma et al. 1978; Suresh et al. 1996), and species diversity, abundance and basic demographic parameters of the tree species in the plot have been reported (Sukumar et al. 1992, 1998). Large mammalian herbivores such as the elephant (*Elephas maximus*), gaur (*Bos gaurus*) and 2 species of deer occur at high densities (Varman & Sukumar 1995). Large carnivores include the tiger (*Panthera tigris*), leopard (*Panthera pardus*) and wild dog (*Cuon alpinus*).

Field methods

We adopted the quadrat-based approach used by Wills et al. (1997) and used dynamic annual census data collected from 1988 to 1996 to examine density-dependence in mortality, recruitment and intrinsic rates of population increase. Of the 70 species recorded in 1988 we chose for this analysis only those species with at least 100 individuals ≥ 1 cm diameter at breast height (DBH). With this cut-off for minimum abundance we could examine only 16 species.

We used 2 measures of density in each quadrat (1) the basal area of trees and (2) the abundance of trees ≥ 1 cm DBH. Basal area weights large trees more than small trees and is an indicator of biomass, whereas abundance represents crowding of trees in the neighbourhood. We also tested the influence of diversity of a quadrat on demographic performance. Diversity was expressed using Fisher's α. We expressed mortality using the measure, $m = 1 - (N_t/N_o)^{1/t}$, where N_o is initial population size and N_t is the number of survivors after time t (Sheil et al. 1995). Recruitment rate was calculated on a *per capita* basis, as the ratio of the number of recruits to the number of trees ≥ 1 cm DBH in each quadrat. The intrinsic rate of increase was expressed as $(b - d)/N$, where b is the number of recruits, d is the number of deaths and N is the initial population size of that species (Wills et al. 1997).

Table 1. Abundance (*A*) and basal area (*B*) of some common tree species in the Mudumalai 50-ha plot (1988). These species account for over 90% of the individuals > 1 cm diameter in each growth form (G); C = canopy tree; U = understorey tree.

Species	Family	G	*A* (ha)	*B* (m^2ha^{-1})
Lagerstroemia microcarpa	*Lythraceae*	C	79.6	3.475
Terminalia crenulata	*Combretaceae*	C	55.4	4.652
Anogeissus latifolia	*Combretaceae*	C	45.6	1.817
Tectona grandis	*Verbenaceae*	C	42.8	6.480
Grewia tiliifolia	*Tiliaceae*	C	10.8	1.538
Syzygium cumini	*Myrtaceae*	C	8.3	0.712
Radermachera xylocarpa	*Bignoniaceae*	C	7.1	0.289
Cordia obliqua	*Boraginaceae*	C	3.8	0.014
Kydia calycina	*Malvaceae*	U	103.5	0.757
Cassia fistula	*Fabaceae*	U	37.7	0.112
Xeromphis spinosa	*Rubiaceae*	U	15.4	0.575
Emblica officinalis	*Euphorbiaceae*	U	11.5	0.375

The analysis was carried out using 100 m × 100 m quadrats; smaller quadrats could not be used due to the low sample size of recruits. In each quadrat, for each species, we obtained the mortality rate, recruitment rate and intrinsic rate of increase, and performed non-parametric Spearman's rank-order correlations with conspecific and heterospecific basal area. Correlation calculations were then repeated with the same demographic parameters but with conspecific and heterospecific abundance and overall diversity. We could calculate recruitment, mortality and diversity for each year using the annual census data, but since girth measurements were taken only once every 4 yr basal areas could only be calculated for 1988, 1992 and 1996. For other years, basal areas were obtained using the most recent measure of DBH for each tree included in the analyses.

Mortality was computed in 2 size classes of trees. For canopy and some large understorey trees the 2 size classes were 1 −< 10 cm DBH (henceforth small trees) and > 10 cm DBH (henceforth large trees). In other understorey trees, the cut-off was 5 - 7 cm DBH depending on the maximum size the tree attained in the plot.

We expected that spatial autocorrelation in tree distributions could result in spurious correlations. Hence we employed a randomization procedure to test for significance of the observed correlations (Wills et al. 1997). We compared each observed correlation with 1000 control, non-parametric correlations obtained using artificially constructed data sets. These artificial data sets were constructed by repeatedly scrambling the tree attributes among individuals of the focal species while retaining the locations of the trees. This scrambling was carried out by picking pairs of individuals of the same species and interchanging their attributes without changing their spatial locations. The attributes included stem diameter and whether the tree had survived, died or been recruited during the census period. For each control correlation, we picked 10 N_s pairs of trees, where N_s is the total number of trees of the focal species in the plot. We then computed the above correlations on these artificial data sets to obtain distributions of control correlations for mortality, recruitment and intrinsic rates of increase.

If the observed correlation was larger or smaller than 95% of the shuffled correlations then it was taken to be significant at the 0.05 level; if larger or smaller than 99% of the shuffled correlations, it was taken to be significant at the 0.01 level; and if larger or smaller than all the shuffled correlations, it was taken to be significant at the 0.001 level.

Results

Density-dependence in mortality among small trees

Since most tree species had very few individuals in the smaller size classes, we could test only 6 species for density-dependence in mortality among small trees, results for the 4 species with the highest sample sizes are shown in Table 2. There were very few significant correlations of conspecific basal area and conspecific abundance with mortality in the small trees. Consistent negative correlations were obtained in *Lagerstroemia microcarpa* though not all were significant. In *Kydia calycina*, the correlations were mostly negative, though again few were statistically significant, and in *Cassia fistula*, the strong and significant correlations were always negative. In other species both positive and negative correlations were obtained with no consistent pattern, With heterospecific basal area and heterospecific abundance both positive and negative correlations were obtained, but again no consistent patterns were found. Diversity-dependent effects varied between species and years. There were negative correlations with diversity in *K. calycina* and both positive and negative correlations in *L. microcarpa* and *Tectona grandis*.

Table 2. Quadrat-based tests for density- and diversity-dependence in small-tree mortality from 1989 to 1996 and the 4-yr intervals. The table entries are results of Spearman's rank-order correlations of conspecific basal area (CB), conspecific abundance (CA), heterospecific basal area (HB), heterospecific abundance (HA) and Diversity (DI) with small-tree mortality rates. Non-significant negative correlations are indicated by '-' and non-significant positive correlations by '+'. An 'x' indicates that sample sizes were too low to perform correlations. The signs '--', '---' and '----' are used to indicate significant negative correlations at α-levels 0.05, 0.01 and 0.001 respectively. Significance is indicated in the same way for positive correlations. Years in which fires occurred are indicated in bold.

	Census year								Interval	
	89	90	**91**	**92**	93	**94**	95	**96**	88-92	92-96
Cassia fistula										
CB	+	+	+	-	+	- - - -	- - -	-	- -	- - -
CA	+++	+	-	-	+	- - -	- - -	-	- -	-
HB	- -	+	-	++	+	-	++	+	+++	+
HA	- -	-	+	- -	-	- -	+	- -	-	-
DI	+	- -	-	-	-	+	+	-	-	+
Kydia calycina										
CB	-	-	- -	-	+	-	x	x	-	+
CA	-	- -	-	-	+	x	x	x	-	x
HB	+	-	+	-	+	+	x	x	+	+
HA	-	+	+	-	-	+	x	x	-	-
DI	- -	- -	-	- -	-	+	x	x	- -	-
Lagerstroemia microcarpa										
CB	-	-	- -	- -	- -	-	- -	- - -	-	- -
CA	-	-	- -	-	- -	-	- -	- - -	-	- -
HB	- - -	-	-	+	+	-	++	-	-	+
HA	-	-	+	++	+++	-	+	+	-	+
DI	++	+	+	+	+	-	-	-	+	-
Tectona grandis										
CB	-	-	+	+	x	+	-	-	+	x
CA	+	-	+	-	x	+	+	+	+	x
HB	- - -	+	-	+	x	-	+	-	+	x
HA	-	+	-	-	x	-	++	-	+	x
DI	++	++	- - -	-	x	-	-	- - -	- - -	x

The 4-yr interval patterns were similar, with negative correlations with conspecific density in *C. fistula* and *L. microcarpa*. There were few significant correlations with heterospecific basal area, heterospecific abundance and diversity for the 4-yr rates and there was no general direction in the sign of the correlations.

Density-dependence in mortality among large trees

We tested 10 species for density-dependence in mortality of large trees. The results for 6 species with the most consistent patterns are shown in Table 3. Though few significant correlations were obtained, the sign of the correlations with conspecific density were largely positive in most species. These include *Anogeissus latifolia*, *Lagerstroemia microcarpa*, *Emblica officinalis*, *Xeromphis spinosa* and *Terminalia crenulata*. In *Kydia calycina*, however, these correlations were mostly negative. In other species there were both positive and negative correlations with no general patterns.

Consistently negative correlations with heterospecific density were obtained in *L. microcarpa*, but the patterns in other species were more variable with both positive and negative correlations. Correlations with diversity were mostly non-significant, but consistent negative correlations were obtained in *Tectona grandis*, *T. crenulata*, *E. officinalis*, *A. latifolia* and *K. calycina*. In *Cassia fistula* and *Xeromphis spinosa*, the correlations were largely positive, but both positive and negative correlations were found in the other species.

The 4-yr interval rates had similar patterns with positive correlations of large tree mortality with conspecific basal area and abundance in many species. Again, the corresponding heterospecific effects were more variable in these species, with both positive and negative correlations. There were significant negative correlations with conspecific abundance in *C. fistula*, *Diospyros montana*, *Eriolaena quinquelocularis* and *T. crenulata*. Heterospecific effects were positive in *T. crenulata*, and both positive and negative effects were found in *Grewia tiliifolia* and *C. fistula* (species with significant correlations for only the 4-yr rates are not shown in Table 3). Correlations with diversity were similar to those obtained for the annual rates.

Density-dependence in recruitment

Strong, consistent negative correlations of recruitment with conspecific basal area were found in *Lagerstroemia microcarpa*, *Tectona grandis*, *Kydia calycina*, *Xeromphis spinosa* and *Cordia obliqua*. Significant negative effects were also present in *C. fistula*, particularly in years when recruitment rates were higher (Table 4). In addition to these negative correlations there were a few positive, but non-significant, correlations in *C. fistula*. All other species had insufficient recruits to obtain correlations. These species include the canopy tree species *Anogeissus latifolia* and *Terminalia crenulata*, which were very common in the plot. These negative effects of conspecific basal area were matched by similar significant negative correlations with conspecific abundance in *L. microcarpa*, *T. grandis*, *K. calycina* and *C. fistula*. In *C. obliqua* and *X. spinosa* there were positive correlations in a few cases, but these were not statistically significant.

Table 3. Density- and diversity-dependence in large-tree mortality rates from 1989 to 1996. For notations see Table 2.

	Census year								Interval	
	89	90	**91**	**92**	93	**94**	95	**96**	88-92	92-96
Anogeissus latifolia										
CB	+	+	+	+	- -	+	+	+	+	+
CA	+	+	+	+	- -	+	+	+	+	+
HB	-	-	-	-	++	-	-	-	-	-
HA	-	-	+	+	-	+	+	+	-	-
DI	-	-	-	-	+	-	- -	+	-	+
Kydia calycina										
CB	- -	- -	- - - -	-	-	-	+	-	-	-
CA	-	-	- - -	- - -	-	-	+	- -	-	-
HB	-	-	+	+	++	+	+	-	+	+
HA	-	+++	+	-	-	- -	-	-	+	-
DI	-	-	-	- -	- -	+	-	-	- -	-
Lagerstroemia microcarpa										
CB	+	+	+	+	+	+	+	++	+	++++
CA	+	+	+	+	+	+	+	++	+	+++
HB	-	-	-	- -	-	-	- -	- -	-	- - -
HA	+	-	-	-	-	-	- -	-	+	- - - -
DI	+++	+	-	+	-	+	-	-	+	-
Emblica officinalis										
CB	- -	+	+	+	x	+	+	++	+	++
CA	-	+	+	-	x	+	+	++	+	++
HB	-	+	-	+	x	-	+	+	+	-
HA	-	+	+	-	x	-	+	-	+	-
DI	-	- - -	-	-	x	+	-	-	-	-
Xeromphis spinosa										
CB	+	+	+	+	+	+	+	-	+	+
CA	+	+	+	+	+	+	+	-	+	+
HB	-	+	-	+	-	-	+	+++	-	+
HA	+	-	+	- -	+	-	+	-	-	+
DI	++	+	+	-	- -	+	-	+	+	-
Terminalia crenulata										
CB	- -	+	+	+	+	+	+	+	-	+
CA	+	- -	- -	+	+	- -	+	+	- -	+
HB	-	+	++	-	+	-	-	-	+++	-
HA	+	+++	+	-	+	+	+	-	++	+
DI	- -	+	+	-	-	-	-	-	-	-

Significant positive correlations of recruitment with heterospecific basal area were obtained in *L. microcarpa* and *T. grandis*, while these correlations were largely negative in *C. obliqua*, *C. fistula* and *X. spinosa*. Recruitment in *L. microcarpa* had strong and consistent positive correlations with the abundance of heterospecific trees, and these were stronger and more pervasive than the correlations with heterospecific basal area. Positive correlations were also obtained in *K. calycina* and *X. spinosa*, but these were weaker than for *L. microcarpa*. In other species, there were both positive and negative correlations with no consistent patterns.

Recruitment was consistently positively correlated with diversity in *T. grandis*, *X. spinosa* and *K. calycina*. There were a small number of significant negative correlations with diversity in *L. microcarpa*, but in all other species the correlations with diversity were non-significant. Correlations involving the 4-yr interval recruitment rates had patterns similar to the annual recruitment rates (Table 4).

We then examined these within-quadrat density- and abundance-dependent effects for 'mass' effects, which are due to recruits that arise from parents outside a given quadrat (Shmida & Wilson 1985). This effect

Table 4. Density- and diversity-dependence in recruitment from 1989 to 1996. The number of recruits (*R*) for each species in each year is listed, for other notations see Table 2. Only the species with the largest number of recruits are shown.

	Census year								Interval	
	89	90	**91**	**92**	93	**94**	95	**96**	88-92	92-96
Cassia fistula										
R	76	285	80	223	570	356	486	216	74	438
CB	+	-	+	+	- -	- - -	- - -	+	- -	-
CA	+	-	+	+	- - -	-	- - - -	+	- -	-
HB	- - - -	-	+	-	+	+	-	-	- - -	+
HA	+	- - - -	-	-	- -	-	- -	-	+	+
DI	+	-	-	-	-	-	+	+	+	+
Lagerstroemia microcarpa										
R	58	143	56	74	55	118	104	35	144	107
CB	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -
CA	- - -	- - -	- - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - -
HB	+	-	-	-	+++	+++	-	+	+	++
HA	+	+	+++	+++	++++	++++	++++	+++	+++	++++
DI	+	+	- -	- -	-	-	-	+++	-	-
Xeromphis spinosa										
R	18	25	6	27	2	12	8	4	54	13
CB	- - - -	- - - -	x	- - - -	x	x	- - -	x	- - -	- - - -
CA	+	+	x	+	x	x	+	x	- - - -	- - - -
HB	- - -	-	x	-	x	x	+	x	-	+
HA	+	+	x	++	x	x	+	x	-	+
DI	++++	++++	x	++++	x	x	++	x	++++	+++
Tectona grandis										
R	57	82	50	33	78	71	94	11	25	21
CB	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -	- - - -
CA	- - - -	- -	- - -	- - - -	- - -	- -	- - -	- - -	- - - -	- - - -
HB	++	-	+	+	-	-	+	++	++	+++
HA	-	-	+	+	-	-	+	+	-	++
DI	+	++++	++++	+	+	+	+	+	+	++

would be especially important when quadrats with few seed-producing adult trees are surrounded by quadrats with many such adults. The effect would also be stronger at small quadrat sizes and would lead to over-estimates of recruitment in low-density quadrats. Since we used a relatively large quadrat size in the analyses reported here, mass effects are unlikely to be important. We nevertheless tested for mass effects by conducting partial parametric regressions of recruitment rate against the number of conspecific adult trees within the quadrat and the number of adults in both the 4 nearest and the 8 nearest neighbouring quadrats (Wills et al. 1997). The first regressions measure the within-quadrat effect and the second the mass effect. The 4 and 8 neighbour regressions gave similar results and we report only the 8 neighbour results here. In *Cassia fistula*, all except one of the partial regressions were non-significant for both within-quadrat and mass effects. For 1995, when recruitment was relatively high, a significant negative within-quadrat effect was found but the mass effect was non-significant. Similarly, in *Lagerstroemia microcarpa*, a significant negative within-quadrat effect was found while the mass effect was non-significant. All other partial regressions were non-significant in this species. In *Tectona grandis*, within-quadrat effects were strong and negative in 5 yr, when most recruitment occurred. Significant positive mass effects were found in 2 yr and a negative mass effect in a single year, but these mass effects were much weaker than within quadrat effects judging by the strength of the regressions. All other species had too few recruits to test for mass effects and we conclude that mass effects are relatively weak for 100 m × 100 m quadrats in the species tested.

Table 5. Density- and diversity-dependence in intrinsic rates of population increase. For notations see Table 2. Only species included in Table 4 are shown.

	Census Year								Interval	
	89	90	**91**	**92**	93	**94**	95	**96**	88-92	92-96
Cassia fistula										
CB	-	-	+	+	- - -	++	- - -	+	+	+
CA	- - -	-	+	-	- - -	++	- - - -	-	-	-
HB	+	- -	+	- - -	+	+	-	-	- -	+
HA	+++	- - - -	+	-	-	+	- - -	+	+	+
DI	-	+	-	-	-	-	+	+	-	+
Lagerstroemia microcarpa										
CB	-	- - - -	+	-	- - - -	-	-	++++	-	++
CA	-	- - - -	+	-	- - -	+	- -	++++	-	+
HB	++	+	+	+	+	+	+	-	+	+
HA	+	++	+	+	++	+	+	- - - -	+	+
DI	- -	+	-	- -	-	- -	+	+	- - -	+
Xeromphis spinosa										
CB	- - -	- - - -	x	-	x	x	-	x	-	-
CA	-	- -	x	-	x	x	-	x	-	-
HB	- -	-	x	-	x	x	+	x	-	+
HA	-	+	x	+	x	x	+	x	-	+
DI	+	+	x	+	x	x	-	x	+	-
Tectona grandis										
CB	+	-	++	+++	- -	+	- - -	++++	++	+++
CA	- -	-	+	++	- -	+	- -	++	-	++
HB	+	-	-	-	-	-	+	-	-	+
HA	-	-	-	+	- -	-	+	-	-	+
DI	-	++	+	- -	+	-	+	-	-	+

Density-dependence in the intrinsic rate of population increase

We performed these correlations only on those species that were included in the recruitment analysis. Intrinsic rates of population increase were largely negatively correlated with conspecific basal area, but some positive correlations were also obtained. Positive correlations were obtained only when fire had occurred, whereas the correlations were negative in the absence of fire (Table 5). Such effects were prominent in *Tectona grandis* and *Lagerstroemia microcarpa*. In *Cassia fistula*, intrinsic rate of increase was negatively correlated with conspecific basal area for the years 1993 and 1995 in which fire was absent and positively correlated in 1994 when fire was present. Similarly, there were positive but non-significant correlations in other years when fire was present. The correlations with conspecific abundance were similar to those with conspecific basal area, but the effects were weaker.

Correlations involving heterospecific basal area were non-significant in most species, with no consistent patterns in the sign of the correlations. In *L. microcarpa*, however, there were positive correlations with heterospecific abundance when fire was absent, and a negative correlation in a year when fire was present. Correlations with diversity were non-significant in most species but there were strong positive correlations in *Kydia calycina* and negative correlations in *L. microcarpa* (Table 5).

For the 4-yr interval rates, significant positive correlations with conspecific basal area were found in *T. grandis* for both 1988-1992 and 1992-1996 and in *L. microcarpa* for 1992-1996. Correlations with heterospecific density and diversity were mostly non-significant (Table 5).

Discussion

Density and diversity effects on mortality

Mortality among small trees was highly elevated due to extensive ground fires in many years during 1988-1996. Since the correlations suggest that in many species small-tree mortality was lower under dense patches of conspecific trees, it is possible that fire intensities are lower in such patches in these species resulting in lower death rates. Field observations and qualitative data on ground vegetation cover suggest that tall grasses and other herbaceous vegetation was relatively sparse underneath dense stands of *Lagerstroemia microcarpa* and *Xeromphis spinosa*, which could potentially explain the small-tree mortality patterns in these species. In some species, small trees were distributed away from dense patches of large trees. These small trees were mostly individuals that had recruited in recent years. Mortality was higher in the patches where small-tree densities were high, resulting in the negative correlations (Fig. 1).

Large-tree mortality rates were generally low in all species with very few adult deaths in any given year, and correlations with density were mostly non-significant. There were few significant correlations even for the 4-yr interval rates. However, the sign of the correlations were consistently positive in many species suggesting the direction in which density was influencing mortality. The positive density-dependence can be seen in Fig. 2 for *L. microcarpa*, where the large tree mortality is clearly concentrated in the high density patches. Such positive density-dependence can potentially have a stabilizing effect on populations in this species and is probably operating in other common tree species in Mudumalai. The data suggest that positive density-dependence in large-tree mortality could be important in *Anogeissus latifolia*, *Emblica officinalis*, *X. spinosa* and *Terminalia crenulata*, all common trees in the plot. However, longer-term data are needed to carry out more rigorous analyses of these patterns and to test more species because mortality rates for large trees have been very low at Mudumalai (< 1% per year for trees > 30 cm DBH) (Sukumar et al. 1998).

Wills et al. (1997) and Wills & Condit (1999) found very few significant effects of basal area or abundance of conspecific trees on tree mortality in the moist forests of BCI and Pasoh. Of the 84 abundant species in BCI that were tested, 20 species had significant negative correlations and 13 species positive correlations with conspecific basal area for both juvenile and adult survival. They conclude that in these forests, once the trees have reached 1 cm DBH, mortality is approximately random, but that non-random processes must be taking place during the period when the trees are small. A

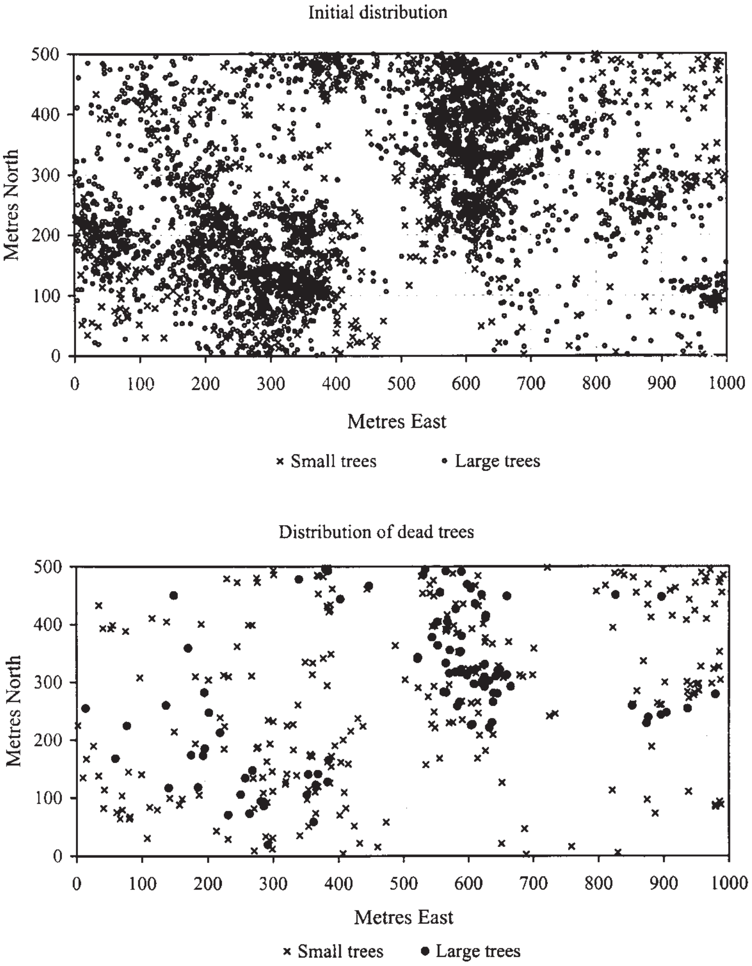

Fig. 1. Spatial patterns of mortality in *Lagerstroemia microcarpa* from 1992 to 1996. The top panel shows the initial distribution of trees in 2 size classes, 1 to < 10 cm diameter at breast height (DBH) (small trees) and ≥ 10 cm DBH (large trees). The distribution is highly clumped with 2 large clusters. The bottom panel shows the distribution of dead trees after the 4-yr interval for the same size classes. Here, the distribution of large trees is highly clumped and occurs mainly in the dense clusters. The distribution of small trees is also clumped, but less so. Density-dependence was negative for small tree mortality and positive for large tree mortality during this period.

direct comparison of the processes in Mudumalai with those at the 2 moist forests is difficult because the forests are so different. Certainly, disturbance by fire is influencing the patterns of mortality in this forest, especially among small trees, but longer-term data with controlled fire conditions would be needed to resolve density-related effects from those caused by disturbance.

Density and diversity effects on recruitment

In a different analysis (R. John & R. Sukumar unpubl.) we had examined recruitment probability of a focal species as a function of distance to the nearest conspecific adult. In that analysis, we found that there was significant inhibition of recruitment near conspecific adults in *Lagerstroemia microcarpa* and *Tectona grandis*. The peak in recruitment probability occurred some distance (20 - 30 m) away from adult trees in these species resulting in a repelled pattern of recruitment. A partially repelled pattern was seen in *Cassia fistula*, with the peak in recruitment 10 - 15 m away but with no inhibition close to adult trees. Here, we report that there is strong negative density-dependence in recruitment in these species when tested at a scale of 1 ha, which included many adult trees. Recruitment was lower in quadrats with a high basal area and abundance of conspecific trees. Though recruitment was poor in most species, strong negative density-dependence in recruitment was found in all species that did have higher recruitment rates. It is possible that these recruitment effects are due to thinning or intraspecific competition. However, we carried out sub-sampling of the plot to assess seedling densities and found that seedlings of these species did not occur at high densities anywhere in the plot, and that recruits had not arisen after thinning from a thick rank of seedlings.

Heterospecific basal area and, in particular, heterospecific abundance were strongly positively correlated with recruitment in *Lagerstroemia microcarpa* and to a lesser extent in *Tectona grandis*. The presence of negative conspecific-density effects and positive heterospecific-density effects in these canopy tree species suggests that inter-specific competition for shared resources such as nutrients and moisture or stress factors such as build-up of waste products or toxins are probably less important factors causing density-dependence. The same concept applies to the understorey species *Kydia calycina* and *Xeromphis spinosa*. We argue here that pests, pathogens or intraspecific effects involving resource-based trade-offs are important influences on recruitment in these species. If interspecific resource competition and stress factors were important high densities, regardless of species, should lower recruitment. Accordingly, the presence of significant negative density-dependence due to both conspecific and heterospecific density in the understorey species *Cordia obliqua* and, to a lesser extent, in *Cassia fistula* suggest that resource competition and/or stress factors have a significant influence on recruitment in these species.

Wills et al. (1997) and Wills & Condit (1999) report strong negative density-dependence in recruitment in both the BCI and Pasoh forests. In BCI, of the 84

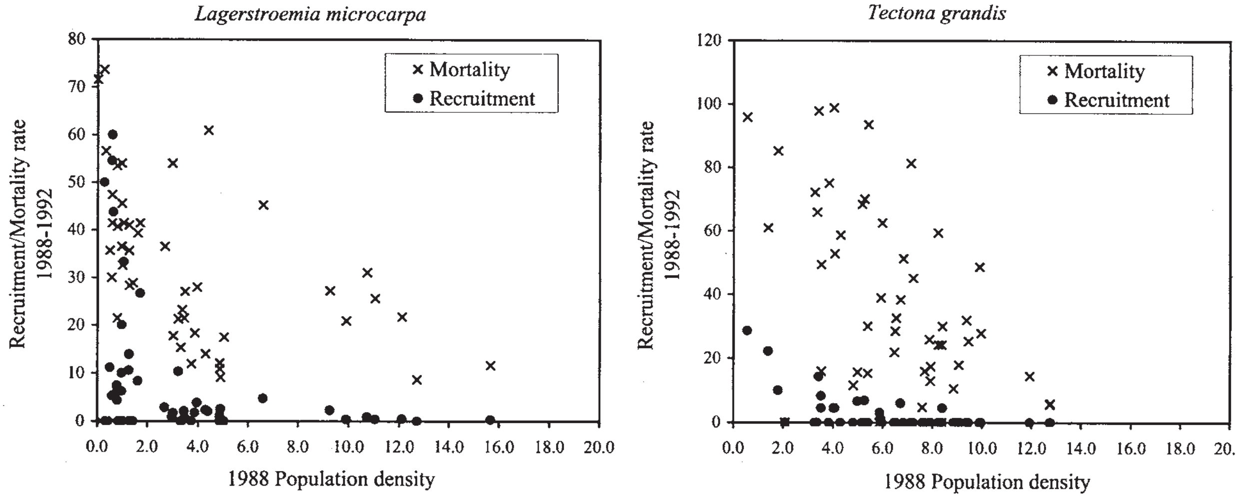

Fig. 2. Density-dependence in the canopy trees *Lagerstroemia microcarpa* (*Lythraceae*) and *Tectona grandis* (*Verbenaceae*), showing density-vague behaviour in both mortality and recruitment rates. Each point represents density (expressed as basal area in m^2) and *per capita* mortality/recruitment (%) in a 100 m × 100 m quadrat.

common species tested, 67 species had significant negative correlations with conspecific basal area, whereas only 5 species had significant positive correlations (Wills et al. 1997). Similarly, for the Pasoh forest, the distribution of mean *t*-values from correlation analyses for 100 common species was significantly negative, indicating that the nature of the correlations between recruitment and conspecific basal area were predominantly negative in the species examined (Wills & Condit 1999). Wills et al. (1997) also report that total abundance, and not total basal area, had strong negative effects on recruitment in a moist forest in BCI, Panama and argue that this crowding effect is an indicator of the importance of biotic influence on density-dependence in that forest. In comparison to the BCI forest, there are considerably fewer trees in Mudumalai, particularly in the smaller sizes, but basal areas are not much lower (Table 6). Thus, one would expect that crowding due to large numbers of trees would be more important in BCI than in Mudumalai, where the trees are sparsely distributed. Thus, while the weak intraspecific abundance-dependent effects in Mudumalai is probably due to less crowding, the factors that result in the observed basal area dependent effects need to be investigated.

In the BCI forest, where density- and frequency-dependent mechanisms have been identified, the mechanisms have been attributable to the actions of predators and pathogens and not to resource-based trade-offs (Hubbell et al. 1990; Wong et al. 1990; Gilbert et al. 1995). For the Mudumalai forest, however, we still do not have a mechanistic explanation for the observed density-dependence. The presence of strong density-dependence in some species indicates that causal factors are time-lagged in their action, because, if they were acting instantaneously, life-history parameters would be continuously ‘corrected’ and we would not be able to observe strong density-dependence (Hubbell 1998; Wills et al. 1997). The presence of time-lags argues strongly for the role of factors such as pests, pathogens or allelopathic effects that might take time to build up, and for a smaller role of seed predators in causing density-dependence (Hubbell 1998). The role of fungal pathogens and symbiotic fungi in influencing the diversity of plant communities has been persuasively argued (Hubbell 1998). The role of pests in deciduous forests is probably evident in the periodic outbreaks of a stem borer beetle that has caused death in a dipterocarp (*Shorea robusta*) over large areas of deciduous forest in central India (Beeson 1941). These forests are silviculturally managed for Sal timber at the expense of other species, thus decreasing the diversity of the community and increasing the density of Sal. In Mudumalai, a related Cerambycid beetle had killed all adults of a related species, *Shorea roxburghii*, in the area before the plot was established (Sukumar et al. 1992). Though our study has found patterns, more field studies are needed before the mechanisms of resource competition and stress factors versus other biotic factors in causing density-dependence in this forest can be properly assessed.

Table 6. Mean number of trees per ha, No. ind. and basal area (B) in the BCI and Mudumalai (Mud) plots. The figures for Mudumalai are for the 1988 census and 1995 for BCI (R. Condit pers. comm.).

Tree size class	No. ind.		B (m^2ha^{-1})	
	BCI	Mud	BCI	Mud
> 1cm DBH	4581.4	511.1	32.86	24.45
> 10cm DBH	429.2	300.7	28.56	23.85
> 30cm DBH	82.7	97.8	20.45	17.60

It should be noted here that strong, negative density effects in recruitment were found despite mortality being lower in high-density quadrats. One would expect that factors promoting survivorship, especially of juvenile trees, in high-density quadrats should also promote recruitment. Therefore, if mortality was lower in high-density quadrats, recruitment should have been higher and positive density-dependence in recruitment should have been found. Thus, the presence of negative density-dependence in recruitment indicates that the forces suppressing recruitment in high-density patches in this forest are strong. These strong density effects on recruitment into the ≥ 1 cm DBH class also indicate that the effects are important in the seed or early seedling stages, which this study has not monitored.

Vegetative coppicing is common in this forest, but field observations indicate that initial recruitment is mostly from seeds (pers. obs.). Shoots of seedlings are repeatedly burnt at very early stages and sprout vegetatively before attaining sizes ≥ 1 cm DBH. Clonal reproduction is limited, and if this were an important means of recruitment in this forest, attracted syndromes of recruitment would have been observed resulting in positive density-dependence in recruitment.

It is possible that the density-dependence detected here may simply be due to averaging i.e. the forest might simply be in a process of ‘smoothing out’ from an originally patchy distribution of trees. For instance, if the adult trees were clumped in distribution and the recruits were randomly distributed, then a quadrat-based test would yield negative density-dependence on per-adult demographic rates. To examine if the forest was indeed smoothing out with respect to these species, we examined whether the coefficients of variation of tree densities in 20 m × 20 m quadrats had changed during 1988-1996. The results are shown in Fig. 2 for 3 species in which strong negative density-dependence in recruitment was found. There was no evidence for decrease in clumping in the tree distributions in any of the species examined.

Diversity related effects were generally positive and higher diversity did seem to promote recruitment, but the patterns were not consistent. In *Lagerstroemia microcarpa* alone, there were some significant negative effects in addition to a positive effect. Positive correlations with recruitment and the quadrat's overall diversity would be expected if biotic factors were important (Wills et al. 1997).

Density and diversity effects on intrinsic rates of population increase

Intrinsic rates of increase, as defined here, summarize the combined effects of mortality and recruitment on population growth. Conspecific density- and abundance-effects on intrinsic rates of increase were generally negative in the absence of fire indicating that population growth was lower in quadrats with higher conspecific density, an effect that could regulate the abundance of such species. On the other hand, when extensive fires occurred intrinsic rates of increase were higher in quadrats of higher conspecific density, an effect that would promote species that show this effect. Further, the stronger effects on recruitment and the relatively few and weak effects on mortality suggest that density-dependence is more important in the very early stages of plant establishment in this forest. This study, focusing only on trees ≥ 1 cm DBH, precludes the possibility of detecting density-dependence in seed and early seedling stages, where much of the density-dependent effects are probably occurring.

Conclusion

We found significant density-related effects on recruitment of the kind that could regulate abundance, in a few common species in the dry deciduous forest in Mudumalai. Such effects, if more prevalent among the species in the community, can maintain tree species diversity in this forest. However, significant statistical correlations did not mean that recruitment or mortality was a direct mathematical function of density in the Mudumalai forest. Thus, for any given value of density, a range of recruitment and mortality rates were obtained (Fig. 3). This was particularly the case for low and intermediate values of density. Hubbell (1998) reports that in the moist forest in BCI, death rates were generally good mathematical functions of density but recruitment rates were not, except that there appeared to an upper boundary for *per capita* recruitment, and this upper boundary declined with density. Thus, recruitment in the BCI forest was density-vague *sensu* Strong (1986). In the Mudumalai forest, however, both mortality and recruitment rates were not good mathematical functions of density. This is expected in such relatively stressed environments, where environmental fluctuations, disturbance and other density-independent effects on mortality are likely to be more important than in moist forests such as BCI or Pasoh. Thus, while there is a broad, but significant, influence of density on mortality in some species, superimposed on these effects are also many density-independent effects. Similarly, recruitment will also be influenced by environmental stochasticity that affects year-to-year fecundity, seed and seedling survival and establishment. Thus, density-dependent regulation of plant populations in the Mudumalai forest, if present, appears density-vague with respect to both mortality and recruitment.

Finally, grass fires seemed to reverse some patterns of density-dependence such that some common species would increase in abundance if fires were frequent. Thus, if the decline in abundance of many species due to poor recruitment and high mortality as seen during 1988-1996 were to persist, an increase in dominance and a decrease in diversity in this forest would be expected even on short time scales. This study was limited to a few species due to the paucity of data for other species (due to the relative rarity of most species), but the species included here account for a substantial proportion of the species and individuals in the community. Clearly, further studies will be needed to disentangle the mechanisms causing density-dependence, and also to examine density-independent effects on tree population dynamics in Mudumalai.

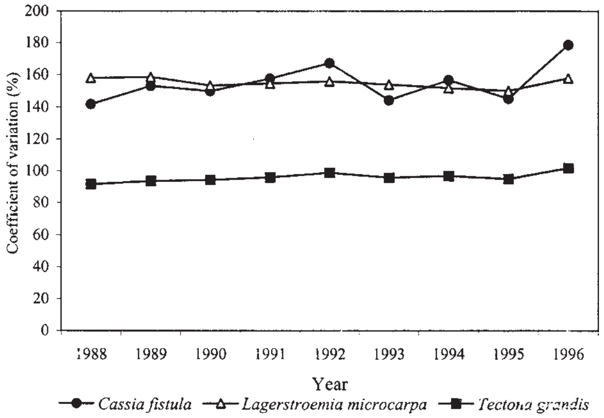

Fig. 3. Coefficients of variation (CV) for tree abundance in 20 m × 20 m quadrats for each year from 1988 to 1996 for 3 species. The CV values indicate that the degree of clumping in tree distributions has not changed in any consistent direction.

Acknowledgements. This study was funded by the Ministry of Environment and Forests, Government of India. We thank the Tamil Nadu Forest Department for permission to carry out the research. We are grateful to Rick Condit, Chris Wills and N.V. Joshi for several ideas and suggestions at various stages and to Steve Hubbell for inspiring this work. We deeply appreciate the untiring work of C.M. Bharanniah, Shivaji and several field assistants throughout the course of the field study. The Center for Tropical Forest Science, STRI gave logistical support at all stages.

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Received 16 March 2001;
Revision received 9 October 2001;
Accepted 9 November 2001.
Coordinating Editor: C. Leuschner.