Matrix model projections of selected canopy species' population dynamics, under different environmental regimes in the Mudumalai dry deciduous forest

Cheryl D. Nath, H. S. Suresh, H. S. Dattaraja, R. Sukumar

Technical Report No. 117
June 2007

Centre for Ecological Sciences
Indian Institute of Science
Bangalore – 560 012, India

Matrix model projections of selected canopy species' population dynamics, under different environmental regimes in the Mudumalai dry deciduous forest

Cheryl D. Nath, H. S. Suresh, H. S. Dattaraja, R. Sukumar

Technical Report No. 117
June 2007

Centre for Ecological Sciences
Indian Institute of Science
Bangalore – 560 012, India

For further information: Email: rsuku@ces.iisc.ernet.in; Tel: + 91 80 2360 0382; Fax: + 91 80 2360 2280

Abstract

The tropical dry forest in Mudumalai Wildlife Sanctuary, southern India, is under great pressure from surrounding human communities for livelihood and livestock related needs. Here we study the impacts of different environmental regimes on the long-term population trajectories of four canopy species in this forest community.

Basic demographic data were obtained between 1988-2000 from a 50hectare permanent vegetation monitoring plot set up in the Mudumalai Sanctuary by the Centre for Ecological Sciences in 1988. Matrix-based population dynamics modeling was carried out for the four dominant species, *Lagerstroemia microcarpa*, *Tectona grandis*, *Terminalia tomentosa* and *Anogeissus latifolia*. Long-term population trajectories were obtained under five different fire regimes and two different "worst case" scenarios in order to explore common species' potential response to changes in the current environmental regime at Mudumalai. The different fire frequency scenarios explored here included lower and higher average fire return intervals, in addition to the current average rate. The two worst case scenarios examined included one in which either the mortality and recruitment rate schedules were made "worse" than current rates, or one in which the mortality, recruitment and growth rate schedules were made worse. Initial transition matrixes were obtained from average annual growth, mortality and recruitment rates over the 12 year period of the study; starting population distributions were obtained from stand data of the 50ha plot in 1988; and population dynamics were projected for 500 years using a deterministic Leslie matrix model.

Populations of all four canopy species declined over the long term, while basal areas initially increased before ultimately declining for two species and increased for the other two species, under current environmental conditions. Results suggested that current recruitment rates from small into large size classes might be a limiting step for long-term population persistence at the Mudumalai dry forest. Recruitment from the smallest into medium size classes also was poor in the four species, and this largely determined year-to-year fluctuations in population abundance. While worst case mortality and recruitment rates caused overall reductions in population abundance and basal area, the use of worst case growth rates caused steeper population declines by making stems vulnerable to high mortality in small size classes, or conversely, could maintain higher than normal basal areas in some populations by preventing large stems from reaching sizes at which they senesce and die.

The results of this study suggest that currently dominant species in the Mudumalai dry deciduous forest could decline severely over the long term under current or worse environmental conditions. Thus improved fire management may be crucial to reduce the impacts of anthropogenically driven community changes in this dry tropical forest.

Acknowledgements

We thank the Ministry of Environment and Forests, Government of India, for providing funding and the Forest Department of Tamilnadu for permission to carry out fieldwork at Mudumalai. We thank Prof. N.V. Joshi for critical comments and help with the analysis. We also thank C.M. Bharanaiah, Shivaji, Sidda, Annadurai, M. Bomman and other Field Assistants at the CES Field Station, Masinagudi, for assistance with collecting tree measurements at the Mudumalai plot, and Mr. Y. G. Kanade at the CES Library for his help with formatting this Technical Report.

Contents

Introduction

The tropical dry forest of Mudumalai, southern India, is under great pressure from surrounding human communities for livelihood and livestock related needs, which include cattle grazing, dung collection, lopping, minor forest produce collection and setting fire to the undergrowth (Sukumar 1990; Narendran et al. 2001; Silori & Mishra 2001). Previous studies have pointed out the potential harmful effects of continued pressure on these forests (Sukumar et al. 1998; Narendran et al. 2004); however, no previously published studies have used a forest dynamics modeling approach to examine how environmental influences and variations are likely to influence the community structure in the long term. Given the paucity of information on tropical dry forest dynamics in India, such studies would provide useful information for long-term management of dry forests in Mudumalai, as well as elsewhere in India.

Here we examine long term population dynamics in the four commonest canopy species' in the Mudumalai dry deciduous forest, using matrix projection modeling (Caswell 1989). The four species were the following: *Lagerstroemia microcarpa*, *Tectona grandis*, *Terminalia tomentosa* and *Anogeissus latifolia*, which together constituted 44% of the population and 67% of the basal area of all trees censused at the initiation of the plot in 1988–89 (Sukumar et al. 2005). Information on growth and other parameters per species are given in Table 1. The matrix model was used to obtain long-term population trajectories under five different fire regimes and two different "worst case" scenarios, in order to find out how the commonest species may respond to improvement or worsening of the current environmental regime, in relation to effects of fire on mortality and recruitment, as well as of other environmental factors on growth.

Methods

1. Plot set up and data collection

A large permanent 50ha plot vegetation monitoring plot was set up in the Mudumalai dry deciduous forest in 1988-89 (Sukumar et al. 1992). Data used for the current analysis were collected from this plot between 1988 and 2000 by staff of the Centre for Ecological Sciences, Indian Institute of Science, Bangalore, using internationally standardized protocols (Condit 1998). Details regarding setting up the plot, data collection methods, topographic description, species composition, demographic rates and community dynamics have been published elsewhere previously (Sukumar et al. 1992; Sukumar et al. 1998; John et al. 2002; John & Sukumar 2004; Sukumar et al. 2004; Sukumar et al. 2005; Nath et al. 2006).

Girth measurements were obtained from all woody tree stems =1cm in diameter every four years during this 12 year period, which provided three intervals of diameter increment data on >13,000 trees. Tree growth data were obtained by manually measuring tree diameters and girths at breast height (dbh at 1.3m from the ground) for all stems in the 50ha plot. Stems that were damaged, deformed or jointed at the point of measurement were excluded, and where appropriate growth rate calculations included the contributions of all stems in multiple-stemmed individuals. Every year all mortalities and new recruits (ie., new stems =1cm dbh that were not recorded during the previous annual census) in the plot have been recorded, thus providing annual data for calculation of mortality and recruitment rates in these species.

2. Demographic rate calculations for matrix models

Data on growth, mortality and recruitment had been collected from trees in the 50-ha plot, as described above. Transition matrixes were obtained using different sets of size classes within the relevant size range per species. Size classes were chosen based on the average annual growth rates per species and on the proportions of individuals per class that were likely to remain within versus grow out of the current size class (in the positive direction) per year. Thus, the size class used for modeling *L. microcarpa* dynamics was 0.5cm, whereas that for the slow growing *T. crenulata* was 0.1cm (Table 1).

Table 1 Species' details and parameter values related to growth used in the model. "LAGL" = *Lagerstroemia microcarpa*; "TECG" = *Tectona grandis*; "TERT" = *Terminalia tomentosa*; "ANOL" = *Anogeissus latifolia.*

Species code	Average annual growth rate (1988-2000)	Worst case average annual growth rate (1992-1996)	Diameter class interval used in the model (cm)	# escape categories used in the model	Maximum diameter in the plot (cm)	Minimum and maximum diameter used in the model (cm)
LAGL	1.03	1.02	0.5	± 3	85.86	1 - 100
TECG	1.007	1.003	0.25	± 3	142.86	1 - 150
TERT	1.005	1.003	0.1	± 7	117.25	6 - 150
ANOL	1.008	1.005	0.2	± 4	75.41	6 - 100

Size-structured population parameters obtained from field data were smoothed within ±0.5cm of the recorded diameter (dbh or diameter at breast height, 1.3m), in order to offset measurement errors during field recordings of girth. In addition, curves were fit to growth and mortality rates across size classes per species, in order to reduce the effects of chance variations in size classes with low sample sizes. Details of calculations used to obtain demographic values per size class are given below.

1) Growth rate calculations

Diameter growth rate per individual was calculated as the average of annual rates obtained from three 4-yr measurement intervals (i.e., average of annual rates obtained from the intervals 1988-92, 1992-96 and 1996-2000). Annual growth rates were calculated assuming exponential growth (these values are quite similar to those obtained by assuming linear rates) between consecutive diameter measurements (Condit et al. 1993a, 1993b). For a "worst-case scenario", the annualised growth rates of 1992-96 were used for all four species, as most species in the plot were found to have experienced lowest-growth during this interval. All injured and broken stems as well as jointed stems were excluded to reduce inaccuracies from growth rate calculations. All stems, including primary and non-primary stems of multiple-stemmed individuals, were included for growth calculation. For each multiple-stemmed tree, the cross-sectional areas of all stems were pooled to obtain an integrated diameter for the whole tree.

Maximum allowable growth limits were set as detailed below, using *L. microcarpa* rates as a guide. These limits were used in order to eliminate the extreme outliers resulting from errors in data collection or entry. The growth limits used (while calculating average growth per size class) were:

1) For dbh 0.5 to <3cm: Max. growth rate = 2.5
2) For dbh 3 to <20cm: Max. growth rate = 1.5
3) For dbh 20cm or greater: Max. growth rate = 1.3
4) For all size classes, minimum growth rate allowed =0.5 (i.e., shrinkage of up to half of the current stem size per year; however, for most classes the actual limits used in the model were set by the maximum number of escape categories and the diameter class interval used per species. See Table 1, column #s 4 and 5)

These growth limits eliminated 2% or less of the data per species. In addition, while simulating population dynamics outlying escape classes were ignored, which depended on few individuals with extreme growth rates (see Table 1, column 5, for escape class limits per species). Thus specific limits of maximum increment were used per species, which eliminated 3% or less of growth rates.

In each size class different proportions of individuals achieved diameter increments per year that either confined them to the same size class in the following year (i.e., the "stay proportion") or allowed them to move out of the current size class in the positive or negative directions (i.e., the "escape proportions"). For those individuals escaping from the current size class, different proportions were able to move into size classes that were one or more steps away. These proportions of individuals escaping into higher or lower size classes were different per size class and per species. The maximum number of such escape categories incorporated into the model per species is given in Table 1 (column #5).

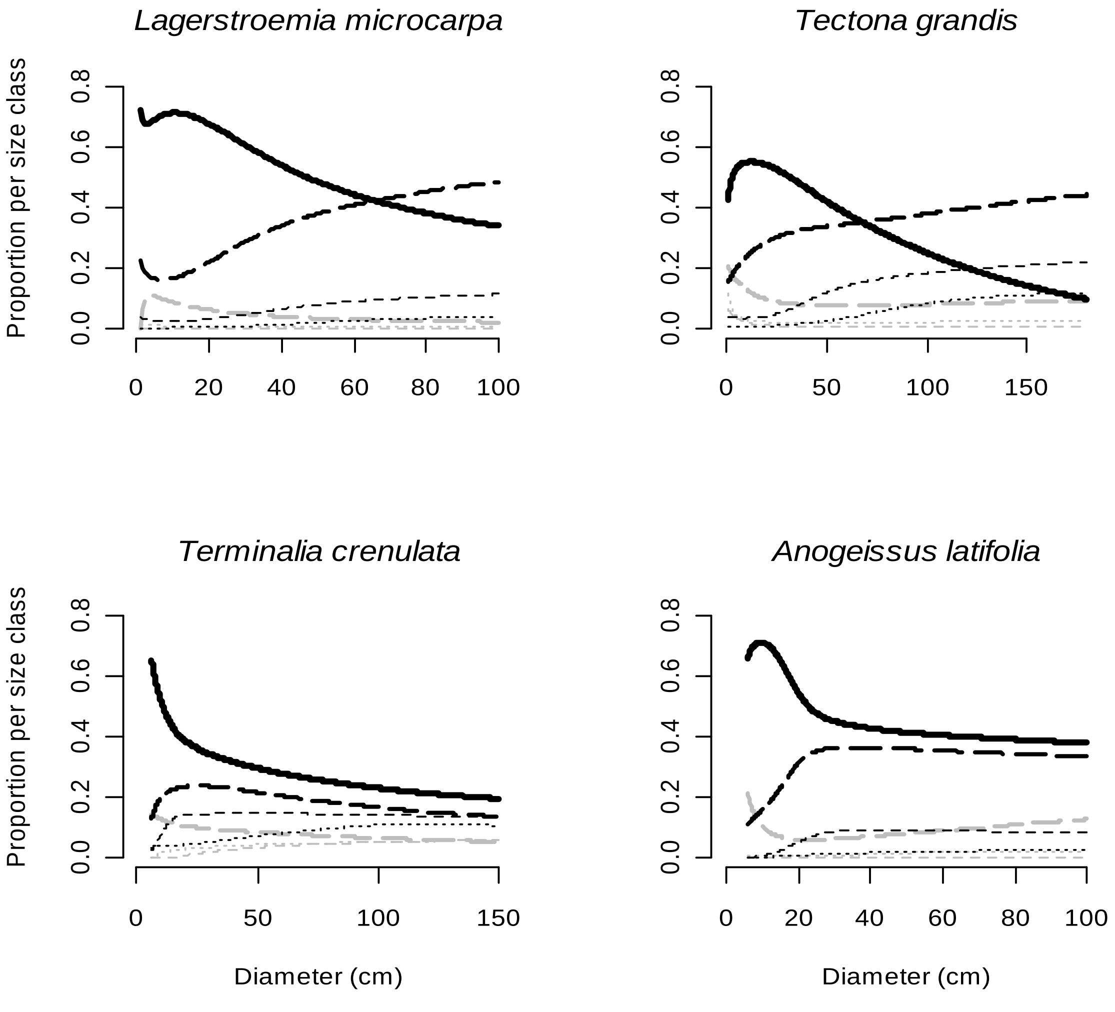
For each stay or escape category per species, curves were fit to escaping or staying individuals across all dbh classes after initially smoothing the data (see Figure 1). Smoothing of growth proportions was as follows: Size classes within the diameter range of 1cm and 10cm were smoothed using growth values of all classes within 0.5cm on either side of them; while classes with diameter =10cm were smoothed using growth values of all classes within ±5% of the current diameter class (incremental smoothing). Only those classes with frequency (after smoothing) of at least 30 individuals were used for obtaining best-fit curves per stay/escape class category, per species. In some cases where the proportions appeared to increase or decrease unreasonably in the highest size classes, the input data for curve fitting was truncated to avoid fitting extreme slopes for the highest size classes. Specific size classes per species that were used for fitting growth curves (i.e., stay and escape curves) are described below. Curve fitting was carried out using CurveExpert (trial version 1.34). Best-fit curves were chosen based on a combination of the following criteria: minimizing the Chi-square value, number of parameters and total of residuals, as well as maximizing the Pearson r-value. After fitting curves for different growth categories per species, all the curves per size class were summed together and normalized to ensure that all the growth category proportions per size class summed to 1.0 (Figure 1)**.**

Details of growth rate calculations per species:

L. microcarpa: Curves were fit to the smoothed data using size classes 1-65 cm for 1988-2000 growth rates, and size classes 1-55 cm for 1992-96 (worst case scenario) growth rates. The total number of escape categories used by the model was three (i.e., ± 1.5cm). Fitted curves include rational function, MMF model, sinusoidal fit, vapor pressure model, exponential association, polynomial fit, logistic model and linear fit (Equations for all curves are given at the end of this Report).

T. grandis: Curves were fit to the smoothed data, using size classes 1-80 cm for 1988-2000 growth rates, and size classes 23.75-75 cm for 1992-96 (worst case scenario) growth rates. Several lower size classes were omitted during curve fitting because of having frequencies, after smoothing, of less

Figure 1 Normalised fitted curves of proportions of individuals that remained in the original size class after one year ("stay" proportion, represented by thick and solid black lines below), or grew out of the existing size class in the positive or negative directions ("escape" proportions, represented by dashed and dotted lines below). Growth rates were based on three four-year intervals between 1988 and 2000, for the four commonest canopy species. Proportions of individuals escaping up to three size classes away in the positive and negative directions are plotted, with positive proportions in black and negative proportions in grey. Details of escape classes represented: one class away: long dashes; two classes away: short dashes; three classes away: dotted lines. The thickness of lines in the plots below becomes progressively reduced as they represent greater distance from the starting size class.



than 30. The total number of escape categories used was three (i.e., ± 0.75cm). Fitted curves include Hoerl model, Weibull model, MMF model, Richards model, geometric fit, exponential association, logistic model and linear fit.

T. crenulata: Due to the absence of small sized stems in the 50ha plot, a lower size class cut-off of 6cm was used in the *T. crenulata* model. Curves were fit to the smoothed data, using size classes 6-

78 cm for 1988-2000, and size classes 9.3-70 cm for 1992-96 (worst case scenario). The total number of escape categories used by the model was seven (i.e., ± 0.7cm). Fitted curves include heat capacity model, vapor pressure model, rational function, logarithmic fit, Hoerl model, MMF model, Harris model, exponential association, logistic model and linear fit.

A. latifolia: A lower size class cut-off of 6cm was used, as for *T. crenulata*. Curves were fit to smoothed data using size classes 7.8-50 cm for 1988-2000 and size classes 8.8-41 cm for 1992-96 (worst case scenario). The total number of escape categories used by the model was four (i.e., ± 0.8cm). Fitted curves include Weibull model, Richards model, heat capacity model, rational function, logarithmic fit, MMF model, quadratic fit, exponential association, logistic model and linear fit.

2) Mortality rate calculations

Mortalities per size class were calculated under four categories related to fire occurrences in the plot:

1. *Average rates*: Weighted average across all 12 years (1988-2000)
2. *Fire rates*: Weighted average across the five fire years (1989, 1991, 1992, 1994, 1996)
3. *nf1 rates*: Weighted average across the four non-fire years occurring one year after fire (1990, 1993, 1995, 1997)
4. *nf2 rates*: Weighted average across the three non-fire years occurring more than one year after fire (1998, 1999, 2000)

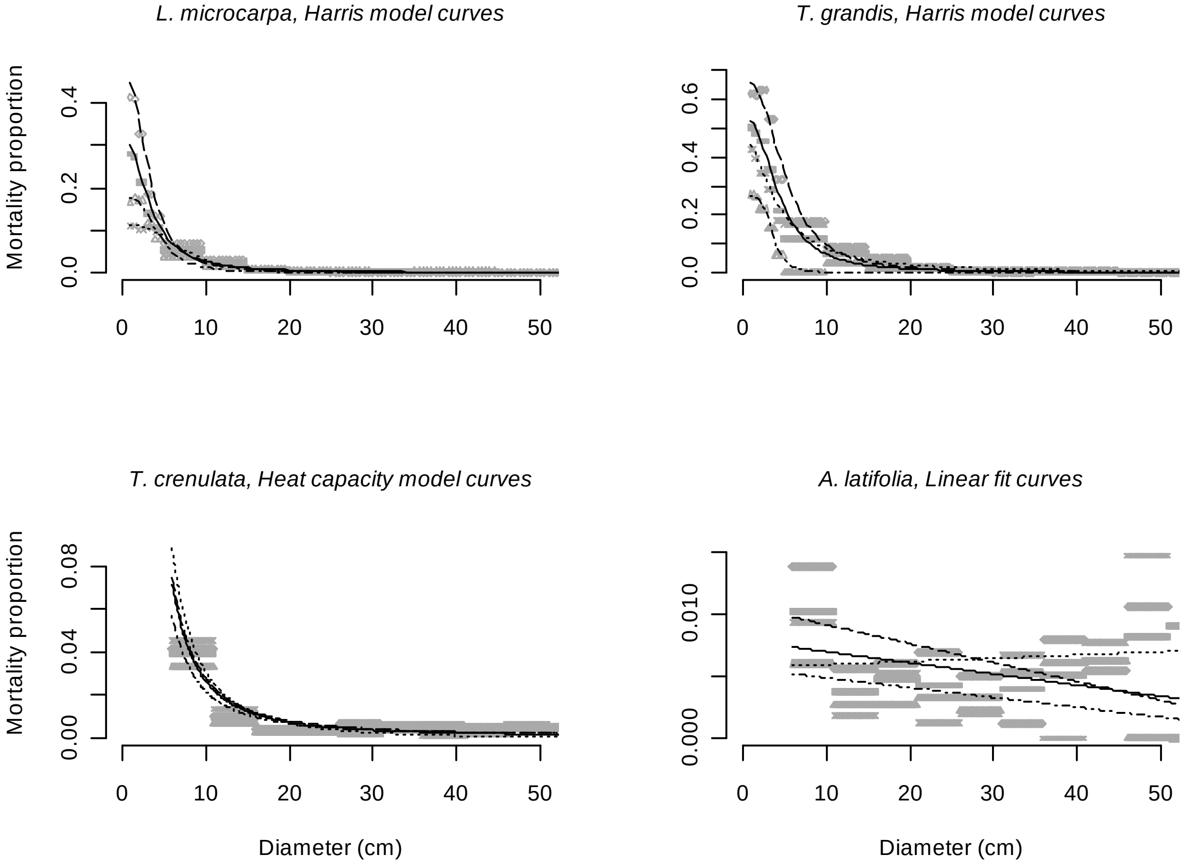
For all species, the average mortalities across size classes were clubbed together into larger size classes as described below:

1-2cm dbh clubbed using 0.5cm class intervals
2-5cm dbh clubbed using 1.0cm class intervals
5cm or greater dbh clubbed using 5.0cm class intervals

These larger group mortality rates were also smoothed using mortality values of the classes within ±0.5cm from the lower and upper group limits, in order to offset field measurement errors. Curves were then fit to the four sets of mortality rates, using a single type of curve per species. Thus, all mortality curves used for *L. microcarpa* and *T. grandis* were of Harris Model, while the Heat Capacity Model and the Linear Fit curves were used for *T. crenulata* and *A. latifolia*, respectively (Figure 2).

For "worst case mortality" values a 95% confidence interval could not be used due to the large variation in sample sizes under different fire conditions. Thus the original mortality curves were multiplied by 1.5 to obtain worst-case mortality values.

Figure 2 Mortality proportions per year in different size classes, in relation to fire occurrence for the four commonest canopy species in the Mudumalai 50ha plot. Mortality rates are based on annual censuses between 1988 and 2000. Diameter class values were clubbed into larger groups before fitting curves. Details of mortality rate calculations in relation to fire occurrence: 1. Averaged across all 12 years of data (represented by squares and solid black lines); 2. Fire years only (represented by diamonds and long dashed lines); 3. One year after fire (represented by triangles and dot-dash lines); 4. More than one year after fire (represented by crosses and dotted lines).

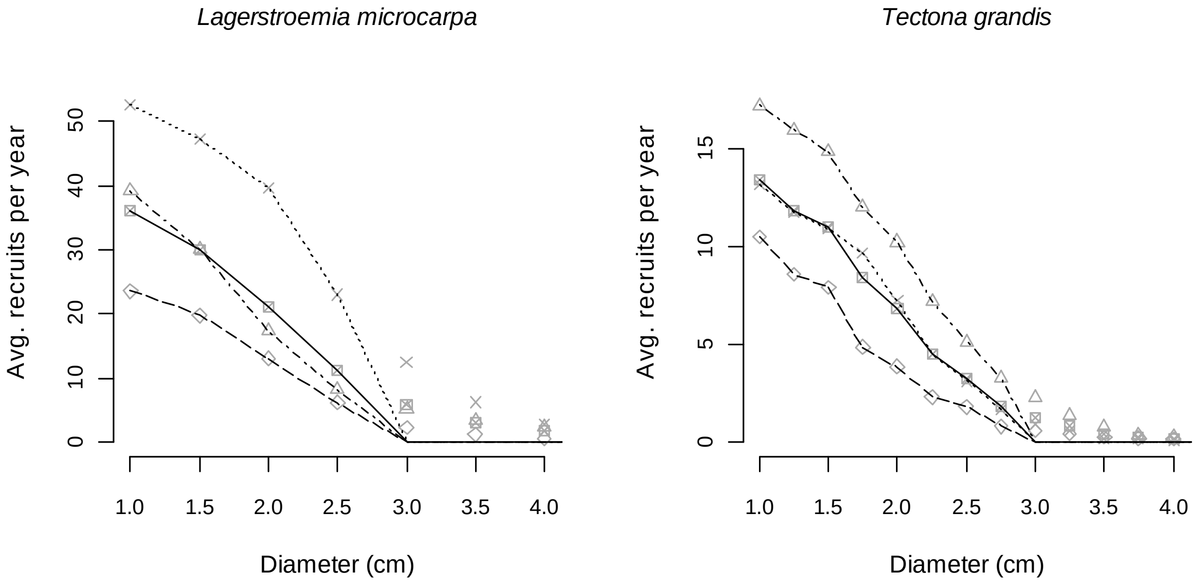


3) Recruitment rate calculations

Recruitment was incorporated into the model by calculating the average number of individuals recruiting per size class, up to 3cm dbh, under the four different types of fire conditions, as described above for mortality rates. As in mortality rate calculations, recruitment averages per size class were smoothed with recruitment values occurring within ±0.5cm from the lower and upper limits of each class, in order to offset field measurement errors. Recruitment was recorded only for *L. microcarpa* and *T. grandis* between 1988-2000 (Figure 3), whereas *T. crenulata* and *A. latifolia* showed no recruitment during this interval. Hence no recruitment was incorporated into the baseline models of *T. crenulata* and *A. latifolia.* The dbh for multi-stemmed recruits was calculated as described in the growth rate calculations section above. Worst-case recruitment values under each of the fire conditions was taken as 2/3 of the average recruitment value per size class.

Previously it has been speculated (Sukumar et al. 2005) that species that do not recruit stems on a regular basis in the Mudumalai dry forest may follow the lottery competition or temporal storage strategy (Chesson & Warner 1981; Warner & Chesson 1985). This strategy is characterised by long intervals without recruitment followed by recruitment bursts during favourable periods when large numbers of seedlings enter the population. For *T. crenulata* and *A. latifolia,* which did not recruit between 1988 and 2000, this strategy was tested for by adding small or large numbers of recruits (i.e., 10 or 50 recruits) into the smallest size class at two different frequencies (every five or 10 years). Three different fire regimes were used (Average, nil or alternate-year, details given below), to see if juvenile populations (i.e., trees up to 15cm dbh) of these species could stabilize under such recruitment influx, over a long time scale.

Figure 3 Average numbers of recruits per year in relation to fire occurrence, for two common canopy species. Recruitment rates are based on annual censuses between 1988 and 2000. Diameter class values were smoothed by ± 0.5cm prior to calculating recruitment rates. Details of recruitment calculations in relation to fire occurrence: 1. Averaged across all 12 years of data (represented by squares and solid black lines); 2. Fire years only (represented by diamonds and long dashed lines); 3. One year after fire (represented by triangles and dot-dash lines); 4. More than one year after fire (represented by crosses and dotted lines. The symbols (squares, diamonds, etc.) represent recruits recorded in the plot; however, in the models only recruits =3cm dbh were included (i.e., represented by lines in the plots below).



4) Other details of the models

Starting population distributions were obtained from stand data of the 50ha plot in 1988. All single and multi-stemmed individuals with dbh of at least 1cm were included. Multi-stemmed individuals' dbh was calculated as described in the growth rates section above. Models were tested to explore the response of species to different kinds of environmental variations. Several different scenarios that incorporate variations in fire regimes and low growth conditions were used for modeling each species' long-term dynamics. Population dynamics were modelled for 500 years and trees that grew beyond the largest dbh class were considered to have left the population (i.e., died).

For each of the four canopy species models of population change were examined under the following five fire regimes:

1) *Average fire regime:* An average of conditions present between 1988 and 2000
2) *Nil fire regime:* No fires
3) *Alternate-year fire regime:* Fire occurring every alternate year
4) *3-year fire regime:* Fire occurring every third year
5) *6-year fire regime:* Fire occurring every sixth year

For each fire regime the relevant set of mortality and recruitment rates was used in simulations (for e.g., under "average fire regime" only the average mortality and recruitment rates per species were used, whereas under "3-year fire regime" the mortality and recruitment rates used included fire rates as well as nf1 and nf2 rates).

In addition to the results obtained when using original parameter rates, two worst case scenarios were modelled under each fire regime:

Worst-case scenario1: the worst-case mortality and recruitment rates were used,

Worst-case scenario2: the worst-case mortality, recruitment and growth rates were used.

In all cases the population distribution at regular intervals was plotted in terms of the total number of individuals per size class, total population size and total basal area.

Results

Lagerstroemia microcarpa

1) Total population size and basal area, when using original rates with five fire regimes

The total number of stems was highest under the nil fire regime and lowest under the average fire regime for around 400 years (Figure 4a). At the end of 500 years, the range of total population sizes under the five different fire regimes was 270-1475 stems. The low trajectory under average fire regime is unexpected. This may have been related to the relatively higher values of the curve fitted to average mortality rates in the medium to high size classes. In conformity with expectations, however, the alternate-year fire regime had a lower population size trajectory than those of nil, 3-year or 6-year fire regimes.

Total population size declined moderately during the first 50-100 years and then more steeply between 200-300 years. These two declines are related to the reduction of juvenile classes initially (see Figure 6) and to the elimination of the largest stems from the population when they exceed the maximum dbh allowed by the model in later years. The relative positions of basal area (BA) trajectories under different fire regimes was reversed, with alternate-year fire regime producing the highest BA (Figure 4b). This may be influenced by the juvenile stems, which were responsible for high population size under nil-fire regime but contributed very little to the total basal area (Figure 6). In all five fire regimes tested, the total basal area of *L. microcarpa* stems in the 50-ha plot increased fourfold or more, from 174m^2 to 650-800 m^2 during the first 200 years, and then declined

2) Using worst case scenarios

Under worst case scenario1 (i.e., worst case mortality rates and recruitments), the trajectories of total population size under all five fire regimes were similar, showing an initial steep decline in population size, a levelling off and then a second steep decline (for e.g., see Figure 5). The shapes of the basal area trajectories were very similar to those obtained using the original parameter rates (with the exception of a small difference in the initial curve under nil fire regime), although the magnitude of final population size was much lower under worst-case mortality and recruitment. However, when using worst-case scenario2 the shape of the population trajectory changed, as worst-case growth rates also were used in the model. The second decline of total stems and the position of the maximum basal area peak were delayed by about 50-100 years. This was caused by the slower growth of stems into larger dbh size classes, resulting in delayed attainment of maximum basal area.

3) Comparison of juvenile versus adult total stems and total basal area per fire regime

Under all fire regimes (for e.g., see Figure 6), the initial decrease or increase in total stems over the first 100 years largely reflected patterns in juvenile stems, whereas the second decline in total stems reflected the pattern of adult stems being eliminated by the model at maximum dbh. In the case of basal areas, however, juvenile basal areas were negligible at all times and under all fire regimes, and the patterns of population basal area closely reflected those of adult stems alone. Thus, in *L. microcarpa*, whereas population size was affected by juvenile and adult stems, basal area was affected by adult stems only.

Figure 4 *Lagerstroemia microcarpa* population abundance and basal area trajectories over 500 yrs under five different fire regimes. The model parameter rates were calculated from field data collected in the 50ha plot during 1988-2000. Details of five different fire regimes used to obtain trajectories: 1. Average regime (represented by thick solid black lines); 2. Alternate-year fire regime (represented by long dashed black lines); 3. No fire (represented by black dotted lines); 4. Fire every third year (represented by grey dashed lines); 5. Fire every sixth year (represented by grey dotted lines).

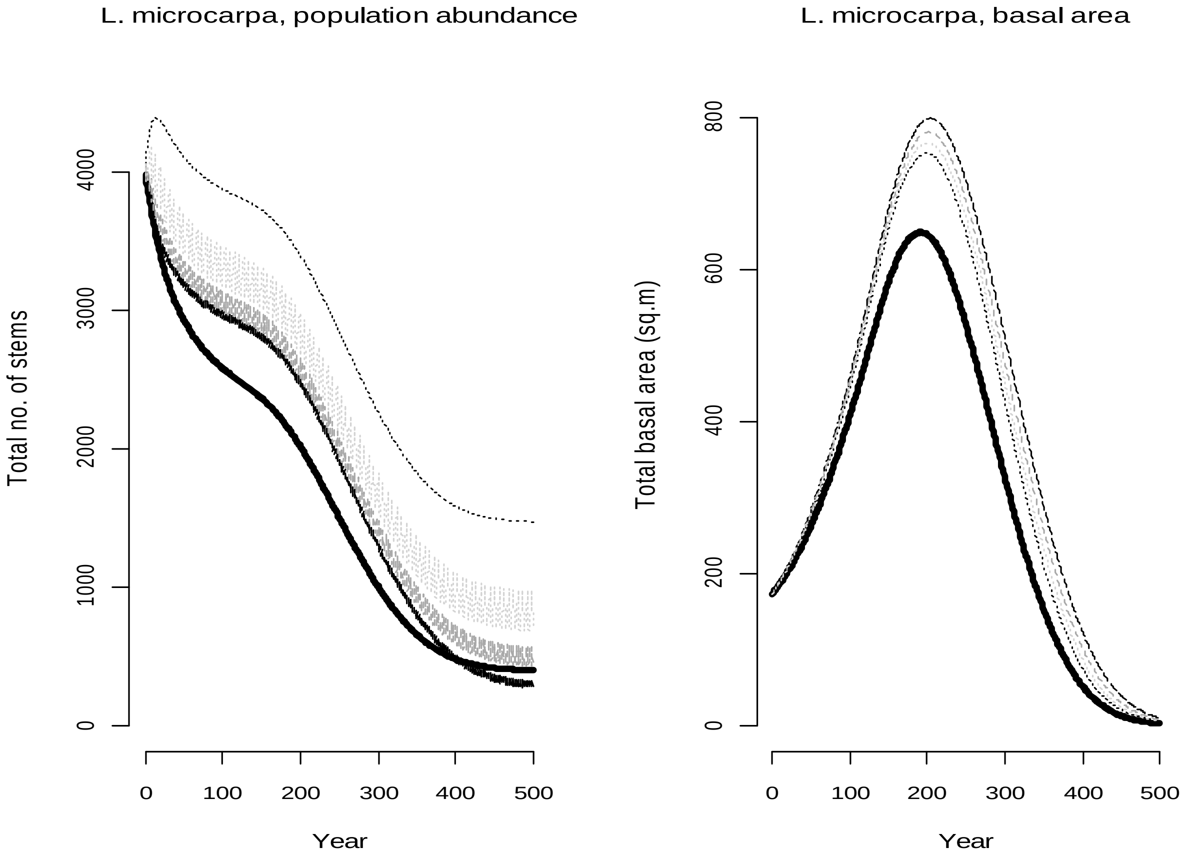


Figure 5 *Lagerstroemia microcarpa* population abundance and basal area trajectories over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values have been used, as well as worst-case scenarios (see text for details), to obtain population abundance (three thinner lines originating in top half of plots) or basal area trajectories (three thicker lines originating in bottom half of plots). The original parameter rates were calculated from field data collected in the 50ha plot during 1988-2000. The average and worst case scenarios used per plot below are the following: 1. Mortality, recruitment and growth rates averaged across 1988-2000 (black solid lines); 2. Worst case mortality and recruitment (dark grey dashed lines); 3. Worst case mortality, recruitment and growth (light grey dotted lines).

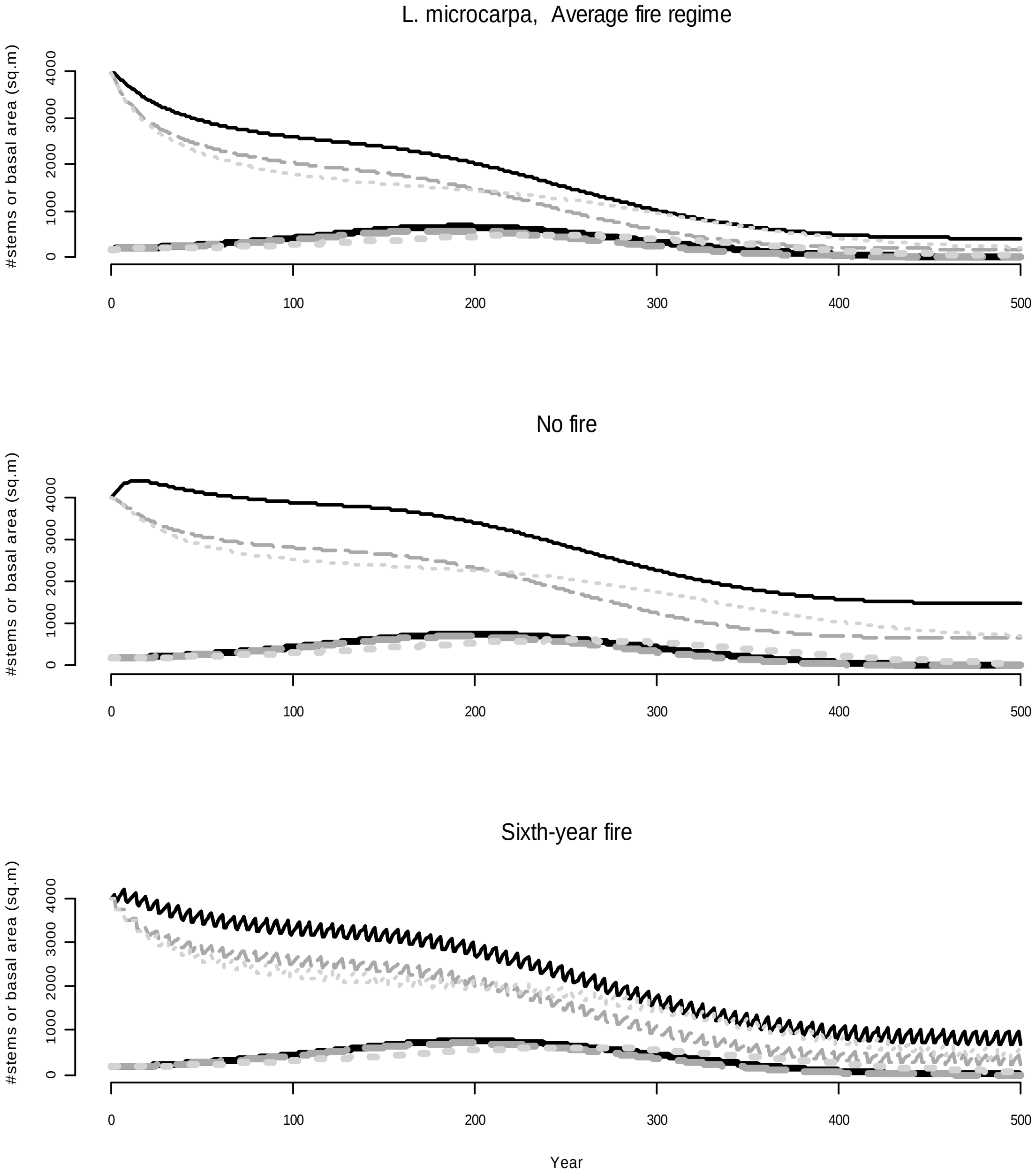
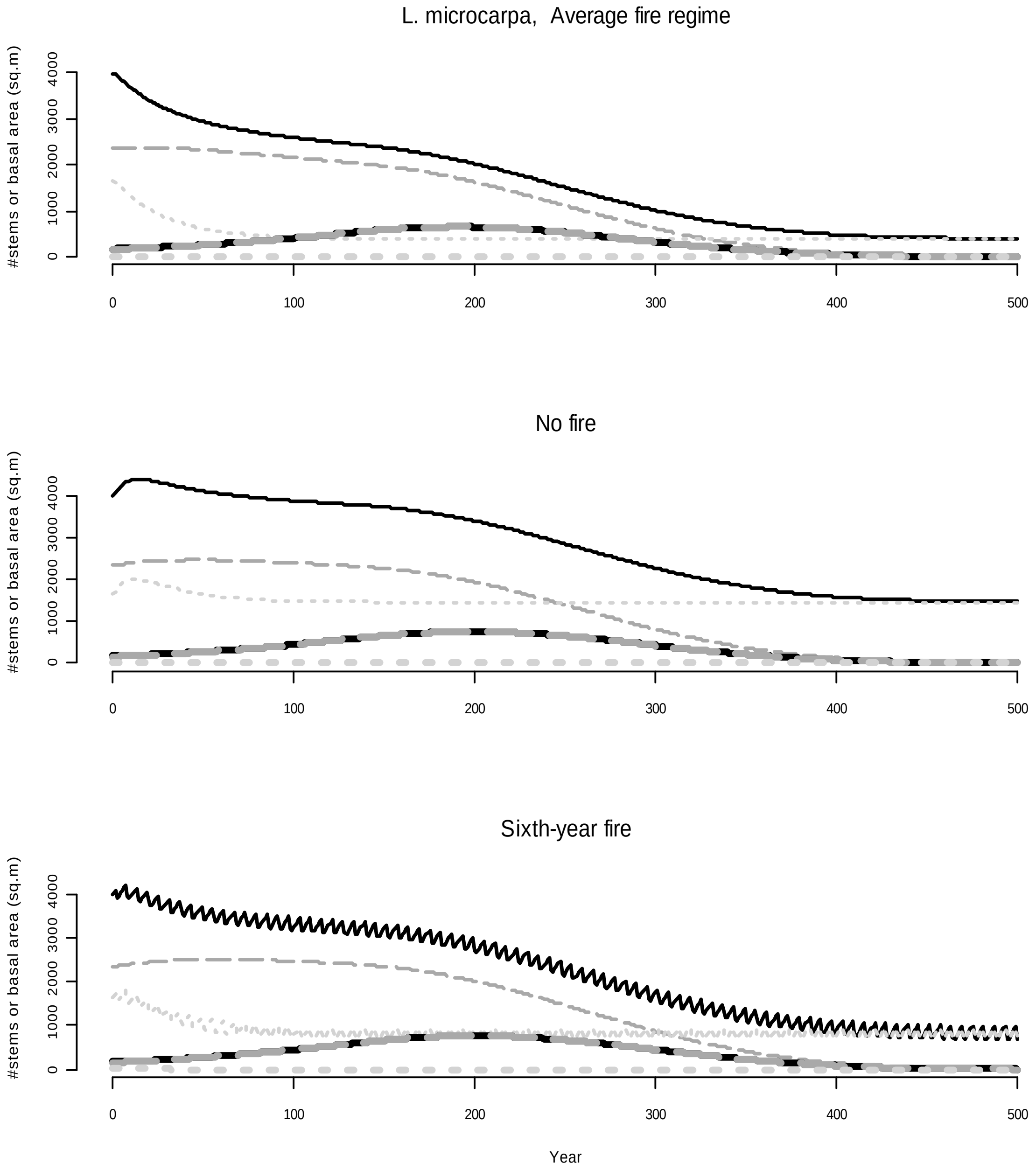


Figure 6 *Lagerstroemia microcarpa* population abundance and basal area trajectories for all stems, adults (>15cm dbh) and sub-adult (non-adults), over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values, calculated from field data collected in the 50ha plot during 1988-2000, were used to obtain population abundance (three thinner lines originating in top half of plots) or basal area trajectories (three thicker lines originating in bottom half of plots). Stems sizes are represented as follows: 1. All stems: black solid lines; 2. Adults: dark grey dashed lines; 3. Sub-adults: light grey dotted lines. Note that basal area of all stems is approximately the same as that of adults, while the sub-adult contribution to basal area is approximately zero throughout.



Tectona grandis

1) Total population size and basal area, when using original rates with five fire regimes

Under all fire regimes the total number of stems monotonically declined, while total basal area increased for the first 400 years and then declined (Figure 7) Contrary to the case of *L. microcarpa*, highest totals of stems and basal area occurred under alternate-year fire and lowest totals occurred under nil fire regime. This may be due to differences in relative positions of fire-related mortality curves in the medium to large size classes. In these classes, the nf2 mortality curve was the highest and probably caused the reversal in the relative positions of BA curves. Also in contrast to *L. microcarpa* was the relatively large difference in total BA, under different fire regimes. *T. grandis* had a higher maximum basal area than *L. microcarpa* (approximately 1,200 sq.m, also representing a fourfold increase). This may be because peak basal area occurs when most of the stems are in the largest dbh classes, and in *T. grandis* the maximum diameter limit used in the model for *T. grandis* (150cm) is 1.5 times that used for *L. microcarpa* (100cm).

2) Using worst case scenarios

Worst-case mortality and recruitment lowered the population trajectory considerably in all fire regimes, although the general shapes of the trajectories were maintained (Figure 8). Total basal area was most affected under nil and 6-year fire regimes. When worst-case growth was used all fire regimes showed steeper initial declines in total population size, while total basal areas declined throughout, under all fire regimes. Thus, in *T. grandis* retarding the already slow growth rate appears to make the larger stems vulnerable to relatively higher mortalities at lower size classes, and hence the population declines at an accelerated rate without gaining in basal area.

3) Comparison of juvenile versus adult total stems and total basal area per fire regime

Unlike in *L. microcarpa*, juvenile stems had very little influence on the population trajectories of *T. grandis*. Thus both, total population size and basal area closely reflected changes in adult stems only, except for a short and sharp decline related to juveniles within the first 10 years (Figure 9). This is probably because the proportion of juvenile stems at the beginning of the time interval was very low in *T. grandis* (around 17%), whereas in *L. microcarpa* the proportion of juveniles was higher (>41%).

From these simulations it appears that the *T. grandis* population trajectory is very sensitive to mortality rates in adult stems, and to relative differences between fire and non-fire mortalities and recruitment rates.

Figure 7 *Tectona grandis* population abundance and basal area trajectories over 500 yrs under different fire regimes. Details of five different fire regimes used to obtain trajectories: 1. Average regime (represented by thick solid black lines); 2. Alternate-year fire regime (represented by long dashed black lines); 3. No fire (represented by black dotted lines); 4. Fire every third year (represented by grey dashed lines); 5. Fire every sixth year (represented by grey dotted lines).

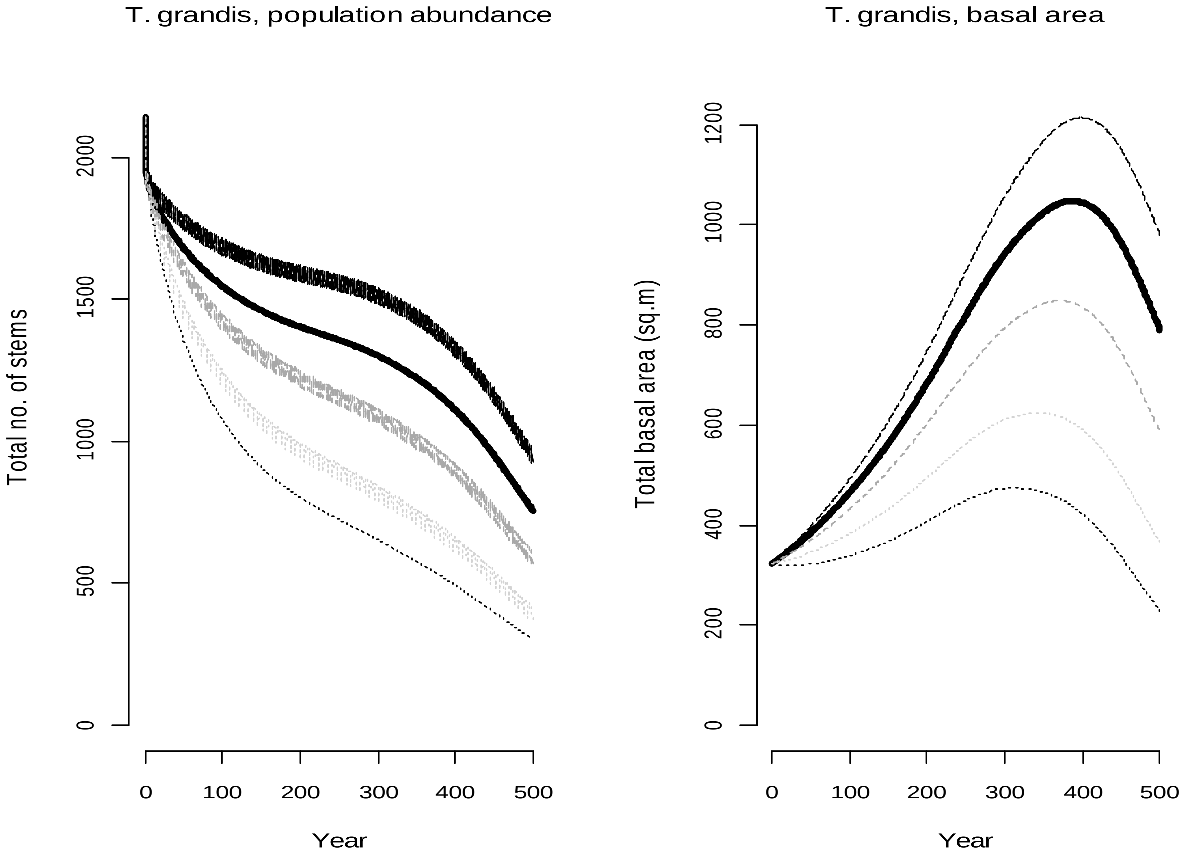


Figure 8 *Tectona grandis* population abundance and basal area trajectories over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values have been used, as well as worst-case scenarios (see text for details), to obtain population abundance (three thinner lines originating in top half of plots) or basal area trajectories (three thicker lines originating in bottom half of plots). The original parameter rates were calculated from field data collected in the 50ha plot during 1988-2000. The average and worst case scenarios used per plot below are the following: 1. Mortality, recruitment and growth rates averaged across 1988-2000 (black solid lines); 2. Worst case mortality and recruitment (dark grey dashed lines); 3. Worst case mortality, recruitment and growth (light grey dotted lines).

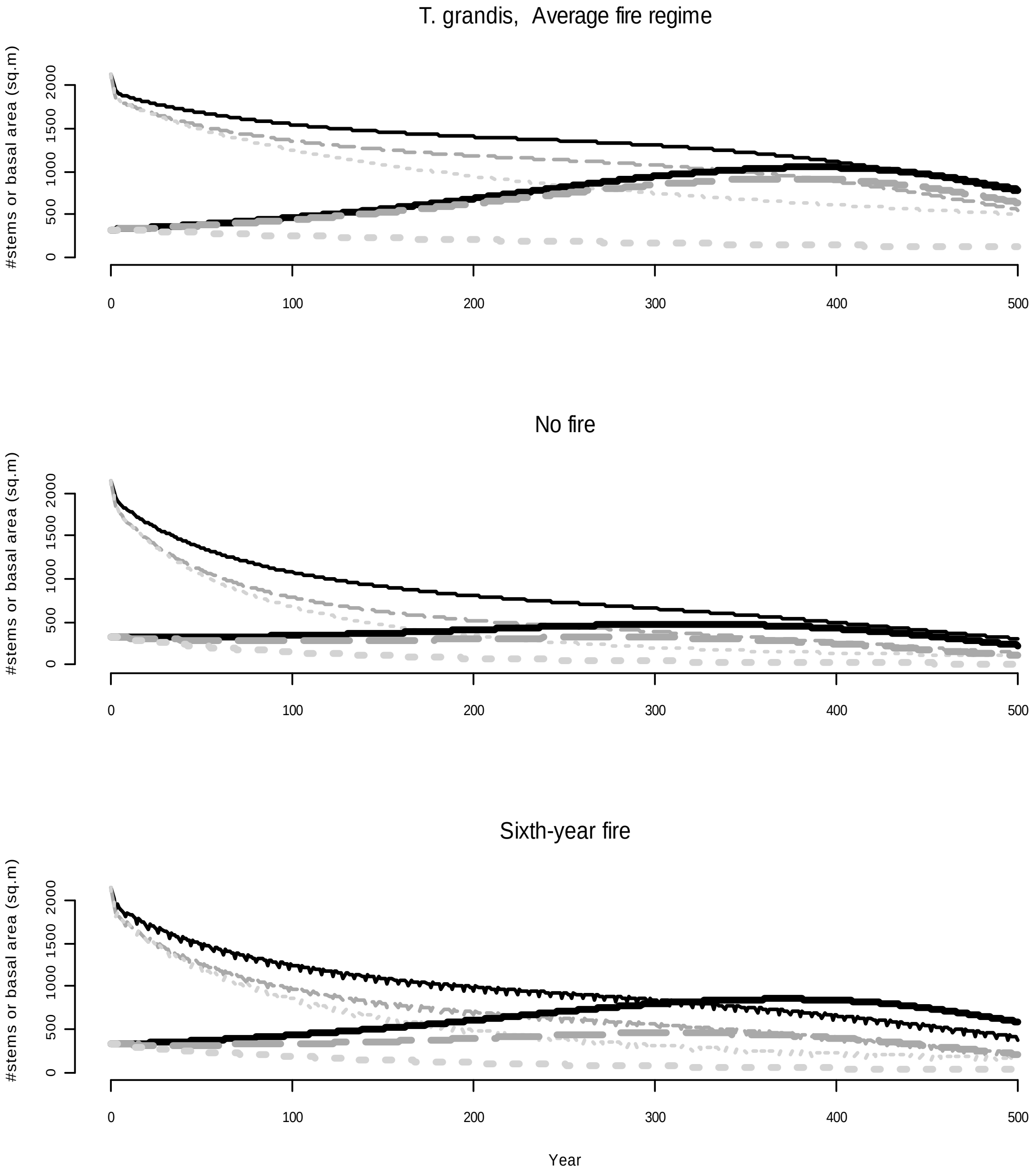
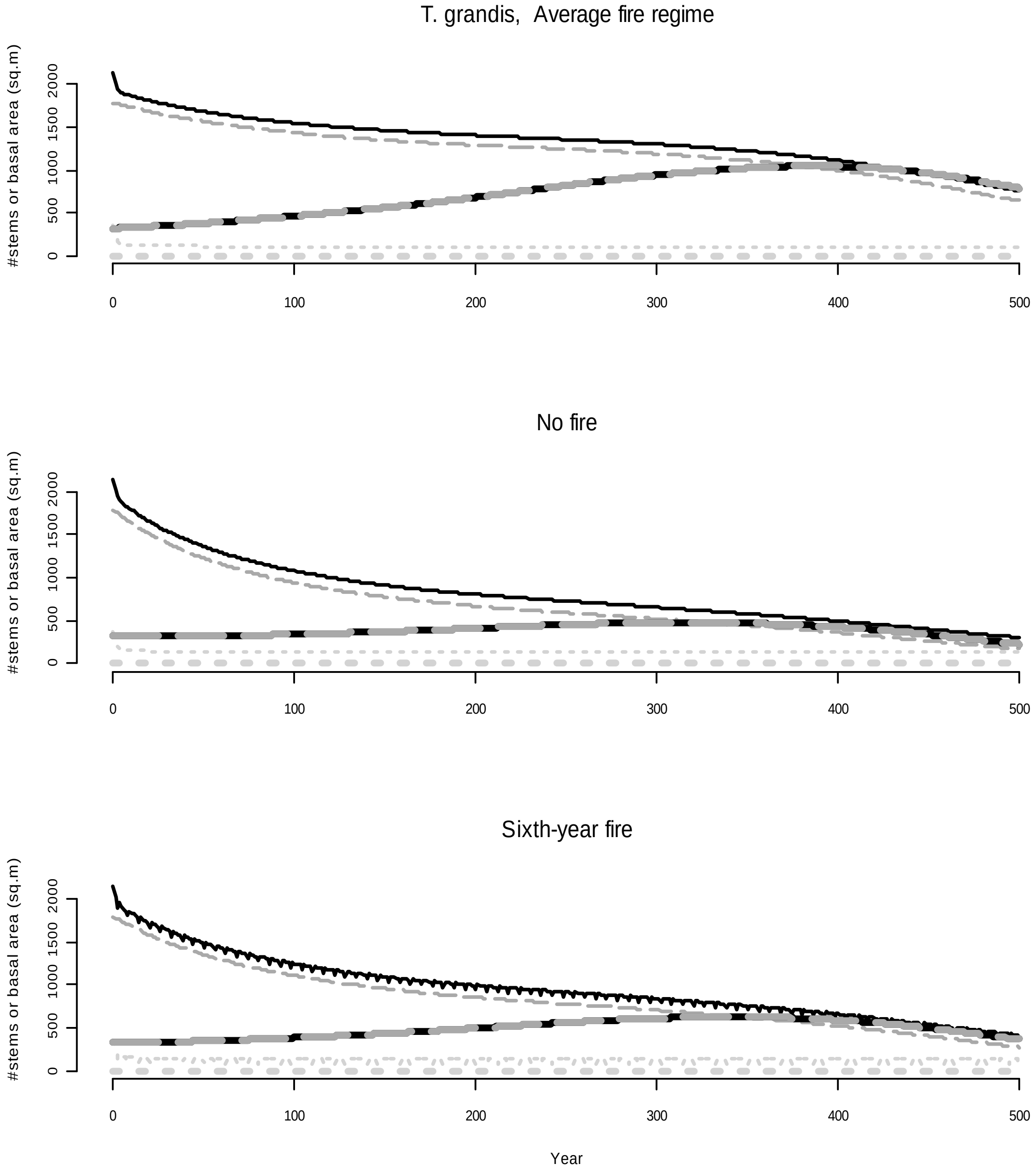


Figure 9 *Tectona grandis* population abundance and basal area trajectories for all stems, adults (>15cm dbh) and sub-adult (non-adults), over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values, calculated from field data collected in the 50ha plot during 1988-2000, were used to obtain population abundance (three thinner lines, two of which originate in the top half of plots) or basal area trajectories (three thicker lines originating in bottom half of plots). Stems sizes are represented as follows: 1. All stems: black solid lines; 2. Adults: dark grey dashed lines; 3. Sub-adults: light grey dotted lines. Note that basal area of all stems is approximately the same as that of adults, while the sub-adult contribution to basal area is approximately zero throughout.



Terminalia crenulata

1) Total population size and basal area, when using original rates with five fire regimes

There was a monotonic decline in total population size under all fire regimes, while total basal area monotonically increased under all fire regimes and showed relatively higher variance than total stem trajectories (Figure 10). As expected, the lowest fire frequency (nil fire regime) produced highest final basal area, roughly doubling the starting basal area, while highest fire frequency (alternate-year fire regime) produced lowest final basal area with a minor increase over the starting value.

2) Using worst case scenarios

Under all fire regimes and both worst-case scenarios there was a steep decline in total number of stems (Figure 11). Worst-case growth rates caused population size to decrease at a faster rate and caused total basal area to switch from originally increasing to a monotonic decline under all fire regimes, as in *T. grandis*. This may be because low growth rates cause stems to stay longer in the lower size classes where they are vulnerable to relatively higher worst-case mortality rates.

3) Comparison of juvenile versus adult total stems and total basal area per fire regime

The proportion of juvenile stems in the population at the initial stage was around 26%. This made the population size trajectory sensitive to juvenile declines in the first 50-100 years (Figure 12). Since juveniles declined almost to zero subsequently under all fire regimes, the population trajectory was essentially the same as the adult trajectory in later years. As in the other species, juvenile stems contributed almost nothing to total basal area, throughout the 500-year interval.

4) Effect of adding recruitment at regular intervals

In general, the rates of recruit addition tested here did not produce juvenile populations that stabilized with greater than 50 individuals under any fire regime, except when the number of recruits added was reasonably large (50) and the no-recruitment interval was relatively short (i.e., five years, see Figure 13) Juvenile basal area was not appreciably different from the original values under any of the recruitment input scenarios tested here. This indicates that enhancing recruitment in *T. crenulata* is unlikely to substantially change the population trajectories unless very large numbers of recruits enter the population very frequently.

In *T. crenulata* relative differences in mortality due to different fire regimes seems to strongly affect the population size and basal area. Population size and basal area are largely dependent on adult stems under current simulation conditions.

Figure 10 *Terminalia crenulata* population abundance and basal area trajectories over 500 yrs. Details of five different fire regimes used to obtain trajectories: 1. Average regime (represented by thick solid black lines); 2. Alternate-year fire regime (represented by long dashed black lines); 3. No fire (represented by black dotted lines); 4. Fire every third year (represented by grey dashed lines); 5. Fire every sixth year (represented by grey dotted lines).

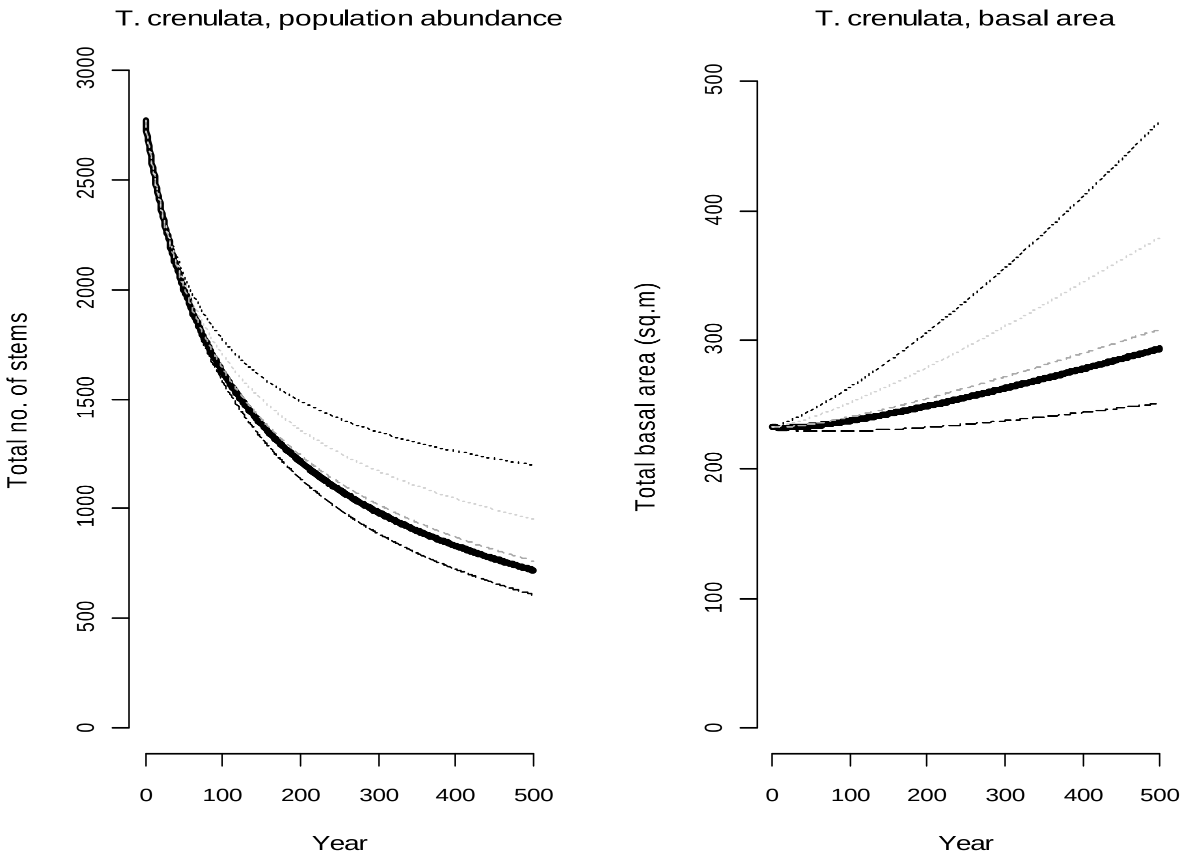


Figure 11 *Terminalia crenulata* population abundance and basal area trajectories over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values have been used, as well as worst-case scenarios (see text for details), to obtain population abundance (three thinner lines originating in top half of plots) or basal area trajectories (three thicker lines originating in bottom half of plots). The original parameter rates were calculated from field data collected in the 50ha plot during 1988-2000. The average and worst case scenarios used per plot below are the following: 1. Mortality, recruitment and growth rates averaged across 1988-2000 (black solid lines); 2. Worst case mortality and recruitment (dark grey dashed lines); 3. Worst case mortality, recruitment and growth (light grey dotted lines).

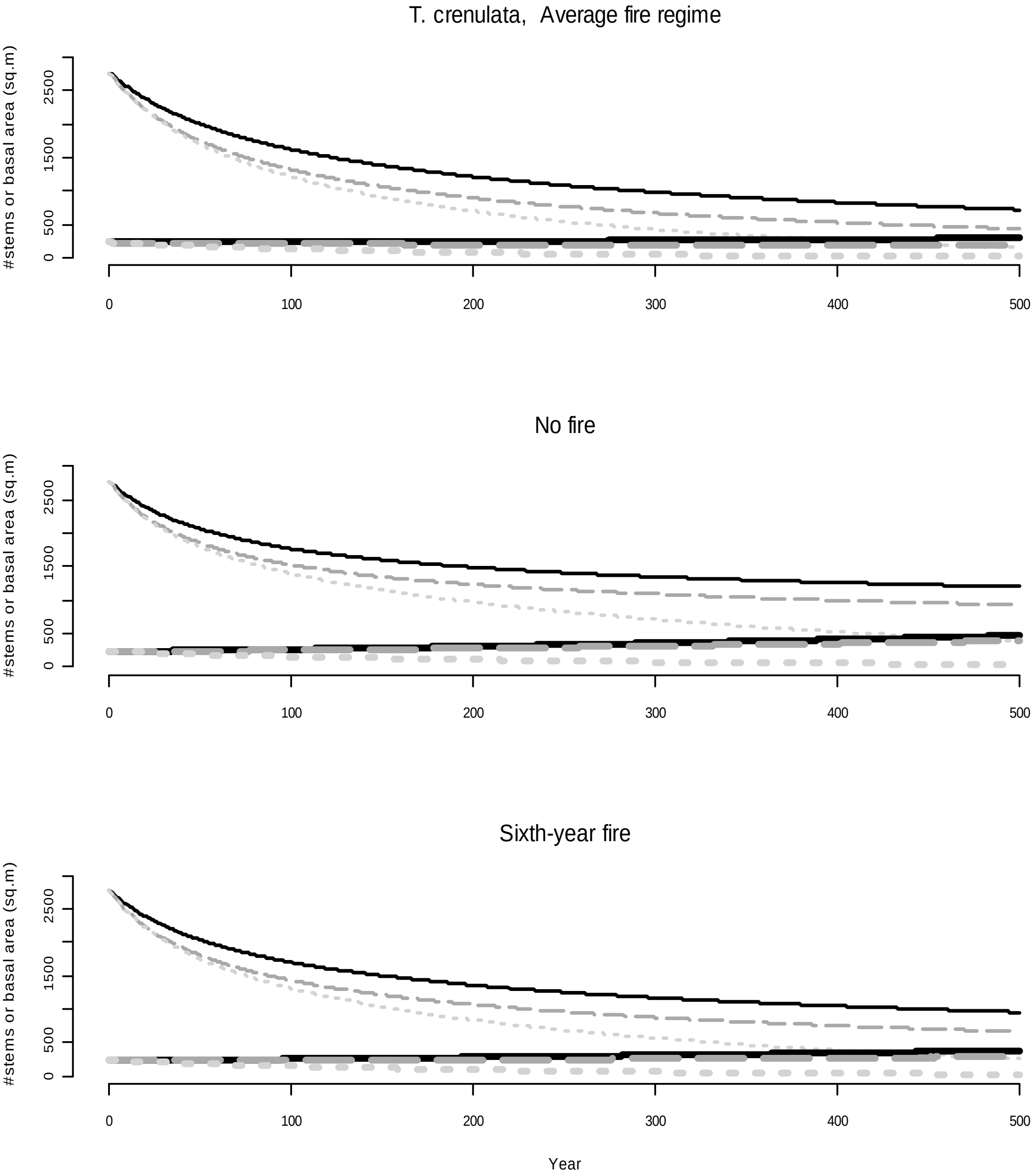


Figure 12 *Terminalia crenulata* population abundance and basal area trajectories for all stems, adults (>15cm dbh) and sub-adult (non-adults), over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values, calculated from field data collected in the 50ha plot during 1988-2000, were used to obtain population abundance (three thinner lines, two of which originate in top half of plots) or basal area trajectories (three thicker lines originating in bottom half of plots). Stems sizes are represented as follows: 1. All stems: black solid lines; 2. Adults: dark grey dashed lines; 3. Sub-adults: light grey dotted lines. Note that basal area of all stems is approximately the same as that of adults, while the sub-adult contribution to basal area is approximately zero throughout.

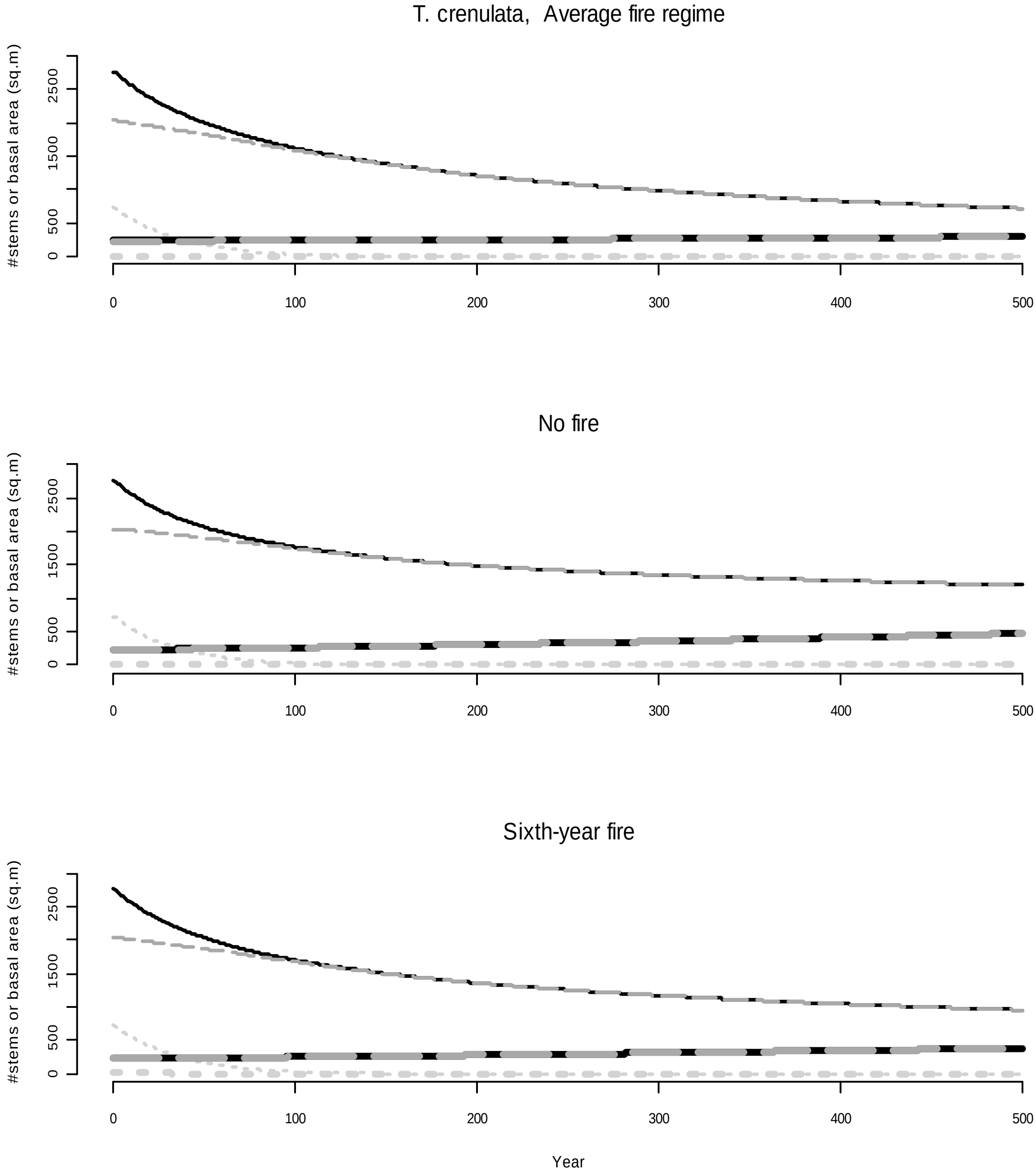
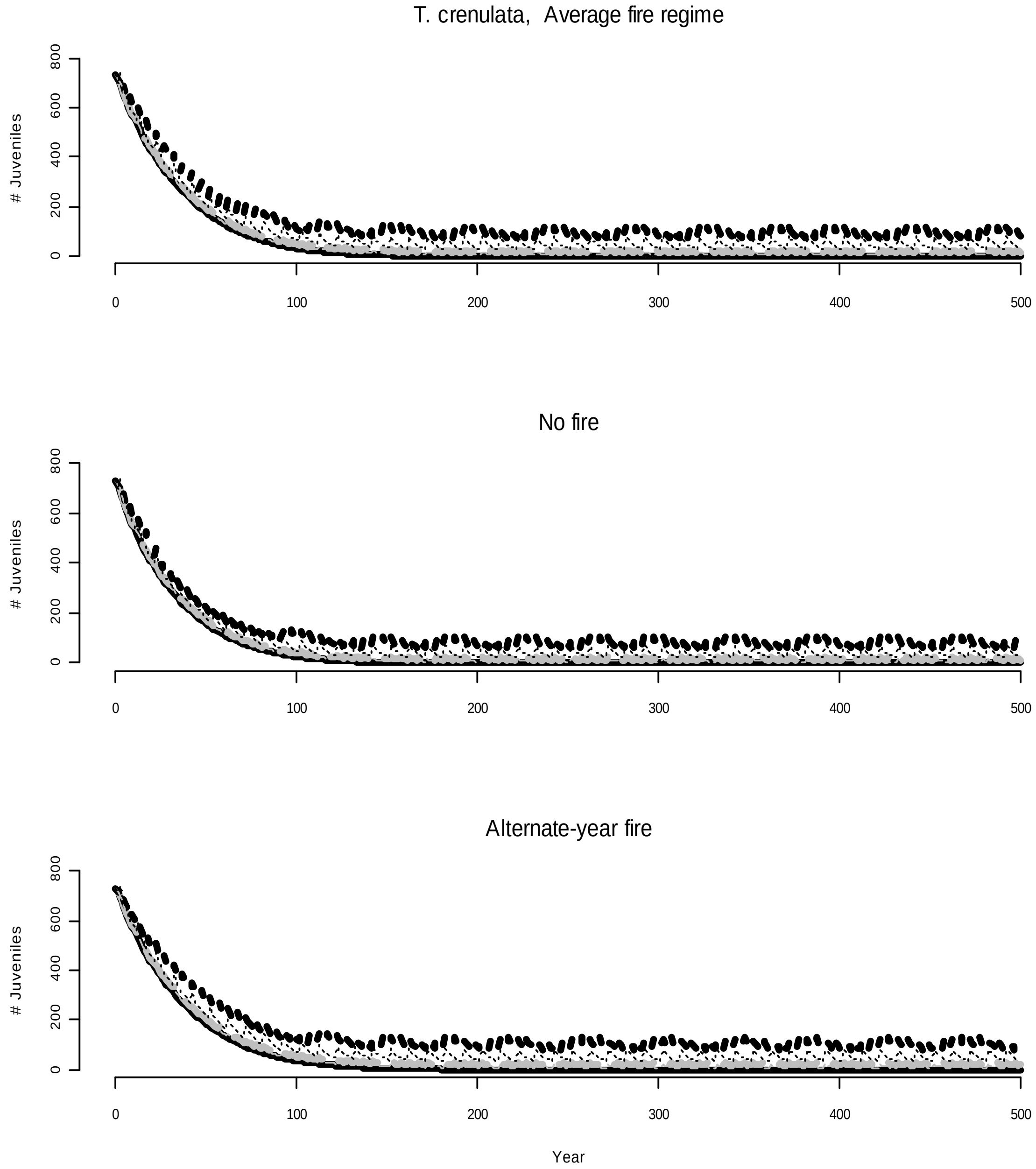


Figure 13 Terminalia crenulata juvenile (<16cm dbh) population abundance trajectories obtained after addition of recruitments every five or 10 years, with total recruitment input sizes of 10 or 50. Original mortality, recruitment and growth values, calculated from field data collected in the 50ha plot during 1988-2000, were used with three different fire regimes (average, nil and alternate-year fire regimes). Trajectories with different recruitment addition schedules are represented with black, grey, solid, dashed or dotted lines, as follows: 1. No recruits added: thickest solid black line showing the lowest baseline trajectory; 2. According to frequency of recruits added: thicker lines = higher frequency (five year intervals), thinner lines = lower frequency (10 year intervals); 3. According to number of recruits added: black dots = more recruits (50), grey dashes = fewer recruits (10).



T. crenulata, Average fire regime

No fire

Alternate-year fire

Anogeissus latifolia

1) Total population size and basal area, when using original rates with five fire regimes

Total population size declined exponentially under all fire regimes, as in the case of *T. crenulata* (Figure 14). The relative positions of the five curves showed unexpected relative trajectory positions, with the highest fire frequency producing the highest population trajectory and vice versa. This was probably due to the negatively sloping fire mortality curve that contrasted with the positively sloping and several-fold higher nf2 mortality curve, in medium to large dbh size classes**.** As a result, total basal areas also showed qualitatively different patterns under different fire regimes: Whereas high fire frequencies produced increasing basal areas, lower fire frequencies produced initially increasing (for the first 50-100 years) and subsequently decreasing basal areas (Figure 14). *A. latifolia* had the lowest maximal basal area of the four species.

2) Using worst-case scenarios

In all cases total population size declined steeply, while basal area showed a similar variation in trajectories across different fire regimes (Figure 15). However, under worst-case scenario2, basal areas declined under all fire regimes, perhaps as a result of large stems becoming vulnerable to higher mortality rates under reduced growth rates.

3) Comparison of juvenile versus adult total stems and total basal area per fire regime

Juvenile declines contributed to total stem decline during the first 100-150 years, as they comprised 31% of the starting population (Figure 16). As in the other species, however, they did not contribute much to total basal area.

4) Effect of adding recruitment at regular intervals

Addition of recruits to the lowest size class produced similar results as in *T. crenulata*. There was a substantial increase in juvenile population size only when the number of recruits added was large (50) and the no-recruitment interval was short (five years, Figure 17). Also, as in the case of *T. crenulata*, juvenile basal area was not appreciably changed by regular addition of recruits. Thus recruitment enhancements in *A. latifolia* also need to be very large and very frequent in order to impact the total population trajectories.

The simulations indicate that *A. latifolia* population size and basal area are highly sensitive to mortality rates in the medium to large dbh size range. Juvenile populations affected total population size initially, while adult trees were responsible for changes in basal area.

Figure 14 *Anogeissus latifolia* population abundance and basal area trajectories over 500 yrs. Details of five different fire regimes used to obtain trajectories: 1. Average regime (represented by thick solid black lines); 2. Alternate-year fire regime (represented by long dashed black lines); 3. No fire (represented by black dotted lines); 4. Fire every third year (represented by grey dashed lines); 5. Fire every sixth year (represented by grey dotted lines).

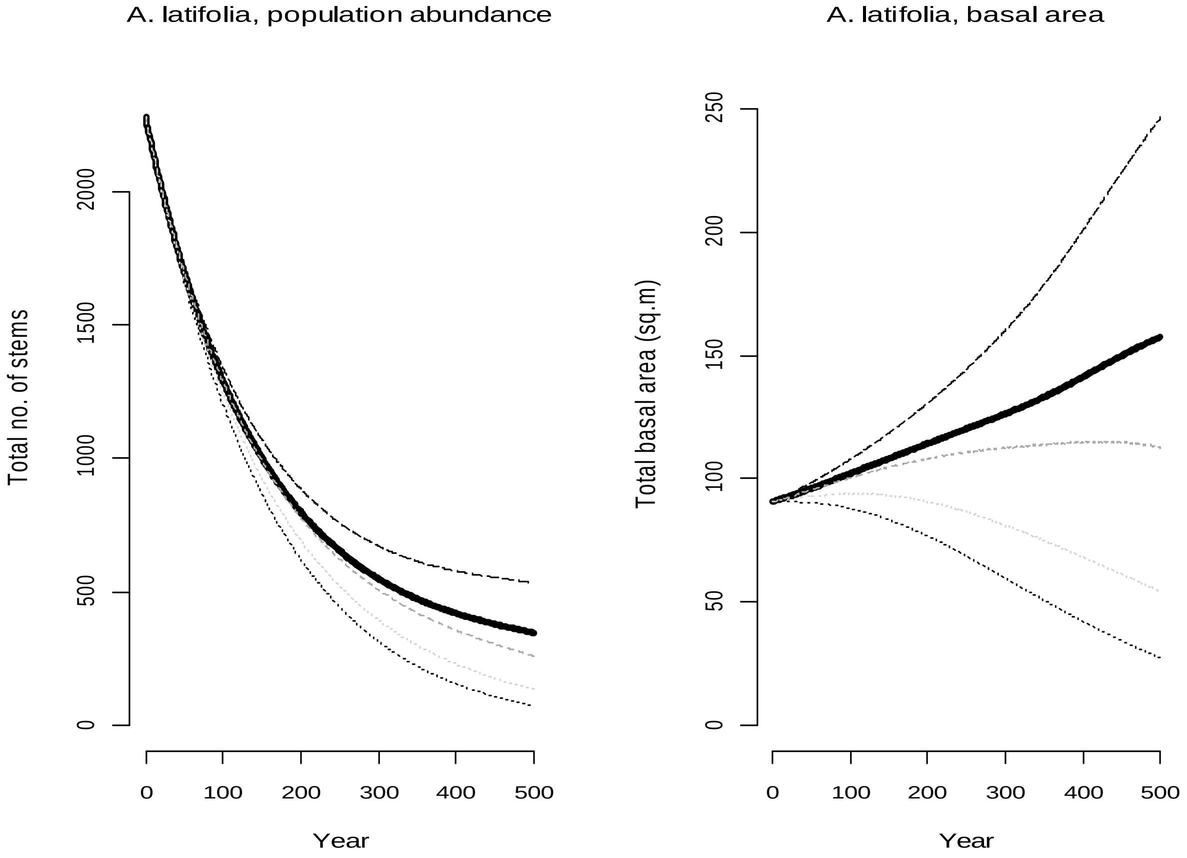
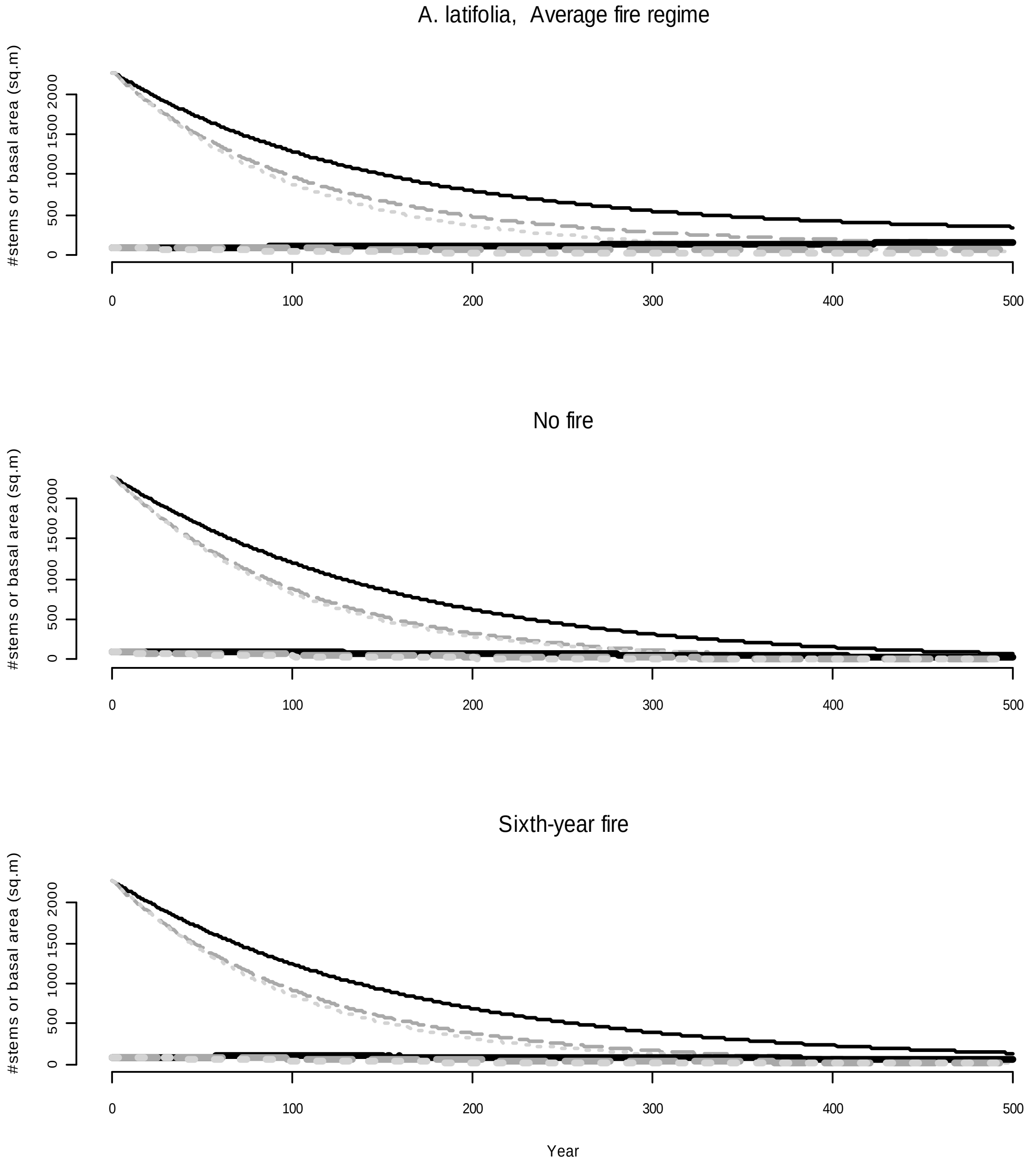


Figure 15 *Anogeissus latifolia* population abundance and basal area trajectories over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values have been used, as well as worst-case scenarios (see text for details), to obtain population abundance (three thinner lines originating in top half of plots) or basal area trajectories (three thicker lines originating in bottom half of plots). The original parameter rates were calculated from field data collected in the 50ha plot during 1988-2000. The average and worst case scenarios used per plot below are the following: 1. Mortality, recruitment and growth rates averaged across 1988-2000 (black solid lines); 2. Worst case mortality and recruitment (dark grey dashed lines); 3. Worst case mortality, recruitment and growth (light grey dotted lines).

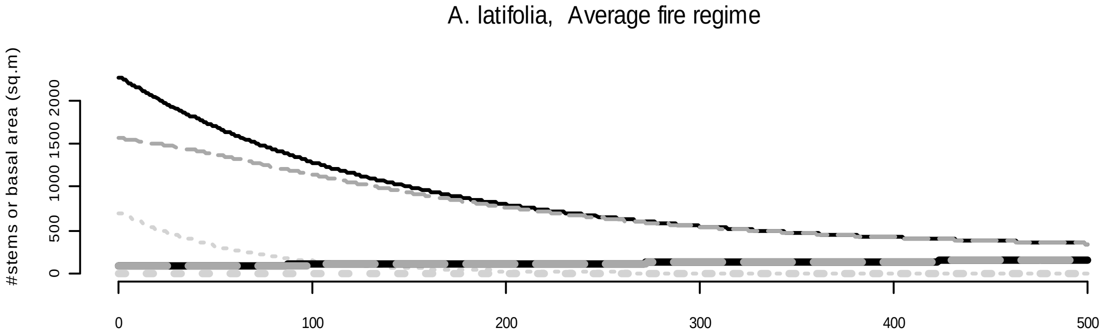


A. latifolia, Average fire regime

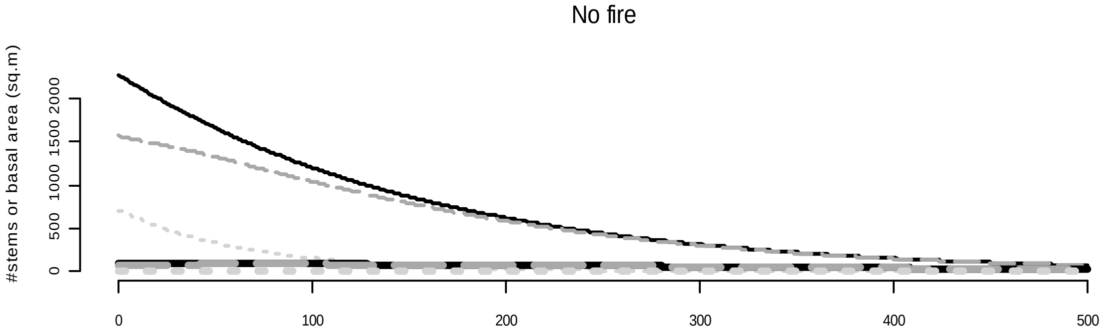
No fire

Sixth-year fire

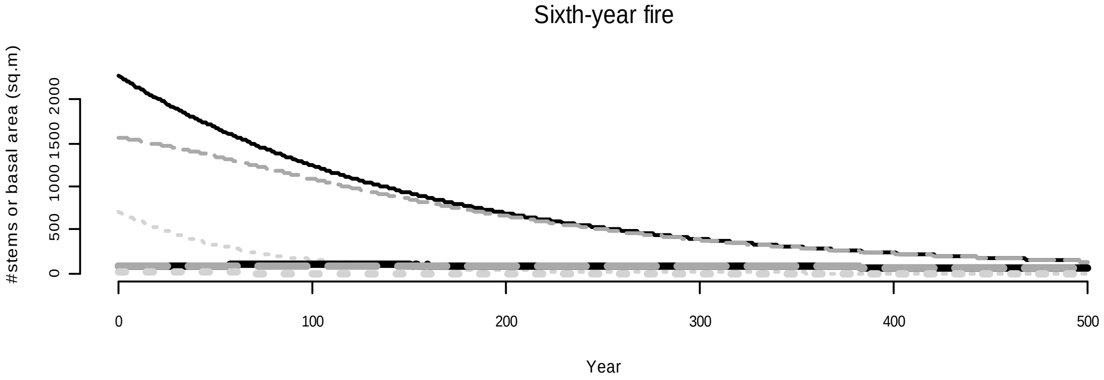
Figure 16 *Anogeissus latifolia* population abundance and basal area trajectories for all stems, adults (>15cm dbh) and sub-adult (non-adults), over 500 yrs under average, nil and 6-yr fire regimes. Original mortality, recruitment and growth values, calculated from field data collected in the 50ha plot during 1988-2000, were used to obtain population abundance (three thinner lines originating in upper section of plots) or basal area trajectories (three thicker lines originating in lower section of plots). Stems sizes are represented as follows: 1. All stems: black solid lines; 2. Adults: dark grey dashed lines; 3. Sub-adults: light grey dotted lines. Note that basal area of all stems is approximately the same as that of adults, while the sub-adult contribution to basal area is approximately zero throughout.



A. latifolia, Average fire regime

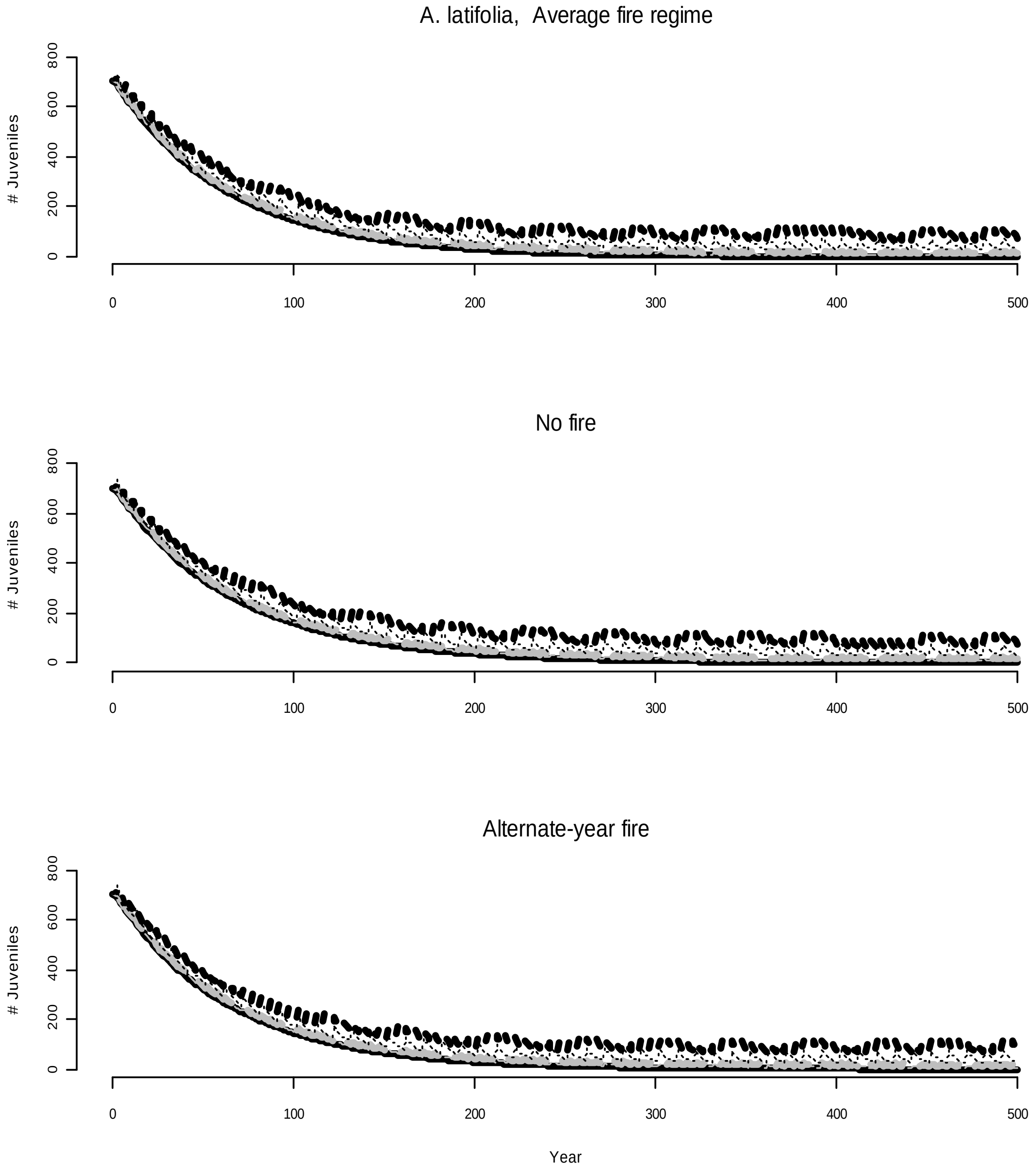


No fire



Sixth-year fire

Figure 17 *Anogeissus latifolia* juvenile (<16cm dbh) population abundance trajectories obtained after addition of recruitments every five or 10 years, with total recruitment input sizes of 10 or 50. Original mortality, recruitment and growth values, calculated from field data collected in the 50ha plot during 1988-2000, were used with three different fire regimes (average, nil and alternate-year fire regimes). Trajectories with different recruitment addition schedules are represented with black, grey, solid, dashed or dotted lines, as follows: 1. No recruits added: thickest solid black line showing the lowest baseline trajectory; 2. According to frequency of recruits added: thicker lines = higher frequency (five year intervals), thinner lines = lower frequency (10 year intervals); 3. According to number of recruits added: black dots = more recruits (50), grey dashes = fewer recruits (10).



Conclusion

This population dynamics simulation study showed that matrix modeling could provide useful information on long-term dynamics of species in the Mudumalai dry deciduous forest, which may not be apparent from examinations of demographic rate tables. The most important results obtained here were that under current environmental scenarios the populations of all four canopy species appeared to decline over the long term, while the basal areas increased during the first 200 years before ultimately declining in at least two species. An additional important result was that recruitment of small stems into medium size classes was poor in all species, and this largely determined the year-to-year fluctuations in population size. Another important pattern observed was that reduced growth rates could potentially cause steep population declines by making stems vulnerable to high mortalities in small size classes, or conversely, could retard population basal area declines by preventing large stems from reaching sizes in which they may be more likely to senesce and die.

Certain unusual or unexpected population trajectories also were observed in most of the species tested with different fire regimes. A possible cause of these anomalies were the fitted curves used for mortality rates. Mortality rates used in the models were obtained by smoothing across neighbouring size classes and fitting curves to the smoothed data in order to overcome effects of small sample sizes in some classes. However, this may not be suitable for very long-term projections, as slight upward or downward trends created by the fitted curves may be magnified over the long term if they occur in sensitive size classes. In the data of the four species used here, fitted mortality curves were most likely to be influenced by low sample sizes in the medium to large size classes. Thus, unexpected patterns in the final population trajectories may have been caused by anomalous fitted mortality rates in medium to large size classes, wherein slight anomalies in the fitted curves may have been magnified in the long-term projections. A sensitivity analysis can be carried out to examine the effects of such parameter variability on the predicted population estimates. Based on the current study, it is expected that population projections of the species tested here may be sensitive to mortality rate variations in the medium to large size classes. In addition, the use of different models (such as stochastic matrix model and individual-based model) can be explored, which incorporate the natural variability of species' parameter rates and thus allow for better resolution of long term variations under different environmental scenarios.

A potentially important result of this study was to show that current rates of recruitment into large size classes are likely to limit very long-term population persistence in these four canopy species. Although the four species appeared to increase in basal area during the first 200 years, this was due to persistence of the largest stems that continued to survive, grow and contribute to population basal area trajectories. Large stems in the Mudumalai dry forest are known to have extremely low mortality rates (Sukumar et al. 1998; Sukumar et al. 2005). However, the apparently positive trend in basal area that was associated with these low mortality rates masks the important dynamics occurring in juvenile size classes, where very little recruitment into medium size classes took place. This was largely due to relatively high juvenile mortality for three of the species (in *A. latifolia* mortality may not be high in juvenile classes, however, the species has shown a general failure to recruit stems above 1cm diameter during the 12 years of this study).

Based on earlier observations of low mortality and recruitment in the Mudumalai 50ha plot, it had been suggested that species such as *A. latifolia* may employ the lottery competitive strategy of showing bursts of very high recruitment during undisturbed intervals, when conditions for recruitment of these species are favourable (Sukumar et al. 2005). The initial tests carried out here did not support this hypothesis for *A. latifolia* and *T. crenulata*. Fairly large inputs of recruitment at high frequency failed to stabilize or turn around the generally decreasing population abundance trajectories for both these species. A recent analysis of fire dynamics at the Mudumalai Wildlife Sanctuary (Narendran et al. 2004) has shown that the current fire return frequency within the Sanctuary is approximately 3.3 years. In addition, a general trend of increasing fire frequency was observed when comparing current fire occurrence data with that from the early twentieth century. Even if we assume that the current fire frequencies may remain unchanged for the next 20-50 years without increasing, there appears to be little scope for *A. latifolia* and *T. crenulata* to recruit sufficient individuals into medium and large size classes under such conditions. The current fire regime also may be a cause for the failure of these species to recruit into the smallest size class of 1-2cm dbh.

Concerns about the conservation threat posed by frequent occurrences of fire in the Mudumalai Wildlife Sanctuary have been expressed in previous studies (Sukumar et al. 1998; Narendran et al. 2004). This modeling study of the four commonest canopy species in the 50-ha plot of the Mudumalai dry deciduous forest also suggests that it would be important to reduce the fire frequency in the Sanctuary, as even the most dominant species' long term persistence may be threatened under the current fire regime. This study hence lends support to the conclusions of Narendran et al (2004), which stated that "..the current fire regime of the Western Ghats poses a severe and persistent conservation threat to forests both within and outside protected reserves".

Equations of curves used to fit growth and mortality rate data:

1. Exponential Association: y = a(1-exp(-bx)
2. Geometric Fit: y = ax^(bx)
3. Heat Capacity Model: y = a+bx+c/x^2
4. Harris model: y = 1/(a+bx^c)
5. Hoerl model: y = a*(b^x)*(x^c)
6. Linear Fit: y = a+bx
7. Logarithm Fit: y = a+b*ln(x)
8. Logistic model: y = a/(1+b*exp(-cx))
9. MMF Model: y = (a*b+c*x^d)/(b+x^d)
10. 3rd degree Polynomial Fit: y = a+bx+cx^2+dx^3
11. Quadratic Fit: y = a+bx+cx^2
12. Rational function: y = (a+bx)/(1+cx+dx^2)
13. Richards Model: y = a / (1 + exp(b - cx))^(1/d)
14. Sinusoidal Fit: y = a+b*cos(cx+d)
15. Vapor pressure model: y = e^(a + (b/x) + c.lnx)
16. Weibull Model: y = a-b*exp(-c*x^d)

LITERATURE CITED

Caswell, H. 1989. *Matrix population models: Construction, analysis and interpretation*. Sinauer Associates Inc., Sunderland, MA.

Chesson, P.L. & Warner, R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist* 117: 923-943.

Condit, R., Hubbell, S.P. & Foster, R.B. 1993a. Mortality and growth of a commercial hardwood 'el cativo', *Prioria copaifera*, in Panama. *Forest Ecology and Management* 62: 107-122.

Condit, R., Hubbell, S.P. & Foster, R.B. 1993b. Identifying fast-growing native trees from the Neotropics using data from a large, permanent census plot. *Forest Ecology and Management* 62: 123-143.

Condit, R. 1998. *Tropical forest census plots: Methods and results from Barro Colorado Island, Panama and a comparison with other plots*. Springer-Verlag and R. G. Landes Company, Berlin, Germany, and Georgetown, Texas.

John, R., Dattaraja, H.S., Suresh, H.S. & Sukumar, R. 2002. Density-dependence in common tree species in a tropical dry forest in Mudumalai, southern India. *Journal of Vegetation Science* 13: 45-56.

John, R. & Sukumar, R. 2004. Distance- and density-related effects in a tropical dry deciduous forest tree community at Mudumalai, southern India. In: Leigh, E.G., Jr. (ed.) *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*, pp. 363-383. University of Chicago Press, Chicago.

Narendran, K., Murthy, I.K., Suresh, H.S., Dattaraja, H.S., Ravindranath, N.H. & Sukumar, R. 2001. Nontimber forest product extraction, utilization and valuation: a case study from the Nilgiri Biosphere Reserve, southern India. *Economic Botany* 55: 528-538.

Narendran, K., Cochrane, M.A. & Sukumar, R. 2004. Conservation threat of increasing fire frequencies in the Western Ghats, India. *Conservation Biology* 18: 1553.

Nath, C.D., Dattaraja, H.S., Suresh, H.S., Joshi, N.V. & Sukumar, R. 2006. Patterns of tree growth in relation to environmental variability in the tropical dry deciduous forest at Mudumalai, southern India. *Journal of Biosciences* 31: 651–669.

Silori, C. & Mishra, B.K. 2001. Assessment of livestock grazing pressure in and around the elephant corridor in Mudumalai Wildlife Sanctuary, south India. *Biodiversity and Conservation* 10: 2181-2195.

Sukumar, R. 1990. Nilgiri Biosphere Reserve - from theory to practice. In: Swarupanandan, K. (ed.) *Tropical forest ecosystem conservation and development in South and Southeast Asia*, pp. 27-33. Kerala Forest Research Institute, Peechi, India.

Sukumar, R., Dattaraja, H.S., Suresh, H.S., Radhakrishnan, J., Vasudeva, R., Nirmala, S. & Joshi, N.V. 1992. Long-term monitoring of vegetation in a tropical deciduous forest in Mudumalai, southern India. *Current Science* 62: 608-616.

Sukumar, R., Suresh, H.S., Dattaraja, H.S. & Joshi, N.V. 1998. Dynamics of a tropical deciduous forest: Population changes (1988 through 1993) in a 50-ha plot at Mudumalai, southern India. In: Comiskey, J.A. (ed.) *Forest biodiversity research, monitoring and modeling: Conceptual background and Old World case studies*, pp. 551-563. United Nations Educational, Scientific and Cultural Organisation, Paris, France.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., John, R. & Joshi, N.V. 2004. Mudumalai Forest Dynamics Plot, India. In: Leigh, E.G., Jr. (ed.) *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*, pp. 551-563. University of Chicago Press, Chicago, USA.

Sukumar, R., Suresh, H.S., Dattaraja, H.S., Srinidhi, S. & Nath, C. 2005. The dynamics of a tropical dry forest in India: Climate, fire, elephants and the evolution of life-history strategies. In: Hartley, S. (ed.) *Biotic Interactions in the Tropics: Their role in the maintenance of species diversity*, pp. 510-529. Cambridge University Press, Cambridge.

Warner, R.R. & Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *The American Naturalist* 125: Jun., 1985.