

Relationship between annual rainfall and tree mortality in a tropical dry forest: Results of a 19-year study at Mudumalai, southern India

H.S. Suresh^a, H.S. Dattaraja^a, R. Sukumar^{a,b,*}

^a Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India

^b Divecha Centre for Climate Change, Indian Institute of Science, Bangalore 560012, India

ARTICLE INFO

Article history:

Received 6 April 2009

Received in revised form 28 August 2009

Accepted 15 September 2009

Keywords:

Forest dynamics
Climate variability
Drought
Tropical dry forest
Western Ghats

ABSTRACT

Variability in rainfall is known to be a major influence on the dynamics of tropical forests, especially rates and patterns of tree mortality. In tropical dry forests a number of contributing factors to tree mortality, including dry season fire and herbivory by large herbivorous mammals, could be related to rainfall patterns, while loss of water potential in trees during the dry season or a wet season drought could also result in enhanced rates of death. While tree mortality as influenced by severe drought has been examined in tropical wet forests there is insufficient understanding of this process in tropical dry forests. We examined these causal factors in relation to inter-annual differences in rainfall in causing tree mortality within a 50-ha Forest Dynamics Plot located in the tropical dry deciduous forests of Mudumalai, southern India, that has been monitored annually since 1988. Over a 19-year period (1988–2007) mean annual mortality rate of all stems >1 cm dbh was $6.9 \pm 4.6\%$ (range = 1.5–17.5%); mortality rates broadly declined from the smaller to the larger size classes with the rates in stems >30 cm dbh being among the lowest recorded in tropical forest globally. Fire was the main agent of mortality in stems 1–5 cm dbh, elephant-herbivory in stems 5–10 cm dbh, and other natural causes in stems >10 cm dbh. Elephant-related mortality did not show any relationship to rainfall. On the other hand, fire-related mortality was significantly negatively correlated to quantity of rainfall during the preceding year. Mortality due to other causes in the larger stem sizes was significantly negatively correlated to rainfall with a 2–3-year lag, suggesting that water deficit from mild or prolonged drought enhanced the risk of death but only with a time lag that was greater than similar lags in tree mortality observed in other forest types. In this respect, tropical dry forests growing in regions of high rainfall variability may have evolved greater resistance to rainfall deficit as compared to tropical moist or temperate forests but are still vulnerable to drought-related mortality.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Dry tropical forests experience distinct seasonality and high inter-annual variability in rainfall (Murphy and Lugo, 1986). Ecological processes of dry tropical forests can be thus expected to be influenced by pattern and variability in rainfall perhaps more than by any other climatic factor (Murphy and Lugo, 1986; Sukumar et al., 2005; Holmgren et al., 2006). Seasonally dry forests that presently occupy an area of about 1 million km² (Miles et al., 2006) account for over 40% of the total vegetation cover of the tropics (Brown and Lugo, 1982) and 77% of the forest cover of India (Singh and Kushwaha, 2005); thus an understanding of their dynamics in relation to environmental variability is important,

especially in the context of possible increasing climatic variability in the future (IPCC, 2001).

Increasing frequency and intensity of ENSO (El Niño Southern Oscillation) related droughts in the southeast Asian tropics (Walsh, 1996) impact the forests of this region. Droughts can have measurable impacts on population structure, species composition, phenology, regeneration and mortality of tropical moist forest communities in southeast Asia (Woods, 1989; Corlett and LaFrankie, 1998; Siegert et al., 2001; Aiba and Kitayama, 2002; Delissio and Primack, 2003) and the Neotropics (Borchert et al., 2002; Condit et al., 1995; Tobin et al., 1999). Droughts also result in higher mortality of trees in forest fragments, especially along their edges, in the Amazon (Laurance et al., 2001). There have been several analyses of tropical moist forest dynamics in relation to ENSO-related drought (Nakagawa et al., 2000; Condit et al., 2004; Nishimura et al., 2007). These studies found elevated mortality rate of trees at some sites as a consequence of severe drought, though a single drought was not necessarily catastrophic for persistence of the forest. However, there has been insufficient understanding of

* Corresponding author at: Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India. Tel.: +91 80 23600382/22933102; fax: +91 80 23602280/23601428.

E-mail address: rsuku@ces.iisc.ernet.in (R. Sukumar).

the role of climatic variability and extreme events such as drought on the ecology of tropical dry forests.

An important aspect of drought-related tree mortality is the time interval between soil water deficit and death of trees. Some studies suggest that tree mortality in tropical moist forest may be enhanced concurrently with or within a year of a wet season drought (e.g. Laurance et al., 2001; Condit et al., 2004). European temperate forests experienced increased mortality with a time lag of 1–2 years following summer drought in 2003 (Breda et al., 2006). How would dry forests that grow in the seasonal tropics, and are presumably adapted to water deficit during the annual dry season, respond to wet season drought?

The 50-ha Forest Dynamics Plot located at Mudumalai in southern India (Sukumar et al., 1992), the driest of the plots in the global network of large-scale plots coordinated by the Center for Tropical Forest Science (CTFS) (Condit, 1995; Losos and Leigh, 2004), provides an opportunity to understand the response of a tropical dry forest to environmental variability. This region is characterized by considerable variability in rainfall, dry season ground fire, high density of large mammals and past extraction of timber (Sukumar et al., 2005). We began monitoring this plot in 1988–1989 with annual census for mortality and recruitment and 4-yearly censuses for stem measurement (Sukumar et al., 1992, 1998). The annual census data provide the opportunity to examine how the variation from year to year in rainfall quantity influenced tree mortality and forest dynamics. In the course of the study there was a prolonged drought (rainfall 20–39% below average, though not necessarily ENSO-related – see Krishna Kumar et al., 1999) during 2000–2003 that also allowed us to observe changes in tree mortality rates.

Mortality of trees in the tropical dry forests of Mudumalai have been basically categorized as due to one of three causes: fire-related death of aboveground stem, elephant-related herbivory, and “other natural causes” that includes a suite of causes including drying of stem from water stress, windfall, pest attack and senescence of old stems (Sukumar et al., 2005). Each of the above factors could be related to precipitation (or other climate-related

variables such as temperature and humidity). For instance, the occurrence of dry season fire would obviously be influenced by rainfall in the preceding year (e.g. Kitzberger et al., 1997), herbivory of woody stems (such as stripping of bark) by elephants may depend on availability of other forage such as grasses whose production is related to rainfall as well as to fire (Sukumar, 2003), while stem drying and senescence could be directly influenced by rainfall and soil moisture (Condit et al., 1995; Camargo and Kapos, 1995). Each of these factors is also broadly responsible for mortality of different sized stems: fire for the smallest stems, elephant-herbivory for the small to medium-sized stems, and other natural causes for the larger stems (Sukumar et al., 1998).

We began by examining the relationship between annual or dry season rainfall and overall tree mortality before going on to examine the relationships between rainfall and tree mortality due to different causes, all of which are expected to go in the same direction. We thus examined the following hypothesis in this study:

- (1) The overall mortality of trees would be negatively related to the preceding dry season rainfall or annual rainfall in the preceding year or years.
- (2) Fire-related mortality of trees, especially in the smaller size classes, would be negatively related to rainfall in the preceding year or years.
- (3) Mortality of trees due to herbivory by elephants would be negatively influenced by rainfall in the corresponding or preceding year.
- (4) Mortality of trees due to other natural causes would be negatively related to rainfall during the preceding year or years.

2. Materials and methods

2.1. Study area

Mudumalai Wildlife Sanctuary (MWLS; 11°30' and 11°39'N latitude, 76°27' and 76°43'E longitude) that cover an area of

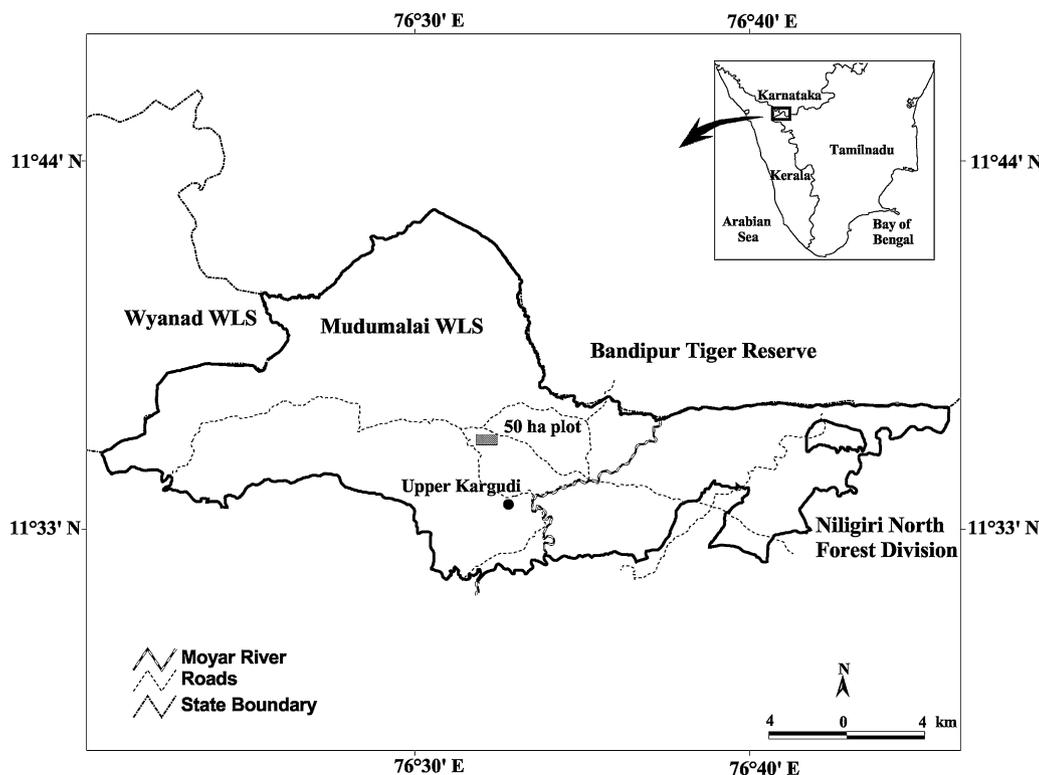


Fig. 1. Location of Mudumalai Wildlife Sanctuary and the 50-ha Forest Dynamics Plot in southern India.

321 km² in the state of Tamilnadu, southern India (Fig. 1), is a part of the Nilgiri Biosphere Reserve (NBR), a designated Elephant Reserve and a Tiger Reserve (Sukumar et al., 2004). The terrain is undulating with elevation ranging from about 300 to 1200 m ASL with a general elevation over most of the reserve of 900–1000 m. The base rock is of the igneous type while the soils of both red and black types have been classified into four orders, Inceptisols, Alfisols, Mollisols and Entisols (George et al., 1988). According to the Koeppen-Geiger global climate classification (Kottek et al., 2006), this region falls under the Equatorial winter dry type. The summer or southwest monsoon brings rains to a large part of the sanctuary during June–September while the retreating monsoon (winter or northeast monsoon) also brings rain to the eastern part during October–November. Across MWLS there is a strong east–west gradient in average annual rainfall that spans a range from about 600+ to 1800+ mm. Correspondingly the vegetation varies from tropical dry thorn forest in the drier east through dry deciduous forest in the central part to moist deciduous forest with patches of semi-evergreen forest in the wetter western region. The flora and vegetation types of MWLS (Sharma et al., 1977; Suresh et al., 1996, 2006), as well as the history and characteristics of dry season fires (Kodandapani et al., 2008), have been well documented. Dry season ground fires are usually caused by humans, though lightning caused fires may also occur rarely; the average fire-return interval is 6 years in the tropical dry deciduous forest and 10 years in dry thorn forest (Kodandapani et al., 2008).

The 50-ha Mudumalai Forest Dynamics Plot (MDFP) is centrally located at MWLS in tropical dry deciduous forest; a more complete description of the MDFP is given elsewhere (Sukumar et al., 2004). Mean annual rainfall recorded by us at Upper Kargudi (11°37'N and 76°31'E), close to the location of the MDFP, has been 1255 ± 292 mm during 1988–2007. Rainfall (>50 mm/month) is spread over a 8-month period, from April to November, with two peaks, the first in June–July corresponding to the southwest monsoon and the second in October from the northeast monsoon (Fig. 2). Mean monthly maximum temperature is 28.2 °C (peak value of 34.0 °C in March) and mean monthly minimum temperature is 17.3 °C (lowest value of 14.2 °C in December).

The MDFP had 72 woody plant species in 1988 and 79 species in 2007 (stems >1 cm dbh). The dominant canopy trees in the MDFP are *Lagerstroemia microcarpa* Wt., *Terminalia crenulata* Roth., *Anogeissus latifolia* (DC.) Bedd. and *Tectona grandis* L. f., while the understory is characterized by *Kydia calycina* Roxb., *Helicteres isora* L., *Cassia fistula* L., *Catunaregam spinosa* (Thunb) Tirveng. and *Phyllanthus emblica* L. The ground vegetation is dominated by perennial tall grasses, mainly *Themeda cymbaria* Hack. and *Cymbopogon flexuosus* (Steudel) Watson. Invasive alien species, such as *Lantana camara* L. and *Chromolaena odorata* (L.) King & Robinson, are also common in the understory. Mudumalai also has an intact community of large mammals characteristic of peninsular India, including the elephant (*Elephas maximus*) that is found at a high density of c.2 elephant/km² (unpublished data). The broad east–west movement of elephants in this region encompasses home range sizes of 500–800 km² (Baskaran et al., 1995) that are typical for this species (Sukumar, 2003).

2.2. Field methods and analyses

The field methods employed in the study have been described in earlier publications (Sukumar et al., 1992, 1998). All woody plants >1 cm dbh were enumerated during the period May 1988–May 1989. The plants were identified, measured for dbh, tagged and mapped to the nearest 0.5 m. As most of the species in this deciduous forest are leafless during December–March, the censuses during subsequent years began in June, just after the onset of the monsoon, by which time they had flushed leaf, making

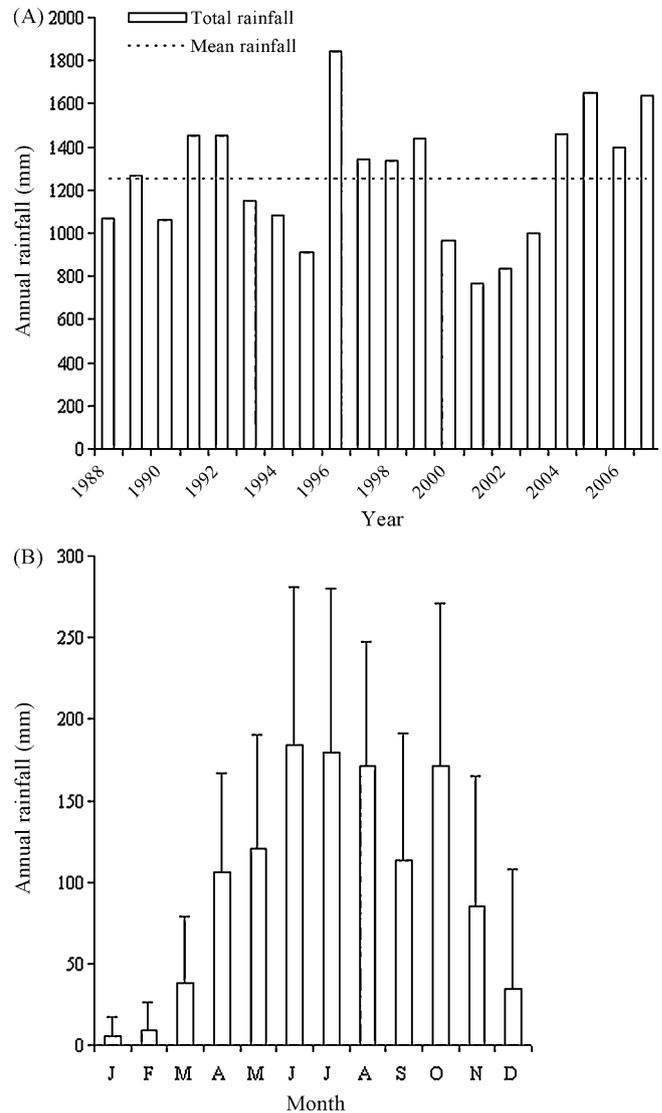


Fig. 2. Rainfall patterns at Upper Kargudi (see text for details). (A) Annual rainfall during 1988–2007; the dotted line represents the mean annual rainfall during the same period. (B) Average monthly rainfall over the same period; the error bars represent 1 SD.

species identification and living status more positive. We followed the CTFS protocol in making decisions on mortality, recruitment and stem sizes during the censuses (Condit, 1998).

The annual censuses recorded mortality of trees that had been alive during the previous year as well as new recruits during that particular year. A tree was considered dead if it showed no visible signs of active meristem (complete absence of green leaves, dried stem and bark showing no living tissue when superficially peeled), and no new root coppice, if any, had reached 1 cm dbh. We differentiated the following three broad causes of mortality in the plot:

- fire-related death of aboveground stem defined as the complete disappearance of above-ground stem due to burning or a standing above-ground stem that was clearly charred by fire and showed no active meristem,
- elephant-related herbivory when a stem had died due to stripping of bark (ring barking), breaking of stem or had been completely uprooted (but not when a stem had been merely broken and was still alive) and
- “other natural causes” (henceforth “other causes”) that includes a suite of causes including drying of stem from water

stress, windfall, pest attack and senescence with no sign of active meristem.

It is, of course, possible that the primary cause of mortality of certain trees was not correctly identified as when a tree pushed over by an elephant or that had dried up naturally was also burnt subsequently. A stem was considered as living if it had been merely broken below 1.3 m but was still alive. Every stem, including those recorded as dead previously, was examined during the annual censuses. There were occasions when a standing tree recorded as “dead” during a given year was, in fact, not dead and began to sprout leaf in a subsequent year. In such instances our dataset was corrected for the earlier periods when the individual was wrongly recorded as dead. A recruit is defined as the appearance of a new stem that has grown >1 cm dbh. At the end of the dry season each year the extent of burning, if any, was mapped at a 10 m × 10 m resolution; a quadrat was recorded as burnt if >50% of the area showed signs of fire. Stem sizes have also been re-measured every 4 years (1992, 1996, 2000 and 2004 censuses). The stem sizes used in the analyses for a particular year refer to the sizes recorded in the preceding year of measurement without correction for possible growth; thus the stem sizes for the stands from 1989 to 1991 use the measurements recorded in 1988, and the stems sizes for 2005–2007 use the sizes for 2004; given the slow rates of tree growth in this plot (Nath et al., 2006) this procedure is not expected to influence the results reported here.

The censuses that began in June each year typically took 4–6 months to complete depending on several factors such as abundance of the understorey plants and rainfall intensity; during the full census years when stems were also measured the enumeration took up to 8 months. The interval between successive censuses in a particular 20 m × 20 m plot is thus not precisely 1 year. For the purposes of this analysis, however, we considered simple annual mortality because the greatest mortality, caused by fire or perhaps drying of stems, certainly occurred during the dry season between successive census intervals. Mortality rate is thus expressed as the percentage of individuals (of a species or of a given size class) dying between two successive census years. All mean annual rates have been calculated as arithmetic means of annual rates. Stems were grouped into six size classes (1–5, 5–10, 10–20, 20–30, 30–60, >60 cm dbh) for describing basic mortality rates and patterns, and later grouped into three classes (1–10, 10–30 and >30 cm dbh) in order to obtain sufficient samples sizes for examining the correlations between cause of mortality and precipitation.

Rainfall data (Fig. 2) come from the weather station we maintain at Upper Kargudi, about 4 km south of the plot. For the period of 1988, prior to the start of our long-term study at Mudumalai, we obtained rainfall data from Gamehut (11°34'N and 76°31'E) and used a regression developed earlier by us for the relationship between rainfall here and at Kargudi (Nath et al., 2006).

We carried out Pearson's Product Moment Correlations between mortality rates for a particular size class or cause and rainfall. Because the annual censuses were conducted during the wet months, and each census took several months to complete, it would not be entirely appropriate to examine correlations between mortality and rainfall during the corresponding year; for instance, some stems would be recorded as dead during the early period of the census in June while rainfall for the corresponding year would include months up to December in the same year. We thus examined mortality rates for all stems from all causes, or a particular size class and a particular cause, with total annual rainfall during the preceding year or years to examine the immediate response (up to 1-year lag) or short-term (up to 2–3-year lag) response of trees to climatic variability. Thus, mortality

rates recorded during census years 1989, 1990...2007 were correlated with rainfall in years 1988, 1989...2006 for 1-year lag relationship, mortality rates recorded during 1990, 1991...2008 were correlated with rainfall in years 1988, 1989...2005 for 2-year lag relationship, etc. We also examined the relationship between dry season (defined for our purposes as rainfall <50 mm per month on average; this is the period of December–March) rainfall and mortality recorded in the following wet season census.

In view of the large number of Pearson's correlations carried out (that could introduce Type 1 errors of statistical interpretation) and possible departure from normality of the variables examined, we also used bootstrap procedures to examine support for the correlations (Manly, 1997). Bootstrap simulations were done in R (R Development Core Team, 2009) using the 'sample()' function to first randomly sample mortalities across years, keeping total annual rainfall constant. A correlation was then derived between observed rainfall and randomized mortality values. This process was repeated 1000 times to derive a distribution of correlations, and 95 and 99 percentile bootstrapped confidence intervals were then used to determine if the observed correlations were non-random.

3. Results

3.1. Mortality rates and patterns

Mean annual mortality rate of all stems >1 cm dbh was $6.9 \pm 4.6\%$ (range = 1.5–17.5%, $N = 19$ years) during the period 1988–2007, with the lowest and the highest rates being observed during the consecutive 2000–2001 and 2001–2002 periods, respectively. Overall, the high mortality rates during the early years of the study (Fig. 3) were largely contributed by the death of the understorey plants, *C. fistula* due to fire, *H. isora* due to fire and elephant-herbivory, and *K. calycina* due to elephant-herbivory. During the later years of the study the lower total mortality rates were associated with the near-absence of fire (the notable exception being the intense fire and high mortality during 2002) but considerable variation in rainfall.

Mortality rates were highest in the smallest size classes and generally declined in a non-linear fashion with increasing stem sizes (Fig. 4). Mean annual mortality of $22.2 \pm 17.4\%$ observed in stems 1–5 cm dbh declined to $0.77 \pm 0.83\%$ in >60 cm dbh class. Across-year variability in annual mortality rates of stem sizes shows a U-shaped pattern with high coefficient of variation (CV) in the smaller and the higher size classes and low CV in the mid-size classes. When causes of mortality are examined across stem sizes, the main cause of mortality in the smallest sized stems (1–5 cm) was fire, while in

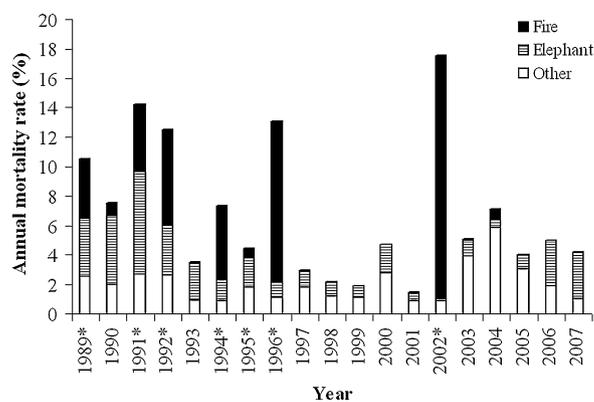


Fig. 3. Annual mortality rate (%) due to different causes during 1989–2007 in the 50-ha plot. Asterisk (*) indicates the occurrence of dry season fire in a particular year; during 1994 and 1995 only a small area (<3%) of the plot was burnt while in other fire years >89% of the plot was burnt.

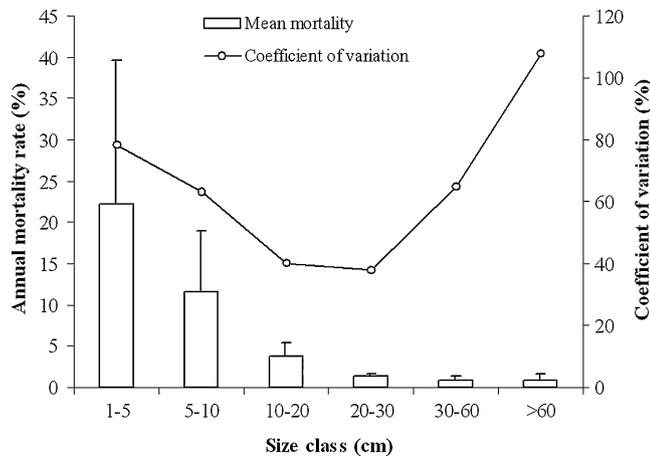


Fig. 4. Mean annual mortality rate (%) with coefficient of variation (CV) in mean mortality (expressed in % as standard deviation/mean mortality) across different size classes of stems in the 50-ha plot during 1989–2007.

stems 5–10 cm this was due to elephant-herbivory; above this size “other causes” was the main cause of stem mortality (Fig. 5). Variability in annual mortality rates was highest in fire-related mortality (CV = 171%) and lower due to elephant-herbivory (82%) and other causes (62%).

The main causes of mortality (i.e. when a particular cause contributed to >3% mortality of the total population of individuals in a year) varied across years (Fig. 3); thus fire-related mortality contributed in large measure to the total mortality during years when extensive burning (>89%) occurred in the plot (years 1989, 1991, 1992, 1996, 2002) while elephant-related mortality was high during the period 1989–1992 and 2006–2007 when this mammalian herbivore’s favoured browse plants of the order Malvales (particularly *K. calycina* and *H. isora*) were available in greater abundance (Fig. 6). Other causes predominated as the major cause of mortality during other years (Fig. 3).

3.2. Correlation of mortality rates and rainfall

Mortality rates of trees were not significantly correlated ($p > 0.05$ in all cases for Pearson’s R) to rainfall during the dry season preceding the wet season census in any of the size classes or total population examined. On the other hand, several significant correlations were obtained between tree mortality and annual rainfall (Table 1). Overall mortality of trees 1–10 cm dbh was

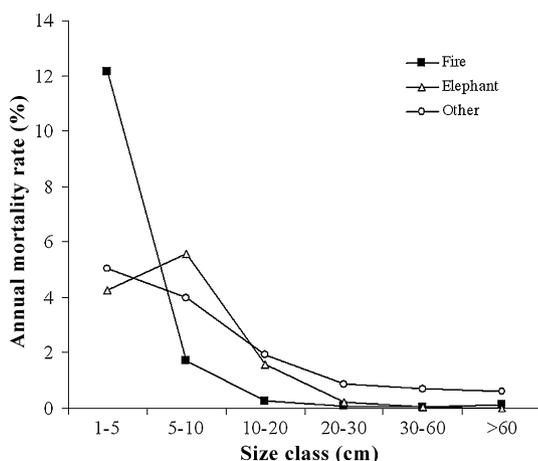


Fig. 5. Size class specific mean annual mortality rates due to various causes during 1989–2007 in the 50-ha plot (see text for details).

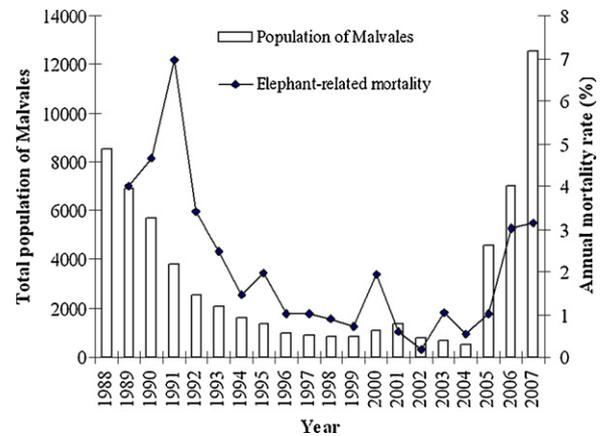


Fig. 6. Annual mortality rate (%) due to elephant-herbivory in relation to the total population (>1 cm dbh) of plants of the order Malvales (mainly *Kydia calycina*, *Helicteres isora*, *Grewia tiliifolia* and *Eriolaena quinquelocularis*) in the plot during 1989–2007.

significantly negatively correlated to annual rainfall with a lag of 1-year; a similar relationship seen in trees of all sizes could have been influenced by the large proportion of small-sized individuals in the sample. Significant negative correlations between mortality in the medium (10–30 cm) and larger (>30 cm) sized trees and annual rainfall were also obtained with 3-year time lags.

Fire-related mortality in each of the three size classes (1–10, 10–30 and >30 cm dbh) examined, as well as of all sizes combined, showed significant negative correlation with rainfall during the preceding year (Table 1) but not with 2-year or 3-year lag in rainfall.

Elephant-related mortality in none of the different size classes showed any significant correlation with rainfall during any of the annual periods examined.

Table 1

Matrix of Pearson’s correlations (R) between annual mortality rates (%) due to different causes across different size classes of stems and annual rainfall in the Mudumalai Forest Dynamics Plot of 50 ha. Degrees of Freedom (df) = 18 for 1-year lag, 17 for 2-year lag and 16 for 3-year lag. p values (in brackets) are provided for Pearson’s correlations in cases of $p < 0.1$. Asterisk (*) indicates bootstrap support ($p < 0.05$ in all cases). None of the correlations were significant when mortality and annual rainfall during the corresponding year or preceding dry season was examined.

Rainfall	1–10 cm dbh	10–30 cm dbh	>30 cm dbh	All stems (>1 cm dbh)
Overall mortality				
1-year lag	$R = -0.534^*$ ($p = 0.018$)	$R = -0.028$	$R = -0.133$	$R = -0.474^*$ ($p = 0.040$)
2-year lag	$R = -0.440$ ($p = 0.068$)	$R = -0.325$	$R = -0.483$ ($p = 0.042$)	$R = -0.370$
3-year lag	$R = 0.013$	$R = -0.465$ ($p = 0.060$)	$R = -0.623^*$ ($p = 0.007$)	$R = -0.001$
Fire-related mortality				
1-year lag	$R = -0.506^*$ ($p = 0.027$)	$R = -0.464^*$ ($p = 0.045$)	$R = -0.493^*$ ($p = 0.032$)	$R = -0.516^*$ ($p = 0.024$)
2-year lag	$R = -0.252$	$R = -0.187$	$R = -0.234$	$R = -0.264$
3-year lag	$R = 0.187$	$R = -0.154$	$R = 0.167$	$R = 0.197$
Elephant-related mortality				
1-year lag	$R = 0.186$	$R = 0.002$	$R = -0.158$	$R = 0.145$
2-year lag	$R = 0.083$	$R = 0.018$	$R = -0.0006$	$R = 0.161$
3-year lag	$R = 0.149$	$R = 0.023$	$R = -0.285$	$R = 0.061$
Other causes related mortality				
1-year lag	$R = -0.145$	$R = 0.134$	$R = -0.035$	$R = -0.084$
2-year lag	$R = -0.583^*$ ($p = 0.011$)	$R = 0.291$	$R = -0.423$ ($p = 0.080$)	$R = -0.576^*$ ($p = 0.012$)
3-year lag	$R = -0.545^*$ ($p = 0.023$)	$R = -0.595^*$ ($p = 0.011$)	$R = -0.624^*$ ($p = 0.007$)	$R = -0.604^*$ ($p = 0.010$)

Mortality due to other causes in the smallest size class (1–10 cm dbh) as well as all stem sizes combined showed significant negative correlation with rainfall with 2-year lag. Mortality due to other causes in each of the three size classes as well as all sizes combined showed significant negative correlation with rainfall with 3-year lag period.

In addition to the above Pearson's correlations that are significant at least at the 5% level (i.e. $p < 0.05$), it is worth noting three other correlations that are significant at the 10% level (i.e. $p < 0.10$); these are mortality due to natural causes in stems >30 cm with rainfall with 2-year lag, mortality due to all causes in stems 1–10 cm with rainfall with 2-year lag, and mortality due to all causes in stems 10–30 cm with rainfall with 3-year lag (this has bootstrap support at $p < 0.05$).

Bootstrap support for Pearson's correlations clearly brought out two patterns in the relationship between annual rainfall and mortality. Fire-related mortality across all size classes of trees was consistently negatively related to rainfall in the preceding year. Similarly, mortality due to other natural causes was significantly negatively related to rainfall with a time lag of 2–3 years.

4. Discussion

Mortality rates as influenced by ground fire, herbivory by large mammals and wet season drought are highly variable in the 50-ha Forest Dynamics Plot at Mudumalai. Overall, mortality rates in the small-sized stems are high and variable, and these generally decline with increase in stem size with the exception of the largest stems that are in senescence. While fire kills the smaller stems of a wide range of species, herbivory by elephants has resulted in mortality of small- to medium-sized stems of a few favoured forage species such as *K. calycina* and other members of the order Malvales as observed in earlier analyses (Sukumar et al., 1998, 2005). On the other hand, this study over a longer time period also found that mortality rates of large trees (>30 cm dbh) were below 1% per annum during 15 of the 19 census intervals, and under 0.5% during four of these years. These rates are the lowest mean mortality rates recorded for larger trees in the CTFS global network of large-scale Forest Dynamics Plots (Condit et al., 1999; Losos and Leigh, 2004; Sukumar et al., 2005). Such low mortality rates could be an adaptive response in a forest subject to considerable climatic stress and disturbance (fire and large mammalian herbivory in this case) in order to enhance long-term persistence (Sukumar et al., 2005).

Rainfall at Mudumalai has been variable through the study period, with phases of very low rainfall (2000–2003) and very high rainfall (2004–2007) following in succession. Fire in tropical moist forests is typically related to ENSO-caused droughts combined with disturbance such as logging resulting in sharply enhanced mortality of trees (Siegert et al., 2001). In a tropical dry forest where the fuel for ground fires include not only dried logs but also perennial grasses, understorey shrubs and litter from leaves shed by the deciduous trees, the enhanced production of these fuel components from higher rainfall could be expected to be positively related to occurrence of fire and fire-related mortality in subsequent years, with a time lag, especially following decreased rainfall that causes the fuel to dry. Over a larger spatial scale at Mudumalai spanning a gradient from tropical dry thorn forest to semi-evergreen forest, the highest fire frequencies are observed in the tropical dry deciduous forests (Kodandapani et al., 2008) that also have the highest non-wood fuel loads (N. Mondal and R. Sukumar, unpublished results). The broad rainfall–fire relationship along a rainfall gradient in northern Patagonia, Argentina, is one of drought promoting fire in the short-term, while above-average moisture levels and fuel production also do so with a lag of 1–2 years as discerned from tree ring chronology (Kitzberger et al., 1997). We would thus have expected in our study a negative

relationship between rainfall and fire-related mortality with a short time lag (i.e. declining rainfall would result in drying up of fuels and make them more inflammable soon after), but a positive relationship between rainfall and fire-related mortality with perhaps a longer time lag. The strong and consistent negative correlation between rainfall and fire-related mortality in the subsequent year across trees of all size classes supports the first expectation; however, the contrary expectation of a positive correlation between rainfall and fire-related mortality with a time lag of >1 year is not supported by our results at the scale of the 50-ha plot. Perhaps this relationship will have to be examined over larger spatial and longer temporal scales.

Elephants are generalist feeders that switch between a diet predominantly of browse during the dry season and of grass during the wet season, though both plant types are consumed round the year (Sukumar, 2003). Inter-annual variation in the browse:grass ratio could also be expected to be related to the considerable inter-annual variation in rainfall. However, our initial hypothesis that elephant-related herbivory of favoured forage plants from the Malvales would also be related to quantity of rainfall is not supported at this time. It is possible that selection of browse (woody) plants by elephants on local scales (in this case a mere 50-ha) could be influenced by several other factors including the abundance, degree of clumping and sizes of trees (Sukumar et al., 1998) as well as foraging decisions over animals' home ranges whose geographical areas in this region are about 3 orders of magnitude larger (Baskaran et al., 1995) than the MFDP. Fire (that is related to rainfall) could also influence the choice of plants by elephants either by causing temporary scarcity of grasses and forcing the elephants to feed on woody plants, or causing the elephants to move to unburnt areas for feeding (Sukumar, 2003). The relationship of woody plant mortality due to elephant-herbivory and rainfall is thus complex and may have to be examined over larger spatial scales for patterns to emerge.

Mortality of trees due to other natural causes in the MFDP shows a strong negative relationship to rainfall with 2–3-year time lags possibly because the process of drying up and death of stems from water stress operates with a lag of those periods in tropical dry forests. A tree can die if the shortage of soil water impacts one or more of several steps of water transport along the soil–root–stem–leaf–atmosphere continuum. In recent years, this ecophysiological response of trees has been extensively investigated and compared across a number of plant functional types in temperate (e.g. Borghetti et al., 1998; Pataki et al., 2000; Breda et al., 2006) and tropical vegetation (e.g. Sobrado, 1993; Eamus, 1999; Rice et al., 2004; Ishida et al., 2006). The most common cause of hydraulic dysfunction in trees is believed to be xylem cavitation or embolism (Sperry and Tyree, 1988), a phenomenon that has been examined in plants from a variety of biomes globally (Maherali et al., 2004). On the other hand, the carbon-deficit hypothesis seeks to explain the death of trees as due to reduction of leaf area index and insufficient storage of carbohydrates and other compounds following soil water deficit (Breda et al., 2006). This may better explain the observations of 1–2-year lag in tree mortality following severe drought in the temperate region, as in the case of the European drought of 2003 (Breda et al., 2006). The hydraulic and carbon balance mechanisms are linked through leaf stomatal control and water use efficiency of the plant. A tree would respond physiologically to water deficit through reduced leaf water potential, stomatal conductance, transpiration and photosynthesis, resulting in reduced growth and loss of shoots, altered roots, and crown die-back that could eventually result in death when these effects are severe (Rood et al., 2003; O'Grady et al., 2005).

Trees of tropical dry forests typically have deep root systems for acquiring water during the dry season or longer periods of soil water deficit, as well as physiological mechanisms including

deciduousness and capacity for stem water storage that help retain sufficient moisture within the plant to tide over lean periods (Borchert, 1994). Deciduous trees in tropical dry forest may also be more resistant to xylem cavitation (Maherali et al., 2004) or adapted to reduced leaf area index when soil water is deficient. Regeneration in fire-prone tropical dry forests is also mainly through sprouts (Sukumar et al., 1998, 2005) that are less vulnerable to dry season water deficit as compared to seedlings (Saha et al., 2005). Thus, deciduous forest trees in the seasonal tropics may show a longer lag response to rainfall deficit before they wilt and die as compared to evergreen forest trees in the aseasonal tropics. Not only we did not find any relationship between dry season rainfall and mortality as indicated in some other studies (Villalba and Veblen, 1998), the deficit in annual rainfall resulted in natural mortality with a time lag greater than values reported for several other tropical and temperate forest communities.

Trees subject to water deficit from severe drought may also die through other indirect mechanisms such as outbreak of insect herbivory (Van Bael et al., 2004), an aspect we have not investigated in the MFDP, though we have observed higher levels of Lepidopteran and Coleopteran herbivory of leaves after the onset of monsoonal rains (Murali and Sukumar, 1993). Ecophysiological studies of plant–water relations, combined with observations of pest and pathogen-mediated mortality, in seasonally dry forest communities of the Western Ghats in southern India are needed if we are to better understand the sensitivity of different tree species here to rainfall variability and drought. Such an understanding would help us model the potential response of tropical dry forest ecosystems to future climate change in southern India.

Acknowledgements

We thank the Ministry of Environment and Forests, Government of India for funding this research, and Tamilnadu Forest Department for permissions to carry out long-term research of forest dynamics at Mudumalai. Two anonymous referees made helpful comments that improved our manuscript. We thank our colleagues C.M. Bharanaiah, R.P. Harish, Dr. H.M. Prakasha, A. Srinidhi, and R. Mohan for their support in the field work and data management, and Shivaji, Krishnan, Bomman, Maran, Kunmari, Siddan and several others for their help during field work. Geetha Ramaswami assisted in carrying out the bootstrap simulations, and K. Avinash and Smita Nair in preparation of figures for publication. HSS would like to acknowledge the financial support by IUFRO for attending the conference at Umea, Sweden, and also thank Dr. Michael Kline, IUFRO, for his support during the conference.

References

- Aiba, S., Kitayama, K., 2002. Effects of the 1997–98 El Niño drought on rain forests of Mount Kinabalu, Borneo. *Journal of Tropical Ecology* 18, 215–230.
- Baskaran, N., Balasubramanian, M., Swaminathan, S., Desai, A.A., 1995. Home range of elephants and its implications for the management of Nilgiri Biosphere Reserve, India. In: Daniel, J.C., Datye, H.S. (Eds.), *A Week with Elephants, Proceedings of the International Seminar on the conservation of Asian elephant, Mudumalai Wildlife Sanctuary, June 1993*. Bombay Natural History Society, Bombay, pp. 296–313.
- Borchert, R., 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. *Ecology* 75, 1437–1449.
- Borchert, R., Rivera, G., Hagnauer, W., 2002. Modification of vegetative phenology in a tropical semi-deciduous forest by abnormal drought and rain. *Biotropica* 34, 27–39.
- Borghetti, M., Cinnirella, S., Magnani, F., Saracino, A., 1998. Impact of long-term drought on xylem embolism and growth in *Pinus halepensis* Mill. *Trees* 12, 187–195.
- Brown, S., Lugo, A.E., 1982. The storage and production of organic matter in tropical forests and their role in global carbon cycle. *Biotropica* 14, 161–187.
- Breda, N., Huc, R., Granier, A., Dreyer, E., 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* 63, 625–644.
- Camargo, J.L.C., Kapos, V., 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology* 11, 205–221.
- Condit, R., 1995. Research in large, long-term tropical forest plots. *Trends in Ecology and Evolution* 10, 18–22.
- 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 and Georgetown.
- Condit, R., Hubbell, S.P., Foster, R.B., 1995. Mortality rates of 205 tropical tree and shrub species and the impact of severe drought. *Ecological Monographs* 65, 419–439.
- Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P., Foster, R.B., 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50-ha plots. *Philosophical Transactions of the Royal Society of London B* 354, 1739–1748.
- Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbell, S.P., Foster, R.B., 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology* 20, 51–72.
- Corlett, R.T., LaFrankie, J.V., 1998. Potential impacts of climate change on tropical Asian forests through an influence on phenology. *Climate Change* 39, 439–453.
- Delissio, J.L., Primack, R.B., 2003. The impact of drought on the population dynamics of canopy-tree seedlings in an aseasonal Malaysian rain forest. *Journal of Tropical Ecology* 19, 489–500.
- Eamus, D., 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends in Ecology and Evolution* 14, 11–16.
- George, M., Gupta, G.M., Singh, J. (Eds.), 1988. Forest Soil Vegetation Survey Report on Mudumalai Forest Division, Tamilnadu. Forest Soil – Vegetation Survey, southern region, Coimbatore, India, February 1988.
- Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutiérrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Mauricio, L., López, B.C., Meserve, P.L., Milstead, B.W., Polis, G.A., Previtali, M.A., Richter, M., Sabaté, S., Squeo, F.A., 2006. Extreme climatic events shape arid and semi-arid ecosystems. *Frontiers in Ecology and Environment* 4, 87–95.
- IPCC, 2001. Climate Change: The Scientific Basis. A report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Ishida, A., Diloksumpun, S., Ladpala, P., Staporn, D., Panuthai, S., Gamo, M., Yazaki, K., Ishizuka, M., Puangchit, L., 2006. Contrasting seasonal leaf habits of canopy trees between tropical dry-deciduous and evergreen forests in Thailand. *Tree Physiology* 26, 643–656.
- Kitzberger, T., Veblen, T.T., Villalba, R., 1997. Climatic influences on fire regimes along a rainforest-to-xeric woodland gradient in northern Patagonia, Argentina. *Journal of Biogeography* 24, 35–47.
- Kodandapani, N., Cochrane, M.A., Sukumar, R., 2008. A comparative analysis of spatial, temporal and ecological characteristics of forest fires in a seasonally dry tropical forest ecosystem in the Western Ghats, India. *Forest Ecology and Management* 256, 607–617.
- Kottek, M., Grieser, J., Beck, C., Bruno Rudolf, B., Rubel, F., 2006. World map of the Köppen–Geiger climate classification updated. *Meteorologische Zeitschrift* 15, 259–263.
- Krishna Kumar, K., Rajagopalan, B., Cane, M.A., 1999. On the weakening relationship between the Indian monsoon and ENSO. *Science* 284, 2156–2159.
- Laurance, W.F., Williamson, B.G., Delamonica, P., Oliveira, A.A., Lovejoy, T.E., Gascon, C., Pohl, L., 2001. Effects of a strong drought on Amazonian forest fragments and edges. *Journal of Tropical Ecology* 17, 771–785.
- Losos, E.C., Leigh, Jr., E.G. (Eds.), 2004. *Tropical Forest Diversity and Dynamism: Findings from a Large-Scale Plot Network*. University of Chicago Press, Chicago.
- Maherali, H., Pockman, W.T., Jackson, R.B., 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. *Ecology* 85, 2184–2199.
- Manly, B.F.J., 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. Chapman & Hall, London.
- Miles, L., Newton, A.C., DeFries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E., 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography* 33, 491–505.
- Murali, K.S., Sukumar, R., 1993. Leaf flushing and herbivory in a tropical deciduous forest, southern India. *Oecologia* 94, 114–119.
- Murphy, P.G., Lugo, A.E., 1986. Ecology of tropical dry forest. *Annual Review of Ecology and Systematics* 17, 67–88.
- Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubot, T., Katott, T., Maedat, T., Sato, K., Miguchi, H., Nagamasu, H., Oginott, K., Teotts, S., Hamid, A.A., Seng, H.L., 2000. Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *Journal of Tropical Ecology* 16, 355–367.
- Nath, C., Dattaraja, H.S., Suresh, H.S., Joshi, N.V., Sukumar, R., 2006. Patterns of tree growth in relation to environmental variability in a tropical dry deciduous forest at Mudumalai, southern India. *Journal of Biosciences* 31, 651–669.
- Nishimura, T.B., Suzuki, E., Kohyama, T., Tsuyuzaki, S., 2007. Mortality and growth of trees in peat-swamp and heath forests in central Kalimantan after severe drought. *Plant Ecology* 188, 165–177.
- O'Grady, A.P., Eamus, D., Cook, P.G., Lamontagne, S., 2005. Comparative water use by the riparian trees *Melaleuca argentea* and *Corymbia bella* in the wet-dry tropics of northern Australia. *Tree Physiology* 26, 219–228.
- Pataki, D.E., Oren, R., Smith, W.K., 2000. Sap flux of co-occurring species in a western subalpine forest during seasonal soil drought. *Ecology* 81, 2557–2566.
- R Development Core Team, 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org>.

- Rice, K.J., Matzner, S.L., Byer, W., Brown, J.R., 2004. Patterns of tree dieback in Queensland, Australia: the importance of drought stress and the role of resistance to cavitation. *Oecologia* 139, 190–198.
- Rood, S.B., Braatne, J.H., Hughes, F.M.R., 2003. Ecophysiology of riparian cottonwoods: stream flow dependency, water relations and restoration. *Tree Physiology* 23, 1113–1124.
- Saha, S., BassiriRad, H., Joseph, G., 2005. Phenology and water relations of tree sprouts and seedlings in a tropical deciduous forest of south India. *Trees* 19, 322–325.
- Sharma, B.D., Shetty, B.V., Vivekanandan, K., Rathakrishnan, N.C., 1977. Flora of Mudumalai Wildlife Sanctuary, Tamilnadu. *Journal of the Bombay Natural History Society* 75, 13–42.
- Siegert, F., Ruecker, G., Hinrichs, A., Hoffmann, A.A., 2001. Increased damage from fires in logged forests during droughts caused by El Niño. *Nature* 414, 437–440.
- Singh, K.P., Kushwaha, C.P., 2005. Emerging paradigms of tree phenology in dry tropics. *Current Science* 89, 964–975.
- Sobrado, M.A., 1993. Trade-off between water transport efficiency and leaf life-span in a tropical dry forest. *Oecologia* 96, 19–23.
- Sperry, J., Tyree, T.M., 1988. Mechanisms of water stress-induced xylem embolism. *Plant Physiology* 88, 581–587.
- 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-hectare plot at Mudumalai, southern India. In: Dallmeier, F., Comiskey, J.A. (Eds.), *Forest Biodiversity Research, Monitoring and Modelling: Conceptual Background and Old World Case Studies*, UNESCO, Paris and The Parthenon Publishing Group, Man and The Biosphere Series, vol. 20. pp. 495–506.
- Sukumar, R., 2003. *The Living Elephants: Evolutionary Ecology, Behavior and Conservation*. Oxford University Press, New York.
- Sukumar, R., Suresh, H.S., Dattaraja, H.S., John, R., Joshi, N.V., 2004. Mudumalai forest dynamics plot, Mudumalai Wildlife Sanctuary, India. In: Losos, E.C., Leigh, E.G. (Eds.), *Tropical Forest Diversity and Dynamism: Findings from a Large-scale Plot Network*. University of Chicago Press, Chicago, pp. 551–563.
- Sukumar, R., Suresh, H.S., Dattaraja, H.S., Srinidhi, S., Nath, C., 2005. Dynamics of a tropical dry forest at Mudumalai (India): climate, fire, elephants and the evolution of life history strategies. In: Burslem, D., Pinard, M., Hartley, S. (Eds.), *Biotic Interactions in the Tropics*. Cambridge University Press, UK, pp. 510–529.
- Suresh, H.S., Dattaraja, H.S., Sukumar, R., 1996. Tree flora of Mudumalai Sanctuary, southern India. *Indian Forester* 122, 507–519.
- Suresh, H.S., Dattaraja, H.S., Bhat, H.R., Sukumar, R., 2006. Revised flora of Mudumalai Wildlife Sanctuary, Tamilnadu, India. *Journal of Economic Botany and Taxonomy* 30, 97–156.
- Tobin, M.F., Lopez, O.R., Kursar, T.A., 1999. Responses of tropical understorey plants to severe drought: tolerance and avoidance of water stress. *Biotropica* 31, 570–578.
- Van Bael, S.A., Aiello, A., Valderrama, A., Medianero, E., Samaniego, M., Wright, S.J., 2004. General herbivore outbreak following an El Niño-related drought in a lowland Panamanian forest. *Journal of Tropical Ecology* 20, 625–633.
- Villalba, R., Veblen, T.T., 1998. Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia. *Ecology* 79, 2624–2640.
- Walsh, R.P.D., 1996. Drought frequency changes in Sabah and adjacent parts of north Borneo since the late nineteenth century and possible implications for tropical rain forest dynamics. *Journal of Tropical Ecology* 12, 385–407.
- Woods, P., 1989. Effects of logging drought and fires on structure and composition of tropical rain forest in Sabah, Malaysia. *Biotropica* 21, 290–298.