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Assessing sustainability of nontimber forest product extractions: how fire affects sustainability

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Abstract. Sustainable use of nontimber forest products (NTFPs) can be affected by levels of extractions as well as by other anthropogenic influences such as fire and grazing. We examined the effects of fire on the demography of *Phyllanthus emblica*, an important NTFP in the forests of Biligiri Rangan Hills, India. We then assessed demographic responses to the combined effects of fire and current fruit harvesting patterns. Fruits of *Phyllanthus* are commercially harvested by an indigenous forest dwelling people. Using matrix population models, we compared demographic indices across a chronosequence of time since last fire. Population growth rates (λ) ranged from 0.7692 to 1.1443 across the five times since last fire. λ was the lowest at times since last fire of 2 and 3 yr. Frequent fires increased time to maturity by altering growth and survival rates, thereby causing a demographic shift from growth to regressions or negative growth. Elasticity analysis revealed that stasis of adults makes the biggest contribution to λ. Simulations of periodic and stochastic fire regimes suggest that higher λ and population persistence can be achieved at fire-return intervals of ≥ 7 and ≥ 9 yr, respectively. These fire-return intervals became longer when the simulations included harvesting and fire. Extinction probabilities under the current fire regimes (every 2–3 yr) suggest that populations will decline to lower densities. Our findings provide critical information for developing guidelines for sustainable use and management of NTFPs in Biligiri Rangan Hills, and demonstrate the need to incorporate various human-generated physical regimes in assessing sustainability of NTFPs.

Introduction

Nontimber forest products (NTFPs) have long been used by indigenous and local communities in the tropics for their subsistence and for commercial sale in local, regional and international markets. Extractions of marketable NTFPs, if done sustainably, may represent a sound long-term approach to tropical forest conservation and can be integrated with other land uses and management practices (Anderson 1992; Salick et al. 1995; Ashton et al. 2001; Pilz and Molina 2002). However, the process of extraction of NTFPs can result in over harvesting leading to declines in yields and degradation of the biota (Chambers et al. 1989; Vasquez and Gentry 1989; Browder 1992; Nepstad et al. 1992; Neumann and Hirsch 2000 and references there in). Furthermore, the scope for sustainable NTFP extractions can be affected by other anthropogenic effects such as fire and grazing.

Our current state of knowledge of NTFP extraction systems mostly pertains to the valuation of NTFP resources (Peters et al. 1989; Malhotra et al. 1991; Grimes et al. 1994; Narendran et al. 2001), and patterns of resource use and demography of the extracted species (Piñero et al. 1984; LaFrankie 1994; Runk 1998; Paoli et al. 2001). Some studies have addressed issues of sustainable extractions in the American tropics (Peters 1991; Pinard 1993; Olmsted and Alvarez-Buylla 1995; Peña-Claros 1996; Ratsirarson et al. 1996) and the influences of a stochastic environment on harvest regimes (Nantel et al. 1996; Zuidema 2000; Ticktin et al. 2003). In the Asian tropics, there is a paucity of demographic data even though NTFPs contribute significantly to the revenues of the countries. In their evaluation of sustainability, the above mentioned studies only include effects of harvesting. Most tropical forests are exploited for multiple purposes, and subjected to different types of disturbances; effects of various human influences (e.g., harvesting of NTFPs, fire, and grazing) on the demography of the resource species need to be examined simultaneously to evaluate sustainability of its use.

In India, millions of people living in and around forests depend on NTFP extractions for their livelihood (World Resource Institute 1990; Tewari 1998 and references therein). Extractions of certain NTFPs (e.g., honey and Indian gooseberry, the focal NTFP of this study), over the years, have gone from subsistence-collections to large-scale commercial extractions for sale in local and regional markets. Yet, little priority has been given to the management and sustainable use of NTFP species. Although there is an extensive protected area network in India, the exact conservation status of NTFP species, which constitute a majority of plant species at any location, is largely unknown. Furthermore, in the process of extraction, extractors can impact forests through other ancillary disturbances like fire. In fact, the various human influences may have interactive effects. Despite the increasing levels of NTFP extractions and the pervasive human influences on Indian forests, there are no studies, to our knowledge, that have systematically addressed issues related to sustainability of NFTP use and anthropogenic influences. There is widespread belief that populations of many NTFP species are being depleted, but hard evidence is lacking.

The forest of Biligiri Rangan Hills (BR Hills), our study area, has had a long history of human influences. First, an indigenous people, the Soligas, have been living within the forests and extracting NTFPs for centuries. Soligas were a hunter-gatherer people who practised shifting cultivation until 1972 when the area was declared a wildlife sanctuary. Today, they have usufruct rights to commercially extract NTFPs. They rely heavily on various NTFP extractions which yield up to 50% of their cash income (S. Lele, personal communication). Second, management practices in the wildlife sanctuary may have changed the fire dynamics. For instance, in the past, Soligas used carefully monitored, low intensity fires to control the ground cover, facilitate collection of fruits from the ground during harvesting, and increase accessibility and visibility. Ever since the area was declared protected, the government has practiced fire suppression as a management tool. Today, despite the ban on use of fire, Soligas deliberately set fires (without the knowledge of local managers), which are not monitored. As such, fires are uncontrolled and often spread over large areas. Typically, any given area in the sanctuary is burned every 2–3 yr. Fires occur between February and April, and coincide with the dry season. Despite the long history of human influences, the effects Soligas may have on the forests through harvesting and fires are not well understood.

We examined the effects of fire, on the demography of *Phyllanthus emblica*, the most economically important NTFP species in the forests of the BR Hills in south India, under the current fruit harvesting patterns. We then modelled the combined effects of fire and fruit harvesting patterns. Specifically, the questions addressed were: (i) how is the population growth rate of *P. emblica* affected by time since last fire?, (ii) which population parameters (fecundity, growth to larger size classes, regression to smaller size classes and stasis) are responsible for the differences in population growth rates at various times since last fire, (iii) how do periodic and stochastic fire regimes affect population growth and persistence, and (iv) what are the demographic responses to the combined effects of fire and harvesting? To the best of our knowledge, our attempt at considering the effects of additional human-induced disturbances on harvested populations of a NTFP in assessing sustainability (defined as minimal or no long term negative effect; Hall and Bawa 1993) is the first of its kind.

Phyllanthus emblica

The study species, *Phyllanthus emblica* L. (Euphorbiaceae), commonly known as Amla or Indian gooseberry, is a medium-sized tree that usually attains a height of 7 m and is found in the deciduous forests of BR Hills. The trees produce small, monoecious flowers from February to April, which coincides with the fire season. Immature fruits appear in May. Fruits are globose, 6-seeded berries, and greenish-yellow in colour when ripe. Fruit dispersal begins only when the fruits fall to the ground around November. The fleshy parts of the fruits are then eaten by mammals, such as sambar (*Cervus unicolor*), barking deer (*Muntiacus muntjak*), mouse deer (*Tragulus meminna*) and Chittal (*Axis axis*), and the pits containing seeds are regurgitated. The fruits then dehisce to release the seeds. Regurgitated fruits dehisce faster than the fruits not eaten by the mammalian dispersers and are less susceptible to fungal attacks (A. Sinha, personal observation). No pre-dispersal predation was observed. Instead, post-dispersal seed predation by insects and rodents from the regurgitation piles was observed (A. Sinha, personal observation). Seed germination begins in June with the onset of the southwest monsoons and continues until October.

The fruits are harvested by the Soligas from December to mid-February. Current harvesting techniques of Amla fruits can range from beating of branches on trees and subsequent collection of fruits from the ground, to, lopping of branches or occasionally cutting of the entire tree. The Soligas harvest an average of 86% (±17.72%) of the fruit production on a per tree basis in *P. emblica* (Sinha and Bawa 2002). At the population level, 64.75% of the productivity is harvested. The fruits are used for making pickles, jams, herbal medicines (Ayurvedic), cosmetics and in tanning and dyeing. They are commercially sold to traders through a tribal co-operative.

We chose to work on *P. emblica* because it is one of the most heavily harvested NTFP species in the region, and yet little is known about its conservation status. The revenue generated from this species and *P. indo-fischeri*, another NTFP species, may be as high as 12% of the total cash income in a typical Soliga household (S. Lele, personal communication). Soligas do not distinguish between the fruits of the two species while trading them.

Study area

The study area is located within the Biligiri Rangaswamy Temple Wildlife Sanctuary in BR Hills, south India. The forests of BR Hills lie at the confluence of two mountain ranges, the Eastern and Western Ghats, that run along the east and west coasts of India, respectively. The wildlife sanctuary lies between 11°40′ to 12°09′N latitude and 77°05′ to 77°15′E longitude and covers 540 km^2 (Figure 1). The elevation ranges from 600 to 1800 m. Climate is tropical monsoonal with the monsoon season extending from June to November. The area receives rainfall from both the southwest and the northeast monsoons. Rainfall is variable, ranging from 941 to 1800 mm with topography and altitude. The dry season extends from February to April.

The deciduous forest, where the study species occurs, is found at elevations between 900 and 1400 m. In most parts of the deciduous forest, elephant grasses (*Themeda cymbaria*, *T. triandra* and *Cymbapogon* spp.) form a very dense ground cover and can grow to heights of about 1.5 m. The forest is classified as *Anogeissus–Pterocarpus–Terminalia* spp. type series based on importance index values and dominant forest associations (Ramesh 1989).

Methods

Matrix population models were used to compare the demography of *P. emblica* across a chronosequence of time since last fire. Demographic data on annual rates of survival, growth to larger size classes, regressions (negative growth) to smaller size classes, and fecundity were used to construct transition matrices. These data were collected from 11 permanent

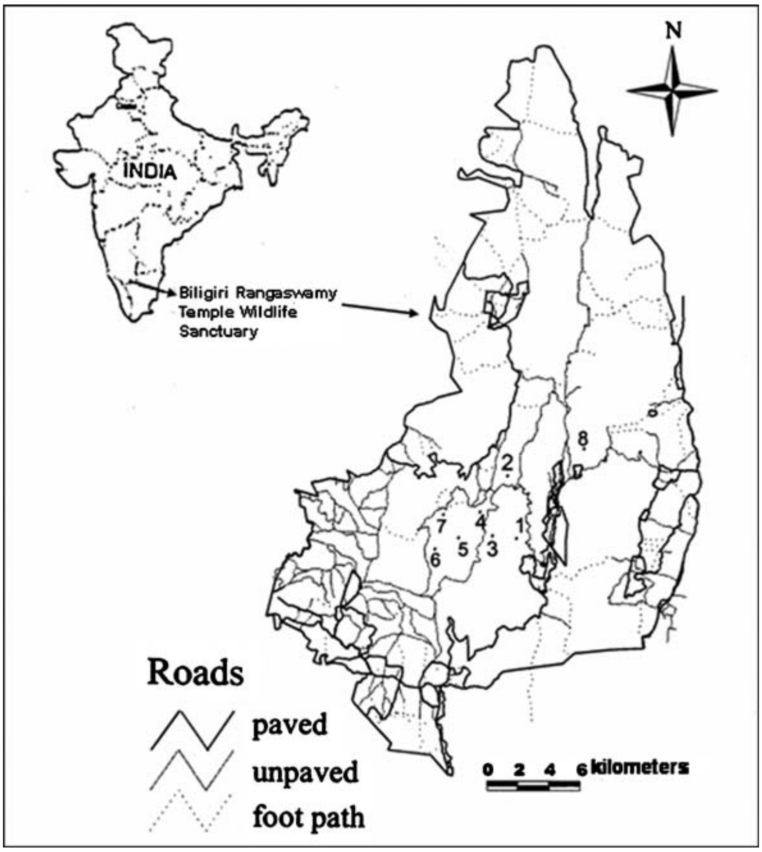

Figure 1. Map of Biligiri Ranga Swamy Temple Wildlife Sanctuary showing the location of the plots: 1. Arlesoneatti, 2. Ganagilarebetta, 3. Thumbebetta, 4. Basavankere, 5. Kumbernaguddae, 6. Tabassigaddae, 7. Thekerguddae, and 8. Arvellibetta.

plots laid in 1995 at eight sites in deciduous forests (Figure 1), with site selection based on time since last fire. A total of 10.5 ha were sampled. Determination of plot size was based on size of the interior habitat (to avoid edge effects from roads) and an adequate number of *P. emblica* individuals (roughly determined by examining size class distributions). Plots ranged from 0.44 to 3.28 ha. Ecological differences among plots were minimized to the extent possible.

We determined time since last fire for each plot by collecting data on the history of fire frequency from informally interviewing Soligas. Information on fire frequencies was validated by multiple independent interviews with Soligas. Time since last fire ranged from 1 to 5 yr with replicates (i.e., plots) in each category (see Table 1). Thus, time since last fire of 2 yr refers to 12–24 months post-fire, 3 yr refers to 24–36 months, etc.

Table 1. Fruit production for plots across the chronosequence of time since last fire.

Plots	Year	*N*	Proportion trees fruited	Total fruit production at the population level
Time since last fire = 5 yr				
Ganagilarebetta	1996–1997	22	0.50	4185
Tabassigaddae II	1996–1997	22	0.68	8400
Time since last fire = 4 yr				
Ganagilarebetta	1995–1996	23	0.17	4794
Tabassigaddae I	1995–1996	64	0.16	5038
Tabassigaddae II	1995–1996	43	0.19	4030
Arlesoneatti	1995–1996	24	0.42	750
Arvellibetta	1995–1996	177	0.56	55,821
Thumbebetta	1996–1997	28	0.86	8040
Time since last fire = 3 yr				
Thumbebetta	1995–1996	71	0.58	5398
Basavanakere	1996–1997	14	0.86	12,262
Time since last fire = 2 yr				
Kumbernaguddae	1995–1996	6	0	0
Basavanakere	1995–1996	15	0.47	16,064
Thekerguddae	1996–1997	85	0.94	25,409
Time since last fire = 1 yr				
Thekerguddae	1995–1996	166	0.02	1091
Kumbernaguddae	1996–1997	6	0	0
Tabassigaddae I	1996–1997	25	0.64	8960
Arlesoneatti	1996–1997	24	0.63	690
Arvellibetta	1996–1997	95	0.13	4242

Twenty-nine reproductive adults were used for estimation of fruit production. *N* in the table represents the number of adults sampled for the estimation of proportion trees fruited during the study period, 1995–1997. The last column of the table represents fruit production/ha.

Demographic data

Survival and growth estimates

We estimated survival, regressions, and growth of individuals from annual censuses of 7372 tagged individuals conducted from 1995 to 1997. Each of the 11 plots was divided into subplots of 20 × 20 m to facilitate enumerations. All individuals were mapped on the subplots. Diameters of all ramets of an individual were measured and used to calculate the basal area of an individual. Basal areas were used instead of diameter at breast height as branching of stems and trunks can occur at variable heights. Each annual census was conducted between December and March/April prior to the occurrence of any fires. However, in three of the plots, census could not be completed prior to the occurrence of fires. As such, data were collected immediately following a burn, providing information on size-based survivorship and population responses in a burn year (time since last fire = 0 yr). However, as this data set was relatively small, it was used only for comparison of size-based survivorship and population growth rates across times since last fire.

We estimated annual survivorship of new seedlings by monitoring them in the subplots three times during their first year of recruitment. This was done because the germination period extends from June to October. The first enumeration was done in July and August when most seeds germinate, the second in November to ensure those seeds that germinated since the first enumeration had been included, and the third when the seedlings were approximately 9 months old. The proportion of seedlings surviving decreased exponentially with time ($Y = 192.47 * e(-0.65x)$, $r^2 = 0.99$, $p < 0.05$, Sinha 2000). This relationship was then used to calculate the annual seedling survival rate from the survival rate through 9 months.

Fecundity estimates

Fecundity estimates (contribution of adults to the seedling stage) for the transition matrix were determined using data on reproductive effort, fruit predation and seed germination (Menges 1990; Caswell 2000a). Multiplying the reproductive effort of each class with the probability of seed germination gave the contributions of each class to the seedling stage (Caswell 2000a). Fecundity estimates appear as the top row entries in a transition matrix.

Reproductive effort of adults was the product of mean fruit production per individual and the proportion of trees that fruited each season. Fruit production per individual (fruit crop size, FCS) was estimated in a subset of reproductive adults in each plot (29 trees, basal area ≥ 63.644 cm^2) during the fruiting seasons of 1995–1996 and 1996–1997 prior to fruit dispersal. FCS was measured by counting the number of fruits on three random branches and multiplying the average number of fruits per branch by number of branches. Mean FCS was then calculated for each plot. Proportion of trees that fruited each season was determined by monitoring a sample of adults in each plot (see Table 1 for sample sizes). In addition, we calculated the total fruit production at the population level by multiplying the total number of trees that fruited in each plot with the mean FCS. Since the area of plots was different, total fruit production was corrected for area.

Probability of seed germination was a function of rates of seed predation and proportions of seeds germinating (Caswell 2000a). We assessed levels of post-dispersal fruit predation (defined as damage or removal of fruits from regurgitation piles) at two locations in the field. Deposits of regurgitated fruits were identified and monitored twice a month from November to April. Numbers of intact regurgitated fruits and fruits showing signs of predation were counted. Missing fruits not found near the deposits were assumed to have suffered predation. Fruits showing signs of predation were removed to avoid confusion during subsequent observations. From the data collected, we calculated the proportion of fruits/seeds that suffered predation. The proportion of seeds germinating was determined by planting and monitoring 50 seeds at the field station in the wildlife sanctuary. No seed dormancy was observed (S. Setty, personal communication; A. Sinha, personal observation). The rates of seed predation and germination used in our analyses were the same regardless of time since last fire.

Fecundity estimates were not corrected for harvesting rates since fruit harvesting is very variable both spatially and temporally, and was very low to none in the focal plots during the study period (A. Sinha, unpublished data). For instance, fruits had not been harvested for the last 5 yr from Arvellibetta, one of our plots. Furthermore, it is possible that there may be spatiotemporal variation in seed germination and predation rates across times since last fire but logistical problems precluded determination of seed predation and germination rates at each plot.

The model

Six classes were used to construct transition matrices, with the first being an age class and the others being size classes based on basal area measurements and the reproductive status (Maschinski et al. 1997; Kaye et al. 2001; H. Caswell personal communication): (1) seedlings up to a year old (S_1, an age class); (2) saplings, S_2 (>1 yr old seedlings ≤ 0.072 cm^2); (3) saplings S_3 ($>0.072 \leq 0.787$ cm^2); (4) juveniles, S_4 (>0.787 ≤ 19.643 cm^2); (5) juveniles S_5 (>19.643 ≤ 63.643 cm^2), and (6) reproductive adults, S_6 (>63.643 cm^2). Individuals that were burned or did not have above ground vegetative parts at the time of census were considered dead if they did not reappear during the next census; if they resprouted, they were put into the appropriate size class based on their new basal area. Data from plots with similar times since fire were pooled together to construct the transition matrices (Caswell 2000a). Prior to data pooling, we analysed the data for each plot and found that plots with same times since last fire had similar population growth rates, indicating very little variation in population trends among the plots in any given pooled category. Thus, our pooling of data across times since fire did not alter our conclusions.

Probabilities of growth, stasis (staying in the same size class), and regressions, as well as fecundity rates were calculated to build the transition matrices. A value of 0.0001 was substituted to estimate transitions that could not be determined due to absence of individuals of a certain size class in a given year (H. Caswell personal communication); this was necessary in order to run the model. All transitions were calculated using Matlab (MathWorks, Inc. 2002).

We used a deterministic, density-independent model of population growth of the form $n(t+1) = An(t)$, where A is the transition matrix, and n, a vector, gives the numbers of individuals in each size class at time t or $t+1$ (Caswell 2000a). From the model, we obtained the asymptotic rate of population increase (λ), given by the dominant eigenvalue, for each time since last fire. Thus, λ for time since last fire of 5 yr refers to population growth during the fifth year after a fire. A λ of 1 indicates a stable population, <1 a declining population, and >1 a growing population. We then calculated confidence intervals for λ using bootstrap resampling with replacement which calculates λ repeatedly for a subset of the total data set (for details, see Caswell 1989; Efron and Tibshirani 1993). The individual with its demographic parameters, i.e., rates of fecundity, growth, stasis and regression constituted a resampling unit. A bootstrap sample size of 5000 was used.

The right eigenvector (w) obtained from the transition matrix represents the population stable stage distribution (SSD). A G-test (Sokal and Rohlf 1994) was used to test for differences between the SSD and the observed stage distribution.

One of the assumptions of our model was density independence, which excludes the effects of density on population growth. Such as assumption may or may not be valid. It is possible that *Phyllanthus* populations are below their carrying capacity given the level of human-induced disturbances in the study area. However, long term demographic studies that explicitly include density-dependence in their models will have greater predictive power than our model and will be of value in providing information required for adaptive management.

Elasticity analysis and life table response experiments

Elasticity analysis was used to evaluate the proportional contributions of survival, growth, fecundity and regressions to λ. Elasticities accurately predict the functional dependence of λ on matrix elements, a_{ij} (Ehrlén et al. 2001). In other words, elasticity measures how a proportional change in the matrix elements causes a proportional change in λ. Elasticity analysis is being increasingly used in conservation and management. Elasticity is given by

$$e_{ij} = \frac{a_{ij}}{\lambda} \cdot \frac{\partial \lambda}{\partial a_{ij}},$$

where $\partial\lambda/\partial a_{ij}$ is the sensitivity of λ to small absolute changes in a matrix element a in row i and column j. All elasticities in a matrix sum to 1 since they give the proportional contribution of the matrix elements to λ (Caswell 2000b; de Kroon et al. 2000).

Various factors may affect λ through their effects on vital rates (reproduction, survival and growth). Variations in λ can be explained as functions of variation in the vital rates using life table response experiments (LTRE) developed by Caswell (1989, 2000a, b) and are given by

$$V(\lambda) = 1/N - 1\left[\sum \lambda_i^2 - \frac{(\sum \lambda_i)^2}{N}\right].$$

Stated differently, LTRE analysis determines the contribution of each vital rate to the overall observed effect of fire on λ. We used LTRE analysis to examine which vital rates contribute most to the overall effect of fire on λ across a chronosequence of times since last fire using methods described by Caswell (1989, 2000a, b) and Caswell and Kaye (2001).

LTRE analysis has great potential for contributing to conservation and management efforts and can be used in conjunction with elasticity analysis (Ehrlén and Groenendael 1998). Since LTRE analysis assesses differences in terms of past variation, it can be extremely valuable in evaluating variations that might result from management practices. However, the use of LTRE as a tool in conservation biology has been limited.

Periodic and stochastic fire regimes

The population model described above is a time-invariant model that does not include the effects of environmental fluctuations on population growth. It is thus important to incorporate environmental variability into the population projection model to make more realistic projections of effects of fire regimes on λ. We considered fire as a dynamic part of the environment of *P. emblica* by simulating the effects of two fire regimes: (i) periodic, and (ii) stochastic, on population responses of *P. emblica* using variable transition matrices. Population projections under the two fire regimes can provide guidance for better management.

A periodic fire regime can be defined by the interval between either burned years or unburned years (Caswell and Kaye 2001). We modelled the periodic regime by defining the fire intervals, i.e., the number of years between fires, and therefore, the order of the transition matrices. Thus, a fire frequency of 0.33 yr (i.e., fire-return interval of approximately 3 yr) can be specified by the following sequence of transition matrices: $A_1A_2A_3A_1A_2A_3\ldots$ We calculated the population growth rate for 1–12 yr fire-return intervals.

The stochastic fire regime measures the outcome of random fires on the population and was simulated by randomly alternating the transition matrices of the different times since last fire following Nantel et al. (1996). This means that the sequence of 'environments' which produce the transition matrices is stochastic. Therefore, in each projection, different random sequences of matrices are used. Average fire-return intervals ranged from 1 to 12 yr. The stochastic growth rate (log λ_s) and it's associated 95% confidence intervals, as well as the population sizes were computed for each simulation. Populations with log $\lambda_s > 0$ are likely to persist while those with log $\lambda_s \leq 0$ will go extinct (Caswell and Kaye 2001).

We determined probabilities of pseudo-extinction and quasi-extinction for the periodic and stochastic fire regimes, respectively. These extinctions can be defined as the probability of populations reaching a specified fraction of the current population (Ginzburg et al. 1982; Burgman et al. 1993) or a critical threshold population size below which no increase in population occurs. We used probability of the population falling below the initial population size as the extinction threshold. This initial population size yielded a $\lambda > 1$ and is therefore relevant to management and conservation concerns.

For both periodic and stochastic regimes, the simulations were run 1000 times and projected for 20 yr since this time frame may be of relevance from the management perspective. Both the periodic and stochastic simulations were performed using Matlab (MathWorks, Inc. 2002).

An assumption of our periodic and stochastic simulations is that the mean and variances of coefficients of our transition matrices represent the means and variances in a larger data set from a longer time series (Nantel et al. 1996). Furthermore, our stochastic simulations do not measure the cumulative effects of fire, i.e., the impact of two fires in subsequent years are equal.

Fire and fruit harvesting

As fruit harvesting was very low to none in the focal plots during the course of the study, we assumed that our demographic model and the periodic and stochastic fire simulations predominantly reflect the effects of fire. We then introduced the effects of harvesting patterns into the periodic and stochastic fire simulations, described above, to assess how our populations would respond to being systematically harvested. This would provide information on how two main anthropogenic pressures, harvesting and fire, may affect sustainability of use of *P. emblica*. The harvest level (intensity) and practices used in our model reflect harvest patterns used by Soligas; typically, 65% of the fruit production at the population level was harvested and main branches were lopped from 5% of the harvested trees (Sinha and Bawa 2002). In our model as well as in reality, such lopping rendered 5% of trees unproductive for a year. Hereafter, we refer to the simulation regimes as: *fire only* (simulations of stochastic and period fire regimes described in the previous section), and *fire + harvest* (harvest of 65% of the productivity accompanied with a lopping rate of 5%). As in the *fire only* model, we calculated population growth rates, and pseudo-extinction and quasi-extinction rates for the *fire + harvest* model.

Results

Effects of fire on fruit production

Fruit production was variable among plots as well as between years for a given plot (Table 1). Typically, high fruit production in one year was followed by low fruit production in the next year or vice versa (e.g., Tabassigaddae II, Arvillebetta, Thekerguddae). These differences in productivity between years were due to the proportion of trees that fruited and were more pronounced in burned plots. For instance, in plots that were burned during the study period (e.g., Thekerguddae, Tabassigaddae I, Arlesoneatti, and Arvellibetta), there was a 1.5–39.06-fold difference in the proportion of trees that fruited in the year following a fire, compared to the 1.5–3.66-fold variation observed in proportion of trees that fruited in unburned plots. In Arvellibetta, 13% of the trees fruited in the year following a fire, i.e., the next fruiting season, whereas

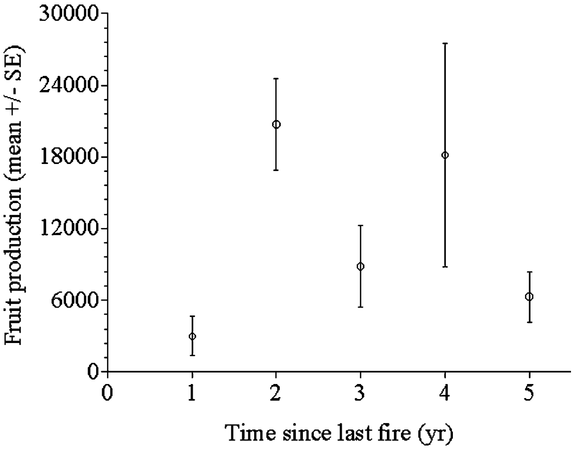

Figure 2. Fruit production (mean ± SE) at different times since last fire. Fruit production data from plots were pooled by time since last fire.

56% trees fruited in the previous year (1995–1996), a nonfire year (Table 1). A similar pattern was also found in another location, Thekerguddae.

When fruit production data from plots were pooled by time since last fire, mean fruit production (per ha) was lowest in the year following a fire, i.e. time since last fire of 1 yr (Figure 2). Plots at times since last fire of 2 and 4 yr had higher levels of mean fruit production and fecundity than those of 1, 3 and 5 yr.

Germination and survivorship

In the germination experiments performed at the field station, the proportion of seeds that germinated was 0.65. Approximately, 59.72% seeds suffered predation in the field. Survivorship of individuals, as expected, increased with individual size (Figure 3). However, this trend was less consistent for the larger size classes, S_4–S_6. The biggest change in rates of survival occurred between the seedling and sapling classes (more than a 2-fold difference) regardless of time since last fire. Generally, rates of survival of seedlings and saplings were lowest in plots second year after fire (time since last fire = 2 yr) with the exception of those in a burn year (time since last fire = 0 yr). Survival rates for burn year are shown for comparison. Adult survivorship was largely unaffected by time since last fire.

Effects on demography

Population growth rates were positive at times since last fire of 1 and 5 yr but not significantly different given by the overlap in the confidence intervals

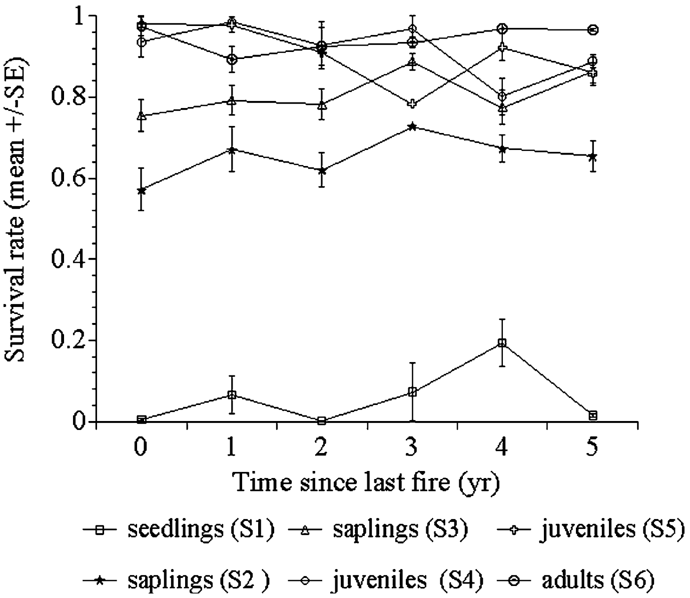

Figure 3. Size-specific survival rate (mean ± SE) as a function of time since last fire. The rates for burn year (time since last fire = 0 yr) are shown for comparison.

Table 2. Population growth rates (±95% CI) at various times since last fire.

Time since last fire (yr)	λ	Confidence intervals	
		Lower limit	Upper limit
0	0.7692	0.6731	0.8653
1	1.1368	1.0565	1.2074
2	0.9502	0.9162	0.9795
3	0.9225	0.8797	0.9637
4	1.0100	0.9862	1.0511
5	1.1443	1.0047	1.2399

Confidence intervals were generated using bootstrap resampling procedure. Population growth rate for burn year (0 yr since last fire) is shown for comparison. A λ of 1 indicates a stable population.

(Table 2). In the fourth year after a fire (time since last fire = 4 yr), the λ of 1.01 was significantly different from that in the first year following a fire. In contrast, in the second and third years after fire, population growth rates were negative and significantly different from λ at all other times since last fire. λ in a burn year declined by 23% and has been shown for comparison (Table 2). For reasons stated above, this data was not used in any further analysis. Appendix 1 gives the transition matrices for the times since last fire.

Seedlings dominated the SSD, making up 22–83% of the SSD, in plots in the first and second years after fire. However, the sapling classes were the most abundant in the SSD (63–84% of the SSD) in the third, fourth and fifth years

Table 3. Total elasticities of population growth rate for each time since last fire.

Classes of individuals	Time since last fire (yr)				
	1	2	3	4	5
Seedlings (S_1)	0.0788	0.0000	0.0022	0.0349	0.0642
Saplings (S_2)	0.1331	0.0000	0.0075	0.0745	0.1138
Saplings (S_3)	0.1343	0.0000	0.0213	0.0830	0.1862
Juveniles (S_4)	0.0550	0.0000	0.0079	0.0988	0.0802
Juveniles (S_5)	0.1598	0.0099	0.0168	0.0509	0.1357
Adults (S_6)	0.4391	0.9900	0.9444	0.6578	0.4199

Elasticities for fecundity, stasis, growth and regression were summed over each class.

since last fire. All the observed stage distributions were significantly different from the SSDs (G values for various times since last fire from 1 to 5 yr are: 353.32, 566.61, 117.42, 157.20, 197.18; $p < 0.001$).

Elasticity analysis

Comparing elasticities across a chronosequence of time since last fire provided information about the response of λ to fire return intervals. The elasticities in Table 3 represent the sum total of all effects of population parameters on λ, i.e., through fecundity, stasis, growth and regression, for each class of individuals. λ was most sensitive to the fate of adults which accounted for 44% to almost 100% of the total elasticity (Table 3). Elasticities for all classes but adults were extremely low at times since last fire of 2 and 3 yr compared to other times since last fire. Thus, a proportional change in the survival, growth, fecundity and regressions of adults would cause the greatest change in λ, in particular, in populations 2 and 3 yr since last fire.

The relative importance of the population parameters in affecting λ was: stasis > growth > fecundity > regression, a pattern more pronounced in plots at times since last fire of 2 and 3 yr (Table 4). This indicates that any small change to stasis of individuals in these plots would have a proportionally greater effect on λ than in other plots. Regardless of time since last fire, stasis of adults had the largest influence on λ. In contrast, elasticities for growth were much lower at times since last fire of 2 and 3 yr compared to other times since last fire. Regression elasticities were an important transition in the first year after fire, and were greatest for regression of individuals to the sapling class for most times since last fire.

Life table response experiments

Changes in survival, growth, regression and fecundity due to fire contributed to the overall effect of fire on λ. Time since last fire of 1 yr was used as a point of comparison, and effects were measured relative to these populations. Contri-

Table 4. Elasticities of population growth rates to changes in stasis, growth, and regression.

Classes of individuals	Time since last fire (yr)				
	1	2	3	4	5
Stasis					
Saplings (S_2)	0.0475	0.0000	0.0042	0.0346	0.0397
Saplings (S_3)	0.0665	0.0000	0.0173	0.0506	0.1149
Juveniles (S_4)	0.0349	0.0000	0.0049	0.0626	0.0481
Juveniles (S_5)	0.0992	0.0061	0.0074	0.0322	0.0712
Adults (S_6)	0.3582	0.9861	0.9350	0.6214	0.3557
Growth					
Seedlings (S_1)	0.0788	0.0000	0.0022	0.0349	0.0642
Saplings (S_2)	0.0856	0.0000	0.0034	0.0399	0.0741
Saplings (S_3)	0.0611	0.0000	0.0029	0.0275	0.0616
Juveniles (S_4)	0.0167	0.0000	0.0022	0.0353	0.0310
Juveniles (S_5)	0.0599	0.0000	0.0093	0.0184	0.0642
Regression					
Saplings (S_3)	0.0067	0.0000	0.0011	0.0049	0.0097
Juveniles (S_4)	0.0034	0.0000	0.0008	0.0010	0.0011
Juveniles (S_5)	0.0007	0.0000	0.0000	0.0002	0.0003
Adults (S_6)	0.0021	0.0038	0.0071	0.0015	0.0000

butions of survival, growth, regression and fecundity were summed over all size classes to get a single value across each time since fire.

Largest reduction in λ was due to the effects of fire on growth followed by survival (Figure 4). At time since last fire of 2 yr, growth and survival contributions to λ were the lowest whereas fecundity showed a maximum increase (Figure 4). Although this increase in fecundity contributed positively to a change in λ, it was not adequate to offset the cumulative negative effects of all

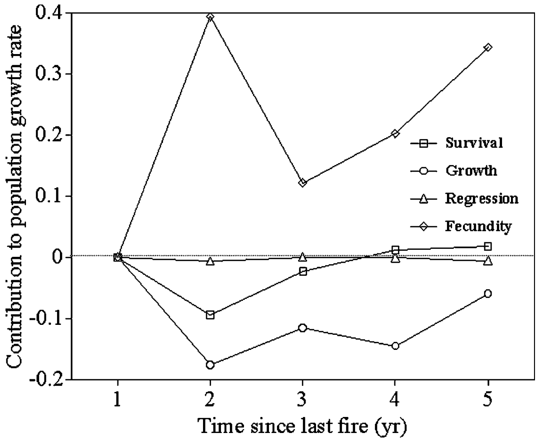

Figure 4. Contributions of population parameters (stasis, growth, regressions and fecundity) to the effects of time since last fire on λ. These contributions were calculated using LTRE analysis.

other parameters. Consequently, the net result of all changes was a decrease to a $\lambda < 1$ (see Table 2). Similarly, at time since last fire of 3 yr, the overall λ was still below 1 due to negative contributions of survival and growth. Contributions of fecundity to λ were higher than in the year after fire, again, with a net result of a declining population. Negative contributions through regressions, which were more pronounced at 2 and 3 yr since last fire than in the year after fire, also ensured declining λ (by 18 and 21% compared to in the year after fire). Good survival and fecundity during the fourth year after fire brought about a net positive λ. In fact, fecundity contributions were at a high point of its two year cycle. However, negative effects of fire on growth of all size classes translated to a negative growth contribution (Figure 4), resulting in a λ fluctuating around the stable λ. Positive contributions of survival and fecundity offset the negative effect of fire on growth in the fifth year after fire leading to a positive λ of 1.1443; both survival and growth across all classes were balanced with very few individuals moving to smaller classes. This was in contrast to the plots at time since fire of 1 yr where regressions were important. Furthermore, following a fire, the surviving population resprouted mainly in the sapling classes. Thus, the effects of fire might be manifested as changes in survival, growth, regression and fecundity depending upon time since last fire. In addition, the causal factors responsible for positive population growth rates (time since fire of 1 and 5 yr) may be different.

Fire regimes and fruit harvesting

Population growth rates increased as fire return intervals became longer under the *fire only* and *fire + harvest* periodic and stochastic regimes (Figure 5a, b). However, population growth rates, for both periodic and stochastic simulations, were lower in the *fire + harvest* regimes than in the *fire only* regimes but these differences were not significant. Critical fire-return intervals that allowed population persistence, not surprisingly, became longer when fire was modelled in combination with harvesting patterns.

A periodic *fire only* regime resulted in a population growth rate that declined ($\lambda < 1$) at fire return intervals of less than 6 yr (Figure 5a). Even though the population was projected to increase at fire intervals of ≥6 yr, the confidence intervals indicated that the population growth rate could fluctuate and decline below 1, the stable population growth rate. The critical fire-return interval was in the order of ≥7 yr given by the positive population growth rate and its confidence intervals (Figure 5a). In contrast, periodic fires accompanied with harvest (*fire + harvest*) required fire-return intervals of ≥8 yr (Figure 5a).

Under a stochastic *fire only* regime, average fire-return intervals of > 6 yr resulted in a stochastic population growth rate slightly greater than zero, indicating that the population may persist (Figure 5b). However, the minimum average fire-return interval that will ensure positive growth was ≥9 yr for a *fire*

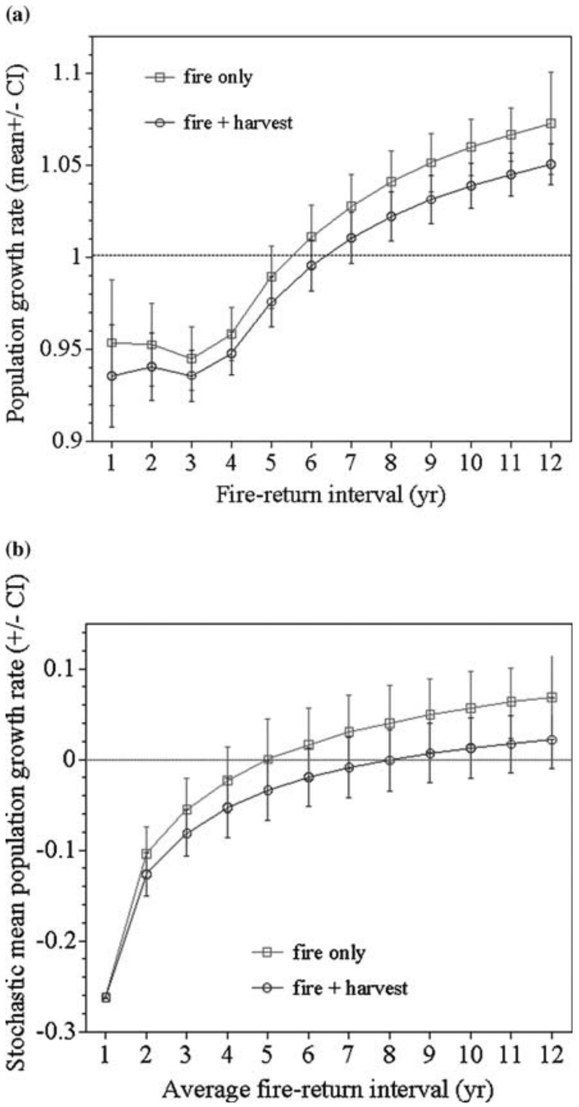

Figure 5. (a) Population growth rate (mean ± 95% confidence intervals) as a function of fire-return interval for *fire only* and *fire + harvest* periodic regimes. The lambdas are means of 1000 simulations for 20 yr. The dashed line represents a stable population. (b) Stochastic population growth rate (mean ± 95% confidence intervals) for *fire only* and *fire + harvest* regimes as a function of average fire-return interval. A stochastic population growth rate > 0 (above the dashed line) indicates a population that is likely to persist. A zero or negative growth rate leads to extinction.

only regime and longer (> 10 yr) for the *fire + harvest* regime (Figure 5b). Under both the stochastic regimes, increase in population growth rates required longer fire return intervals than the periodic fire regimes.

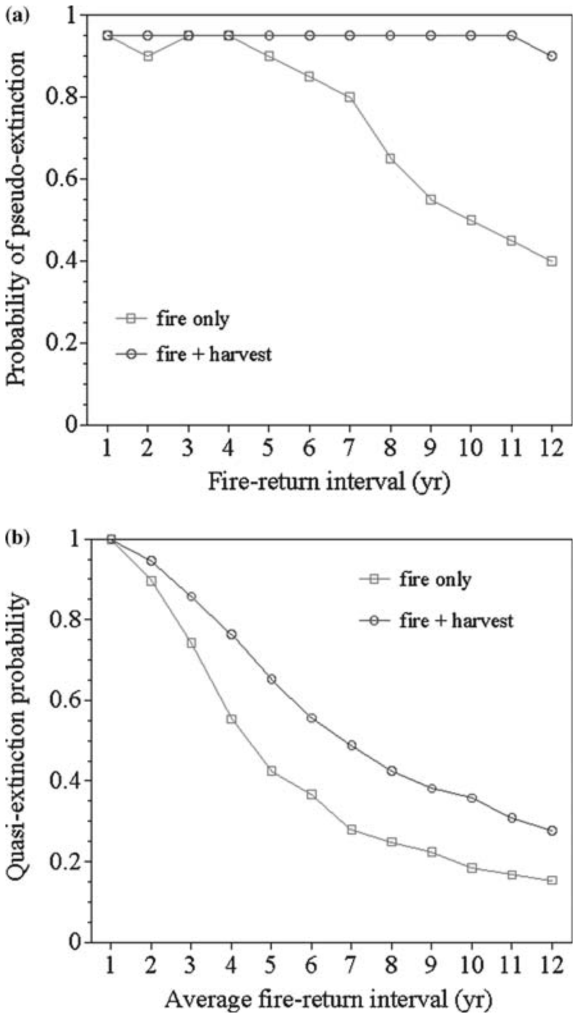

Figure 6. (a) Probability of pseudo-extinction as a function of fire-return interval under a periodic fire regime. Results are for a time horizon of 20 yr. (b) Quasi-extinction probability as a function of average fire-return interval under a stochastic fire regime. Results are for a time horizon of 20 yr.

Persistence of the population over the 20 yr projection period was greater under stochastic regimes than if fires were to occur periodically (Figure 6a, b). In the presence of periodic *fires only*, probability of pseudo-extinction decreased with longer intervals between fires (Figure 6a). Pseudo-extinction probabilities at fire regimes of 1–5 yr fluctuated between 90 and 95% and fell rapidly thereafter for a *fire only* regime whereas the probability of pseudo-extinction remained high (>90%) for the *fire + harvest* regime. In contrast, the stochastic simulations predicted a declining trend in quasi-extinction probabilities for both regimes, *fire only* and *fire + harvest* (Figure 6b). Compared to the periodic regimes, the likelihood of extinctions were much lower in the stochastic regimes. There was a greater than 50% likelihood of population persistence associated with random fire occurrence with an average return time of >5 yr. This likelihood increased to over 75% if average fire-return intervals were ≥ 9 yr; this fire return interval would ensure positive growth rates (Figure 4b). In both periodic and stochastic regimes, if fire returned every year, extinction probability would be 1 indicating that the populations would continue to decline exponentially to lower densities.

Discussion

Our findings provide valuable information about fire frequencies conducive for long term-persistence of *P. emblica* and help focus attention on aspects of the life stages and population parameters that need management efforts. To the best of our knowledge, our study is the only one that characterizes population responses of a long lived tree species in terms of 5 yr of post-fire recovery times.

Effects of fire on fruit production

Long-term studies in BR Hills have observed high levels of fruit production in *P. emblica* in alternate years (S. Setty, personal communication). Our findings suggest that alternate years of heavy fruiting might be intrinsic to the species though fire might set the pattern. Fire negatively impacted fruit production in *P. emblica* because the alternating high/low fruit production we observed was more pronounced in response to fire. The biggest year-to-year differences in fruit production were observed following a fire, with fruit production being considerably lower in the year after a fire (e.g., Arvellibetta and Thekerguddae). Similar responses to fire have been observed in other woody species that either have no seed set or lowered fruit production for a few years following a burn (Hoffmann 1999).

In some plots (e.g., Arvellibetta 1996–1997, and Thekerguddae 1995–1996) where the fires coincided with the flowering season, trees did not produce fruits that year. *P. emblica* flowers at a time (February–April) when most fires occur in BR Hills. When such fires reach *Phyllanthus* canopies, they burn the buds and flowers resulting in low or no fruit production in the subsequent fruiting season (A. Sinha, personal observation). However, late season fires that occurred after the flowering season had little effect on fruit production (e.g., Tabassigaddae I 1996–1997). Such negative effects of timing of fires during a burn season on leaf flush and seed production have been previously documented (Setterfield 1997). Our findings and observations suggests that the timing of fires may be critical in determining fruit production and fecundity rates of trees in the following fruiting season. However, the effects of timing of fire need further exploration.

Demographic responses to fire

Disturbances, natural or human-induced, may not necessarily reduce population growth rates. West (1995) reported similar annual population growth rates for tree populations at different ends of the disturbance gradient, i.e., completely unlogged and 60% logged. Similarly, rates of population growth for pre- and post-hurricane tree populations were not significantly different (Batista et al. 1998). In *Phyllanthus*, population growth rates from the two ends of the disturbance gradient, i.e., time since last fire, seemed to converge.

Instead, the impacts of disturbance might be manifested in other aspects of the life history of a species. The positive population growth rate in the first year after fire may be because fire opened up spaces and reduced competition from elephant grass and weedy species, which are common ground cover; λ, indeed, was sustained by both higher levels of seed germination (Sinha 2000) and increased regressions to the sapling classes. However, as time since last fire increased, survival and growth balanced each other and regressions had a small effect on λ. This suggests that populations can increase at similar rates yet how they achieve that increase might differ based on disturbance regimes.

Furthermore, disturbance can increase selection pressures on certain stages that maintain the population at or close to pre-disturbance levels or alter the importance of population parameters. Significant shifts in contributions of population parameters to λ have been documented in disturbed populations (Batista et al. 1998). Our results from the LTRE analyses, indeed, support this.

As fires become more frequent, deterministic and stochastic population growth rates have been observed to increase in herbaceous species (Silva et al. 1991; Canales et al. 1994; Caswell and Kaye 2001; Quintana-Ascencio et al. 2003), as well as decline in savanna woody species (Hoffmann 1999). In addition, intermediate patterns, where the population growth rate peaks at intermediate fire frequencies, have also been documented (Gross et al. 1998). Our matrix models predicted that longer fire return intervals were more conducive to *Phyllanthus* populations than frequent fires in the forests of BR Hills. If the current fire frequencies of every 2–3 yr should persist, the populations will continue to decline to lower densities. If fire were the only human-induced disturbance in these forests, the periodic and stochastic simulations suggest that fire intervals must be at least ≥7 to ≥9 yr, respectively, in order to ensure the persistence of this NTFP species. Since the cumulative demographic effects of fire and harvesting were more severe than if each of these were to occur alone, our findings suggest long fire return intervals (≥8 yr for periodic and ≥10 yr for stochastic). Such long intervals between fires can be explained in terms of growth form and stature. Typically, woody species prefer either low frequencies of fire or fire exclusion (Frost et al. 1986; Schmalzer and Hinkle 1996; Hoffmann 1999).

Moreover, frequent fires, e.g., annual burning, would cause a demographic shift from growth (to larger size classes) to regressions. Such regressions (negative growth) reduced mean individual sizes, delayed time to maturity and growth, and increased the probability of stasis or further regressions. Delayed time to maturity, in turn, may increase the risk of mortality, especially since survival in *Phyllanthus* is a function of size of individuals. Hoffmann (1999) reported similar responses to frequent fire in trees of the Brazilian Cerrado. Thus, despite the 13.68% increase in λ in the first year after fire, a rate of increase very similar to that obtained in the fifth year after fire (14.43%), annual burnings may be detrimental to *Phyllanthus* populations in the long term.

Furthermore, differences between the observed and stable stage distributions at different recovery times may be due to past disturbance regimes. Since fires are a frequent disturbance type that occur on a short time scale, the populations are not given enough time to attain the stable stage distributions; instead they appear to persist under nonequilibrium conditions.

Critical population parameters and life stages

The extent to which the population growth rates of species are affected by stasis, growth and fecundity differ greatly among species and habit. Fecundity has been shown to be important in short-lived species, whereas in long-lived woody plants, survival was the most important determinant of λ (Caswell and Werner 1978; Caswell 1986). Typically, fecundity makes very small contributions to the population growth rates ($<1\%$) of *Araucaria cunninghamii*, a gymnosperm (Enright and Watson 1991) and *Astrocaryum mexicanum*, a palm (Pinero et al. 1984). Our findings (from LTRE and elasticity analyses) revealed that fecundity was a relatively unimportant parameter in increasing λ, pointing to the fact that extraction of fruits *per se* may be less of a limiting factor for λ than other population parameters. These results must be treated with caution because ancillary disturbances associated with fruit-extractions, such as lopping of branches and trees during harvesting, lowered fruit production in the subsequent year (Sinha and Bawa 2002); harvesting techniques combined with the effects of fire may significantly reduce λ.

In contrast to fecundity, changes in stasis, in particular of the adult size class, affected λ the most in *Phyllanthus*, a pattern observed in other woody plants as well (Enright and Watson 1991; Silverton et al. 1993; West 1995) including palms (Piñero et al. 1984; Pinard 1993; Olmsted and Alvarez-Buylla 1995; Ratsirarson et al. 1996). The implication of this finding is that increasing survival of adults (e.g. through reduced lopping during harvesting) may significantly increase λ; most lopped individuals died (A. Sinha, personal observation).

The effects of fire on population parameters determine the contribution of that parameter to the overall change in λ. Effects of fire on stasis, growth, regressions and fecundity changed with time since last fire, thereby causing a shift in contributions of these parameters to λ. As time since last fire increased, contributions of regression to λ (e.g., 1 yr since last fire) were replaced by contributions of growth and stasis (e.g., 4 and 5 yr since last fire). This shift can be explained by the fact that fire reduced the probabilities of growth and stasis but increased the likelihood of regressions. Somewhat low contributions of growth and stasis to λ 2 and 3 yr since last fire may be due to increased competition from elephant grasses that have very different growth rates and reproductive biology compared to the focal species (A. Sinha, personal observation). Furthermore individuals of woody species may allocate more energy towards growth and getting back their vegetative structures following disturbance by fire than growing out of a size class.

Long term fate of P. emblica populations

Human influences in the forests of BR Hills are very pervasive and their dominance has increased over the years due to increase in the human population and its demands. The intensity of use of the forests and the impacts thereof has changed over the years. For instance, fires have become more frequent and intense, and harvesting of *P. emblica* fruits has gone from a subsistence level activity to a commercial one (K.S. Bawa, personal communication).

Our results are of direct relevance to fostering sustainable use and management of the most important NTFP resource of this region and demonstrate a need to modify current management practices. A few recommendations may be made based on the findings of this study. First, frequent fires had negative effects on the population growth rates, levels of fruit production, time to maturity, and would ultimately reduce the harvest potential. As described in 'the Introduction', the current frequency of fire, on an average, is 2–3 yr. Our results revealed that such frequent fires were detrimental to population growth and persistence. The impacts of harvesting on populations subjected to fires need special management attention in terms of fire-return intervals.

Second, management in terms of fruit production alone would suggest a 2-yr burn frequency based on the high fruit yields that could be harvested (Figure 2). In the long-term, however, this strategy would fail since λ is also low during the second year since last fire. Since persistence of *Phyllanthus* is critical to the economy of Soligas and the region, fire frequencies in the forests of BR Hills must be kept low for continued extraction of fruits. In addition, Sinha and Bawa (2002) recommended a change in harvesting techniques to increase yields.

Even though our study did not explicitly examine the relationship between fire timing and fruit production and population growth rates, our findings point to the fact that timing of fires during the flowering season was critical in determining fruit production in the subsequent fruiting season. Fires that coincide with the budding and flowering season should be prevented since such fires negatively affected fruit production (Sinha 2000).

Fostering sustainability of NTFP harvest, such as in our case, requires a simultaneous focus on other anthropogenic effects (e.g., fire). This assumes more importance since *Phyllanthus* fruits might be an important component in the diet of animals. Moreover, long term monitoring of the effects of fire exclusion on NTFPs as well as on woody plants and the dominant ground cover (*Themeda* spp. and *Cymbapogon* spp.) will further increase our understanding on how to sustainably manage the forests of BR Hills. Furthermore, cumulative effects of harvesting and fire over the long term need to be monitored to determine optimal disturbance/fire regimes among co-occurring species.

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Appendix 1. (a)–(f): Transition matrices for the various times since last fire.

Size at time $t + 1$	Size at time t					
	S_1	S_2	S_3	S_4	S_5	S_6
(a) Time since last fire = 0 (burn year)						
S_1	0	0	0	0	0	533.1390
S_2	0.0099	0.0167	0.0151	0.0116	0	0
S_3	0	0.0024	0.0681	0.0058	0	0
S_4	0	0	0.0030	0.0233	0	0
S_5	0	0	0	0.0001	0.2069	0
S_6	0	0	0	0	0.0690	0.7692
(b) Time since last fire = 1 yr (first year after a fire)						
S_1	0	0	0	0	0	151.2628

Appendix 1. Continued.

S_2	0.3431	0.4060	0.1632	0.0074	0	0
S_3	0	0.1907	0.5629	0.2353	0	0
S_4	0	0.0027	0.0415	0.7206	0.0588	0.0052
S_5	0	0.0014	0.0069	0.0147	0.7059	0.0104
S_6	0	0	0.0014	0.0074	0.2157	0.9275
(c) Time since last fire = 2 yr (second year after a fire)						
S_1	0	0	0	0	0	805.8012
S_2	0.08	0.2872	0.0627	0.0426	0	0
S_3	0	0.1638	0.2889	0.2128	0	0
S_4	0	0.0021	0.0046	0.1702	0	0
S_5	0	0	0	0.0001	0.5833	0.0053
S_6	0	0	0	0	0.25	0.9465
(d) Time since last fire = 3 yr (third year after a fire)						
S_1	0	0	0	0	0	353.3790
S_2	0.2178	0.5098	0.0897	0.0571	0	0
S_3	0	0.2141	0.7484	0.3143	0.0909	0.0157
S_4	0	0.0016	0.0350	0.5714	0.0909	0
S_5	0	0	0	0.001	0.4091	0.0157
S_6	0	0	0	0	0.2273	0.9134
(e) Time since last fire = 4 yr (fourth year after a fire)						
S_1	0	0	0	0	0	487.7722
S_2	0.3015	0.4695	0.1337	0.0186	0	0
S_3	0	0.1912	0.6153	0.1925	0.1860	0.0086
S_4	0	0.0025	0.0163	0.6398	0.0465	0.0086
S_5	0	0	0	0.0155	0.6395	0.0115
S_6	0	0	0	0.0031	0.0698	0.9540
(f) Time since last fire = 5 yr (fifth year after a fire)						
S_1	0	0	0	0	0	723.4584
S_2	0.2258	0.3992	0.1299	0.0381	0	0
S_3	0	0.3244	0.7060	0.1238	0	0
S_4	0	0.0019	0.0194	0.6857	0.0400	0
S_5	0	0	0.0015	0.0286	0.6000	0
S_6	0	0	0	0	0.2000	0.9692

See Table 1 for information on plots included under the different times since last fire. Data for the burn year matrix came from three plots that were burnt prior to data collection; since this data set was relatively small, we have used it only to compare size-based survivorship and population growth rates across times since last fire. The top row of the matrix gives the contributions of each class to the seedling stage. Entries along the diagonal are probabilities of stasis and those along the subdiagonal represent growth probabilities. All other nonzero entries are regression probabilities.

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