

## FIRE AND POPULATION DYNAMICS OF WOODY PLANTS IN A NEOTROPICAL SAVANNA: MATRIX MODEL PROJECTIONS

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**Abstract.** Human activity has resulted in high fire frequency in many moist tropical savannas. To simulate the effects of increased fire frequency on woody plants of the cerrado savannas of Brazil, I constructed matrix population models for five species, including a subshrub, two shrubs, and two trees, using four years of demographic data. The models projected that four of the five species will decline under frequent burning but will increase in abundance under infrequent burning. For these four, fire intervals of 2–9 yr are required for long-term persistence, depending on the species. The fifth species, a shrub, was virtually unaffected by burning.

Similar data for three herbaceous species were obtained from literature sources. Among the eight species, there was a negative relationship between population growth under annual burning and population growth under unburned conditions. Woody plant species performed best under low fire frequency, and herbaceous species performed best under high fire frequency.

Three of the study species propagate vegetatively by producing root suckers. Fire stimulates vegetative propagation in all three species but reduces sexual reproduction. Elasticity analysis revealed that vegetative propagation is more important than sexual reproduction for population maintenance of these three species, and that vegetative propagation is relatively more important under frequent burning. However, stasis and progression were always much more important than either mode of reproduction, with stasis making the largest contribution to population growth.

Analyses of life history response experiments were performed to determine what demographic variables contributed most to the population decline under frequent burning. The effect of fire on sexual reproduction contributed little to the overall effect of fire on population growth, particularly for clonal species. Fire-induced mortality also had little effect on population growth, except for *Miconia albicans*, which has extremely fire-sensitive seedlings. The negative effect of fire on individual size tended to make the greatest contribution to the overall negative effect of fire on population growth, and this effect was greater for the two trees than for the shrub species.

The results indicate that growth form was the primary determinant of fire response, while ability to reproduce vegetatively is important to a lesser extent. Current fire regimes are predicted to reduce woody plant density and to favor smaller life forms and species capable of clonal propagation.

**Key words:** Brazil; cerrado; demography; elasticity; fire; fire frequency; life table response experiment; matrix model; savanna; shrub; subshrub; tree.

### INTRODUCTION

Humans have had a large impact on fire regimes of tropical savannas. At present, the moist savannas of Australia, Africa, Asia, and South America commonly burn at intervals of 1–3 yr (Eiten and Goodland 1979, Lacey et al. 1982, Trollope 1984, Coutinho 1990, Stott 1990, Menaut et al. 1991, Russell-Smith et al. 1997), primarily due to anthropogenic causes. There is little doubt that burning would be less frequent in the absence of humans, although it is uncertain what range

of fire frequencies are natural for such savannas. In the savannas of the Brazilian cerrado, it has been estimated that burning intervals ranged from 3–10 yr under indigenous occupation (Ratter et al. 1973, Eiten 1975, Eiten and Goodland 1979).

Predicting the long-term effects of humans on savanna diversity and structure will require an understanding of the effects of fire on woody plants. Woody cover plays an important role in nutrient cycling (Kellman 1979, Belsky et al. 1989, Isichei and Muoghalu 1992, Mordelet et al. 1993, Archer 1995), soil carbon storage (Belsky et al. 1989, Weltzin and Coughenour 1990, Dunham 1991, Garcia-Miragaya et al. 1994, Scholes and Archer 1997), seedling establishment (Kellman and Miyanishi 1982, Kellman 1985, Bowman and Panton 1993, Hoffmann 1996a), and the distri-

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bution of animals (Dall'Aglio 1992, Alho 1994), so changes in woody plant density can have widespread effects on savanna ecology. However, predicting the effects of fire on woody-plant dynamics is complicated by the need to consider interspecific variability in fire sensitivity, as well as temporal variation in fire frequency.

The difficulty in predicting the effects of burning on populations is largely due to the complexity of fire effects. Fire simultaneously affects sexual reproduction, vegetative reproduction, seedling establishment, individual size, growth, and mortality. These effects interact to alter the growth rate of a population, complicating attempts to determine which plant traits are most important for determining success or failure under a particular fire regime. Matrix population models are a valuable tool for predicting population responses to burning and for determining which demographic traits are critical for long-term success in frequently burned savannas (Silva et al. 1991, Canales et al. 1994, Caswell and Kaye 1996). In this paper, I use matrix population models to address the following questions for five species of woody plants of the savannas of the Brazilian cerrado:

*How does fire frequency affect the population growth rate of woody plants of the cerrado?*—The relationship between fire frequency and population growth rate will determine whether a species will decline toward extinction or become abundant under a particular fire regime. The range of fire frequencies that permit positive population growth is particularly important, as this will determine how well a species can cope with long-term changes in fire frequency. If each species is able to persist only under a narrow range of fire frequencies, we would expect large shifts in species composition in response to changes in fire frequency. However, if many cerrado species are able to maintain relatively stable populations under a wide range of fire frequencies, we should expect high ecosystem resilience (*sensu* Holling 1973).

*How does fire frequency affect the mean individual size?*—Within a species, individual size may span several orders of magnitude. Even if burning were to have little effect on population size, shifts in the size distribution can have large effects on the physical structure of cerrado vegetation. Understanding the long-term effects of burning upon woody cover may be just as valuable as understanding the effects upon numbers of individuals.

*Is there a trade-off between fire tolerance and success in unburned conditions?*—Species in fire-prone ecosystems exhibit a diversity of adaptations to burning, such as large carbohydrate reserves (Miyaniishi and Kellman 1986, Bowen and Pate 1993, Bell et al. 1996) and thick bark (Landers 1991). Such traits require resources that could otherwise be allocated for reproduction or resource capture, so they may limit population growth in the absence of fire. I hypothesized that

there is a negative relationship between success under frequent burning and success under protection from fire.

*Which demographic parameters contribute most to the overall effect of burning on population growth?*—Fire has an impact on all components of the life cycle of the study species, thus changing the population growth rate. We do not know which demographic parameters contribute most to this change in the population growth rate. A large effect of fire upon a particular demographic parameter cannot be taken as proof that the population growth rate will be greatly affected. The impact upon population growth rate also depends upon the sensitivity of the population growth rate to changes in the particular demographic parameter.

Understanding which demographic parameters contribute most to population decline under frequent burning will be useful for identifying traits that make species susceptible to frequent burning. This information could also be used to make better informed predictions of species responses to burning, when complete information of their life histories is unavailable. This question will be addressed using analysis of life table response experiments (LTRE) (Caswell 1989b).

*How much do sexual and vegetative reproduction contribute to population growth, and how do their contributions change with fire frequency?*—Vegetative reproduction is known to be important for many woody plant species in tropical savannas, but the relative importance of vegetative and sexual reproduction has never been determined. Although vegetative reproduction has been frequently purported to be more important than sexual reproduction in the cerrado, this has never been demonstrated (Hay and Moreira 1992). Furthermore, because vegetative reproduction is stimulated by fire (Hoffmann 1998), and sexual reproduction is often reduced by fire (Hoffmann 1998), the relative importance of these two forms of reproduction are expected to depend on fire frequency. These comparisons were performed with elasticity analysis (de Kroon et al. 1986).

## METHODS

### *Research site*

The cerrado is a savanna ecosystem occupying  $\sim 2 \times 10^6$  km<sup>2</sup> or nearly one-quarter the area of Brazil (Adámoli et al. 1985). All research was conducted within the Ecological Reserve of the Brazilian Institute of Geography and Statistics (IBGE) and the adjacent Botanical Garden of Brasília (JBB). The site is located  $\sim 35$  km south of Brasília, D.F., Brazil, at 15°56' S and 47°53' W. Mean annual rainfall (1980–1994) at the site is 1480 mm, of which 91% occurs in the summer months of October–April. Mean annual temperature (1980–1994) is 21.8°C. The soil at the site is a dark red latosol of the Brazilian Soil Classification system, corresponding to Oxisol of the U.S. Soil Taxonomy

TABLE 1. Important attributes of the study species.

Attribute	<i>Periandra mediterranea</i> Taub.	<i>Miconia albicans</i> Steud.	<i>Rourea induta</i> Planch.	<i>Myrsine guianensis</i> Aubl.	<i>Roupala montana</i> Aubl.
Family	Leguminosae	Melastomataceae	Connaraceae	Myrsinaceae	Proteaceae
Growth form	subshrub	shrub	shrub	tree	tree
Maximum height (approximate)	1.5 m	3 m	3 m	8 m	8 m
Vegetatively reproducing†	no	no	yes	yes	yes
Fire-induced mortality (adults)‡	9%	6%	3%	3%	3%
Fire-induced mortality (seedlings)†§	52%	100%	33%	86%	63%
Fire-induced mortality (suckers)†§	...	...	7%	47%	30%

† Data from Hoffmann (1998).

‡ Data from Hoffmann (1996b).

§ Mortality rates of seedlings and suckers were obtained from individuals burned during their first year of growth.

system and Ferralsol of the Food and Agriculture Organization (FAO) System (Sanchez 1976). The soils are deep and well drained.

#### Field data

Five species were chosen for this study (Table 1). All five are abundant at the study site. As is common among woody plants of the cerrado, all five species are evergreen, and all resprout vigorously following fire.

I collected demographic data within a large fire project established at the study site in 1991. The experimental area of the fire project is divided into six blocks of five 10-ha plots. Each plot within a block is subjected to one of five fire regimes. I established one 15 × 25 m study within each of 12 of these 10-ha experimental plots. Six were established in unburned plots and six were established in plots that were to be burned biennially, late in the dry season. Late-season burns were chosen because cerrado fires are most common at this time of the year. The vegetation within the fire project ranges from open shrub savanna to closed savanna woodland.

Within the plots, all individuals of the study species were mapped and marked with numbered aluminum tags. For the two tree species, additional large individuals outside the permanent plots were similarly marked and sampled. Annual censuses were conducted in 1992, 1993, 1994, and 1995, during the dry season, when annual growth ceases or greatly declines. At each census, stem diameter was measured for each individual. Stem diameter was measured at 30 cm height, for individuals <60 cm tall. For smaller individuals, stem diameter was measured at half the stem height.

Burning increased mortality of all species, but primarily among the smallest size classes. Among adults, fire-induced mortality was much lower (Table 1). Topkill, defined as death of the aboveground stem, was much more prevalent than true mortality. Only large individuals escaped topkill, so the subshrub *Periandra* experienced 100% topkill, and the two shrubs experienced nearly 100% topkill. The two trees experienced considerably lower topkill among the larger size classes. Resprouting began shortly after burning.

Censuses of seed production were performed in the study plots, and in additional transects, as described by Hoffmann (1998). These transects were established in areas with other fire treatments, including biennial early dry-season burns, biennial mid dry-season burns, biennial late dry-season burns, and quadrennial mid dry-season burns. Seedling establishment data were obtained from a series of experimental plots in which seeds were placed, as is presented by Hoffmann (1996a). Additional establishment data collected in an identical manner were since obtained for *Periandra* and *Myrsine* (Hoffmann, unpublished data).

These studies revealed that sexual reproduction is unsuccessful in years that burning occurs, because fire destroys seeds, flower buds, or developing fruit. In subsequent years, size-specific seed production of *Periandra* is the equal to the preburn level. For *Miconia*, few fruit are produced in the first year after burning, but, in the second and third years after burning, size-specific seed production is greater than the preburn level. For *Rourea*, size-specific seed production is greatest in the first year after burning, and decreases in subsequent years. For both *Myrsine* and *Roupala*, seed production is low in the first year after burning, and gradually increases to preburn levels in subsequent years.

*Rourea*, *Myrsine*, and *Roupala* reproduce vegetatively by producing root suckers (Hoffmann 1998). These root suckers are defined as new individuals originating from root buds at some distance from the parent stem. Hoffmann (1998) describes estimation of sucker production. Following the method of Ribbens et al. (1994), I used a maximum-likelihood estimator to fit the allometric relationship between stem diameter and sucker production, within the study plots. Fire significantly stimulated the production of root suckers by all three species. Suckers have lower rates of fire-induced mortality than do seedlings of similar age (Table 1; Hoffmann 1998).

For estimating demographic parameters, an individual was defined as a stem, or a group of stems, connected at the root crown. Stems not connected at the root crown were considered separate individuals. According to this definition, root suckers were not con-

sidered part of the parent individual, so there may have been physiological connections between stems considered to be separate individuals. However, for *Myrsine* and *Roupala*, the connection between parent and offspring typically disintegrated within one year. For individuals with more than one stem connected at the root crown, individual size was taken to be the diameter of the largest stem.

*Model parameterization*

Several stem diameter classes were delimited for each species. The number of classes differed among species, depending on the maximum individual size (see the *Appendix*). The lower bound for the largest size class was approximately half the largest diameter observed for each species. In addition to size classes, several distinct stages were distinguishable for different classes of offspring. In the case of *Miconia*, dormant seeds and seedlings were recognized as additional classes. For *Rourea*, *Myrsine*, and *Roupala*, seedlings and root suckers were distinct classes.

Transitions among these life history stages were grouped into five categories (Fig. 1). *Sexual reproduction* is the production of dormant seeds or seedlings by adults. Seed production and seedling establishment are subsumed into a single step when necessary. *Vegetative reproduction* is the production of new individuals by root suckering. *Stasis* is persistence within the same class. *Progression* is transition to a later category, including the transition of dormant seeds into seedlings for *Miconia*. *Retgression* is the transition of an individual to a smaller size class. Burning was the primary cause of retrogression, but even in the absence of fire, some individuals suffered loss of the main stem and resprouted.

I used the demographic data to construct matrix models based on the observed transition probabilities. Three matrices were constructed per species, each simulating population dynamics at a different stage of the fire cycle. Matrix **B** simulates dynamics in the year the population is burned. Burning occurred at the beginning of the one-year period simulated by **B**, so resprouting had occurred during this time. Matrix **A** simulates dynamics in the year following burning. Matrix **U** simulates dynamics of unburned populations. The matrices appear in the *Appendix*.

The survival and size transition data for constructing each matrix were obtained by pooling the data from all the relevant permanent plots and seedling plots, for all relevant years. Transition probabilities were calculated directly from counts of individuals involved in each transition. The four annual censuses yielded three years of transition data for the permanent plots, along with an additional census of the seedling plots in 1996. Sample sizes for growth and survival varied among species. Sample sizes (measured in plant-years) were *Miconia*, 4746; *Myrsine*, 5102; *Periandra*, 1069; *Roupala*, 3539; and *Rourea*, 3527.

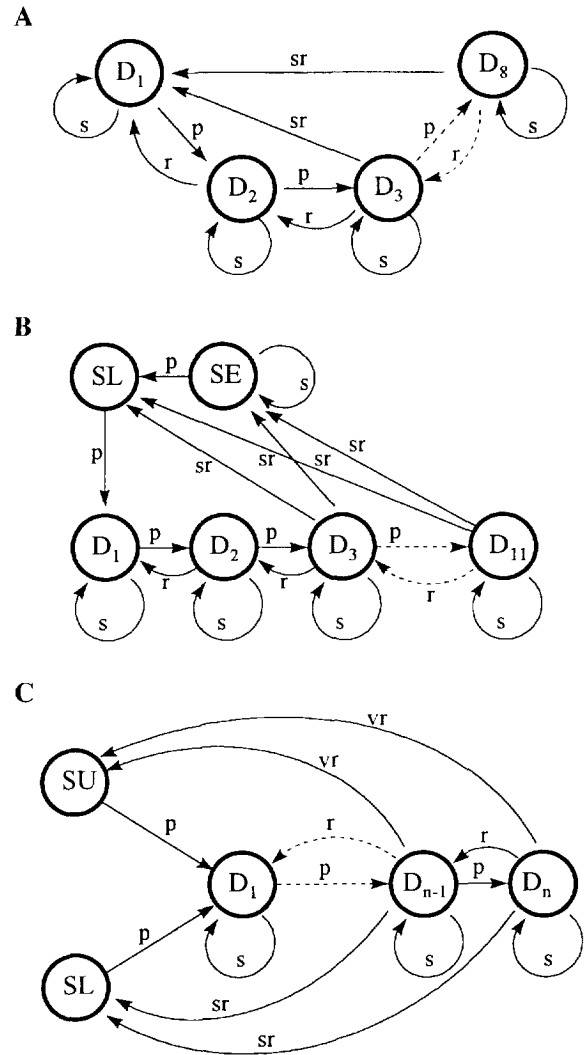


FIG. 1. Life cycle diagrams for the study species. (A) *Periandra mediterranea*; (B) *Miconia albicans*; (C) *Rourea induta*, *Myrsine guianensis*, and *Roupala montana*. The life stages include seedlings (SL), dormant seeds (SE), root suckers (SU), and stem diameter classes (D). Transitions include progression (p), stasis (s), retrogression (r), sexual reproduction (sr), and vegetative reproduction (vr). Progression and retrogression transitions often skipped one or more size classes, but for clarity, these transitions are not shown. Dashed lines indicate where size classes were omitted from the diagram.

For *Periandra*, *Miconia*, and *Roupala*, seedling production for each size class was estimated by multiplying the number of seeds per individual by the fraction of seeds developing into seedlings. For *Myrsine* and *Rourea*, seed production was extremely variable among individuals. Rather than estimate seed production for each size class independently, regression was used to estimate seed production for these two species, as described by Hoffmann (1998).

For *Miconia*, the survival and germination rates of

dormant seeds were calculated from the numbers of new seedlings emerging in the seedling plots in the three years after the seeds were sown. To estimate these values it was assumed that annual rates of seed survival and germination remained constant, regardless of seed age.

#### Population projections

The matrices **B**, **A**, and **U** were used to simulate the effect of different fire frequencies on population dynamics. It was assumed that population dynamics in the second and subsequent years following burning are similar to unburned populations. For example, to simulate population dynamics during the 4-yr period in which burning occurs in the first year, we can use

$$\mathbf{N}_4 = \mathbf{U} \cdot \mathbf{U} \cdot \mathbf{A} \cdot \mathbf{B} \cdot \mathbf{N}_0.$$

The vectors  $\mathbf{N}_0$  and  $\mathbf{N}_4$  are the population vectors at year 0 and year 4, respectively.

For several species, a modification of this model was necessary. For *Myrsine* and *Miconia*, it was observed that the effect of burning on reproduction continued for more than a single year; thus, additional matrices were required for the second and third years after burning. For *Rourea*, a matrix for the second year after burning was included.

For each fire frequency, two distinct fire regimes were simulated. The first fire regime was deterministic, so the number of years between burns remained fixed. Under the fixed fire return interval, the population vector converges onto a stable size distribution, although the size distribution depends on what stage of the fire cycle is observed. The mean annual growth rate  $\lambda$  is the  $T$ th root of the dominant eigenvalue of the matrix formed by the product of the matrices used to simulate the fire regime (e.g.,  $\mathbf{U} \cdot \mathbf{U} \cdot \mathbf{A} \cdot \mathbf{B}$ , for the above example).  $T$  is the fire return interval, defined as the number of years between burns. The dominant eigenvectors and eigenvalues of the matrix models were obtained by use of a computer program that was written to simulate a fire regime until a stable size distribution is reached.

For the second fire regime, I simulated a random fire return interval by maintaining a constant probability of burning, regardless of fire history. In this case, the probability of burning in any year is  $1/T$ , where  $T$  is the average fire return interval. The mean population growth rate,  $\bar{\lambda}$ , was calculated as the geometric mean of the annual population growth rates. Each simulation was run for 6000 yr, with the first 1000 yr omitted from the calculation of  $\bar{\lambda}$ .

#### Elasticity analysis

Elasticity, the proportional change in  $\lambda$  resulting from a proportional change in a matrix element  $a_{ij}$ , is defined as follows (de Kroon et al. 1986):

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

where  $\partial \lambda / \partial a_{ij}$  is the sensitivity of  $\lambda$  to changes in the matrix element  $a_{ij}$ , holding all other matrix elements constant. The elasticities of all the matrix elements sum to one for simple matrix models (de Kroon et al. 1986) as well as periodic matrix models (Caswell and Trevisan 1994). The elasticity of a matrix element can be interpreted as the contribution of that element to the population growth rate (de Kroon et al. 1986). Elasticities were calculated for fixed fire return intervals, and were pooled to obtain sums for each of five principal transition types, shown in Fig. 1: sexual reproduction, vegetative reproduction, retrogression, stasis, and progression.

The sensitivity used to calculate each elasticity, and to perform the analysis of life table response experiments, was calculated by making a small perturbation ( $\Delta a = 0.001$ ) to each matrix element and applying the following formula:

$$s_{ij} = \frac{\partial \lambda}{\partial a_{ij}} \cong \frac{\lambda(a_{ij} + \Delta a_{ij}) - \lambda(a_{ij})}{\Delta a}.$$

The sum of the elasticities produced in this manner closely approximated the actual value of one. In no case did the sum differ from one by  $>0.0013$ , and the average absolute deviation was 0.00026.

It will be useful to note that the matrix elements  $a_{ij}$ , corresponding to retrogression, stasis, and progression, can be rewritten as  $G_{ij}S_j$ , where  $S_j$  is the probability of survival for an individual in size class  $j$ , and  $G_{ij}$  is the probability of transition from class  $j$  to class  $i$ , provided that the individual survives. I will refer to  $G_{ij}$  as the probability of growth, with the realization that growth can be negative in the case of retrogression, or neutral in the case of stasis.

The sum of the elasticities for survival ( $S_j$ ) is equal to total sum of the elasticities of progression, retrogression, and stasis:

$$\sum_{j=1}^n \frac{S_j}{\lambda} \frac{\partial \lambda}{\partial S_j} = \sum_{j=1}^n \left( \frac{S_j}{\lambda} \sum_{i=1}^n \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial S_j} \right) = \sum_{j=1}^n \sum_{i=1}^n \frac{\partial \lambda}{\partial a_{ij}} \frac{S_j G_{ij}}{\lambda}$$

where differentiation with respect to  $S_i$  is carried out with all  $S_{j \neq i}$  held constant. Similarly, it can be shown that the sum of the elasticities for growth ( $G_{ij}$ ) is also equal to the total sum of the elasticities for progression, retrogression, and stasis. Although the elasticities for  $S_j$  and  $G_{ij}$  can be interpreted as the relative sensitivities of survival and growth, they can not be interpreted as contributions of survival and growth to  $\lambda$ .

#### Analysis of life table response experiments

Fire affects all stages of the life cycle of the study species, so it is not evident whether the effect of fire on the population growth rate is predominantly due to increased mortality, reduced individual size, or a reduction in size-specific reproduction. The analysis of life table response experiments (LTRE), which has been developed by Caswell (1989a, b, 1996a, b), permits us

to determine which component of the life cycle contributes most to the overall effect of fire on the population growth rate.

To estimate the contribution of a particular component of the life cycle, a linear approximation is used to estimate the change in the population growth rate,  $\lambda$ , resulting from a fire-induced change in some demographic parameter,  $x_i$ , with all other parameters  $x_j$  unchanging. The predicted change in  $\lambda$  is

$$\Delta\lambda_i \cong \Delta x_i \cdot \frac{\partial\lambda}{\partial x_i} \tag{1}$$

where  $\Delta\lambda_i$  is the change in  $\lambda$  due to the change in  $x_i$ , and  $\Delta x_i$  is the observed effect of fire on  $x_i$ .

The overall effect of burning on  $\lambda$  is approximated as the sum of these individual contributions:

$$\Delta\lambda \cong \sum_i \Delta x_i \cdot \frac{\partial\lambda}{\partial x_i} \tag{2}$$

This approximation is valid for any sufficient set of parameters (Caswell 1996a), i.e., any set of parameters which is sufficient to reconstruct the entire matrix model. The set of sufficient parameters may be simply the matrix elements; alternatively, it may be given by either of the alternative parameterizations presented by Caswell (1996a, b). Here I use another parameterization that is suited for interpreting the data at hand.

The following parameterization can be used to decompose the treatment effect on  $\lambda$  into the contributions due to survival, growth, and fecundity for population matrices of any form:

$$\begin{bmatrix} G_{11}S_1 + F_1 & G_{12}S_2 + F_2 & G_{13}S_3 + F_3 & G_{14}S_4 + F_4 \\ G_{21}S_1 & G_{22}S_2 & G_{23}S_3 & G_{24}S_4 \\ G_{31}S_1 & G_{32}S_2 & G_{33}S_3 & G_{34}S_4 \\ G_{41}S_1 & G_{42}S_2 & G_{43}S_3 & G_{44}S_4 \end{bmatrix} \tag{3}$$

where  $S_j$  is the probability of survival,  $G_{ij}$  is the probability of growth from class  $j$  to class  $i$ , provided that the individual survives, and  $F_i$  is fecundity. The parameterization in Expression 3 must be modified for matrices that include more than one mode of reproduction. The decomposition of the effect of burning is given by

$$\Delta\lambda \cong \sum_{ij} \Delta F_i \frac{\partial\lambda}{\partial F_i} + \sum_i \Delta S_i \frac{\partial\lambda}{\partial S_i} + \sum_{ij} \Delta G_{ij} \frac{\partial\lambda}{\partial G_{ij}} \tag{4}$$

The  $\Delta F_i$ ,  $\Delta S_i$ , and  $\Delta G_{ij}$  are the changes in the  $F_i$ ,  $S_i$ , and  $G_{ij}$  due to burning. The derivatives are evaluated from the mean of the burn and unburn matrices. The contributions of the individual  $G_{ij}$  will probably be of little interest. Instead, the sum of the contributions of the  $G_{ij}$  for a column provides the total contribution due to changes in growth of surviving individuals.

This analysis decomposes the change in  $\lambda$  into the contributions caused by changes in fecundity, survival,

and growth under annual burning. To extend this analysis to other fire frequencies, additional modifications are necessary. For example, the difference between the population growth rate for an unburned population and the population growth rate of a population burned every three years can be decomposed as follows:

$$\Delta\lambda \cong \sum_i \Delta x_i^{(B)} \frac{\partial\lambda}{\partial x_i^{(B)}} + \sum_i \Delta x_i^{(A)} \frac{\partial\lambda}{\partial x_i^{(A)}} \tag{5}$$

where  $\Delta x_i^{(B)}$  is the change in the parameter  $x$  due to burning, relative to an unburned population, and  $\Delta x_i^{(A)}$  is the change in the parameter in the year after burning, relative to an unburned population. The sensitivities  $\partial\lambda/\partial x_i^{(B)}$  and  $\partial\lambda/\partial x_i^{(A)}$  are evaluated within the sequence of matrices  $\mathbf{U} \cdot \mathbf{A}' \cdot \mathbf{B}'$ , where the matrices  $\mathbf{A}'$  and  $\mathbf{B}'$  are defined as  $\mathbf{A}' = (\mathbf{U} + \mathbf{A})/2$ , and  $\mathbf{B}' = (\mathbf{U} + \mathbf{B})/2$ .

The decomposition of Eq. 5 can be applied to Eq. 4 to decompose the effect of burning into the contributions due to fire-induced changes in survival, growth, and fecundity for any fire frequency. For each of these classes of parameters, the contributions were summed over all size classes to obtain a single value. For each fire frequency, the contributions for the year after burning were combined with the contributions for the year of burning. These analyses were performed for fixed fire return intervals.

For all species, certain size classes were absent in the year after burning, because the regrowth rate in the year of burning was insufficient to produce individuals in some size classes. The transition values for these size classes are undefined for the year after burning, and changing these values does not affect population projections, since there are no individuals in these size classes in the year after burning. However, the LTRE analysis requires transition estimates for all size classes, so data from unburned plots were used to fill missing matrix elements for the year after burning. For the LTRE analysis, this approach results in zero contribution for these undefined elements, since the corresponding  $\Delta x_i$  will be zero.

#### Model validation

Although the fire history of the study site is not known precisely, sufficient information is available to test model performance. The study site was used for cattle grazing from the early 1910s to the late 1950s. During this time, the area was managed by burning biennially (B. Dias, *personal communication*). Burning continued to occur approximately once every two years, except for the IBGE reserve, which has been successfully protected from burning since 1973. In the JBB reserve, burning occurred until 1987.

To test the ability of the models to predict the relative abundance of each species in JBB and IBGE, data from Moreira (1992) were used. These data consisted of counts of individuals along 10 100-m transects in each

of the two reserves. The transects were located alongside the fence separating the two reserves.

To generate predictions for a species, it was assumed that abundance and size distributions in JBB and IBGE were identical before 1910. It was not necessary to estimate the absolute abundance in 1910, because I compared only the relative abundance in IBGE and JBB. The size distribution in 1910 was arbitrarily chosen to be the stable size distribution generated by the matrix model under a 5-yr fire interval, which may be typical in remote areas of cerrado (Ratter et al. 1973, Eiten 1975). After 1910, biennial burning was simulated in the model populations of both reserves. This model fire regime was continued in JBB until 1987 and in IBGE until 1973. After these times, a fire-free regime was continued until 1989, the year the data was collected (Moreira 1992). The  $t$  test was used to test if the observed difference in abundance between the two reserves differed significantly from the predicted difference.

## RESULTS

### Effect of fire frequency on population growth rate

The matrix models yielded qualitatively similar results for four of the five study species. *Periandra*, *Miconia*, *Myrsine*, and *Roupala* are predicted to decline under annual burning, but, as the time between burns increases, the population growth rate ( $\lambda$ ) increases monotonically for these species (Fig. 2). Despite the similarities, there are important quantitative differences in their rates of population growth under fixed fire return intervals. Under annual burning, the population growth rates for *Periandra*, *Miconia*, *Myrsine*, and *Roupala* were 0.91, 0.84, 0.87, and 0.84, respectively. Under fire exclusion, the population growth rates were 1.07, 1.19, 1.10, and 1.05. The minimum fire return intervals permitting persistence of *Periandra*, *Miconia*, *Myrsine*, and *Roupala* were 3, 5, 3, and 9 yr, respectively.

The fifth species, *Rourea*, exhibited a response that differed fundamentally from the others. Population growth is predicted to remain nearly constant over the entire range of fire frequencies. Under fixed fire return intervals,  $\lambda$  was slightly  $<1$ , except for fire intervals of 2 and 3 yr, which permitted population increase (Fig. 2).

The stochastic fire regimes affected population growth rates differently than the deterministic fire regimes, except for *Periandra* (Fig. 2). For *Rourea*, *Myrsine*, and *Roupala*, a random fire regime resulted in a lower population growth rate, at least for some range of fire frequencies. Under the random fire regime, *Myrsine* requires an average fire return interval of  $\geq 4$  yr for positive population growth, as compared to the 3 yr required under a constant fire interval. Likewise, under a random fire regime, *Rourea* is predicted to have a negative growth rate under all fire frequencies. Only *Miconia* exhibited greater population growth rates un-

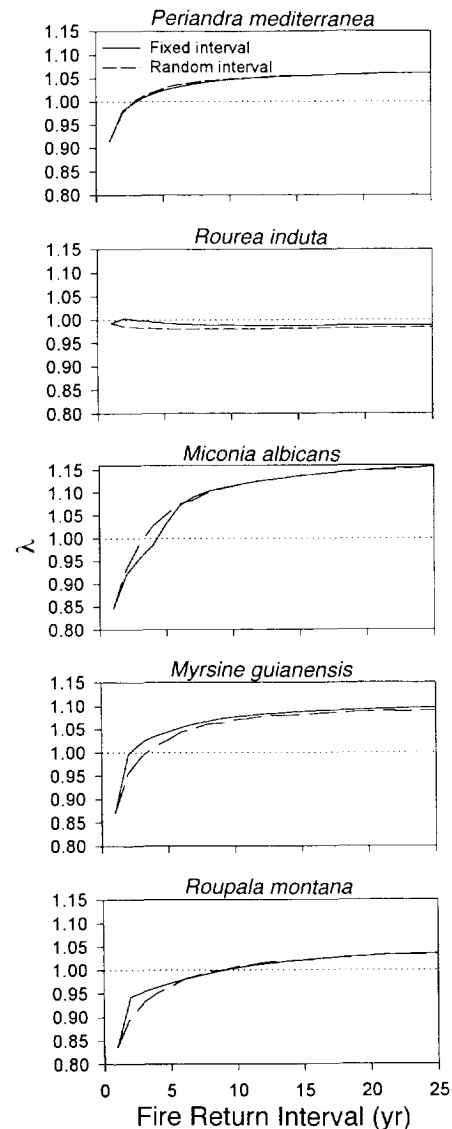


FIG. 2. The effect of fire return interval upon the population growth rate ( $\lambda$ ), as simulated by the matrix models. The fixed interval was simulated by maintaining a constant number of years between burns. The random interval was simulated by maintaining a fixed probability of burning, regardless of fire history. For the random fire regime, each  $\lambda$  is the geometric mean of 5000 yr of simulation.

der a variable fire return interval than under a fixed fire return interval. For this species, population persistence is possible under an average fire interval of 4 yr, rather than 5 yr under a fixed fire regime (Fig. 2).

### Effect of fire frequency on individual size

Mean basal area at the end of the fire cycle (i.e., immediately prior to burning) tended to increase in response to longer fire return intervals (Fig. 3), with the two tree species showing the greatest response. For *Myrsine*, basal area was  $14\times$  greater in unburned pop-

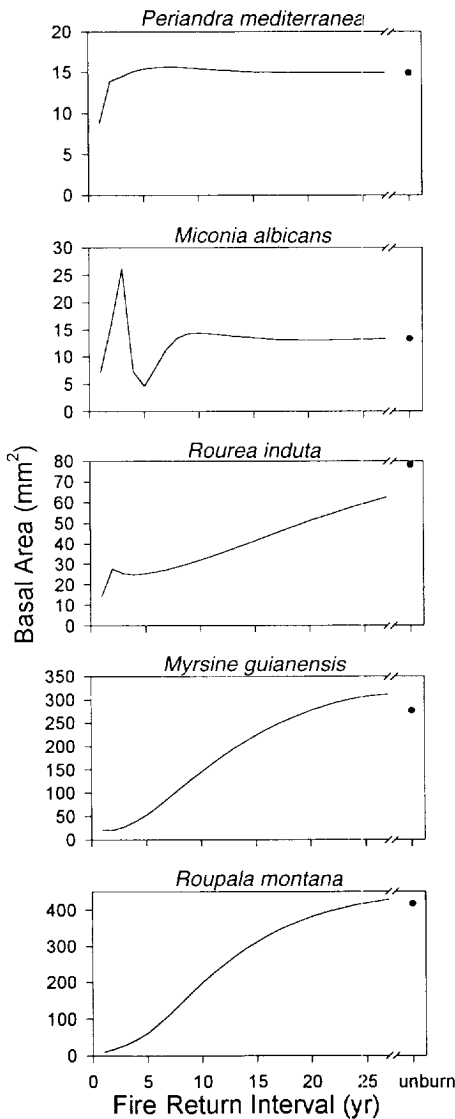


FIG. 3. The effect of fire return interval upon mean plant basal area. Basal area was estimated from the stable size distribution, using a fixed fire return interval. Mean basal area was estimated at the end of the fire cycle, i.e., at the end of the fire-free interval.

ulations than in annually burned populations, while *Roupala* showed a 38-fold increase. These two species exhibit slight declines in basal area with very infrequent burning (Fig. 3), due to an increase in the abundance of seedlings. Similarly, basal area of *Miconia* reaches a peak under triennial burning, because there is sufficient time for resprouting; yet there is not sufficient time for substantial seedling establishment, which reduces the mean considerably under less frequent burning.

*Elasticity analysis*

The elasticities of vegetative and sexual reproduction were highly dependent upon fire frequency (Fig. 4).

Sexual reproduction did not contribute to population growth under annual burning for any species. As the fire return interval increased, the importance of sexual reproduction increased, although it eventually declined somewhat for *Rourea*. In contrast, the importance of vegetative reproduction was high under frequent burning (Fig. 4). As the fire return interval increased, the importance of vegetative reproduction decreased or remained relatively constant. Therefore, the relative importance of sexual reproduction to vegetative reproduction was greatest under less frequent burning for all three clonal species. Nevertheless, even in the absence of burning, vegetative reproduction was more important than sexual reproduction. In unburned populations, the ratios of vegetative elasticity to sexual elasticity were 2.1, 3.1, and 5.8 for *Rourea*, *Myrsine*, and *Roupala*, respectively. Nonclonal species had higher elasticities for sexual reproduction than did clonal species (Fig. 4), indicating that nonclonal species relied more heavily on sexual reproduction. However, it must

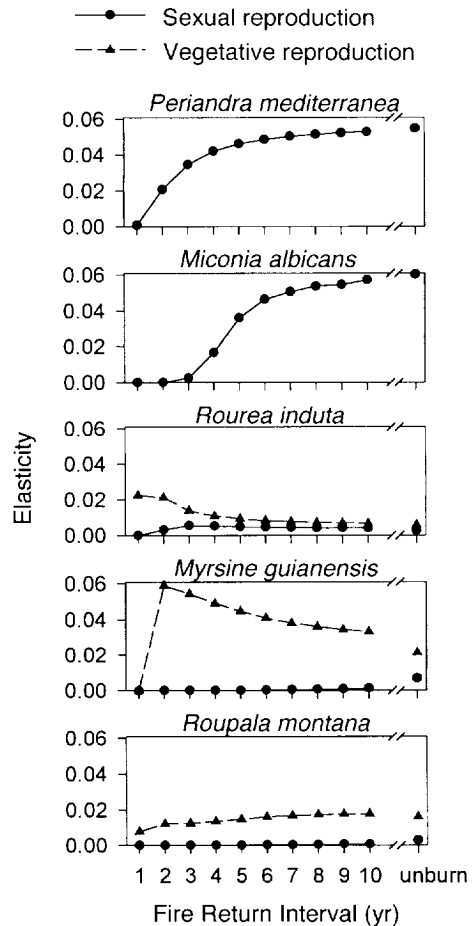


FIG. 4. The elasticities of vegetative and sexual reproduction, using the periodic matrix models with fixed fire return intervals. Elasticities for each mode of reproduction were summed over all size classes, yielding a single value for each fire frequency.

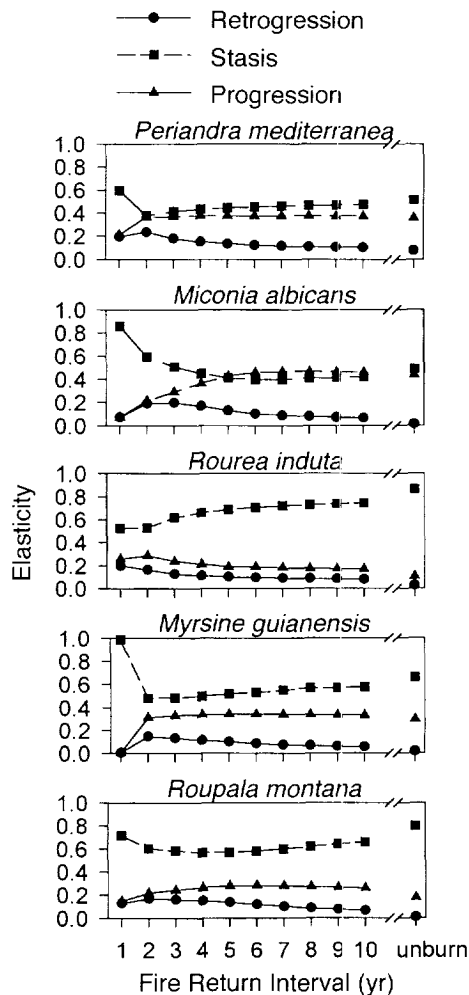


FIG. 5. The elasticities for retrogression, stasis, and growth, using fixed fire return intervals. Elasticities for each type of transition were summed over all size classes, yielding a single value for each fire frequency. Note that the scale of the vertical axis differs from Fig. 4.

be cautioned that elasticities depend considerably on the choice of size categories, making interspecific comparisons problematic (Enright et al. 1995).

The elasticities for retrogression, stasis, and progression (Fig. 5) were consistently much larger than the elasticities for vegetative and sexual reproduction (Fig. 4). The elasticities for stasis were typically the largest component, regardless of fire interval, indicating that these populations are maintained predominantly by surviving and remaining in the same size class. The elasticities for progression were usually the second largest component, indicating the importance of individual growth to  $\lambda$ . For all species, the elasticities for retrogression were greatest for frequent burning, but declined as burning became less frequent.

#### Analysis of the life table response experiments

Fire affected survival, sexual reproduction, vegetative reproduction, and growth of the study species.

These changes all contributed to the overall effect of fire on the population growth rate ( $\lambda$ ) (Fig. 6). For the two trees, the largest reduction in  $\lambda$  was caused by the effects of fire on growth (Fig. 6). Because burning reduces individual size, there was a shift from positive growth (progression) to negative growth (retrogression). The effect of fire on individual growth was also the largest contributor to population decline of *Miconia*, except for fire return intervals  $\leq 6$  yr. For the subshrub *Periandra* and the shrub *Rourea*, the effect of fire on individual growth had relatively little impact on  $\lambda$  (Fig. 6).

The effect of fire on survival made a negative contribution to the population growth rate of all five species (Fig. 6), because burning increases mortality. However, the contribution of fire-induced mortality tended to be small, except for *Miconia*, which exhibits high fire mortality among small size classes.

Burning stimulated vegetative reproduction of the three clonal species, making a positive contribution to the population growth rate. This positive contribution was particularly large for *Myrsine* (Fig. 6). In contrast, fire tended to have a negative effect on sexual reproduction, but this typically had little effect on the population growth rate, especially for the clonal species (Fig. 6). However, for *Miconia* the effect on  $\lambda$  was positive for fire intervals of  $\geq 3$  yr. For this species, size-specific reproduction is greater in the second and third years after burning than in unburned plots (Hoffmann 1998), offsetting the negative effects of fire on reproduction in the year burning occurs and the year after burning.

In all cases, the contribution of each life history component to the overall effect of fire approaches zero as the fire return interval increases (Fig. 6), because the population growth rate approaches the growth rate of unburned populations. However, the relative contributions of the various components depend on the fire return interval. For example, in *Myrsine* and *Roupala*, the contribution of fire-induced mortality tends to approach zero more quickly than other components (Fig. 6).

#### Model validation

For all five species, the observed difference in abundance between the two reserves with differing fire histories, JBB and IBGE, did not differ significantly from the differences predicted based upon historical fire regimes (Fig. 7). Values of the  $t$  test ranged 0.41–1.40 ( $df = 18$ ), corresponding to probabilities of 0.69–18.

#### DISCUSSION

##### Population responses to fire frequency

The matrix models predict that current fire frequencies are reducing woody plant density in the Brazilian cerrado. Two species, *Miconia* and *Roupala*, are predicted to decline under current fire return intervals of

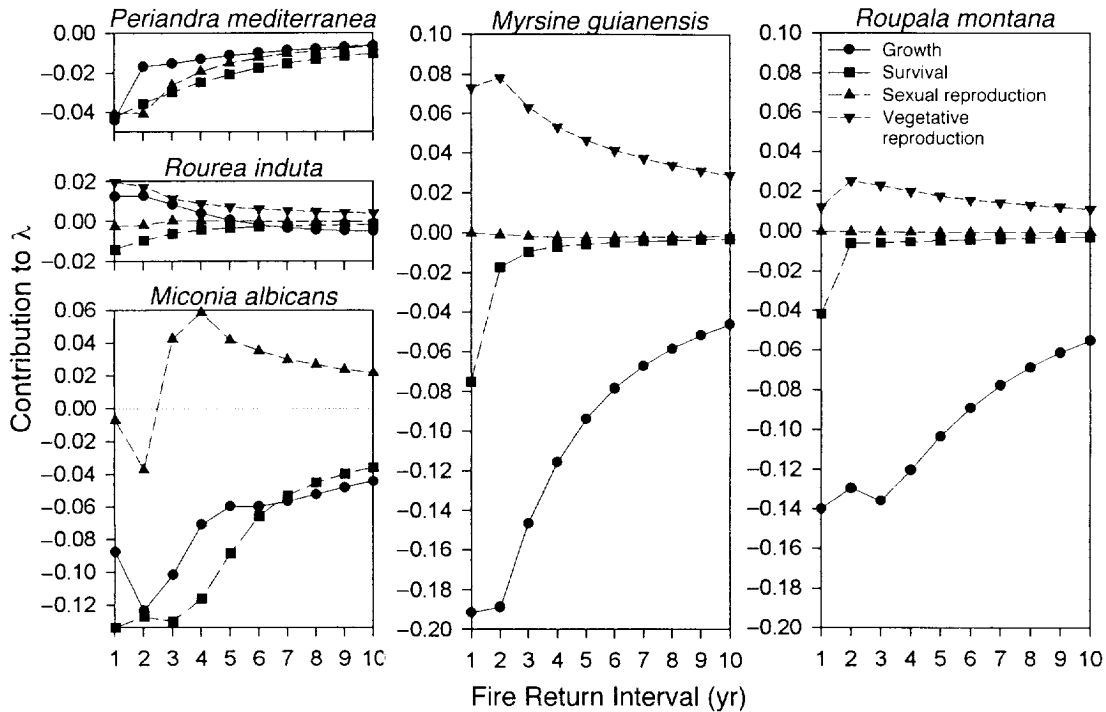


FIG. 6. The contributions of growth, survival, sexual reproduction, and vegetative reproduction to the overall effect of fire on  $\lambda$ . The contributions were obtained from the analysis of life history response experiments (LTRE), applied to the periodic matrix models, with a fixed fire return interval.

1–3 yr. Two species, *Periandra* and *Myrsine* are also predicted to decline under annual or biennial burning, but increase under triennial burning, so they should experience less extensive decline. Only *Rourea* is predicted to be unaffected by fire return intervals of 1–3 yr.

In addition to reducing population density, frequent fire will reduce mean individual size, especially for one shrub and both tree species. This is due to reductions in the size of established individuals, as well as increased production of small-diameter suckers, which reduce the overall mean. Neither *Periandra* nor *Miconia* exhibited a dramatic increase in mean basal area under less frequent burning, due to the increase in seedling production under fire protection.

The predicted decrease in tree and shrub density contrasts with observations in some savannas and grasslands where woody plant density has increased in historical times, often following cattle grazing. Reduced fire frequency probably contributes to shrub encroachment in these systems (Harrington and Hodgkinson 1986, Adámoli et al. 1990, Bahre and Shelton 1993, Archer 1995). In the cerrado and many other moist savannas, the combination of low soil nutrient availability and high rainfall permits frequent burning in spite of grazing (Frost et al. 1986). High rainfall results in high biomass production, and the low forage quality in nutrient-poor savannas ensures that grazing will not greatly reduce the herbaceous biomass (Frost et al.

1986, Scholes 1990). The resulting fuel availability permits very high fire frequency in the cerrado.

However, if fire were eliminated, woody plant cover would increase, as predicted for four of the five species. Indeed, tree density has been shown to increase following fire exclusion in the cerrado (Moreira 1992) and other moist tropical savannas (San Jose and Farinas 1991, Hopkins 1992, Swaine et al. 1992, Bowman and Panton 1995). Clearly, the high population growth rates could not continue indefinitely, because increased density will result in greater competition and lower population growth. It must be noted that simulations based on matrix models are merely projections of how the population would behave if environmental conditions were to remain as they are when the data are collected. The effects of increased tree density is probably not a serious problem for predicting the effects of current fire regimes, as fire frequency in the cerrado is rarely low enough to permit great increases in vegetation density.

Variability among sites and among years may also compromise the generality of the model results. Here, a stochastic fire interval was the only source of environmental variability introduced into the models. Including this source of variation reduced population growth rates for *Rourea*, *Myrsine*, and *Roupala*, but increased population growth of *Miconia*. This change is easily explained in the case of *Miconia*, a species that requires at least five fire-free years for substantial

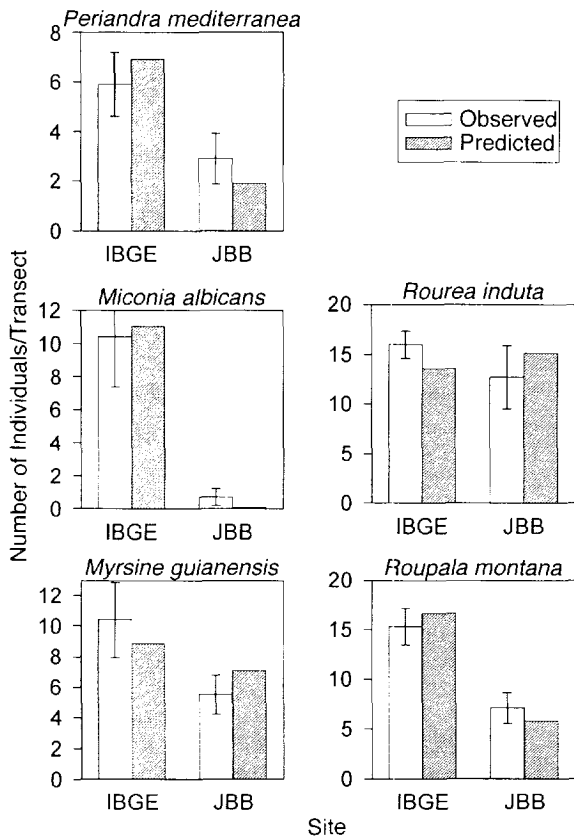


FIG. 7. Validation of the model. The model was used to predict the relative abundance in two adjacent reserves, Brazilian Institute of Geography and Statistics (IBGE) and Botanical Garden of Brasília (JBB), with different fire frequencies. IBGE has been protected from fire since 1973, whereas JBB was burned approximately biennially until 1987. Observed abundances (mean  $\pm$  1 SE) were obtained in 1989 from 10 transects in each reserve (data from Moreira [1992]). None of the model predictions differed significantly from the observations ( $0.41 < t < 1.40$ ,  $df = 18$ ,  $0.69 < P < 0.18$ ).

recruitment to occur (Hoffmann 1998). Under the random fire regime, there are occasional fire-free intervals of long duration, permitting occasional recruitment, even when the mean fire return interval is  $< 5$  yr.

Season and intensity of fire are important sources of variation that were not included explicitly in the models. However, the models were parameterized with data from numerous burns that varied considerably in fire intensity. While fire intensity may affect mortality and reproduction, its clearest effect is on individual size, since more intense fires result in more topkill. The season of burning can be important, because it affects fire intensity (Glitzenstein et al. 1995), but also because it curtails phenological events, such as leaf flush and reproduction (Setterfield 1997). Although variation in fire intensity and season were not explicitly included in the model, the validation indicated that these models generate reasonable estimates of fire effects. For each of the five species, the observed difference in abun-

dance between two adjacent reserves with different fire histories did not differ significantly from predictions.

*Performance in burned vs. unburned environments*

The five study species differed greatly in vulnerability to fire. The population growth of one species, *Rourea*, was virtually unaffected by fire frequency. For the four fire-sensitive species, the fire return interval necessary for population maintenance 3–9 yr, depending upon species. These differences represent an enormous variation in fire susceptibility, considering the high fire frequency in the cerrado. Furthermore, there was considerable interspecific variation in population growth rate under annual burning (range, 0.84–0.99) and under fire protection (range, 0.99–1.19). Based on different population-level responses to fire frequency, it can be concluded that changes in fire frequency should cause shifts in the relative abundance of the study species, in addition to changes in the overall abundance of woody plants.

The results from these species were compared with three other studies in which similar matrix models were developed for herbaceous species in savanna and grassland environments (Silva et al. 1991, Canales et al. 1994, Caswell and Kaye 1996). A comparison among species revealed a negative relationship between population growth rate under annual burning and population growth rate under fire exclusion (Fig. 8; Spearman's rank correlation,  $-0.833$ ,  $n = 8$ ,  $P = 0.007$ ).

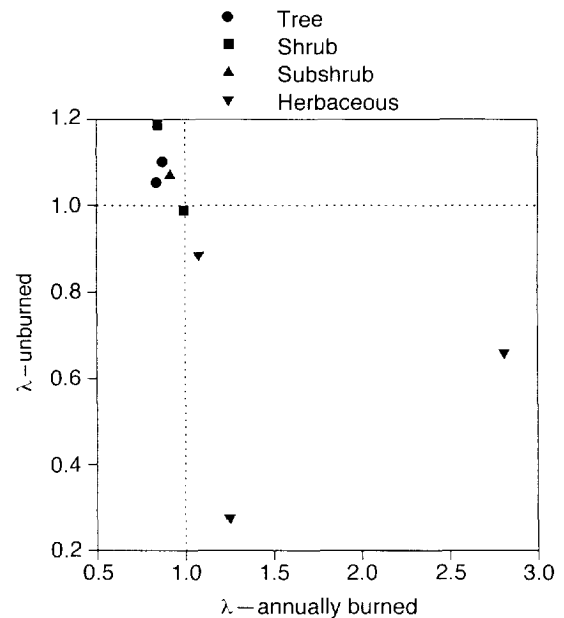


FIG. 8. The relationship between population growth rate ( $\lambda$ ) under annual burning and the population growth rate under unburned conditions. Each point represents one species. Values for the three herbaceous species were obtained from Caswell and Kaye (1996), Canales et al. (1994) and Silva et al. (1991). The relationship is significant (Spearman's rank correlation =  $-0.833$ ,  $P = 0.007$ ).

Much of the variation in response to fire can be attributed to differences in growth form. There was a negative relationship between plant stature and growth rate under annual burning (Spearman's rank correlation,  $-0.81$ ,  $n = 8$ ,  $P = 0.01$ ), where the rankings used for stature are tree > shrub > subshrub > herb. Similarly, there was a positive relationship between plant stature and growth rate under fire exclusion (Spearman's rank correlation,  $-0.75$ ,  $n = 8$ ,  $P = 0.02$ ). This relationship is consistent with observations that burning promotes success of grasses and forbs, whereas fire exclusion promotes success of woody plants (Fröst et al. 1986).

#### *Traits responsible for population decline under frequent burning*

Population decline under frequent burning was the net result of changes in sexual reproduction, vegetative reproduction, survival, and growth. To quantify the contribution of each of these components to the decline in the population growth rate, analysis of life table response experiments (LTRE) was used. The contribution of a parameter to the overall change in  $\lambda$  depends on how strongly fire affects the parameter, as well as the sensitivity of  $\lambda$  to changes in the parameter. This analysis revealed that fire-induced mortality tended to have little effect on the population growth rate of most species, although all populations were very sensitive to changes in survival. As explained in *Methods*, the sum of the elasticities for survival is equal to the total sum of the elasticities for progression, stasis, and retrogression. The sum of these components was never  $<0.94$ , indicating that  $\lambda$  is highly sensitive to changes in survival. Therefore, the low impact of fire-induced mortality can only be explained by the fact that fire causes little mortality to most of the study species. Mortality had a large impact on  $\lambda$  only for *Miconia*, a species suffering from high rates of fire-induced mortality among seedlings and other small individuals. In fact, the large negative effect of mortality in this species was primarily due to the contributions in these smallest size classes. For example, under triennial burning, 61% of the mortality effect is due to the high mortality of seedlings under burning (data not shown).

In contrast to survival, the impact of fire on individual growth had a large effect on  $\lambda$  for three species. The sum of the elasticities for growth is equal to the sum of the elasticities for survival, so survival and growth do not differ in their relative sensitivities. However, fire affected the probabilities of growth much more than it affected the probabilities of survival. Recall that growth is defined as the probability of transition from size class  $j$  to size class  $i$ , provided that the individual survives. Therefore, growth can be negative (retrogression), neutral (stasis), or positive (progression). By reducing individual size, burning greatly increased the probability of negative growth and decreased the probability of positive and neutral growth. The large changes in the parameters, combined with

the large sensitivities, had a large effect on  $\lambda$  for *Miconia*, *Myrsine*, and *Roupala*.

This growth effect of the LTRE varied profoundly among species, with larger growth forms being more negatively affected. The contribution was smallest for the subshrub *Periandra* and the shrub *Rourea*, and largest for the trees *Myrsine* and *Roupala* (Fig. 6). In contrast, changes in the other parameters did not affect population growth in a way that varied consistently among growth forms, indicating that the relationship between life form and fire susceptibility may be primarily due to the effect of fire on growth. All growth forms were very sensitive to changes in growth (sum of elasticities  $\geq 0.94$ ), so the relationship between growth form and the growth component of the LTRE cannot be explained by differences in sensitivities. Instead, growth forms differ in how fire affects individual size. Fire causes a much larger absolute reduction in the size of large individuals, provided that topkill has occurred. A small subshrub can regain its preburn size much more quickly than a large tree because of the small amount of woody tissue to be replaced by the subshrub. This can confer a large advantage to the subshrub, since the growth effect under annual burning reduced the  $\lambda$  of *Periandra* by only 0.04, but reduced the  $\lambda$  of the two trees by  $\geq 0.14$  (Fig. 6).

Even though fire reduced the probability of stasis, this remained the most important contributor to population growth under frequent burning, as determined by elasticity analysis. Moreover, for *Periandra*, *Miconia*, and *Myrsine*, stasis elasticity was greater under frequent burning than under fire protection. This indicates that these species depend heavily on those individuals that remain in their size class despite burning.

#### *Sexual vs. vegetative reproduction*

Fire affected both vegetative and sexual reproduction. The importance of sexual reproduction was greatly reduced by frequent burning, whereas the importance of vegetative reproduction remained high (Fig. 4). The difference is due to several factors. First, suckers are more tolerant of burning than are seedlings (Table 1). Second, vegetative reproduction was greatly stimulated by fire, whereas none of the species successfully reproduced sexually in the year of burning, because fire destroyed seeds, flowers, or developing reproductive structures. Similarly, seed production of the two trees was greatly reduced for several years following fire. Finally, for the three clonal species, individuals reproduce vegetatively at a smaller size than they reproduce sexually, so sexual reproduction is more strongly curtailed by the reductions in mean individual size.

For the three clonal species, the increase in vegetative reproduction following fire made a positive contribution to population growth, offsetting much of the negative effects of fire on mortality and growth. For these same species, the effect of burning on seed production had virtually no effect on  $\lambda$ , although fire great-

ly reduced seed production of *Myrsine* and *Roupala*. The  $\lambda$  was largely unaffected because sexual reproduction is unimportant for these species, as shown by elasticity analysis. The tendency for clonal species to rely little on sexual reproduction has been frequently observed (Abrahamson 1980, Cook 1985, Eriksson 1992). Similarly, Silvertown et al. (1993) found a negative correlation between elasticities for vegetative and sexual reproduction among species.

For *Periandra* and *Miconia*, which depend entirely on sexual reproduction, the effect of fire on sexual reproduction had a moderate effect on  $\lambda$ . For *Miconia*, fire-induced changes in sexual reproduction actually have a positive effect on population growth, except under annual and biennial burning. For this species, seed production is reduced shortly after burning, but reaches a peak several years after fire (Hoffmann 1998), having a net positive effect on population growth.

Even though vegetative and sexual reproduction contributed  $\leq 6\%$  to the population growth rate, as determined by elasticities, they often made a moderate to large contribution to the overall effect of fire, as determined by LTRE. This is possible because of the large magnitude of the changes in sexual and vegetative reproduction. Similarly, Ehrlén and van Groenendael (1998) and Pfister (1998) showed that demographic parameters with small elasticities are often subject to high variability, and therefore can have substantial effects on the population growth rate.

#### *Plant strategies in the cerrado*

Four of the study species appear to be unable to cope with current fire regimes in the cerrado, suggesting they are not adapted to such frequent burning. Nonetheless, fire has long been present in the cerrado, albeit at lower frequencies than the present. Behling (1995) found high incidence of carbonized particles at 9720 yr BP, and Vicentini (1993) found evidence of several fires before 27 000 yr BP, both in sediment cores from cerrado areas. Undoubtedly, woody plants of the cerrado have evolved under some influence of fire.

This study indicates that populations of cerrado woody plants are very sensitive to increases in mortality. This strong selective pressure very likely explains why fire has relatively little impact on the survival of established individuals. However, low mortality is not sufficient to ensure that a species will succeed under frequent burning. In particular, the effect of fire on individual size had a very large negative impact on population growth of several species. This suggests a strong selective pressure for traits that minimize the impact of fire on individual size or that hasten the rate of regrowth. Many cerrado species develop thick bark that protects stems from high fire temperatures, thus preventing topkill. Similarly, large investment in belowground nutrient and carbohydrate reserves, as evidenced by the large storage organs (Rawitscher and Rachid 1946, Rizzini and Heringer 1962), minimizes

the impact of fire on individual size by permitting rapid regrowth of lost tissues. These same traits should also contribute to the high capacity of individuals to survive fire.

Low investment in aboveground woody stems can also reduce the impact of fire on individual size. Because smaller growth forms have less woody biomass to replace, they can recover their preburn size more quickly. Indeed, woody plants of the cerrado tend to be much smaller than closely related forest species, with many savanna subshrubs having evolved from forest tree species (Sarmiento and Monasterio 1983, Prance 1992), likely as an adaptation to fire. The openness of the savanna environment may also have selected for smaller growth forms, because the high light availability reduces the need for height growth. Nevertheless, to the extent that fire is responsible for the open structure of the cerrado, this selective pressure may be indirectly attributed to fire.

These same traits, adaptive under frequent burning, may be detrimental to plant success under unburned conditions. Investment in reserves and bark represents an opportunity cost because of forgone investment in growth or reproduction (Chapin et al. 1990). Similarly, low investment in woody structures will reduce competitiveness for light in the unburned environment where overtopping will be more likely. These potential trade-offs may largely explain the negative relationship between success under frequent burning and success under fire protection.

We would also expect frequent burning to select for vegetative reproduction. Since vegetative reproduction is stimulated by fire, it offsets much of the negative effects of fire on survival and individual size. Indeed, vegetative reproduction is known to occur in many species of cerrado trees and shrubs (Rawitscher et al. 1943, Ferri 1962, Rizzini and Heringer 1962, Raw and Hay 1985). However, sexual reproduction offers the advantage of dispersal to isolated sites with favorable fire regimes. *Miconia*, though very sensitive to frequent fire, appears to be very capable of colonizing new sites because of its small, bird-dispersed seeds. This species has very high growth rates in the absence of fire, >16 of 21 woody plant species reviewed by Silvertown et al. (1993). This high rate of growth has allowed it to become one of the most abundant woody plant species in the IBGE reserve during 16 yr of fire protection (Moreira 1992). Heavy dependence upon vegetative reproduction at the expense of sexual reproduction would seem to prevent species from rapidly taking advantage of such sites.

Although fire had a negative impact on the importance of sexual reproduction, this may not be necessarily true of all species. Fire stimulates flowering of many subshrubs and herbs in the cerrado (Coutinho 1977), and several species have fruits that protect seeds from burning (Coutinho 1990, Landim and Hay 1996). A postfire peak in seed production had a positive effect

on population growth of *Miconia*, but this peak occurred two and three years after burning. Had this peak occurred earlier, as is the case of some species, the benefits could have been greater under frequent burning.

#### CONCLUSIONS

While rapid conversion to agriculture remains the most imminent threat to the cerrado region (Klink et al. 1995), frequent burning will continue to have a serious impact on remaining cerrado. Frequent fire in the cerrado is causing reductions in the density and size of woody plants, but the population-level effects of fire vary considerably among species. The best performers under frequent burning were the poorest performers under fire exclusion, and vice versa. Growth form was an important determinant of fire response, so current fire regimes are predicted to favor smaller life forms. To a lesser extent, there should also be selection for clonal species. The loss of fire-sensitive species is certain to have a negative impact on the high diversity of woody plants in the cerrado.

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#### APPENDIX

The matrices used in the models are available in ESA's Electronic Data Archive: *Ecological Archives* E080-010. Unburn, burn, and year after burn matrices are given for each of the study species. In addition, for several species, matrices for the second and/or third year after burning are given.