

**Population Responses to Fire in a Tropical Savanna Grass, *Andropogon Semiberbis*: A Matrix Model Approach**



Juan F. Silva; Jose Raventos; Hal Caswell; Maria Cristina Trevisan

*Journal of Ecology*, Volume 79, Issue 2 (Jun., 1991), 345-355.

Stable URL:

<http://links.jstor.org/sici?sici=0022-0477%28199106%2979%3A2%3C345%3APRTFIA%3E2.0.CO%3B2-L>

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

*Journal of Ecology* is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

---

*Journal of Ecology*

©1991 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact [jstor-info@umich.edu](mailto:jstor-info@umich.edu).

©2003 JSTOR

<http://www.jstor.org/>  
Mon May 19 15:44:37 2003

## POPULATION RESPONSES TO FIRE IN A TROPICAL SAVANNA GRASS, *ANDROPOGON SEMIBERBIS*: A MATRIX MODEL APPROACH

JUAN F. SILVA,\* JOSÉ RAVENTOS,\* HAL CASWELL† AND MARIA CRISTINA TREVISAN‡

\* *Centro de Investigaciones Ecológicas de los Andes Tropicales (CIELAT) and ‡ Departamento de Matemáticas, Facultad de Ciencias, Universidad de los Andes, Mérida, Venezuela and † Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, U.S.A.*

### SUMMARY

(1) To study the population-level effects of fire on the savanna grass *Andropogon semiberbis*, size-classified matrix population models were constructed for an annually burnt population and for a population protected from fire. These models were used to examine the effects of fire on population growth rate, stable size distributions and reproductive value, and to simulate different fire regimes.

(2) The burnt population is capable of increasing rapidly ( $\lambda_1 = 1.2524$ ,  $r = 0.2251$ ), whereas the unburnt population is unable to persist ( $\lambda_1 = 0.2762$ ,  $r = -1.2886$ ). Most of this difference is due to effects on the growth, survival and reproduction of the smallest two size classes, which are shown by elasticity analysis to be the most important to population growth in both populations. The stable size distributions and reproductive values are similar in the two populations.

(3) Both deterministic and stochastic analyses reveal a critical frequency of fire ( $\approx 0.85$ ) below which this species is unable to maintain itself. This apparent reliance on fire frequency suggests that the spread and evolution of this species has been closely related to human occupation of neotropical savannas.

### INTRODUCTION

Savanna fires, naturally occurring and anthropogenic, have important direct and indirect effects on several ecological processes. They are considered to be a determinant of tropical savannas, and play an important role in maintaining savanna composition and physiognomy (Gillon 1983; Frost *et al.* 1986; Frost & Robertson 1987). Several experiments with fire regimes have been conducted (O'Connor 1985) and changes in community composition as a result of fire exclusion documented (Menaut 1977; San José & Farinas 1983; Farinas & San José 1987). There are also several descriptive studies on the role of fire on plant growth and population dynamics of savanna species (Coutinho 1982; Lacey, Walker & Noble 1982; Trollope 1982; Mott & Andrew 1985b; Canales & Silva 1987; Silva & Castro 1989). Mathematical models of the population processes involved in the effects of fire on the structure of savanna communities are still lacking, however (Silva 1987). Studies on the ecology and dynamics of tropical plant populations are scarce (Sarukhán 1978), but models have been used to predict population behaviour of tropical rain-forest

trees (Hartshorn 1975; Piñero, Martínez-Ramos & Sarukhán 1984). Mathematical tools for the demographic analysis of complex life cycles (Hubbell & Werner 1979; Caswell 1986, 1989a) are now available, and overcome difficulties arising from the nature of plant populations.

As part of an international effort to study tropical savanna ecosystems (Responses of Savannas to Stress and Disturbance, a programme of the International Union of Biological Sciences), we are addressing the response of plant populations to changes in prevailing environmental factors, especially fire regimes. In this paper, matrix population models are used to compare population responses under regimes of annual burning and fire exclusion for a common savanna grass species, *Andropogon semiberbis*.

### THE SPECIES AND THE MODEL

*Andropogon semiberbis* (Nees) Kunth. is a perennial grass species common in seasonal savannas in the Orinoco Llanos of Venezuela (Sarmiento 1983). We have studied several aspects of populations of this species in Farm Palma Sola, near the city of Barinas in western Venezuela (8°38' N, 70°12' W) in annually burnt savannas, focusing on its reproductive ecology (Silva & Ataroff 1985) and seasonal regrowth related to competitive interference (Raventos & Silva 1988). These studies show that this C<sub>4</sub> grass is a late-growing species with an erect habit, with a relatively high reproductive output and higher competitive ability than the accompanying species *Leptocoryphium lanatum* (H.B.K.) Nees and *Elyonurus adustus* (Trin.) Ekman.

In this study, four size classes were distinguished, based on the number of tillers plant<sup>-1</sup>: 1 tiller, 2–10 tillers, 11–20 tillers and >20 tillers. Size-classified matrix models were constructed for two populations, one burnt annually at the end of the dry season and the other protected from fire for 1 year. The coefficients in each matrix were obtained by combining growth and survival data from two previous demographic field studies in the same area. One of these studies followed two cohorts of seedlings for 6 years in an annually burnt plot (Silva & Castro 1989). The other study followed a cohort of seedlings and a sample of adults in two plots for 2 years. One plot was burnt at the end of the dry season and the other one was protected from fire (Silva, Raventos & Caswell 1990). These studies recorded survivorship, growth and flowering for *A. semiberbis* plants of different sizes. Fecundity values were obtained by multiplying the number of inflorescences for each size class by the average number of germinating seeds inflorescence<sup>-1</sup> (Silva & Ataroff 1985). These data provide no information on temporal variability in demographic rates within the treatments; such variability is an important factor to be explored in future population dynamic studies.

A linear time-invariant matrix population model is given by

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t), \quad (1)$$

where the state vector  $\mathbf{n}(t)$  gives the abundance of each size class and the population projection matrix  $\mathbf{A}$  determines the dynamics of the population. The projection interval from  $t$  to  $t+1$  in the present case is 1 year. The solution to Eqn 1 can be written

$$\mathbf{n}(t) = \mathbf{A}^t \mathbf{n}(0), \quad (2)$$

where  $\mathbf{n}(0)$  is an arbitrary initial population vector.

Population matrices  $\mathbf{U}$  and  $\mathbf{B}$  for the unburnt and burnt populations are shown in graphical form in Fig. 1. Both matrices are irreducible and primitive, and have distinct eigenvalues. Thus the solution to Eqn 2 can be written in terms of the eigenvalues  $\lambda_i$  and the right ( $\mathbf{w}_i$ ) and left ( $\mathbf{v}_i$ ) eigenvectors of the projection matrix:

$$\mathbf{n}(t) = \sum_i c_i \mathbf{w}_i \lambda_i^t \tag{3}$$

where  $c_i = \mathbf{v}_i' \mathbf{n}(0)$ . The Perron–Frobenius theorem guarantees the existence of a real dominant eigenvalue  $\lambda_1$ ; when the transient effects due to the other eigenvalues have decayed, as  $t$  gets large:

$$\mathbf{n}(t) \rightarrow c_1 \mathbf{w}_1 \lambda_1^t \tag{4}$$

A population described by Eqn 4 grows exponentially at a rate  $\lambda_1$  (in continuous time, the familiar intrinsic rate of increase  $r = \ln \lambda_1$ ) with a stable stage distribution given by the right eigenvector  $\mathbf{w}_1$ . The rate of increase  $\lambda_1$  is an integrative measure of the population's response to its environment, combining as it does stage-specific rates of survival, growth and reproduction. It is the appropriate measure of fitness in age- or stage-classified selection models (Charlesworth 1980; Lande 1982).

To evaluate the importance of the different parts of the life cycle (and thus the different entries in the population projection matrix), elasticities were calculated (DeKroon *et al.* 1986). The elasticities give the proportional changes in  $\lambda_1$  due to proportional changes in the matrix coefficients, and are given by

$$e_{ij} = \frac{a_{ij} \partial \lambda_1}{\lambda_1 \partial a_{ij}} \tag{5}$$

The elasticities  $e_{ij}$  give the proportional contribution of the transition  $a_{ij}$  to population growth.

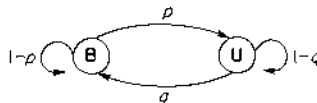
This analysis, applied to the matrices  $\mathbf{U}$  and  $\mathbf{B}$  provides information about the differences between burnt and unburnt environments. To go beyond this, the matrices must be combined to characterize a variable environment with a specified frequency of fire.

A simple deterministic model of an environment with a fire frequency of  $x/m$  is given by

$$\mathbf{n}(t + m) = \mathbf{B}^x \mathbf{U}^{m-x} \mathbf{n}(t) \tag{6}$$

for any value of  $m$ . The dominant eigenvalue of the matrix  $\mathbf{B}^x \mathbf{U}^{m-x}$  gives the eventual rate of growth of the population over a period of  $m$  years; this rate can be converted to a per-year basis by taking the  $m$ th root.

Equation 6 describes an environment in which fire occurs in exactly  $x$  years out of  $m$ . Fire, however, is a stochastic process, so that an environment with a given long-term fire frequency will occasionally experience much longer and much shorter intervals between fires than expected. A simple stochastic environment model is provided by a first-order Markov chain with the transition graph:



where  $p$  is the probability of an unburnt year following a burnt year and  $q$  is the probability of a burnt year following an unburnt year. This environmental model can be characterized by two parameters: the frequency of burning,  $\pi$ , and the autocorrelation,  $\rho$ . A negative autocorrelation indicates that burnt and unburnt years tend to alternate, while positive values indicate that the environment tends to produce long sequences of burnt years, followed by sequences of unburnt years. If  $\rho = 0$ , successive years are independent. It is known that both the frequency of different environmental states and their autocorrelation can have significant effects on population dynamics (e.g. Tuljapurkar & Orzack 1980; Tuljapurkar 1989). The relation between the environmental transition probabilities  $p$  and  $q$  and the fire frequency  $\pi$  and the autocorrelation  $\rho$  is given by

$$\pi = \frac{q}{1 - \rho}, \quad (7)$$

$$\rho = 1 - p - q. \quad (8)$$

The population dynamics in this environment are described by

$$\mathbf{n}(t) = \mathbf{A}_{t-1}\mathbf{A}_{t-2}\cdots\mathbf{A}_0\mathbf{n}(0), \quad (9)$$

where the projection matrix  $\mathbf{A}_t$  is  $\mathbf{U}$  or  $\mathbf{B}$ , as determined by the stochastic environment model.

The appropriate measure of population growth in a stochastic environment is the stochastic growth rate  $\lambda_s$ , defined by

$$\log \lambda_s = \lim_{t \rightarrow \infty} \frac{1}{t} E(\log N(t)), \quad (10)$$

where  $N(t)$  is the abundance of any stage or group of stages in the population (see Tuljapurkar 1989 for a review). This index gives, with probability 1, the asymptotic growth rate of a population experiencing the stochastic environment. If  $\log \lambda_s < 0$ , eventual extinction is certain. The appropriate measure of fitness in stochastic environments is  $\log \lambda_s$  (Tuljapurkar 1982).

Because the analytical computation of  $\log \lambda_s$  is not feasible, we used the numerical method of Cohen, Christensen & Goodyear (1983) and Heyde & Cohen (1985). This method uses the Markov model to generate a sequence of  $T$  matrices ( $T = 3000$  in this study), which are then used to project an arbitrary initial population. At each time  $t$  an instantaneous growth rate is calculated from

$$\log \lambda(t) = \log N(t+1) - \log N(t). \quad (11)$$

The estimate of the stochastic growth rate is the mean of these instantaneous estimates:

$$\widehat{\log \lambda_s} = \frac{1}{T-1} \sum_{t=1}^{T-1} \log \lambda(t). \quad (12)$$

Approximate 95% confidence intervals on this estimate are given by

$$\widehat{\log \lambda_s} \pm 1.96 \sqrt{V(\log \lambda(t))/T}, \quad (13)$$

where  $V(\log \lambda(t))$  is the variance of the  $\log \lambda(t)$ .

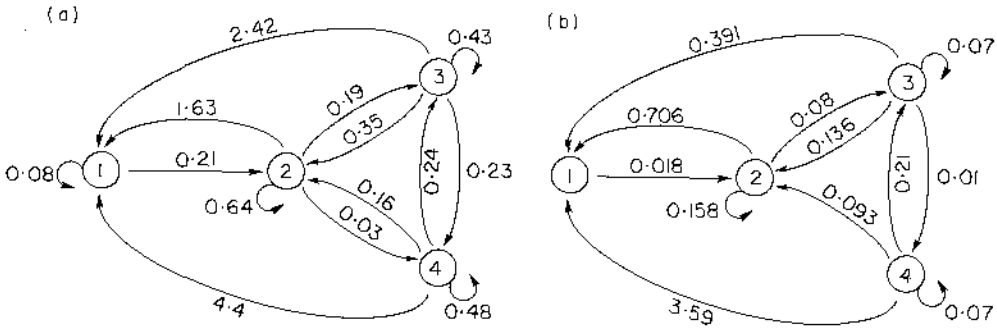


FIG. 1. Life-cycle graphs for two populations of *Andropogon semiberbis* in savanna grassland. The nodes represent stages (1: 1 tiller; 2: 2–10 tillers; 3: 11–20 tillers; 4: > 20 tillers) and the arrows indicate transitions between stages. The  $(i, j)$  element of the projection matrix is the coefficient on the arrow from stage  $j$  to stage  $i$ . (a) An annually burnt population. (b) A population protected from fire for 1 year.

### RESULTS

Fire exclusion has a dramatic and unambiguous effect on the population dynamics of *Andropogon semiberbis* (Fig. 1). Almost all the entries in the burnt matrix **B** are greater than the corresponding entries of the unburnt matrix **U**. The sum of fertilities is 9.25 in **B** and only 4.69 in **U**. These effects are highly significant, according to log-linear analysis applied to matrices describing growth and mortality of individual plants (Silva, Raventos & Caswell 1990). Here, the consequences of these differences for population growth rate, population structure and growth-rate sensitivities will be examined.

#### Growth rates

The population growth rates under the two treatments are  $\lambda_1 = 1.2524$  ( $r = 0.2251$ ) for **B** and  $\lambda_1 = 0.2762$  ( $r = -1.2866$ ) for **U**. Thus the conditions resulting from even a single year of fire exclusion would lead to rapid extinction.

Comparison of the two matrices reveals differences in almost every transition in the life cycle (Fig. 1). Because  $\lambda_1$  is differentially sensitive to these changes, the method of Caswell (1989b) was used to evaluate the contributions of these differences to the effect of fire on population growth. Let  $\Delta\lambda = 1.2524 - 0.2762$  denote the effect of fire on population growth rate. A first approximation to  $\Delta\lambda$  is

$$\Delta\lambda \approx \sum_{i,j} \Delta a_{ij} \frac{\partial \lambda}{\partial a_{ij}}, \tag{14}$$

where the sensitivities  $\partial\lambda/\partial a_{ij}$  are calculated from the mean of the two matrices. The terms in this summation give the contributions of the differences in the matrix entries to the effect on growth rate. The matrix of these contributions is

$$\begin{pmatrix} 0.0163 & 0.0711 & 0.0459 & 0.0061 \\ 0.2560 & 0.2423 & 0.0316 & 0.0033 \\ & 0.0724 & 0.0696 & 0.0019 \\ & 0.0305 & 0.0658 & 0.0411 \end{pmatrix} \tag{15}$$

By far the most important contributions come from the upper left corner of the matrix, from the transitions involving size classes 1 and 2. These four terms contribute 61% of the effect of burning on population growth, emphasizing the importance of fire effects on the growth, survival and reproduction of small plants.

#### *Stable size distribution and reproductive value*

The stable size distributions are given by the right eigenvectors of the two projection matrices. They are very similar and have the typical inverted-J shape (Table 1). The observed size distribution in the burnt plot was not significantly different from that predicted from the eigenvector of the matrix **B** (Kolmogorov–Smirnov test,  $P > 0.05$ ). The size distribution in the unburnt plot was not measured because the population had declined to such low numbers.

The reproductive values for the two models, calculated from the left eigenvectors of the projection matrices, show the same trend (Table 1): the reproductive values of the three largest size classes, which comprise juveniles and adults, are similar and about an order of magnitude greater than those of the one-tiller plants.

#### *Elasticity analysis*

In the burnt population, stage 2 (2–10 tillers) makes the largest contribution (50%) to population growth (Fig. 2a). Including the transition from stage 1 to stage 2 increases the total elasticity to 70% of the total. The subgraph formed by stages 1 and 2 accounts for 58.6% of the total elasticity.

In the unburnt population the contribution of the second stage is even larger (61%) than in the former model (Fig. 2b). In this case the subgraph defined by the first two stages contributes 74.5% of the population growth rate. In both models the largest stage (> 20 tillers) contributes less than 10% of the population growth rate.

#### *Effects of fire regime*

In the deterministic model, population growth rate (measured as  $\log \lambda$  to facilitate comparison with the stochastic model) increases with the frequency of fire (Fig. 3a). The critical fire frequency, below which the population cannot persist, is approximately 0.85.

TABLE 1. Observed size distribution (for a burnt treatment) of *Andropogon semiberbis* and the predicted stable size distribution and reproductive values for both burnt and unburnt treatments.

Stage	Tillers	Size distribution			Reproductive value	
		Observed (burnt)	Predicted		burnt	unburnt
			burnt	unburnt		
1	1	0.639	0.633	0.705	1.00	1.00
2	2–10	0.284	0.266	0.207	5.57	15.34
3	11–10	0.041	0.070	0.084	7.92	13.88
4	> 20	0.035	0.031	0.004	9.31	38.49

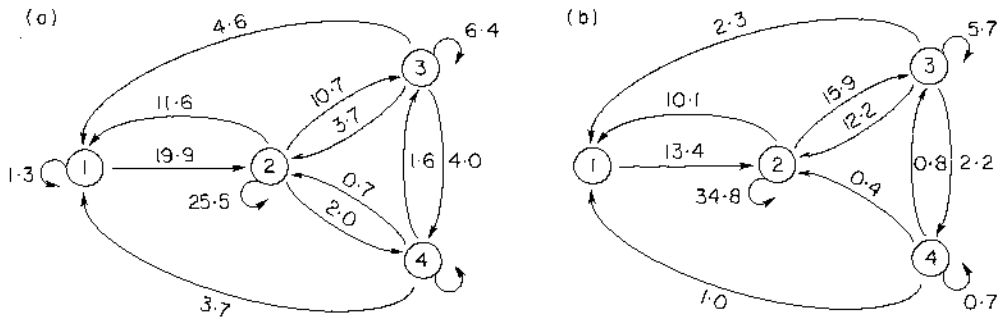


FIG. 2. Elasticity analysis for two populations of *Andropogon semiberbis* in savanna grassland. The graphs correspond to the life-cycle graphs in Fig. 1, but the coefficients are elasticities of  $\lambda$  with respect to the corresponding matrix entry. Elasticities have been scaled to sum to 100, so the coefficients give the percentage of  $\lambda$  contributed by the corresponding transition. Values less than 1 are not shown. (a) An annually burnt population. (b) A population protected from fire for 1 year.

The stochastic growth rate ( $\log \lambda_s$ ) also increases with fire frequency (Fig. 3b). The environmental autocorrelation pattern has no significant effect on  $\log \lambda_s$ . Confidence intervals, calculated using Eqn 13, were never larger than  $\pm 0.025$ , and are not shown in the Fig. 3b. In this case (and it need not be so in other cases) the stochastic results are close to the deterministic ones. All three models predict a critical fire frequency of approximately 0.85.

## DISCUSSION

The lack of basic studies on the population dynamics of savanna plant species makes it difficult to understand the dynamics of savanna communities and their response to changing conditions, particularly fire regimes. This study has used field data to feed theoretical but biologically sound models in order to contrast the demographic properties of *Andropogon semiberbis* in habitats subjected to annual burning and in those protected from fire. The results show that *A. semiberbis* is drastically affected by even a single year of fire exclusion, but that the population can grow rapidly under an annual fire regime. These differences are due mainly to the effects of fire, or its exclusion, on the growth, survival and reproduction of the first two size classes in our model; the elasticity analysis shows that these size classes are the most important determinants of population growth in either environment.

These effects agree with what has been reported from other areas protected from fire and grazing (Farinas & San José 1987). In temperate and tropical grasslands, standing necromass accumulation resulting from low decomposition rates stifles new growth by shading, limiting space and slowing nutrient recycling (Vogl 1974). Radiation reaching the ground is five to twenty times less in unburnt than in burnt plots by the end of the growing season after dry-season fire exclusion, and this difference is even greater at the beginning of the following growing season (Silva, Raventos & Caswell 1990). This excessive shading probably impairs the energy balance of the  $C_4$  species and boosts air and topsoil humidity promoting death and decay of underground plant parts. Prolonged exclusion of fire and grazing, the two main factors reducing litter accumulation in savanna communities, may lead to a



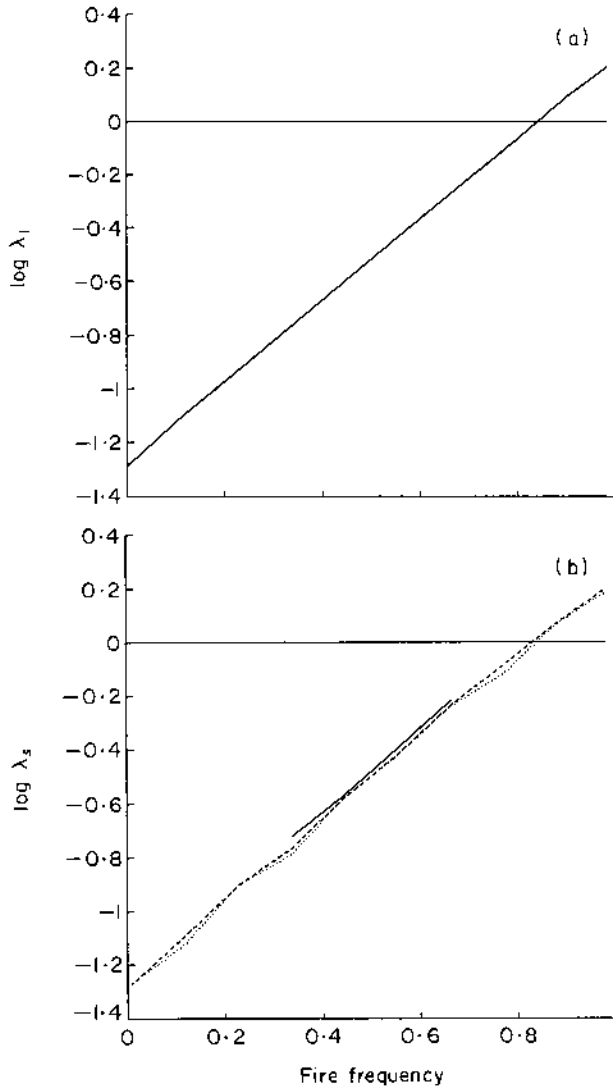
Responses to fire of *Andropogon semiberbis*

FIG. 3. (a) Population growth rate of *Andropogon semiberbis*, measured by  $\log \lambda_1$ , as a function of fire frequency in a deterministic, periodic environment. (b) The stochastic population growth rate  $\log \lambda_s$ , as a function of mean fire frequency in an autocorrelated stochastic environment. Environmental autocorrelation  $\rho = -0.5$  (solid line), 0 (dashed line) and 0.5 (dotted line). (The line for  $\rho = -0.5$  is truncated because fire frequencies outside this range are impossible with this autocorrelation.)

substantial decrease in grass cover and grass diversity and an increase in tree density and diversity (Menaut 1977; San José & Farinas 1983).

Therefore, plant growth is high in burnt savannas, and this is reflected in high transition rates and high survival in the burnt model. More vigorous growth resulted in higher fertilities and recruitment in the annually burnt population. The beneficial effects of fire on the production of the grass layer has already been reported for several savanna and grassland communities (San José & Medina 1976; Gillon

1983; Frost 1985); however, the promotion of flowering has only been reported for precocious and early species (Coutinho 1982).

Caswell (1986) used elasticity analysis to compare the relative contributions of survival in the same size class, growth to the next size class, and reproduction to the population growth rate of five tree species. In these species, survival contributed the most and reproduction the least; a similar trend can be found in the perennial herb *Arisaema triphyllum* (Bierzychudek 1982) and the shrub *Alnus incana* ssp. *rugosa* (Huenneke & Marks 1987). Caswell (1986) suggested that this pattern might be typical of long-lived, slow-growing species. In the *Andropogon semiberbis* populations examined here, the relative contribution of growth (transitions to larger size classes) is the most important, and reproduction the least. Growth is also the most important transition in the biennial *Dipsacus sylvestris* (Caswell & Werner 1978; DeKroon *et al.* 1986) and the annual *Phlox drummondii* (Leverich & Levin 1977). It seems plausible that in short-lived species transitions to larger size classes is the most important parameter determining population growth rate.

The deterministic and stochastic models for variable environments both show that a high frequency (0.85 or greater) of fire is required for population persistence. Savannas are very prone to be burnt annually, and have probably been under an annual regime of fire since European settlement. Savanna fires tend to be patchy, however, with sites being burnt every year, whereas others remain several years without fire.

The fact that, when grazing is excluded, *A. semiberbis* needs frequent fires to persist suggests that the spread and evolution of this species is closely related to human occupation of neotropical savanna ecosystems, because natural fires are unlikely to occur very frequently. Also, the only large herbivores in these seasonal savannas are cattle, introduced by Europeans a few centuries ago. We suggest that changes in the fire regime of neotropical savannas as a consequence of European settlement may have induced evolutionary change from fire tolerance to dependence on fire in this species.

In both models the reproductive value of *A. semiberbis* increases with size, with a tendency to reach a plateau in the B model. This seems to be a general feature of size-classified populations of trees (Caswell 1986), herbs (Caswell & Werner 1978; Bierzychudek 1982) and shrubs (Huenneke & Marks 1987). In contrast, age-classified populations usually show a decline in reproductive value after the beginning of reproduction. This difference could be explained by the lack of senescence in the size-classified populations, or by the fact that large plants are killed by other than physiological causes (Sarukhán 1980; Monasterio 1986). The pattern is also predicted on evolutionary grounds, because selection should act to reduce growth rate into any size class in which reproductive value declines (Caswell 1986).

Stable size distributions for *A. semiberbis* are similar in the two models, showing the inverted-J shape found in other plant species (Werner & Caswell 1977; Bierzychudek 1982; Piñero, Martínez-Ramos & Sarukhán 1984). This pattern seems to be relatively independent of whether individuals are classified by age, size or stage.

Our results suggest several avenues for further research. First, characterizing habitats as 'burnt' or 'unburnt' is an obvious oversimplification, especially for other species in which the immediate effect of a single year of fire exclusion might be smaller. A larger series of matrices, characterizing population dynamics as a function of the time since the last fire, would be an improvement. Such a series could be

coupled with data on fire frequency to construct a much more detailed stochastic analysis. Secondly, our data do not permit examination of other sources of environmental variability. Although we found that the burnt population is close to its stable size distribution, which suggests that other fluctuations do not have a major effect, it would be valuable to characterize the population response to other factors (e.g. rainfall) as well as fire. Thirdly, our analysis does not address the important issue of density-dependent and competitive effects, which may well be important.

#### ACKNOWLEDGMENTS

Thanks are due to Don Luis Nieto for technical assistance. This research was funded by grants from the Consejo Nacional de Investigaciones Científicas y Tecnológicas de Venezuela and from the Consejo de Desarrollo Científico y Humanístico de la Universidad de los Andes to Juan Silva and by grants from the National Science Foundation and the Environmental Protection Agency and a Fellowship from the John Simon Guggenheim Foundation to Hal Caswell. We thank the Latin American Botanical Network for its support of the First International Course in Plant Population Ecology, where this work was begun. Woods Hole Oceanographic Institution Contribution 7326.

#### REFERENCES

- Bierzzychudek, P. (1982). The demography of jack-in-the-pulpit, a forest perennial that changes sex. *Ecological Monographs*, **52**, 335–351.
- Canales, J. & Silva, J.F. (1987). Efecto de una quema sobre el crecimiento y demografía de vástagos en *Sporobolus cubensis*. *Acta Oecologica, Oecologia Generalis*, **8**, 391–401.
- Caswell, H. (1986). Life cycle models for plants. *Lectures on Mathematics in the Life Sciences*, **18**, 171–233.
- Caswell, H. (1989a). *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, MA.
- Caswell, H. (1989b). Analysis of life table response experiments. I. Decomposition of effects on population growth rate. *Ecological Modelling*, **46**, 221–237.
- Caswell, H. & Werner, P.A. (1978). Transient behaviour and life history analysis of teasel (*Dipsacus sylvestris* Huds.). *Ecology*, **59**, 53–66.
- Charlesworth, B. (1980). *Evolution in Age-Structured Populations*. Cambridge University Press, Cambridge.
- Cohen, J. E., Christensen, S.W. & Goodyear, C.P. (1983). A stochastic age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. *Canadian Journal of Fisheries and Aquatic Sciences*, **40**, 2170–2183.
- Coutinho, L.M. (1982). Ecological effects of fire in Brazilian cerrado. *Ecology of Tropical Savannas* (Ed by B.J. Huntley & B.H. Walker), pp. 273–291. Springer-Verlag, Berlin.
- DeKroon, H., Plaisier, A., van Groenendael, J. & Caswell, H. (1986). Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology*, **67**, 1427–1431.
- Farinas, M. & San José, J. J. (1987). Cambios en el estrato herbáceo de una parcela de sabana protegida del fuego y del pastoreo durante 23 años. Calabozo, Venezuela. *Acta Científica Venezolana*, **36**, 199–200.
- Frost, P.G.H. (1985). Organic matter and nutrient dynamics in a broadleaved African savanna. *Ecology and Management of the World's Savannas* (Ed by J. C. Tothill & J. J. Mott), pp. 200–206. Australian Academy of Sciences, Canberra.
- Frost, P.G.H., Medina, E., Menaut, J.C., Solbrig, O.T., Swift, M. & Walker, B.H. (1986). *Responses of Savannas to Stress and Disturbance*. Biology International, Special Issue 10. International Union of Biological Sciences, Paris.
- Frost, P.G.H. & Robertson, F. (1987). The ecological effects of fire in savannas. *Determinants of Tropical Savannas* (Ed by B.H. Walker), pp. 93–140. International Union of Biological Sciences Monograph Series No. 3, IRL Press, Paris.
- Gillon, D. (1983). The fire problem in tropical savannas. *Tropical Savannas* (Ed by F. Bourliere), pp. 617–641. Elsevier, Amsterdam.
- Hartshorn, G.S. (1975). A matrix model of tree population dynamics. *Tropical Ecological Systems* (Ed by F. B. Golley & E. Medina), pp. 41–51. Springer-Verlag, New York.

- Hubbell, S.P. & Werner, P.A. (1979). On measuring the intrinsic rate of increase of populations with heterogeneous life histories. *American Naturalist*, **113**, 277–293.
- Hueneke, L.F. & Marks, P.L. (1987). Stem dynamics of the shrub *Alnus incana* ssp. *rugosa*: transition matrix models. *Ecology*, **68**, 1234–1242.
- Heyde, C. C. & Cohen, J. E. (1985). Confidence intervals for demographic projections based on products of random matrices. *Theoretical Population Biology*, **27**, 120–153.
- Lacey, C. J., Walker, J. & Noble, I. R. (1982). Fire in Australian tropical savannas. *Ecology of Tropical Savannas* (Ed by B.J. Huntley & B.H. Walker), pp. 246–272. Springer-Verlag, Berlin.
- Lande, R. (1982). A quantitative genetic theory of life history evolution. *Ecology*, **63**, 607–615.
- Leverich, W. J. & Levin, D.A. (1977). Age-specific survivorship and reproduction in *Phlox drummondii*. *American Naturalist*, **113**, 881–903.
- Menaut, J.C. (1977). Evolution of plots protected from fire since years in a guinea savanna of Ivory Coast. *Actas del IV Simposium Internacional de Ecología Tropical. Tomo II*, pp. 543–558. Instituto Nacional de Cultura, Panama.
- Monasterio, M. (1986). *Recherches écologiques sur les Espeletia du paramo désertique des hautes Andes tropicales du Venezuela*. Thèse de Doctorat d'état, Université Paris VI, Paris.
- Mott, J.J. & Andrew, M.H. (1985a). Effect of fire on the grass understorey of Australian savanna. *Towards an Expert System for Fire Management at Kakadu National Park* (Ed by J. Walker, J.R. Davis & A.M. Gill). CSIRO, Institute of Biological Resources, Technical Memorandum 85/2, 77–92. Canberra.
- Mott, J.J. & Andrew, M.H. (1985b). The effect of fire on the population dynamics of native grasses in tropical savannas of north-west Australia. *Proceedings of the Ecological Society of Australia*, **13**, 231–239.
- O'Connor, T.G. (1985). A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa. *South African National Scientific Progress Report*, **114**, 1–119.
- Piñero, D., Martínez-Ramos, M. & Sarukhán, J. (1984). A population model of *Astrocaryum mexicanum* and a sensitivity analysis of its finite rate of increase. *Journal of Ecology*, **72**, 977–991.
- Raventos, J. & Silva, J.F. (1988). Architecture, seasonal growth and interference in three grass species with different flowering phenologies in a tropical savanna. *Vegetatio*, **75**, 115–123.
- San José J.J. & Farinas, M.R. (1983). Changes in tree density and species composition in a protected *Trachypogon* savanna, Venezuela. *Ecology*, **64**, 447–453.
- San José J.J. & Medina, E. (1975). Effect of fire on organic matter production and water balance in a tropical savanna. *Tropical Ecological Systems* (Ed by F.B. Golley & E. Medina), pp. 251–264. Springer-Verlag, New York.
- Sarmiento, G. (1983). The savannas of tropical America. *Tropical Savannas* (Ed by F. Bourliere), pp. 245–288. Elsevier, Amsterdam.
- Sarukhán, J. (1978). Studies on the demography of tropical trees. *Tropical Trees as Living Systems* (Ed by P.B. Tomlinson & M. H. Zimmermann), pp. 163–184. Cambridge University Press, Cambridge.
- Sarukhán, J. (1980). Demographic problems in tropical systems. *Demography and Evolution in Plant Populations* (Ed by O.T. Solbrig), pp. 161–188. Blackwell Scientific Publications, Oxford.
- Silva, J.F. (1987). Responses of savannas to stress and disturbance: species dynamics. *Determinants of Tropical Savannas* (Ed by B.H. Walker), pp. 141–156. International Union of Biological Sciences Monograph Series No. 3, IRL Press, Paris.
- Silva J.F. & Ataroff, M. (1985). Phenology, seed crop and germination of coexisting grass species from a tropical savanna in Western Venezuela. *Acta Oecologica, Oecologia Plantarum*, **6**, 41–51.
- Silva, J.F. & Castro, F. (1989). Fire, growth and survivorship in a Neotropical savanna grass (*Andropogon semiberbis* (Ness) Kunth) in Venezuela. *Journal of Tropical Ecology*, **5**, 387–400.
- Silva, J.F., Raventos, J. & Caswell, H. (1990). Growth, survivorship and the effects of fire exclusion in two savanna grasses. *Acta Oecologica* **11**, 783–800.
- Trollope, W.S.W. (1982). Ecological effects of fire in South African savannas. *Ecology of Tropical Savannas* (Ed by B.J. Huntley & B.H. Walker), pp. 292–306. Springer-Verlag, Berlin.
- Tuljapurkar, S. D. (1982). Population dynamics in variable environments. III. Evolutionary dynamics of *r*-selection. *Theoretical Population Biology*, **21**, 141–165.
- Tuljapurkar, S. D. (1989). An uncertain life: demography in random environments. *Theoretical Population Biology*, **35**, 227–294.
- Tuljapurkar, S. D. & Orzack, S. H. (1980). Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theoretical Population Biology*, **18**, 314–342.
- Vogl, R.J. (1974). Effects of fire on grasslands. *Fire and Ecosystems* (Ed by T.T. Kozlowski & C.E. Ahlgren), pp. 139–194. Academic Press, New York.
- Werner, P. & Caswell, H. (1977). Population growth rates and age versus stage-distribution models for teasel (*Dipsacus sylvestris* Huds.). *Ecology*, **58**, 1103–1111.

(Received 8 March 1990; revision received 16 January 1991)