

A Demographic Study of an Annual Grass (*Andropogon brevifolius* Schwarz) in Burnt and Unburnt Savanna

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Abstract

We used demographic models to examine the effects of fire and fire exclusion on the annual grass *Andropogon brevifolius* in Venezuelan savannas. Seed germination, vegetative survival, seed production, and seed survival were measured in experiments in burned and unburned plots. From these data we calculated the population growth rate, stable age distribution, reproductive value, growth rate sensitivities, and the critical fire frequency necessary for persistence of the population. The annual growth rate of the population in the burned plot was 2.81, whereas the growth rate of the population in the unburned plot was only 0.66. Thus *A. brevifolius* will decline to extinction under fire exclusion. Population growth rate is most sensitive to changes in survival, but most of the effect of fire exclusion was contributed by reductions in fertility, including both seed production and seedling recruitment. We estimate that a fire frequency of at least 0.29 is needed for *A. brevifolius* to persist.

Keywords: Population dynamics, fire, plant demography, tropical savanna, annual plants, Poaceae.

Résumé

Des modèles démographiques ont été utilisés pour examiner les effets du feu et de son exclusion sur l'herbacée annuelle *Andropogon brevifolius* dans des savanes vénézuéliennes. La germination des graines, la survie végétative, la production de semences et la survie des graines ont été mesurées au cours d'expériences sur des parcelles brûlées et non brûlées. A partir de ces données, nous avons calculé le taux de croissance de la population, la distribution à un âge stable, la valeur reproductive, les sensibilités de taux de croissance et la fréquence de feu critique nécessaires à la persistance de la population. Le taux annuel de croissance de la population sur la parcelle brûlée est de 2,81, mais de 0,66 seulement sur la parcelle non brûlée. En l'absence de feu, *A. brevifolius* déclinera donc jusqu'à l'extinction. Le taux de croissance de la population est très sensible aux modifications de la survie, mais l'effet d'exclusion du feu se traduit essentiellement par des réductions de la fertilité, incluant la production de semences et le recrutement de plantules. Nous estimons qu'une fréquence de feu d'au moins 0,29 est nécessaire à la persistance d'*A. brevifolius*.

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INTRODUCTION

Tropical savannas are characterized by a herbaceous layer largely dominated by grasses and sedges, by a strongly seasonal rainfall regime and by the regular occurrence of fire and grazing (SARMIENTO & MONASTERIO, 1983). Little is known of the population dynamics of neotropical savanna plants, and thus far the primary focus of interest has been the dominant perennial grasses (SILVA & ATAROFF, 1985; SILVA & CASTRO, 1989; SILVA *et al.*, 1990, 1991). The lack of studies on annuals is probably due to their small contribution to total herbaceous biomass, although their representation may be highly variable. Common annual species in Venezuelan savannas belong to the genera *Andropogon*, *Aristida*, *Diectomis* and *Gymnopogon* (SARMIENTO & MONASTERIO, 1983).

Fire, which usually occurs annually at the end of the dry season, is a major environmental factor in tropical savannas. It acts as a selective filter for fire-sensitive species (SARMIENTO & MONASTERIO, 1975). Although fire can increase mortality and reduce growth in some perennial grasses (CANALES & SILVA, 1987; SILVA & CASTRO, 1989), exclusion of fire has a net detrimental effect on individual and population growth of perennial grasses due to the accumulation of standing necromass in the herbaceous layer (SILVA *et al.*, 1990). Fire should be even more beneficial to annual grasses since they are short and slender plants, unable to outgrow the standing dry mass. The seedlings of annuals themselves are unaffected by dry season fires, since they germinate only after the rainy season has started.

In this paper we report the results of a field study of the effects of fire exclusion on an annual savanna grass, *Andropogon brevifolius*. Our experiments measure the effects of fire exclusion on the survival and reproduction of individual plants. We incorporate these measurements into a matrix population model, and use that model to explore the consequences of fire and fire exclusion for population growth. Our models should be interpreted as explorations of current environmental conditions, not as predictions of future population dynamics.

MATERIALS AND METHODS

Study area

The study area is located in Paraima Ranch, near the city of San Carlos, State of Cojedes, in Venezuela (9 25' N, 68 15' W). Soils are Ultisols (Haplustuls) with medium to light textures, slow drainage, little organic matter, low pH and high content of A1 (BILBAO, 1988). The climate is strongly isothermic, with a mean annual temperature of 27 °C. Rainfall is markedly seasonal with a rainy season from May to November, and a dry season from December to April. Mean annual rainfall is 1 200 mm.

The vegetation is an open savanna, dominated by the perennial grasses, *Trachypogon plumosus* and *Thrasya petrosa*, with scattered trees (*Curatella americana*, *Byrsonima crassifolia* and *Bowdichia virgiloides*) and small forest islands. The area is subjected to cattle grazing of variable intensity. In May 1987, an experimental area of approximately 15 ha was fenced and cattle and fire excluded.

The species

Andropogon brevifolius is a slender, decumbent annual grass with small leaves, broadly distributed in the seasonal savannas of the Orinoco Llanos. Seeds germinate between June and July, and the vegetative growth phase extends until November, when the plants flower. The spikelets are dispersed

between December and January, remaining in the surface of the soil during the dry period and the beginning of the rainy season. We assume that the seed bank is transient, as has been found for several savanna perennial grasses (SILVA & ATAROFF, 1985). This means that after the dormant period, seeds either germinate or die. This assumption is strongly, although not conclusively, supported by our field observations. Direct inspection of soil samples in these and other similar savannas for many years of field work, as well as observations on small plots excluded from seed rain in this area, make us believe that there is no permanent seed bank in the soil for this and other grass species.

Field work

In April 1989, we established two experimental plots (15 sq m each) within the excluded area. One plot was burnt in April and the other remained protected from fire. During the following three months we monitored germination. At the peak of germination in the beginning of July we labelled one thousand seedlings in each plot. The method used to label was as follows: in each plot we scanned through consecutive 1.5 m transects and labelled all seedlings found until we completed one thousand seedlings. The two groups were monitored monthly for survival until December 1989. The two areas occupied by the cohorts within each plot were roughly similar, and from a parallel experiment conducted in the vicinity (CANALES, 1992) we learned that initial seedling densities were similar at that spatial scale.

To evaluate seed survival and germination, one thousand awned spikelets were randomly selected from a sample gathered within the enclosure, in the vicinity of the experimental plots. These spikelets were sown in two additional sub-plots (0.5 × 2 m). One was burnt in April and the other one remained protected from fire. Germination was monitored from May to July.

Within each large plot and without interfering with the labelled cohort, we took a sample of plants to determine fecundity (number of seeds per plant) as follows. Fifteen flowering plants in each plot were randomly selected and labelled in November 1989, after anthesis. Each inflorescence was enclosed in a cheese cloth bag. In December, when dispersal was taking place, the plants were harvested and taken to the laboratory, where spikelets were counted. We observed that only those spikelets holding awns carry a seed. Therefore the proportion of fertile spikelets was estimated by counting the awned spikelets from a sample of 2000 spikelets in each group.

DEMOGRAPHIC ANALYSIS

The life cycle of *A. brevifolius* is very simple. It is a semelparous annual plant with relatively limited periods of flowering and seed germination and without a seed bank. We consider two phases: the plant phase that goes from seedling to senescent adult and the seed phase that goes from seed dispersal to germination. In spite of this simplicity, we apply the analytical machinery of life cycle graphs and matrix population models (CASWELL, 1989). Unlike other approaches used to study annual plants, these methods can be extended directly to annual life cycles with additional complexities (e.g., a seed bank, an extended seed germination period, multiple reproductive events).

We use a linear age-classified model to describe the dynamics in discrete time of the grass population. We express the model initially in the form of the life cycle graph that corresponds to the population projection matrix. The characteristic equation and the right and left eigenvectors can be derived directly from the z -transform of this graph, and these results in turn permit a sensitivity analysis to explore the consequences of the structure of the life cycle (CASWELL, 1989).

To construct the z -transformed life cycle graph, the plant phase (July to December) was divided into six monthly age classes (fig. 1). The nodes n_1 to n_6

represent the classes in the plant phase and P_i is the monthly survival coefficient of class i . The seed phase is depicted as a single seven-month transition from senescent adults (class 6) to seedlings (class 1). F is the fertility value, which represents the number of seeds germinating in July per individual 7 months earlier; thus F includes not only seed production (fecundity) but also seed survival and germination. Following CASWELL (1989), the z -transformed graph is obtained by multiplying each coefficient by λ^{-i} , where i indicates the time, in months, required for the transition. The transition coefficients for the burned (B) and unburned (U) populations are given in table I. The fertility coefficient in B is more than twice that in U. This coefficient is the product of fecundity and seed survival to germination; both these quantities are greater in B (303, 0.011) than in U (182, 0.007). Plant survival probabilities are slightly greater in B than in U, and fairly constant throughout the season in both populations.

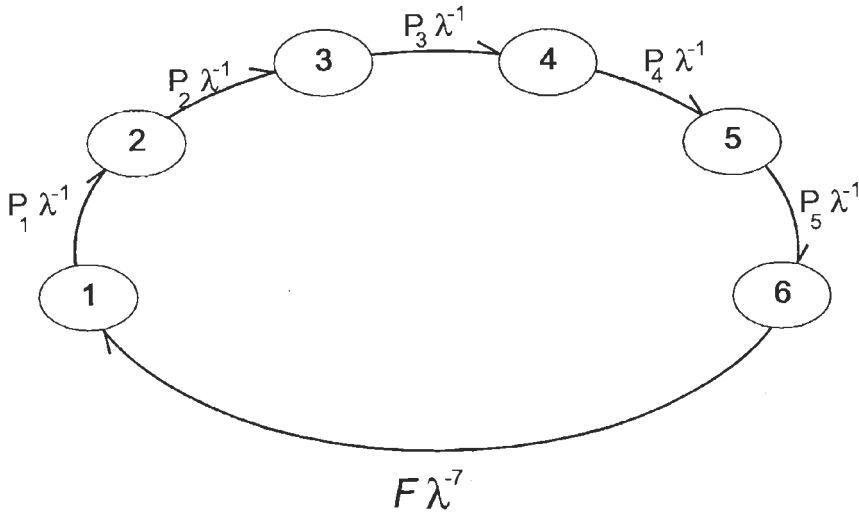


FIG. 1. – Z -transformed life cycle graph. The plant phase is represented by six monthly age classes and five transitions, whereas the seed phase is represented as a single seven-month transition from senescent adults (6) to seedlings (1). P_i is the monthly survival coefficient. F is the fertility value.

TABLE I. – Transition coefficients for the two population models, burnt (B) and unburnt (U). P_1 to P_5 correspond to the plant phase from July to December. F is fertility, the average number of descendants per plant after seven months of the seed phase; this results from multiplying fecundity (f , the average number of seeds produced per plant) by the probability of seed survival and germination (s).

Treatment	P_1	P_2	P_3	P_4	P_5	F	(f)	(s)
burnt (B)	0.98	0.97	0.98	0.96	0.95	3.33	303	0.011
unburnt (U)	0.87	0.86	0.86	0.93	0.87	1.27	182	0.007

The method of z -transforms applied to the graph produces the characteristic equation

$$(1) \quad \lambda^{12} - \left(\prod_{i=1}^5 P_i \right) F = 0$$

where λ is to the 12th power because there are twelve transitions as explained above. The roots of this equation are the eigenvalues of the associated population projection matrix. We denote by λ_1 the unique positive eigenvalue:

$$(2) \quad \lambda_1 = R_o^{1/12}$$

where $R_o = \left(\prod_{i=1}^5 P_i \right) F$ is the net reproductive rate, or expected number of surviving offspring per generation. The right (\mathbf{w}) and left (\mathbf{v}) eigenvectors corresponding to λ_1 are calculated recursively by:

$$(3) \quad \begin{aligned} w_1 &= 1 \\ w_i &= P_{i-1} \lambda_1^{-1} w_{i-1} \quad \text{for } i = 2, \dots, 6 \end{aligned}$$

$$(4) \quad \begin{aligned} v_1 &= 1 \\ v_6 &= F \lambda_1^{-7} \\ v_i &= P_i \lambda_1^{-1} v_{i+1} \quad \text{for } i = 2, \dots, 5 \end{aligned}$$

Most analysis of matrix population models focus on the dominant eigenvalue of the matrix. However, because the life cycle graph consists of a single loop, the associated matrix does not have a dominant eigenvalue (*i.e.* it is imprimitive). Thus the population does not converge to a stable age distribution. Instead, the age distribution cycles, with a period equal to the length of the loop in the life cycle graph (12 months, in this case). This, of course, is precisely the kind of behavior that a real population of annual plants exhibits on a within-year time scale. The structure of the population at any time will depend on the initial population structure. Because generations do not overlap in this species, the relevant initial conditions consist of a single age class. Assuming that this class is the first class, the population $\mathbf{n}(t)$ at time t will contain only one non-zero component; in month j only age class j will be non-empty.

On a year-to-year time scale, however, the mean population structure does converge to stability. CULL and VOGT (1974) show that

$$\lim_{t \rightarrow \infty} \frac{1}{12} \frac{n_j(12t+j)}{\lambda_1^{12t+j}} = cw_j$$

for some constant c . This means that asymptotically, $n_j(12t+j) \cong 12cw_j \lambda_1^{12t+j}$ for any class, and the growth rate of age class j from one year to the next periods is given by:

$$\frac{n_j(12(t+1)+j)}{n_j(12t+j)} \cong \lambda_1^{12} = R_o$$

This shows that the annual growth rate of the population is given by λ_1^{12} . Therefore, if $\lambda_1 < 1$ population decays to extinction, while if $\lambda_1 > 1$ population grows exponentially.

The resulting annual population growth rate for B was $\lambda_B = 2.8105$, whereas for U it was only $\lambda_U = 0.6635$. Since instantaneous growth rate, $r = \log \lambda$, these

values are equivalent to $r_B = 1.03$ and $r_U = -0.41$. Thus, *A. brevifolius* can increase rapidly under the conditions produced by burning, but will decrease to extinction under the conditions produced by fire exclusion.

The effect of fire exclusion on the population growth of *A. brevifolius* is measured by the difference $|\lambda_B - \lambda_U|$ between the growth rates in the burned and unburned treatments. To test the statistical significance of this effect, we used a Monte Carlo test which is a slight modification of the randomization test used by BRAULT and CASWELL (1993; see MANLY, 1991, for a general description of randomization tests). Our data consist of two sets of 1000 seeds from which germination was estimated, two sets of 1000 seedlings from which plant survival was estimated, and two sets of 15 flowering plants from which fecundity was estimated. The null hypothesis is that the fate of an individual seed, seedling or flowering plant is independent of its assignment to the burnt or unburnt treatment. By randomly permuting the individuals between treatments many times, and generating model parameters and a treatment effect $|\Delta\lambda| = |\lambda_B - \lambda_U|$ for each permutation, we generate a distribution of $|\Delta\lambda|$ under the null hypothesis. The statistical significance of the observed effect is given by the probability of an equal or greater effect under the null hypothesis.

Because the seed germination and seedling survival portions of the experiment are simple binomial outcomes with large sample sizes, instead of permuting individuals, we used the normal approximation to the binomial distribution to generate survival probabilities according to the null hypothesis. We find that the observed effect of fire exclusion is highly significant ($p < 0.005$) according to the randomization test.

The right eigenvector \mathbf{w} represents the stable age distribution (in the average sense given above) and the left eigenvector \mathbf{v} gives the reproductive value. From equations (3) and (4) we obtain

$$(5) \quad \frac{w_{i+1}}{w_i} = \frac{P_i}{\lambda_1} \quad \frac{v_{i+1}}{v_i} = \frac{\lambda_1}{P_i}$$

and the stable age distribution and the reproductive value are, respectively, monotonically decreasing and increasing if $P_i \leq \lambda_1$.

Since the survival coefficients for each population are all less than their respective growth rates, according to (5) the stable age distributions and the reproductive values (fig. 2) are monotonically decreasing and increasing respectively. Whereas the stable age distributions in both populations are very similar, reproductive values are greater in B than in U.

To investigate how the growth rate λ_1 varies due to changes in the life history, sensitivities are calculated from the partial derivatives of (1) with respect to each of these coefficients. Sensitivities to survival and to fertility are given by:

$$(6) \quad \frac{\partial \lambda_1}{\partial P_i} = \frac{1}{12} \frac{\lambda_1}{P_i}$$

$$(7) \quad \frac{\partial \lambda_1}{\partial F} = \frac{1}{12} \frac{\lambda_1}{F}$$

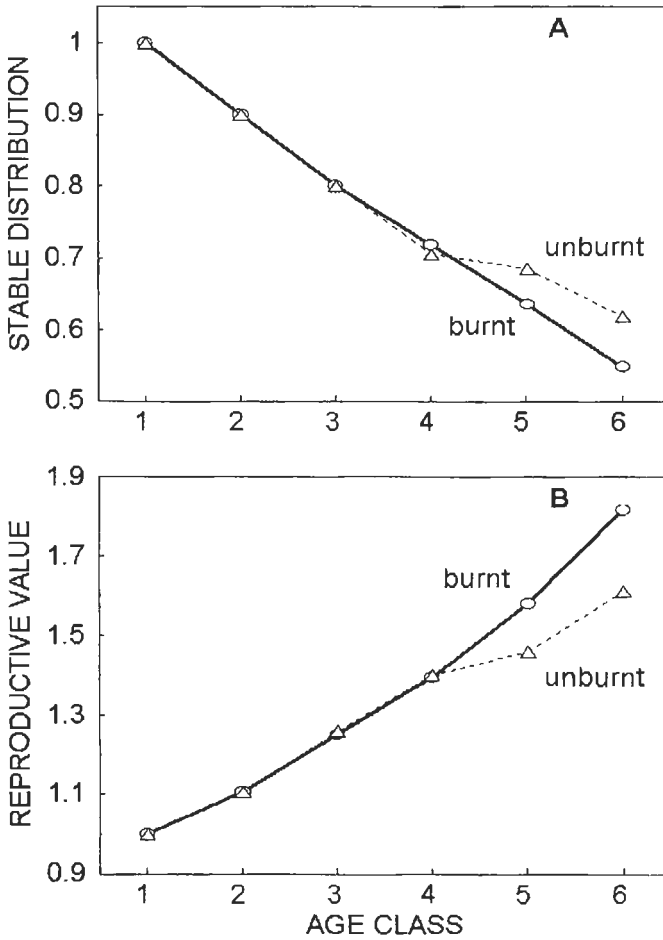


FIG. 2. - Stable age distribution (A) and age-specific reproductive values (B) for the two populations models, burnt (circles) and unburnt (triangles).

Sensitivities of both populations are shown in figure 3. The growth rates of both populations are less sensitive to changes in the fertility coefficient than to changes in monthly survival. In B, the sensitivity to fertility is less than one third the sensitivities to monthly survival, while in U it is only 30 % lower.

The elasticities of λ_1 give the results of proportional changes in survival and fertility. For this life history they have the particularly simple form

$$(8) \quad e_{P_i} = \frac{P_i}{\lambda_1} \frac{\partial \lambda_1}{\partial P_i} = \frac{1}{12}$$

$$(9) \quad e_F = \frac{F}{\lambda_1} \frac{\partial \lambda_1}{\partial F} = \frac{1}{12}$$

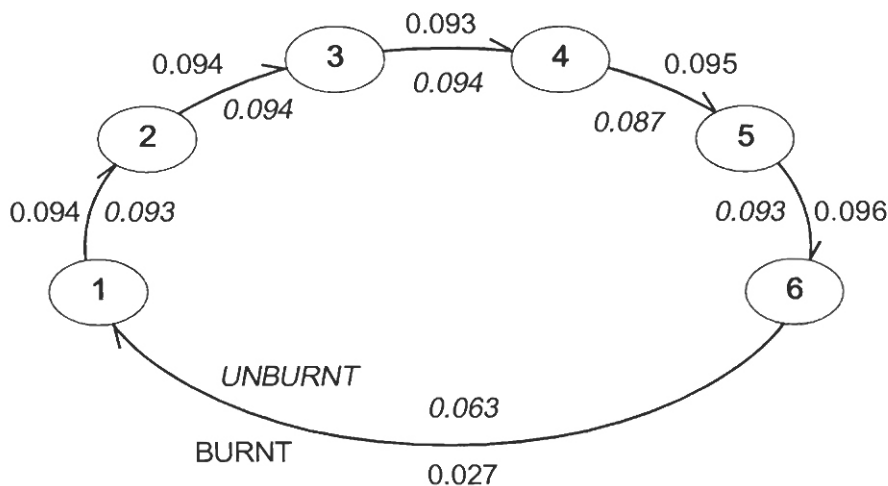


FIG. 3. – Values of sensitivity of population growth rate to transition coefficients in the burnt (outside the graph) and unburnt (inside the graph) models.

because F is a multi-step transition, rather than a matrix element, these elasticities do not sum to 1 and cannot be interpreted as contributions to λ_1 . If we calculated the elasticities of λ_1 with respect to the monthly transitions that make up F , they would all equal $1/12$. That is, because this life cycle contains only a single loop, with no alternative reproductive pathways, each transition makes the same contribution to population growth.

The difference in population growth rate between the burned and unburned treatments integrates the effect of fire exclusion on all the survival and fertility parameters. Indeed, this is one of the main benefits of such an analysis. However, it is also useful to quantify the contributions of each of the survival and fertility rates to the overall effect. To do so, we used LTRE (Life Table Response Experiments) method of CASWELL (1989). If $\Delta\lambda_1$ denotes the difference between the monthly growth rates of burnt and unburnt populations, a first approximation to it is given by

$$(10) \quad \Delta\lambda_1 \cong \sum_{i=1}^5 \Delta P_i \frac{\partial \lambda_1}{\partial P_i} + \Delta F \frac{\partial \lambda_1}{\partial F}$$

Each of the terms in these summations represents the contribution of one of the vital rates to the overall effect on λ_1 .

The contributions of the differences in the vital rates to the effect of fire on population growth, given by the summation terms in equation (10), are shown in table II. About 65 % of the difference between monthly growth rates ($\Delta\lambda = 0.1235$) is contributed by the fertility coefficient. During the plant phase, survival to the first three months contributes more than survival to the last two months.

TABLE II. – Contributions of the differences in the various transition coefficients to the effect of fire on population growth given by equation (10). Terms in parentheses are percents. P_1 to P_5 are transitions during the plant phase; F is fertility.

P_1	P_2	P_3	P_4	P_5	F
0.0102 (8.6)	0.0103 (8.7)	0.0102 (8.6)	0.0027 (2.3)	0.0075 (6.4)	0.0769 (65.3)

These analyses document the differences between the burned and unburned treatments. However, they can also be used to explore the long-term consequences of different frequencies of fire. We approach this problem by constructing the population projection matrix model corresponding to the life cycle graph of figure 1

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

where \mathbf{A} is a 12×12 matrix with the P_i on the subdiagonal in the first 6 columns, and with the subdiagonal in the last 6 columns and $a_{1,12}$ occupied by arbitrary non-negative entries whose product equals the multistep transition F . These matrices are then used to simulate different annual fire regimes with a deterministic model described in SILVA *et al.* (1990). In this model, population growth in an environment with a fire frequency of s/m is given by

$$\mathbf{n}(t+m) = \mathbf{A}_1^s \mathbf{A}_2^{m-s} \mathbf{n}(t)$$

for any value of m , where $\mathbf{A}_1 = \mathbf{B}^{12}$ and $\mathbf{A}_2 = \mathbf{U}^{12}$ with \mathbf{B} and \mathbf{U} being the corresponding projection matrices for the burnt and unburnt populations.

The environment in this model cycles deterministically between s years with fire and $m-s$ years without fire. Following SILVA *et al.* (1991) we also used a stochastic model to generate random sequences of years with and without fire. The model is characterized by the mean frequency of fire and the autocorrelation of fire in successive years. We characterized population growth in this model by the stochastic growth rate (e.g., TULJAPURKAR, 1990).

Figure 4 shows the effects of fire frequency on long-term population growth, according to the deterministic and stochastic models. Both models require a fire frequency of about 0.29 to permit *A. brevifolius* to persist; that is at least one year with fire out of every three years. The autocorrelation has little or no effect on the long-term stochastic growth rate.

DISCUSSION

The effects of fire in savanna ecosystems are complex. Savanna fires kill seedlings (SILVA & CASTRO, 1989) and small trees (FROST *et al.*, 1986), but its absence results in the accumulation of standing necromass, increasing shade and inhibiting grass regrowth. This affects both fertility and survival of perennial grasses (SILVA *et al.*, 1990). Although fire may have other effects, especially on nutrient cycling (MEDINA, 1987), the removal of shading standing mass is probably the most important effect. Our results show that fire exclusion substantially reduces population growth of the annual grass *A. brevifolius*. After two years of fire exclusion *A. brevifolius* populations are declining. In contrast, one burn creates favorable conditions for the population to grow rapidly.

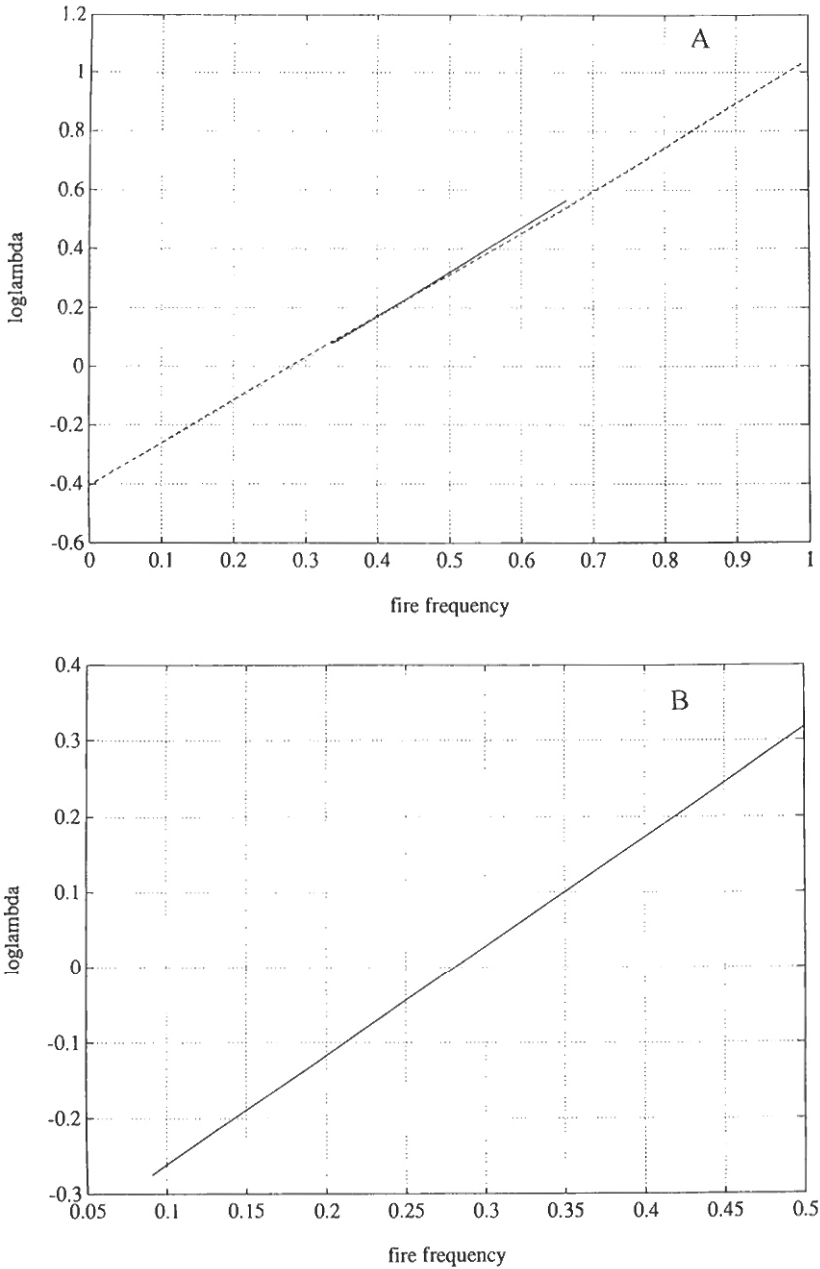


FIG. 4. – Effects of fire frequency on population growth ($\log \lambda$) in an autocorrelated stochastic environment (A) and in a deterministic periodic environment (B). Environmental autocorrelation $\rho = 0.5$ (solid line), 0 (dashed line) and 0.5 (dotted line) produced similar results. (The line for $\rho = 0.5$ is truncated because fire frequencies outside this range are impossible with this autocorrelation.)

In our study, fire exclusion reduced monthly survival probabilities by about 11-12 % in the first three months of life, and by 3-8 % in months 4 and 5. This corresponds to increases in the instantaneous mortality rate of 400-600 % in months 1-3 and 80-170 % in months 4 and 5. Fire exclusion also reduced fertility by about 62 %, through reductions in both seed production and seed-to-seedling survival. Our contribution analysis shows that the reduction in fertility is the most important of these effects, contributing over 60 % of the overall effect on population growth rate. Effects during the plant phase are also important, however, particularly during the first three age classes. This can be contrasted with the results for the perennial *A. semiberbis*, in which only 12 % of the effect of fire exclusion was contributed by fertility reductions, and over 50 % was due to effects on survival and growth of the two smallest size classes in the model (SILVA *et al.*, 1991).

We can say little about the mechanisms by which fertility is reduced by fire exclusion. The decreased seed production could reflect reduced individual growth rates, as reported for perennial savanna grasses (SILVA *et al.*, 1990) and for annual plants from different communities (WATKINSON & HARPER, 1978; Mc CONNAUGHAY & BAZZAZ, 1990; SCHWAEGERLE & LEVIN, 1990). The reduction in the transition from seeds to seedlings could be due to increased mortality during seedling emergence rather than to any effects upon germination. Even small quantities of litter have a negative effect on some grass seedlings (FOWLER, 1988). Microenvironmental light and humidity conditions below the litter in the unburnt plot may increase mortality by favoring the growth of pathogens (SYDES & GRIME, 1981), and the litter itself may mechanically impede seedling emergence (FACELLI & PICKETT, 1991).

According to these analyses, *Andropogon brevifolius* cannot persist without fire. Our models for fire frequency suggest that *A. brevifolius* requires fire at least once every three years. This is less than the frequency (0.83) required by *A. semiberbis* (SILVA *et al.*, 1991). Therefore, *A. brevifolius* seems to be more resistant to fire exclusion than *A. semiberbis*. The latter is an erect, tall grass, very shade-intolerant, whereas the small and slender *A. brevifolius* is more shade-tolerant. However, in agreement with the results of this study, we have observed that this annual grass is able to take quick advantage of disturbances opening gaps in the perennial grass layer.

In this model, sensitivities are inversely proportional to the magnitude of the vital rates and directly proportional to population growth rate (equations 6 and 7). If we reduce the plant phase to a single transition and calculate the sensitivity of λ_1 to this multi-step transition, we can compare the sensitivity of the plant phase to that of the seed phase in both populations, as shown in table III. In both populations, λ_1 is more sensitive to changes in the plant phase than in the seed phase, and that difference is higher in B than in U. It is important to emphasize that whereas fertility contributes the most to the differences between growth rates, both populations are more sensitive to changes in survival. Also, both populations

TABLE III. - Sensitivities of population growth rates to the plant and the seed phases in the burnt and unburnt models, calculated after reducing the plant phase to a single transition.

	burnt (B)	unburnt (U)
to plant phase	0.107	0.155
to seed phase	0.027	0.063

had similar age-specific reproductive values and stable age distribution, showing no effect from burning treatment upon these demographic properties.

Because sensitivities are higher in U than in B, especially sensitivity to changes in the seed phase, population growth of *A. brevifolius* will be particularly susceptible to factors affecting survival or fertility when growing in areas protected from fire. Such analyses may lead to predictions with relevance to applications. For instance, the combination of fire exclusion with grazing late in the growing season should have negative consequences for persistence of the population.

Our results are limited by being restricted to one annual cycle. There is no doubt that vital rates fluctuate from year to year, and it would be important to measure those changes. However, our results strongly suggest that annual savanna grasses, like the dominant perennial grasses, depend on the periodic removal of standing necromass by fire in order to persist. The demographic analysis of more complicated models of annual populations raises interesting questions about sensitivity and elasticity properties which deserve further study.

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