A Publication of the International Association
of Science and Technology for Development - IASTED

The Fifth IASTED International Conference on

MODELLING, SIMULATION, AND OPTIMIZATION

Editor: Giorgio Tonella

August 29 – 31, 2005
Oranjestad, Aruba

ACTA Press

Anaheim | Calgary | Zurich

BN: 0-88986-524-8

Proceedings of the Fifth IASTED International Conference
MODELLING, SIMULATION, AND OPTIMIZATION
August 29-31, 2005, Oranjestad, Aruba

MODELLING THE EFFECTS OF FIRE AND COMPETITION ON THE DYNAMICS OF NEOTROPICAL SAVANNAS: FROM PLANTS TO COMMUNITY

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ABSTRACT

Savannas are one of the most extensive biomes of the world and are subject to intense pressures due to large human populations using this ecosystem, even though it is characterized by low crop yields and poor nutritional quality of natural pastures. Conversion to agriculture and fragmentation of Neotropical savannas, and increasing population pressures are promoting the extent and use of anthropogenic fire.

In this paper we develop a mathematical model to account for spatial dynamics of the savanna grass community. This model is based on a matrix model of growth of three dominant grasses of the Neotropical savanna (*Elyonurus adustus*, *Leptocoryphium lanatum* and *Andropogon semiberbis*). The model integrates plant architecture and competition to simulate the dynamics of this system.

Our model focuses on fire as an essential event in the dynamics of the savanna community, especially frequency of occurrence. We study the current frequency of one fire a year and how changes in fire frequency tend to destabilize the system. The phenology of the species is a key point to understand the behaviour of these species on relation to fire. Late growth species (i.e. *A. semiberbis*) are more adapted to the current frequency than early ones, showing a higher competitive ability.

Our results suggest that if there is a change of the actual fire frequency this system could undergo a decrease of phenological and plant form diversity.

KEY WORDS

Savannas; Matrix model; Fire; Competition; Grasses; Venezuela; Phenology

INTRODUCTION

Savannas are considered one of the largest biomes of the world (ca. 1/6 of the emerged lands). They may significantly feed back to the global climate system since they are characterized by huge energy and water budgets producing considerable emissions of greenhouse gases. Also, savannas are special because of the coexistence of C4-grasses and trees, two usually exclusive life forms. Understanding the savanna ecosystems is a complex problem because we need to integrate the structure (e.g., spatial patterns), the function (e.g., water and nutrient status) and dynamics (e.g., recruitment and growth of plants) of this system [1]. One way to study this complex problem is by means of simulation models (see [2], [3], [4], [5], [1]).

We have undertaken the modelling of one of the two main components of the savanna (grasses) using successive approximations. We began with an individual module model, using Richards' equation to model the elongation of the shoots and leaves, plus some simple geometric considerations to account for both the vertical and horizontal dimensions of three savanna grasses differing in phenology and architecture [6]. Then we converted this individual shoot model to a matrix model to scale up from individual shoots to plants [7], [8]. These three species differ widely in the spatial and temporal patterns of occupation of aboveground space, showing important neighbourhood interference. Consequently, we have recently incorporated the aboveground inter-specific competition into the model. Also, we suggested a possible mechanism for the growth inhibition of the basal meristems by older shoots within the same plant [9].

In this paper we use the competition model to analyse the responses of these three grasses to different regimens of fire that mimic probable scenarios derived from the effect of climate change on savannas ecosystems.

DATA COLLECTION

The field data for this paper came from an earlier study conducted in a savanna near Barinas, Venezuela (8° 38'N, 70° 12'W). Mean annual temperature is 27ºC and mean annual rainfall is 1700 mm, with a rainy season from May to November and a dry season from January to March. Burning usually takes place at the end of the dry season. The selected species are: *Elyonurus adustus* (Trin,) Ekman; (*E*), a precocious bunch grass species that flowers after the annual burning at the end of the dry season. *Leptocoryphium lanatum* (H.B.K.) Nees; (*L*), another bunch grass but with long scleromorphic leaves, is an early species that flowers in May, 1 month after the onset of rains. This species grows and blooms three months after fire, and *Andropogon semiberbis* (Ness) Kunth ; (*A*), an erect and late flowering grass with short leaves that blooms at the end of the wet season (for more details see [10]).

MATHEMATICAL MODEL

Plant growth

We use a projection matrix $\mathbf{M}_U$ ([8]) to project grass growth based on:

$$\mathbf{w}_U(t+1) = \mathbf{M}_U \mathbf{w}_U(t) + \mathbf{w}_U 0 \qquad (1)$$

where U denotes the species that in our case may be 1 (E), 2 (L) or 3 (A), $\mathbf{w}_U(t)$ is a state vector giving the abundance of each height class in time t, and $\mathbf{w}_U\,0$ is the number of new shoots produced in each time interval here corresponding to one month. Using our field data we constructed matrices $\mathbf{M}_1$ for E, $\mathbf{M}_2$ for L and $\mathbf{M}_3$ for A. Each height class is 10 cm.

$$\mathbf{M}_1 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 \\ .18 & .82 & 0 & 0 & 0 \\ 0 & .44 & .56 & 0 & 0 \\ 0 & 0 & .39 & .61 & 0 \\ 0 & 0 & 0 & .07 & .93 \end{pmatrix}$$

$$\mathbf{M}_2 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ .24 & .76 & 0 & 0 & 0 & 0 & 0 \\ .096 & .9 & .004 & 0 & 0 & 0 & 0 \\ 0 & .03 & .52 & .45 & 0 & 0 & 0 \\ 0 & 0 & 0 & .4 & .6 & 0 & 0 \\ 0 & 0 & 0 & 0 & .22 & .78 & 0 \\ 0 & 0 & 0 & 0 & 0 & .07 & .93 \end{pmatrix}$$

$$\mathbf{M}_3 = \begin{pmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ .25 & .75 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1.78 & .11 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & .32 & .84 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & .37 & .63 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & .66 & .34 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & .03 & .97 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & .27 & .73 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & .51 & .49 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & .90 & .1 & 0 & 0 \end{pmatrix}$$

Note that *E. adustus* has only five height classes (maximum height 50 cm), *L. lanatum* has seven height classes (maximum height 70 cm), and *A. semiberbis* has ten height classes (maximum height 100 cm).

Equation (1) can be used to scale up spatially by augmenting the state vector $\mathbf{w}_U(t)$ to obtain a matrix $\mathbf{N}_U(t)$ that gives the number of shoots in each size class (rows) for all the plants of a species along a transect formed by a number of space units (columns). For example, the matrix below gives the number of shoots in each one of five height classes formed by 10 space units (pixels) along a transect.

$$\mathbf{N}_U(t) = \begin{pmatrix} 23 & 0 & 2 & 33 & 9 & 0 & 0 & 16 & 3 & 9 \\ 11 & 0 & 0 & 12 & 5 & 0 & 0 & 8 & 1 & 4 \\ 3 & 0 & 0 & 6 & 1 & 0 & 0 & 3 & 0 & 1 \\ 1 & 0 & 0 & 2 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{pmatrix}$$

In this hypothetical case, $\mathbf{N}_U(t)$ contains plants in only seven pixels whose shoot height structure is given by columns 1, 3, 4, 5, 8, 9 and 10. For example, the plant in pixel one has 23 shoots at first level (height 10 cm), 11 shoots at second level (height 20 cm), 3 shoots at third level (height 30 cm), 1 shoot at fourth level (height 40 cm), and no shoots at the fifth level (height 50 cm).

Matrix $\mathbf{N}_U(t)$ gives the distribution of shoots of each height belonging to different plants of the same species along a linear transect. So, a different matrix, $\mathbf{N}_U(t)$, should be defined for each species. In order to model a two-dimensional space we define a set of matrices matrix $\mathbf{N}^i_U(t)$ formed by several $\mathbf{N}_U(t)$ matrices, one for each pixel or location i of the second spatial dimension. These new matrices could be used to replace the state vector $\mathbf{w}_U(t)$ of equation (1), to obtain a set of equations

$$\mathbf{N}^i_U(t+1) = \mathbf{M}_U \mathbf{N}^i_U(t) \qquad (2)$$

one for each pixel i of the second spatial dimension.

Shoot recruitment

Hereafter operations involving vectors and matrices are performed by pairs of elements. For instance, the product of two vectors **v1** and **v2** (**v1v2**) is obtained by multiplying the first element of **v1** by the first element of **v2** to obtain the first element of the new vector, the second element of **v1** multiplied by the second element of **v2** to obtain the second element of the new vector and so on and so forth.

The recruitment of new shoots by means of the $\mathbf{w}_U 0$ vector in equation (1) is given by the first row of all the matrices which form the matrix $\mathbf{N}^i_U(t)$. This row is the vector $\mathbf{n}_U(t)$ which represents the basal height in the plant.

$$\begin{gathered} \mathbf{n}_u(t+1) = \mathbf{n}_u(t) + n_u 0 - \sum_{V \neq U} \alpha_{uv} \mathbf{n}_u(t) \mathbf{n}_v(t) \\ \mathbf{n}_u(t) > 0, \sum_{i=1}^{3} \frac{\mathbf{n}_i(t)}{k_i} < 1 \end{gathered} \qquad (3)$$

The equation in (3) shows the monthly recruitment of new shoots based on the scalar $n_U 0$ minus the effect of inter-specific competition by means of the coefficient α_{UV}. The inequalities shown that this equation is true only for those values of vector $\mathbf{n}_U(t)$ that are not zero and the sum of the relative values of the species is lower than 1. The first condition implies that there are plants and the second that they do not occupy all the space. Parameter k_i is the maximum number of shoots for species i.

Once recruitment is calculated, vector $\mathbf{n}_U(t)$ is added to the upper row in matrix $\mathbf{N}^i_U(t)$.

Seed dispersal

Once the reproductive month of each species is reached, a fraction of shoots from the largest size (the lowest row in matrix $\mathbf{N}^i_U(t)$) becomes reproductive and therefore is capable to disperse new seeds. We assume seeds are randomly dispersed, and thus we adjust dispersal to a gaussian distribution centered in the reproductive shoot. To simulate seed dispersal we obtain a new matrix $\mathbf{B}_U(t)$ from $\mathbf{N}^i_U(t)$. This new matrix $\mathbf{B}_U(t)$ has zeros where the plants have not reached the highest size (no reproduction takes place) and have ones where the highest size is reached. Using this matrix we calculate seed distribution from all reproductive plants according to the following equation,

$$\mathbf{S}_U(t) = \int_{-\infty}^{+\infty}\int_{-\infty}^{+\infty} \mathbf{B}_U(t) K_D \, dy dx \qquad (4)$$

where $\mathbf{S}_U(,t)$ is the matrix giving the frequency of seed dispersed in each point of the modeled surface and K_D is the kernel of seed dispersal following a bidimensional gaussian distribution:

$$K_D(x,y,t) = \frac{1}{4\pi Dt}\exp\left[-\frac{x^2+y^2}{4Dt}\right] \qquad (5)$$

In this equation, D is the dispersal coefficient.

In fact, in our case the time t has always value 1, because we only take into account dispersion once a year, after the seeds are dispersed by the plant, and the variance of the distribution over time is always the same. So, we can rewrite equation (5) as

$$K_D(x,y) = \frac{1}{4\pi D}\exp\left[-\frac{x^2+y^2}{4D}\right] \qquad (6)$$

The number of seeds of species U in each point of the surface $SN_U(t)$ is attained by multiplying the normalized matrix $S_U(t)$ by the total number of seeds produced by all plants of species U ($N_U(t)$), which comes from the product of ns_U, the average number of seeds per plant, and the number of reproductive plants, nr_U:

$$SN_U(t) = S_U(t) ns_U nr_U \qquad (7)$$

Finally, we calculated the matrix $PG_U(t)$, giving the probabilities of germination of at least one seed in each point of the surface,

$$PG_U(t) = 1-(1-p_U)^{SN_U(t)} \qquad (8)$$

where p_U is the probability of germination of a seed from species U.

RESULTS AND DISCUSSION

This model helps us to understand the response of savanna grasses to different fire frequency regimes. The predictions of climate change for neotropical ecosystems points to an increase in the frequency of events of fire. Usually savannas burn once a year almost every year during the dry season. The modelled dynamics of the three species together showed that under a fire regime of one fire in February of every year the three species coexist (Fig 1 and 2).

We explored the species responses to a fire regime with burning twice in the same year using all sorts of combinations. Table 1 presents the combinations that had a deleterious effect on each species growing alone. Bunch grasses (E and L) have similar response, going extinct only as a result of the combination of a March fire with a fire in any other month, and the combination of an April fire with a fire in any other month of the dry season. On the other hand, the erect species (A) went extinct when fires in August, September or October where combined with another fire taking place in any month of the year. Dry season fires affect more the precocious-early species, and late-season fires affect more the late species. Therefore, the effects of these two types of fires in one year may result from the timing of the fire events rather than from the frequency. We are exploring this possibility but have no results to show yet.

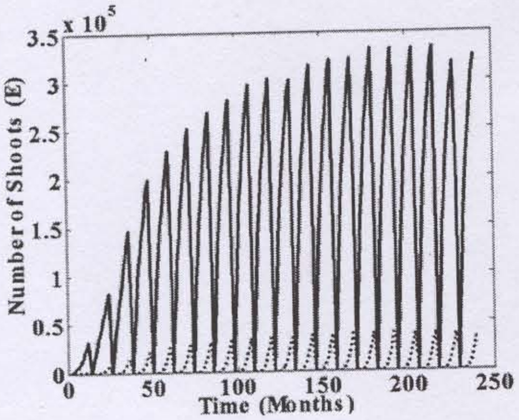
The response of the three species to fire exclusion is presented in Fig. 3. *Andropogon semiberbis* (A), an erect and late flowering species, is the most susceptible to fire exclusion. It occupied little space and soon lost it going virtually extinct. This result agrees with a previous non spatial matrix model simulation on different fire regimes applied to the same species by [11]. The other two species could stand up substantial more years without fire. The hypothesis that basal, precocious and early species (such as *Elyonurus adustus* (E) and *Leptocoyrphium lanatum* (L)) may be more tolerant to fire exclusion than late species was already suggested [12] when comparing the population dynamics of *A. semiberbis* and another precocious species, *Sporobolus cubensis*. Our results emphasize the role of phenology and architecture in the response of savanna grasses to fire regime.

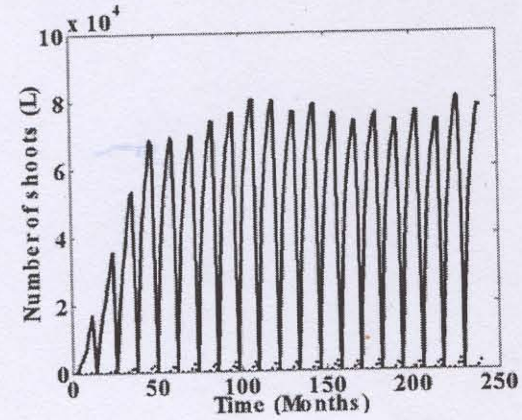
The response of the three species to interspecific competition is presented as the effect of the competition coefficient of one species on the persistence of another species when growing in pairs (Fig. 4). In this competition experiment fire regime was a January fire every year. *A. semiberbis* (A) is a superior competitor over the other two species even at competition coefficients as low as 0.008 shoots^{-1}, and does not suffer any effect from them. *L. lanatum* (L) is the poorest competitor since it has no effect on the other two and suffers the effects of both. *E. adustus* (E) had an important effect on L but no effect on A. Our model output is similar to field results reported by [10] for these three species in an annually burnt savanna.

As a general conclusion, our model shows different responses of these three grass species to fire regime and competitive ability, and these responses seem related to phenological and architectural differences between the species. The three species seem to be well adapted to an annual fire regime taking place in the dry season and coexist under these circumstances, although they differ in their responses to inter-specific competition. On the other hand, they showed different ability to cope with fire exclusion, which would be more detrimental to the erect, competitively superior species than to the bunch grasses. A possible way to explore the coexistence of these grass species in the savanna may be based on the paradigm of competition and disturbance if we consider exclusion of fire as a recurrent uncommon perturbation. Biodiversity of the grass layer in savannas is indeed important and relevant from the point of view of land use. Understanding the responses of these communities to global change, and the mechanisms underlying these responses, is important from a theoretical but also from a practical point of view.

Table 1. Combinations of months with fire events resulting in local population extinction of species *E* and *L* and *A*. All other combinations did not result in local extinction.

	L and *E*		*A*			
	MAR	APR	JUL	AUG	SEP	OCT
JAN	X	X		X	X	X
FEB	X	X		X	X	X
MAR	X	X		X	X	X
APR	X			X	X	X
MAY	X		X	X	X	X
JUN	X		X	X	X	X
JUL	X		X	X	X	X
AUG	X		X	X	X	X
SEP	X		X	X	X	X
OCT	X		X	X	X	X
NOV	X		X	X	X	X
DEC	X	X	X	X	X	X





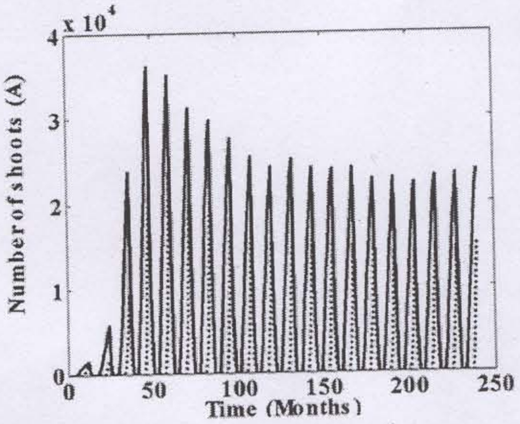


Fig 1. Shoot density dynamics of the three species (E, L, and A) during a 20-year period under a fire regime of one annual fire every February. Continuous line is for basal level shoots and dotted line means top-level shoots.

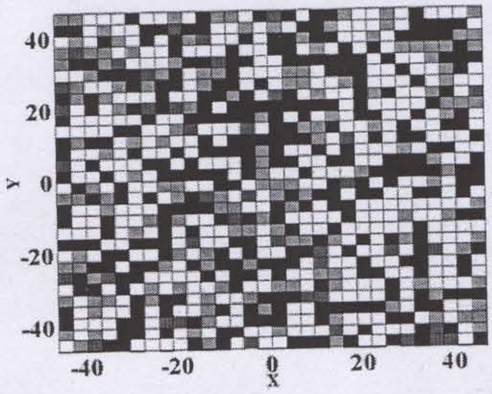


Fig 2 Spatial distribution of the three species (E=black, L=light gray, A=dark gray) and bare soil (white) at the end of the simulation

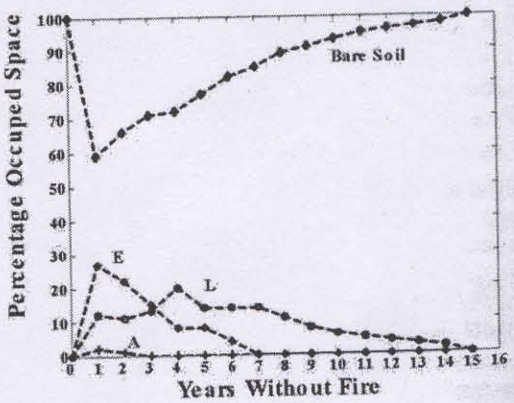


Fig 3. Dynamics of occupied space under a fire-exclusion regime.

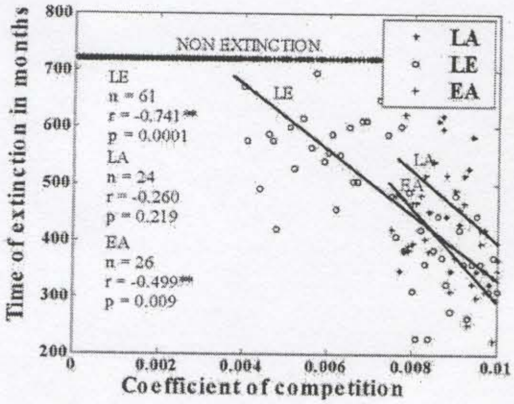


Fig 4. Regression of time to population extinction as a function of competition intensity. Only the three cases of competitive exclusion are shown. In each pair the first letter denotes the target species and the second letter the competitor species. *L= L. lanatum; E= E. adustuts; A= A. semiberbis*. n = number of cases when the target species goes extinct; r = coefficient of correlation; $p^* < 0.005$ and $p^{**} < 0.001$.

IMPLICATIONS FOR LINKING WITH SOCIAL SYSTEMS

Almost one-fifth of the world's population lives in areas that are at present, or were recently, covered with savanna vegetation ([13], [14]). Per capita food production in these communities is usually low because rainfall in these regions is highly seasonal and variable. Primary production is uneven and unpredictable in space and time, reflected in low crop yields and poor nutritional quality of natural pastures. Most savanna soils are nutrient-poor, and that in turn is translated in low crop yields and poor nutritional quality of natural pastures. In the last decade these ecosystem has been undergoing pressure from rapid growth of human population that in turn has changed the traditional land use of extensive cattle grazing to high-input cash crops [15].

Conversion to agriculture and fragmentation of Neotropical savannas, and increasing population pressures are promoting the extent and use of anthropogenic fire. [16] showed that the tropical savanna fires account for the majority of fires globally. Land use changes are also encouraging invasion by exotic species, especially African grasses such as *Hyparrenia rufa* that are aggressively displacing native species and reducing biodiversity

There is a long list of publications on the effect of fire and fire regime on savannas (see for instance [17]). In African savannas as well as in Neotropical savannas there are reports of increasing tree cover at the expense of grassland cover, even under regular annual fire ([18], [19], [20]). However, the long-term experiments suffered from design problems and furthermore, there is scarce information about the effects of repeated fires on the savanna grass layer, specially studies taking into account phenological and architectural parameters

CONCLUSIONS

Mathematical models are very useful tools for integrating the empirical and field data, in order to discover the hidden relations between the components of the system, and make predictions about different scenarios.

Our model can be expanded to include a higher number of grass species, taking into account explicitly their structure and phenology.

We focused in two aspects: the competition between dominant grasses of the savanna and the effect of fire on their dynamics, because both aspects are intimately linked.

Our model suggest that with the usual frequency of fire (more or less, once a year), the late-growth species (*A. semiberbis*) is the better adapted, and the other two (the precocious *E. adustus* and the intermediate *L. lanatum*) have poor competing ability. However, confronted with scenarios of less frequency of fire, *A. semiberbis* is the most vulnerable. In fact, this species becomes extinct only with a frequency less than one fire every two years.

We examined the effects of an increase in fire frequency as a possible consequence of climate change. Our model predicts extinction of some species with two fires in one year, which impede formation of flowering shoots deterring sexual reproduction.

ACKNOWLEDGMENTS

We thank Miguel F. Acevedo, special session organizer, for constructive and useful comments and feedback. This work was partially supported by NSF INT-0104728 for US-Spain Cooperative Research.

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