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J. Raventós

M. F. Acevedo

J. Segarra

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J. Raventós[1], M. F. Acevedo[2] and J. Segarra[1]

[1]*Departamento de Ecología, Universidad de Alicante, Alicante, España (Jraventos@ua.es)*

[2]*Institute of Applied Sciences and Department of Geography, University of North Texas, Denton, Texas 76203 (acevedo@unt.edu)*

Abstract: We developed a model of grass plant growth as a collection of the individual dynamic behavior of shoots inspired in data for plants of three species (*Elyonurus adustus*, *Leptocoryphium lanatum* and *Andropogon semiberbis*) of common grasses in the Venezuelan savannas. These species represent various types of architecture and regeneration response to fire. The individual-shoot model is based on shoot emergence, mortality, and elongation given by Richards' equation, plus a few simple geometric considerations. Model output is shoot density in each cell of a square grid at several vertical levels. Differences in patterns of shoot density among species are explained by changing a set of parameter values related to growth form and phenology. Vertical distribution of shoot density was calculated from the simulation results and the field data with the purpose of deriving a simpler lumped shoot-population model. This simpler demographic model is based on a projection matrix that predicts the essential dynamics of growth in the vertical dimension. The final and transient behavior of vertical distribution of shoot density are calculated with the matrix model and compared to field data yielding good fit. The matrix model can be used for scaling-up the individual-shoot model to larger areas, or applied to generate plant functional types for analysis of savanna dynamics subject to fire.

Keywords: grass plants; savanna; individual-based models; matrix models

1 INTRODUCTION

Savannas are very important tropical ecosystems characterized by co-dominance of herbaceous vegetation and less abundant trees and shrubs. Aboveground vegetation cover is strongly influenced by climate, herbivores and fire [Walker 1987, Skarpe 1996]. Studies of herbaceous vegetation have focused on demography of plant components [Harper et al. 1986] as well as their arrangement in horizontal and vertical dimensions [Raventós and Silva 1988]. Competition for belowground resources in grassland models has been recognized as a determinant process in community composition [Coffin and Lauenroth 1990].

Competition for light has been less emphasized in modeling efforts, although it also determines important properties of plant growth and dynamics, such as shoot survivorship [Raventós and Silva 1988]. In addition, aboveground distribution of plant components affects fire intensity and propagation and, in turn, fire regime is one of the main determinants of tropical savanna dynamics. Therefore, there is a need for models explaining how the dynamics of individual aboveground components link to the architectural expression of grass plants in the vertical and horizontal dimensions.

In a previous paper [Acevedo and Raventós 2002] we developed an individual-shoot model to analyze seasonal aboveground growth dynamics of perennial tropical grass plants. In that paper, a grass plant is modelled by a population of modules (shoots, leaves and flowering shoots) developing in both spatial dimensions. Our aim in this paper is to scale up from this previously developed mechanistic individual-shoot model by building simple transition models capable of predicting vertical distribution of shoot density.

2 DATA COLLECTION

We use data from a study conducted in a savanna near Barinas, Venezuela (8° 38' N, 70° 12' W). This area is subject to frequent burning. Mean annual temperature is 27° C 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 once a year, during February and April, before the onset of the rainy season. We selected three species with different phenologies and architectures: 1) *Elyonurus adustus*, a precocious grower with long and slender leaves b) *Leptocoryphium lanatum*, another bunch grass but with long scleromorphic leaves, c) *Andropogon semiberbis*, an erect and late flowering grass with short soft leaves. These

species represent different plant functional types [Smith et al. 1993].

Three individuals (replicates) of each species were measured using a structure in which we could set a horizontal frame of 225 (15x15) cells of 5x5 cm at different heights. For one year, we performed monthly measurements from 10 to 100 cm above ground at 10 cm intervals (vertical levels). The maximum number of levels achieved by a plant during the year varies by replicate and species; typically five levels for *E. adustus*, seven for *L. lanatum*, and ten for *A. semiberbis*.

For each level and cell, module density was obtained by counting all module intersections with the grid. This was repeated every month from September 1984 to August 1985, except July 1985. Fire occurred sometime after the January 1985 measurement, and thus the data for February 1985 yield non-zero values only in the first level. Details on sampling method are described by Raventós and Silva [1988].

3 MECHANISTIC MODEL

In Acevedo and Raventós [2002] we demonstrated that an individual-based model including shoot emergence and mortality, shoot and leaf elongation and geometrical arrangement can explain the dynamics of the horizontal and vertical distribution given by the data described in the previous section. Each shoot and leaf is considered to grow in length according to the Richards' differential equation [Causton and Venus 1981]. A number of shoots are converted into flowering shoots. Height and horizontal distance reached at any time by a point on a shoot are a function of its length and elevation angle attained by the shoot with respect to ground (using the sine and cosine of this angle). The shoot elevation angle was assumed to vary from 90° to a minimum elevation angle (a species specific parameter).

A shoot generates one leaf at the end of each inter-node length. Leaf elevation angle is less than the corresponding shoot elevation angle; a minimum leaf elevation angle is established as a parameter; but the maximum angle is a function parameterized by the difference between the minimum angle and the shoot angle. A power function accounts for increasing curvature radius with decreasing elevation angle that varies from 1 to the maximum horizontal extent that would occur at the minimum angle. The radius of curvature is a parameter of a parabolic function to relate leaf height and horizontal projection to a given point of the leaf.

The slope of the leaf at any particular time is given by the derivative of the rate function of the logistic equation. For the horizontal distribution, an azimuth angle was used and the coordinates of any point of the leaf or shoot were calculated using spherical coordinates. The elevation angle for each shoot and its leaves, as well as azimuth angle were chosen at random from a uniform distribution. All shoots were initialized with a height equal to 0.1 m and the corresponding shoot length was held constant during a fixed time lag or latency to start growth to the second vertical level. During the senescence months shoots were removed randomly with probabilities assigned as parameters. Also, shoot generation stops at the beginning of this period.

As shoots and leaves elongate and increase in height, they intersect the model grid at different height levels and cell coordinates and are counted to derive a simulated module density at each cell for each level i at month t. We then summed the number of shoots and leaves in all cells of each level i for each month t to obtain a simulated total module density $n_{i,t}$ for the level and month. The total in each level $n_{i,t}$ is divided by the total of all levels $i=1,\ldots,K$ for the month t to obtain proportions $P_{i,t}$ by level, where K is the maximum number of levels for the species.

4 MATRIX MODEL

Right after a fire event (February), all proportions $P_{1,1}$ are equal to 1, i.e. all shoots are at level 1. This proportion decreases with time while the other proportions gradually increase (Figures 4-6). By January the following year, right before the next fire, the proportions $P_{i,t}$ reach a final distribution similar among data replicates and different among species (Figures 1-3). This behavior is simulated rather well by the individual-module model described in the previous section.

In this section we explore the possibility of explaining the vertical distribution of module density by a simpler matrix model with entries given by the month-to-month transitions of modules from one level to the next

$$\mathbf{n_{t+1}} = \mathbf{Mn_t} + \mathbf{s_t} \qquad (1)$$

where $\mathbf{n_t}$ is the vector of module density (with entries given by densities $n_{i,t}$ at each level i) with dimension K, $\mathbf{M}$ is a transition matrix with entries representing the transition from level i to level j, and $\mathbf{s_t}$ is vector of shoot emergence defined as $\mathbf{0}$ for $t \le t_1$ and $\mathbf{s}$ for $t > t_1$. Where t_1 is the latency (in months) in shoot emergence incorporated in the individual-based model. Only the first position of $\mathbf{s}$ is non-zero and represents emergence at first level. All other entries are equal to zero. The first entry of $\mathbf{M}$ is made equal to 1 in order to hold all shoots generated at the first level constant from one month to the next.

The entries of the transition matrix were determined from runs of the individual-based model by calculating the fraction $q_{i,j}$ of modules that move from level i to level j at one-month time intervals. We considered the possibility that a module could stay at the same level or step to the level immediately above or step two levels at a time. In this last case, we must take into account that to pass from level i to level $i+2$ the module must go through level $i+1$.

The coefficients of the transition matrix are calculated from the $q_{i,j}$ values. Using the above example with a species that could reach two levels from one month to the next, we will have

$$
\begin{aligned}
n_{1,t+1} &= n_{1,t} \\
n_{2,t+1} &= n_{2,t} + (n_{1,t} - n_{2,t})q_{1,2} \\
&= n_{1,t}q_{1,2} + n_{2,t}(1 - q_{1,2}) \\
&\ldots \\
n_{i+1,t+1} &= n_{i-1,t} + (n_{i-1,t} - n_{i,t})q_{i-1,i+1} \\
&\quad + (n_{i,t} - n_{i+1,t})(1 - q_{i,i+1})
\end{aligned}
\tag{2}
$$

From these equations we obtain different transition matrices depending on the phenology and architectural arrangement of the aerial part of these grass species.

For *E. adustus* and *L. lanatum* every shoot has only one leaf generated at level 1; the resultant transition matrices are

$$
\mathbf{M} = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 \\
.17 & .83 & 0 & 0 & 0 \\
0 & .38 & .62 & 0 & 0 \\
0 & 0 & .31 & .69 & 0 \\
0 & 0 & 0 & .05 & .95
\end{pmatrix}
\tag{3}
$$

and

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

respectively. The emergence vectors are

$$
\mathbf{s} = \begin{bmatrix} 80 & 0 & 0 & 0 & 0 \end{bmatrix}^T
$$
$$
\mathbf{s} = \begin{bmatrix} 50 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}^T
\tag{5}
$$

for *E. adustus* and *L. lanatum* respectively. Here T denotes transpose. The latency is $t_1=2$ months for both species.

The architecture of *A. semiberbis* is more complex because shoots can produce more than one leaf, and leafing occurs at several levels. We have a system of equations defined by:

$$
\begin{aligned}
\mathbf{n}^v_{t+1} &= \mathbf{M}_v \mathbf{n}^v_t + \mathbf{s}^v \\
\mathbf{n}^f_{t+1} &= \mathbf{M}_f \mathbf{n}^f_t + \mathbf{s}^f \\
\mathbf{n}^l_{t+1} &= \mathbf{M}_l \mathbf{n}^v_t \\
\mathbf{n}_t &= \mathbf{n}^v_t + \mathbf{n}^f_t + \mathbf{n}^l_t
\end{aligned}
\tag{6}
$$

where the vectors $\mathbf{n}^v_t$, $\mathbf{n}^f_t$, $\mathbf{n}^l_t$ refer to the number of vegetative shoots, flowering shoots and leaves respectively, all at time t; the matrices $\mathbf{M}_v$, $\mathbf{M}_f$ and $\mathbf{M}_l$ apply to the projection of each one of these types of shoots; $\mathbf{s}_v$ and $\mathbf{s}_f$ are emergence vectors for each type of shoot. We obtained the following values for each one of these matrices

$$
\mathbf{M}_f = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
.28 & .72 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
.05 & .94 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & .50 & .50 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & .33 & .67 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & .75 & .25 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & .25 & .75 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & .50 & .28 & .02 & -.65 & .85
\end{pmatrix}
\tag{7}
$$

$$
\mathbf{M}_v = \begin{pmatrix}
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
.13 & .87 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
.03 & .97 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & .50 & .50 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}
\tag{8}
$$

$$
\mathbf{M}_l = \begin{pmatrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{pmatrix}
\tag{9}
$$

and

$$
\mathbf{s}v = \begin{bmatrix} 15 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}^T
$$
$$
\mathbf{s}f = \begin{bmatrix} 20 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix}^T
\tag{10}
$$

The latency is $t_1=6$ months. We have used three matrices to simulate three different processes. The structure of the $\mathbf{M}_f$ matrix is equivalent to the one for *E. adustus* and *L. lanatum*. The structure of $\mathbf{M}_l$ shows that leaves are produced at several levels.

5   RESULTS AND DISCUSSION

In this section we discuss the results obtained by simulating proportions $P_{i,t}$ using the matrix model. We will discuss the simulated final (12 months after the fire) and transient behavior.

5.1   Final distribution

The *E. adustus,* the transition matrix **M** has only elements on the principal diagonal (shoots remaining on the same level) and on the sub diagonal (shoots stepping up one level at a time). The same was truth for *L. lanatum* except for the extra elements on levels 1 and 2 accounting for shoots promoted two levels at a time. For *E.adustus,* the values of the estimated coefficients
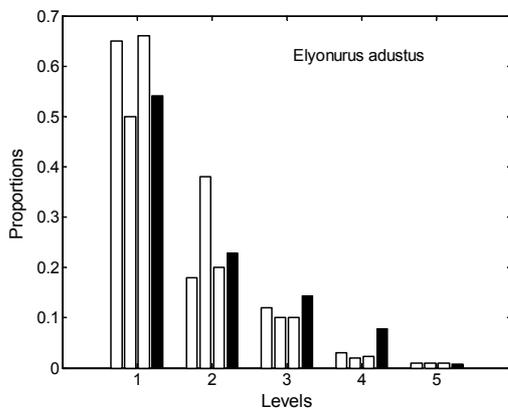
Figure 1. *E. adustus* comparison of final distribution obtained by matrix model (black bars) against observed data (white bars).
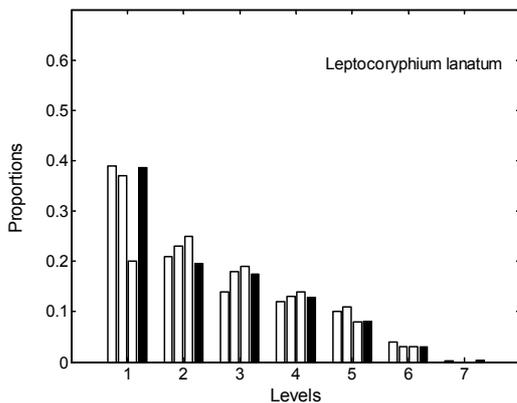

Figure 2. *L. lanatum* comparison of final distribution obtained by the matrix model (black bars) against observed data (white bars).

decrease with increasing height.

For these two species, modules remain on the same level or pass to the following level. For *E. adustus,* the coefficients in the diagonal show higher values,

leading to higher proportions at lower height levels (Figure 1). However, for *L. lanatum,* transitions from levels 2 and 3 have higher values, leading to a less pronounced difference in proportions with height (Figure 2). The two species show a good fit between modeled vertical distribution and the field data. Also, for these two species only one type of module suffices to fit the data.
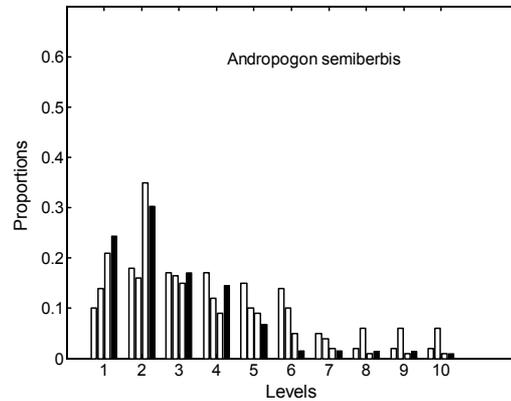

Figure 3. *A. semiberbis* comparison of final distribution obtained by the matrix model (black bars) against observed data (white bars).

A. semiberbis shows a different pattern (Figure 3). The higher proportions at level 2 when compared to level 1 are due to the additional process of leafing at the 2 and 3 levels (Figure 3). Variability among replicates is higher in *A. semiberbis* than *E. adustus* and *L. lanatum.* These results emphasize the different architecture of leafing in *A. semiberbis* compared to *E. adustus* and *L. lanatum*.

5.2   Transient behavior

Figures 4, 5 and 6 show the dynamics of proportions $P_{i,t}$ of vertical distribution for the average of the three field data replicates starting in February (month 1 in X axis, that is right after the fire event) and ending in January the following year (month 12 in X axis, that is just preceding the next fire event). No values are shown for July (month 6 in X axis) because data were not collected that month. The corresponding simulated dynamics by the matrix model are shown in Figure 7, 8 and 9. The simulated curves fit the data relatively well but with some exceptions.

For *E. adustus,* the transients for all levels are well characterized by the model. For *L. lanatum,* at levels 2 and 3 the model underestimated the sudden initial pulse of growth after the latency. For *A. semiberbis,* level 2 shows a sudden increase at month 6 after the latency. Level 3 shows a lower increase in the model than in the data. Goodness of

fit was assessed by calculating root mean square (RMS) errors between the data and the values simulated by the matrix model. For the three species the error between replicates are of the same order of magnitude that the obtained by the matrix model (Table 1). In general the RMS error between the model and replicates are of the same magnitude that the RMS among field replicates.
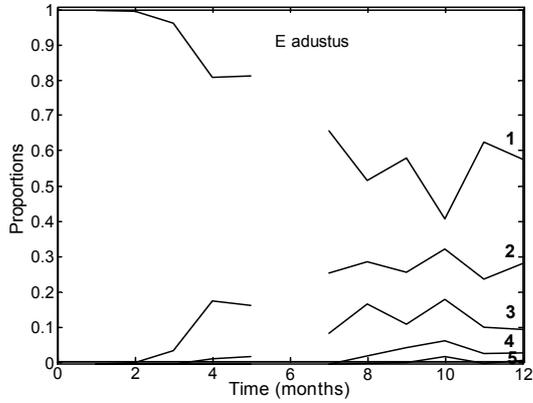
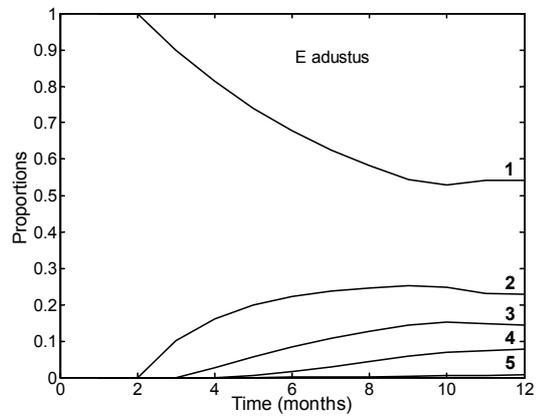**Figure 4.** Observed transients of vertical distribution for *E. adustus.*

Figure 7. Simulated transients of vertical distribution for *E. adustus.*
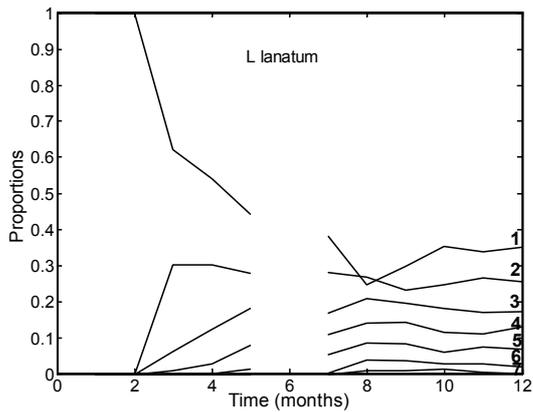
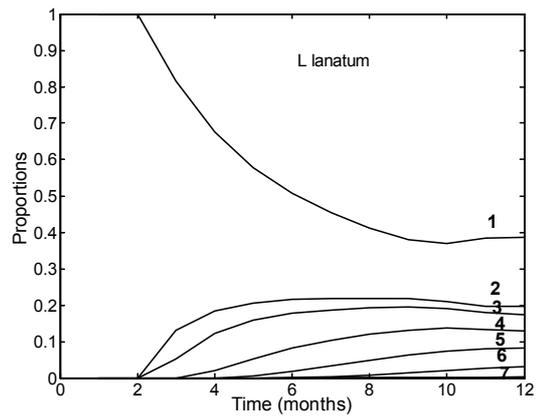**Figure 5.** Observed transients of vertical distribution for *L. lanatum*

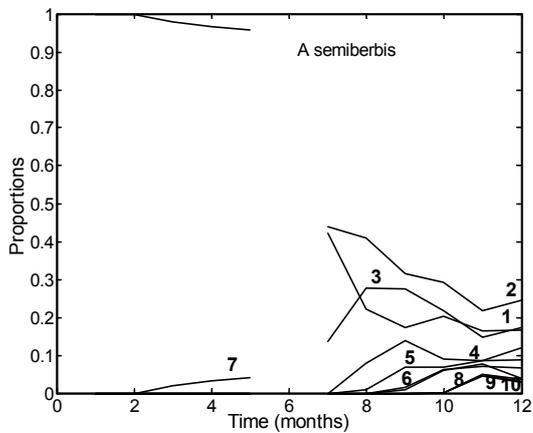**Figure 8.** Simulated transients of vertical distribution for *L. lanatum.*

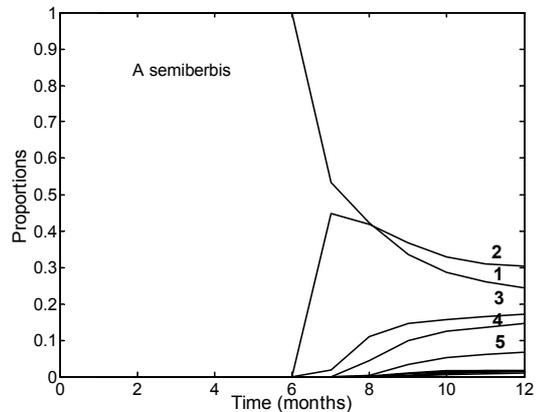**Figure 6.** Observed transients of vertical distribution for *A. semiberbis.*

Figure 9. Simulated transients of vertical distribution for *A. semiberbis.*

Table 1. Comparison of RMS error between field data replicates and matrix model (m).

	E. adustus rms	L. lanatum rms	A. semiberbis rms
Replicate 1vs 2	-	28,6	-
Replicate 1vs 3	-	108,2	-
Replicate 2vs 3	95,6	112	21
Replicate 1vs m	-	51	-
Replicate 2vs m	84	56	24
Replicate 3vs m	123	87	21

6 CONCLUSIONS

Starting with runs of an individual-shoot mechanistic model, we have developed a simplified discrete-time matrix model. The resulting matrix structure has direct connection to the architecture of the three species. *E. adustus* and *L. lanatum* have similar architecture, with shoot emergence and leafing at basal level, lower stature plants, higher shoot density and early or precocious growth after the fire. The different values of coefficients obtained for *E. adustus* and *L. lanatum* reflect architectural differences between these two species. The lower transition coefficients of *E. adustus* reflect a bunch grass with curved shoots. The higher transition coefficients of *L. lanatum* reflect a taller grass with straight shoots.

A. semiberbis is different from both *E. adustus* and *L. lanatum*. The higher values for transition coefficients at all levels are due to taller plants and lower shoot density. Extra matrices were required for *A. semiberbis* due to leafing at different levels. This architecture is more complex than *E. adustus* and *L. lanatum*.

The final vertical distribution of shoots of individual plants can be predicted rather well from a simple matrix model based on level-to-level transitions. However, the simulated transients yield higher errors. The matrix models integrate information on architectural design, conspecific interactions and fire response. Our data include population responses to fire [Silva et al. 1991], competition effects and responses to a variable number of neighbors [Raventos and Silva 1995] and herbivory [Silva and Raventos 1999] for some of these plant functional types. This information can be incorporated in our individual-shoot models and then simplified into matrix models that could be used in analysis of savanna dynamics subject to repetitive fire events. Our current efforts include incorporating competition among plant functional types with different number of neighbors. The approach proposed in this paper is potentially applicable to other grass plants and other grassland ecosystems.

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