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MODELLING RESPONSES OF SAVANNA GRASS SPECIES TO WATER SUPPLY AND COMPETITION

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ABSTRACT
Neotropical savannas are one of the largest biomes in the world. These ecosystems are composed basically of trees and codominant grasses. In this paper we simulate the effect of soil moisture on the growth of three different phenological and architectural savanna grasses when these species grow alone and in pairs. Rainfall simulation is performed based on historical data. We also examined the effect of soil moisture potential decrease to 20% of the usual soil moisture. The results show that when growing alone *Andropogon semiberbis* (A), a late erect species, is the one most affected by this soil moisture decrease. When growing under competition we found a clear relation between phenology and competition ability of these grasses. The late species (A) is the best competitor, and displays a larger decrease in the number of shoots than the other two species *Elionurus adustus* (E) and *Leptocoryphium lanatum* (L), and is less affected by these two other species. The contrary is true for the precocious species (L). There seems to be a trade off between the ability of competition and the ability to withstand a decrease of soil moisture of these codominant grass species. This trade off could be a key point explaining the coexistence of these three different phenological and architectural savanna grasses.

KEY WORDS
soil moisture, niche differentiation, fire, phenology, plant architecture

1. Introduction

Savannas are considered as one of the largest biomes in the world (ca. 1/6 of the emerged lands). Almost one-fifth of the world's population lives in areas that are at present, or were recently, covered with savanna vegetation ([1],[2]). Grasses from Neotropical savannas differ in the patterns of shoot biomass production. Several phenological groups based on flowering time can be distinguished [3]. These phenological differences in the pattern of shoot growth and the time of flowering are related to other traits such as above-ground architecture and competitive ability ([4]). Furthemore, these phenophases of shoot growth seem to depend on soil moisture, which in turn depends on seasonal rainfall and the capacity of the soil to store water. All of this taken together could allow for further differentiation along other axes of their "regeneration niche" (sensus [5]) and permit the existence of the Neotropical savanna ecosystem with codominant savanna grasses.

Despite the importance of soil moisture effects on vegetation dynamics, using real data to simulate long-term fluctuation in rainfall have not been quantitatively incorporated in existing models of savanna dynamics with the exception of few papers (i.e. [6]). In recent years, we built a modular model to simulate the structure and dynamics of a Neotropical savanna. As a first step, we created an individual-based model for shoots based on Richard's equation ([7]) that allowed us to model the different architecture and phenologies of the grasses just by changing the values of certain parameters. The second step involved scaling up this individual-based model to using simple matrix models ([8]). These two models did not explicitly take into account the level of competition among grasses. Our next step was to incorporate aerial competition ([9]) and the effect of fire depending on the timing and the phenology of the grass species ([10]). In this paper we modify the previous models by adding the dynamics of soil water and developed a mechanistic model coupling rainfall, soil water availability, phenology and architectural design using three different savanna grasses. The aim of this model is to integrate the process of competition for soil moisture using real long-term rainfall to understand the coexistence of Neotropical savanna grasses differing in phenology and plant architecture. We also want to simulate possible responses of these codominant grass species to diminishing water supply during the growth season which may eventually result from climatic change ([11]).

2. Material and Methods

2.1. Data collection:

The field data was collected in a seasonal open savanna located near the city of Barinas, Venezuela (8º 38'N; 70º 12' W). The mean annual temperature is 27ºC and the average annual rainfall is 1500 mm, with a wet season between May and November and a dry season from January and March. April and December are transitional months. We selected three perennial different codominant savanna grasses with different flowering phenologies: *Elionurus adustus* (E), a precocious bunch grass species that flowers after the annual burning at the end of the dry season; *Leptocoryphium lanatum* (L), an early scleromorphic bunch grass that flowers in May, one month after the onset of rains; and *Andropogon semiberbis* (A), an erect late species that flowers in November.

3. Model of water dynamics in a neotropical savanna

We used moisture balance equation at a site

$$wZ_r \frac{ds(t)}{dt} = I(s,t) - E(s,t) - L(s,t) \qquad (1)$$

Where:
w: Porosity;
Zr: Depth of soil;
s(*t*): Relative soil moisture content;
I(*s,t*): Infiltration rate from rainfall;
E(*s,t*): Evapotranspiration rate;
L(*s,t*): Leakage or deep infiltration rate.

To simulate rainfall we have used monthly precipitation data from 34 meteorological stations near Barinas, Venezuela. The average length of the precipitation series was 30 years. The data were first tested for homogeneity ([12]) and shown to fit reasonably well to a gamma distribution (Fig. 1). We used this gamma distribution to simulate the monthly precipitation for five year simulations

$$f(h) = \frac{\alpha^p}{\Gamma(p)} e^{-\alpha h} h^{p-1}$$

Where:
f(h) is the probability to obtain the total rainfall *h* in a given month;
$\Gamma(p)$ is an Euler gamma function;
α and p are parameters calculated from the sample mean ($\bar{h}$) and sample variance (s_h) of precipitations defined as:

$$\alpha = \frac{\bar{h}}{s_h}$$

$$p = \frac{\bar{h}^2}{s_h}$$

The amount of rainfall that infiltrates into the soil is assumed to be equal to the depth of rainfall minus the runoff. To obtain an estimate of the monthly precipitation we generated a random number (rn) uniformly distributed on the interval [0,1]. This number is used to generate a gamma distributed rainfall by assigning it as the portion of area under *f(h)* from zero to h_{month} value. That means h_{month} is the value of rainfall for this month.

$$\int_0^{h_{month}} f(h)dh = rn$$

From this estimate we subtracted a constant rainfall threshold, 0.05 cm, to account for the interception parameter ([13]), which we held constant. In future developments, interception will be made a function of shoot density. If the effective rainfall (value after interception) is less than zero, then we make effective rainfall it to zero. As a final step, we divide by wZ_r, the maximum quantity of soil moisture, to normalize the input of soil moisture that can be hold by the soil profile. If rainfall exceeds the infiltration volume, runoff is generated.

To model the losses of the system (Evapotranspiration and Runoff) we follow [13], who model the losses of water by the soil under five different moisture soil conditions.

$$\rho(s) = \frac{\chi(s)}{wZ_r} = \frac{E(s) + L(s)}{wZ_r}$$

$$= \begin{cases} 0, & 0 < s \le s_h, \\ \eta_w \dfrac{s - s_h}{s_w - s_h}, & s_h < s \le s_w, \\ \eta_w + (\eta - \eta_w)\dfrac{s - s_w}{s^* - s_w}, & s_w < s \le s^*, \\ \eta, & s^* < s \le s_{fc}, \\ \eta + m\left(e^{\beta(s - s_{fc})} - 1\right), & s_{fc} < s \le 1, \end{cases}$$

Where:
η_w η m are normalized quantities

$$\eta_w = \frac{E_w}{wZ_r}, \qquad \eta = \frac{E_p}{wZ_r},$$

$$m = \frac{K_s}{wZ_r\left(e^{\beta(s-s_{fc})}-1\right)}.$$

s_{fc}: Soil field capacity
s_h: Hygroscopic Point or soil moisture level below which water can not be extracted from the soil through evaporation.
s_w: Permanent Wilting Point or soil moisture level below which plants stop transpiring and begin to wilt. (following [13]).
s^*: Soil moisture level below which plants begin closing their stomata.

We numerically integrated equation (1) using Matlab's ode45 method with a time step of one day. Daily rainfall is assumed to be a marked Poisson process in time, characterized by the average daily rainfall value. For simplicity and due to lack of daily climate data, we used a Poisson distribution to obtain the daily rainfall. The average daily rainfall was assumed to be equal to the monthly rainfall divided by the number of days of the month. We generate another uniformly distributed random number rn in [0, 1], and use it to assign the daily rainfall, h_{day}, satisfying

$$\int_0^{h_{day}} p(h)dh = rn$$

Where:
$p(h)$ is the Poisson probability density.

The evapotranspiration rate per plant, Ep, is a function of the number of shoots (n_s) per plant following the equation

$$E_p = n_s E_s$$

Where
E_s: Rate of evapotranspiration per shoot (cm d^{-1}).

The water absorption pattern per plant is defined by a normal distribution

$$D_N = \frac{e^{-(x)^2/2\sigma_a^2}}{\sigma_a\sqrt{2\pi}}$$

Where
x: Spatial coordinate (cm).
σ_a: Standard deviation of water absorption by plants.

The convolution between this normal distribution and the evapotranspiration rate of the plant at position x_i allow us to know the pattern of water absorption for an isolated plant i.

$$P_i = \int_{-\infty}^{\infty} E_{pi} D_N dx$$

To determine the absorption of water for all the plants we made a convolution between the normal distribution and the spatial pattern of evapotranspiration rate. That means the amount of ovelap of one function (E_{pT}) as it is shifted over the other function (D_N).

$$P_T = \int_{-\infty}^{\infty} E_{pT} D_N dx$$

Then the quantity of water absorbed by the plant i on the point x is given by:

$$A_i(x) = s(x)\frac{P_i(x)}{P_T(x)}$$

The above equation allowed us to calculate the soil moisture shared among two or more plants that are on the same neighbourhood as a function of the water absorbed by each plant.

3.1. Shoot growth: According to our previous works ([8], [9]) the monthly shoot growth follows a Richard equation (for more details see [10]).

$$\frac{dn_s}{dt} = \frac{r}{g} n_s \left(1 - \left(\frac{n_s}{K}\right)^g\right) \quad (2)$$

For this case we have used the solution of (2)

$$n_s = K\left(1+\exp(\beta - rt)\right)^{-1/g}$$

Where β is one auxiliary variable which value is given by

$$\beta = \ln\left(\exp\left(g \ln\frac{K}{n_s}\right) - 1\right)$$

r: Rate of regrowth of new shoots
K: Maximum number of shoots
g: Parameter of Richard's equation
The simulation time is one month, because is the calculated monthly increase in number of shoots and the parameters on this equation were measured in the field with this periodicity.

3.2. Shoot mortality: Shoot mortality begins for a plant when the soil moisture drops below the wilting point (s_w). At this point, the number of shoots loses is proportional to the difference $(s_w - s(t))$ according to the following equation:

$$n_s = n_s\left(1 - \frac{s_w - s(t)}{s_w - s_h}\right) \qquad for \quad s_h \le s(t) \le s_w$$

4. Parameters of the model

A_i: Water absorbed by i plant (dimensionless).
D_N: Normal Distribution.
E: Rate of Evapotranspiration (cm d^{-1}).
E_s: Rate of Evapotranspiration per Shoot (cm d^{-1}).
E_p: Rate of Evapotranspiration per Plant (cm d^{-1}).
E_{pi}: Rate of Evapotranspiration per Plant at position x_i (cm d^{-1}).
E_{pT}: Rate of Evapotranspiration for the whole Plants (cm d^{-1}).
E_w: Rate of Evapotranspiration when $s=s_w$ (cm d^{-1}).
g: Parameter of Richard's Equation (dimensionless).
h: Total monthly rainfall (mm).
$\bar{h}$: Mean monthly Rainfall (mm).
K: Maximum Number of Shoots.
K_s: saturated hydraulic conductivity (cm d^{-1}).
m: Parameter used in the representation of the Leakage Loss Rate (d^{-1}).
n_s: Number of Shoots
P_i: Pattern of Absorption of Water by the Plant on Position i.
P_T: Pattern of Absorption of Water for the Whole Plants
r: Rate of Regrowth of New Shoots ($month^{-1}$).
s: Soil Moisture (dimensionless).
s_{fc}: Soil Field Capacity (dimensionless).
s_h: Hygroscopic Point or Soil Moisture Level below which Water can not be Extracted from the Soil through Evaporation (dimensionless).
s_w: Permanent Wilting Point or Soil Moisture Level below which Plants Stop Transpiring and Begin to Wilt (dimensionless).
s^*: Soil Moisture Level below which Plants begin closing their Stomata (dimensionless).
w: Soil Porosity (adimensional).
x: Spatial Coordinate (cm).
x_i: Spatial Coordinate of Plant i (cm).
Z_r: Depth of Soil or Roots (cm).
β: Parameter defining, along with K_s, the relationship between soil moisture and hydraulic conductivity when an exponential law is used (dimensionless).
ζ: Static Water Stress (dimensionless).
η: Normalized Diary Rate of Evatranspiration under Unrestricted Soil Moisture conditions (d^{-1}).
η_w: Normalized Average Daily Evaporation Rate al $s=s_w$ (d^{-1}).
ρ: Loss of Normalized Water (d^{-1}).
σ_a: Standard Deviation of Water Absorption by Plants.
σ_h: Standard Deviationof Rainfall.
φ: Rate of Infiltration due to Rainfall (cm d^{-1}).
χ: Loss Rate of Soil Moisture (cm d^{-1}).

5. Results

The upper panel of Fig 3 shows the dynamics of soil moisture for average conditions and a scenario of 20% of reduction on the precipitation. The lower panel of this figure shows the corresponding dynamics of the number of shoots for the three species for the same conditions during five years. On February of every year the fire remove a substantial (~90 %) number of dry shoots.

The soil moisture of *Andropogon semiberbis* (A) conditions fluctuate from 0.2, dry season, to 0.6, wet season, to another time 0.2 on the first months of the year before the fire took place. This pattern of fluctuation of soil moisture is followed by the dynamics of shoot numbers. The precipitation reduction to 20% produces on this species a very strong decrease in the number of shoots (~ 75%) and occasionally the death of the plants. The same graphs are shown for a precocious, *Leptocoryphium lanatum* (L) and early *Elionurus adustus* (E) species. On L species, the reduction of 20% of the soil moisture produces a 40% reduction of the number of shoots. Whereas on early species, E, the same precipitation reduction produces a substantial reduction (~.55%) on their number of shoots. The three species show a high variability associated to this process.

Fig 4 shows the average precipitation effect of competition when one species grows on the neighbourhood of the other different phenological and architectural species. The late species, A, is not affected neither by the other two species. On the contrary, this late species, A, affects strongly the other two species, especially the precocious L, species. The effect of L upon E and E upon L is similar. On both cases the neighbour species causes a 50% of reduction on the number of shoots on the target species. These effects are associated with a high variability.

6. Conclusion

The explicit incorporation of the soil moisture competition on a previous mechanistic growth shoot model ([7]) allows us to compare to earlier work on competition for these three species ([4]). On this earlier work we detected a substantial decrease on the number of shoots when these three species were growing together but we could not assign a specific factor responsible for this aboveground decrease. This paper provides a model to link this decrease to belowground water competition. This allows our model to conform to the prevalent notion that belowground competition is a determinant factor in community composition of savannas ([14]).

The general conclusion is that there is a trade off between the intensity of the competition and the capacity to withstand the dry spell for a given species. Furthermore, these results agree with our previous work ([10]) where the species with a higher competitive ability (A) was the species that performs the worst in absence of fire. The contrary results were found for L, the less competitive species.

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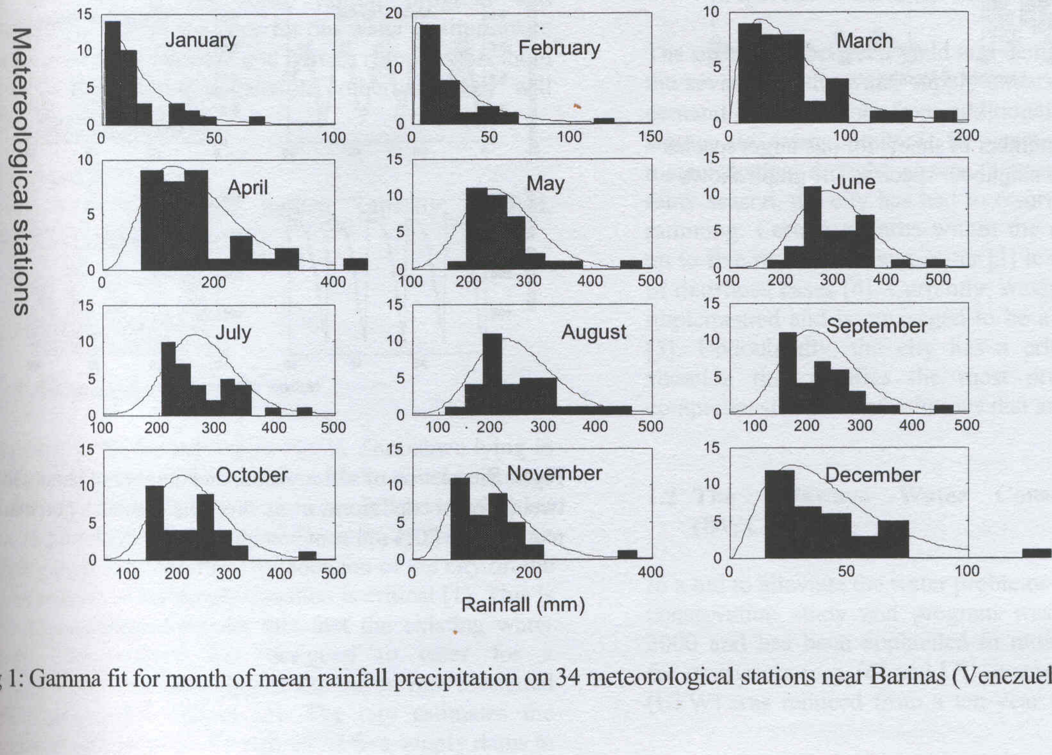

Fig 1: Gamma fit for month of mean rainfall precipitation on 34 meteorological stations near Barinas (Venezuela).

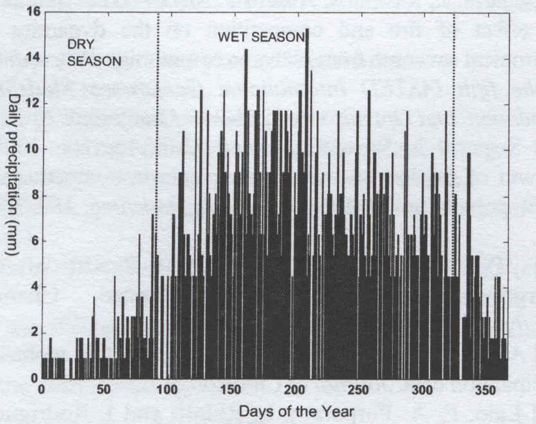

Fig 2. A simulation of daily precipitation estimated though a Poisson distribution.

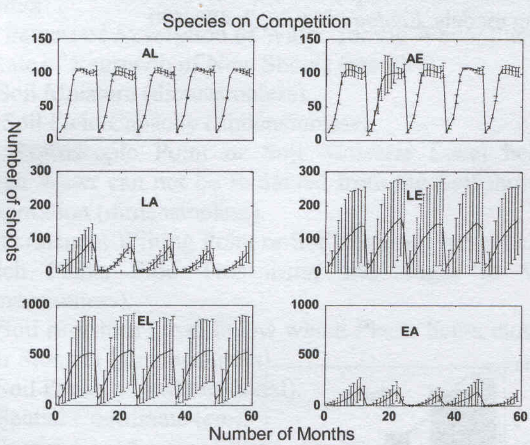

Fig 4. Simulation of number of shoots for one target species when growing with a neighbour species. The graph shows all pair interactions

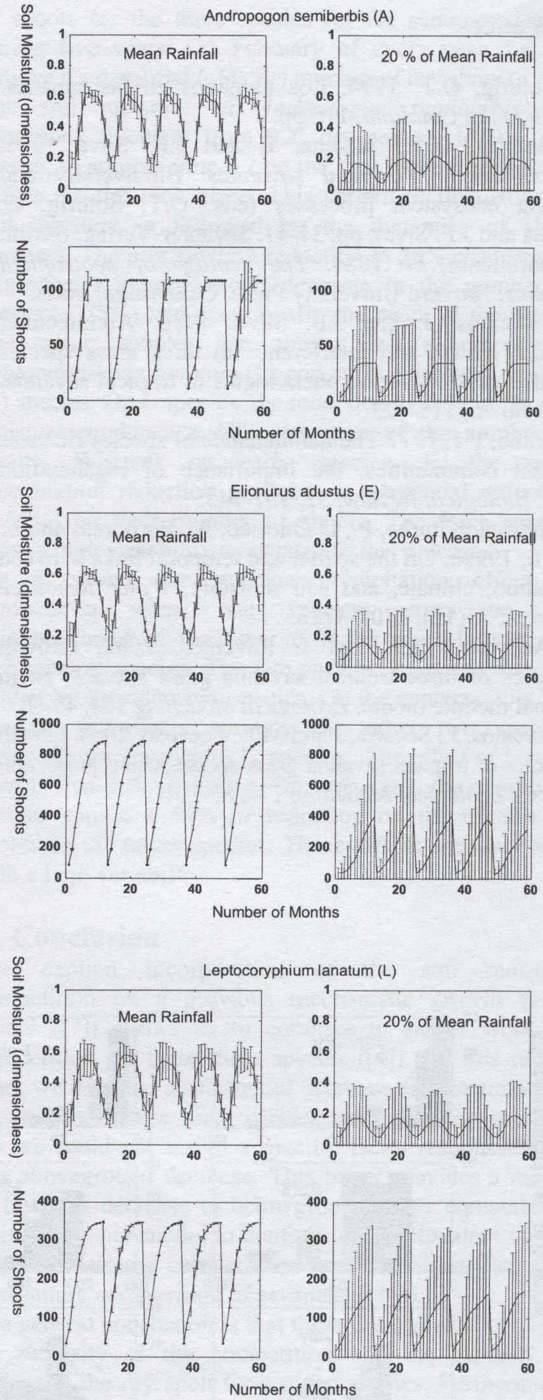

Fig 3. Simulation of soil moisture and number of shoots for two different conditions: mean precipitation and a potential reduction to 20% of mean precipitation for A, L and E.