



Coupling soil water and shoot dynamics in three grass species: A spatial stochastic model on water competition in Neotropical savanna

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ABSTRACT

Savannas are ecosystems known for their high environmental and economic value. They cover at least 20% of the global land surface and, in some cases, can act as a boundary between tropical rainforest and deserts. Water is an important determinant of savanna ecosystems.

In this paper, we present a theoretical stochastic model of root competition for water, which couples, soil water availability, phenology, and root and shoot architecture applied to three Neotropical savanna grasses. Soil moisture was simulated using a daily balance, as proposed by Rodriguez-Iturbe et al. [Rodriguez-Iturbe, I., Porporato, A., Ridolfi, L., Isham, V., Cox, D.R., 1999. Probabilistic modelling of water balance at a point: the role of climate, soil and vegetation. *Proc. R. Soc. London, Ser. A* 455, 3789–3805.]. To simulate rainfall stochasticity, we used daily precipitation data from the airport weather station in the State of Barinas, Venezuela, for the period 1991–2007. Competition among neighbouring plants took into account the spatial distribution of the individuals. As a final step, the model allowed us to calculate the shoot dynamic of the species as a function of soil water availability.

Using these data, we compared the behaviour of isolated plants, pairs and trios, and we found below-ground competition to be a fundamental component of global (shoot + root) competition. Finally, our model suggests various circumstances that allow poor competitor plants to coexist in competition for water with more successful competitors. Apparently, this is not only due to transpiration rates, but also to differences in shoot emergence and shoot growth.

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1. Introduction

In terrestrial plant communities, root competition is a ubiquitous process which plays a major role in determining interactions among individual plants and, consequently, shaping community structure and ecosystem functions. More than 70% of published root competition studies report significant interactions of this process with plant performance (Wilson, 1988; Coomes and Grubb, 2000).

Species composition affects the nature and intensity of root interactions in a plant community, and root interactions can, in turn, affect the diversity of local species through competitive exclusion, niche partitioning and facilitation. Root interactions are of primary interest when discussing the relationships between plant species diversity, ecosystem functions such as primary productiv-

ity, and community invasibility (Wilson and Tilman, 2002; Cahill, 2003; Rajaniemi, 2003; Rajaniemi et al., 2003). Understanding such relationships requires a knowledge of plant interactions, of which root interactions are at least a major, and sometimes a dominant, component (Schenk, 2006).

In this paper, we present a theoretical stochastic model of root competition for water, which couples, soil water availability, phenology, and root and shoot architecture applied to three Neotropical savanna grasses. Soil moisture was simulated using a daily balance as proposed by Rodriguez-Iturbe et al. (1999). Finally, competition among neighbouring plants took into account the spatial distribution of the individuals.

We balanced gain (precipitation) and losses (percolation, evapotranspiration and runoff) using only vertical flows. Although this model does not account for explicit horizontal flow between contiguous soil columns, it has been shown that this simplification works equally well as more complex models that include this component (Guswa et al., 2002). Furthermore, the model implicitly incorporates a horizontal flow since in each iteration soil moisture is made equal throughout the area, taking into account water flows from higher to lower moisture content.

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Nomenclature

$a_h(i)$	average leaf surface area per shoot (m^2)
$b(s)$	growth rate of new shoots (month^{-1})
b_{max}	growth rate of new shoots from water above s^* (month^{-1})
$B(x, y)$	water demand for each point of coordinates (x, y) due to all competing species (cm day^{-1})
$B_j(x, y)$	water demand from species j at each point of coordinates (x, y) (cm day^{-1})
c	auxiliary variable (dimensionless)
$d(k)$	number of days in month k
$D_j(x, y)$	kernel of root density over space x, y , for species j
E_{max}	maximum evaporation rate (cm day^{-1})
$E(s, t)$	soil water loss rate by evaporation (cm day^{-1})
F	daily probability of a rainfall event $t_d(i)$ (dimensionless)
g	parameter of Richard's equation (dimensionless)
$h_{\text{day}(l)}$	rainfall in a day l (cm day^{-1})
$H_d(k)$	rainfall average for each rainy day in month k (cm day^{-1})
H_m	mean monthly precipitation (cm)
$I(s, t)$	soil infiltration rate (cm day^{-1})
J_m	average number of rainy days in each month (day)
$j_m(k)$	frequency of rainy days in month k (dimensionless)
K_s	saturated hydraulic conductivity (cm day^{-1})
$L(s, t)$	soil water loss rate which includes deep percolation rate, transpiration and evaporation (cm day^{-1})
$M(s, t)$	soil water loss rate by leakage (cm day^{-1})
n	soil porosity (dimensionless)
$n_h(i)$	number of shoots
N	maximum number of shoots
r	rate of change in number of shoots (month^{-1})
s	soil moisture (dimensionless)
s_{fc}	soil field capacity (dimensionless)
s_h	hygroscopic point, or soil moisture level below which water cannot 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)
t_c	constant rainfall threshold (cm day^{-1})
$t_{\text{max}}(i)$	maximum transpiration rate for species i (cm day^{-1})
$t'_{\text{max}}(i)$	transpiration capacity per unit of leaf surface for each species ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$)
$T(s, t)$	soil water loss rate by transpiration (cm day^{-1})
T_{max}	average of maximum transpiration rates in modelled plants (cm day^{-1})
$w_{ij}(x_i, y_i)$	root water uptake of each individual i of species j located in position (x_i, y_i) (cm day^{-1})
$W_j(x, y)$	total root water uptake of species j (cm day^{-1})
x	spatial coordinate (m)
x_i	spatial coordinate of individual i (m)
y	spatial coordinate (m)
y_i	spatial coordinate of individual i (m)
z	maximum distance at which soil humidity affects transpiration of an individual plant (m)
Z_r	depth of soil (cm)
σ_a	standard deviation of water absorption by plants
β	parameter defining the exponential relationship between soil moisture and hydraulic conductivity (dimensionless)

$\mu(s)$	mortality rate (month^{-1})
μ_{max}	mortality rate as result of soil water content falling below s_h (month^{-1})

We assigned a portion of soil moisture availability to each individual plant according to its rate of root absorption, which is directly dependent on the rate of shoot transpiration (Larcher, 2003). As a function of soil moisture availability, each plant could produce new shoots, grow them according to Richard's equation (Causton and Venus, 1981), or eliminate a fraction of the current shoots.

In previous research, we modelled the growth dynamics of Neotropical savanna grasses (Raventos et al., 2004; Segarra et al., 2005a,b), modelling competition as an interaction term parameterized by a coefficient, following the typical pattern of Lotka–Volterra models. Here, we went beyond the use of a coefficient and took a first step in formulating a process-based model, taking into account eco-physiology and root measurements. This model is able to provide a better explanation for the mechanics of water competition among savanna grass plants.

We centred the model on water, because competition interactions do not seem to change when soil fertility decreases (Tilman, 1982; DiTommaso and Aarssen, 1989; Wilson and Tilman, 1991; Silletti et al., 2004), although some studies point to a more complex relationship between water stress and competition ability (Chapin, 1980; Aerts and Chapin, 2000; Lambers et al., 1998, 2008). Furthermore, it has been argued that water is more important than nutrients on the whole below-ground competition process (Briguglio et al., 2000), as a shortage of water may kill the plants, but scarcity of nutrients only pushes plants to atrophy (Coomes and Grubb, 2000).

Our goals in this paper are to: (a) test our plant competition model against field measurements, and (b) test the often stated hypothesis (Casper and Jackson, 1997; Schenk, 2006), that below-ground competition is more important than shoot competition for savanna grass ecosystems. Although we apply this model to some Neotropical savanna grasses, it can be easily transformed for use with different species and different grassland ecosystems. The use of stochastic- and spatial-dependent water competition models like these is a powerful tool in understanding and mitigating the effect of climate change on savanna ecosystems which can be affected by a decrease in rainfall precipitation (IPCC WGI Fourth Assessment Report, 2007, page 16, Figure SPM-7).

2. Site and species

This model is designed to simulate soil water competition among grass plants representative of the Neotropical savanna in Barinas, Venezuela ($8^{\circ}38'N$; $70^{\circ}12'W$). This savanna shows high hydric seasonality, high evapo-transpiration rates, oligotrophic soils and frequent fires. These conditions favour the presence of C4 grasses as a dominant vegetation. The mean annual temperature is $27^{\circ}C$ and the average annual rainfall is 1250 mm, with a wet season between May and November and a dry season from January to March. Fire often occurs at the end of the dry season. We tested our model on three perennial co-dominant grasses with different architecture and flowering phenologies: *Elionurus adustus* (Trin.) Ekman (*E*), a precocious bunch grass species that flowers after the annual burning at the end of the dry season; *Leptocoryphium lanatum* (Kunth) Nees (*L*), an early scleromorphous bunch grass that flowers in May, one month after the onset of rains; and *Andropogon semiberbis* (Nees) Kunth (*A*), an erect late species that flowers in November.

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