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Tree–grass co-existence in savanna: Interactions of rain and fire

Francesco Accatino [a], Carlo De Michele [a,*], Renata Vezzoli [a], Davide Donzelli [a], Robert J. Scholes [b]

[a] DIIAR, Politecnico di Milano, P.zza L. da Vinci 32, 20133 Milano, Italy
[b] CSIR, Pretoria, South Africa

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ABSTRACT

The mechanisms permitting the co-existence of tree and grass in savannas have been a source of contention for many years. The two main classes of explanations involve either competition for resources, or differential sensitivity to disturbances. Published models focus principally on one or the other of these mechanisms. Here we introduce a simple ecohydrologic model of savanna vegetation involving *both* competition for water, and differential sensitivity of trees and grasses to fire disturbances. We show how the co-existence of trees and grasses in savannas can be simultaneously controlled by rainfall and fire, and how the relative importance of the two factors distinguishes between *dry* and *moist* savannas. The stability map allows to predict the changes in vegetation structure along gradients of rainfall and fire disturbances realistically, and to clarify the distinction between *climate-* and *disturbance-dependent* ecosystems.

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1. Introduction

The term *savanna* describes ecosystems characterized by the co-dominance of trees and grasses. The proportions of tree and grass can vary greatly. Savannas occur in areas with annual rainfall from 300 to 1800 mm, and are commonly split into *dry* and *moist* forms (semi-arid and wet, nutrient-rich and nutrient-poor, fine-leafed, and broad-leafed are all synonyms for this division). In *dry* savannas, the grass primary production is a strongly increasing function of annual rainfall, while in *moist* savannas the relation is weak or absent. The transition between *dry* and *moist* savannas can be located around 500 – 700 mm of annual rainfall (e.g., Scholes and Walker, 1993; Sankaran et al., 2005).

What is special about the savanna environment that allows trees and grasses to coexist, as opposed to the general pattern in other areas of the world where either one or the other functional type is dominant?

This has been referred to as the '*savanna question*' (Sarmiento, 1984). The question has attracted the interest of many scientists in the last forty years: Walter (1971), Walker and Noy-Meir (1982), Scholes and Walker (1993), Scholes and Archer (1997), Sankaran et al. (2004), Sankaran et al. (2005), D'Odorico et al. (2006), Scheiter and Higgins (2007), Lüttge (2008), Hanan et al. (2008), and Leibold (2008), among others.

According to rangeland ecology literature (e.g.,Westoby et al., 1989; Briske et al., 2003), savannas can be viewed in light of range succession or state-and-transition models. In range succession models, savannas are a point in a continuous spectrum whose extremes are grassland and forest. Disturbances like fire or herbivores just modify the tree–grass ratio along this spectrum with reversible transformations. In state-and-transition models multiple stable states are possible, and the rangeland dynamics is explained through transitions (reversible or irreversible and abrupt) due to disturbances between steady states. The existence of multiple stable states has been pointed out by Dublin (1995), van de Koppel et al. (1997), Anderies et al. (2002), van Langevelde et al. (2003), D'Odorico et al. (2006), Hanan et al. (2008), Okin et al. (2009), Baudena et al. (2010).

According to savannas ecology literature (e.g., Sankaran et al., 2004), the 'savanna question' is addressed within paradigms of equilibrium and disequilibrium. The former interprets the savanna as a long term stable state due to internal factors, being disturbances modifiers of the tree–grass ratio. According to the latter, savanna is an unstable state and its existence is due to disturbances which maintain the tree–grass mixture, preventing the achievement of the complete dominance of trees or grasses.

Within the equilibrium paradigm, the tree–grass co-existence has been explained through competition based mechanisms (e.g., root niche separation or balanced competition), while demographic bottleneck mechanisms are related to the disequilibrium paradigm (see Sankaran et al., 2004).

The archetypal competition-based model of tree–grass co-existence in savannas is based on the 'Walter hypothesis' (Walter, 1971), which assumes soil water to be the limiting resource, with

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* Corresponding author. Tel.:+39 0223996233, fax: +39 0223996207.
E-mail addresses: francesco.accatino@mail.polimi.it (F. Accatino), carlo.demichele@polimi.it (C. De Michele), renata.vezzoli@polimi.it (R. Vezzoli), davide.donzelli@mail.polimi.it (D. Donzelli), BScholes@csir.co.za (R.J. Scholes).

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grasses as the superior competitor, but having roots restricted to the topsoil layer whereas trees roots both in the topsoil and subsoil. The niche separation avoids the tree–grass competition and allows the stable co-existence. The absence of niche separation in fact would lead to one plant functional group equilibrium. Models based on the ‘Walter hypothesis’ have been widely applied in literature (Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segarra, 1985; van Langevelde et al., 2003).

Some experiments and observations have supported ‘Walter hypothesis’ (Knoop and Walker, 1985; Sala et al., 1989; Pelaez et al., 1994) but many others have cast doubts on the existence of vertical rooting niche separation (Scholes and Walker, 1993; Belsky, 1990; Le Roux et al., 1995; Mordelet et al., 1997; Smit and Rethman, 2000; Hipondoka et al., 2003).

In ‘balanced competition’ models, the superior competitor limits its own abundance and the inferior competitor can grow; in other terms the intra-specific competition of the superior competitor is stronger than the inter-specific competition (Amarasekare, 2003). For example, the water scarcity can limit the abundance of trees in savanna so that grass can grow.

In the past two decades, the disequilibrium paradigm has gained favor over the equilibrium one (Higgins et al., 2000; Jeltsch et al., 2000; van Langevelde et al., 2003; D’Odorico et al., 2006; Gardner, 2006; Hanan et al., 2008). The near-universal finding that tree cover increased when fires are excluded from savannas (Trapnell, 1959; Shackleton and Scholes, 2000) and that elephants (see the several studies reviewed in Kerley et al., 2008), giraffes (Pellew, 1983) and other herbivores can substantially modify savanna structure, lend evidence to this school of thought.

Fire is an intrinsic characteristic of many savanna ecosystem allowing tree–grass co-existence: trees at the seedling stage can be easily attachable by flames, thus fire acts as bottleneck in trees demography preventing the canopy closure. Fire has been explicitly included in many savanna models (Hochberg et al., 1994; Anderies et al., 2002; van Langevelde et al., 2003; D’Odorico et al., 2006; Beckage et al., 2009) and has often been described as dependent on the availability of fuel load, that in arid ecosystems is given by dead grass. Hanan et al. (2008) and Baudena et al. (2010) have considered explicitly the demography of trees underlining the asymmetry of the fire effects between saplings and adult trees. This asymmetry can allow the survivorship of trees population at low densities thanks to mechanisms of ‘storage effect’ that compensate the loss of young trees due to demographic bottlenecks with a very low mortality of adult trees (Warner and Chesson, 1985). In addition, various studies focused on fire as cause of bistability in rangelands (Anderies et al., 2002; van Langevelde et al., 2003; Okin et al., 2009).

Simple (non-spatial) models of savanna dynamics, available in literature, focus the attention principally on one mechanism at a time. Competition mechanisms are considered by Walker et al. (1981), Walker and Noy-Meir (1982), Eagleson and Segarra (1985), Fernandez-Illescas and Rodriguez-Iturbe (2004), Baudena et al. (2010), while disturbances-driven mechanisms are used by Casagrandi and Rinaldi (1999), D’Odorico et al. (2006), Hanan et al. (2008), Beckage et al. (2009).

Sankaran et al. (2004) point out the necessity to take into account both disturbances and competition for resources simultaneously in order to capture their relative importance in shaping the different types of savannas.

Based on data from 854 sites in Africa, Sankaran et al. (2005) identify a distinction between savannas receiving less that $\sim$650–700 mm of annual rainfall (*dry savannas*) and those receiving more (*moist savannas*). The former are stable, and disturbances modify the woody cover, but are not necessary for tree–grass co-existence; the latter are unstable and maintained by disturbances, in this case they are essential for the maintenance of a savanna.

van Langevelde et al. (2003) represent the savanna vegetation through a simple model of two equations (one for tree and one for grass) considering the joint role of water (through the root niche separation mechanism) and disturbances (fire and herbivores) that remove grasses and trees. In arid and semi-arid ecosystems the dynamics of soil water is closely linked to the dynamics of vegetation (Scholes and Walker, 1993; Rodriguez-Iturbe and Porporato, 2004), thus in our approach, we will consider explicitly the soil water in the root zone as a state variable.

Here, we address the ‘savanna question’ including in an ecohydrologic model balanced competition and bottleneck mechanisms. We propose a space implicit model of tree–grass dynamics competiting for soil water and perturbated by fire. In Section 2, the savanna is described through a set of three differential equations including the dynamics of trees, grasses, and soil water, fed by rainfall, and disturbed by fire. The variability of the model’s parameters is investigated and the stability analysis is presented. In Section 3, changes of vegetation structure along gradients of rainfall and fire frequency are predicted using the stability map in the rainfall–fire frequency space. The role of rainfall and fire frequency in maintaining dry and moist savannas is illustrated.

2. Materials and Methods

2.1. Tree–grass dynamics

Let us consider the space implicit model introduced by Tilman (1994) to represent the temporal dynamics of tree and grass

$$\begin{cases} \dfrac{dT}{dt} = c_T T(1-T) - \delta_T T \\ \dfrac{dG}{dt} = c_G G(1-G-T) - c_T TG - \delta_G G, \end{cases} \tag{1}$$

where T and G are the fractions of area occupied, respectively, by tree and grass. T and G are dimensionless, and range in the closed interval [0, 1]: $T=0$ means that trees are not present in the area, $T=1$ means that the area is fully covered by trees, and similarly for grasses. In addition, the values of T and G must satisfy also the condition $0 \le T+G \le 1$. c_T and c_G are the colonization rates, whereas δ_T and δ_G are the ‘offtake’ rates for trees and grasses, respectively. c_T, c_G, δ_T, and δ_G are all positive and carry dimension $[1/t]$, where t is the time. In Eq. (1), trees are the *superior competitor*, while grasses are the *inferior competitor*. Trees can displace grasses (the term $-c_T TG$), and colonize places where trees are absent (the term $(1-T)$), while grasses can colonize places where both trees and grass are absent (the term $(1-G-T)$). See Tilman (1994) for further details.

2.2. Fire forcings and tree–grass dynamics

There is much evidence that fire influences the balance between tree and grass in savannas (e.g., Scholes and Walker, 1993). The occurrence and spread of fires depends on the presence of sufficient mass of dry plant material to provide a near-continuous fuel load. The fuel for savannas fires is mostly provided by dead grass: the fire may only burn following years of adequate rainfall and low herbivory, when sufficient grass biomass has accumulated (Bond and van Wilgen, 1996).

The fire acts differently on grass and tree. Fire occurs mainly in the dry season, when the perennial grasses are dormant. It consumes grass leaves as fuel, but does not generally kill the dormant grass buds at/or below the soil surface. The fire also consumes tree leaf litter, but if grass is completely absent it is very difficult for fire to propagate. The living tree biomass is

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