Journal of Theoretical Biology 289 (2011) 74–82

Contents lists available at SciVerse ScienceDirect

Journal of Theoretical Biology

journal homepage: www.elsevier.com/locate/yjtbi

Savanna domain in the herbivores-fire parameter space exploiting a tree–grass–soil water dynamic model

C. De Michele[a],*, F. Accatino[a], R. Vezzoli[a], R.J. Scholes[b]

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

ARTICLE INFO

Article history:
Received 17 February 2011
Received in revised form
4 August 2011
Accepted 13 August 2011
Available online 24 August 2011

Keywords:
Herbivores
Fire
Savanna
State transition
Gradient

ABSTRACT

The tree–grass co-existence in savannas involves multiple and sometimes connected biogeophysical conditions. The savanna domain, its boundaries, and transitions (gradual or abrupt) to other vegetation types (i.e., grassland or forest) are fundamental for the management of ecosystems and for preserving the biodiversity in present conditions and in future changing scenarios. Here we investigate the savanna domain within grazers-fire and browsers-fire parameter planes through a simple ecohydrological model of tree–grass–soil water dynamics. Stability maps allow to identify savanna domains and to show the behavior of vegetation under increasing pressure of grazing and browsing. Stability maps shed light on the causes behind possible vegetation abrupt transitions (e.g., forest collapse and bush encroachment). An application to 15 African savannas sites is presented and discussed with the support of a local sensitivity analysis of the model's parameters.

1. Introduction

The dynamics of vegetated ecosystems are controlled and driven by climate, substrate, and disturbances such as fire, herbivory, and human activities. Vegetated ecosystems whose dynamics are dominated by climate are called *climate dependent ecosystems* (Bond et al., 2003), whereas in the cases where other perturbations, like fires or herbivores, are prominent, they are labeled *fire dependent ecosystems*, or *consumer controlled ecosystems* (Bond et al., 2003; Bond and Keeley, 2005).

Where do savannas – that are ecosystems co-dominated by trees and grass – fit in this classification?

Field observations (Sankaran et al., 2005; Bucini and Hanan, 2007) reveal a complex situation: savannas can be either *climate*, or *disturbance dependent ecosystems*, depending on the environment they occur in.

Early models of savannas emphasized the role of soil water availability and inferred savannas to be *climate dependent*. Walter (1971) describes savannas as 'broad ecotones' between grasslands and forests depending on the mean annual rainfall; Shmida and Burgess (1988) illustrate the *subtropical succession* (*desert → grassland → open savanna → closed savanna → forest*) as the sequence of ecosystem types observed along a rainfall gradient. In general under these conceptual models, water scarcity permits the co-existence of trees and grasses by limiting the abundance of trees allowing grass to persist: this is a mechanism of *balanced competition* (Amarasekare, 2003).

More recent works have considered the role of fire in permitting the tree–grass co-existence in savannas (Hanan et al., 2008; D'Odorico et al., 2006; Bond et al., 2003; Baudena et al., 2010; Accatino et al., 2010), indicating savannas as possible *fire dependent ecosystems*. In ecosystems where water scarcity already limits the tree density and allows tree–grass co-existence, fire influences only the tree–grass ratio. On the other hand, if water is sufficient to support the growth of trees, fire can be a limiting factor for tree cover, permitting again the tree–grass co-existence, through a *bottleneck* mechanism in tree demography. Under these conditions, savannas can be viewed as fire subclimaxes of forests (Scholes and Walker, 1993).

Yet other studies have suggested a role for herbivores in maintaining savannas (Scholes and Archer, 1997; Bond and Keeley, 2005; Baxter and Getz, 2005; Holdo, 2007). Particular attention has been paid to elephants, which are able to 're-engineer' the tree layer (Dublin, 1995).

Accatino et al. (2010), considering the joint role of rainfall and fire, have suggested that arid savannas are *climate dependent*, while moist savannas can be *fire dependent*.

In the savanna literature, tree–grass co-existence is often discussed in relation to the existence of multiple steady states. Bifurcation analyses (van Langevelde et al., 2003; Baudena et al., 2010; Accatino et al., 2010) have pointed out the possibility that

---

* Corresponding author. Tel: +39 02 2399 6233.
E-mail addresses: carlo.demichele@polimi.it (C. De Michele), francesco.accatino@mail.polimi.it (F. Accatino), renata.vezzoli@polimi.it (R. Vezzoli), bscholes@csir.co.za (R.J. Scholes).

0022-5193/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jtbi.2011.08.014

savannas may represent a bistability condition with forests. Beyond the mathematical formalism, the existence of multiple steady states appears evident in field observations. Among the several cases that can be mentioned, we recall the macro-mosaics observable in tropical dry forests, where fire plays a fundamental role in the abrupt transitions from forest to savanna (Murphy and Lugo, 1986), the savanna-forest hysteresis cycle in the Amazon basin (da Silveira Lobo Sternberg, 2001), and the changes observed in the Serengeti–Maara vegetation due to variations in fire and grazing regimes during the rinderpest pandemic period (Dublin, 1995). The key pieces of evidence offered in favor of multiple steady states are abrupt state transitions over time (hysteresis cycles) and space (macro-mosaics), bimodal state variable frequency or distribution, and dual response to driving parameters (Schröder et al., 2005). The space variability plays an important role in maintaining savannas, and several spatial models were built in order to account the dynamics in space of the vegetation (see e.g., Klausmeier, 1999; Rietkerk et al., 2002; Gilad et al., 2007; Borgogno et al., 2009). However, in this work we point the attention on a spatially implicit model.

In particular, we extend the spatially implicit ecohydrological model of water dynamics in a tree–grass–soil system forced by rainfall and fire proposed by Accatino et al. (2010) to explicitly consider disturbances by herbivores, distinguishing grazers from browsers. By doing so, we are able to underline the different contributions of fire and herbivore disturbances to the tree–grass co-existence in savannas.

Then, we use stability maps in the grazers-fire and browsers-fire parameter planes to identify savanna domain and to show the behavior of vegetation under an increasing pressure of grazing or browsing. In this way, we try to answer fundamental questions about the controls on savanna structure and function and explore the causes of abrupt transitions in savanna ecosystems dynamics.

We discuss the theoretical results using observed data collected in 15 savanna sites and characterized by particularly high or low values of fire occurrences and browsers density. The data are extracted by the database reported in Sankaran et al. (2005). The comparison between model outputs and observed data is commented with the help of a local sensitivity analysis of the model's parameters.

2. The action of fire, grazing, and browsing on savannas

Fires and herbivores are 'direct' disturbances to the demography of vegetated ecosystems (Hobbs and Huenneke, 1992). The interactions among rainfall, fire, and herbivores in shaping the vegetation are sketched in Fig. 1(a). The fire shapes savanna structure by acting as a determinant of the tree layer composition (Frost et al., 1986; Bond and van Wilgen, 1996). The quantity of tree biomass is, in general, negatively correlated with fire frequency (Scholes and Walker, 1993). The spread and intensity of fire is supported by the abundance of dead grasses (fuel load) during the dry seasons (Scholes and Archer, 1997; Govender et al., 2006). Fires seldom damage adult trees, but kill or knock back tree seedlings and, the height of which is determined by the abundance of dead grass. Thus the fire acts as a demographic bottleneck, restricting the recruitment of small trees to the adult class.

Large mammal herbivores in African savannas form a continuum from eaters of grass only (grazers) to eaters of trees only (browsers) (McNaughton and Georgiadis, 1986). It is nevertheless useful to split them into two discrete classes, grazers and browsers, to evidence their different feedbacks on fire via the quantity of dead grass (fire's fuel load). Grazers directly reduce the quantity of dead grass which controls the spread and intensity

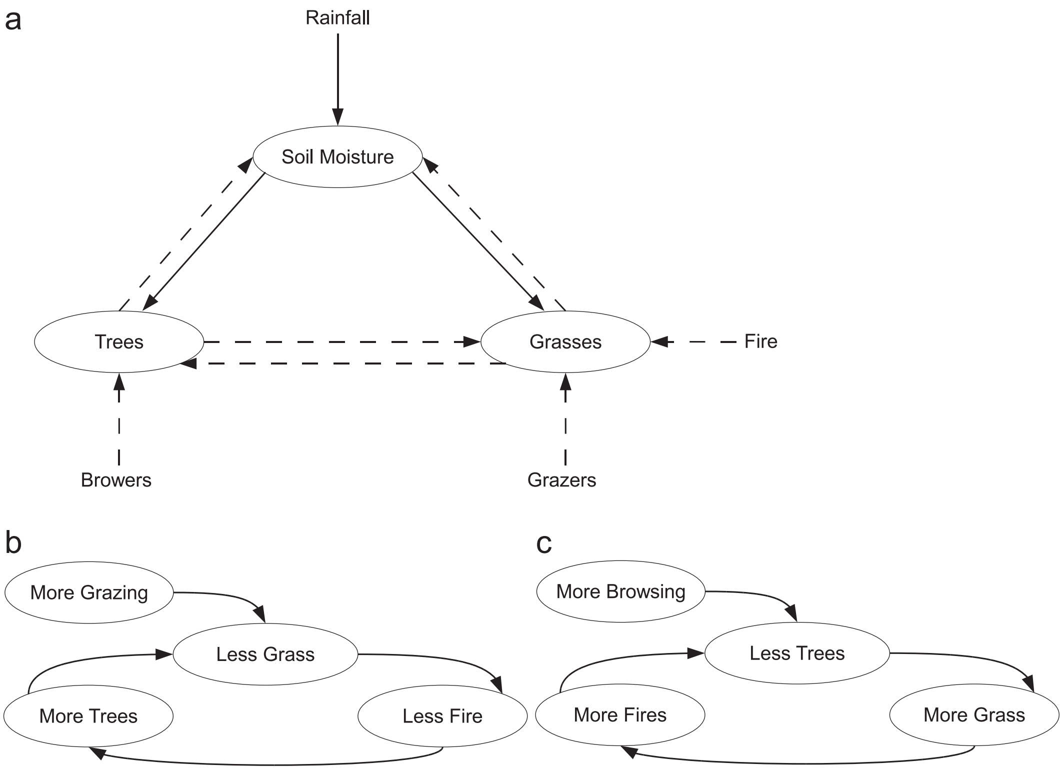

Fig. 1. Panel (a) sketches interactions among rainfall, fire, herbivores, soil moisture, trees and grass. Continuous (dashed) lines indicate positive (negative) interactions. Panels (b) and (c) show respectively feedbacks of grazers-fire and browsers-fire on trees and grass.