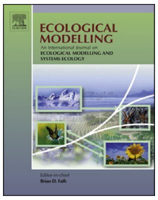
Ecological Modelling 304 (2015) 11–21

Contents lists available at ScienceDirect

Ecological Modelling

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



Facilitation in drylands: Modeling a neglected driver of savanna dynamics

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ARTICLE INFO

Article history:
Received 1 December 2014
Received in revised form 20 February 2015
Accepted 23 February 2015
Available online 21 March 2015

Keywords:
Ecohydrological modeling
ODE model
Coexistence
Biome shifts
Fire
Grazing

ABSTRACT

Our current understanding regarding the functioning of the savanna ecosystem describes savannas as either competition- or disturbance-dependent. Within this generalized view, the role and importance of facilitation have been mostly neglected. This study presents a mathematical model of savannas with coupled soil moisture–vegetation dynamics, which includes interspecific competition and environmental disturbance. We find that there exist environmental and climatic conditions where grass facilitation toward trees plays an important role in supporting tree cover and by extension preserving the savanna biome. We, therefore, argue that our theoretical results in combination with the first empirical studies on the subject should stimulate further research into the role of facilitation in the savanna ecosystem, particularly when analyzing the impact of past and projected climatic changes on it.

1. Introduction

Savannas have been generally defined as ecosystems with a more or less continuous grass layer and scattered trees, distinct in function from grassland, forest and desert biomes (e.g. Scholes and Archer, 1997). Here, we refer to all woody plants as trees, while grasses encompass all the herbaceous vegetation. Given that these two life-forms would normally be regarded as either mutually exclusive or unequal competitors, savanna research has focused on understanding the mechanisms that allow for their continued coexistence (Baudena et al., 2010; Bond and Midgley, 2012; Bond, 2008; Bond et al., 2003; Gillson, 2004; Gil-Romera et al., 2010; Jeltsch et al., 1998, 1996; Scheiter and Higgins, 2007; Tietjen et al., 2010; Van Langevelde et al., 2003). This research has led to the identification of two principal coexistence mechanisms: competition for resources (water) and environmental disturbance. Competition-based theories started with Walter's two-layer hypothesis, which predicted stable tree–grass coexistence via a resource niche differentiation (Walter, 1972; Walker et al., 1981; Walker and Noy-Meir, 1982; Belsky, 1990). However, the general validity of the original two-layer hypothesis was questioned (Higgins et al., 2000; Sankaran et al., 2004; Scholes and Archer, 1997), leading to refinements proposing that grasses dominate the 'topsoil' layer and regulate the amount of water that infiltrates deeper into the soil, from where trees access their resources (Kulmatiski et al., 2010; Ward et al., 2013). In the meantime, alternative coexistence theories surfaced, in which water availability ceases to be the sole driving force. These postulate that the savanna ecosystem is not necessarily stable and, lying in the middle of a continuous spectrum of vegetation starting from open grasslands and ending at a closed-canopy forest, it requires environmental disturbances to preserve it from shifting to either end of the vegetation spectrum (Augustine and Mcnaughton, 2004; Bond et al., 2005; D'Odorico et al., 2006; Higgins et al., 2000; Scholes and Archer, 1997). A different formulation, not hinging on defining savannas as an equilibrium or a non-equilibrium system, focused on how such disturbances act as 'buffering mechanisms' to preserve the savanna ecosystem (Jeltsch et al., 2000).

Sankaran et al. (2004) proposed an aggregation of the different theories to best describe savanna dynamics, with later studies demonstrating how incorporating both competition and disturbances into models can yield more realistic results for a broad range of rainfall regimes (Calabrese et al., 2010; De Michele et al., 2011; Higgins et al., 2010; Sankaran et al., 2005; Staver et al.,

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http://dx.doi.org/10.1016/j.ecolmodel.2015.02.015
0304-3800/

2011). This has led to the current widely accepted perception that competition becomes the primary coexistence mechanism under strong resource limitation (rainfall below ~650 mm/year), while disturbances stop the ecosystem from shifting to a different biome when water is theoretically sufficient for trees to form a closed canopy.

Facilitation has been largely absent from the aforementioned savanna debate, even though some recent empirical studies have investigated the impact of a facilitative relationship between grasses and trees at small spatial scales. Some studies found evidence of grass facilitation toward tree seedlings through the amelioration of harsh conditions or through the protection from grazers (Anthelme and Michalet, 2009; Good et al., 2014; Iacona et al., 2012; Maestre and Cortina, 2004). Others observed how trees facilitated grasses by improving moisture conditions in their vicinity (Dohn et al., 2013; Holzapfel et al., 2006; Moustakas et al., 2013). Nevertheless, there has been no systematic effort to study facilitation as a possible tree–grass coexistence mechanism in savannas at the ecosystem level until now, despite some first signs of its possible significance (Baudena and Rietkerk, 2013). Due to this lack of facilitation studies at the savanna level, we are not in a position to assess its possible impact as a coexistence mechanism nor are we able to identify certain climatic and environmental patterns which may cause facilitative tree–grass interactions to support savannas.

In this study we use a new deterministic mathematical model of coupled soil moisture–vegetation cover dynamics to investigate the role of facilitation as a mechanism preserving arid and semi-arid savannas. In these climatic conditions where tree cover is low and savannas can potentially be replaced by grasslands (Bond, 2008), we focus on the notion of grass facilitation toward trees only. Our model includes inter- and intra-specific competition for resources and space, as well as environmental disturbances such as fire, grazing and browsing. We realized positive feedbacks that allow for facilitation among growth types by a positive impact of vegetation cover on infiltration and shading. We apply the model to evaluate, under which conditions grasses can facilitate trees and to assess the impact of grass facilitation on the vegetation composition at the ecosystem level. We finally discuss how our theoretical results, combined with existing empirical studies, should stimulate further investigation into the role of facilitation in savannas.

2. Methods

Previous Ordinary Differential Equation (ODE) models of grassland and savanna dynamics focused on the roles of competition (Tilman, 1994), herbivory (De Knegt et al., 2008), fire (Beckage et al., 2009) or on a combination thereof (Van Langevelde et al., 2003). We used the ecohydrological ODE model of Accatino et al. (2010) as our starting point to simultaneously model interactions between the two vegetation types (grasses and trees) and between the vegetation cover and soil moisture. This model of coupled vegetation–soil moisture includes competitive interactions (resource competition), environmental disturbance (fire) and herbivory (grazing and browsing). We have also included positive vegetation–soil moisture feedbacks (infiltration and shading). In this section we first present the model design and its assumptions as well as the model parameterization. Afterwards, we describe the simulated scenarios and the methods used to evaluate the results.

2.1. Model design

We designed a deterministic ecohydrological model of Ordinary Differential Equations (ODEs) to describe the dynamics of soil moisture (M), grasses (G) and trees (T) based on the model of Accatino et al. (2010). Soil moisture content is given by the rate of change in the saturation of the soil which is determined by infiltrated rainfall, evaporation and transpiration:

$$\frac{dM}{dt} = \delta(G, T)\left(\frac{p}{v_1}\right)(1 - M) - \varepsilon M(1 - T - G) - w_G MG - w_T MT \quad (1)$$

We assume that trees and grasses extract water from the same depth (Kulmatiski et al., 2010) and that the water table is so deep that it does not affect the water dynamics in the root zone (Accatino et al., 2010). Then M, defined as the water volume present in the root zone relative to the maximum volume of water that can be held in this zone, increases with rainfall p $[l/t]$, which is normalized by the unitary volume porosity, v_1 $[l]$, and controlled by infiltration $\delta(G, T) = (1 - a)(G + T) + a$. The unitary volume porosity, v_1 $[l]$, is the product of the soil depth, z $[l]$, and soil porosity, n $[-]$. Parameter a $[-]$ from the infiltration function represents the proportion of infiltrated water in a bare landscape. A fraction of infiltrated rainfall is lost through percolation into deeper soil layers, $-\delta(G, T)(p/v_1)M$ (Accatino et al., 2010). Additional soil moisture losses occur via evaporation over bare ground at a rate ε $[1/t]$, and through grass and tree transpiration, at respective rates w_G $[1/t]$ and w_T $[1/t]$.

The rate of change of grass cover G is determined by the expansion of grass cover minus losses:

$$\frac{dG}{dt} = c_G MG(1 - T - G) - d_G G - \gamma(G) \quad (2)$$

Here, we assume that grasses only colonize empty space $(1 - T - G)$ at rate c_G $[1/t]$ and that grass cover growth is linearly dependent on soil moisture content, M. Grass cover is lost due to a constant natural mortality rate d_G $[1/t]$ and grazing, $\gamma(G) = a_G G^{b(1-G)}$ $[1/t]$. Grazing is defined as a non-linear, increasing saturating function of grass cover (details are given in Section 2.2).

The rate of tree cover change follows the same principle as that of grass cover, colonization minus mortality:

$$\frac{dT}{dt} = c_T MT(1 - f(G) - T) - d_T T - \beta(T) \quad (3)$$

Tree cover, T, dynamics (Eq. (3)) are similar to those of grass cover with different rates for colonization, c_T $[1/t]$, and natural mortality, d_T $[1/t]$, and a non-linear function $\beta(T) = a_T T^{b(1-T)}$ $[1/t]$ for browsing rather than grazing. The density-regulating term of trees in the growth term, $(1 - f(G) - T)$, includes the impact of fire, $f(G) = a_S G^{b(1-G)}$ $[-]$. Because our model does not explicitly describe the age structure of trees, we represent the demographic bottleneck principle (Higgins et al., 2000; Jeltsch et al., 2000; Sankaran et al., 2005) as a hindrance on the establishment of new trees, which impacts the overall growth of tree cover, following the proposal of Hanan et al. (2008).

2.2. Model assumptions

Competition: Inter-specific competition for resources occurs via transpiration (Eq. (1)), where both vegetation types remove moisture from the soil. In addition, intra-specific competition for space is represented by a density-regulating term (Eqs. (2) and (3)). Trees are additionally able to displace grasses (Accatino et al., 2010; De Michele et al., 2011), whereas grasses can only establish in unoccupied space.

Environmental disturbance: The environmental disturbance in the establishment of trees is represented by fire, which is fueled by existing grasses cover (Bond, 2008; D'Odorico et al., 2012). Furthermore, we assumed that fire intensity has a sigmoidal response to increasing grass cover (Staver et al., 2011). Grazing and browsing have a direct negative impact on grass and tree cover, respectively. Losses by grazing impact grass cover additionally to the natural mortality rate and are defined as a non-linear, increasing saturating