ECOLOGICAL MODELLING 209 (2007) 377–391

available at www.sciencedirect.com

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

SATCHMO: A spatial simulation model of growth, competition, and mortality in cycling savanna patches

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ARTICLE INFO

Article history:
Received 22 May 2006
Received in revised form
25 April 2007
Accepted 2 July 2007
Published on line 8 August 2007

Keywords:
Patch-dynamics
Cyclical succession
Shrub encroachment
Spatially explicit root growth
Computer simulation model
Validation
Latin Hypercube sensitivity analysis
Acacia mellifera

ABSTRACT

Many mechanisms have been suggested to explain the coexistence of woody species and grasses in savannas, yet, evidence from field studies and simulation models has been mixed. Shrub encroachment is an ecological and economic problem in savannas worldwide which generally is attributed to overgrazing. Patch-dynamics is a new mechanism explaining tree-grass coexistence and the natural occurrence of shrub encroachment in savannas. A patch-dynamic savanna consists of patches in which cyclical succession between grassy and woody dominance proceeds spatially asynchronously. The spatially explicit, individual-based patch-scale simulation model SATCHMO was developed to investigate cyclical succession in the paradigm of patch-dynamics for arid and semi-arid savannas. SATCHMO is designed to capture within-patch shrub population dynamics based on a grid of 51 m side length and a resolution of 10 cm. The model shrub characteristics were derived from *Acacia mellifera*, the main encroaching species in African savannas. The aim of SATCHMO is to give a detailed small-scale understanding of above- and belowground growth, competition, and mortality of savanna woody plants and the influence of precipitation and fire on patch transition frequencies, shrub growth rates, and shrub size frequencies. With SATCHMO, we want to identify the conditions leading to cyclical successions in general and shrub encroachment in particular. Soil moisture is the most important parameter in SATCHMO influencing growth, reproduction, and mortality of shrubs and grass tufts, and that mediates competition. To acknowledge the importance of belowground interactions in savannas, shrub root growth and competition are modelled spatially explicitly. The model output was successfully validated with morphometrical and spatial data from the field site in the South African Kalahari thornveld and with recent literature data on savanna woody species cover. Global sensitivity analysis with Latin hypercube sampling shows that soil moisture is the most important driver of shrub cover dynamics in semi-arid savannas.

1. Introduction

Savannas are ecosystems co-dominated by woody species and grasses in varying relative proportions. The widely discussed 'savanna question' is concerned with the factors that promote tree-grass coexistence and prevent savannas from being driven to open grassland or forests with a closed canopy. Many empirical studies and savanna models have proposed

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doi:10.1016/j.ecolmodel.2007.07.001

solutions to the savanna question (Walter, 1971; Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segarra, 1985; Menaut et al., 1990; Hochberg et al., 1994; Jeltsch et al., 1996, 1998, 2000; Higgins et al., 2000; Fernandez-Illescas et al., 2001; van Wijk and Bouten, 2001; van Langevelde et al., 2003). In the majority of studies, there is agreement on the four key factors determining savanna dynamics: water, nutrients, herbivory, and fire (Frost et al., 1986; Sankaran et al., 2004), but their relative importance has long been unclear. Recently, the analysis of data from 854 African field sites showed the paramount impact of mean annual precipitation (MAP) on woody cover as a switch effect at 650 mm MAP (Sankaran et al., 2005). Below this threshold, in arid and semi-arid savannas, herbivory, fire, and soil properties can only reduce woody cover below its maximum which depends linearly on MAP. Above this threshold, savannas are unstable and disturbances such as fire or herbivory are necessary to prevent canopy closure (Sankaran et al., 2005). The dominant role of water among the key determinants of savanna structure also highlights the greater importance of belowground interactions in arid and semi-arid savannas compared to aboveground interactions. Unfortunately, field methods for belowground investigations come at a much greater cost than aboveground methods so that simulation models provide an efficient alternative for capturing a reasonable amount of detail with similar effort for above- or belowground systems.

With respect to the mechanisms underlying tree-grass coexistence, both empirical evidence and model results are mixed and emphasize different aspects of savanna dynamics for the explanation of tree-grass coexistence. In their comprehensive review of savanna models, Sankaran et al. (2004) consider explanations focusing on the limiting role of demographic bottlenecks in woody species populations (Higgins et al., 2000; Jeltsch et al., 2000) to be superior to the traditional competition-based explanations (Walter, 1971; Walker et al., 1981; Walker and Noy-Meir, 1982; Eagleson and Segarra, 1985) because empirical evidence for rooting-niche separation and other competitive mechanisms is equivocal (Scholes and Archer, 1997; Sankaran et al., 2004; Wiegand et al., 2005) and resource competition alone does not produce coexistence in spatially explicit models (Jeltsch et al., 2000). Still, a unifying mechanism explaining tree-grass coexistence in savannas is lacking.

Furthermore, the 'savanna question' is not only an ecological issue but also has a socio-economic dimension. Shrub encroachment, i.e. the increase in density of woody plants often unpalatable to livestock, is observed in savannas all over the world reducing the amount and quality of grazing lands dramatically. So far, it was generally believed that overgrazing in combination with rooting-niche separation is primarily responsible for shrub encroachment. However, recent research has not only questioned the universality of the rooting-niche separation in particular and competition-based models in general but also the paramount importance of overgrazing for fostering shrub encroachment (Wiegand et al., 2005, 2006).

Wiegand et al. (2006) propose the patch-dynamics paradigm as a mechanism explaining tree-grass coexistence in arid savannas. The patch-dynamics concept is based on a cyclical succession that proceeds asynchronously in spatially distinct patches that constitute the savanna landscape. Patches cycle between woody and grassy dominance so that shrub encroachment is a natural phase in the cyclical succession. Patch-dynamics and overgrazing are not mutually exclusive explanations for shrub encroachment, but may enhance each other. If overgrazing occurs during the naturally encroached phase of the successional cycle, its effect on shrub cover increase will be greater than if it occurred during a non-encroached phase of the cycle. Moreover, the patch-dynamics paradigm does not exclude other theories about tree-grass coexistence, but can integrate many of the savanna theories put forward thus far because cyclical succession can be driven by a range of processes. For instance, the spatial and temporal overlap of localized rain events in arid savannas may induce mass germination of a shrub cohort and promote the transition of a grass-dominated patch to woody dominance. Empirical support for patch-dynamics is offered from paleoecological long-term studies in east African savannas that revealed cyclical changes in the relative abundance of trees and grasses at the local scale but stable proportions at the landscape scale (Gillson, 2004). The advantage – but also the challenge – of the patch-dynamics concept is its explicit consideration of spatial and temporal scales. While field studies are rarely able to cover several spatial and temporal scales (but see Gillson, 2004), simulation models do not suffer from such restrictions. In simulation models, processes can be implemented at one scale generating patterns at the next greater scale (Jeltsch et al., 1996; Wiegand et al., 2003). For this procedure to be successful, the processes prevailing at small scales have to be understood in detail before they can be generalized to larger scales. The great amount of detail necessary for a good understanding of small-scale processes with simulation models is supported by the accessibility of small-scale field data for model parameterization relative to data at larger scales.

In order to investigate cyclical succession at the patch-scale, we developed the small-scale spatially explicit, individual-based Savanna Patch Model (SATCHMO) for arid and semi-arid savannas (MAP < 650 mm). The focus of our model lies on savannas that receive less than 650 mm MAP because the continental-scale analysis of Sankaran et al. (2005) shows that water is the most limiting factor for woody cover and permits tree-grass coexistence in these savannas. The purpose of SATCHMO is to model within-patch population dynamics that give a detailed small-scale understanding of above- and belowground growth, competition, and mortality of savanna woody plants and the conditions leading to cyclical successions in general and shrub encroachment in particular.

2. Methods

2.1. Study area

SATCHMO is based on field data that were collected in semi-arid savanna in the Kalahari thornveld at Pniel Estates (28°35′S, 24°29′E), 30 km north of Kimberley, South Africa, between 2003 and 2005 (see also Meyer et al., 2005). Mean annual precipitation is 377 mm and mostly occurs as thunderstorms throughout the summer months (September–March).