Are savannas patch-dynamic systems? A landscape model

Aristides Moustakas[a,*], Konstantinos Sakkos[b], Kerstin Wiegand[a,1],
David Ward[c], Katrin M. Meyer[a,1], Dirk Eisinger[d]

[a] *Institute of Ecology, Friedrich Schiller University, Dornburger Str. 159, 07743 Jena, Germany*
[b] *Departament de Fisica i Enginyeria Nuclear, Universitat Politecnica de Catalunya, Campus Nord B4-B5, E-08034 Barcelona, Spain*
[c] *School of Biological and Conservation Sciences, University of KwaZulu-Natal, P. Bag X1, Scottsville 3209, South Africa*
[d] *Department of Ecological Modelling, UFZ-Centre of Environmental Research, P.O. Box 500136, 04301 Leipzig, Germany*

ARTICLE INFO

ABSTRACT

Savannas are ecosystems characterized by the coexistence of woody species (trees and bushes) and grasses. Given that savanna characteristics are mainly formed from competition, herbivory, fire, woodcutting, and patchy soil and precipitation characteristics, we propose a spatially explicit model to examine the effects of the above-mentioned parameters on savanna vegetation dynamics in space and time. Furthermore, we investigate the effects of the above-mentioned parameters on tree–bush–grass ratios, as well as the degrees of aggregation of tree–bush–grass biomass. We parameterized our model for an arid savanna with shallow soil depth as well as a mesic one with generally deeper and more variable soil depths. Our model was able to reproduce savanna vegetation characteristics for periods of time over 2000 years with daily updated time steps. According to our results, tree biomass was higher than bush biomass in the arid savanna but bush biomass exceeded tree and grass biomass in the simulated mesic savanna. Woody biomass increased in our simulations when the soil's porosity values were increased (mesic savanna), in combination with higher precipitation. Savanna vegetation varied from open savanna to woodland and back to open savanna again. Vegetation cycles varied over ~300-year cycles in the arid and ~220-year cycles in the mesic-simulated savanna. Autocorrelation values indicated that there are both temporal and spatial vegetation cycles. Our model indicated cycling savanna vegetation at the landscape scale, cycles in cells, and patchiness, i.e. patch dynamics.

1. Introduction

Savannas are ecosystems characterized by the coexistence of woody species (trees and bushes) and grasses (Scholes and Archer, 1997). The ratio between grass and woody vegetation as well as the total aboveground biomass characterizes the phases of savanna. Theoretically, tree–grass coexistence is possible if competition within life forms (tree–grass) is stronger than competition between life forms (Scholes and Archer, 1997). In savannas, usually the limiting factors to total aboveground green biomass are soil moisture and nutrient availability (Scholes and Archer, 1997). Savannas have annual precipitation that can vary from as little as 100 mm per year to 1300 mm per year (Belsky, 1990; Wiegand et al., 2006). Rain has a high degree of patchiness in time and space (Zucchini et al., 1992; Ward et al., 2004; Ward, 2009). Germination and seedling

survival of trees and bushes depends mainly on soil moisture, making recruitment episodic and rare (Sy et al., 2001; Barnes, 2001a). Thus, soil moisture is a key factor for savanna vegetation (Laio et al., 2002). Soil moisture is mainly a function of rainfall and soil properties such as porosity, water-holding capacity and soil depth (Rodriguez-Iturbe et al., 2001a,b; Fernandez-Illescas et al., 2001). These soil properties are patchily distributed within the savanna landscape (Scholes, 1990).

Fire plays an important but unclear role in savanna ecology because there are several contradictory studies on the effect of fire on savanna vegetation (Higgins et al., 2000; Russell-Smith et al., 2003). Even though fire has been proposed as a factor explaining tree–grass coexistence in savannas, the general applicability of these results is questionable. In arid savannas, the grass fuel load is often too low to support fires (Bond and Midgley, 1995; Ward, 2005; Meyer et al., 2005). Grazing, browsing, and woodcutting play an important role in savannas because selective suppression of some species favours the dominance of other species (Walker et al., 1987; Shipley et al., 1999). Furthermore, megaherbivores such as elephants and giraffes have been shown to be significant modifiers of woody–grass composition (Bond and Loffell, 2001). The effects of megaherbivores are reported to be more profound in

* Corresponding author. Current address: Institute of Integrative & Comparative Biology, Faculty of Biological Sciences, University of Leeds, Leeds LS2 9JT, UK.
 E-mail address: arismoustakas@gmail.com (A. Moustakas).
 [1] Current address: Ecosystem Modelling, University of Göttingen, Büsgenweg 4, 37077 Göttingen, Germany.

savannas receiving mean annual precipitation >650 mm (Walker, 1993; Sankaran et al., 2005).

Woody invasion, i.e. the increased dominance of woody species, often unpalatable to livestock, reduces livestock carrying capacity and biodiversity of savannas and is a widespread economic and ecological problem (Moleele et al., 2002). Woody invasion is a phenomenon observed in African (O'Connor and Crow, 2000) as well as in American (Archer, 1989) and Australian (Burrows et al., 1990) savannas. The causes of woody invasion (in South Africa often referred as "bush encroachment", or shrub invasion in the US) are poorly known (Ward, 2005). There are several studies attempting to explain the phenomenon (e.g. Walker and Langridge, 1996, 1997; Polley et al., 2002; Ward, 2005; Bond et al., 2003). Management techniques to prevent bush encroachment have been proposed (e.g. Winter, 1990). The techniques proposed focus mainly on grazing intensity and fire. However, given that savanna soil and vegetation cycles outlive researchers (Bernhard-Reverserat, 1982) it is difficult to follow savanna landscape patterns and vegetation composition in the field. Therefore, modelling is a useful tool for predicting future scenarios.

Much of the difficulty in savanna modelling and management arises from dealing with very different scales in time, space, and species interactions (see e.g. Wiegand et al., 2006). Multiple spatial scales are particularly difficult to address using differential equations, because these models focus mainly on population dynamics but not on their spatial distribution. An alternative approach is to focus on the spatial distribution of trees, grass, and bushes, and to develop models which focus on the factors affecting their growth based on their neighbouring plants, rather than trying to add interaction mechanisms to models based on more uniform population dynamics. One way to do this is by the use of grid-based simulation models. In these models, a grid of cells represents the spatial distribution of vegetation, e.g. cells may be occupied by grass, bushes, or trees (e.g. Jeltsch et al., 1996). Grid-based discrete time models depict spatial dynamics with rules describing how the occupancy of the grid cells changes from one time step to the next. In classic cellular automata, the state of each cell depends only on the content of that cell and adjoining cells during the previous time step (Wolfram, 1983; Ermentrout and Edelstein-Keshet, 1993). In contrast, in grid-based models, spatial interaction is possible on all scales.

Due to the advantages of spatially explicit models in such heterogeneous environments as savannas, savanna models are increasingly often spatial (e.g. Jeltsch et al., 1996; Higgins et al., 2000; Wiegand et al., 2006, 2008; Meyer et al., 2007b). While there are several good savanna models, there is still space for improvement as a combination of competition-based and demographic modelling approach is needed (Sankaran et al., 2004). The need for spatial models is also acknowledged (Jørgensen et al., 2008). Furthermore, most models focus either on one location exclusively, and/or they assume spatial homogeneity in terms of soil properties and moisture characteristics.

The globally reported increase of woody species in savannas (Sankaran et al., 2005), is not well understood (Ward, 2005). As a result, there is a need for a new theory explaining savanna dynamics. Recently, Gillson (2004a,b) and Wiegand et al. (2005, 2006) developed the idea that savannas are patch-dynamic systems. According to this theory, savannas are patch-dynamic systems composed of many patches in different states of transition between grassy and woody dominance. While there is evidence that savannas are patchy (Gillson, 2004a; Wiegand et al., 2005), the spatiotemporal dynamics of the patchiness might be a key to understanding tree–grass coexistence (Wiegand et al., 2006). The patch dynamics hypothesis is based on two different spatial scales, the patch scale and the landscape scale, and ultimately requires investigations at both scales (Meyer et al., 2007a). Following the results from patch scale modelling (Meyer et al., 2007a,b), in this study, we focus on the landscape scale.

Given that a key to understanding savanna dynamics may lie in recognizing their patchiness (Wiegand et al., 2006), we propose a spatially explicit model that includes the spatial variance of precipitation and soil characteristics on large spatial scales and their effects on the patchy characteristics of aboveground biomass. The aim of this paper is to introduce the model and to investigate basic properties of the spatiotemporal vegetation dynamics exemplified by two model parameterizations, representing an arid and a mesic savanna.

2. Problem formulation

2.1. Overview

The purpose of the model is to improve our understanding of the ecology of savannas at the landscape scale. To keep things simple, we focus on two hierarchical levels: vegetation patches and the landscape. The main purpose of this model is to detect (if any) vegetation cycles in savanna ecosystems.

Based on this purpose, we used a grid-based, spatially explicit, individual-based model (Silvert, 1993) to follow the dynamics of three life forms, following trees and bushes on an individual basis and grass biomass within a cell. The model represents part of a savanna by a rectangular grid of cells. Each cell is characterized by a number of trees and bushes and grass biomass. Admittedly there is no clear definition of what a tree and a bush is, as in different areas woody species are found both as bushes as well as trees (e.g. *Acacia tortilis*, pers. obs.). In this model we define as bushes woody species that are normally multi-stemmed, their maximum height rarely exceeds 2 m and may reproduce vegetatively, such as *Acacia mellifera*. We define as trees woody species with maximum height normally exceeding 2 m and reproducing sexually (e.g. *Acacia erioloba*). Each tree and bush has a unique biomass (size) and age. Grass is characterized by grass biomass only. Additionally, each cell has a value of soil porosity and soil depth. The biomass of trees, bushes, and grass in each cell changes on a daily basis through a set of rules. These rules are the key part of the model and are intended to represent the dynamics of savanna vegetation as realistically and parsimoniously as possible.

For the simulations shown in this paper, we chose a grid (X, Y) of 100×100 cells. Each cell corresponds approximately to 3 km on a side, giving a total area of about 90,000 km^2. The cell is updated with a daily time step, meaning that the trees, bushes, and grass might grow on a daily basis depending on soil moisture and season of the year (seasonality). The number of simulation years (S) was 2100. The first 100-year results were omitted as the model reached a stable savanna state on average at a maximum of 100 years. In the results presented, we start numbering simulation years from year 100, the year that the model has reached a stable savanna state.

2.2. Vegetation properties

Several size-classes of bushes and trees can exist within each cell. Thus each cell represents a savanna patch even though several cells together can form larger savanna patches.

Tree and bush individuals are attributed by size and age. Grass has only size as an attribute, which corresponds to grass biomass. This rule is based on the idea that vegetation biomass is constrained by environmental conditions, predominantly rain and active soil depth (Wiegand et al., 2005). Limits to tree height and thus to tree biomass derive from hydraulic lift limits as described by Ryan and Yoder (1997) and Koch et al. (2004). Given that trees are usu-