Ecological Modelling 326 (2016) 13–22

Contents lists available at ScienceDirect

Ecological Modelling

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

Same rainfall amount different vegetation—How environmental conditions and their interactions influence savanna dynamics

Britta Tietjen[a,b,*]

[a] Freie Universität Berlin, Institute of Biology, Biodiversity and Ecological Modeling, Altensteinstr. 6, D-14195 Berlin, Germany
[b] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), D-14195 Berlin, Germany

ARTICLE INFO

Article history:
Available online 29 June 2015

Keywords:
Dryland
Ecohydrology
Soil texture
Spatial heterogeneity
Water availability
Water-vegetation-interactions

ABSTRACT

Water limited ecosystems such as savannas are characterized by strong interactions between water fluxes and vegetation. However, the fraction of mean annual rainfall that is transformed into plant available water, is not only dependent on the prevailing vegetation cover, but also on abiotic factors such as soil texture and topography as well as intra-annual precipitation patterns. Most models projecting savanna vegetation cover dynamics have not accounted for these factors until now. Here, it is highlighted how and why spatial heterogeneity in water availability and vegetation cover is closely related to abiotic conditions. The role of soil texture, slope and precipitation patterns on water availability and emergent vegetation patterns are systematically tested by using the process-based, spatially explicit model EcoHyD. The analysis shows that the same overall precipitation will result in qualitatively different vegetation cover, depending on environmental conditions. This highlights that models of savanna systems should indeed resolve water dynamics and the feedbacks between water and vegetation with care. In addition the study discusses that future savanna models should go one step further and include phenotypic plasticity and demographic processes to better resolve individual plant responses towards water stress.

1. Introduction

In water limited ecosystems such as savannas, one might think that regions that receive more precipitation are the more productive ones. However, the truth is not as simple, as drylands are characterized by complex interactions between biotic (Maestre et al., 2010) and abiotic (Nano and Clarke, 2010) factors, which can strongly impact each other (Maestre et al., 2005, 2006). Their interplay determines the share of rain that will in the end contribute to plant growth. A key determinant in this interaction is soil texture (Lane et al., 1998), which directly impacts water fluxes into the soil, within the soil and to the plant. The landscape structure, e.g., in terms of its heterogeneity or slope, is also decisive for the speed of runoff and erosion processes and for degradation of vegetation (Ludwig et al., 2005). Last but not least, precipitation is not evenly distributed within a year, and the magnitude of single precipitation pulses determines how much water is stored in the soil at different depths (Loik et al., 2004) and how plants respond in terms of germination and growth to this temporally limited water availability. The hierarchy of ecosystem responses to precipitation pulses of different intensity was described in a general framework that Schwinning and Sala (2004) developed for arid and semi-arid ecosystems. Their examples clearly show that the magnitude of single rainfall events plays a key role in the specific ecosystem responses that are triggered: For example carbon fixation can already be detected for a rainfall event of 3 mm (Schwinning et al., 2003), while germination of many desert plants requires a rainfall event of at least 25 mm (Beatley, 1974).

In dryland systems, not only is water availability controlling plant growth and thus standing vegetation, but vegetation also exhibits strong impacts on water dynamics. Plants regulate water fluxes to the atmosphere by transpiration or lead to reduced evaporation by shading (Huxman et al., 2005). In addition, they control water fluxes into the soil (e.g., directly by preferential flow paths along root systems and indirectly by impacting the abundance of ground dwelling organisms) by increasing the infiltration capacity (HilleRisLambers et al., 2001, Walker et al., 1981) or by decreasing overland fluxes due to higher surface roughness at vegetated patches (Bartley et al., 2006).

Since these complex interactions between water and vegetation have gained large attention during the past century, the aim of this study is to demonstrate model advances in the description of

* Corresponding author at: Freie Universität Berlin, Institute of Biology, Biodiversity and Ecological Modeling, Altensteinstr. 6, D-14195 Berlin, Germany.
Tel.: +49 30 838 53158.
E-mail address: britta.tietjen@fu-berlin.de

http://dx.doi.org/10.1016/j.ecolmodel.2015.06.013
0304-3800/

ecohydrological processes and to point out where the future generation of ecohydrological model approaches of savanna ecosystems could head. For this, a short history of dryland vegetation models is presented in the following. Afterwards, a fully coupled ecohydrological model will be introduced to demonstrate present modeling potential to investigate the impact of environmental conditions on savanna dynamics, and to motivate future model developments.

Ecological modeling of dryland ecosystems began in the late 1970s (Noy-Meir, 1978; Tadmor et al., 1977). These first models were spatially implicit ordinary differential equations (ODEs) that include very simplified feedbacks between water and vegetation. They were used to analyze equilibrium conditions for grasses and woody vegetation under different grazing intensity (e.g., Walker et al., 1981) or for different nutrient levels (e.g., McMurtrie and Wolf, 1983) and were thoroughly investigated during the subsequent decade (e.g., Rietkerk and van de Koppel, 1997). ODE models typically do not assess the impact of slope or intra-annual rainfall variability (cf. Baudena et al., 2007 for a study that works around this shortcoming for the case of rainfall intermittency in an ODE model).

Since the importance of spatial heterogeneity was increasingly acknowledged (Fowler, 1986; Snyder and Tartowski, 2006), ODEs were extended by the consideration of space, leading to partial differential equations (PDEs), e.g., to account for water redistribution by diffusion or runoff (e.g., HilleRisLambers et al., 2001). PDEs are able to produce fascinating spatial patterns of vegetation, including stripes, rings or dotted spots of vegetated landscape (e.g., Meron et al., 2004, Rietkerk et al., 2002; von Hardenberg et al., 2001). However, they are normally solely driven by climatic means and neglect seasonality, the impact of rainfall intensity of single events, or demographic processes. Differing soil properties can only be implicitly included by changing for example the rate of infiltration or evaporation, which was for example discussed in an analysis on self-organizing ecosystems by Rietkerk et al. (2002). Therefore, the ability of PDE models to assess whether and how the same rainfall amount translates into water availability to plants for different soil textures, slopes or intra-annual rainfall variability, in an applied ecological context, is very limited.

In addition to these rather abstract differential equation models that describe gradual changes in time, a new type of model evolved, namely those that simulate spatially explicit, individual plant behavior, and are called agent-based or individual-based models (IBMs). These models include for example the demographic behavior of trees (e.g., Wiegand et al., 1995), or allow for variation between individuals (e.g., SATCHMO model, Meyer et al., 2007), but cannot be traced analytically any longer. However, although these models usually describe biological processes in more detail than differential equations models, such as the impact of plant age on seed production, they largely neglect the role of water for vegetation dynamics and assess water availability on an annual basis (e.g., see a review on model structures in Tietjen and Jeltsch, 2007). Often, annual rainfall is directly used to assess water availability without considering soil texture, topography or the intra-annual rainfall distribution, although for example Jeltsch et al. (1997) showed with a grid-based vegetation model including two soil layers that variable rainfall can be easily included.

In the past decade, trans-disciplinary models such as the ecohydrological model EcoHyD (Lohmann et al., 2012, 2014; Tietjen et al., 2009, 2010) started to bridge the enormous gap between the insufficient description of water dynamics in many vegetation models and the tradition of classical models on soil water dynamics to include vegetation as time series without accounting for full feedback mechanisms (e.g., SOILWAT: Bradford and Lauenroth, 2006; SWAT: overview in Douglas-Mankin et al., 2010).

In this study, it is demonstrated, how ecohydrological models such as EcoHyD, which include full feedback loops between water and vegetation, can assess how rainfall is transformed to plant available water and the productivity of vegetation under different environmental conditions. These conditions include annual precipitation, its intra-annual variability, soil texture, and topography. The results are used to highlight the major advantages of fully coupled ecohydrological models compared to previous approaches, which are too simplistic in their description of abiotic conditions, and to discuss ideas, where the next generation of ecohydrological model approaches should head.

2. Methods

This study is an application of the ecohydrological, spatially explicit savanna model EcoHyD (Tietjen et al., 2009, 2010). EcoHyD was selected for its ability to describe fully coupled water dynamics and vegetation dynamics. Model experiments were designed to assess the impact of mean annual rainfall, intra-annual variability of rainfall, soil texture and slope on water availability and vegetation cover. Model results were evaluated in terms of mean values and emerging spatial patterns. The following sections provide an overview of the model, its parameterization, and the post-processing of model output into the results of this study.

2.1. Model description

The model description roughly follows the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006, 2010), with greater detail on the overview part, since model details can be found in Tietjen et al. (2009, 2010).

2.1.1. Purpose

The model EcoHyD was developed to assess the impact of climate change on different savanna sites. It was a first attempt to overcome the shortcoming of dryland grazing models to resolve the impacts of climate change on the coupled dynamics of water and vegetation adequately, especially in terms of changes in hydrological fluxes (Tietjen and Jeltsch, 2007). The model was afterwards refined in several studies to investigate the role of different management strategies in terms of manual shrub reduction (Jeltsch et al., 2010), grazing intensity (Lohmann et al., 2012) and the application of prescribed fires (Lohmann et al., 2014). It was also coupled to an erosion model to study erosion risks dependent on prevailing vegetation cover (Mueller et al., in press). In the context of this study, the model was used to demonstrate the importance of mean annual precipitation and its intra-annual variability, soil texture, and topography for mean water availability to plants and for resulting plant cover and their emerging spatial heterogeneity.

2.1.2. Entities, state variables, and scales

EcoHyD consists of a landscape, in the parameterization for this study totaling 6.25 ha, that is divided into 50 by 50 grid cells, each with a size of 5 m by 5 m (Fig. 1). It consists of a hydrological and a vegetation sub-model that are closely interlinked and that act on different time resolutions to adequately describe relevant fluxes and changes (hydrological model: hours to days, vegetation model: biweekly to yearly processes).

The hydrological sub-model describes soil moisture in two soil layers as well as surface water. In the vegetation model, the cover of two broad plant function types is distinguished, namely perennial herbaceous vegetation and woody vegetation (hereafter referred to as grass and shrubs). The dynamics of these five variables are driven by hourly data on temperature and precipitation. Hydrological fluxes are strongly influenced by site-specific values of soil texture and topography.