Applied Mathematical Modelling 40 (2016) 6165–6197

Contents lists available at ScienceDirect

Applied Mathematical Modelling

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

Tree–grass interaction dynamics and pulsed fires: Mathematical and numerical studies

A. Tchuinté Tamen [a,f], Y. Dumont [b,*], J.J. Tewa [c,f], S. Bowong [c,f], P. Couteron [d,e]

[a] Faculty of Science, University of Yaounde 1, Cameroon
[b] CIRAD, Umr AMAP, Montpellier 34398, France
[c] LIRIMA, GRIMCAPE, University of Yaounde 1, Cameroon
[d] IRD, Umr AMAP, Montpellier, France
[e] Plant Systematic and Ecology Laboratory, Department of Biology, Higher Teachers' Training College, University of Yaounde I, P.O. Box 047 Yaounde, Cameroon
[f] CETIC project, University of Yaounde I, Cameroon

ARTICLE INFO

Article history:
Received 11 February 2015
Revised 16 December 2015
Accepted 13 January 2016
Available online 3 February 2016

Keywords:
Savanna
Tree–grass competition
Fires
Impulsive differential equations (IDE)
Bifurcation
Nonstandard numerical scheme

ABSTRACT

Savannas are dynamical systems where grasses and trees can either dominate or coexist. Fires are known to be central in the functioning of the savanna biome although their characteristics are expected to vary along the rainfall gradients as observed in Sub-Saharan Africa. In this paper, we model the tree–grass dynamics using impulsive differential equations that consider fires as discrete events. This framework allows us to carry out a comprehensive qualitative mathematical analysis that revealed more diverse possible outcomes than the analogous continuous model. We investigated local and global properties of the equilibria and we showed that various states exist for the physiognomy of vegetation. Though several shifts between vegetation states appeared to be determined by fire periodicity, we showed that direct shading of grasses by trees is also an influential process embodied in the model by a competition parameter leading to bifurcations. Relying on a suitable nonstandard simulation scheme, we carried out numerical simulations in reference to three main climatic zones as observable in Central Africa.

1. Introduction

In savannas, trees and grasses typically coexist (Menaut [1]). Fire is recognized as playing a major part in the dynamics of this biome. The nature of tree–grass interactions and fire regimes strongly vary along environmental gradients in tropical savannas. Fire is more intense in wet than in arid savannas, where lower water availability leads to lower grass, i.e., fuel load, production. Thus fire is expected to control tree–grass dynamics in wet savannas (Frost et al. [2]). But two non mutually exclusive hypotheses for tree–grass coexistence have been introduced during these last decades. First, Walter [3] proposed the idea that trees and grass exploit two different rooting niches. Grasses are rooted in superficial soil layers and first use the incoming water, whereas tree roots are situated in subsoil, so that trees could grow only where enough water reached deeper soil horizons. This idea was developed analytically by Walker and Noy-Meir [4] using a Lotka–Volterra theory of co-existence between competitors. The second hypothesis says that tree–grass coexistence is driven by limited opportunities for seedlings to escape both droughts and the flame zone into the adult stage (Hochberg et al. [5]; Higgins et al. [6]). In areas where tree seedlings succeed to establish in spite of competition with grasses, they are burnt by frequent grass fires (Higgins et al. [6]).

* Corresponding author. Tel.: +33 467 614 908.
E-mail address: yves.dumont@cirad.fr (Y. Dumont).

http://dx.doi.org/10.1016/j.apm.2016.01.019

Savanna fires are frequent, occurring up to every 1–5 years in wet savannas (Frost & Robertson [11]) though the fire return time is usually a decreasing function of mean annual precipitation (MAP). Fuel load made of dead aerial grass parts typically ranges between 2 and 10 t.ha^{-1} of dry matter (Lacey et al. [7]; Stronach & Mac-Naughton [8]; Menaut et al. [9]; Mordelet [10]) and flame height is usually 2–3 m high (Frost & Robertson [11]). Although the fire burns most or all the aboveground grass biomass, the large underground root systems of perennial grass species enable most of the tufts to survive even the most intense fires and to rapidly establish new shoots before the onset of the rainy season. In contrast to grasses, trees which are less than 2 m high may either succumb to fire or have to resprout from roots and have their growth delayed (Bond and Midgley [12]). Mature trees (>8 m) and shrubs beyond 2 m are more fire resistant and only experience partial die-back (Menaut & César [13]; Gillon [14]). Early fires (in the beginning of the dry season) are less violent than late fires and have a lower impact on tree regeneration (Abbadie et al. [15]).

Africa is a land of extreme contrasts in rainfall distribution and the time of year during which rainfall occurs (Janowiak [16]). Hence essential resource availability (e.g., water) is discontinuously available and the availability of these resources impacts the ecosystem as discrete pulse events interspersed among long periods of limited resource availability (Schwinning et al. [17]). When soil resource supply (e.g., moisture) is temporally variable, trees and grasses will experience two distinct phases of resource availability: pulse and inter-pulse periods. Pulse periods occur when resources are high, production is enhanced and biomass accumulation (notably grass fuel load) occurs. In contrast inter-pulse periods occur when resources are too low for most tree and grass to take up and more mortality due to resource deficits takes place (Goldberg & Novoplansky [18]; Noy-Meir [19]).

Fires are sudden events that consume trees and grass biomass (Scheiter [20]). The broad objective of this study is to examine the influence of pulse events with regard to fires' impacts on the tree–grass dynamics along the rainfall gradient in Africa. Tree–grass savanna dynamics cannot be modeled without integrating the important role of fires (Tilman [21]; Higgins et al. [22]; Sankaran et al. [23], [24]; D'Odorico et al. [25]; Accatino et al. [26]; Beckage et al. [27]; Staver et al. [28]; Yatat et al. [29] and Tchuinté Tamen et al. [30]). This paper extends our earlier work (Tchuinté Tamen et al. [30]) where we considered a time-continuous tree–grass interaction model that featured a fairly generic family of nonlinear functions of grass biomass to model fire intensity and its impact on trees. We have shown that the continuous model is able to predict a variety of dynamical outcomes. Notably, the number of equilibria featuring tree–grass coexistence depends on the characteristics of fairly generic Monod functions used to model the fire impact on tree dynamics. Moreover, we have shown that various bistability situations occur among forest, grassland and tree–grass (i.e., savanna) equilibria (for more detail see Tchuinté Tamen et al. [30]). Of course, in practice, fires are not continuous. Recent studies of the interactions between fire and vegetation are based on stochastic approaches because of the random and unpredictable nature of fire occurrences (D'Odorico et al. [25]; Beckage et al. [27]).

In Section 2 we will present the model with pulse fires. The theoretical analysis is developed in Section 3. We show that the system admits four equilibria among which two trivial equilibria (the bare soil and the forest equilibria), and two periodic equilibria (the periodic grassland and the periodic savanna equilibria). We show that there are various bistabilities: between forest and grassland; between forest and savanna. Local and global stabilities are distinguished using classical tools such as Floquet multipliers and comparison theorem. We highlight thresholds that summarize the dynamics of the model and explain the theoretical and ecological meanings of these thresholds. Prior to illustrate our theoretical results numerically in Section 5, based on the scheme developed in [30] we develop a reliable nonstandard finite difference method (NSFD) that preserves the qualitative properties of the system (Anguelov et al. [31–33]) in Section 4. Section 6 concludes the paper. Some mathematical details are included in appendices.

2. The mathematical model

In savanna environment, fire intensity is tightly linked to dried grass biomass that remains during the dry season (Higgins et al. [22]). During the last decades, the effects of fire on vegetation dynamics have been studied (Scholes et al. [34]; Higgins et al. [6]). Most of the models associated to or derived from these studies are ordinary differential equations (ODE) which assume that fires occur continuously with a fixed frequency. However fires are sudden event that consume grass biomasses and kill or harm tree seedlings (Scheiter [20]). The season of burning and the time between recurring fires determine trees and grass physioniomies in most ecosystems and especially in the savanna biome (Thonicke et al. [35]). In this paper we present a new tree–grass model that aim to contribute to our understanding about how pulse fire shapes vegetation dynamics in fire-prone savanna-like ecosystems. We consider fire as discrete events and derive the following impulsive differential system

$$
\begin{cases}
\left.\begin{aligned}
\frac{dG}{dt} &= \gamma_G G\left(1-\frac{G}{K_G}\right)-\delta_{G0}G-\gamma_{TG}TG,\\
\frac{dT}{dt} &= \gamma_T T\left(1-\frac{T}{K_T}\right)-\delta_T T,
\end{aligned}\right\}, \quad t \neq t_n, n = 1, 2, \ldots, N_\tau \\
\left.\begin{aligned}
\Delta G(t_n) &= G(t_n^+) - G(t_n) = -\lambda_{fG}G(t_n),\\
\Delta T(t_n) &= T(t_n^+) - T(t_n) = -\lambda_{fT}\omega(\lambda_{fG}G(t_n))T(t_n),
\end{aligned}\right\}, \quad t = t_n, n = 1, 2, \ldots, N_\tau \\
G(t_0^+) = G_0,\\
T(t_0^+) = T_0,
\end{cases}
\tag{1}
$$