

Analysis of Catastrophic Shifts between Different Moving Vegetation Patterns

Stefano De Gennaro^a, Lucia Russo^{b*}, Francesco Giannino^c, Pier Luca Maffettone^a, Stefano Mazzoleni^c, Constantinos Siettos^d

^aDipartimento di Ingegneria Chimica, dei Materiali e della Produzione Industriale, Università Federico II, Napoli, Italy

^bIstituto di Ricerche sulla Combustione, CNR, Napoli, Italy

^cDipartimento di Scienze Agrarie, Università Federico II, Portici, Italy.

^dDipartimento di Matematica e Applicazioni, Università Federico II, Napoli, Italy.

lucia.russo@irc.cnr.it

There are many ecological evidences that regular vegetation patterns in semi-arid regions may be interpreted has early warning signals of catastrophic transitions to an irreversible homogeneous bare-soil state (desertification). In this framework, the paper analyses the occurrence of catastrophic shifts between different moving vegetation patterns. The study is conducted by numerical simulations of a system of partial differential equation which describes the dynamics of the biomass and water as a reaction-diffusion process. The model also includes the effect of self-toxicity produced by the biomass, which increases the capability of the system to self-organize in the space and time. The analysis reveals the existence of a variety of different periodic patterns moving in the space, like travelling waves and/ or pulse-like backfiring solutions. The precipitation rate is considered as system parameter and its effect on the vegetation patterns evolutions is analysed.

1. Introduction

Climate changes are becoming the most serious and dangerous environmental phenomena which may cause catastrophic shifts with irreversible and abrupt changes in the ecosystems (e.g. desertification, extinction of species, etc.). Even if climate changes may appear gradual and slow, changes in ecosystems may appear, abruptly and thus catastrophically leading to irreversible mutations of the ecosystems itself. However, while there are more and more confirming observations which attribute many catastrophic shifts to climate changes, it is not clear yet in ecology how climate changes interfere at different scale in time and space on these phenomena (Scheffer et al. 2001). Many studies have attributed such catastrophes to the presence of two possible, alternative stable states in which the ecosystem can maintain its equilibrium (Scheffer and Carpenter, 2003). From a nonlinear dynamical point of view, this means that the ecosystem should be modelled as a dynamical system which has at least two attracting (stable) steady states, that is, it should be bistable. Commonly, the nonlinearity, which is responsible of the bistability, comes from the modelling of the positive feedback control between consumers (e.g. biomass/vegetation) and limiting resource (e.g. water/nutrients) which is the main mechanism that has been considered the reason of the catastrophic ecosystem shifts (Rietkerk and van de Koppel, 1997). When the distribution of the consumer/resource on the space is not important, the feedback control law can be lumped, giving rise to O.D.Es (mean field approach) which do not take into account spatial interactions. While the mean field analysis can give reasonable predictions for ecosystems where the catastrophic shifts occurs at intrinsically homogeneous level (Russo et al. 2016, Spiliotis and Russo 2016, Russo et al. 2017), there are many ecosystems in which self-organized regular/irregular spatial patterns are the demonstration of an essential link between a feedback control at different spatial scales (Scheffer et al. 2004).

An important example of these bistable ecosystems are the vegetation ecosystems in arid and semi-arid areas (van de Koppel et al. 1997; Rietkerk et al. 1997, 2004; Scheffer et al. 2009). Indeed, for the vegetation systems the spatial re-organizations and interactions between biomass and water is of fundamental importance, as a consequence the feedback control is scale-dependent (Scheffer et al. 2004). Many are the

observations confirming these modelling ideas (Klausmeier, 1999; Couteron and Lejeune 2001, HilleRisLambers et al. 2001; Von Hardenberg et al. 2001; Rietkerk et al. 2002; Shnerb et al. 2003; Lejeune et al. 2004). For these reasons, many studies propose models in form of partial differential equations (P.D.E.s) like pattern forming reaction/diffusion type systems (e.g. Klausmeier, 1999,). The underlying mechanism is a feedback control of the water on the biomass/vegetation which at short range acts positively, whereas at long range negatively (Rietkerk et al. 2000). From the other hand, the biomass diffuses very slowly in the space whereas the water diffuses fast. The nonlinear feedback control together with the different diffusion rates of the biomass and the water resembles the inhibitor/activator mechanism proposed by Turing to model the morphogenesis (Turing, 1952). Such reaction/diffusion models, indeed, exhibit bistability between a specific spatially structured and homogeneous state. Thus, PDEs in the form of Turing-type reaction/diffusion models may predict catastrophic shifts at large spatial scales between coexisting stable states in vegetation distributed ecosystems (Rietkerk et al. 2004). Thus, since the global climate changes include the gradual reduction of the rainfall in semi-arid areas, the understanding of the effect of the precipitation rate on the vegetation patterns is crucial for preventing the catastrophic shifts toward the bare soil state which represents the irreversible desertification of the landscape.

To this aim, following the work of Carteni et al. (2012) and Marasco et al. (2014), the paper analyses the effect of the precipitation rate on the vegetation patterns, the coexistence between different vegetation patterns as well as the possible catastrophic shifts which may be observed in vegetation distributed ecosystems. The model is a couple PDEs of reaction-diffusion type, in term of biomass and water (Klausmeier, 1999), which also includes a local negative feedback due to a toxic compounds produced by the biomass itself (Carteni et al., 2012). For a preliminary investigation, the model is considered one-dimensional in the space with periodic-boundary conditions.

2. The reaction/diffusion PDEs model

The analysed model stems by the ones of Klausmeier (1999) and Carteni et al. (2012). It is based on three state variables B , W and T representing biomass, soil water and toxic compounds respectively.

The dynamics of this soil-plant-atmosphere system is modelled taking into account the following mechanisms:

- plant biomass grows according to water availability
- soil water content is affected by rain, evaporation and plant uptake (considered as equal to transpiration)
- litter produces toxic compounds that are degraded in the soil according to environmental conditions (precipitation and temperature), exerting a negative effect on plant growth performance

Under these assumptions, the mathematical model consists of the following set of nonlinear partial differential equations:

$$\begin{cases} \frac{\partial B}{\partial t} = cB^2W - (d + sT)B + D_B \Delta B \\ \frac{\partial W}{\partial t} = p - rB^2W - lW + D_W \Delta(W - \beta B) \\ \frac{\partial T}{\partial t} = \gamma(d + sT)B - (k + \varepsilon p)T \end{cases} \quad (1)$$

The plant biomass exponentially grows proportionally to water availability, whereas the mortality is due to a constant loss rate d and an extra loss induced by T concentration due to the negative feedback, whose effect depends on plant sensibility s . Plant vegetative propagation is represented by a dispersal term of coefficient D_B . Furthermore, water W , representing both deep soil and surface water, is supplied uniformly due to precipitation at rate p and lost due to evaporation at rate l ; plants take up water at rate r , and finally water diffusion is modelled as in Von Hardenberg et al.(2001) in which the coefficient D_w is reduced by the presence of the plant biomass with a constant factor β . Finally, toxic compounds are produced by a fraction of the dead biomass and are reduced by decay and water precipitation processes by means of the parameters k and ε , respectively.

The parameters c , d , p , r and γ are required to be positive since we presume that biomass-water dynamics cannot be decoupled and that it would not be realistic to suppose the non-existence of an intrinsic mortality for the plants or the total absence of precipitation, especially because timings related to the emergence of ring patterns are considerably extended. Moreover, l , s , ε , k , D_B , D_W are all supposed to be non negative in order to respect their biological meaning. The definition of the parameters and their fixed values are reported in Table 1.

Table 1 : Definition and values of parameters

Parameter	Description	Units	Values
c	Growth rate of B due to water uptake	$\text{m}^4 \text{d}^{-1} \text{kg}^{-2}$	0.002
d	Death rate of biomass B	d^{-1}	0.001
k	Decay rate of toxicity T	d^{-1}	0.01
l	Water loss due to evaporation and drainage	d^{-1}	0.01
p	Precipitation rate	$\text{kg d}^{-1} \text{m}^{-2}$	[0, 4]
q	Proportion of toxins in dead biomass	–	0.05
r	Rate of water uptake	$\text{m}^4 \text{d}^{-1} \text{kg}^{-2}$	0.035
s	Sensitivity of plants to toxicity T	$\text{m}^2 \text{d}^{-1} \text{kg}^{-1}$	0 or 0.2
w	Washing out of toxins by precipitation	$\text{kg day}^{-2} \text{m}^{-2}$	0.001
D_B	“Diffusion coefficient” for biomass	$\text{m}^2 \text{d}^{-1}$	0.01
D_W	“Diffusion coefficient” for water	$\text{m}^2 \text{d}^{-1}$	0.8

3. Moving vegetation patterns and range of stability

The present study analyses the vegetation patterns appearing changing the precipitation rate p by numerical simulations of the system Eq. (1). To this aim numerical simulations has been performed by applying a finite different central scheme to the PDE system (Eq.1) in one dimensional domain and periodic boundary conditions. The numerical results reveal that, depending on the precipitation rate p and on the initial conditions, different vegetation patterns may be found. In particular, three kind of different solutions have been found. The contour plots of these solutions, in terms of space and time, are reported in Fig.1 where, for the sake of simplicity, just the biomass has been represented as state variable. All the solutions show periodicity in time and space. In particular, in Fig.1 (a) it is reported a travelling wave with one peak (TW1), that is a wave of biomass (Fig.2 (a)) which travels with constant velocity and with one maximum along the domain. Of course, the other two variables, W and T , will also travel with the same velocity (Fig.2 (b) and (c)). This solution is, thus, defined by the following equation:

$$u(x, t) = f(x \pm ct) \quad (2)$$

where c is the velocity of the travelling wave. The second type of solution, reported in Fig. 1 (b) is still a travelling wave but now the periodicity is the half both in space and in time. Two peaks appears along the domain and, of course, the velocity is doubled. This solution will be called TW2. The third and last type of solution, reported in Fig. 1 (c), is the most intriguing and unusual. It is characterized by two peaks which travel along the domain in opposite directions. When they meet, they annihilate and then they re-fire changing both directions.

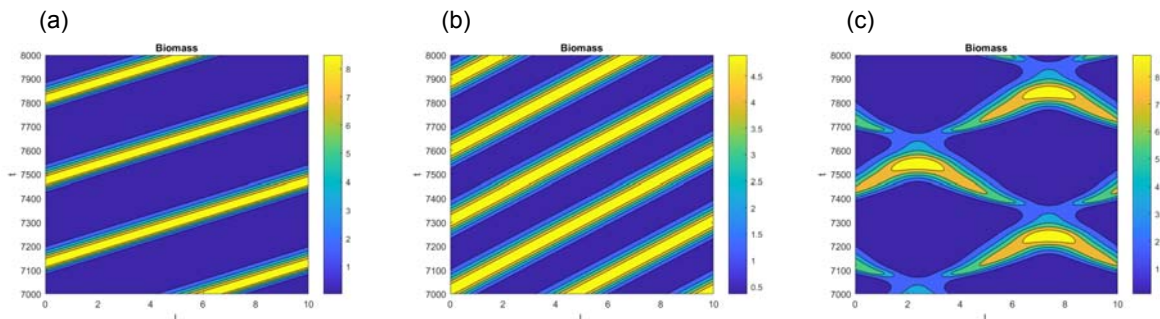


Figure 1: Contour plots of the different solutions for the biomass. (a) Traveling wave with one peak: TW1 (b) Traveling wave with two peaks: TW2 (c) Backfiring.

The solution is still periodic in the time but not anymore in the space and it will be called backfiring (BF) as defined in Zimmermann et al. (1997) for a pattern forming catalytic surface.

From a biological point of view, the following explanation may be given for the formation of vegetation patterns continuously moving in the space. The biomass generates toxic compounds (also called auto-toxicity (Marasco et al. 2014)), which, in turn, reduce the rate of biomass growing (see Figure 2 (a) and (c)): there is a negative feedback between biomass and auto-toxicity. In practice, the substance produced by degradation from plants is harmful to the plants themselves. For this reason, the biomass spreads in virgin areas, free from toxicity. But again, after the shift, biomass will produce new toxicity and so it spreads continuously: the result is a wave that travels over time. Moreover, as we can see in Figure 2, there is a synergy between biomass and water. The first needs water to grow up, so when we have the maximum of biomass, we expect the minimum of water (Figure 2 (a) and (b)).

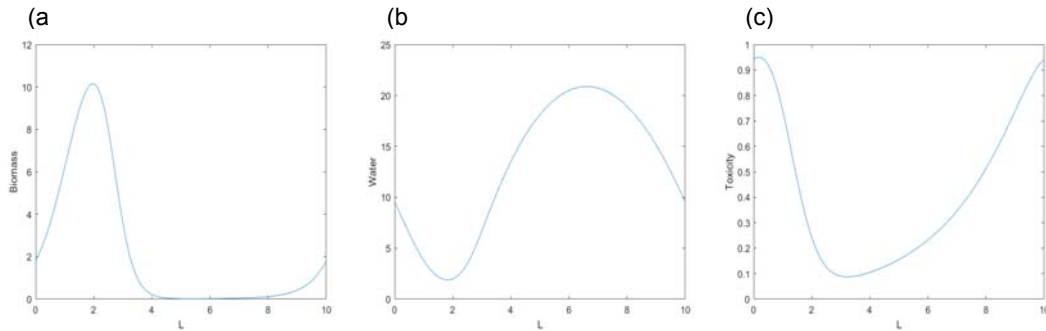


Figure 2: Spatial profiles of the traveling wave solution with one peak at a fixed time value. (a) Biomass. (b) Water. (c) Toxicity.

Finally, we computed by numerical simulations the range of stability of the three kind of solutions over the parameter range $p \in [0,4]$. The results are reported in Figure 3. It can be observed that there are wide ranges of the parameter, where the solutions are all stable.

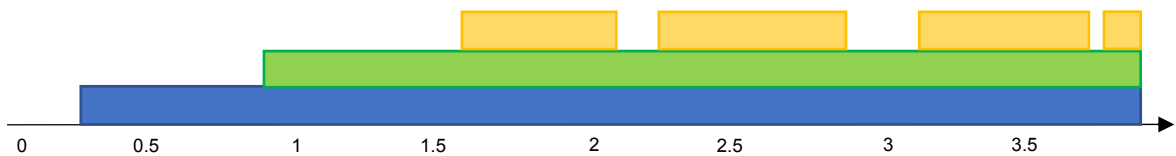


Figure 3: Range of stability of the different solution. ■ Traveling wave with one peak. ■ Traveling wave with two peaks. ■ Backfiring.

4. Catastrophic shifts between different moving vegetation patterns

As a consequence of the observed multistability, different types of catastrophic shifts may manifest. In particular, for a fixed value of the precipitation rate and in a region where multistability is present, catastrophic shifts may manifest as consequence of a perturbation of the state variable. Indeed, because each stable solutions will be characterized by its own basin of attraction (the set of initial conditions which will end to the considered stable solution), a perturbation of the state variable can cause the crossing of the basins boundaries, letting the system to shift from one solution to another. From the other hand, catastrophic shifts may also appear as consequence of a perturbation of the parameter. This is the case in which the parameter value is very close to a critical point (a bifurcation) for which the solution of the system is losing its stability. Thus a perturbation on the parameter may lead to the loss of stability or the disappearance of the solution, giving rise to a catastrophic shift of the system toward a new stable solution.

4.1 Transitions as effect of a vector state perturbation

First, we report some examples of possible catastrophic shifts as consequence of a perturbation of the state variables. The precipitation rate is fixed in a region where all the three solutions are stable ($p = 2$). Then, we consider an initial condition for which the final regime solution is a travelling wave with two peaks (TW2), we give a perturbation on the biomass at a fixed time value and we leave the system to evolve toward the new regime solution. The numerical results are reported in Figure 4. The perturbation is given at $t=2000$ imposing zero biomass in the first half of the domain. As it can be observed in Figure 4, at $t=2000$, there is a clear catastrophic shift from the TW2 to the TW1. It should be also noted that passing from two peaks to one peak,

the biomass self-organizes in the space so that the peak of TW1 is much bigger than the peak of the TW2 (Figure 4 (b)). The motivation may be that the average content of biomass in the space remains the same.

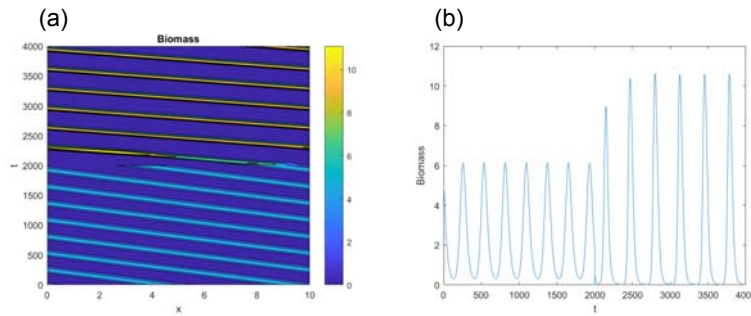


Figure 4: Transition from a traveling wave solution with two peaks to a traveling wave solution with one peak at $p=2$ with a perturbation on the biomass at $t=2000$. (a) Contour plot of the biomass. (b) Time series of the biomass in one point of the domain.

Similarly, for the same precipitation rate value, an initial condition giving the backfiring solution as a regime solution has been considered. The vector state perturbation is again on the biomass. As we can see in Figure 5, at the time $t = 2000$, after the perturbation, the system shifts from the backfiring solution to a travelling wave with one peak.

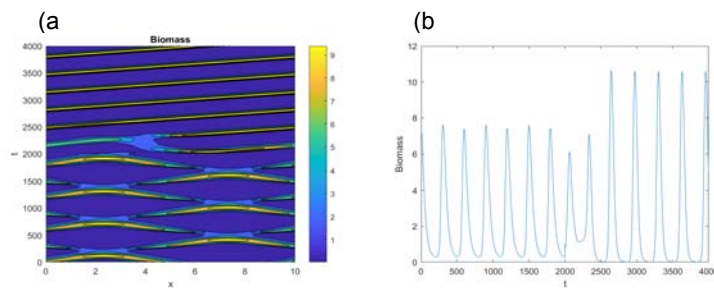


Figure 5: Transition from backfiring solution to traveling wave solution with one peak at $p=2$ with a perturbation on the biomass at $t=2000$. (a) Contour plot of the biomass. (b) Time series of the biomass in one point of the domain.

4.2 Transitions as effect of parameter perturbation

As climate changes are reducing the precipitation rate in arid and semi-arid regions, it is important to analyse catastrophic shifts as consequence of a perturbation on the precipitation rate for low parameter values. Fixing the parameter $p=0.25$, and, after choosing an initial condition leading to the regime solution corresponding to the TW1, we give a perturbation which reduces the parameter at $t=2000$.

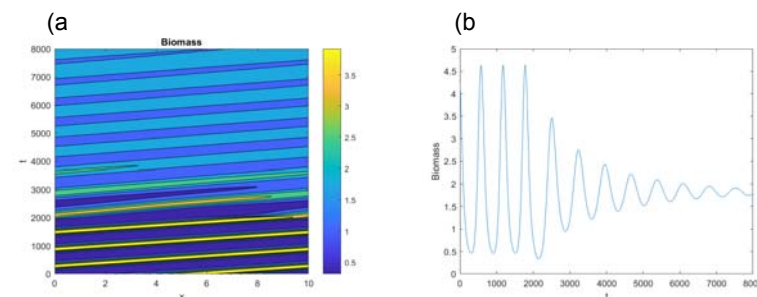


Figure 6: Transition from traveling wave solution with one peak (TW1) to homogeneous solution corresponding to the bare soil giving a reducing perturbation of $p=0.25$ at $t=2000$. (a) Contour plot of the biomass. (b) Time series of the biomass in one point of the domain.

Figure 6 shows the contour plot and the time series which represent the evolution of the biomass before and after the parameter perturbation. From Figure 6, it is clear that after the perturbation the system evolves from the TW1 to the regime solution corresponding to homogeneous bare soil solution. It should be noted that for higher parameter values other catastrophic shifts may be observed which mark the disappearance (or the loss of stability) of the solutions BF and TW2.

5. Conclusions

We analyzed the dynamics of vegetation moving patterns along a landscape which is modelled by reaction - diffusion system of PDEs with periodic boundary conditions. The analysis has been focused on the effect of precipitation rate on the patterns formation. The analysis has been conducted by numerical simulations by considering 1D-dimensional PDEs system. The numerical results has revealed that in the range of precipitation rate [0,4] a variety of patterns are found and multi-stability is possible. In particular, three kind of solutions have been found: travelling waves with one peak, travelling waves with two peaks and backfiring solutions. Catastrophic shifts between these different moving vegetation patterns are possible as consequence of perturbation of vector state and/or of the parameter.

Acknowledgments

Lucia Russo would like to thank Marco Imparato for his technical support.

References

- Callaway M. et al., *Nature* 417, 844 (2002).
- Carteni F, Marasco A, Bonanomi G, Mazzoleni S, Rietkerk M and Giannino F (2012) Negative plant soil feedback and ring formation in clonal plants. *J Theor Biol* 313:153–161
- Couteron P. and O. Lejeune, *J. Ecol.* 89, 616 (2001).
- Klausmeier C., *Science* 284, 1826 (1999).
- HilleRisLambers R. et al., *Ecology* 82, 50 (2001).
- Marasco A., Iuorio A. Fabrizio Carteni F., Bonanomi G., Tartakovsky D.M., Mazzoleni S., Giannino F., *Bull. Math. Biol.* (2014) 76:2866–2883.
- Russo, L., Spiliotis, K.G., Giannino, F.c, Siettos, C.I.b, Mazzoleni, S.c, (2017), *AIP Conference Proceedings*, 1906, Article number 100010
- Russo, L., Spiliotis, C., Siettos, C., *Catastrophic transitions in a forest-grassland ecosystem*, 53, 2016, Pages 229-234.
- Rietkerk M., J. van de Koppel, *Oikos* 79, 69 (1997).
- Rietkerk M. et al., *Plant Ecol.* 148, 207 (2000).
- Rietkerk M., Dekker S.C., de Ruiter P.C., van de Koppel J. (2004), *Science*, 305, 1926-1929.
- Rietkerk M. et al., *Am. Nat.* 160, 524 (2002).
- Scheffer M. et al., *Nature* 413, 591 (2001). 2.
- Scheffer M., S. R. Carpenter, *Trends Ecol. Evol.* 18, 648 (2003)
- Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) *Nature* 461(3):53–59.
- Shnerb N. M. et al., *Phys. Rev. Lett.* 90, 038101 (2003).
- Spiliotis, K.G., and Russo, L. , (2016), *AIP Conference Proceedings*, 1790, Article number 110005.
- Turing A., *Philos. Trans. R. Soc. London Ser. B* 273, 37 (1952).
- Von Hardenberg J. Meron E., Shachak M., Zarmi Y., *Phys. Rev. Lett.* 87, 198101 (2001).
- Zimmermann, S. O. Firlé, M. A. Natiello, M. Hildebrand, M. Eiswirth, M. Bär, A. K. Bangia, and I. G. Kevrekidis, *Physica D* 110, 92 (1997).