



Original Research Article

Species coexistence by front pinning

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ABSTRACT

The spatial competition between two plant species that make different compromises in capturing soil water and sunlight is studied using a mathematical model. A precipitation range along the rainfall gradient is identified where two alternative stable states coexist. The first state describes a uniform distribution of a plant species that specializes in capturing soil water, whereas the second state describes a periodic pattern of a species that specializes in capturing light. We show that this bistability range generally divides into three parts according to the dynamics of the front or ecotone that separates the two plant populations: a low precipitation range where the superior competitor for water displaces the superior competitor for light, a high precipitation range where the displacement is reversed, and an intermediate range where neither species displaces the other. While in the low and high precipitation ranges one species outcompetes the other, the intermediate range allows for species coexistence in the form of a multitude of stable localized solutions consisting of fixed domains of one species in areas otherwise occupied by the other species. These localized solutions can only be realized when one of the alternative stable states is spatially patterned. We further study two factors that affect the size of the species coexistence range: the strength of the competition for light and the form of the tradeoff between the competitive abilities to capture water and light.

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1. Introduction

Water-limited vegetation is generally patchy. According to the traditional view, vegetation patchiness is a result of an underlying physical template, often formed by slow geologic and geomorphologic processes, that creates favorable vegetation-growth areas (Sheffer et al., 2013). A different view of vegetation patchiness has been motivated by recent field observations of banded vegetation and other forms of regular vegetation patterns in nearly homogeneous landscapes (Tongway et al., 2001; Deblauwe et al., 2008). According to this view vegetation patterns can result from small-scale biomass-water feedbacks that give rise to self-organization at large scales even in spatially uniform systems (Rietkerk and van de Koppel, 2008; Meron, 2012). Mathematical models that capture these feedbacks have been very instrumental in understanding the causes of self-organized vegetation patchiness and the specific forms it takes along the rainfall gradient (Borgogno et al., 2009). Studies of such models

have first identified five basic vegetation states along the rainfall gradient (von Hardenberg et al., 2001; Rietkerk et al., 2002): uniform vegetation, hexagonal gap patterns, stripes or labyrinthine patterns, hexagonal spot patterns, and bare soil, which are in good agreement with field observations. They further suggest richer forms of self-organized vegetation patchiness: disordered spatial mixtures of basic states in bistability ranges, and amorphous patches that span wide patch-size distributions under conditions of global competition (von Hardenberg et al., 2010; Meron, 2012).

Most model studies have considered a single plant species, overlooking the large plant communities that generally exist in water-limited landscapes (Shachak et al., 2005). The tendency of water-limited ecosystems to self-organize in patchy landscapes raises the question: what impact does vegetation pattern formation have on species coexistence and diversity? This is a significant question, particularly nowadays, when transitions between different vegetation states become more likely due to the ongoing global climate change and the environmental fluctuations associated with it (Field et al., 2013). Understanding the response of plant communities to such transitions is important for maintaining the diversity of water-limited ecosystems and securing their function and stability.

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Very few model studies have addressed the interaction between different species in water-limited vegetation, taking into account mechanisms of vegetation pattern formation. All of them have considered a pattern-forming species that acts as an ecosystem engineer (Jones et al., 1994, 1997) by concentrating the water resource, thereby facilitating the growth of the other species understory (Pugnaire and Luque, 2001; Holzapfel et al., 2006; Maestre et al., 2005). One set of studies has focused on the interplay between biomass-water feedbacks that have opposite effects on the soil-water distribution, and the development ecosystem engineering under conditions of water stress (Gilad et al., 2007a,b; Meron, 2012). Two other studies focused on species coexistence where a pattern-forming ecosystem engineer is an inferior competitor that survives the competition with a superior competitor because of the highly dispersive character of the latter (Baudena and Rietkerk, 2013; Nathan et al., 2013).

In this paper we propose a new pattern-formation mechanism of species coexistence that is based on a generic mathematical property associated with bistability of a uniform state and a periodic-pattern state – the possible existence of a multitude of stable localized structures (or homoclinic orbits in an appropriately defined dynamical system) (Knobloch, 2008). These structures consist of confined domains of the patterned state in a background of the other, spatially uniform, alternative stable state, and vice versa. Their existence is related to the dynamics of the transition zones that separate the two alternative stable states, i.e. the fronts that are bi-asymptotic to the two states (Pomeau, 1986). When the two alternative stable states are spatially uniform the fronts propagate in one direction or another, except for a particular value of the control parameter (the Maxwell point) at which the fronts are stationary (Pismen, 2006). By contrast, when one of the alternative stable states is spatially patterned there might exist a finite range of the control parameter within which fronts are stationary or pinned. It is within this range that localized structures are found. The mathematical property described above is commonly referred to as “homoclinic snaking”, because of the snake-like forms of the solution branches that describe the localized structures in the corresponding bifurcation diagrams (Knobloch, 2008). Localized structures of this kind were found also in a vegetation model for a single plant species in a bistability range of periodic vegetation pattern and bare soil (Lejeune et al., 2002; Zelnik et al., 2013).

To study species coexistence associated with bistability of uniform and patterned states we consider two plant species in water limited ecosystems that are related to one another by a tradeoff between investment in growing taller shoots and investment in increasing root-to-shoot ratio. Taller plants have an advantage in capturing light whereas plants with higher root-to-shoot ratios have an advantage in capturing soil water. We study the interaction between these two species along a rainfall gradient using a modified version of the vegetation model introduced by Gilad et al. (2004) that includes inter-specific competition for light. Since the proposed coexistence mechanism is based on a generic mathematical property of bistable pattern-forming systems, the results presented here may be applicable to many other contexts of ecological communities.

2. Modeling community dynamics

The model we study is based on the multi-species vegetation model introduced by Gilad et al. (Gilad et al., 2007a; Meron, 2011). The Gilad et al. model describes the evolution of a plant community in a water limited system where species interact through competition for water. In its most general form the model consists of a system of integro-differential equations that models non-local water uptake by laterally extended root zones. Here we study a

modified version of this model that takes into account competition for light too, but simplifies it in other respects.

2.1. Model equations

The original model consists of equations for the above-ground biomass densities B_i of N interacting species ($i = 1, \dots, N$), the soil water content per unit ground area W and the height of a surface-water layer above ground level H . We simplify it first by assuming that the infiltration rate of surface water into the ground is approximately constant, independent of the plants' biomass. Quite often the infiltration rate in bare soil is lower than that in vegetated soil because it is covered by physical and biogenic crust that makes the infiltration slower (Eldridge and Zaady, 2012). This effect can be negligible in sandy soils which are often uncrusted. When the infiltration rate is constant the equation for H decouples from the equations for W and the B_i s and the variable H can be eliminated (Zelnik et al., 2013). The model equations in one dimension (1d) then read

$$\frac{\partial B_i}{\partial t} = \Lambda_i(B)G_{B_i}(B_i, W)(1 - B_i/K_i)B_i - M_i B_i + D_{B_i} \frac{\partial^2 B_i}{\partial x^2}, \quad (2.1a)$$

$$\frac{\partial W}{\partial t} = P - LW - G_W(B)W + D_W \frac{\partial^2 W}{\partial x^2}, \quad (2.1b)$$

where $B = (B_1, \dots, B_N)$ and x represents a 1d lateral direction. The nonlinear growth rate of the i th species includes a water dependent factor, $G_{B_i}(B_i, W)$, that represents water uptake by the plants' roots, and a biomass dependent factor, $\Lambda_i(B)$, that accounts for light attenuation by competing plant species. The growth rate of grown plants is also limited by genetic factors, such as stem strength, whose effects are lumped in the parameter K_i . In the case of annuals K_i can also represent the limited size a plant can develop in its life cycle. Biomass growth is also limited by mortality and grazing that are represented by the parameter M_i . Spatial biomass expansion is accounted for by a diffusion term that represents short-distance seed dispersal or clonal growth, where the “biomass diffusivity”, D_{B_i} , is assumed to be a constant parameter. In the soil water Eq. (2.1b), the parameter P represents the precipitation rate while L represents the evaporation rate, which in general may also depend on the above-ground biomass to account for reduced evaporation by shading. The factor $G_W(B)$ is the rate of water uptake by the plants' roots, and its biomass dependence reflects the increase in the root-zone size as the above-ground increases, i.e. the root-to-shoot ratio. Lastly, the term $D_W \partial^2 W / \partial x^2$ models water transport in a non-saturated soil with D_W being a diffusivity constant.

2.2. Competition for water

Plants compete for water through water uptake by their roots. For laterally extended root zones the uptake is nonlocal and is captured by the following form (Gilad et al., 2007b),

$$G_W(x, t) = \sum_{i=1}^N \Gamma_i \int g_i(x', x, t) B_i(x', t) dx',$$

where the kernel $g_i(x', x, t)$ represents the roots architecture, and the integration is over the root zone of plants located at x . We use the form

$$g_i(x, x', t) = \frac{1}{\sigma_i \sqrt{2\pi}} \exp\left(-\frac{|x - x'|^2}{2\sigma_i^2(1 + E_i B_i(x, t))^2}\right),$$

where E_i quantify the root augmentation per unit of above-ground biomass, which is a measure of the root-to-shoot ratio. Note that

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