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Banded vegetation: biological productivity and resilience

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Abstract

Vegetation band patterns on hill slopes are studied using a mathematical model. The model applies to drylands, where the limiting resource is water, and takes into account positive feedback effects between biomass and water. Multiple band patterns coexisting in wide precipitation ranges are found. For given precipitation and slope conditions band patterns with higher wavenumbers are more biologically productive. High-wavenumber patterns, however, are less resilient to environmental changes.

1. Introduction

Arid and semi-arid ecosystems are characterized by patchy vegetation; the limited availability of the water resource forces plant species to self-organize in various vegetation patterns. A striking example is banded vegetation. Vegetation bands on hill slopes, consisting primarily of trees and shrubs, have been observed in arid and semi-arid regions throughout the world [1]. The bands are normally oriented perpendicular to the slope direction and are a few tens of meters apart.

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The view of vegetation patchiness as a symmetry-breaking pattern formation phenomenon is quiet recent. It has been motivated and supported by mathematical models that relate vegetation patterns to finite wavenumber instabilities of uniform vegetation states [2–4]. The instabilities result from two positive feedback mechanisms between biomass and water: (a) increased surface-water infiltration induced by vegetation [5], and (b) soil water uptake by the plants' roots [6]. According to the first mechanism, a growing plant induces further local infiltration of surface water which accelerates its growth. According to the second mechanism, as a plant grows its roots become longer. The longer the roots the more soil water they take up and the faster the plant grows. In both mechanisms, the depletion of soil water from the plant surrounding, and the plant competition for water resource, lead to symmetry breaking and pattern formation.

In this paper we study the structural and dynamical aspects of banded vegetation using a recent model that captures the two positive feedbacks discussed above. Understanding these aspects is significant for the conservation and rehabilitation of desertified regions [7].

2. The model

The model we study has been introduced in Ref. [6]. It contains three dynamical variables: (a) a biomass density, $b(\mathbf{r}, t)$, representing the plant biomass above ground level, (b) a soil-water density, $w(\mathbf{r}, t)$, describing the amount of soil–water available to the plant per unit area of ground surface, and (c) a surface water variable, $h(\mathbf{r}, t)$, describing the height of a thin water layer above ground level. The model equations in non-dimensional form are:

$$\partial_t b = G_b b(1-b) - b + \delta_b \nabla^2 b \,,$$

$$\partial_t w = Ih - \nu(1-\rho b)w - G_w w + \delta_w \nabla^2 w \,,$$

$$\partial_t h = p - Ih + \delta_h \nabla^2 (h^2) + 2\delta_h \nabla h \cdot \nabla \zeta + 2\delta_h h \nabla^2 \zeta \,, \tag{1}$$

where G_b represents the biomass growth rate, G_w is the rate of soil–water consumption by the vegetation, I is the infiltration rate of surface water into the soil, p is the precipitation rate, and the function $\zeta(\mathbf{r})$ describes the ground topography.

The two positive feedback effects between biomass and water are included in the explicit forms of the infiltration term I and the biomass growth rate G_b. The infiltration I is assumed to depend on the biomass b according to $I = \alpha(\mathbf{r}, t)[b(\mathbf{r}, t) + qf]/[b(\mathbf{r}, t) + q]$ [5,4]. The smaller the f the lower the infiltration rate at bare soil, as compared with vegetated soil, and the stronger the water–biomass feedback [6]). The biomass growth rate is modeled by $G_b(\mathbf{r}, t) = \nu \int_\Omega g(\mathbf{r}, \mathbf{r}', t) w(\mathbf{r}', t)\, \mathrm{d}\mathbf{r}'$, where $g(\mathbf{r}, \mathbf{r}', t) = \frac{1}{2\pi} \exp\left[-\frac{|\mathbf{r}-\mathbf{r}'|^2}{2[(1+\eta b(\mathbf{r}, t))]^2}\right]$ and the integration is over the entire domain Ω. According to this form the biomass growth rate depends not only on the amount of soil water at the plant location, but also on the amount of soil water in the neighborhood which the plant's roots extend to. The positive feedback effect due to water uptake by the roots is captured by the dependence of the root length (Gaussian width) on biomass; the larger the biomass the longer the roots and the higher the water uptake. The water consumption rate at a point $\mathbf{r}$ is similarly given by $G_w(\mathbf{r},t) = \gamma \int_\Omega g(\mathbf{r}',\mathbf{r},t) b(\mathbf{r}',t)\,d\mathbf{r}'$. For more details regarding the model the reader is referred to Ref. [6].

3. Uniform and pattern solutions

Eqs. (1) have two stationary uniform states representing bare soil and uniform vegetation, as well as patterned states. The bifurcation diagram in Fig. 1 shows the uniform states and their stability properties. The insets show two basic patterned states; spot patterns at low precipitation rates and band patterns at higher precipitation rates. Stable spot patterns appear at precipitation values where the bare soil state is still stable. Likewise, stable band patterns appear at precipitation values where spot patterns are still stable. With appropriate parameter choices a tristability of bare state, spots and bands can be obtained. These

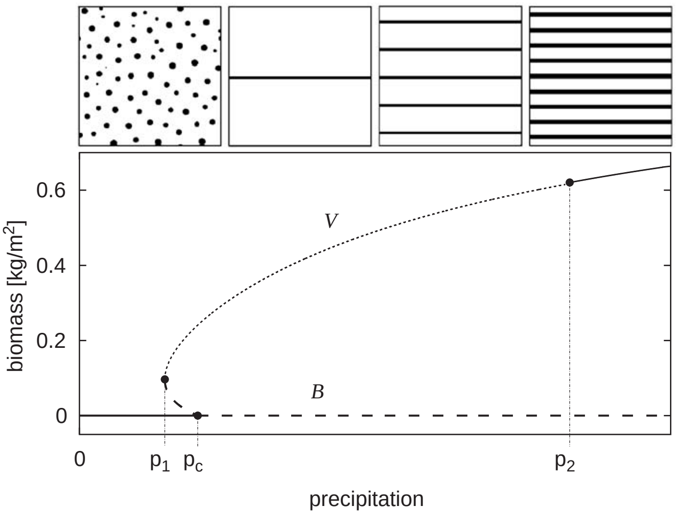

Fig. 1. A bifurcation diagram showing biomass b vs. precipitation p for a uniform slope. The branch $\mathscr{B}$ represents a uniform bare soil solution and the branch $\mathscr{V}$ represents a uniform vegetation state. The precipitation axis spans the range 0–1250 mm/yr. The bare state becomes unstable at $p_c = 1$ (250 mm/yr). The uniform vegetation state becomes unstable at $p_2 = 4.146$ (1036.5 mm/yr). The insets show typical patterns along the precipitation gradient, spots at low p (200 mm/yr) and bands at higher p (200, 250 and 500 mm/yr for a single, five and nine bands, respectively). Dark shades of gray represent high biomass. Parameter values used are: $\nu = 2$, $\eta = 5$, $\alpha = 160$, $f = 0.1$, $q = 0.05$, $\gamma = 5$, $\rho = 1$, $\delta_b = 0.02$, $\delta_w = 2$, $\delta_h = 200$ and slope = 3 degrees.

ranges of multistability have significant implications on desertification [3] and habitat diversity [6].

4. Multiple band states

Multistability of stable states also exists within the precipitation range of stable bands where the bare state and spot patterns are unstable. The coexisting stable states correspond to band patterns with different wavenumbers. At relatively low precipitation, where the bare state is still stable, single-band patterns are possible (second inset from the left in Fig. 1). At higher precipitations stable patterns with higher wavenumbers appear but many of the lower wavenumber patterns remain stable. These states are likely to be related to the discrete families of Eckhaus stable solutions that have been found in simpler models of finite systems, such as the Ginzburg–Landau model [8] and the complex Swift–Hohenberg model [9,10]. The existence of a discrete family of stable banded patterns suggests two principal responses to a gradual precipitation downshift: (i) an increase in the ratio of the interband distance to the band width (interband–bandratio, or IBR index [11]) without a change in the pattern's wavenumber, and (ii) a decrease in the pattern's wavenumber. Fig. 2 shows how the IBR index changes with precipitation. The numerical data fit an exponential function well, in agreement with field observations [11].

The multistability of band states bears on the rate at which vegetation consumes water, and as a result on the biological productivity of the ecosystem; the smaller this rate the higher the productivity. We evaluated the water consumption rate per unit

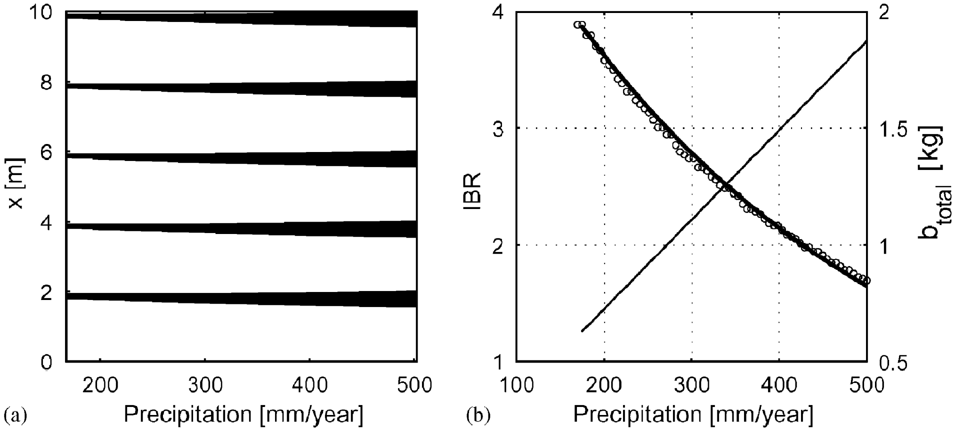

Fig. 2. The effect of precipitation on the widths of vegetation bands for a pattern with a given wavenumber. The numerically computed Interband–bandratio (IBR) (circles in part (b)) fits an exponentially decreasing function (thick solid line) quite well. The total biomass grows linearly with precipitation (thin solid line). The parameters are the same as in Fig. 1.

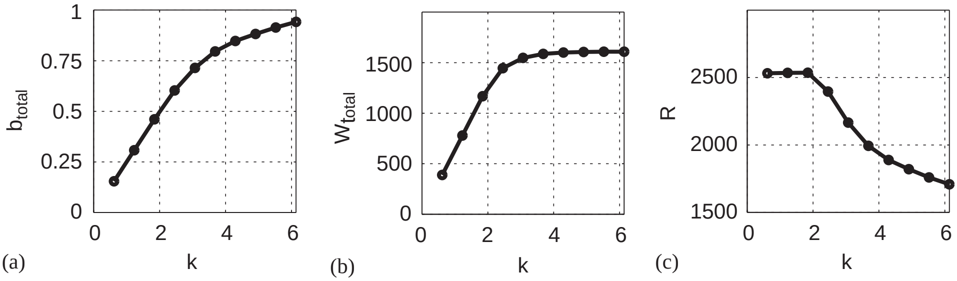

Fig. 3. The dependence of biological productivity on the pattern's wavenumber k. Both total biomass, b_{total}, and total amount of water consumed by the vegetation, w_{total}, increase with k, but the ratio $R = w_{total}/b_{total}$ decreases. Thus, high wavenumber patterns consume less water and are therefore more productive. Parameters $p = 0.8$ (200 mm/year) and all other parameter values are the same as in Fig. 1.

of biomass for all band solutions that coexist for given precipitation and slope values by calculating the total water consumption rate $w_{total} = \int G_w w d\mathbf{x}$, the total biomass, $b_{total} = \int b d\mathbf{x}$ and the ratio w_{total}/b_{total}. The results are shown in Fig. 3. Both w_{total} and b_{total} increase with the pattern's wavenumber (or number of bands) but w_{total} increases more slowly. As a consequence the water consumption per unit biomass decreases as the pattern's wavenumber increases. This result suggests that establishing higher wavenumber patterns in rehabilitating desertified regions will increase the biological productivity of these regions.

5. Resilience of band states

Banded patterns with higher wavenumbers are more biologically productive but are less resilient to environmental changes. We demonstrate this property by studying the response of banded vegetation to a precipitation downshift. Fig. 4 shows the response of a relatively high wavenumber pattern ($k_0 = 8.8$) to a precipitation downshift within the range of multistability of band states. The downshift leads to an Eckhaus-type instability [12] that culminates in a significantly lower wavenumber ($k = k_0/2$). An identical downshift of a band pattern with an intermediate wavenumber ($k_0 < 8$) leaves the wavenumber unchanged. Thus, lower wavenumber patterns which are less productive are more resilient to precipitation downshifts such as prolonged droughts.

6. Conclusion

The results of this study are significant for rehabilitation of desertified regions. In choosing the inter-band distances in rehabilitation projects [13] of two conflicting factors should be carefully considered; short distances increase the biological

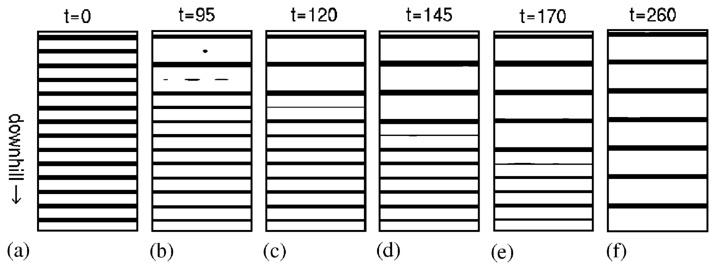

Fig. 4. Low resilience of vegetation bands to precipitation downshifts. A high wavenumber pattern ($k_0 = 8.8$) which is stable at $p = 2$ (500 mm/yr) responds to a precipitation downshift to $p = 1.2$ (300 mm/yr) by gradual downhill elimination of every second band. Parameter values are the same as in Fig. 1.

productivity but also increase the vulnerability of the system to environmental changes such as a precipitation downshift.

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[13] The inter-band distance is determined by the distance between successive contour ditches along which the vegetation is planted. The ditches trap runoff from the bare areas uphill and thereby provide conditions for growth.