

VEGETATION PATTERN FORMATION IN SEMI-ARID GRAZING SYSTEMS

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Abstract. Hypotheses about the origin of vegetation pattern formation in semi-arid areas around the world almost all include a common feature of semi-arid areas: the presence of a positive feedback between plant density and water infiltration. We investigate whether this positive feedback and the spatial redistribution of runoff water are sufficient to explain vegetation pattern formation. For this purpose, we analyze a spatially explicit model consisting of partial differential equations using a method for demonstrating pattern formation (Turing analysis). Our analysis reveals that pattern formation can occur in semi-arid areas given only the positive feedback between plant density and local water infiltration coupled with the spatial redistribution of runoff water. Thus, slope and underlying heterogeneity are not essential conditions. Other factors in the model, such as herbivory, plant dispersal, rainfall, and drought tolerance of plants, appear to determine under what conditions pattern formation is likely but are not the primary factors that generate the patterns. The model is in agreement with field observations and indicates the conditions for which vegetation pattern formation can be expected in arid and semi-arid grazing systems.

Key words: grazing; herbivory; patchiness; plant dispersal; plant–soil interaction; positive feedback; runoff; semi-arid grazing systems; spatially explicit model; Turing analysis; vegetation patterns.

INTRODUCTION

The occurrence of patches of vegetation alternating with patches of (almost) bare soil (“vegetation pattern formation”) is a common feature in arid and semi-arid grazing systems throughout the world. These systems cover nearly 30% of the earth’s land surface. Vegetation patches vary in form, ranging from irregular mosaics to regular bands, and patch sizes range from approximately one to hundreds of meters (Belsky 1986, 1989, Mabbut and Fanning 1987, Tongway and Ludwig 1990, Cornet et al. 1992, Kellner and Bosch 1992, Montaña 1992, Haase et al. 1996, Bromley et al. 1997, Jeltsch et al. 1997, Hiernaux and Gérard 1999, Rietkerk et al. 2000). Vegetation pattern formation may occur on flat ground as well as on gentle slopes. An illustrative example of vegetation pattern formation is the so called “tiger bush” on gentle slopes in sub-Saharan Africa

(Macfaydan 1950a, b, Boaler and Hodge 1962). In this particular case, vegetation patches consisting of grasses, shrubs, trees, or any combination of these functional groups, appear as regular bands alternating with bare soil resembling stripes of a tiger skin when seen from the air.

A large number of hypotheses have been suggested about the origin of this vegetation pattern formation. Yet no consensus has been reached. For instance, Boaler and Hodge (1962) attributed the presence of vegetation stripes to the variation in texture of soil parent material. Belsky (1986) suggested that the initiation of the vegetation mosaics was caused by soil sodicity and salinity through differential leaching of salts from the sodic soils. Kellner and Bosch (1992) suggested that vegetation patterns in semi-arid grasslands were created through selective grazing by herbivores. Thiery et al. (1995) demonstrated that patterns such as those in tiger bush can be generated if plants are positively affected by lateral and down-slope plants, but negatively affected by up-slope plants. Jeltsch et al. (1997) related vegetation patterns to the interplay of factors such as competition, colonization, and changes in the vegetation caused by fire and grazing. Similarly Bromley et al. (1997) suggested that vegetation mosaics develop out of a complete cover of vegetation through the creation of patches by termites, grazing, or fire.

Manuscript received 8 March 1999; revised 22 November 1999; accepted 22 December 1999; final version received 31 January 2000.

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Lefever and Lejeune (1997:263) found vegetation mosaics resulting from the “interplay between short-range cooperative interactions controlling plant reproduction and long range self inhibitory interactions originating from plant competition for environmental resources.”

One common feature of semi-arid areas, especially of those areas exhibiting vegetation patterning, is a positive feedback between plant density and water infiltration. This positive feedback is often included in hypotheses concerning possible agents for vegetation pattern formation (Belsky 1986, Montaña 1992, Mauchamp et al. 1994, Ludwig and Tongway 1995, Thiery et al. 1995, Bromley et al. 1997, Rietkerk and Van de Koppel 1997, Rietkerk et al. 2000). The nature of this positive feedback is that at higher plant densities more water infiltrates into the soil than at lower plant densities. In vegetation mosaics, rain falling on bare patches of soil will barely infiltrate and run off. This runoff water subsequently accumulates in the vegetated patches, where it can infiltrate more easily. The presence of a positive feedback between plant density and water infiltration is an important generalization that can be made about semi-arid areas exhibiting vegetation patterning. In this paper, we propose that this positive feedback is the main process generating vegetation pattern formation in semi-arid areas throughout the world. Our hypothesis is that the positive feedback between plant density and water infiltration and runoff–run-on processes such as those found in semi-arid grazing systems is sufficient to explain vegetation pattern formation. Many authors have suggested that plant dispersal and herbivory may have important effects on vegetation pattern formation. We therefore examine how changes in these parameter values, as well as changes in other parameters related to rainfall, soil properties, and plant properties, affect vegetation pattern formation.

Rietkerk et al. (1997) and Rietkerk and Van de Koppel (1997) developed a model of semi-arid grazing systems predicting the possibility of irreversible vegetation collapse at high levels of herbivory as a consequence of the positive feedback between plant density and water infiltration. However, their model did not take space into account. In this paper, we develop a model of a semi-arid grazing system describing the dynamics of surface water, soil water, and plant density in time as well as in space by using a set of partial differential equations. This approach enables us to model plant dispersal and the net exchange of surface water and soil water with surrounding areas. We analyze the model using a method developed by Turing (1952) for demonstrating pattern formation. Turing analysis has been applied extensively in ontogenetic analysis of mammal coat patterns, but is relatively new to this field (Lefever and Lejeune 1997).

METHODS

Model description

We develop a model describing the dynamics of three state variables in time as well as in space: surface water,

soil water, and plant density. Surface water during rain showers is related to rainfall, infiltration rates, and runoff/run-on processes. Soil water is related to infiltration rates, water uptake by plants, evaporation, drainage, and subsurface flow. Plant density is related to plant growth, which is water limited; a natural mortality rate and herbivore-induced loss rate; and plant dispersal through seed or vegetative propagation. We assume space to be an infinite two-dimensional surface, implying no boundaries.

Surface water

Rain in semi-arid areas falls in short periods of time during intense rain showers. Furthermore, water infiltration into the soil is a relatively slow process, so that a major proportion of the rainfall first collects above ground. This water will either infiltrate into the soil at that position, or flow towards other areas and subsequently infiltrate in those regions (“surface water motion”). We consider a two-dimensional area of land. A position in this space has coordinates $\vec{x} = (x_1, x_2)$. The amount of water on the soil surface at position \vec{x} and at time t will be denoted by $O(\vec{x}, t)$. The rate of change of the amount of water on the surface $\partial O(\vec{x}, t)/\partial t$ is governed by the equation

$$\begin{aligned} \frac{\partial O(\vec{x}, t)}{\partial t} = & \text{[rainfall rate at } \vec{x} \text{ at } t] \\ & - \text{[infiltration rate at } \vec{x} \text{ at } t] \\ & \pm \text{[overland flow]}. \end{aligned} \quad (1)$$

We assume that during rain showers rainfall is constant and homogeneous so that

$$\text{[rainfall rate at } \vec{x} \text{ at } t] = R. \quad (2)$$

Infiltration rate $W_{in}(\vec{x}, t)$ depends on the amount of water on the surface, plant density, and soil characteristics. In semi-arid areas there is a positive relationship between plant density and water infiltration. We model this as

$$\text{[infiltration rate at } \vec{x} \text{ at } t] = \alpha O(\vec{x}, t) \frac{P(\vec{x}, t) + k_2 W_0}{P(\vec{x}, t) + k_2} \quad (3)$$

(Walker et al. 1981). Here $P(\vec{x}, t)$ refers to plant density at a certain spot at a certain time, $\alpha O(\vec{x}, t)$ is a term describing maximum infiltration rate of surface water, $\alpha O(\vec{x}, t) W_0$ is the minimum water infiltration in the absence of plants (if $P(\vec{x}, t) = 0$), and k_2 is a half-saturation constant (Fig. 1, Table 1). A high W_0 corresponds to sandy soils, whereas a low W_0 is typical for clayey soils. Parameter k_2 corresponds to the rate at which water infiltration increases with plant density and can be interpreted as the capacity for vegetation to improve structural and water-holding capacities of the soil (Rietkerk et al. 1997). Empirical evidence for the shape of this equation can be found in van Wijngaarden (1986) and Rietkerk (1998).

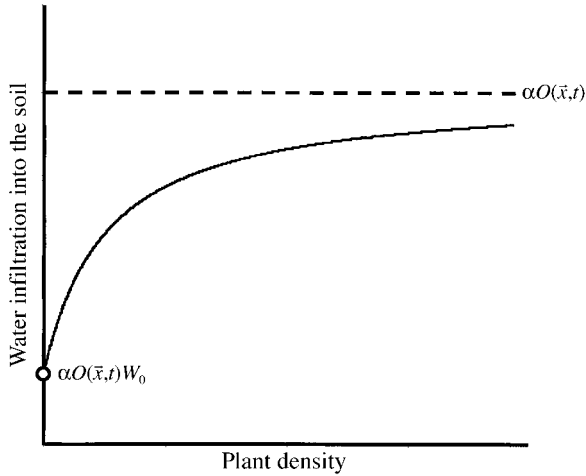


FIG. 1. The relationship between water infiltration into the soil and plant density. The minimum water infiltration rate in the absence of plants is $\alpha O(\bar{x}, t)W_0$. The asymptote $\alpha O(\bar{x}, t)$, represents the maximum water infiltration rate.

To model run-on/runoff water we adopted the type of model used in groundwater flow in aquifers by Bear and Verruyt (1990). In the model, the net displacement of surface water on a perfectly horizontal terrain during a rain shower is due to the fact that water infiltration in vegetated ground is much faster than in unvegetated ground. The water on the bare surface will then flow to places with vegetation where all water has already infiltrated, induced by pressure differences measured by the slope of the thickness of the water layer (given by $\partial O(\bar{x}, t)/\partial x$). This type of description of surface water motion incorporates the flow due to pressure differences into a single parameter, D_o , so that rainwater movement can be described by the term

$$\begin{aligned} & \text{[surface water motion]} \\ & = D_o \left\{ \frac{\partial^2 O(\bar{x}, t)}{\partial x_1^2} + \frac{\partial^2 O(\bar{x}, t)}{\partial x_2^2} \right\}. \end{aligned} \quad (4)$$

This component describes the net exchange of surface water with surrounding areas.

During rain showers of at least some considerable length, a steady state will develop between rainfall, surface water motion, and water infiltration. This steady state is calculated from $[\partial O(\bar{x}, t)]/\partial t = 0$. Certainly, rain showers are discrete events. For the sake of model analysis, however, we assume that water infiltration rate is at steady state. In other words, water infiltration is a continuous water supply to the system at position \bar{x} . To calculate the rate of water supply from our continuous time model we have to multiply the infiltration rate $W_{in}(\bar{x}, t)$ by the fraction of time it rains (f). Thus the water supply is $W_{in}(\bar{x}, t) = f\bar{W}_{in}(\bar{x}, t)$, where f is incorporated into parameter α in Eq. 3.

Soil water

Soil water at a certain spot may be taken up by plants growing at that spot, evaporate, percolate to deep soil layers, or flow to other spots. The rate of change in soil water content $W(\bar{x}, t)$ is governed by

$$\begin{aligned} \frac{\partial W(\bar{x}, t)}{\partial t} &= \text{[infiltration rate at } \bar{x} \text{ at } t] \\ &\quad - \text{[plant water uptake at } \bar{x} \text{ at } t] \\ &\quad - \text{[evaporation and drainage at } \bar{x} \text{ at } t] \\ &\quad \pm \text{[water movement]}. \end{aligned} \quad (5)$$

Here the infiltration rate at \bar{x} at t is given by Eq. 3. We assume that plant water uptake is a saturating function of soil water:

$$\begin{aligned} & \text{[plant water uptake at } \bar{x} \text{ at } t] \\ & = g_{\max} \times \frac{W(\bar{x}, t)}{W(\bar{x}, t) + k_1} \times P(\bar{x}, t) \end{aligned} \quad (6)$$

(Rietkerk et al. 1997). Here g_{\max} is the maximum specific soil water uptake by plants and k_1 is a half-saturation constant (Fig. 2). Plants with a lower k_1 are less effective in soil water uptake, and so, when compared with a higher k_1 , experience the same soil water levels as being "drier."

For the sake of simplicity, we assume that evaporation and soil water loss by drainage is a linear function of water availability as shown in the following equation:

TABLE 1. Interpretation of the symbols used.

Symbol	Interpretation	Units
P	Plant density	g/m^2
W	Soil water	mm
O	Surface water	mm
c	Conversion of water uptake by plants to plant growth	$g \cdot mm^{-1} \cdot m^{-2}$
g_{\max}	Maximum specific water uptake	$mm \cdot g^{-1} \cdot m^2 \cdot d^{-1}$
k_1	Half saturation constant of specific plant growth and water uptake	mm
d	Specific loss of plant density due to mortality	d^{-1}
β	Specific loss of plant density due to grazing	d^{-1}
D_p	Plant dispersal	m^2/d
α	Proportion of surface water available for infiltration	d^{-1}
k_2	Rate at which infiltration increases with specific plant density	g/m^2
W_0	Minimum water infiltration in the absence of plants	...
r_w	Specific soil water loss due to evaporation and drainage	d^{-1}
D_w	Diffusion coefficient for soil water	m^2/d
R	Rainfall	mm/d
D_o	Diffusion coefficient for surface water	m^2/d

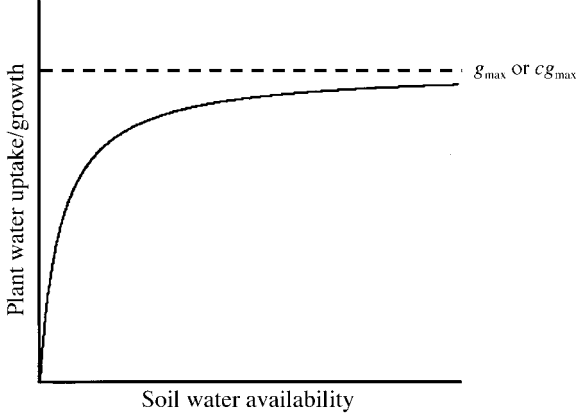


FIG. 2. The relationship between soil water availability and plant water uptake and growth is modeled as a Michaelis equation. The maximum specific soil water uptake is given by the parameter g_{\max} , and maximum specific plant growth by cg_{\max} .

$$\begin{aligned} \text{[evaporation and drainage at } \vec{x} \text{ at } t] \\ = r_w \times W(\vec{x}, t). \end{aligned} \quad (7)$$

Soil water movement is described by the diffusion term:

$$\begin{aligned} \text{[soil water movement]} \\ = D_w \left\{ \frac{\partial^2 W(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 W(\vec{x}, t)}{\partial x_2^2} \right\}. \end{aligned} \quad (8)$$

Plant density

Plant density $P(\vec{x}, t)$ is related to plant growth, plant loss, and dispersal into and out of other areas. The rate of change of plant density is governed by the following equation:

$$\begin{aligned} \frac{\partial P(\vec{x}, t)}{\partial t} = \text{[plant growth at } \vec{x} \text{ at } t] - \text{[plant loss at } \vec{x} \text{ at } t] \\ \pm \text{[plant dispersal]}. \end{aligned} \quad (9)$$

Plant growth is assumed to be water limited. Furthermore, we assume that specific plant growth increases linearly with increasing specific soil water uptake and is at its maximum at full plant turgor when the availability of soil water permits maximum specific soil water uptake (De Wit 1958). Therefore, the plant growth function is related to plant water uptake by a constant conversion factor c :

$$\begin{aligned} \text{[plant growth at } \vec{x} \text{ at } t] \\ = cg_{\max} \times \frac{W(\vec{x}, t)}{W(\vec{x}, t) + k_1} \times P(\vec{x}, t). \end{aligned} \quad (10)$$

Here specific plant growth is given by $cg(W)$, where the maximum asymptotic plant growth is given by cg_{\max} .

Plant biomass may be lost either through natural

mortality (d) or through removal by herbivores (β). For the sake of simplicity, the functional response of herbivores to changes in plant availability is assumed to be linear:

$$\text{[plant loss at } \vec{x} \text{ at } t] = (d + \beta)P(\vec{x}, t). \quad (11)$$

Plant movement, either through seed dispersal or lateral growth, is given by the diffusion term:

$$\text{[plant dispersal]} = D_p \left\{ \frac{\partial^2 P(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 P(\vec{x}, t)}{\partial x_2^2} \right\}. \quad (12)$$

Thus, summarizing, the whole model system is defined by three partial differential equations for plant density, soil water, and surface water, respectively:

$$\begin{aligned} \frac{\partial P(\vec{x}, t)}{\partial t} = cg_{\max} \times \frac{W(\vec{x}, t)}{W(\vec{x}, t) + k_1} \times P(\vec{x}, t) \\ - (d + \beta)P(\vec{x}, t) \\ + D_p \left\{ \frac{\partial^2 P(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 P(\vec{x}, t)}{\partial x_2^2} \right\} \end{aligned} \quad (13a)$$

$$\begin{aligned} \frac{\partial W(\vec{x}, t)}{\partial t} = \alpha O(\vec{x}, t) \frac{P(\vec{x}, t) + k_2 W_0}{P(\vec{x}, t) + k_2} \\ - g_{\max} \times \frac{W(\vec{x}, t)}{W(\vec{x}, t) + k_1} \times P(\vec{x}, t) \\ - r_w W(\vec{x}, t) + D_w \left\{ \frac{\partial^2 W(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 W(\vec{x}, t)}{\partial x_2^2} \right\} \end{aligned} \quad (13b)$$

$$\begin{aligned} 0 = R - \alpha O(\vec{x}, t) \frac{P(\vec{x}, t) + k_2 W_0}{P(\vec{x}, t) + k_2} \\ + D_o \left\{ \frac{\partial^2 O(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 O(\vec{x}, t)}{\partial x_2^2} \right\} \end{aligned} \quad (13c)$$

(see Table 1 for a survey of symbols used with interpretations and units).

Turing conditions for pattern formation

We analyze our model using a method developed by the British mathematician A. M. Turing (1952). This method is based on the principle that pattern formation in a system of partial differential equations can occur if a system is stable to spatially homogeneous perturbations but unstable if spatially heterogeneously perturbed. This method of demonstrating pattern formation has been used extensively in ontogenetic work, for example when explaining stripe patterns on tiger skin (Murray 1981).

In the biological terms of the present model the analysis proceeds as follows: The model equations allow for a spatially homogeneous steady state of plant density, soil water availability, and surface water. Starting from this steady state we add or remove a small and spatially homogeneous amount of plants, soil water, and surface water, and then let the system follow its

own course again in time. The model analysis requires that such a perturbation allows for the system to return to its original spatially homogeneous steady state. In other words, the homogeneous steady state should be stable with respect to spatially homogeneous perturbations. Again, starting from the spatially homogeneous steady state, we add or remove a small but spatially heterogeneous amount of plants, soil water, and surface water, and then let the system follow its own course in time. In other words, we perturb plants, soil water, and surface water more at some places than at others: if these perturbations diverge, then the system will develop to a new, spatially patterned, steady-state (diffusion-driven instability). The mathematical analysis is described in detail in the following section, where we derive analytical solutions for spatial pattern formation in the model.

MATHEMATICAL ANALYSIS

Scaling of the model

Scaling our model given in Eq. 13 with coefficients given in Table 2 reduces the number of parameters from 13 to 7 and gives us the following equations:

$$\frac{\partial P}{\partial t} = \frac{W}{W+1} \times P - bP + D_{po} \left\{ \frac{\partial^2 P}{\partial x_1^2} + \frac{\partial^2 P}{\partial x_2^2} \right\} \quad (14a)$$

$$\frac{\partial W}{\partial t} = O \times \frac{P+W_0}{P+1} - \frac{W}{W+1} \times kW - rW + D_{wo} \left\{ \frac{\partial^2 W}{\partial x_1^2} + \frac{\partial^2 W}{\partial x_2^2} \right\} \quad (14b)$$

$$\frac{cg_{\max}}{\alpha} \times \frac{\partial O}{\partial t} = 0 = R_s - O \times \frac{P+W_0}{P+1} + \left\{ \frac{\partial^2 O}{\partial x_1^2} + \frac{\partial^2 O}{\partial x_2^2} \right\}. \quad (14c)$$

Turing analysis

Analysis of these equations with the method as developed by Turing (1952) requires that the model (Eq. 14) has a locally stable nontrivial equilibrium with respect to spatially homogeneous perturbations, and that these equilibria be unstable to at least one type of spatially heterogeneous perturbation.

Spatially homogeneous equilibria

The spatially homogeneous internal steady states are $P(\bar{x}, t) = \bar{P}$, $W(\bar{x}, t) = \bar{W}$, and $O(\bar{x}, t) = \bar{O}$. Equilibria are as follows:

TABLE 2. Coefficients and their scaling for parameters in equations.

Coefficient	Scaling
b	$\frac{d + \beta}{cg_{\max}}$
k	$\frac{k_2}{k_1 c}$
r	$\frac{r_w}{cg_{\max}}$
R_s	$\frac{R}{cg_{\max} k_1}$
D_{po}	$\frac{D_p \alpha}{D_o cg_{\max}}$
D_{wo}	$\frac{D_w \alpha}{D_o cg_{\max}}$
P_{scaled}	$\frac{P_{\text{original}}}{k_2}$
W_{scaled}	$\frac{W_{\text{original}}}{k_1}$
O_{scaled}	$\frac{O_{\text{original}} \alpha}{k_1 cg_{\max}}$
t_{scaled}	$t_{\text{original}} cg_{\max}$
x_{scaled}	$x_{\text{original}} \sqrt{D_o / \alpha}$

$$\bar{W} = \frac{b}{1-b} \quad (15a)$$

$$\bar{P} = \frac{R_s - r\bar{W}}{kb} \quad (15b)$$

$$\bar{O} = R_s \times \frac{\bar{P} + 1}{\bar{P} + W_0}. \quad (15c)$$

Since the dynamics of surface water act on a much faster time scale than change in soil water availability and plant density, a quasi-steady-state approach (Edelstein-Keshet 1988) can be adopted, and one may assume that the rate of change of O is equal to zero. Thus it can be shown that the internal steady state is locally stable with respect to spatially homogeneous perturbation if

$$-\left(\frac{k\bar{P}}{(\bar{W} + 1)^2} + r \right) < 0 \quad (16)$$

and

$$\frac{kb\bar{P}}{(\bar{W} + 1)^2} > 0. \quad (17)$$

Since all coefficients in Eqs. 16 and 17 are positive as long as the internal steady state exists, these inequalities are always valid and equilibria in Eq. 15 are stable.

Spatially heterogeneous perturbations

We now analyze the behavior of a spatially heterogeneous perturbation of the system around the equilib-

ria (Eqs. 15). We perturb these equations with a spatially heterogeneous perturbation of wavelength l and analyze what happens to the equilibria: pattern formation occurs when these equilibria are unstable.

Linearizing Eqs. 14 around local steady states with

$$P(\vec{x}, t) = \bar{P} + \varepsilon(\vec{x}, t) \quad (18a)$$

$$W(\vec{x}, t) = \bar{W} + \psi(\vec{x}, t) \quad (18b)$$

$$O(\vec{x}, t) = \bar{O} + \theta(\vec{x}, t) \quad (18c)$$

gives us

$$\begin{aligned} \frac{\partial \varepsilon(\vec{x}, t)}{\partial t} &= a_{11}\varepsilon(\vec{x}, t) + a_{12}\psi(\vec{x}, t) + a_{13}\theta(\vec{x}, t) \\ &+ D_{po} \left\{ \frac{\partial^2 \varepsilon(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 \varepsilon(\vec{x}, t)}{\partial x_2^2} \right\} \end{aligned} \quad (19a)$$

$$\begin{aligned} \frac{\partial \psi(\vec{x}, t)}{\partial t} &= a_{21}\varepsilon(\vec{x}, t) + a_{22}\psi(\vec{x}, t) + a_{23}\theta(\vec{x}, t) \\ &+ D_{wo} \left\{ \frac{\partial^2 \psi(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 \psi(\vec{x}, t)}{\partial x_2^2} \right\} \end{aligned} \quad (19b)$$

$$\begin{aligned} 0 &= a_{31}\varepsilon(\vec{x}, t) + a_{32}\psi(\vec{x}, t) + a_{33}\theta(\vec{x}, t) \\ &+ \left\{ \frac{\partial^2 \theta(\vec{x}, t)}{\partial x_1^2} + \frac{\partial^2 \theta(\vec{x}, t)}{\partial x_2^2} \right\} \end{aligned} \quad (19c)$$

where a_{ij} is given by:

$$\begin{aligned} a_{11} &= 0 & a_{12} &= \frac{\bar{P}}{(\bar{W} + 1)^2} & a_{13} &= 0 \\ a_{21} &= \bar{O} \times \frac{1 - W_0}{\bar{P} + 1} - kb & a_{22} &= -\left(\frac{k\bar{P}}{(\bar{W} + 1)^2} + r \right) \\ a_{23} &= \frac{\bar{P} + W_0}{\bar{P} + 1} & a_{31} &= -\bar{O} \times \frac{1 - W_0}{\bar{P} + 1} & a_{32} &= 0 \\ a_{33} &= -\frac{\bar{P} + W_0}{\bar{P} + 1}. \end{aligned}$$

We next substitute perturbations of the following form:

$$\varepsilon(\vec{x}, t) = \bar{\varepsilon}(t)\cos(q_1x_1) \times \cos(q_2x_2) \quad (20a)$$

$$\psi(\vec{x}, t) = \bar{\psi}(t)\cos(q_1x_1) \times \cos(q_2x_2) \quad (20b)$$

$$\theta(\vec{x}, t) = \bar{\theta}(t)\cos(q_1x_1) \times \cos(q_2x_2). \quad (20c)$$

With $q_i = 1/l_i$, the inverse of the wavelength of the perturbation in the x_1 or x_2 direction results in

$$\frac{\partial \bar{\varepsilon}(t)}{\partial t} = a_{11}\bar{\varepsilon}(t) + a_{12}\bar{\psi}(t) + a_{13}\bar{\theta}(t) - D_{po}\bar{\varepsilon}(t)Q^2 \quad (21a)$$

$$\frac{\partial \bar{\psi}(t)}{\partial t} = a_{21}\bar{\varepsilon}(t) + a_{22}\bar{\psi}(t) + a_{23}\bar{\theta}(t) - D_{wo}\bar{\psi}(t)Q^2 \quad (21b)$$

$$0 = a_{31}\bar{\varepsilon}(t) + a_{32}\bar{\psi}(t) + a_{33}\bar{\theta}(t) - \bar{\theta}(t)Q^2 \quad (21c)$$

where $Q^2 = q_1^2 + q_2^2$.

Since we adopted a quasi-steady-state approach and assumed that the rate of change of O is zero, the rate of change of O around its equilibrium is also equal to zero, thus from Eq. 21c we find

$$\bar{\theta}(t) = \frac{a_{31}\bar{\varepsilon}(t) + a_{32}\bar{\psi}(t)}{Q^2 - a_{33}}. \quad (22)$$

Together with the fact that a_{11} , a_{13} , and $a_{32} = 0$, this allows us to reduce Eq. 21 to a system of two ordinary differential equations:

$$\frac{\partial \bar{\varepsilon}(t)}{\partial t} = -(D_{po}Q^2) \times \bar{\varepsilon}(t) + a_{12}\bar{\psi}(t) \quad (23a)$$

$$\begin{aligned} \frac{\partial \bar{\psi}(t)}{\partial t} &= \left(a_{21} - a_{23} \times \frac{a_{31}}{(a_{33} - Q^2)} \right) \times \bar{\varepsilon}(t) \\ &+ (a_{22} - D_{wo}Q^2) \times \bar{\psi}(t). \end{aligned} \quad (23b)$$

The Jacobean matrix

$$\mathbf{J} = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix}$$

has elements:

$$\begin{aligned} b_{11} &= -(D_{po}Q^2) & b_{12} &= a_{12} \\ b_{21} &= a_{21} - a_{23} \times \frac{a_{31}}{(a_{33} - Q^2)} & b_{22} &= a_{22} - D_{wo}Q^2 \end{aligned}$$

and stability is assured when

$$b_{11} + b_{22} < 0 \quad (24)$$

and $F(Q^2) > 0$ with

$$F(Q^2) = b_{11}b_{22} - b_{21}b_{12}. \quad (25)$$

For pattern formation to occur instability is required, which means that one or both of the above inequalities must be false.

Because b_{11} and b_{22} are both negative, Eq. 24 is always true. $F(Q^2)$, however, can be both positive or negative depending on the parameter values and Q^2 .

We conclude that pattern formation occurs when $F(Q^2) < 0$ with

$$\begin{aligned} F(Q^2) &= D_{po}Q^2 \times \{kA + r + D_{wo}Q^2\} \\ &- \left\{ \frac{Q^2B}{C + Q^2} - kb \right\} \times A \end{aligned} \quad (26)$$

where

$$\begin{aligned} A &= \frac{\bar{P}}{(\bar{W} + 1)^2} \\ B &= \frac{1 - W_0}{(\bar{P} + 1)^2} \times \bar{O} \\ C &= \frac{\bar{P} + W_0}{\bar{P} + 1}. \end{aligned}$$

Further, it can be established that a minimal requirement for pattern formation is that $D_p/D_o < AB/(kA + r)$

with the biological meaning that plant dispersal should be low with respect to surface water motion.

General shape of $F(Q^2)$ and parameter plane pictures

$F(Q^2)$ has first derivative

$$F'(Q^2) = D_{p0} \times \{kA + r + 2D_{w0}Q^2\} - \left\{ \frac{BCA}{(C + Q^2)^2} \right\} \quad (27)$$

and second derivative

$$F''(Q^2) = 2D_{p0}D_{w0} + \left\{ \frac{BCA}{(C + Q^2)^3} \right\}. \quad (28)$$

$F'(Q^2)$ is first negative and then positive with increasing Q^2 , and $F''(Q^2)$ is always positive. Therefore, $F(Q^2)$ is of a concave form, increasing toward infinity at high Q^2 . Thus the transition from a state with no patterns to a state with patterns is given by the parameter combinations at which both $F(Q^2) = 0$ and $F'(Q^2) = 0$.

We present our results visually as diagrams showing the transition from one state to another on two parameter axes, given by $F(Q^2) = 0$ and $F'(Q^2) = 0$. By formulating the equations derived from $F(Q^2) = 0$ and $F'(Q^2) = 0$ in terms of D_{p0} we can derive an expression for the condition for pattern formation in terms of D_{p0} . Subtracting these two expressions from each other yields

$$R(Q^2) = \frac{\left\{ \frac{Q^2 B}{C + Q^2} - kb \right\} \times A}{Q^2 \times \{kA + r + D_{w0}Q^2\}} - \frac{CBA}{(C + Q^2)^2} \cdot \frac{1}{kA + r + 2D_{w0}Q^2}. \quad (29)$$

When $R(Q^2)$ is 0, the expressions for D_{p0} are valid. Solving $R(Q^2)$ numerically for different parameters allows the creation of diagrams showing the bounds of regions with patterning with D_{p0} on the y-axis and a parameter of choice (e.g., herbivory) on the x-axis.

In addition, the level of herbivory for which plants cannot exist is derived from the expression for the non-trivial plant equilibrium (Eq. 15b):

$$\bar{p} = \frac{R_s - r\bar{W}}{kb}.$$

Plants cannot exist when this equilibrium is < 0 . At a system in equilibrium this occurs when

$$b < \frac{R_s}{r + R_s} \quad (30)$$

which is the criterion under which plant cover can exist.

RESULTS

General modeling results

Pattern formation occurs in the model given spatially homogeneous initial conditions. In Fig. 3 is a parameter

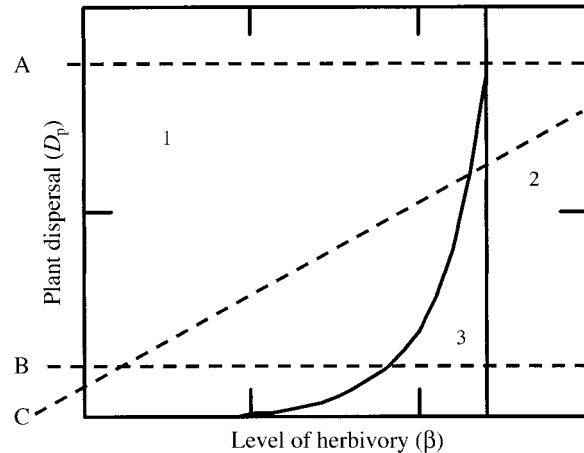


FIG. 3. Phase plane picture showing three states: (1) closed vegetation cover, (2) bare soil, and (3) pattern formation. Dashed line A depicts high plant dispersal: as herbivory increases, transition is from state 1 (closed vegetation cover) to state 2 (bare soil). Dashed line B depicts low plant dispersal: as herbivory increases transition is from state 1 (closed vegetation cover) through state 3 (pattern formation) to state 2 (bare soil). Dashed line C depicts the case when plant dispersal increases with herbivory: there is not necessarily a qualitative difference between line C and line B. Parameter values: $c = 10$, $g_{\max} = 0.05$, $k_1 = 3$, $d = 0.1$, $\alpha = 0.1$, $k_2 = 5$, $W_0 = 0.1$, $D_w = 1$, $D_o = 1 \times 10^4$, $r_w = 0.1$.

plane picture showing the combinations of herbivory and plant dispersal for which vegetation pattern formation will occur. The curved line is a line separating parameter combinations resulting in pattern formation from those that do not. The vertical line is a boundary separating the parameter plane into a state where vegetation is able to exist, and a state where no vegetation is able to exist. Together these two boundaries delimit three system states: (1) closed vegetation cover, (2) bare soil, and (3) spatial vegetation patterns.

Fig. 3 shows that for low levels of plant dispersal, an increase in herbivory leads from regions with a closed vegetation cover, through regions with pattern formation, to regions where vegetation is not able to exist (Fig. 3, line B). At higher levels of plant dispersal the range of herbivory for which pattern formation occurs is lowered, and eventually disappears (Fig. 3, line A).

Belsky (1986) suggests that an increased disturbance by animals increases lateral plant growth, as clonal grass plants may be more spread out by trampling. If this is true, plant dispersal will increase with herbivory, and lines denoting the transitions between states with increasing disturbance will follow a different path, indicating higher levels of plant dispersal with higher levels of herbivory (see Fig. 3, line C). This type of interaction between plant dispersal and herbivory may have a negative effect on pattern formation, but our results indicate that the same type of behavior is possible as in cases where plant dispersal does not increase

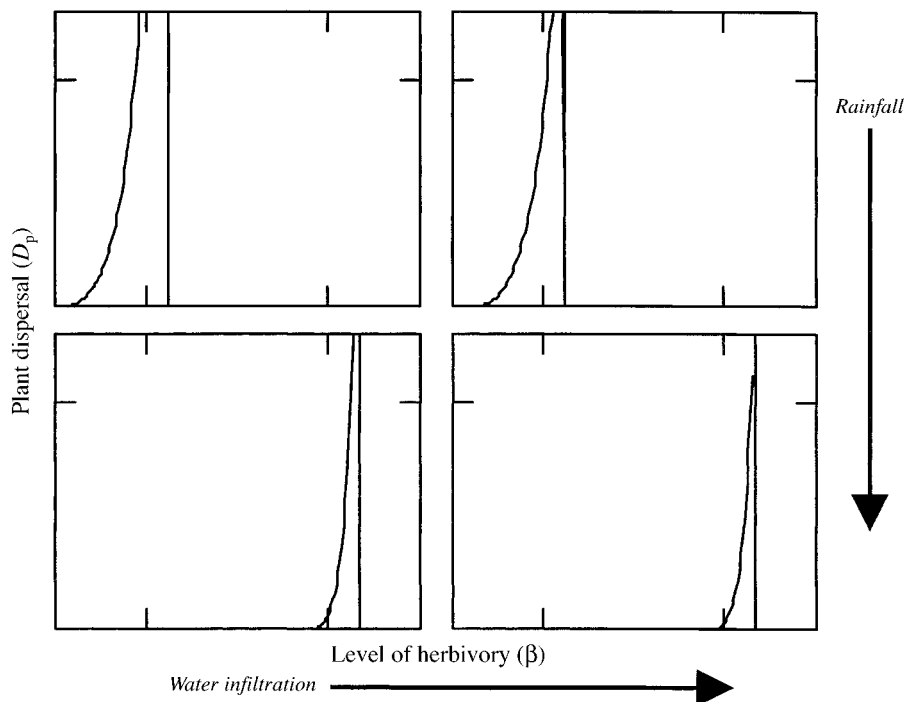


FIG. 4. Phase plane pictures showing the effect of different levels of water infiltration in the absence of plants ($W_0 = 0.05$ and 0.15) and different levels of rainfall ($R = 0.05$ and 1.5) on the area for which vegetation patterning occurs. An increase in W_0 leads to smaller areas for which pattern formation occurs. An increase in rainfall increases the area across which vegetation can exist but decreases the area for which pattern formation occurs. Parameter values: $c = 10$, $g_{\max} = 0.05$, $k_1 = 3$, $d = 0.1$, $\alpha = 0.1$, $k_2 = 5$, $D_w = 1$, $D_o = 1 \times 10^4$, $r_w = 0.1$.

with herbivory. We now examine the effects of other parameters on pattern formation by studying how changes in these parameter values affect the phase plane picture of Fig. 3.

Effects of rainfall and soil properties

The amount of rainfall received by the system is important in determining the level of herbivory for which a closed vegetation cover can be maintained, but also on the range of herbivory for which vegetation pattern formation occurs (Fig. 4). Higher levels of rainfall increase the levels of herbivory for which vegetation can exist and decrease the parameter area in which pattern formation occurs. Further, an increase in water infiltration capacity (W_0 from Eq. 3 describing water infiltration into the soil in the absence of plants) decreases the area across which pattern formation occurs for all rainfall levels. Recall that a high water infiltration capacity corresponds to sandy soils, whereas a low water infiltration capacity is typical for loamy or clayey soils. Thus, given a certain rainfall level, loamy or clayey soils are more likely to exhibit vegetation pattern formation than sandy soils. Additionally, the level of herbivory for which vegetation pattern formation can be expected is lower for loamy or clayey soils than for sandy soils.

Effects of plant properties

Vegetation composed of perennial grasses is more likely to improve soil structure than vegetation composed of annual grasses (Kelly and Walker 1976, Rietkerk et al. 2000). Note that the capacity of the vegetation for soil improvement is reflected by the parameter k_2 (Eq. 3); a higher k_2 represents a lower capacity of the vegetation for soil improvement. Such lower capacity results in vegetation pattern formation for a larger parameter area and at lower levels of herbivory (Fig. 5). This indicates that a vegetation cover comprised of annual grasses is more likely to exhibit pattern formation than a vegetation cover made up of perennial grasses, and that a vegetation cover consisting of annual grasses will exhibit pattern formation at lower levels of herbivory than a vegetation cover formed of perennial grasses.

It is recalled that given a certain soil water level, plants with a higher k_1 (Eqs. 6 and 10) take up less water and grow slower than plants with a lower k_1 and thus experience the same soil water levels as being "drier." An increase in k_1 decreases the parameter area across which plants are able to survive and increases the parameter area across which pattern formation may occur (Fig. 6). Thus, vegetation not adapted to drought is more likely to exhibit pattern formation than vegetation adapted to drought.

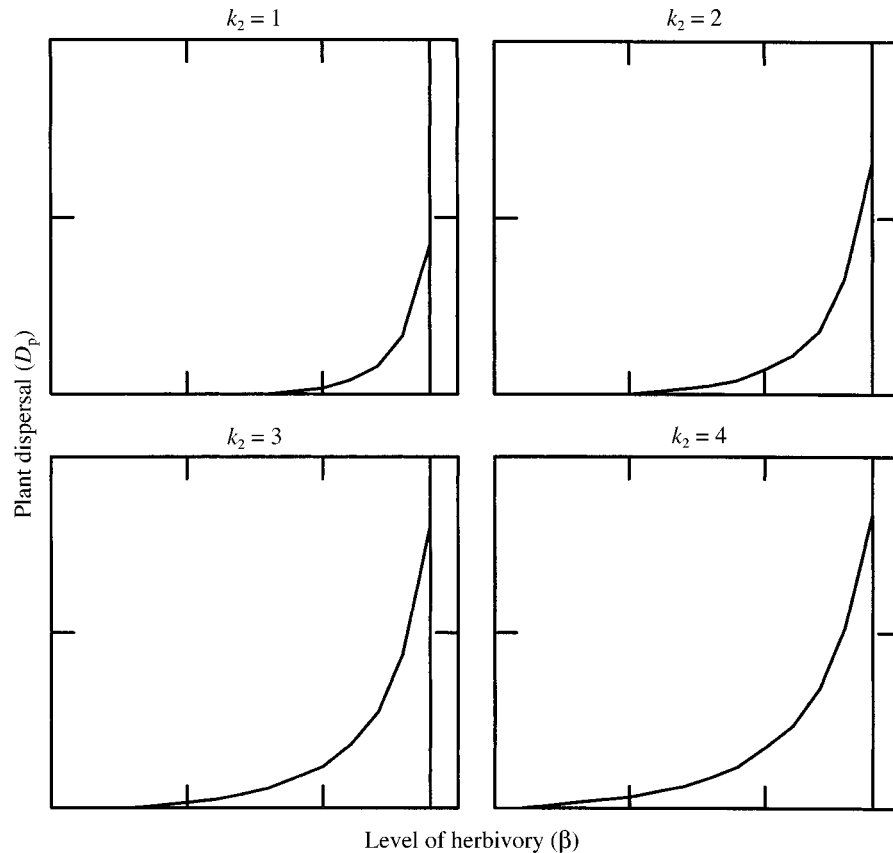


FIG. 5. Phase plane pictures showing the effect of a decrease in the capacity of vegetation for the improvement of soil structure (increasing k_2) on the area for which pattern formation occurs. An increase in k_2 results in a larger area for which pattern formation occurs. Parameter values: $R = 2$, $c = 10$, $g_{\max} = 0.05$, $k_1 = 3$, $d = 0.1$, $\alpha = 0.1$, $W_0 = 0.1$, $D_w = 1$, $D_o = 1 \times 10^4$, $r_w = 0.1$.

DISCUSSION

Many authors have included the positive feedback between plant density and water infiltration in their hypotheses concerning possible agents for vegetation pattern formation in semi-arid grazing systems. We proposed that this positive feedback is the main process generating vegetation pattern formation in semi-arid areas throughout the world. Our model results indeed suggest that it is the combination of this positive feedback and runoff/run-on processes that generate vegetation pattern formation in semi-arid grazing systems. Without the positive feedback between plant density and water infiltration, pattern formation is not found in our model. Thus we conclude that slope and underlying heterogeneity are no essential conditions for vegetation pattern formation. Other factors in the model, such as herbivory, plant dispersal, rainfall, the rate at which water infiltration increases with plant density, and drought tolerance of plants, appear to determine under what conditions pattern formation is likely (as discussed below), but are not the primary factors that generate the patterns.

Our model predicts that, provided the rate of plant

dispersal is low, an increase in the level of herbivory would lead to transitions from a state with a closed vegetation cover, to a state with spatial vegetation patterning, to a state with bare soil. Higher levels of plant dispersal have a negative effect on pattern formation. However, if plant dispersal increases as herbivory increases, the same qualitative behavior is still possible, though less likely. These theoretical results are in line with empirical findings of Rietkerk et al. (2000). On a gradient of herbivore impact they found areas with a closed vegetation cover at low herbivore impact, areas of spatial vegetation patterning at levels of intermediate impact, and areas of bare soil at high herbivore impact. Rietkerk et al. (2000) also provided evidence for the positive feedback between plant density and water infiltration in areas where vegetated patches alternated with bare soil. Vegetated patches positively affected soil moisture through less runoff and higher infiltration of rainwater that could not infiltrate into the bare soil elsewhere (see also Anderson and Hodgkinson 1997, Bromley et al. 1997).

Our model also revealed the effect of rainfall on the incidence of vegetation patterns. While a decrease in

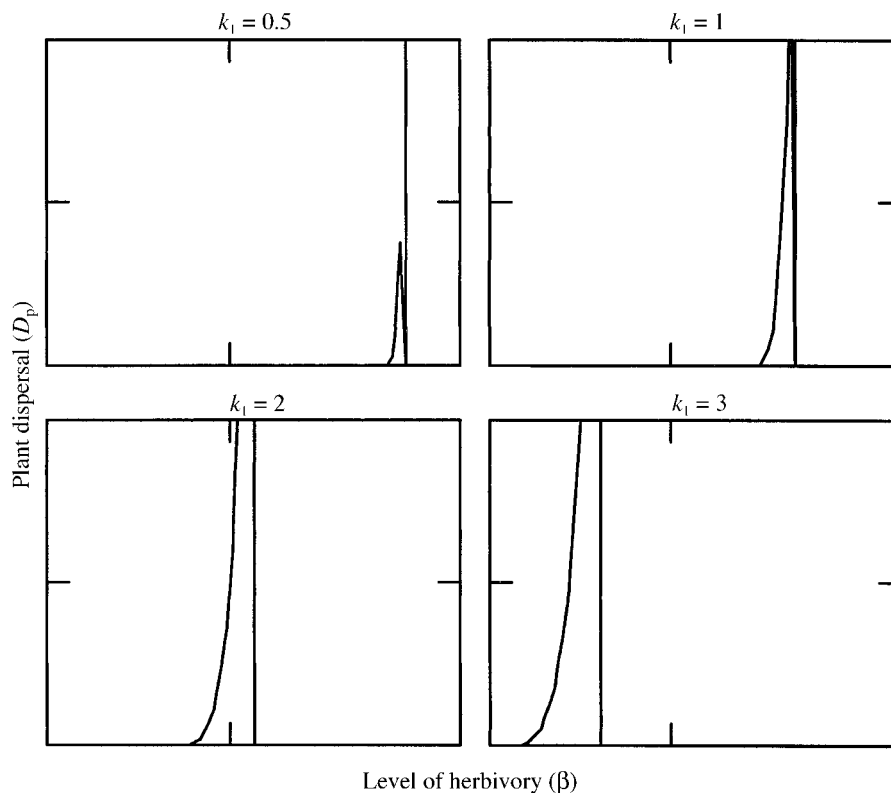


FIG. 6. Phase plane pictures showing the effect of a decrease in the ability of plants to take up water (increasing k_1) on the area for which pattern formation occurs. An increase in k_1 results in a larger area across which pattern formation occurs for lower levels of herbivory. Parameter values: $R = 2$, $c = 10$, $g_{\max} = 0.05$, $d = 0.1$, $\alpha = 0.1$, $k_2 = 5$, $W_0 = 0.1$, $D_w = 1$, $D_o = 1 \times 10^4$, $r_w = 0.1$.

rainfall reduced the level of herbivory below which plants could survive, the parameter area in which pattern formation occurred increased. This is in line with the observation that vegetation change following borehole installation is generally restricted to a limited radius around the boreholes, which expands if rainfall decreases and contracts if rainfall increases (Hanan et al. 1991, Helldén 1991). Following these authors, analyzing remote sensing images around boreholes can be used to further test the hypotheses generated by our model.

Our model indicates that slope is not a necessary condition for the appearance of vegetation patterns (see also Lefever and Lejeune 1997). However, the soil surface regularly slopes gently in areas where vegetation patterning occurs (Mabbut and Fanning 1987, Bromley et al. 1997) favoring runoff water flowing towards certain directions without forming gullies. Slope, together with plant interactions, as proposed by Thiery et al. (1995) and Lefever and Lejeune (1997), may explain the varying forms of pattern, and that in some regions bands of vegetation seem to migrate slowly upslope, while in other regions they seem to be stable (Klausmeier 1999). Furthermore, we have shown that on flat ground underlying heterogeneity is not an essential

condition either. It is important to further investigate the varying forms and movement of patterns in the case of directional overland flow along a slope and in the case of flat ground. These will be the next steps in our research.

It is of interest to compare the predictions of the models of Rietkerk et al. (1997) and Rietkerk and van de Koppel (1997), with the predictions put forward in this paper. In their models, soil water that cannot be retained and used by the vegetation is completely lost from the system. Our model, however, permits surface water that does not infiltrate at a certain location still to be potentially available for vegetation elsewhere. The marked difference in assumptions between these models also results in different predictions. For instance, our model does not predict sudden, irreversible vegetation collapse at high levels of herbivory. Instead, we predict that vegetation pattern formation functions as a buffer against sudden vegetation collapse, and that vegetation changes are reversible if herbivory decreases. This illustrates the imperative need to explicitly take the effects of different spatial scales into account when predicting vegetation collapse and pattern formation at a real-world level.

Plant communities are likely to exhibit pattern for-

mation if they are not able to improve soil structure, if they are growing on loamy or clayey soils with low infiltration capacity, and if they comprise plant species that are not very drought tolerant. Apparently, the occurrence of vegetation patterning is coupled to conditions under which plants are severely stressed, either because of climatic properties (low rainfall), soil properties (low infiltration capacity), or plant properties (hardly able to improve soil structure and not very drought tolerant). This is in line with the observation that the regions within which patterned vegetation occurs share a harsh semi-arid climate with a severe dry season and a tendency to develop low-permeability surface crusts if vegetation is absent (Bromley et al. 1997). In these regions, plants can only survive if they facilitate their own growth by improving their microenvironment. Our model analysis suggests that vegetation pattern formation in semi-arid grazing systems may be attributed mainly to such facilitation.

Most evidence of facilitation comes from ecosystems where plants are exposed to severe abiotic stress, for instance from salt marshes (high soil salinity due to evaporative salt concentration), from arid deserts (high temperatures resulting in high soil evaporation leading to low water supply), and from arctic tundras (low temperatures and low soil nutrient availability) (Bertness and Callaway 1994, Brooker and Callaghan 1997, Holmgren et al. 1997). The question arises if patterned vegetation occurs in these ecosystems as well, and if exposure to severe abiotic stress and vegetation pattern formation may be linked with the process of facilitation in general. Indeed, evidence from arctic salt marshes shows that plants decrease soil evaporation, thereby decreasing sodium concentration of soil water, and that persistent vegetation mosaics develop composed of densely vegetated patches alternating with almost bare soil (Srivastava and Jefferies 1995, 1996, Van de Koppel et al. 1997). The generation of such vegetation patterning may thus be a general phenomenon in ecosystems sharing harsh abiotic conditions, and this phenomenon may be mechanistically linked with the process of facilitation.

ACKNOWLEDGMENTS

We thank Johan Grasman, John Hearne, Pierre Hiernaux, Johan van de Koppel, Christopher Klausmeier, Lalit Kumar, Frank van Langevelde, René Lefever, Emiel van Loon, and Han Olf for useful discussions and comments on the manuscript. The research of Max Rietkerk was supported by the Netherlands Organisation for Scientific Research (NWO-WOTRO programme FLARE project number WAB 76-198). IACR receives grant-aided support from the Biotechnology and Biological Sciences Research council of the United Kingdom.

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