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Effects of overgrazing and rainfall variability on the dynamics of semiarid banded vegetation patterns: A simulation study with cellular automata

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ABSTRACT

The effects of factors acting at small scale (grass/grass and grass/shrub biological interactions) and landscape scale (overgrazing and rainfall changes) on the development and permanence of banded vegetation patterns (VB) are assessed with a spatially explicit cellular automaton model. In particular, the influence of two environmental factors that are changing in many VB arid lands (rainfall and grazing pressures) is studied. Three rainfall regimes (representing 0.5, 1.0, and 2.0 times the long-term rainfall average), five grazing intensities, two types (reversible and irreversible) of grazing disturbance, two grazing periodicities (chronic and pulse), two levels of grass colonization ability, positive and negative interactions between shrubs and grasses, and the efficiency of endozoochorous seed dispersal are simulated.

The results show that the permanence of undisturbed VB depends on the interaction of two factors, rainfall regime and grass colonization ability. Type and intensity of grazing also modify VB cover and permanence; furthermore, long-term overgrazing may convert mixed grass/shrub plant communities to pure scrublands dominated by endozoochorous-dispersed shrubs due to competitive interactions between shrubs and grasses.

Besides providing an adequate representation of the system's dynamics, the model is a useful tool that may be used to explore the consequences of climate change on management scenarios.

1. Introduction

Vegetation bands (VB) constitute a particular type of aggregate vegetation pattern that has been observed in deserts of Africa, America, Asia, and Australia. They appear in nearly flat areas (rarely more than 1% slope) where rain is scarce and occurs in intense bursts (Worrall, 1960; Boaler and Hodge, 1964; Valentin et al., 1999). The spatial patterns consist of dense plant aggregations surrounded by bare soil; viewed from the air, they appear as bands perpendicular to contour lines (Montaña et al., 2001; Fig. 1). Such an orientation facilitates the interception of run-off water flows, and water infiltration is greater inside the band because of its edaphic properties (Cornet et al., 1992). This extra input of water favors the survival and recruitment of plants, permitting the development of a vegetation cover – inside the bands – that would not exist if rainwater was evenly distributed across the landscape (Mauchamp et al., 1993; Valentin et al., 1999; Tongway and Ludwig, 2001).

Physical factors (mainly topography, soil properties, and rain regime) influencing the dynamics (Dunkerley, 1997b) and formation (Klausmeier, 1999) of VB, and biotic factors such as species interactions (Thiéry et al., 1995) inside VB have been studied through model simulation. But there are factors acting at small scale (the level of biological interactions) and others acting at landscape scale (overgrazing and rainfall changes) that affect the stability of banded vegetation patterns (VB) and have not been studied simultaneously with models allowing the assessment of direct effects as well as the effect of their interactions. In particular, this paper aims to study the stability of VB in the face of changes in rainfall and grazing pressures, two environmental factors that are changing in many arid lands where VB are present. For that purpose, "small" and "landscape" scale processes were integrated in an automaton model.

The first small-scale process studied here is the colonization capacity of grasses. The influence on VB development of the ability of grasses to explore and colonize nearby patches that are rich in

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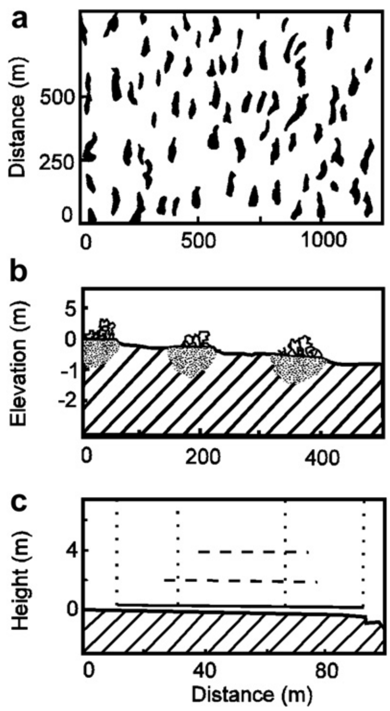

Fig. 1. Schematic representation of banded vegetation patterns from the Southern Chihuahuan Desert (Mexico). (a) Aerial view at 1:25,000 scale showing the vegetation bands (in black) surrounded by almost bare areas. (b) Idealized cross-section of the landscape showing the distribution of vegetation and soil water moisture after rain (dotted areas on the soil profile). (c) Idealized cross-section of a vegetated band. Horizontal straight lines indicate the vegetated range and the height of herbaceous species (solid line), shrubs (lower dotted line), and small trees (upper dotted line). Dotted vertical lines indicate the three subdivisions of the bands used in this study: (i) upslope, (ii) main body, and (iii) downslope (modified from Fig. 1 of Montaña, 1992).

resources (e.g., through a seed bank or clonal propagation) was considered. The second small-scale process comprises the biological interactions among plants of different life forms. When VB have a dense herbaceous stratum, there is the possibility that the colonization capacity of grasses will be altered by density-dependent competition (Cain et al., 1995). The establishment of shrub seedlings may also be hindered by the presence of a dense grass cover (Bush and van Auken, 1990), despite the fact that adult grasses and shrubs can coexist as their root systems do not overlap (Brown and Archer, 1990; Briones et al., 1996). The first "landscape-scale" factor studied here, overgrazing by livestock, has also been studied through modeling (Dunkerley, 1997a; Hillerislambers et al., 2001), but perhaps not enough. It is a very common type of disturbance in arid lands and far surpasses the overall effect of native herbivores (Brown and Archer, 1987). In a given region, it can occur continuously for long periods of time or constitute events that are localized in time and space—as is the case for rotational grazing systems. Besides grazing intensity, the influence of this disturbance on VB dynamics also depends on the part of the system that is affected. For example, if disturbance results only in the removal of grass biomass, the system may recover its original biomass levels, as long as the environmental modification is not severe. If, however, the soil is affected—for example, its structure is altered by trampling and subsequent erosion (Prose et al., 1987)—run-off properties are modified in a practically irreversible way. Periodicity is also an important factor. A constant regime of low-intensity disturbance modifies communities differently than a short, intense event (Brown and Archer, 1989). Grazing may also facilitate the establishment of shrub species (Brown and Archer, 1987); in consequence, VB systems may be radically modified. The second "landscape-scale" process that has not been studied in depth is rainfall variability, including both interannual rainfall variability and changes in the long-term rainfall annual average.

Mathematical simulation is a common approach used for studying vegetation band dynamics. There are two main groups of VB models. One comprises the continuous models (based on simultaneous differential partial equations), which have focused on the effect of water dynamics on band formation (Klausmeier, 1999) and on the interaction between physical and biotic factors (Hillerislambers et al., 2001; Meron et al., 2004). The other group consists of discrete models inspired on cellular automata systems (Wolfram, 1984). These models were used to analyze intraspecific interactions (Thiéry et al., 1995) and climate variation (Dunkerley, 1997a,b) on VB.

One advantage of cellular automaton models is that their numerical implementation is usually much simpler than that of continuous models, especially in the way that they represent explicit space and the effect of neighborhoods on the system's global dynamics. They are also extremely versatile, as both physico-chemical and biological processes can be simulated. It is worth noting that they make it possible to simultaneously model processes that occur on different temporal and spatial scales. The difference in the speed and intensity of the demographic response of shrubs and grasses to variations in rainfall and grazing is one such example.

In this study, a cellular automaton modeling approach is used to study the effects of the interaction between two small scale factors (colonization capacity of grasses and biological interactions between shrubs and grasses) and two landscape scale factors (overgrazing and rainfall variability) on the functioning of VB composed by two interacting species with contrasting life forms (phreatophyte shrubs propagated by endozoochory and grasses). The information gathered in the VB pattern of the southern Chihuahuan Desert (Montaña, 1992) is used for that purpose.

2. Materials and methods

2.1. Model set-up

Cellular automata (CA) are discrete, dynamic systems composed of the following: a) a lattice of cells; b) state variables that acquire discrete and finite values in each cell; and c) an evolutionary rule that controls temporal and spatial changes in the values of state variables (Wolfram, 1984). Their system dynamics develop in discrete units of time. The updating of time (t) to time ($t+1$) for each individual cell depends on its state and neighborhood, which can vary in size and shape. The effect of explicit space on the dynamics of these systems is represented as a "neighborhood function" that evaluates conditions in a cell's neighborhood and determines the value that it will acquire at the following time step, which was considered as annual. All of the crucial processes that vary in space are incorporated into this neighborhood function.

The model consists of four 80×30 cell rectangular lattices (two to simulate water flow at times (t) and ($t+1$), and another two to simulate vegetation dynamics at the same time intervals). The two lattices for time (t) and the two for time ($t+1$) appear in pairs, so that the columns and rows of the lattices of each pair coincide. On each lattice, the upper and lower edges are joined as are the right and left side, thus simulating a continuous surface. The values for water flow cells influence the state of vegetation cells and vice versa, through functions that represent the processes that will be modeled. On the basis of water and vegetation conditions at time (t), the conditions for time ($t+1$) are calculated. The model code