

# Chapter 13

## Case Study of Self-Organized Vegetation Patterning in Dryland Regions of Central Africa

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**Abstract** A growing body of empirical evidence supporting or opposing the mechanistic hypotheses and predictions of self-organization models exist which have been applied to the case of spatially periodic vegetation patterns found in semi-arid and arid areas around hot deserts in Africa. Overall, remarkable qualitative – and sometimes quantitative – agreement is found and presented here between the rich theoretical framework and predictions of self-organization models and the results of field and remotely sensed investigations for dryland areas in Niger, Morocco and Sudan.

### 13.1 Introduction

This chapter presents a case study of a self-organized semi-arid ecogeomorphic system integrating current research across disciplines and scales. It analyzes particular spatial organizations of vegetation cover in the form of spatially periodic alternations of vegetated and bare or nearly bare zones that have been described at the border of every hot desert (Deblauwe et al. 2008). The first descriptions of such striking patterns date back to the colonial period and the strategic aerial surveys that were carried out after World War II (MacFadyen 1950; Clos-Arceuduc 1956). Tiger bush (i.e. banded) patterns were initially assumed to be related to geomorphic and hydrological processes, with the stripes clearly following topographic contours.

A large number of studies have since then documented the hydrology, pedology and ecology of comparable vegetation patterns around the globe. As the interactions of small-scale processes which lead to self-organization phenomena are often non-intuitive, it became possible to reproduce the whole set of pattern morphologies

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observed in nature – whether in the form of banding or the more isotropic arrangements of labyrinthine, spotted or gapped structures – through numerical approaches in the form of spatial symmetry-breaking models (Lefever and Lejeune 1997; Rietkerk and van de Koppel 2008; Borgogno et al. 2009) (see also the discussion in Chap. 3). The models enabled an understanding of the modulation of pattern morphologies along gradients of external (environmental) constraints on the system, as well as parsimonious explanations in terms of the local processes liable to produce such emergent behaviours.

In the following section, we will summarize and test hypotheses on the mechanisms that trigger the spatial patterning. Some quantitative testing of model predictions on pattern dynamics are given in the subsequent section.

### 13.2 Testing the Hypothesized Ecohydrological Processes

Several self-organization models have been published recently that were able to reproduce the intrinsic vegetation patterning observed in drylands (Rietkerk and van de Koppel 2008; Borgogno et al. 2009). Functionally, these vegetation models can all be conceptually interpreted as expressing a balance between the mechanisms of short-range activation (positive feedback) and long-range inhibition (negative feedback) of biomass with surrounding vegetation modulating the local dynamics of water and vegetation biomass. The hydrological and biological processes invoked in these models differ fundamentally, especially when it comes to generating patterns in isotropous conditions (i.e. without a slope gradient and substantial water advection). Two hypothesized mechanisms for pattern generation can be distinguished:

- **M1:** a spatial diffusion of both water (unconcentrated overland flow) and vegetation with a feedback of vegetation on water infiltration. Patterns emerge because of a large difference in the diffusion coefficients of water and vegetation (HilleRisLambers et al. 2001; von Hardenberg et al. 2001);
- **M2:** the existence of positive and negative spatial feedbacks of plants on the soil-water budget via the contrasting effects induced by plant organs above ground (e.g. shade) and below ground (extended root systems). Patterns emerge because resource competition at the lateral range exceeds the facilitation range of a plant (Lefever and Lejeune 1997; Lefever et al. 2009).

Our work on isotropous gapped vegetation patterns in SW Niger (detailed in Chap. 4) shed new light on these opposing hypotheses. Using a combination of direct observation of plant organs (crowns and root systems), soil-moisture monitoring through space and time and stable isotope ( $^2\text{H}$ ) labelling, it was found (Barbier 2006; Barbier et al. 2008) that:

1. there was no significant difference between bare and vegetated patches in recharge within the shallow root zone (350 mm mean depth above the iron pan) after average rainstorm events (30–40 mm);
2. the water half-life time in the soil was three times higher within thickets, an effect that was statistically more strongly related to the physical presence of a shrub crown above than to other soil quirks, such as improved texture, bulk density or organic matter content;
3. the root system of the dominant shrub (*Combretum micranthum*, G. Don) was mainly distributed in the upper soil layers. It was laterally very extensive and spreading under areas of bare soil. Shrubs could tap water (as confirmed through deuterium labelling) up to lateral distances equivalent to ten times their crown radius.

The above elements lend support to the second hypothesised mechanism **M2** in self-organization models and provide limited evidence for the first explanation **M1**, at least in the particular context of the study area. Moreover, it appeared that when parameterized using field data from our Niger site (i.e. adult plant size, facilitation and competition ranges and allometry exponent), the (Lefever et al. 2009) model – although deprived of any remaining degrees of freedom – is able to reproduce the observed morphology (gaps in vegetation cover) and wavelengths (the added widths of two successive sparse and dense areas) of patterns (of about 50 m). A key role in the parameterization is played by the ratio between above and below-ground plant ranges and plant size via a measurable allometry exponent (Lefever et al. 2009).

### 13.3 Testing Predictions on Pattern Emergence and Modulation

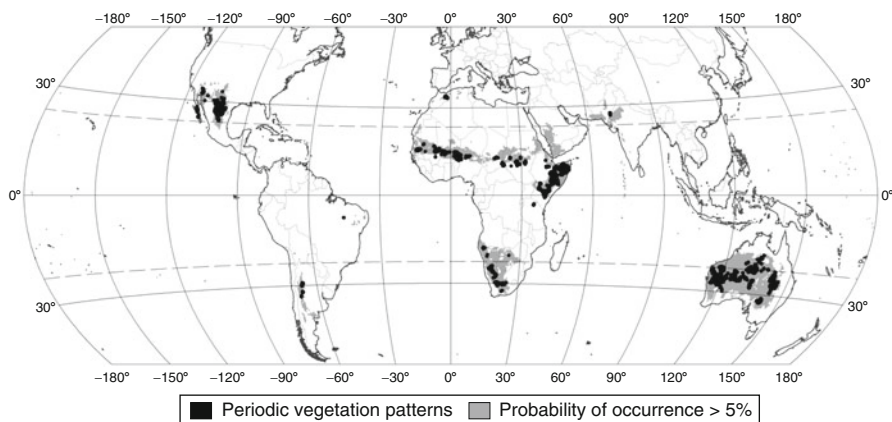
Whether they employ the M1 or M2 mechanism, self-organization models converge on several predictions regarding the spatial or temporal dynamics of pattern morphologies under varying environmental stressors affecting plant productivity or mortality (e.g. aridity, grazing, wood collection). Due to the size and life span of individual shrubs and the even larger space and time scales characterizing the emerging structures, testing the two mechanisms requires working at landscape to regional scales and across decadal to centennial time scales. Remote sensing surveys are starting to deliver the required coverage, while at the same time providing a sufficient horizontal resolution to allow the quantification of pattern morphology and to allow the testing of model predictions in terms of symmetry, orientation, travelling waves and dominant frequencies. Deblauwe et al. (2011) give a comprehensive summary of the predictions of self-organization models on pattern modulation:

- **P1:** Under homogeneous and isotropic conditions (i.e. on non-sloping terrain and in the absence of an influential dominant wind), stress in the form of decreased

biomass productivity and/or increased mortality induced by increasing levels of aridity, grazing or woodcutting provokes a predictable succession of pattern changes. Round gaps first appear in the uniform vegetation cover and then elongate and coalesce to form a labyrinthine structure. As the aridity further increases, round spots are the only remnant of the vegetation within a bare soil matrix, preceding a final transition to bare soil (desert) (Lejeune and Tlidi 1999; Couteron and Lejeune 2001; Rietkerk et al. 2002; Meron et al. 2004; D'Odorico et al. 2006; Guttal and Jayaprakash 2007; Lefever et al. 2009).

- **P2:** Lower annual rainfall (increased aridity) results in patterns with larger wavelengths (Lefever and Lejeune 1997; Lejeune et al. 2004; Sherratt and Lord 2007).
- **P3a:** In the presence of a sufficient anisotropic environmental influence, for instance due to the presence of a slope gradient or dominant winds, all the above morphologies are forced into parallel bands elongated in a direction perpendicular to the environmental anisotropy, forming the so-called tiger bush (Lefever and Lejeune 1997; Lefever et al. 2000; von Hardenberg et al. 2001; Rietkerk et al. 2002).
- **P3b:** Runoff intensifies as the slope steepens and the competition range increases in the upslope direction, inducing an increase in the wavelength of banded patterns (Sherratt 2005).
- **P3c:** Bands are predicted to migrate in the upslope direction (Lefever and Lejeune 1997; Klausmeier 1999; Sherratt and Lord 2007).
- **P4:** Several self-organization modelling approaches have also pointed to the possibility of hysteresis loops and critical points in aridity-driven succession of vegetation states. Transitions between desert and spotted patterns (Lejeune et al. 2002), between uniform cover and gapped patterns and among the different pattern morphologies and wavelength may not occur at the same critical aridity levels during drying and wetting phases and are therefore dependent on initial conditions (Lejeune et al. 2004; Meron et al. 2004; Sherratt and Lord 2007). In this case, multiple stable vegetation states may coexist within some range(s) on the aridity scale. Since spotted patterns and bare land may represent alternative stable states, several authors have proposed that periodic vegetation may serve as warning signals of imminent and rapid ecosystem collapse or “catastrophic shift” (Rietkerk et al. 2004; Kefi et al. 2007; but see also the discussion in Chap. 3).

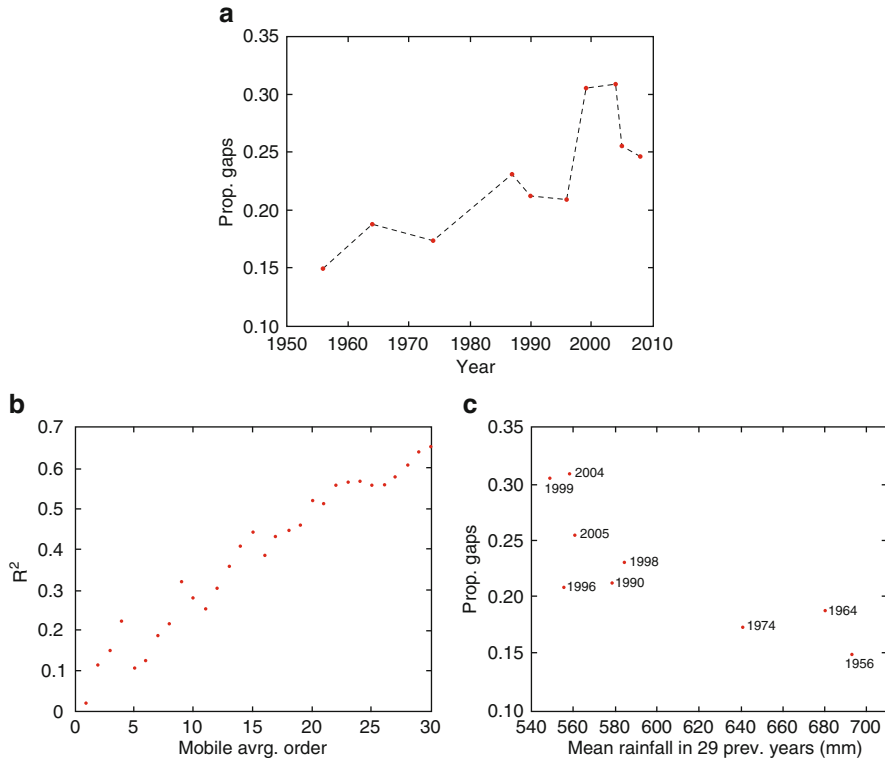
The map in Fig. 13.1 represents a global analysis of periodic pattern distributions (predicted and actual) obtained using pattern-occurrence data from written and digital records overlain on Landsat satellite imagery using the model MaxEnt by Phillips et al. (2006), which is a geographic distribution and habitat model. Using data on the spatial variation of a number of environmental variables related to topography, soil and climate, the MaxEnt model determines the regions where vegetation patterning might occur. Existing empirical approaches allowed sorting the relative importance of environmental variables on pattern existence (Deblauwe et al. 2008). The most important driver was the humidity index, obtained as the ratio of mean annual rainfall to mean annual evapotranspiration, with vegetation



**Fig. 13.1** Actual and predicted distribution of periodic vegetation patterns using the MaxEnt method

patterns occurring consistently in hot and arid to semi-arid regions. Other significant variables include the soil wilting point (mainly related to soil texture), temperature and rainfall seasonality. A number of new locations were discovered worldwide, including the first evidence of spotted patterns in Sudan and of periodic patterns in South America. Most importantly, periodic vegetation patterning appeared under predictable environmental conditions at biome scale across all longitudes, despite very different phylogenetic histories, i.e. different plant families, although possibly with a limited number of convergent life forms. These results confirmed the generality of aridity-mediated pattern emergence at the border of every tropical desert (P1).

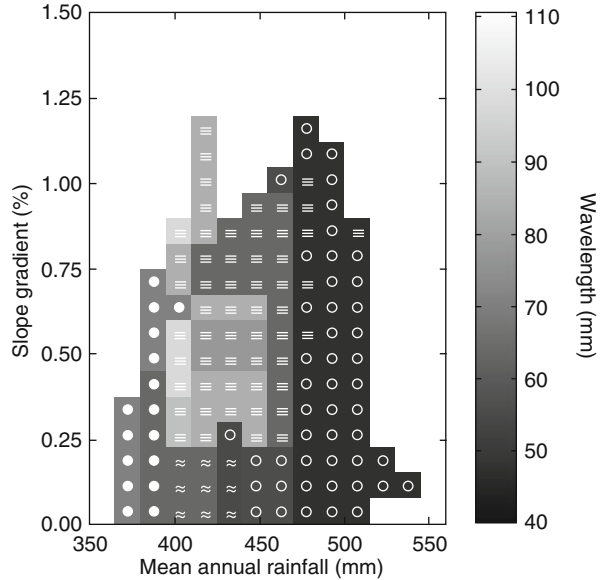
At a smaller (regional) scale, we endeavoured to analyze pattern modulation in a quantitative way within the framework of the Fourier textural ordination methods presented in Chap. 9. In a first study, we investigated pattern emergence from homogeneous savannah cover in isotropous substratum conditions, by placing ourselves at the most humid end of the distribution of periodic patterns in the south west of the Republic of Niger (Barbier et al. 2006). The objective was to observe over time if a decrease in rainfall could trigger the emergence of gapped patterns. Using historical imagery records (from both satellite- and air-borne sensors), we were able to quantify at different points in time the proportion of gapped patterns in a 3,000 km<sup>2</sup> area, including a protected area (W National Park) and areas increasingly impacted by human exploitation (for wood and pasture) (Barbier et al. 2006). We thereby demonstrated that patterned areas had increased between 1956 and 1996 because of drought alone (i.e. in the National Park, where grazers and browsers density remained relatively low) and that this increase became more marked as a result of human land use and biomass uptakes. We present here data from the same protected area with a higher temporal resolution (Fig. 13.2a): from 1956 to 2010, the figure shows how patterned area first increased until early 2000s followed by a slight decrease afterwards. As a result, the area covered by gapped (and labyrinthine) pat-



**Fig. 13.2** Dynamics of gapped vegetation patterns in the W National Park (Niger) as a function of mean annual rainfall. Vegetation structure was characterized on the basis of a Fourier textural gradient analysis (see Sect. 9.3) using a set of superimposed panchromatic data sources (aerial and Spot imagery). Image spatial resolution: 10 m; analysis window size:  $250 \times 250$  m; total window number: 14,592 windows. Rainfall statistics at the Say meteorological station (Source: DMN, Niger) (**a**) proportion of gapped patterns through time; (**b**) coefficient of determination obtained in linear regressions of gap proportion as a function of the average rainfall of previous years (number of years = mobile average order); (**c**) scatter plot of gap proportion versus the average yearly rainfall of the 29 previous years

terns had doubled in the early 2000s relative to the 1956 figure. When trying to relate pattern area statistics to mean annual rainfall, the best fits ( $R^2 \sim 0.7$ ;  $p < 0.001$ ) were found for the longest averaging periods, i.e. 29 years (Fig. 13.2b, c). The results suggest a notable inertia in the response of the system, which may be related to the large number of woody components in the study region. However, a potential caveat with this particular case is that, as both rainfall and pattern area present temporal linear trends, one cannot be definitive about the existence of a cause-and-effect relationship being of the observed correlation. An ideal case would have been to observe several concomitant progressions and regressions in the pattern dynamics and climatic conditions. In any case, the study brought for the first time a strong empirical support for aridity-mediated pattern emergence (part of prediction **P1**).

**Fig. 13.3** Pattern wavelength as a function of mean annual rainfall and slope in central Sudan. Grey-scale level is proportional to the mean wavelength of the dominant pattern morphology: spotted ( $\bullet$ ), labyrinthine ( $\approx$ ), gapped ( $\circ$ ) and banded pattern ( $\equiv$ ). White areas represent the environmental domain where vegetation is not organised into periodic patterns (less than 15 windows featuring periodic vegetation pattern per slope–rainfall bin). Analysis based on a synchronic (2001) coverage of SPOT images (Modified from Deblauwe et al. 2011)



In a second study, in the Kurdufan province of Sudan (north-central Africa), we studied the spatial and temporal transitions between all possible morphologies (gaps, labyrinths, spots and bands) and both rainfall and slope gradients (Deblauwe et al. 2011). SPOT and Corona satellite images taken at three dates over a 35-year period were subdivided into  $410 \times 410$ -m windows and classified into the following pattern classes: non-periodic, gapped, labyrinthine, spotted and banded. The results are summarised in Fig. 13.3. The images gave some large-scale evidence that the predicted modulation sequence is valid in terms of both morphology and wavelength. Along the aridity gradient, we indeed observed the predicted sequence of gapped, labyrinthine and spotted patterns (**P1**). Above a critical slope threshold, the patterns aligned into parallel bands (**P3a**). For all slope gradients, the pattern wavelength was proportional to aridity (**P2**). Furthermore, both the sequence of morphologies and the wavelength variations were observed not only across space (synchronous comparisons) but also through time (diachronous comparisons). However, for increasing slope gradients, prediction **P3b** – which had relied on a very limited number of modelling studies – was not observed in the data, as banded pattern wavelengths appeared to decrease with slope. Hysteresis loops (multiple stable states) in pattern succession dynamics, as well as the unaccounted influence of soil factors could explain the important share of unexplained wavelength variance in the study (78 % for the banded pattern). On the other hand, no evidence supported irreversible transitions from spotted patterns to bare soils (desert) (**P4**). We even observed cases of reappearance of spotted structures after clearing for cultivation in the diachronous image series. This apparent contradiction may be due to some favourable conditions of certain soil properties (structure, texture, organic matter content, etc.) that had improved under thickets prior to cultivation. Regarding band

orientation, a detailed study (Koffi et al. 2007; Deblauwe 2010) in the same region evidenced systematic deviations of band orientations in contours orthogonal to slope direction. As these deviations systematically pointed towards the direction of the dominant winds (Harmattan), this result brought some alteration to the water runoff hypothesis (**M1**), which was generally assumed applicable to sloping conditions. In particular, the role of sediment and seed redistribution by wind should be explored in more detail (see Chap. 12 for a case study on sediment transfers in Australia).

Another aspect of banded pattern dynamics that has generated long-standing debates (Tongway et al. 2001) is the prediction that bands would travel in the upslope direction (**P3c**). Multi-temporal remote sensing data allowed us to test the prediction at a number of sites in Northern America, Northern Africa and Australia (Deblauwe et al. 2012). Using Fourier analysis and a 2D cross-spectral approach (Barbier et al. 2010), we were able to quantify band-migration speed in a systematic way across regions sufficiently large enough to be statistically representative. We discovered that, not only did bands move upslope in a number of regions (up to  $0.8 \text{ m year}^{-1}$  for both a Moroccan and a Somalian sites), but also they did so at a speed proportional to pattern wavelength – a finding matching observed behaviour of some self-organization models (Sherratt and Lord 2007). Analyzing the rate of band migration in the Chihuahuan Desert (Northern America), for example, suggested that upslope colonization and downslope regression episodes did not occur synchronously, but rather in response to wet and dry spells, respectively. Upslope migration might therefore be interpreted rather as a reaction to climate variability than as an endogenous property of all banded systems. However, the question of band migration remains largely open as most of the variability in dynamics is still unexplained. For instance, the monitored dryland systems in Australia did not show any movement during the 40-years observation period.

## 13.4 Conclusions

What this study has highlighted is the usefulness of self-organization models as a theoretical framework allowing the guidance of empirical research. Indeed, despite their simplistic nature and the sometimes diverse mechanisms invoked, a number of convergent predictions were produced, which were very consistent – at least qualitatively and, sometimes, quantitatively (Lefever et al. 2009) – with the behaviours of real systems. Sadly, the prospect of calibrating fully quantitative models of these ecosystems seem a long way ahead, principally because of the very limited research efforts dedicated to estimating parameters in arid and semiarid landscapes within which periodic patterns extensively occur. In practice, competences from a range of fields is required, spanning ecology, hydrology, soil physics, remote sensing and non-linear systems modelling. Although studies from each of these individual fields have been carried out and published, a lack of integration has until now hampered



decisive breakthroughs. Manipulative experiments in the field or in shadehouses may also help to disentangle imbricated spatial effects mediated by plants on their environment and resources.

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