

Self-organized vegetation patterning as a fingerprint of climate and human impact on semi-arid ecosystems

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Summary

1 Spatially periodic vegetation patterns are well known in arid and semi-arid regions around the world.

2 Mathematical models have been developed that attribute this phenomenon to a symmetry-breaking instability. Such models are based on the interplay between competitive and facilitative influences that the vegetation exerts on its own dynamics when it is constrained by arid conditions, but evidence for these predictions is still lacking. Moreover, not all models can account for the development of regularly spaced spots of bare ground in the absence of a soil prepattern.

3 We applied Fourier analysis to high-resolution, remotely sensed data taken at either end of a 40-year interval in southern Niger. Statistical comparisons based on this textural characterization gave us broad-scale evidence that the decrease in rainfall over recent decades in the sub-Saharan Sahel has been accompanied by a detectable shift from homogeneous vegetation cover to spotted patterns marked by a spatial frequency of about 20 cycles km⁻¹.

4 Wood cutting and grazing by domestic animals have led to a much more marked transition in unprotected areas than in a protected reserve.

5 Field measurements demonstrated that the dominant spatial frequency was endogenous rather than reflecting the spatial variation of any pre-existing heterogeneity in soil properties.

6 All these results support the use of models that can account for periodic vegetation patterns without invoking substrate heterogeneity or anisotropy, and provide new elements for further developments, refinements and tests.

7 This study underlines the potential of studying vegetation pattern properties for monitoring climatic and human impacts on the extensive fragile areas bordering hot deserts. Explicit consideration of vegetation self-patterning may also improve our understanding of vegetation and climate interactions in arid areas.

Key-words: aridity, climate variability, ecosystem monitoring, Fourier transform, human pressure, pattern classification, remote sensing, self-organization, symmetry-breaking instability, vegetation patterns

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Introduction

The existence in the then British Somaliland of regular, landscape-scale patterns, in which dense patches of

vegetation alternate with bare soils, was first revealed by aerial photographs taken during the Second World War. They were first described scientifically by Macfadyen (1950), whose insight was that ‘they are manifestly within the province of botany and ecology; the essential background concerns geomorphology and meteorology; the causes must be investigated by physics

and mathematics; and the whole matter must be studied on air photographs'. Striped, spotted or arc-shaped patterns of different plant life-forms (grass, shrub and tree) have since been described in dry zones of Africa, Australia, Mexico and the Middle East, on soils ranging from sandy and silty to clayey (Tongway *et al.* 2001), and their occurrence at the transition between tropical savannas and hot deserts suggests aridity as the probable triggering factor. Non-formalized explanations of the phenomenon have led to the assumption that vegetation patches overcome aridity as a result of water sheet flow from upslope bare ground.

Recent modelling studies have mathematically formalized this theory of water redistribution through runoff (Thiéry *et al.* 1995; Dunkerley 1997). As sloping ground is necessary for resource redistribution, and thus for pattern formation, vegetation stripes always develop along elevation contours, and soil heterogeneity has been called on to explain the existence of regularly spaced bare spots on nearly flat territory (Klausmeier 1999). By contrast, another class of models is able to generate spots and stripes even in strictly homogeneous and isotropic (non-sloping) environments (Lefever & Lejeune 1997; von Hardenberg *et al.* 2001; HilleRisLambers *et al.* 2001; Okayazu & Aizawa 2001). The pattern is generated by an instability that leads to the disruption of spatial symmetry: the approach is derived from the seminal work of Turing (1952), which has already inspired many applications in physics, chemistry and biology (Cross & Hohenberg 1993; Murray 2003). The slope-induced anisotropy, if present, is then merely interpreted as a secondary factor that leads to the formation of stripes rather than spots, and potentially drives the progressive motion of the pattern.

The general contribution of mathematical modelling has been to show that interactions between plants at scales of the order of a few metres may result in the emergence of spatially periodic distributions of vegetation having wavelengths (i.e. the distance between two consecutive highs or lows in vegetation density) in the order of tens or hundreds of metres. It can be demonstrated that all these models of vegetation dynamics involve the interplay of competitive effects related to soil water consumption and facilitative effects resulting from soil water budget enhancement by vegetation. For pattern formation to occur, negative interactions (competition) must have a larger range than positive interactions (facilitation), analogous to the well-known condition of short-range activation and long-range inhibition in reaction-diffusion systems (Nicolis & Prigogine 1977). Moreover, all models agree that patterning occurs when vegetation growth decreases, for instance as a result of reduced water availability, and therefore view patterns as a self-organized response of vegetation to resource scarcity (Lejeune *et al.* 2002). However, different classes of models predict distinct patterning scenarios below a critical aridity threshold. In the absence of prepatterning in substrate properties, slope-based models always show a transition from homogeneous to striped vegetation, whereas the second class

consistently shows a shift from homogeneous cover to vegetation punctuated by bare spots. The distribution of bare spots is spatially periodic and displays a clear dominant spatial frequency (i.e. the number of repetitions of the pattern within a given window; the inverse of the wavelength) in Fourier space (Lejeune *et al.* 1999; Couteron & Lejeune 2001). In simulations, as aridity increases further, bare spots merge into 'labyrinthine' stripes, which subsequently become a bare matrix surrounding spots of vegetation that eventually disappear and leave a complete desert.

The main purpose of this paper is to provide broad-scale empirical evidence for the emergence of self-organized patterns of bare spots in response to increased aridity. A general trend towards lower rainfall, observed across the African Sahel during the second half of the last century (Nicholson 2001; IPCC 2001), allowed us to monitor changes in the spatial distribution of vegetation. Our study area in south-west Niger is located at the wetter end of the climatic range in which periodic patterns are presently observed in subsaharan West Africa (Couteron & Lejeune 2001) and encompasses both a protected area, experiencing only rainfall decrease, and adjacent, unprotected areas subjected to both decreasing rainfall and increasing human pressure. Extensive remote sensing data taken over a period of 40 years, coupled with intensive field measurements, allow us to address the following questions. (i) Can decreased rainfall drive the emergence of spatially periodic spots of bare ground – i.e. spotted patterns – in vegetation, all other things being equal? (ii) If so, is the phenomenon intrinsic to plant population dynamics or does it reveal pre-existing soil heterogeneity? (iii) What is the relative influence of climatic and anthropogenic factors on the process?

Materials and methods

STUDY AREA

Our investigations were carried out in south-west Niger at the southern (and wettest) extremity of a latitudinal climatic gradient between 12°N and 15°N (1951–89 average annual rainfall ranges from 700 mm to 300 mm; L'Hôte & Mahé 1996). Periodic patterns of alternating bare ground and dense vegetation are systematically observed all along the gradient on iron-capped plateaus, with spotted patterns being predominant in the south and banding in the northern stretches. In West Africa, such patterns are formed by dense thickets of tall shrubs (especially *Combretum micranthum* G. Don), in association with annual grasses (Couteron & Lejeune 2001). South of 12°N, periodic patterns are no longer observable, even on iron-capped plateaus, and the vegetation cover, which no longer displays regular patches of bare soil, can be described as a tree savanna, with mixed cover of both tall perennial and annual grasses associated with scattered trees and shrubs. Dry season fires, which are regular events in these savannas, rarely affect spotted

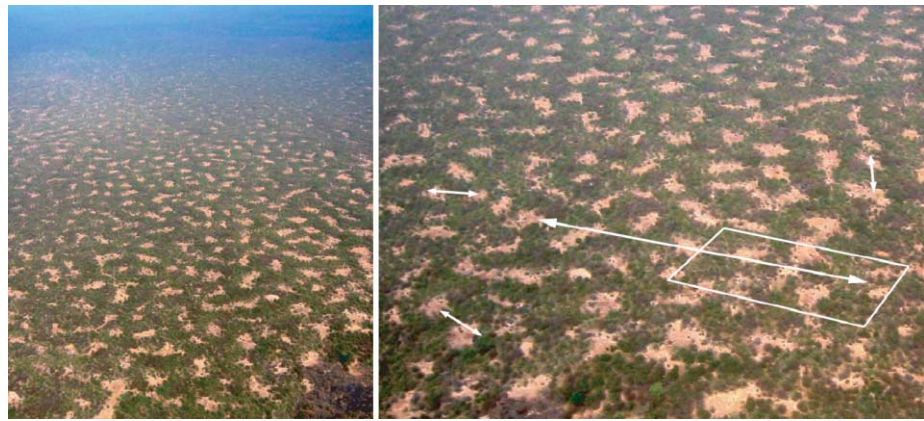


Fig. 1 Typical spotted pattern (bare soil is light coloured) and field study set up: perspective oblique view showing transects (three 50-m transects for soil survey, one 250-m transect for vegetation-relief correlation study) and a 120-m by 70-m area for topographical mapping.

vegetation due to both the lower quantity and the fragmented distribution of ignitable herbaceous biomass.

The influence of drought on vegetation pattern formation was addressed by monitoring vegetation change in a protected area (Niger part of the W Trans boundary Biosphere Reserve – 12°14'–12°30' N, 2°14'–2°45' E) while the combined influences of drought and human activities were considered by monitoring the immediate surroundings on the opposite (east) bank of the River Niger (district of Birnin Gaoure). In the reserve, as well as in the surrounding districts, extensive areas of periodic spotted vegetation patterns (Fig. 1) are presently observed on iron-capped plateaus, which are more xeric than other topographic positions. Official statistics for the district of Birnin Gaoure give a human density of 50 inhabitants km⁻² with a demographic annual growth rate of around 4% over the last decade. Except for the reserve, the whole region of south-west Niger is, in fact, characterized by a human population (density > 20 km⁻² and growth rate > 3%; Raynaut 2001) that is comparatively denser and is expanding faster than the African Sahel average. On iron-capped plateaus, neither crops nor settlements are generally observed and human pressure is mostly exerted via wood-cutting and grazing of domestic herds, which both result in a diffuse suppression of plant biomass. Since establishment in 1954, the reserve has been kept free from major human influences, except for the limited poaching of wildlife and brief night crossing of domestic herds (Leberre & Messan 1995).

The local rainfall series (Fig. 2) shows the difference between the years before the late 1960s (1921–68), with average rainfall of 670 mm yr⁻¹, and the subsequent years, characterized by both lower average rainfall (550 mm yr⁻¹) and limited, but severe, drought periods, particularly in the early 1970s and 1980s. There is a regular latitudinal gradient in average rainfall of approximately –1 mm yr⁻¹ for each kilometre northwards (L'Hôte & Mahé 1996), and similar variation was found for locations in and around the study area (series of Say, Tamou, La Tapoa and Kandi; data not shown). The study set-up was orientated

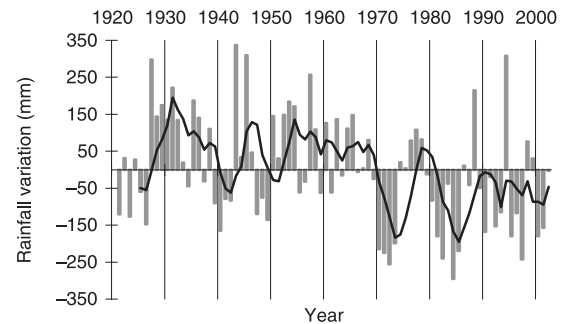


Fig. 2 Rainfall data for 1921–2002 at the meteorological station of Say (source: Direction Météorologique Nationale, Niger) expressed as annual variation (bars) around the interval mean (619.5 mm). The continuous line shows the moving average of the five preceding years.

longitudinally, with protected and unprotected sites at similar latitude to avoid the effects of this gradient.

REMOTELY SENSED DATA

Diachronic aerial photographs were used to survey both temporal and spatial variation of vegetation patterns. Panchromatic contacts (IGN-Niger, 1 : 50 000, December 1956 and December 1996) were digitized into greyscale levels with a pixel size of 2 m that was sufficient to study decametric-scale patterns. Tests with higher resolution, i.e. 1 m pixel⁻¹ or less, led to similar results for all analyses. On the digitized images, bright pixels correspond to bare soil, whereas dark pixels result from woody vegetation, and intermediate greyscale pixels relate to continuous grass cover. At first approximation, greyscale values can be considered as a monotonic function of phytomass.

We systematically sampled a rectangular study region of *c.* 100 × 30 km (with the longer dimension orientated east–west) via 29 square areas of 9 km² (total sampling rate of 8.7%), about half of which (14) were located in the park. These areas were sampled according to a 10-km by 10-km grid, with some local adjustments to

ensure that each sample area was found close to the centres of a picture from each of the two dates. This allowed a relatively precise superimposition of 1956 and 1996 digitized photographs without requesting geometrical corrections. Geographical invariants were found within each area and superposition was achieved with a root mean square error of less than 4 m. The 29 areas were then subdivided into square windows of 300 m on a side. At each date, 2900 such windows were submitted to quantitative pattern analysis.

QUANTITATIVE PATTERN ANALYSIS AND CLASSIFICATION

We used the two-dimensional (2D) Fourier transform and the subsequent computation of the 2D periodogram (Mugglestone & Renshaw 1998), also known as the power spectrum in engineering sciences, to obtain a quantitative characterization of the patterns observable in the greyscale images. This method is known to be appropriate when spatial periodicity is present in the signal under study, as periodogram amplitude values directly express the proportions of image variance that are accounted for by periodic functions of explicit spatial frequencies and orientations. The characterization is independent of the actual mean and variance of the images, making it a powerful tool to compare images without the need to request time-consuming radiometric corrections (Couteron 2002). Our approach differs from the method used by Ares *et al.* (2003) in that we computed spectra from 2D image periodograms (rather than 1D periodograms from transects), and we used these spectral values instead of a unique signal-to-noise ratio to compare and interpret spectra.

Two-dimensional periodograms were simplified so as to capture separately pattern information relative to spatial frequency and to spatial orientation. This was done by summing periodogram values on either ring-shaped or wedge-shaped concentric frequency regions to compute the r - and θ -spectra, respectively (Mugglestone & Renshaw 1998; Couteron 2002). The r -spectrum expresses the partition of the image variance among spatial frequencies while the θ -spectrum expresses the partition among spatial orientations. We further derived a synthetic index of pattern isotropy by computing Shannon's entropy (Legendre & Legendre 1998) on the values of the θ -spectrum. Highly anisotropic patterns (dominated by a particular orientation) show a unique prominent peak in their θ -spectra and a low entropy value. Conversely, isotropic patterns whose variance is scattered among all orientations (fairly flat θ -spectrum) should yield high entropy figures. [The maximum value for a strictly flat θ -spectrum would be 2.9, i.e. $\ln(18)/18$, as we partitioned the 0–180° range into 18 direction classes of 10°.]

Pairwise comparisons of r -spectra were carried out using the log-ratio technique, which is well suited for the computation of confidence intervals (F -distribution; Diggle 1990). In Fig. 3 we illustrate the method by

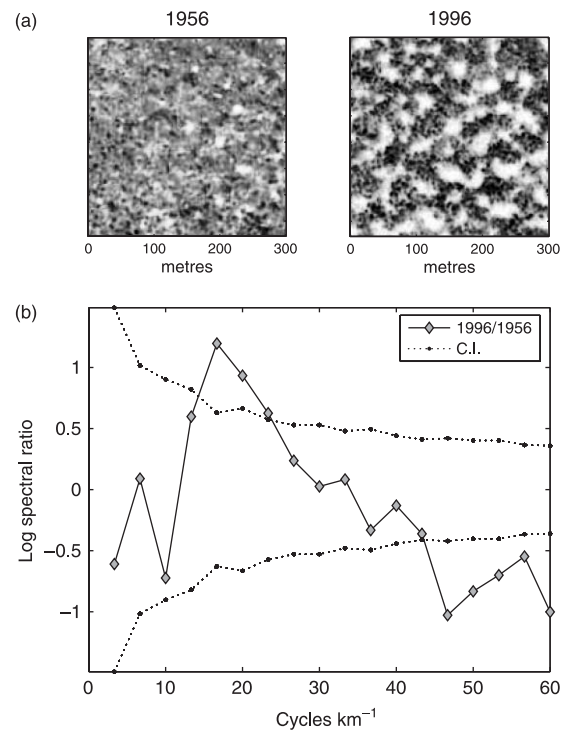


Fig. 3 Diachronic comparison of vegetation aspect in a particular window: (a) aerial photographs (windows 300 m on a side); bare soil appears in white and vegetation in grey (light to medium for herbaceous cover, dark for bushes, thickets and trees). (b) Log ratio between the 1996 and 1956 Fourier r -spectra. Dashed lines represent the 95% confidence interval (CI) computed under the null hypothesis of absence of change between 1956 and 1996.

comparing two diachronic versions of the same window (Fig. 3a). The shift from homogeneous savanna to spotted vegetation is clearly characterized by the emergence of a peak in the r -spectrum, while the log-ratio between r -spectra (Fig. 3b) shows which spatial frequencies have undergone a statistically significant increase (i.e. those having values above the upper confidence envelopes). Note that for generality spatial frequencies are expressed in cycles km^{-1} rather than in wavenumbers.

Each temporal version of a window is characterized by its r -spectrum, and can be seen as being described by quantitative variables (or 'features'; Tang & Stewart 2000), which are the contributions of successive spatial frequencies to image variance (we restrict ourselves to the first 25 wavenumbers, i.e. spatial frequencies smaller than 83 cycles km^{-1} or wavelengths above 12 m). Non-hierarchical, unsupervised clustering using the K-means algorithm and the Euclidean distance (Legendre & Legendre 1998) was performed on the r -spectra table (after standardization, i.e. centring of each variable by its mean and division by its standard deviation) to classify windows objectively into four classes. The two dates ($n = 5800$ windows) were analysed together in order to obtain a common frame of reference for observing pattern dynamics between the dates. We further built two-way contingency tables between dates and classes in order to test the significance of interdate variations in class

frequencies (Bishop's critical values on Freeman–Tukey deviates). Finally, we mapped the categories on the digitized aerial photographs by superimposing categorical symbols at the centre of each 300-m sampling window.

FIELD MEASUREMENTS

In order to assess whether the observed periodic spatial patterning could derive from pre-existing substratum heterogeneities, we selected a typical spotted vegetation site, located in the middle of the protected park, for intensive field investigations (Fig. 1). The vegetation, geomorphology and soil properties were characteristic of the iron-capped plateaus of the whole region, and the selected site had witnessed the overall emergence of spotted patterns that are described and analysed below. Topographical mapping was carried out (instrumental error less than 5 mm) in a 120-m by 70-m area and along a 250-m transect using an optical theodolite (Metland MTX0™) and a laser meter (Leica Disto™) adapted on the theodolite. Along the transect, vegetation cover was visually estimated in quadrats of 1 m on a side. To evaluate the spatial correlation between cover and local elevation along a transect, the Fourier coherence spectrum (Diggle 1990) was computed between vegetation cover and detrended elevation. This spectrum is derived from the cross-periodogram built from the two processes and is interpreted as a series of correlation coefficients (ranging from 0 to 1) between the spatial frequencies of the two processes. Envelopes were built from the standard error of the coherence spectrum (computed following Diggle 1990).

Other soil parameters such as soil depth above the ironpan, depth of the layer of iron nodules, particle size (proportions in seven classes) and bulk density were measured from 32 soil pits regularly sampled every 5 m along three transects (Fig. 1). A two-way ANOVA (Sokal & Rohlf 1995), using vegetation cover (either bare or vegetated) and transects as factors, was performed to explore the variability of soil parameters in relation to the vegetation pattern. Spatial dependency between residuals of the ANOVA was tested using Young's test for serial independence.

Results

PERIODIC PATTERN AND SUBSTRATUM VARIATION

Two-dimensional topographical mapping revealed that vegetation was not restricted to local depressions (Fig. 4a), contradicting the idea that spotted patterns may directly match slight pre-existing substratum irregularities. The coherence spectrum, giving the correlation coefficients between the spatial frequencies of two different processes, was computed between detrended local elevation and vegetation cover measured along a transect. This spectrum showed the absence of any significant relationship at relevant spatial frequencies. In particular,

coherency estimates did not differ significantly from zero for the spatial frequencies of *c.* 20 cycles km⁻¹ (see below) characterizing the periodic vegetation pattern (Fig. 4b). By contrast, the mapped area proved not to be completely isotropic as a general slope of *c.* 0.6% was observed. It is interesting to note that in the central part of the mapped area, where the slope was highest (i.e. 1.7%), the spotted (isotropic) pattern of vegetation tended to become anisotropic (i.e. banded) by aligning perpendicularly to the slope. The two-way ANOVA on soil parameters showed that the only significant difference between bare and vegetated areas was found for bulk density. Although other parameters whose spatial variation might be expected to determine vegetation patterns did not show any significant relationship with vegetation cover, they did show significant differences between transects. The scale of this spatial variability was not, however, reflected by the periodic vegetation pattern. Residuals of the ANOVA did not show spatial autocorrelation along transects.

CLASSIFICATION OF LAND COVER SPATIAL PATTERNS

We submitted the 5800 (two temporal versions of 2900 windows) individual standardized r-spectra to K-means clustering. The r-spectrum gives the signature of each window in terms of spatial frequencies, and the purpose of applying this clustering algorithm was therefore to classify windows on the basis of their resemblance (Euclidian distance) with respect to the coarseness or fineness of the texture. The resulting four classes gave a clear interpretation in terms of textural properties of the windows (Fig. 5) and therefore in terms of land cover features or vegetation types (Fig. 6). Class C1 (spotted) was characterized by a strong peak of the mean standardized r-spectrum in the range 20–30 cycles km⁻¹, i.e. for spatial frequencies that were identified by preliminary analyses as characterizing spotted periodic vegetation (Fig. 3). The three remaining classes were ordered along a textural gradient according to the relative importance of small vs. large spatial frequencies in the r-spectrum: C3 (macro) was characterized by a peak in the small spatial frequencies (< 20 cycles km⁻¹), corresponding to windows marked by large landscape features, such as crops, hamlets, gallery forests or rocky escarpments, whereas C4 (fine textured) had a mean standardized r-spectrum dominated by large frequencies and corresponded mainly to fine-grained homogeneous savanna vegetation, as seen clearly in Fig. 6(a,c). Class C2 (slight macro) had intermediate textural properties, a virtually flat standardized r-spectrum and featured windows that were often slightly macro-heterogeneous.

TEMPORAL DYNAMICS

The particular images displayed in Fig. 6 illustrate the temporal change in land cover patterns. In 1956, after

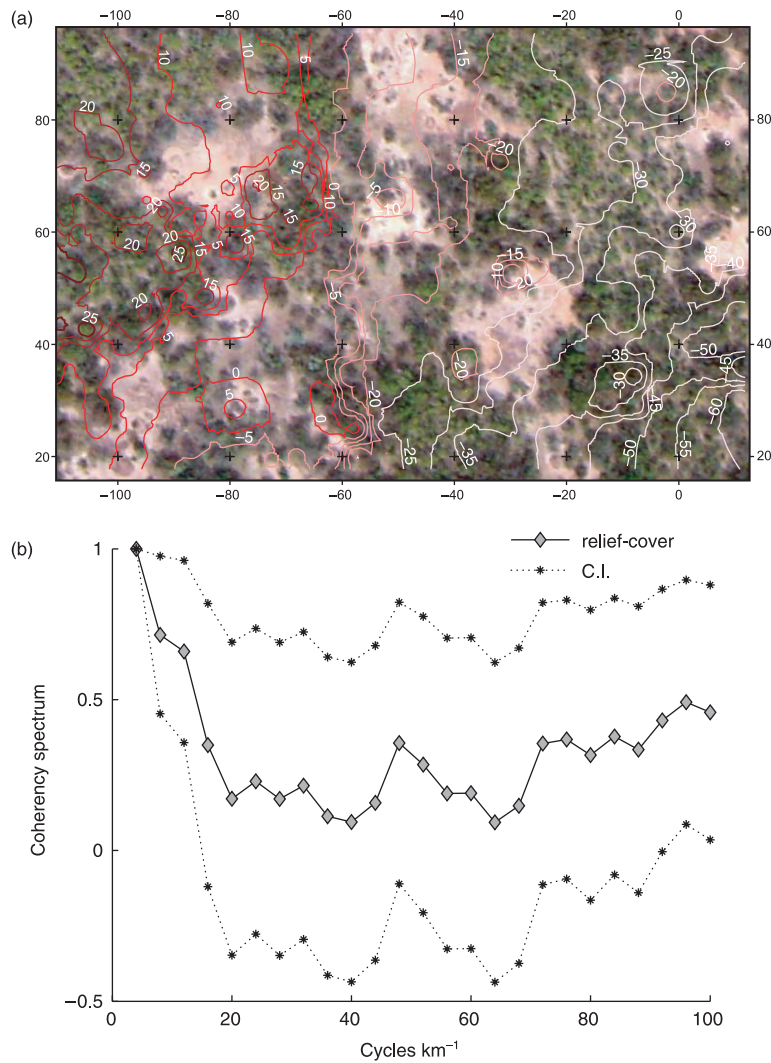


Fig. 4 Test of independence between vegetation pattern and microelevation. (a) Contour levels (5-cm spacing, relative altitudes in cm, distances in m) superimposed on a vertical view in the 120-m by 70-m quadrat. (b) Coherence spectrum between cover and local elevation along the transect. The dashed lines represent the 95% pointwise confidence interval (CI) based on two standard errors in each direction.

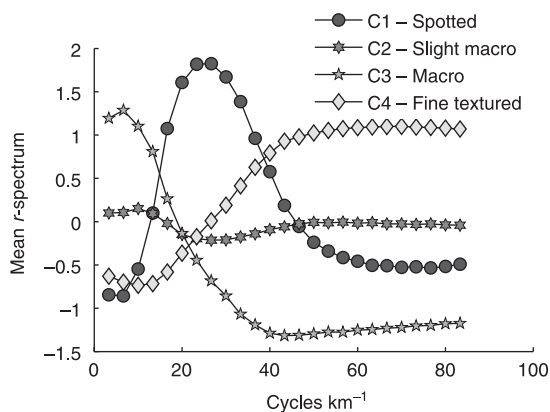


Fig. 5 Standardized mean r -spectrum of each class of land-cover pattern (K-means clustering).

three decades of rainfall of around 670 mm yr^{-1} , both images (Fig. 6a,c) displayed an extended, rather uniform, vegetation cover dominated by homogeneous savannas, and most windows were classified as C4, with very little bare soil. The iron-capped plateaus, present in

both images, were only identifiable by the geomorphological features marking their boundaries, and windows within these areas were classified as macro-heterogeneous (classes C2 and C3). During the drought period, i.e. three decades of rainfall around 550 mm yr^{-1} , the protected area (Fig. 6c,d) showed limited change, although spotted patterns developed on the plateaus, but under heavy human pressure (Fig. 6a,b) extensive spotted patterns, easily identifiable to the naked eye, developed across the plateaus, while most of the slopes and valleys (sandy soils) were cleared for crops. Areas where natural vegetation was removed display a smooth light-grey to white aspect, which contrasts sharply with residual gallery forest (black, e.g. in the middle of Fig. 6b) and fallows, leading to a macro-heterogeneous appearance (class C3) for the 1996 version of many windows. The homogeneous savannas predominant in 1956 appear to have been wiped off the landscape.

To address the generality of these changes, we first turned to the systematic classification and mapping of windows to assess the change in spatial extent of the

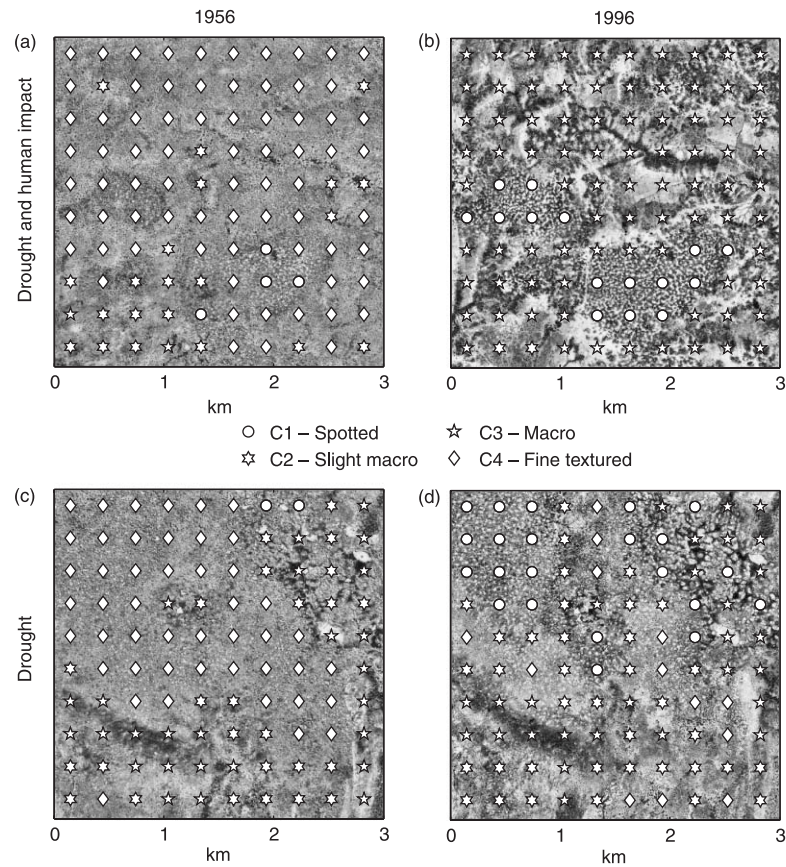


Fig. 6 Maps of land-cover patterns illustrating the temporal dynamics in two particular square areas of 3000 m on a side: (a,b) outside the park, under human pressure; (c,d) in the park.

Table 1 Diachronic change in the relative area covered by each class of vegetation pattern (K-means clustering) between 1956 and 1996 for protected (drought impact) vs. unprotected situations (drought + human impact). Values are percentages of the surveyed areas under each protection status. Values significantly under or above expectation for the null hypothesis (no diachronic change in each cover class) are indicated by (+) and (-), respectively. Significance levels: * $0.05 \geq P > 0.01$; ** $0.01 \geq P > 0.001$; *** $P \geq 0.001$ (Bishop's critical values on Freeman–Tukey deviates)

		Spotted	Slight macro	Macro	Fine textured
Drought	1956	6.93	40.71	16.71	35.64
	1996	8.50 (*)	41.93 (NS)	12.07 (***)	37.50 (NS)
Drought and human impact	1956	2.83	25.67	22.67	48.83
	1996	12.83 (***)	10.67 (***)	74.17 (***)	2.33 (***)

different types of land cover patterns (Table 1). In the park there was a slight, yet significant, increase in spotted patterns (6.9% to 8.5% of the area, i.e. a relative increase of 23%). A decrease was also noted in areas classified as macro-heterogeneous, possibly as a consequence of progressive fading of the impacts of previous human occupation. In the unprotected area, the change was very different. The share of fine-textured windows (i.e. homogeneous savannas) fell from 49% to 2%, while

the share of macro-heterogeneous windows soared from 23% to 74%. Areas covered by spotted patterns rose from 3% to 13%, an increase in area of 353%. This important spatial extension of spotted pattern was clearly made at the expense of homogeneous savannas.

To assess the intensity of these changes with respect to spatial frequency, we then computed the log-ratio between the 1996 and 1956 mean r-spectra separately for conserved and non-conserved areas (Fig. 7a). In the park, the log-ratio of mean spectra exhibited a significant concentration around 20 cycles km^{-1} , confirming the fact that drought mainly resulted in the appearance of spotted patterns. In inhabited areas, a significant concentration was observed, not only around 20 cycles km^{-1} , but also for all smaller frequencies, due to the appearance of large human-induced features, such as fields or hamlets, that resulted in many windows becoming macro-heterogeneous. We extended our analysis of spotted pattern establishment by computing the 1996/1956 log-ratio of mean spectra just for those windows exhibiting an identifiable spotted pattern in 1996 and classified as C1 (Fig. 7b). Concentration around spatial frequencies in the range 15–35 cycles km^{-1} was apparent and significant independent of the conservation status, but the amplitude of the peak was nearly three times higher outside the park, showing that the intensity of the patterning process during the 1956–96 interval was exacerbated by human activities.

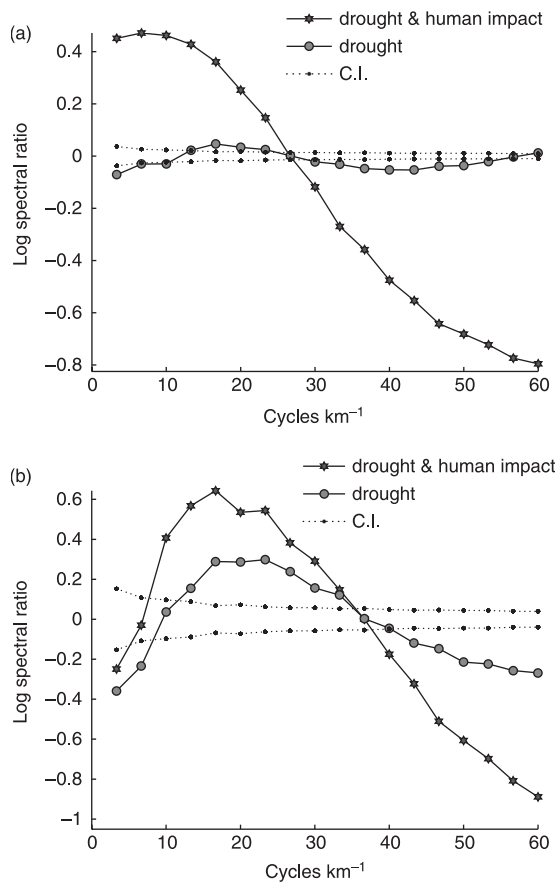


Fig. 7 Diachronic change in vegetation spatial patterns for protected (drought impact) vs. unprotected (drought + human impact) situations analysed using the log-ratios of mean 1996–56 Fourier r-spectra. The dashed lines represent the 95% confidence interval (CI) computed under the null hypothesis of absence of change between 1956 and 1996. (a) Log-ratios computed for all windows; (b) log-ratios computed for the windows classified as spotted in 1996.

The above analyses were only concerned with the appearance of periodicity in vegetation. To test whether the increase of a dominant frequency had been accompanied by the appearance of dominant orientations, we performed a factorial ANOVA (using protection status and date as factors) on the entropy (Shannon) of all the θ -spectra of the windows classified as ‘spotted’ in 1996. A significant decrease in average entropy (from 2.86 to 2.84), i.e. a less isotropic aspect, was observed in the unprotected area but not in the park. This decrease corresponded in the most extreme cases (10% of the windows classified as C1 in the unprotected area) to a shift to entropy values of less than 2.8, characterizing labyrinthine or even banded periodic patterns (Fig. 8).

Discussion

By comparing signatures in the Fourier space of vegetation patterns before and after a prolonged period of drought, in a study region of *c.* 3000 km² in south-west Niger, we have shown that the vegetation on iron-capped plateaus exhibited a dramatic and systematic shift from homogeneous (as illustrated in Figs 3 & 6) to periodic

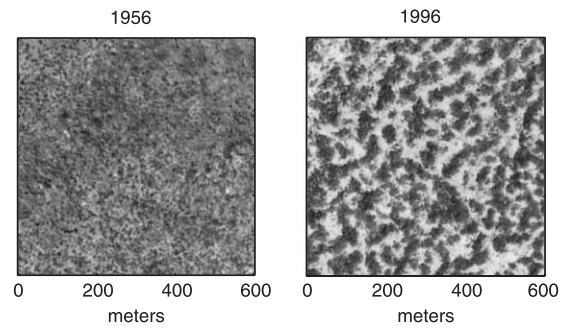


Fig. 8 Diachronic aspects of a reference area exemplifying an exceptional shift towards labyrinthine/banded pattern, i.e. the appearance of a dominant wavelength accompanied by a substantial loss of isotropy, with entropy figures of less than 2.8 in the banded parts of the right picture.

patterns comprising spots of bare ground. These patterns were characterized by the dominance of a well-defined peak around spatial frequencies of 20 cycles km⁻¹ in the radial spectrum (Fig. 7), and are clearly discriminated from human-induced land-cover patterns, such as crops and villages, which are generally not observed on the plateaus and which are, moreover, dominated by spatial frequencies of 3–10 cycles km⁻¹ (Fig. 7). On a selected plateau in a protected area, field measurements of soil properties (including relief, texture and depth) along transects crossing successive patches of plants and bare ground showed that the spatial variation of soil parameters was uncorrelated with the vegetation pattern, except for bulk density, a parameter known to be strongly influenced by vegetation (Tongway *et al.* 2001). Marked slopes (above 1%) appeared to be able to influence the symmetry of the periodic patterns, but our results show that periodic patterns can appear even in the absence of pre-existing spatial heterogeneity or anisotropy. These results invalidate the class of models that can only generate stripes in an environment devoid of prepattern. We should therefore base subsequent research efforts on models that are able to generate periodic spotted patterns without calling on environmental heterogeneities (Lejeune *et al.* 1999; Rietkerk *et al.* 2002; Gilad *et al.* 2004).

The shift from homogeneous savanna to vegetation punctuated by bare spots occurred during a sequence of years marked both by intense drought periods and by a general decreasing trend in rainfall. This points towards increased aridity as a triggering factor, an explanation confirmed by the fact that significant, albeit limited, patterning developed in the protected area. The initial intensity of this dynamic change (due to droughts occurring in the mid 1970s and 1980s) may actually have been underestimated on the 1996 photographs (i.e. after several years of fairly good rainfall). Other potential causes of patterning in the park can be ruled out. During the last five decades, the park has been effectively protected from major human disturbances such as clearing for crops, woodcutting and systematic grazing (Leberre & Messan 1995). Migrating cattle herds are known occasionally to cross the park at the end of the dry season,

but they avoid the plateaus as these are devoid of watering points. In spite of protection, the density of wild ungulates has remained low (Hibert *et al.* 2004) with respect to the carrying capacity of the vegetation. The savannas in the park are pyrophilous and the fires that regularly occur there cannot cause sudden large-scale physiognomical changes (Sankaran *et al.* 2005). The fact that the emergence of spotted patterns has been observed in most of the 14 sampling areas located in the park confirms the generality of the change in vegetation patterning. In fact, some windows are located up to 100 km from each other and can be considered as fairly independent replicates that underwent the same dynamics under similar climate variation and substratum conditions.

The strongest patterning dynamics occurred outside the park, where the deflection in Fourier spectral space was three times higher than in the park. We can thus be confident of the importance of the interaction between human activities and drought for triggering the appearance of periodic patterns. It is worthwhile comparing our results regarding protected and unprotected areas with those of models that relate the change in plant biomass to the dynamic balance between production and suppression. In these models aridity decreases production, while human-induced biomass uptake contributes to the suppression of vegetation biomass. Models predict that, below a certain threshold, decreasing production will cause the emergence of a pattern of periodic bare spots from an initial homogeneous vegetation distribution. By contrast, increasing suppression enlarges the domain of existence of periodic patterns (Rietkerk *et al.* 2002). This is consistent with our observation of amplified pattern formation on those unprotected plateaus where human-induced diffuse biomass uptake (wood-cutting and domestic herd grazing) took place in addition to the overall decrease in rainfall. However, this uptake may be considered as fairly independent of the standing biomass, while the suppression term is proportional to it in all existing models. Hence, it would be interesting to investigate the relative influence of aridity and human pressure on vegetation patterning with a constant biomass removal to mimic human-induced uptake, in addition to the natural mortality term.

Our results also showed that, in particular parts of the unprotected area, the emergence of a dominant wavelength coincided with a significant loss of isotropy, corresponding to the appearance of flexuous bands of vegetation. The symmetry (spotted, labyrinthine, banded) of patterns as well as their periodicity may thus be useful indicators of stress or disturbance. The sequence of patterns formed under increasing stress is predicted to be spots of bare ground, 'labyrinths' (i.e. flexuous bands) and spots of vegetation (Lejeune & Tlidi 1999; von Hardenberg *et al.* 2001; Rietkerk *et al.* 2002), and this is consistent with our findings. However, as slope values were not available, we cannot draw conclusions regarding the endogenous nature of the observed anisotropic patterns. Other theoretical predictions, such as those

regarding the wavelength of the periodic patterns, are worth testing in the light of broad-scale, remotely sensed images of metre-scale resolution. The wavelength of the pattern is indeed predicted to be a monotonically increasing function of aridity.

An increasing set of evidence thus indicates that the spatial properties of plant distributions are potential indicators of the climatic and anthropogenic constraints experienced by arid ecosystems. This fact has yet to be recognized in the literature: studies of climate impact on ecosystems have instead largely relied on abundances and range shifts of species or functional groups (Brown *et al.* 1997; Smith *et al.* 1997; Allen & Breshears 1998; Walther *et al.* 2002), or on photosynthetic activity (Nicholson *et al.* 1998; Roerink *et al.* 2003). Systematically applying Fourier analysis to remotely sensed images, so as to study vegetation spatial distributions in sensitive arid regions bordering hot deserts, may make a valuable contribution to the worldwide monitoring of the impacts of climate change. Moreover, Fourier analysis is not only relevant to detect and characterize periodic patterns, as in the present paper, but is also a reliable tool for multi-scale quantification and classification of non-periodic patterns, including forest canopy aspects (Couteron *et al.* 2005) or landscape features (Couteron *et al.* in press).

Vegetation is acknowledged to have a critical effect on essential biogeochemical processes (Schlesinger *et al.* 1990) and on climate (Zeng *et al.* 1999; Higgins *et al.* 2002). The extension of bare ground, for instance, is known to influence the atmospheric energy and water budget in a nonlinear way, i.e. spatial patterns may matter. In addition, broad-scale shifts from fire-prone savanna to fire-resistant patterned vegetation may have significant consequences on carbon fluxes. Yet the landscape-scale self-organization of vegetation has been largely ignored in studies on the interactions between climate and land cover. Rietkerk *et al.* (2004) have recently reviewed the potential for catastrophic shifts to occur in pattern-generating models that feature both patterned vegetation and desert as alternative stable states (i.e. bistability) due to the positive feedback exerted by vegetation on itself (May 1977; Scheffer & Carpenter 2003). However, the possibility of an abrupt transition from periodic vegetation to desert still needs confirmation from broad-scale field data. Coupled remote sensing and field monitoring in the most arid areas where periodic vegetation is encountered in the African Sahel may well be able to provide such data. In fact, vegetation self-organization is an important issue that should be accounted for in order to establish more realistic models of interactions between vegetation and climate as well as to understand better and mitigate 'desertification' and degradation of arid land capabilities.

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