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Fine-scale spatial distribution of plants and resources on a sandy soil in the Sahel

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Abstract

We studied fine-scale spatial plant distribution in relation to the spatial distribution of erodible soil particles, organic matter, nutrients and soil water on a sandy to sandy loam soil in the Sahel. We hypothesized that the distribution of annual plants would be highly spatially autocorrelated and that this would be positively linked with the spatial distribution of erodible soil particles, soil organic matter and nutrients. Further, we hypothesized that larger vegetated patches (a relatively high vegetation cover at coarser spatial scale) will be stronger linked with erodible soil particles, organic matter and nutrients than smaller vegetated patches (a relatively low vegetation cover at coarser spatial scale). Generally, for 'low cover' and 'high cover' plots, spatially confined micro-elevations with a relatively high volume percentage of erodible very fine – medium sand (50–400 μm), were linked with a higher cover of annual plants. The robustness of vegetation patchiness (expressed as the proportion of the total variance accounted for by spatial dependent variance) was significantly higher for the 'high cover' plots. For the 'low cover' plots, higher vegetation cover was associated with higher elevations, soil moisture, and volume percentage of very fine to medium sand, but lower organic matter, total N and P. For the 'high cover' plots, micro-elevations also consisted of a relatively high volume percentage of very fine to medium sand, and this was associated with dryer conditions and higher total N. Additionally, dryer conditions were weakly correlated with higher organic matter. So, micro-elevations were indirectly associated with dryer and more fertile conditions, which was opposite to what we found for the 'low cover' plots.

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We propose that for the 'low cover' plots, micro-elevations or textural patches could become sparsely vegetated as seeds of annuals were not easily washed away from their surface. The micro-elevations became islands of humidity and infertility through their different textural origin and leaching by infiltrating rainwater. For the 'high cover' plots, surface water in micro-depressions was not only working as an erosive agent, but also induced a higher soil water content and leaching of nutrients when the surface water is more stagnant. Additionally, we speculate that in the 'high cover' plots, annual plants on micro-elevations were more successful in holding the soil, and increasing organic matter and nutrients than in the 'low cover' plots. In conclusion, highly dynamical physical soil surface processes and soil surface characteristics are overriding factors explaining spatial plant distribution on a sandy soil in the Sahel.

Introduction

The occurrence of patches of vegetation alternating with patches of (almost) bare soil on multiple scales (local and landscape scale) is a common feature in semi-arid areas (Bromley et al., 1997; Ludwig et al., 1999; Montaña, 1992; Rietkerk et al., 2000). The redistribution of surface water is considered as an important factor explaining spatial plant distribution. Rain falling on bare patches of soil will fail to infiltrate and run off. This run-off water subsequently accumulates in the vegetated patches where it can infiltrate more easily (Bromley et al., 1997; Hiernaux and Gérard, 1999; HilleRisLambers et al., 2001; Klausmeier, 1999; Rietkerk and Van de Koppel, 1997).

However, not only is surface water redistributed by run-off; soil particles, organic matter and nutrients are also transported by surface water, as well as by wind. Soil erodibility by water and wind depends on aggregate size, aggregate stability and particle size. The term soil erodibiity reflects that different soils erode at different rates with the value of soil erodibility generally increasing with an increasing sand content and a decreasing clay content, since sandy soil particles are more easily detached (Bagnold, 1941; Evans, 1980). While soil particles, organic matter and nutrients can be easily transported by wind or surface water, vegetation positively influences the retention of these elements (Kellman and Sanmugadas, 1985; Rietkerk and Van de Koppel, 1997). Hence, especially on sandy soils, the redistribution of soil particles, organic matter and nutrients could be important in explaining fine-scale spatial plant distribution.

We studied fine-scale spatial plant distribution in relation to the distribution of erodible soil particles, organic matter, nutrients and soil water on a sandy to sandy loam soil in the Sahel of northern Burkina Faso, West Africa. We hypothesized that the distribution of plants would be spatially autocorrelated, and linked with the spatial distribution of soil particles, organic matter and nutrients. Further, we hypothesized that larger vegetated patches (a relatively high vegetation cover at coarser spatial scale) are stronger linked with erodible soil particles, organic matter and nutrients than smaller vegetated patches (a relatively low vegetation cover at coarser spatial scale). Our aim is to understand the relation between the fine-scale spatial distribution of plants and redistribution of resources since this is essential for explaining vegetation patchiness and its function for conserving soil resources within the landscape (Ludwig et al., 2000; Tongway and Ludwig, 1997).

Materials and methods

Site description

Field work was carried out in the Sahelian zone of Burkina Faso (West Africa) in August and September 1999, at the Katchari research station of INERA (13° 55′ – 15° 05′ N, 0° 00′ – 0°10′ W), about 10 km west of Dori, capital of the province of Séno. Mean annual rainfall (1960–1999) is 485 mm (rainfall station Dori) and the rains fall in summer during 2–4 months; the rest of the year is dry. Mean monthly temperature ranges between 21 °C in January and 35 °C in May, with maximum temperatures of well over 40 °C. Katchari research area has a surface of 36.9 km^2 with a population density of 19 inhabitants per km^2 in 1996. Characteristic soils (FAQ-UNESCO) of the area are Lithosols (I), sandy to sandy loam Arenosols (Q) and Regosols (R). The coverage of woody species is generally low but heterogeneous and the vegetation cover is dominated by the annual grasses Schoenfeldia gracilis Kunth. and Cenchrus biflorus Roxb. The main land use in the area is grazing by cattle.

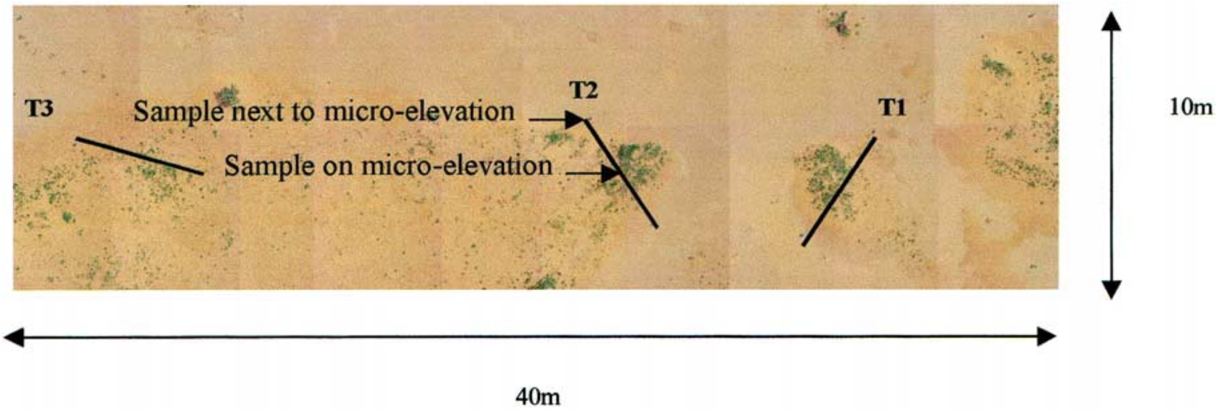

Figure 1. Composite image of plot 1 of 10 × 40 m with location of the 3 transects. Vegetation cover is 3.8%. Note the differences in soil colour indicating abiotic heterogeneity, caused by runoff-runon processes and transport of soil particles by wind. Yellow-brown soil colour indicates micro-elevations on which the annual vegetation occurs. T1, T2 and T3 indicate the position of the 3 transects of this plot, which were laid out in different directions, in a way that each individual transect represented maximum visible local spatial variability. Note the locations of two the samples, of which characteristic differential volume curves of particle diameters are illustrated in Figure 2.

Plots and transects

At the Katchari research station, 6 plots were selected of 10 × 40 m via stratified random sampling; 3 plots with relatively small vegetated patches (estimated by eye) resulting in a vegetation cover of 2.0, 2.9 and 3.8% ('low cover' plots), and 3 plots with relatively large vegetated patches (estimated by eye) resulting in a vegetation cover of 17.7, 19.1 and 19.7% ('high cover' plots). No suitable plots with fragmented vegetation of this scale were present in the study area outside of this cover range. The size and orientation of the plots was chosen in a way to include maximum visible spatial variability of soil characteristics and annual plant distribution in the area. All plots were situated within an area of 1 km2 with the same sandy to sandy loam soil on a gentle slope of 1–3%. Within the area of study, no grazing gradients were apparent such as studied by Rietkerk et al. (2000). From the plots, images were taken to obtain vegetation cover (%) data with a digital camera (Sony MVC FD91) attached on an upright pole 7.5 m above the ground. The size of a single image was 6 × 5 m, and single images were put together to form composite images representing the plots (Figure 1). At each plot, a 41 × 11 matrix of 451 sampling points representing a 1 × 1 m grid was established to measure microrelief (elevation) using a surveyor's level and levelling staff with an accuracy of 1 mm.

Additionally, at each of the 6 plots, 3 transects of 5 m length were laid out in different directions as to avoid effects of orientation and in a way that each individual transect represented maximum visible local spatial variability (Figure 1). At 0.5 m intervals along each of the transects (representing 11 sampling points per transect and 33 sampling points per plot), elevation was measured and soil samples were taken (0–5 cm depth) to measure soil moisture, particle size distribution, organic matter, total nitrogen (N) and phosphorus (P). The soil samples were put in sealed plastic bags and the bags were put immediately in a closed coolbox and transported by car to the lab where fresh mass of the samples were weighed at the end of the day at which the samples were taken. No evaporation of soil water from the samples could occur during transportation. Soil moisture (weight %) was measured gravimetrically. Particle size distribution was measured by laser diffraction using a Coulter LS230 Particle Size Analyser (Coulter Electronics Ltd.) that is able to determine the volume percentage of 116 particle size classes between 0.040 and 2000 μm (Buurman et al. 1997). For further analysis the volume percentages of 50–150 μm ('very fine–fine' sand) and 150–400 μ (fine–medium sand) (USDA/FAO classification) were determined. This was based on the characteristic differential volume curves derived from each sample and on an approximation of particle size classes that are relatively easily removed by wind and water erosion respectively (Bagnold, 1941; Hjulström, Morgan, 1986; Savat, 1982). Before measuring, the samples were treated with 5 min ultrasound to eliminate the effects of aggregation by soil organic matter. Soil organic matter (weight %) was measured by loss on ignition. Total N and P (weight %) were determined

Table 1. Spearman's correlation coefficients between elevation and vegetation cover for each plot (grid data). Mean robustness and range of patchiness compared between the 'low cover' plots and 'high cover' plots. Significant differences between means (Mann–Whitney U test, $p < 0.05$) are indicated by different letters. The parameters 'robustness' and 'range' are derived from the grid data and explained in the text.

Variable	Plots	
	'Low cover' plots	'High cover' plots
Spearman's rho (elevation-cover)	(1) 0.175** ($n = 451$)	(1) 0.203** ($n = 451$)
	(2) 0.075 ($n = 451$)	(2) 0.112* ($n = 451$)
	(3) 0.198** ($n = 451$)	(3) 0.243** ($n = 451$)
Mean robustness patchiness elevation	0.95a ($n = 3$)	1.00a ($n = 3$)
Mean range patchiness elevation (m)	11.82a ($n = 3$)	15.10a ($n = 3$)
Mean robustness patchiness vegetation cover	0.33a ($n = 3$)	0.70b ($n = 3$)
Mean range patchiness vegetation cover (m)	5.56a ($n = 2$)	1.06a ($n = 3$)

*Correlation is significant at the 0.05 level; **Correlation is significant at the 0.01 level.

with an auto-analyser after digestion with H_2SO_4 – salicylic acid – H_2O_2.

Infiltration capacity (ml min $^{-1}$) was measured on 0.25 × 0.25 m plots with different aerial vegetation cover by using a small rainfall simulator (Kamphorst, 1987; Rietkerk et al., 2000). Water infiltration was calculated by subtracting run-off from simulated rainfall. Each simulation consisted of a rain shower with a duration of 5 min and an intensity of 6.3 mm min^{-1} on 0.25 × 0.25 m plots). Aerial vegetation cover in these plots was estimated visually using a quadrat with 10 × 10 subdivisions.

Cover classification and statistical analysis

Pixels from the digital camera images were aggregated to obtain 10 × 10 cm vegetation cover (scale 0–100). For each plot, these data were resampled for values corresponding with the 451 coordinates for which elevation was measured ('grid data'), and with the 33 sampling locations along the 3 transects ('transect data'). No normal distribution was assumed for the data. Correlation between elevation and vegetation cover was determined for each plot by calculating Spearman's correlation coefficient for the grid data. Spatial variation of elevation and vegetation cover was evaluated for each plot by semivariance analysis of the grid data and calculating the 'robustness' and 'range' of patchiness by fitting optimal models to the form of the semivariograms (GS^+ 3.1, Gamma Design Software). Robustness is the proportion of the total variance accounted for by spatially dependent variance (ranging from 0 for random patterns to 1 for robust patches with sharp boundaries) and range is the spatial scale over which autocorrelation occurs (patch size) (Robertson and Gross, 1994). GS^+ calculates default values of the parameters robustness and range of five models: spherical, exponential, linear, linear to sill and Gaussian. Each of the models has the same amount of parameters and the same complexity. The parameter values of robustness and range that we used for further analysis are of the calculated best-fit models based on minimizing the reduced sum of squares. The means of robustness and range of patchiness were compared between the 'low cover' plots and 'high cover' plots by Mann–Whitney *U* tests.

The transect data were pooled for each group of plots ('low cover' plots and 'high cover' plots) and evaluated by calculating a Spearman's correlation coefficient matrix in order to test the link between spatial distribution of plants and micro-elevation, soil water, particle size distribution, organic matter, total N and total P. Means of the pooled transect data were compared between groups with Mann-Whitney U tests. Linear regression analysis was performed to test the dependence of infiltration capacity on aerial cover of annual grasses.

Results

Plants were occuring on micro-elevations, as indicated by the positive significant correlation coefficients between elevation and vegetation cover (Table 1). Elevation was highly spatially autocorrelated; 95% of the variation of the 'low cover' plots and 100% of the 'high cover' plots could be spatially explained. Dia-

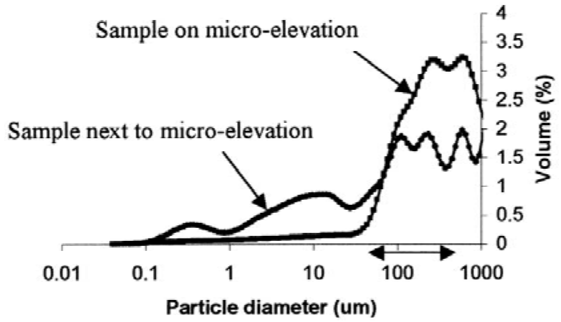

Figure 2. Characteristic differential volume curves of particle diameters ranging from 0.040 to 1000 μm for two samples. For location of the two samples see Figure 1. On the x-axis the particle size classes of very fine–medium sand that are relatively easily removed by wind and water erosion are indicated ⟵⟶).

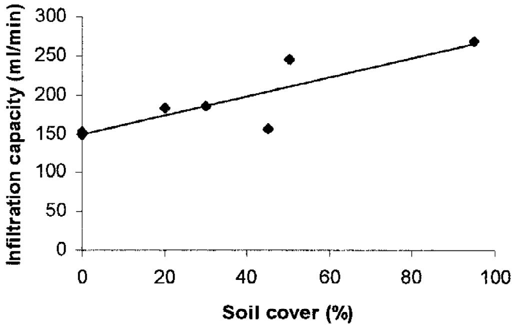

Figure 3. Linear regression between infiltration capacity and soil cover of annual grasses for a sandy soil ($p < 0.05$, $R^2 = 0.73$).

Table 2. Mean values of relevant transect data for 'low cover' plots and 'high cover' plots ($n = 99$). Significant differences between means (Mann–Whitney U test, $p < 0.05$) are indicated by different letters.

Variable	Plots	
	'Low cover' plots	'High cover' plots
Vegetation cover (%)	14.96a	28.41b
Soil moisture (%)	5.70a	6.49b
Very fine–fine sand (%)	18.53b	16.58a
Fine–medium sand (%)	28.59a	29.10a
Very fine–medium sand (%)	47.12a	45.68a
Organic matter (%)	1.23b	0.82b
Nitrogen (%)	1.13×10^{-2}b	0.64×10^{-2}a
Phosphorus (%)	6.05×10^{-3}b	4.30×10^{-3}a

meters of these micro-elevations ranged from 10 to 20 m.

Vegetation was more randomly distributed than elevation, especially in case of the 'low cover' plots. Here, only 33% of the variation in cover could be spatially explained. For one of these plots spatial plant distribution was 100% random (robustness of zero). Therefore, no range of patchiness could be determined for that particular plot. This explains the $n = 2$ for this particular 'low cover' group and not $n = 3$ as for all the other groups in Table 1. Vegetation in the 'high cover' plots showed a significantly higher spatial autocorrelation, but there was no strong patchiness as for elevation. Range of patchiness for vegetation cover varied between 1 and 8 m, which becomes an arbitrary parameter if no strong patchiness could be detected.

Annual plants mainly occurred on micro-elevations, which can be recognized by the yellow-brown colour on composite images (e.g. Figure 1). The soil sample taken on the micro-elevation had a remarkably higher volume percentage of fine–coarse sand (150–1000 μm) and lower volume percentage of silt (2–50 μm) than the sample taken on the flat surface around the micro-elevation (e.g. Figure 2). The particle size class of 50–400 μm (very fine - medium sand) is especially vulnerable to removal by wind and water erosion (double arrow on the x-axis in Figure 2). All samples were taken on a depth of only 0 - 5 cm, therefore they characterize the soil surface.

Mean value differences of the transect data between 'low cover' plots and 'high cover' plots were relatively small (Table 2), except for vegetation cover. However, soil moisture was significantly higher in the 'high cover' plots, while organic matter, total N and P were significantly higher in the 'low cover' plots. Furthermore, the particle size class for very fine–fine sand, which is relatively easily removed by wind, was significantly higher in the 'low cover' plots while no differences were found in the other particle size classes. Although soil cover by vegetation was significantly higher for transects in 'high cover' plots, this can not be interpreted as larger vegetated patches as no significant difference was found between mean range patchiness vegetation cover (Table 1).

For the 'low cover' plots, higher vegetation cover along the transects was associated with higher elevations, soil moisture, and volume percentage of very fine–medium sand, but lower organic matter, total N and P (Table 3). On the micro-elevations, infiltration capacity was higher. In the absence of vegetation infiltration capacity was 150 ml min^{-1} ($n = 2$) (Figure 3). We measured an infiltration capacity of 78 ml min^{-1} ($n = 2$) next to these micro-elevations, where the soil contained a higher volume percentage of silt. The

Table 3. Spearman's correlation coefficient matrix for 'low cover' plots and 'high cover' plots (transect data) ($n = 99$).

Plots	Variables	Vegetation cover (%)	Elevation (mm)	Soil moisture (%)	Very fine–medium sand (%)	Organic matter (%)	Nirtrogen (%)	Phosphorus (%)
'Low cover'	Vegetation cover (%)	1						
	Elevation (mm)	**0.372****	1					
	Soil moisture (%)	**0.267****	0.015	1				
	Very fine-medium sand (%)	**0.261****	**0.658****	0.075	1			
	Organic matter (%)	**−0.301****	**−0.746****	−0.005	**−0.637****	1		
	Nitrogen (%)	**−0.211***	−0.052	**−0.203***	−0.036	**0.296****	1	
	Phosphorus (%)	**−0.355****	**−0.471****	**−0.360****	**−0.339****	**0.565****	**0.393****	1
'High cover'	Vegetation cover (%)	1						
	Elevation (mm)	0.051	1					
	Soil moisture (%)	0.040	**−0.641****	1				
	Very fine-medium sand (%)	0.178	**0.636****	**−0.359****	1			
	Organic matter (%)	0.006	0.075	**−0.202***	−0.060	1		
	Nitrogen (%)	0.045	0.167	−0.086	**0.281****	**0.398****	1	
	Phosphorus (%)	−0.013	0.046	−0.087	−0.114	**0.663****	**0.283****	1

*Correlation is significant at the 0.05 level; **Correlation is significant at the 0.01 level.

resulting higher cover of annual grasses could lead to even higher infiltration rates of rain water (Figure 3).

For the 'high cover' plots, the picture along the transects was different. Vegetation cover was not directly associated with any of the other parameters measured along the transects (Table 3). Micro-elevations also consisted of a relatively high volume percentage very fine–medium sand, but these were associated with dryer conditions. No relation with organic matter and nutrients could be detected, although volume percentage of very fine–medium sand was associated with higher total N, and dryer conditions were weakly correlated with higher organic matter.

Discussion

We hypothesized that the distribution of plants would be highly spatially autocorrelated and that this would be positively linked with the spatial distribution of erodible soil particles, soil organic matter and nutrients. Further, we hypothesized that larger vegetated patches (a relatively high vegetation cover at coarser spatial scale) are stronger linked with these soil elements than smaller vegetated patches (a relatively low vegetation cover at coarser spatial scale). However, in contrast with what we expected, a higher vegetation cover was clearly associated with lower organic matter and soil nutrients for the 'low cover' plots. For the 'high cover' plots no clear direct link between vegetation cover on the one hand and soil organic matter and nutrients on the other hand could be found. Nonetheless, the micro-elevations in these plots on which a higher cover of annual plants could be found, was indirectly associated with more fertile conditions. This was opposite to what we found in 'low cover' plots.

Based on our results, we propose that highly dynamic physical soil surface processes, like erosion-deposition of soil elements by water and wind, and spatial differences in water infiltration rate, are overriding factors explaining fine-scale in spatial plant distribution. Evidently, plants could establish more easily on micro-elevations. Based on a feedback between plant cover and retention of soil particles, organic matter and nutrients, we hypothesized that the distribution of plants would be spatially autocorrelated; sharp boundaries of vegetated patches coinciding with those of the textural patches (Wilson and Agnew, 1992). This would indicate that annual plants could not only establish themselves more easily on these textural patches, but that they are also successful in entrapping and retaining erodible soil particles (*cf.* Tongway and Ludwig, 1997; Wilson and Agnew, 1992).

However, despite the fact that 95–100% of the variation in elevation could be spatially explained and that higher vegetation cover was associated with micro-elevations of erodible soil particles, we could not detect strong vegetation patchiness. This could indicate that, especially for the 'low cover' plots, cover of annual plants was more determined by the spatial (re)distribution of soil particles than vice versa. During the dry season (October–April) and the early wet season (May–July), erosive winds that exceed a certain threshold wind speed induce saltating sand particles jumping over the soil surface (Sterk, 1997). During the early wet season, these strong winds are typically followed by heavy thunderstorms with intense rains leading to soil erosion by run-off water. Vegetation of annual plants, which only becomes established in the late wet season (August–September), is not successful in retaining and entrapping soil particles, especially if cover is low. It may even take a series of wet years before enough cover and biomass of annuals is accumulated to 'hold the soil' and increase organic matter and nutrients (Westoby, 1980). In our study, factors other than the distribution of annual plants determined the detachment and entrapment of erodible soil particles (e.g. surface roughness or the random occurrence of stones and dead wood) (Casenave and Valentin, 1992), especially for the 'low cover' plots.

Although spatial plant distribution was strongly linked with the distribution of soil particles, the relationship with organic matter and soil nutrients was less apparent (for the 'high cover' plots) or even converse (for the 'low cover' plots) of what we hypothesized. On the 'low cover' plots, higher plant cover on the micro-elevations was associated with lower organic matter, total N and P (Table 3). At the same time, we found a higher infiltration capacity in the absence of vegetation and higher soil moisture on those locations. We propose that annual plants could become established on these sandy islands of infertility and humidity because of their physical surface characteristics. It has been long recognized that physical surface condition is an important factor explaining germination and establishment of vegetation (Casenave and Valentin, 1992; Valentin and Bresson, 1992). A high infiltration capacity on these (sparsely) vegetated micro-elevations prevents run-off and induces leaching of soil nutrients (Bouma et al., 1995; Brouwer and Powell, 1996). Overland flow on the surrounding, more fertile, silty and compacted soil swirls around these micro-elevations, preventing that annual seeds and seedlings wash away from them. Furthermore, soil crusting associated with the presence of fine soil particles (Hoogmoed and Stroosnijder, 1984; Morgan, 1986) prevents the establishment of seeds (Hien et al., 1997; Valentin and Bresson, 1992), although the soil is more fertile.

For the 'high cover' plots, no straightforward relation between vegetation cover at one side, and soil water, organic matter and soil nutrients at the other side, could be detected. However, the higher volume percentages of very fine–medium sand on the micro-elevations were associated with dryer conditions and higher total N, and these conditions were weakly correlated with higher organic matter. So, micro-elevations were indirectly associated with dryer and more fertile conditions, which was opposite to what we found for the 'low cover' plots. Higher cover of annual plants, for which the spatial autocorrelation was significantly higher than for the 'low cover' plots, probably contributed to this. At the same time, surface water in micro-depressions of the 'high cover' plots was not only working as an erosive agent of top soil but also induced a higher soil water content and leaching when the surface water is more stagnant (Bouma et al., 1995; Brouwer and Powell, 1996).

According to Breman and De Wit (1983), nitrogen and phosporus determine plant growth at an annual rainfall above 300 mm, especially on soils not vulnerable for surface crusting and soil compaction. Spatial patterns may develop most rapidly for resources which are typically most limiting to plant growth (Ryel et al., 1996; Rietkerk et al., 2000; Schlesinger et al., 1996). Although based on a snapshot in time, we did not find patterns of total N and P coinciding with spatial plant distribution, as would be expected. However, we only measured top soil characteristics and measuring nutrients in deeper soil layers could have given different findings. At the same time, even for sandy to sandy loam soils, high rainfall intensities can result in rain splash, surface crusting and soil compaction, leading to high runoff (Hoogmoed and Stroosnijder, 1984). Even for annual rainfall above 300 mm, nitrogen and phosporus deficiencies are not necessarily the prime limiting factors determining plant distribution (Breman et al., 1982).

We acknowledge that our data only provide a one-off description of the status of the vegetation community and environmental conditions. This data can only be used to make indirect inferences about dynamic processes and the mechanims that generate spatial patterns in plant distribution. One of the main difficulties with inferring mechanisms from static data is that identifying the causes of spatial patterns in vegetation is complicated by the multiple confounding abiotic and biotic factors that determine the dispersal, germination and establishment of plants. A wide range of potential mechanims may explain spatial patterns in plant distribution in general. It is a common observation that most if not all plant species are clumped at one or more scales (Condit et al., 2000; Rietkerk et al., 2000). The convential explanation for spatial patterns in other systems such as tropical forests is seed dispersal limitation. However, the annuals studied produce a large amount of seeds in terms of biomass and number, characteristic for semi-arid grasslands, while dispersal by wind and water is usually not a limiting factor (Breman et al., 1979; Veenendaal et al., 1996). This means that germination and establishments of the seeds is crucial, and earlier studies have recognized that the substrate is very important for this due to its influence on the effective rainfall, through texture, microrelief and surface characteristics (Breman et al., 1979; Casenave and Valentin, 1992; Hien et al., 1997). Although our study was based on a snapshot in time, we suggest that highly dynamic physical soil surface processes and soil surface characteristics are overriding factors explaining spatial plant distribution on this sandy soil in the Sahel.

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References

Bagnold R A 1941. The physics of blown sand and desert dunes. Chapman and Hall, London.

Bouma J, Brouwer J, Verhagen A and Booltink H W G 1995 Site specific management on field level: High and low-tech approaches. *In* Eco-regional Approaches for Sustainable Land Use and Food Production. Eds. J Bouma et al. pp 453–473. Kluwer Academic Press, Dordrecht, The Netherlands.

Breman H, Cissé I B and Djitèye M A 1982 Exploitation, degradation et desertification. *In* La Productivité des Pâturages Sahéliens; Une Étude des Sols, des Végétations et de l'Exploitation de Cette Ressource Naturelle. Eds. F W T Penning de Vries and M A Djitèye. pp 352–384. Pudoc, Wageningen, The Netherlands.

Breman H, Cissé A M, Djiteye M A and Elberse W Th 1979 Pasture dynamics and forage availability in the Sahel. Israel J. Bot. 28: 227–251.

Breman H and De Wit C T 1983 Rangeland productivity and exploitation in the Sahel. Science 221, 1341–1347.

Bromley J, Brouwer J, Barker A P, Gaze S R and Valentin C 1997 The role of surface water redistribution in an area of patterned vegetation in a semi-arid environment, southwest Niger. J. Hydrol. 198, 1–29.

Brouwer J and Powell J M 1996 Soil aspects of nutrient cycling in a manure experiment in Niger. *In* Livestock and Sustainable Nutrient Cycling in Mixed Farming Systems of Sub-Saharan Africa. Vol. 2. Technical papers. Proc. of an Int. Conf., Int. Livestock Centre for Africa (ILCA) 22–26 Nov. 1993. Eds. J M Powell et al. pp 211–226. Addis Abeba, Ethiopia.

Buurman P, Pape Th and Muggler C C 1997 Laser grain-size determination in soil genetic studies. 1. Practical problems. Soil Sci. 162, 211–218.

Casenave A and Valentin C 1992 A runoff capability classification system based on surface features criteria in semi-arid areas of West Africa. J. Hydrol. 130, 231–249.

Condit R, Ashton P S, Baker P, Bunyavejchewin S, Gunatilleke S, Gunatilleke N, Hubbell S P, Foster R B, Itoh A, LaFrankie J V, Lee H S, Losos E, Manokaran N, Sukumar R and Yamakura T 2000 Soatial patterns in the distribution of tropical tree species. Science 288: 1414–1418

Evans R 1980 Mechanics of water erosion and their spatial and temporal controls: An emperical viewpoint. *In* Soil Erosion. Eds. M J Kirkby and R P C Morgan. pp 109–128. Wiley, Chichester.

Hien F G, Rietkerk M and Stroosnijder L 1997 Soil variability and effectiveness of soil and water conservation in the Sahel. Arid Soil Res. Rehab. 11, 1–8.

Hiernaux P and Gérard B 1999 The influence of vegetation pattern on productivity, diversity and stability of vegetation: The case of 'brousse tigrée' in the Sahel. Acta Qecologica 20, 147–158.

HilleRisLambers R, Rietkerk M, Van den Bosch F, Prins H H T and De Kroon H 2001 Vegetation pattern formation in semi-arid grazing systems. Ecology 82(1), 50–61.

Hjulström F 1935 Studies of the morphological activity of rivers as illustrated by the River Fyries. Bull. Geol. Inst. Univ. Uppsala 25, 221–527.

Hoogmoed W B and Stroosnijder L 1984 Crust formation on sandy soils in the Sahel I Rainfall and infiltration. Soil & Tillage Res. 4, 4–23.

Kamphorst A 1987 A small rainfall simulator for the determination of soil erodibiity. Neth. J. Agric. Sci. 35, 407–414.

Kellman M and Sanmugadas K 1985 Nutrient retention by savanna ecosystems. I Retention of the absence of fire. J. Ecol. 73, 935–951.

Klausmeier C A 1999 Regular and irregular patterns in semiarid vegetation. Science 284, 1826–1828.

Ludwig J A, Tongway D J, Eager R W, Williams R J and Cook G D 1999 Fine-scale vegetation patchiness decline in size and cover with increasing rainfall in Australian savannas. Landscape Ecol. 14, 557–566.

Ludwig J A, Wiens J A and Tongway D J 2000 A scaling rule for landscape patches and how it applies to conserving soil resources in savannas. Ecosystems 3, 84–97.

Montaña C 1992 The colonisation of bare areas in two-phase mosaics of an arid ecosystem. J. Ecol. 80, 315–327.

Morgan R P C 1986 Soil erosion and conservation. Longman Scientific & Technical, Essex.

Rietkerk M and Van de Koppel J 1997 Alternate stable states and threshold effects in semi-arid grazing systems. Oikos 79, 69–76.

Rietkerk M, Ketner P, Burger J, Hoorens B and Olff H 2000 Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa. Plant Ecol. 148, 207–224.

Robertson G P and Gross K L 1994 Assessing the heterogeneity of below ground resources: Quantifying pattern and scale. *In* Exploitation of Environmental Heterogeneity by Plants. Eds. M M Caldwell and R W Pearcy. pp 237–252. Academic Press, New York.

Ryel R J, Caldwell M M and Manwaring J H 1996 Temporal dynamics of spatial heterogeneity in sagebrush-wheatgrass steppe during a growing season. Plant Soil 184, 299–309.

Savat J 1982 Common and uncommon selectivity in the process of fluid transportation: Field observations and laboratory experiments on bare surfaces. Catena Suppl. 1, 139–160.

Schlesinger W H, Raikes J A, Hartley H E and Cross A F 1996 On the spatial pattern of soil nutrients in desert ecosystems. Ecology 77, 364–374.

Sterk G 1997 Wind erosion in the Sahelian zone of Niger: processes, models, and control techniques. Tropical Resource Management Papers 15. Also published as doctoral thesis. Wageningen Agricultural University, Wageningen.

Tongway D J and Ludwig J A 1997 The conservation of water and nutrients within landscapes. *In* Landscape Ecology, Function and Management: Principles from Australia's Rangelands. Eds. J Ludwig, D Tongway, D Freudenberger, J Noble and K Hodgkinson. pp 237–252. CSIRO Publishing, Melboume.

Valentin C and Bresson L-M 1992 Morphology, genesis and classification of surface crusts in loamy and sandy soils. Geoderma 55, 225–245.

Veenendaal E M, Ernst W H 0 and Modise G 5 1996 Reproductive effort and phenology of seed production of savanna grasses with different growth form and life history. Vegetatio 123, 91–100.

Westoby M 1980 Elements of a theory of vegetation dynamics in arid rangelands. Israel J. Bot. 28, 169–194.

Wilson J B and Agnew A D Q 1992 Positive feedback switches in plant communities. Adv. Ecol. Res. 23, 263–336.

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