Multiscale soil and vegetation patchiness along a gradient of herbivore impact in a semi-arid grazing system in West Africa

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Abstract

We studied the degree and scale of patchiness of vegetation and selected soil variables along a gradient of herbivore impact. The gradient consisted of a radial pattern of 'high', 'intermediate' and 'low' herbivore impact around a watering point in a semi-arid environment in Burkina Faso (West Africa). We hypothesised that, at a certain range of herbivore impact, vegetated patches alternating with patches of bare soil would occur as a consequence of plant-soil feedbacks and run-off-run-on patterns. Indeed, our transect data collected along the gradient showed that vegetated patches with a scale of about 5–10 m, alternating with bare soil, occurred at intermediate herbivore impact. When analysing the data from the experimental sites along the gradient, however, we also found a high degree of patchiness of vegetation and soil variables in case of low and high herbivore impact. For low herbivore impact, most variation was spatially explained, up to 100% for vegetation biomass and soil temperature, with a patch scale of about 0.50 m. This was due to the presence of perennial grass tufts of *Cymbopogon schoenanthus*. Patterns of soil organic matter and NH_4-N were highly correlated with these patterns of biomass and soil temperature, up to $r = 0.7$ ($P < 0.05$) for the *in situ* correlation between biomass and NH_4-N. For high herbivore impact, we also found that most variation was spatially explained, up to 100% for biomass and soil temperature, and 84% for soil moisture, with three distinct scales of patchiness (about 0.50 m, 1.80 m and 2.80 m). Here, microrelief had a corresponding patchy structure. For intermediate herbivore impact, again most variation was spatially explained, up to 100% for biomass and soil temperature, and 84% for soil moisture, with a patch scale of about 0.95 m. Here, we found evidence that vegetated patches positively affected soil moisture through less run-off and higher infiltration of rainwater that could not infiltrate into the bare soil elsewhere, which was not due to microrelief. Thus, we conclude that our findings are in line with our initial hypothesis that, at intermediate herbivore impact, vegetated patches alternating with patches of bare soil persist in time due to positive plant-soil feedbacks.

Introduction

Several studies have shown that in semi-arid areas plant cover and biomass has major effects on soil resources and physical properties (Jackson & Caldwell 1993; Vinton & Burke 1995; Schlesinger et al. 1996). This indicates the possibility of feedbacks between plants and their micro-environment in these areas, such as positive feedbacks between plant cover and nutrient cycling, or between plant cover and infiltration of rain water (Schlesinger et al. 1990; Wedin & Tilman 1990; Vinton & Burke 1995). The importance of these plant-soil relations for ecosystem functioning lies in the potential for plant-induced soil changes to

persist, as positive feedbacks are by definition self-reinforcing, and for yielding relatively high levels of primary productivity (Van Breemen 1993).

Overgrazing may disrupt these *in situ* plant-soil relations and create spatial heterogeneity (Schlesinger et al. 1990, 1996). Grazing and trampling by domestic livestock in semi-arid regions, concentrated around watering points and villages, often leads to a reduction of plant cover and to soil compaction. This causes rainfall running off instead of infiltrating into the soil (Elwell & Stocking 1976; Kelly & Walker 1976; Breman & De Wit 1983; Stroosnijder 1996), leading to spatial redistribution of soil moisture, erodible material and nutrients. The resulting spatial variation may be structured at certain scales, whereby vegetated patches concentrate soil water and nutrients lost from patches of bare, compacted soil (Schlesinger et al. 1990; Wilson & Agnew 1992; Ludwig & Tongway 1995).

Geostatistics are indispensable for analysing the degree and scale of spatial variation, and for comparing spatial patterns (Burrough 1995; Stein et al. 1997). Comparison of spatial patterns of vegetation and selected soil variables at a field scale has received little attention in ecological studies (but see Jackson & Caldwell 1993; Ryel et al. 1996). Comparison of such patterns may elucidate spatial relationships that were hitherto undemonstrated or unknown. In this study, we linked spatial patterns of different selected soil and vegetation variables, and analysed these links in relation to herbivore impact. We focussed on the conditions under which the spatial redistribution of soil resources and erodible material by run-off and run-on could lead to the formation and likely persistence of spatial patterns.

The first objective of our study was to investigate the degree and scale of patchiness (spatial autocorrelation) of vegetation and selected soil variables along a gradient of herbivore impact. The gradient in this study consisted of a radial pattern of cattle impact around a 20-year-old man-made watering point. Our second objective was to determine similarities between spatial vegetation and soil patterns along this gradient of herbivore impact. This was done by studying five transects and three experimental sites that were laid out radially from the watering point.

Herbivore impact in dry areas is typically focussed around livestock watering points (Valentin 1985; Andrew 1988). Therefore, we refer to the zone closely encircling the watering point we selected as being exposed to 'high' herbivore impact. Further, intense grazing and trampling around foci of herbivore impact generally result in bare, compacted soil without vegetation (Valentin 1985; Andrew 1988). Thus, at high herbivore impact we expected a relatively homogeneous soil with no vegetation patchiness.

We refer to the zone far off from the watering point where the intensity of livestock trails is low as being exposed to 'low' herbivore impact. We hypothesised that, at low herbivore impact, the degree of patchiness would be relatively low, and that scales of patchiness could be attributed to differences in *in situ* effects that functional plant groups have on soil resources and physical properties (Jackson & Caldwell 1993; Vinton & Burke 1995; Schlesinger et al. 1996).

The zone between the zones of high and low herbivore impact is being exposed to 'intermediate' herbivore impact. Note the ordinal nature of the scale. Further, note that in theory, when the spatial pattern of herbivore impact depends on the location of the watering point only, zones with equal herbivore impact surrounding the watering point should be concentric, but this is in reality not the case. At intermediate herbivore impact, it was hypothesised that the degree and scale of patchiness would be relatively high as patches of bare, crusted and compacted soil could cause run-off of water and erodible material. Resources could subsequently become available for vegetated patches because of run-on. The rationale behind this hypothesis was derived from Rietkerk & Van de Koppel (1997) and Rietkerk et al. (1997). Their theoretical models showed that within certain ranges of herbivore impact, small initial differences in plant cover and amount of soil resources can magnify to alternative states of the system that persist in time due to positive plant-soil feedbacks.

The relative abundance of different functional plant groups changed with herbivore impact. Consequently, the effects of functional plant groups and herbivore impact on selected soil variables could interact (Vinton & Burke 1995). Therefore, we also measured the effects of the main functional plant groups (annual and perennial grasses) on some selected soil variables, by comparing soil variables between plots with bare soil, annual grasses and perennial grasses respectively. It was not our aim to elucidate mechanistically how grazing and trampling affected the different functional groups and the interaction between those groups.
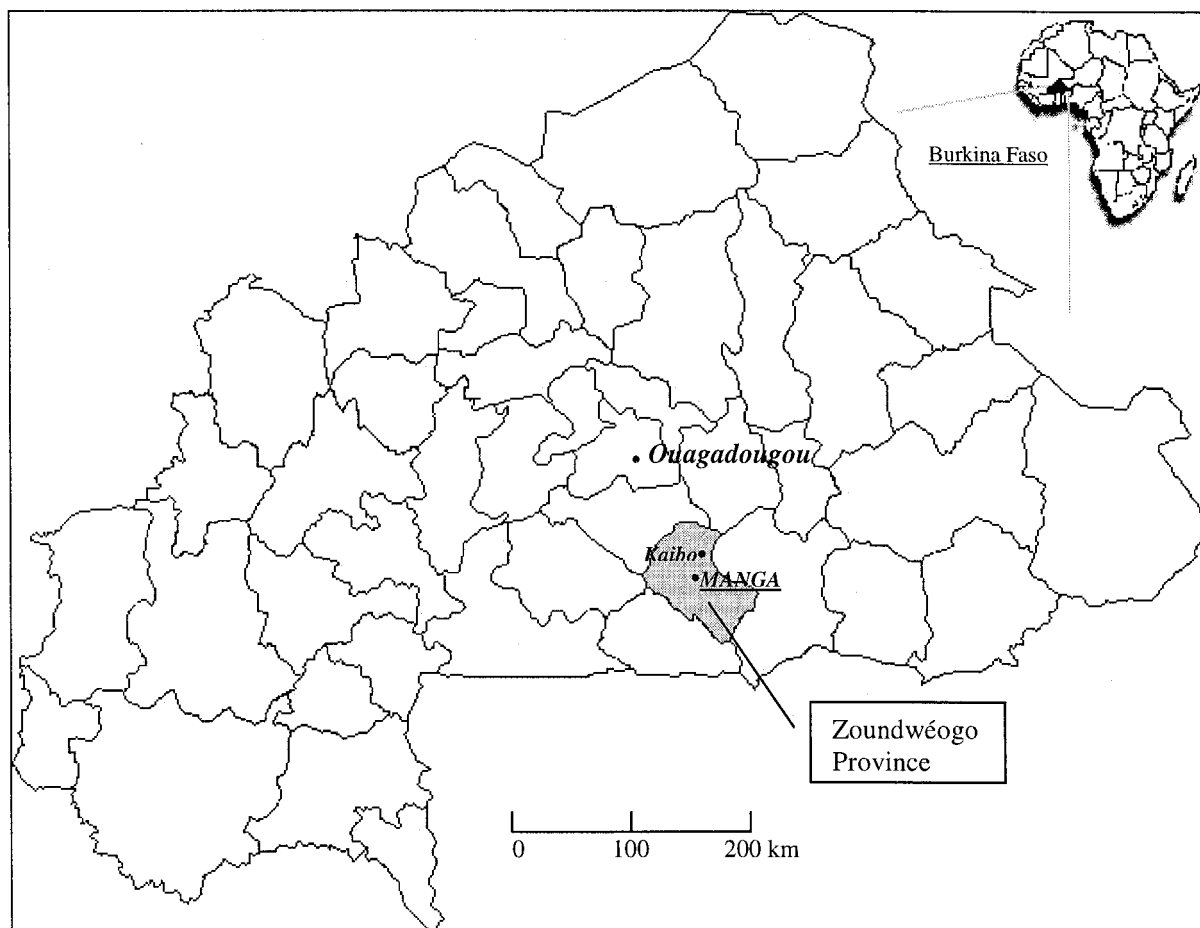
Figure 1. Geographic location of the study area in Burkina Faso, West Africa.

Material and methods

Field sampling and laboratory analysis

Site description

Fieldwork was carried out in Burkina Faso (West Africa) from June–September 1996 and the same period in 1997 near the village of Kaibo Sud V6, Zoundwéogo province ($11°7'$ N, $0°9'$ W), approximately 100 km south-east of the capital Ouagadougou (Figure 1). Average annual rainfall is 800–900 mm (North Sudanian ecoclimatic zone); the rainy season lasts from May–September. Average annual temperature is 28 °C. The soils of the area are Eutric Regosols (75%). and Eutric Leptosols (18%). Landcover varies from tree savannah of low to medium (2–10%) coverage of trees and low (10–25%) coverage of agricultural fields, to medium (5–10%) coverage of trees and high (>70%) agricultural field coverage around the villages (Mulders 1996). The (semi-) natural vegetation shows a high (10–20%) coverage of shrubs and low trees with an understorey of the perennial grass *Cymbopogon schoenanthus* (L.) Spreng. and annual grasses and herbs. It has been extensively grazed by cattle from the Mossi and the Fulani for about 20 years, since the area was recolonised after eradication of onchocerciasis (river blindness).

For this study, a grazing area with a watering point was selected. The watering point consisted of a 20-year-old waterpump at the southern edge of the village where spoiled water used for households is collected in a trough enabling livestock to drink. The research site was only gently sloping at 2–3%. All field measurements took place in July 1996 and July 1997.

Transects

To verify an underlying gradient of herbivore impact, five transects of approximately 200 m were laid out ra-

dially from the watering point. Cattle faeces countings were carried out in series of 10 × 10 m quadrats laid out over each transect with the underlying assumption that the accumulation of faeces correlates with herbivore impact. The transects were used as axes of the series of quadrats, and for the design of the quadrats consecutive tracts of 10 m of the transect itself and 5 m at each side of the transect were used. In each of these quadrats, the total number of faecal droppings was counted.

Further, vegetation height (cm), type of functional plant group (perennial grasses, perennial herbs, annual grasses and annual herbs) and the presence of bare soil and litter were recorded at 0.1 m intervals along two (Transect 1 and 2) of the five transects. This was not done for the remaining three transects because of the occurrence of too many human tracks and other disturbances. Transect 1 (183.5 m long) consisted of 1836 sampling points and transect 2 (230.0 m long) of 2301 sampling points. Vegetation height was measured by lowering a perforated foam disc (diameter 0.1 m, weight 7 g) onto the vegetation along a gauged stick.

Soil variables in relation to functional plant groups

The dominant functional plant groups were perennial grasses and annual grasses. To investigate the relation between these plant groups and different soil variables, an area of approximately 15 × 15 m was selected in the zone far off (about 2 km) from the watering point. Plots of 0.25 × 0.25 m were selected within this area, five replicates for each functional plant group and five plots with bare soil. Samples from the upper 5 cm of the soil were taken at each plot to determine soil moisture content, organic matter content and soil texture. Soil moisture content (weight% on basis of oven-dry soil) was determined gravimetrically, organic matter content (weight% on basis of oven-dry soil) by loss on ignition and soil texture (weight% on basis of oven-dry soil) by sieve and pipette. Bulk density (g cm^{-3}) was determined by taking undisturbed samples of 100 cm^3 from the upper 5 cm of the soil and placing them in an oven at 105 °C until constant weight was reached.

Additionally, infiltration capacity (ml min^{-1}) on 0.25 × 0.25 m plots with different aerial vegetation cover of perennial grasses and annual grasses was measured by using a small rainfall simulator. Each simulation consisted of a rain shower with a duration of 4–5 min and an intensity of 6 mm min^{-1} (375 ml min^{-1} on 0.25 × 0.25 m plots) (Kamphorst 1987, Eijkelkamp Agrisearch Equipment). Theoreti-

cally, with a constant rainfall, infiltration decreases asymptotically to a certain final constant value as time increases (Stroosnijder 1976; Kiepe 1995). Therefore, each simulation was repeated until run-off was constant and at its maximum, so that final constant infiltration (infiltration capacity) could be calculated by subtracting run-off from simulated rainfall. Two series of measurements were performed, for plots with annual grasses only (in the absence of perennial grass tufts), and for plots including perennial grass tufts. The coverage of perennial grasses, annual grasses, litter and bare ground was estimated by eye using a quadrat with 10 × 10 subdivisions.

Experimental sites

Based on the findings of the transects, three sites (A, B and C) were selected which differed in herbivore impact because of their relative distance from the watering point (50–130 m) and the nearby village (120–230 m); the longer these distances, the lower the herbivore impact. Herbivore impact was high for site A, intermediate for site B and low for site C. At each site, a 7 × 5 matrix of 35 sampling points was established at 1 m interspaces. At each of these so-called base points, two additional sampling points were located in a randomly assigned direction (N, NE, E, SE, S, SW, W, NW), at 0.2 and 0.4 m from each base point (Gross et al. 1995). This resulted in a total of 105 sampling points per site (315 in total) in a stratified-nested design.

Run-off-run-on patterns were quantified by randomly scattering coloured plastic beads (available at local markets) over the sites and measuring their spatial distribution before and after rainfall. This was done by counting the number of beads on a 1 dm^2 surface at each sampling point, directly after scattering and after rainfall. 8400 beads of type 1 and 650 beads of type 2 were scattered per site, counted, and recounted after 51.4 mm of rain with a duration of 237 min. Type 1 beads were round, with an average diameter of 4.0 mm and an average weight of 0.026 g. Type 2 beads were oval shaped, on average 9.0 mm long, with an average diameter of 5.0 mm and an average weight of 0.109 g.

To quantify microrelief within each site, the height differences between all sampling points were measured by a using a surveyor's level and levelling staff with an accuracy of 1 mm. Soil moisture content (vol%) was measured with the Trime TDR (Time Domain Reflectometry) measuring system (Eijkelkamp Agrisearch Equipment) at 5 cm soil depth, 12–16 h

after a rain shower of 31.4 mm with a duration of 201 min. Soil temperature (°C) was measured at midday and 34–38 h after the same shower, with an electronic soil thermometer at 2.5 cm soil depth. Penetrability (kN) was measured 37–41 h after a rain shower of 6.2 mm with a duration of 32 min, with a soil penetrometer as a measure of topsoil compaction and crust formation.

At each sampling point the aboveground biomass (g dm^{-2}) of 1 dm^2 was harvested, air dried, sorted into different functional plant groups (annual grasses, annual herbs, perennial grasses, perennial herbs) and litter, and weighed with an electronic balance. Prior to harvesting, the height of the vegetation (cm) was measured, and aerial coverage (%) of annuals, perennials, litter and bare ground for each sampling point of 1 dm^2 was estimated by eye using a quadrat with 4×4 subdivisions.

Finally, after sampling the aboveground biomass, a soil core of 5 cm diameter was taken at each sampling point at 0–5 cm depth. The soil samples were put in small plastic bags and air-dried. In the laboratory, the air-dried samples were sieved with a 2 mm sieve. Per sample, two subsamples were taken of approximately 30 g, one for determining particle size distribution and one for chemical analyses. 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). As variable for further analysis the volume percentage of 1–100 μm was used, based on the characteristic differential volume curves derived from each sample. Before measuring, the samples were treated with a 300 g l^{-1} hydrogen peroxide (H$_2$O$_2$) solution and 3 min ultrasound to eliminate the effects of aggregation by soil organic matter. Organic matter content (weight% on basis of oven-dry soil) was determined by loss on ignition. Available PO$_4$-P, NO$_3$-N and NH$_4$-N (mg kg^{-1}), were determined with an auto-analyser after extraction with 0.01 M calcium chloride (CaCl$_2$).

Statistical analysis

Transects

Linear regression analysis was carried out to explore the relationships between distance from the watering point and the number of faecal droppings counted in the quadrats along the different transects. Moving averages of vegetation height and moving relative abundance of functional plant groups ($n = 100$) along transect 1 and 2 were calculated for a graphical exploration of the transect data. The spatial variation of vegetation height along transect 1 and 2 was evaluated by semivariance analysis, which analyses the variance between measurements taken at increasing distance from each other (Burrough 1995; Robertson & Gross 1994). The semivariance γ for a certain distance interval h is calculated as half the average of squared differences of pairs of observations for which the distance between the observations falls within that interval:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [y(x_i) - y(x_i + h)]^2,$$

where $N(h)$ is the total number of pairs that are separated by distance interval h, and $y(x_i + h)$ is the value of a variable at a distance interval h from x_i (Burrough 1995; Robertson & Gross 1994). Multiple spatial resolutions (minimum distance intervals) varying from 0.1 m to 2.0 m were used to optimally analyse different scales of patchiness.

Models were used in order of increasing complexity to fit the form of the semivariograms (Robertson et al. 1988; Jackson & Caldwell 1993; Schlesinger et al. 1996; Robertson et al. 1997). In the linear model with a sill, $\gamma(h) = C_0 + (C_1/A_1)h$ if $h < A_1$, and $\gamma = C_0 + C_1$ if $h > A_1$, where γ is the semivariance, h is the lag, A_1 is the range, C_0 is the nugget variance, and C_1 the structural variance. In the spherical model, $\gamma(h) = C_0 + C_1 [1.5(h/A_1) - 0.5(h/A_1)^3]$ if $h < A_1$, and $\gamma = C_0 + C_1$ if $h > A_1$. In the two-level Gaussian model, $\gamma(h) = C_0 + C_1 [1 - \exp(-1\{h^2/A_1^2\})]$ if $h < q_1$, and $\gamma(h) = [C_0 + C_1] + C_2[1 - \exp(-1\{[h - q_1]^2/A_2^2\})]$ if $h > q_1$, where q_1 is the transition point from semivariogram 1 to semivariogram 2, C_2 is the structural variance of semivariogram 2, and A_2 the range of semivariogram 2. In the three-level Gaussian model, a third semivariogram could be distinguished. Thus, $\gamma(h) = [C_0 + C_1 + C_2] + C_3[1 - \exp(-1\{[h - q_2]^2/A_3^2\})]$ if $h > q_2$, where q_2 is the transition point from semivariogram 2 to semivariogram 3, C_3 the structural variance of semivariogram 3, and A_3 the range of semivariogram 3. The proportion of the total variance accounted for by structural or spatially dependent variance is calculated by $C_1/(C_0 + C_1)$ in case of a one-level model (linear model with a sill or spherical model). In case of a two-level and three-level model the proportion structural variation is calculated by $(C_1 + C_2)/(C_0 + C_1 + C_2)$ and $(C_1 + C_2 + C_3)/(C_0 + C_1 + C_2 + C_3)$, respectively.

The simplest model with the highest R^2 was considered as optimal. A more complex model was chosen if its R^2 was at least 0.05 higher than the R^2 of a less complex one. If according to this standard procedure the optimal model was a linear model, then this model was only chosen if its $P < 0.05$. If $P > 0.05$, then the random model was considered appropriate.

Soil variables in relation to functional plant groups

Soil variables as measured for the 0.25×0.25 m plots were compared using the Mann–Whitney U-test. Linear regression analysis was performed to test the dependence of infiltration capacity on aerial cover of annual grasses and perennial grasses.

Experimental sites

Site means were compared pairwise using the Mann–Whitney U-test. The magnitude of within-site variability was evaluated by comparing coefficients of variation (%). To explore the correlation structure of the data set, Principal Component Analysis (PCA) was used. Further analysis and discussion was mainly focussed on the variables with the highest eigenvectors for the first component.

The spatial variation of the variables was evaluated by calculating the semivariograms and fitting optimal models. For each variable of the three sites, the lag interval evaluated was 0–4 m (approximately half the maximum distance between sampling points) with a spatial resolution (minimum distance interval) of 0.2 m. The cross-correlogram was used to compare spatial patterns of those variables with the highest eigenvectors for the first component. The cross-correlogram plots the cross-correlation $r_{ab}(h)$ between two variables as a function of the distance interval h between sampling points. To calculate $r_{ab}(h)$ from available data, consider pairs of observations $a(x_i)$ and $b(x_i + h)$, separated by distance interval h. For $N(h)$ pairs of observations, $r_{ab}(h)$ is calculated as:

$$r_{ab}(h) = \frac{\sum_{i=1}^{N(h)} a(x_i)b(x_i + h) - m_a m_b}{s_a s_b},$$

where m_a and m_b and s_a and s_b denote sample mean and standard deviation of a and b respectively (Stein et al. 1997). If patterns are completely similar and overlapping, $r_{ab}(0)$ is equal to 1; if patterns are completely opposite and overlapping, $r_{ab}(0)$ is equal to -1. Commonly, the cross-correlation gradually shifts towards zero for increasing values of h, indicating a range of spatial dependence. For totally unrelated patterns, $r_{ab}(h)$ equals zero. If patterns show similarities for certain distances larger than zero, $r_{ab}(h)$ may show a peak for those specific distances.

Linear trends and data transformation

If significant ($P < 0.01$) linear trend lines or trend surfaces were present for the variables evaluated, the given variables were represented by the deviations from the trends for the geostatistical analyses, as well as for the PCA. This was the case for most of the variables. This caused most (detrended) variables to approach a normal distribution. Therefore, and because unbiased comparisons of scales of patchiness between variables and between sites were needed, data were not transformed. For comparisons between means, non-parametric tests were used.

Results

Transects

The average number of faecal droppings across the five transects showed a significant ($P < 0.001$, $R^2 = 0.21$) decrease with increasing distance. Therefore, the assumption of an underlying gradient of herbivore impact radial to this watering point was justified. For transect 1, a significant decrease in the number of faecal droppings with increasing distance from the water point was found ($P < 0.001$, $R^2 = 0.64$), but not for transect 2 (Figure 2). At an intermediate distance from the watering point, the moving average of vegetation height ($n = 100$) as well as the moving relative abundance of annual and perennial grasses showed a clear periodic signal for transect 1 with the underlying gradient of herbivore impact, but not for transect 2, which did not show a significant gradient.

For transect 1, four different scales of patchiness emerged while for transect 2, two scales of patchiness were found (Figure 3). For both transects, the smallest scale of patchiness (about 0.75 m) consisted of perennial grass tufts (Figures 3a, d; see Table 1 for parameter values of optimal models). The next scale of patchiness of about 5–10 m (Figures 3b, e) consisted of vegetation patches of co-occurring annuals and perennials alternating with bare soil. Two additional scales of patchiness were recognised for transect 1 (Figure 3c), representing relatively homogeneous parts of the transect (bare soil close to the watering point and a continuous vegetation cover at the end
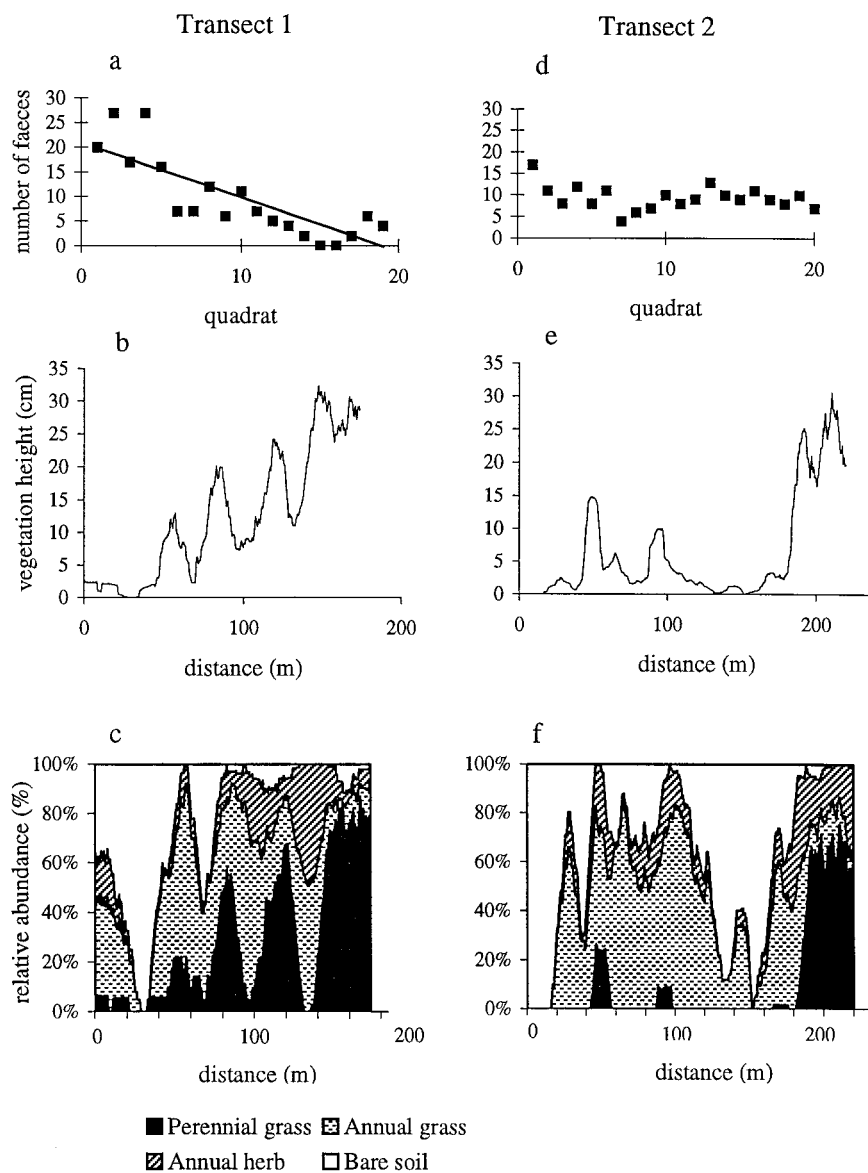
Transect 1

a

b

c

Transect 2

d

e

f

■ Perennial grass ⊠ Annual grass
▨ Annual herb □ Bare soil

Figure 2. Results of transects 1 (a–c) and 2 (d–f). (a, d) Number of faecal droppings as a function of quadrat number (which equals distance from watering point if multiplied by 10) (linear regression transect 1: $P < 0.001$, $R^2 = 0.64$; linear regression transect 2: not significant). (b, e) Moving average ($n = 100$) of vegetation height. (c, f) Moving relative abundance ($n = 100$) of bare soil, annual herbs, annual grasses and perennial grasses.

of the transect), and the remaining intermediate part where the periodic signal occurred. The periodicity of this signal can be recognised by the cyclic pattern in the semivariogram. Analysed at a lag interval of 0–100 m, transect 2 was optimally fitted by a linear model without a sill (Figure 3f), indicating increasing deviations from the linear trend with increasing distance interval.

Soil variables in relation to functional plant groups

Soil organic matter and moisture were significantly higher in vegetated plots than in bare soil plots (Table 2). Bulk density of bare soil was significantly higher than in perennial grass plots. Soil samples taken from annual grass plots contained significantly more clay and less sand than samples taken from bare soil plots. Infiltration capacity increased both with increas-

Table 1. Parameters of the optimal models of the transect semivariograms of vegetation height. In order of increasing complexity the models we have tested were: linear model (=linear), linear model with a sill (=sill), and spherical model (=spher). If appropriate, a two-level or three-level Gaussian model (=gauss) was applied. The parameters C_0, C_1, C_2, C_3, A_1, A_2, A_3, q_1 and q_2 are explained in the text.

Transect	Lag interval (m)	Model	R^2	C_0	C_1	Proportion structured variance	A_1 (m)	C_2	A_2 (m)	C_3	A_3 (m)	q_1 (m)	q_2 (m)
Transect 1	0–2	Sill	0.97	0.00	44.15	1.00	0.71	–	–	–	–	–	–
Transect 1	0–65	Gauss	0.91	34.92	60.24	0.74	7.48	40.44	6.32	–	–	35.16	–
Transect 1	0–100	Gauss	0.95	34.89	60.11	0.77	7.48	38.59	6.13	19.71	7.48	35.00	65.00
Transect 2	0–2	Sill	0.88	0.33	8.30	0.96	0.87	–	–	–	–	–	–
Transect 2	0–10	Sill	0.90	4.43	13.92	0.76	4.99	–	–	–	–	–	–
Transect 2	0–100	Linear	0.98	8.70	–	–	–	–	–	–	–	–	–

As significant linear trends ($P < 0.01$) were present in the data evaluated, the given data was represented by the deviations from the trend before calculation of the semivariograms.

Table 2. Mean values of soil variables for different functional plant groups and bare soil, and number of observations (n). Significant differences between means (Mann–Whitney U-test, $P < 0.05$) are indicated by different letters.

Variable	Mean (n)		
	Bare soil	Annual grass	Perennial grass
Soil moisture (%)	10.76 (5) a	14.30 (5) b	15.72 (5) b
Soil organic matter (%)	1.32 (10) a	1.95 (10) b	2.11 (10) b
Bulk density (g cm^{-3})	1.62 (5) b	1.55 (5) ab	1.36 (5) a
Clay (%)	34 (8) a	40 (8) b	40 (8) ab
Loam (%)	31 (8) a	29 (8) a	28 (8) a
Sand (%)	35 (8) a	31 (8) b	32 (8) ab

ing annual grass cover (linear regression, $P < 0.05$, $R^2 = 0.30$) and perennial grass cover (linear regression, $P < 0.001$, $R^2 = 0.81$) (Figure 4). Given a certain aerial vegetation cover, plots with perennial grass cover had a higher infiltration capacity than plots with annual grass cover.

Experimental sites

The number of beads found after rainfall indicated that run-off was higher for site A and site B as compared to site C (Table 3). Mean biomass, aerial biomass cover, vegetation height, soil moisture and available PO_4-P ($n = 105$) increased significantly from site A (high herbivore impact) to site B (intermediate herbivore impact), and from site B to site C (low herbivore impact). Site A and B were characterised by an absence of perennial vegetation and litter, the vegetation only consisted of annuals. In site C, average aerial cover of perennials (mainly grass tufts of *Cymbopogon schoenanthus*) was about 14% and that of litter was about 19%.

NH_4-N was about two to three times higher in site C than in site A and B. NO_3-N was about four times higher in site B than in site A and C (Table 3). Soil organic matter in site B and C was significantly higher than in site A. Soil compaction and soil temperature of the top soil was lowest in site C. Soil texture differed significantly between the sites; volume% of soil particle diameter from 1–100 μm was highest for site B and lowest for site C. Coefficients of variation were generally low for altitude, soil temperature, soil organic matter and texture ($<20\%$). Higher coefficients of variation were found for vegetation height, soil moisture, NO_3-N and penetrability (approximately 20–100%). Coefficients of variation higher than 100% were found for the other variables.

Correlation structure

For all sites, four principal components together contributed for more than 65% in explaining the total variation in the data (Table 4). Component I contributed relatively much in explaining this variation,
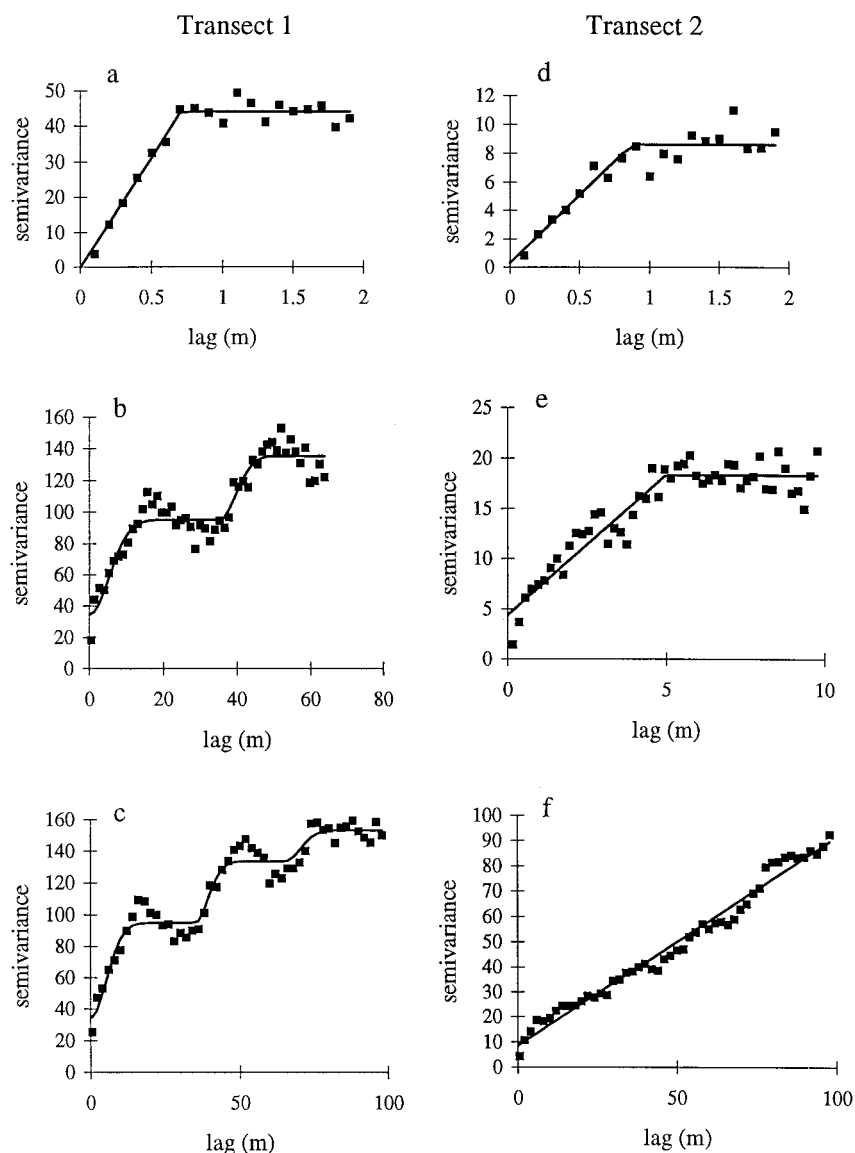
Transect 1

Transect 2

Figure 3. (a–f) Semivariograms for vegetation height (cm) of transect 1 and 2 for different lag intervals. Maximum lag interval was 0–100 m, approximately half the length of the transects. For parameters of optimal models, see Table 1.

29.2%, 32.1% and 31.6% for site A, B and C respectively. For site A and B, the highest weightings for this component were soil temperature, biomass, soil moisture, number of beads and penetrability. This means that these variables were more or less correlated for these sites and that together they are relatively important in explaining the total variation in the data. Thus, in site A and B, higher biomass, higher soil moisture and less run-off were associated with lower soil temperature and less soil compaction. In site C, soil moisture, run-off and penetrability did not con-

tribute to component I; the highest eigenvectors for this component were biomass, NH_4-N, soil organic matter, soil temperature and altitude. Thus, in site C, higher biomass, higher soil organic matter and higher NH_4-N were associated with micro-elevations and lower soil temperatures. This can be understood by the presence of perennial grass tufts in this site, which consist of micro-elevations through the accumulation of organic material. Soil organic matter became increasingly important with decreasing herbivore impact (going from site A to site B to site C).

Table 3. Mean values and coefficients of variation (sd/mean × 100%) of 105 sampling points. Significant differences between means (Mann–Whitney U-test, $P < 0.05$) are indicated by different letters.

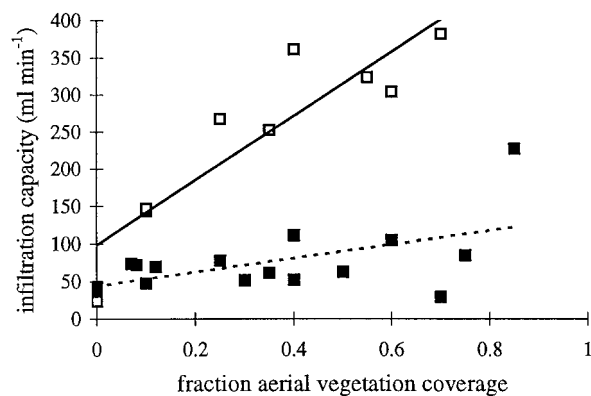| Variable	High herbivore impact Site A		Intermediate herbivore impact Site B		Low herbivore impact Site C	
	Mean	CV(%)	Mean	CV(%)	Mean	CV(%)
Number of beads before rain (dm^{-2})	3.21a	104.8	3.77b	71.2	2.27a	104.1
Number of beads after rain (dm^{-2})	0.62 a	268.2	0.49 a	233.9	2.16 b	147.3
Relative altitude (mm)	−1110.76 b	2.2	−1519.39 a	1.1	−1115.92 b	2.4
Biomass ($g\,dm^{-2}$)	0.48 a	150.2	0.69 b	93.0	6.18 c	166.2
Biomass cover (%)	15.17 a	144.0	23.67 b	101.8	76.22 c	35.9
Vegetation height (cm)	3.70 a	68.2	5.18 b	68.0	21.56 c	79.7
Soil moisture (vol.%)	5.59 a	40.3	6.30 b	23.4	8.52 c	35.3
Soil temperature (°C)	41.47 b	5.8	42.07 c	7.1	33.10 a	7.4
Soil organic matter (%)	2.67 a	13.8	3.80 b	11.8	3.99 b	17.8
NH_4-N ($mg\,kg^{-1}$)	1.37 a	69.9	1.34 a	68.2	3.76 b	155.9
NO_3-N ($mg\,kg^{-1}$)	3.25 a	102.3	13.20 c	66.7	3.76 b	73.2
PO_4-P ($mg\,kg^{-1}$)	9.52×10^{-3} a	371.9	98.76×10^{-3} b	117.9	106.57×10^{-3} c	179.5
Penetrability (kN)	0.11 b	38.8	0.11 b	44.9	0.05 a	68.3
Texture (vol.% 1-100 μm)	51.28 a	13.3	77.42 c	6.5	60.17 b	11.5

Figure 4. Linear regression between infiltration capacity on 0.25 × 0.25 m plots and annual grass coverage (■) ($P < 0.05$, $R^2 = 0.30$) and perennial grass coverage (□) ($P < 0.001$, $R^2 = 0.81$). For the measurement series of annual grass coverage, vegetation cover consisted only of annual grasses. For the measurement series of perennial grass coverage, vegetation cover consisted of perennial grass as well as annual grasses and litter, but only perennial grass coverage was used in the regression analysis.

Cross-correlograms shed a more detailed light on the correlations between variables for the different sites (see section Cross-correlograms).

Semivariograms
Beads showed a more or less patchy distribution after scattering (Figure 5 and Table 5). Heavy and intense rain (51.4 mm with a total duration of 237 min) caused severe run-off from site A and site B. Most beads were washed away from these two sites (Table 3), leading to low semivariances and leaving no robust spatial structures within these sites after the rain. Note the similarity of the two semivariograms for beads before and after rain for site C, indicating no spatial redistribution for this site.

For each site, the semivariograms of biomass, soil temperature and soil moisture showed similar scales of patchiness, except for soil moisture at site C (Figures 6b–d and Table 5). Note that for site A, the optimal model fitted through the semivariograms of biomass, soil temperature and soil moisture was a three-level Gaussian curve, indicating three distinct levels of spatial structure at this site. For site B, the semivariograms of these variables showed a clear range (A_1) of about 1 m. For site C, this range was much smaller, but not for soil moisture which did not have a clear patchy structure at this site. The semivariograms of altitude showed a relatively large scale of patchiness ($A_1 = 2.89$ m) for site A, a smaller scale for site B and no clear patchy structure for site C (Figure 6a). Note the high R^2 (0.99) of the linear model with a sill for this variable for site A (Table 5). Interestingly, also a three-level Gaussian curve accurately fitted the altitude semivariance data for this site,

Table 4. Eigenvalues, percentages of variation (%Var) explained and eigenvectors of variables for each component and each site, evaluated by PCA. Bold values indicate highest eigenvector scores for a given variable.

Site	Parameter PCA	Variable	Component I	Component II	Component III	Component IV
A	Eigenvalue		3.22	1.56	1.32	1.13
	%Var		29.2	14.2	12.0	10.2
	Eigenvector	Soil temperature∗	**−0.86**	0.08	−0.05	0.35
		Biomass∗	**0.83**	−0.04	−0.05	0.19
		Soil moisture∗	**0.77**	0.08	−0.03	−0.36
		Penetrability*	**−0.65**	−0.39	0.11	0.15
		Beads∗	**0.50**	−0.48	0.19	0.42
		Soil organic matter	0.43	**0.60**	0.31	0.11
		PO$_4$-P∗	−0.33	**0.51**	−0.04	0.09
		Texture∗	−0.19	0.50	**0.61**	0.16
		NH$_4$-N	0.20	−0.41	**0.65**	0.25
		Altitude∗	−0.28	−0.10	0.60	**−0.63**
		NO$_3$-N	0.25	0.33	0.00	**0.35**
B	Eigenvalue		3.53	1.53	1.25	1.10
	%Var		32.1	13.9	11.3	10.0
	Eigenvector	Soil temperature∗	**−0.91**	0.10	0.09	0.19
		Biomass∗	**0.83**	−0.22	0.06	−0.10
		Soil moisture∗	**0.75**	−0.17	−0.21	−0.20
		Penetrability	**−0.72**	−0.16	−0.01	−0.05
		Soil organic matter∗	**0.72**	0.44	0.01	0.03
		Beads	**0.46**	−0.19	0.32	0.37
		PO$_4$-P∗	0.20	**0.64**	0.44	−0.27
		NH$_4$-N∗	−0.25	0.23	**0.62**	−0.45
		Altitude∗	−0.11	−0.45	**0.51**	0.16
		Texture∗	−0.30	0.45	**−0.49**	−0.16
		NO$_3$-N	0.12	0.55	0.09	**0.73**
C	Eigenvalue		3.47	2.02	1.26	1.06
	%Var		31.6	18.4	11.4	9.6
	Eigenvector	NH$_4$-N∗	**0.86**	−0.11	0.06	−0.18
		Biomass	**0.85**	0.09	0.24	−0.02
		Soil organic matter	**0.78**	0.06	0.14	0.20
		Soil temperature∗	**−0.68**	0.48	0.21	−0.16
		Altitude∗	**0.61**	0.49	−0.24	0.25
		Texture∗	−0.12	**−0.77**	0.13	−0.10
		Penetrability	−0.53	**0.62**	0.29	−0.17
		Soil moisture∗	−0.02	−0.51	**0.56**	−0.15
		NO$_3$-N	0.09	0.36	**0.59**	0.49
		Beads	−0.30	−0.31	0.37	**0.50**
		PO$_4$-P	0.41	0.24	0.41	**−0.59**

If significant linear trend surfaces ($P < 0.01$) were present in the variables evaluated, the given variables (indicated by ∗) were represented by the deviations from the trend surface before evaluation by PCA.

Table 5. Parameters of the optimal model of the semivariograms. In order of increasing complexity the models we have tested were: random model (=rand), linear model (=linear), linear model with a sill (=sill), and spherical model (=spher). If appropriate, a three-level Gaussian model (=gauss) was applied. Minimum distance interval: 0.2 m; number of lags: 20; lag interval: 0–4 m. The parameters $C_0, C_1, C_2, C_3, A_1, A_2, A_3, q_1$ and q_2 are explained in the text.

Site	Variable	Model	R^2	C_0	C_1	Proportion structured variance	A_1 (m)	C_2	A_2 (m)	C_3	A_3 (m)	q_1 (m)	q_2 (m)
A	Beads before rain	Sill	0.52	1.07	6.50	0.86	0.64	–	–	–	–	–	–
	Beads after rain	Linear	0.56	0.37	–	–	–	–	–	–	–	–	–
	Altitude	Sill	0.99	0.00	45.12	1.00	2.89	–	–	–	–	–	–
	Altitude	Gauss	0.98	0.56	15.00	0.99	0.50	19.20	0.52	10.00	0.15	1.20	2.40
	Biomass	Gauss	0.84	0.00	0.10	1.00	0.43	0.07	0.22	0.05	0.10	1.60	2.80
	Soil moisture	Gauss	0.95	0.46	1.34	0.84	0.59	0.66	0.20	0.41	0.12	1.60	2.60
	Soil temperature	Gauss	0.98	0.00	1.45	1.00	0.49	1.39	0.27	1.01	0.23	1.60	2.60
	Soil organic matter	Spher	0.39	0.03	0.08	0.73	0.72	–	–	–	–	–	–
	NH$_4$-N	Sill	0.46	0.14	0.37	0.73	0.70	–	–	–	–	–	–
	NO$_3$-N	Linear	0.57	1.48	–	–	–	–	–	–	–	–	–
	PO$_4$-P	Linear	0.90	0.00	–	–	–	–	–	–	–	–	–
	Penetrability	Sill	0.59	2.84×10^{-4}	12.15×10^{-4}	0.81	1.62	–	–	–	–	–	–
	Texture	Sill	0.82	0.00	25.15	1.00	1.31	–	–	–	–	–	–
B	Beads before rain	Sill	0.31	0.68	5.64	0.89	0.49	–	–	–	–	–	–
	Beads after rain	Spher	0.13	0.00	0.11	1.00	0.56	–	–	–	–	–	–
	Altitude	Sill	0.83	0.00	41.39	1.00	1.60	–	–	–	–	–	–
	Biomass	Sill	0.78	0.00	0.38	1.00	0.99	–	–	–	–	–	–
	Soil moisture	Sill	0.64	0.31	1.57	0.84	0.81	–	–	–	–	–	–
	Soil temperature	Sill	0.79	0.00	8.98	1.00	1.02	–	–	–	–	–	–
	Soil organic matter	Sill	0.80	0.03	0.07	0.70	1.34	–	–	–	–	–	–
	NH$_4$-N	Sill	0.42	0.29	0.30	0.51	0.89	–	–	–	–	–	–
	NO$_3$-N	Linear	0.33	31.34	–	–	–	–	–	–	–	–	–
	PO$_4$-P	Sill	0.48	2.08×10^{-3}	3.06×10^{-3}	0.60	1.62	–	–	–	–	–	–
	Penetrability	Spher	0.57	6.31×10^{-4}	17.88×10^{-4}	0.74	1.62	–	–	–	–	–	–
	Texture	Linear	0.60	13.97	–	–	–	–	–	–	–	–	–
C	Beads before rain	Spher	0.35	1.57	2.46	0.61	1.94	–	–	–	–	–	–
	Beads after rain	Spher	0.23	2.41	1.92	0.44	2.00	–	–	–	–	–	–
	Altitude	Linear	0.87	58.27	–	–	–	–	–	–	–	–	–
	Biomass	Sill	0.58	0.00	27.88	1.00	0.56	–	–	–	–	–	–
	Soil moisture	Linear	0.69	5.07	–	–	–	–	–	–	–	–	–
	Soil temperature	Sill	0.56	0.00	5.18	1.00	0.49	–	–	–	–	–	–
	Soil organic matter	Sill	0.77	0.07	0.31	0.82	1.29	–	–	–	–	–	–
	NH$_4$-N	Linear	0.69	2.61	–	–	–	–	–	–	–	–	–
	NO$_3$-N	Sill	0.33	0.69	2.70	0.80	0.46	–	–	–	–	–	–
	PO$_4$-P	Linear	0.64	8.22×10^{-4}	–	–	–	–	–	–	–	–	–
	Penetrability	Sill	0.64	1.08×10^{-4}	5.16×10^{-4}	0.83	1.43	–	–	–	–	–	–
	Texture	Sill	0.63	10.57	29.60	0.74	1.14	–	–	–	–	–	–

If significant linear trend surfaces ($P<0.01$) were present in the variables evaluated (see Table 4), the given variables were represented by the deviations from the trend surface before calculation of the semivariograms.
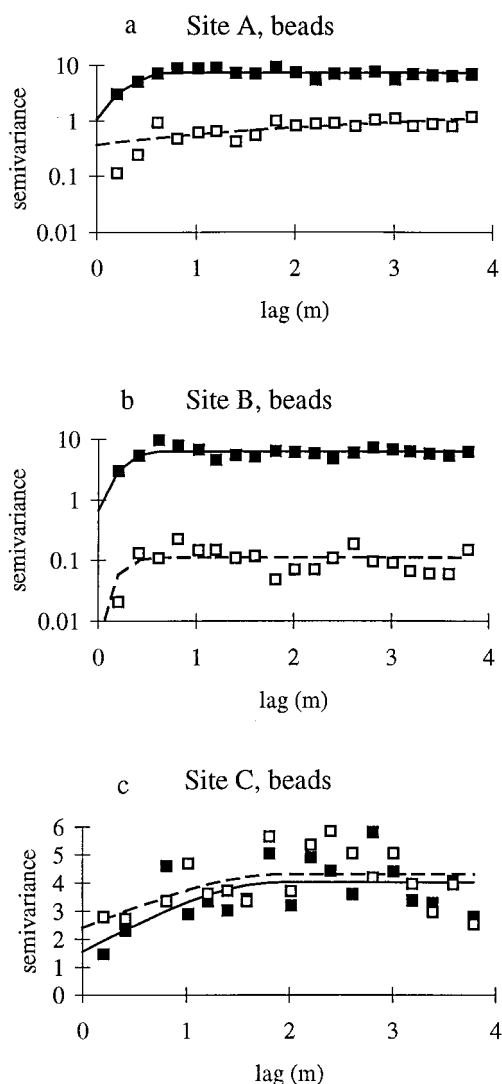
Figure 5. (a–c) Semivariograms of amount of beads counted before rain (■) and after rain (□) for each site. Lines represent optimal models. For parameters and types of optimal models, see Table 5. A log semivariance scale is used if semivariances of the amount of beads showed large differences between observations before and after rain.

its R^2 was 0.98, only 0.01 lower than that of the optimal model. So, semivariograms of altitude, biomass, soil moisture and temperature showed a corresponding patchy structure for site A.

Soil organic matter showed a comparable proportion structured variance for the three sites, and the scale of patchiness was relatively small for site A as compared to site B and C (Figure 6e). NH_4-N showed a more or less similar patchy structure for site A and B, but for site C no clear sill could be detected (Figure 6f).

Semivariances of both soil organic matter and NH_4-N were higher at site C as compared to the other sites.

Cross-correlograms

Biomass showed a significant positive correlation with soil moisture at a lag interval of 0–0.5 m for site A and B, but for site C no significant cross-correlations occurred (Figure 7a), meaning that biomass and moisture patterns were overlapping for site A and B, but not for site C. A significant positive cross-correlation at a lag interval of 0–0.2 m could be detected for sites A and B between beads counted after rainfall on the one hand, and biomass and soil moisture on the other hand (Figures 7b, c), which could not be attributed to microrelief (Figure 7d). This means that run-off was less on locations close to or in vegetated patches in site A and B (but not in site C) resulting in higher soil moisture. The cross-correlograms soil organic matter – biomass showed an increasing similarity between spatial patterns going from site A to site B and from site B to site C (Figure 7e). The range across which significant spatial dependence occurred was relatively high (0–0.7 m) for site B as compared to the other sites. Cross-correlations of NH_4-N with biomass showed that higher amounts of NH_4-N were associated with higher biomass for site C, due to the presence of perennial grass tufts, but not for site A and B (Figure 7f).

We further found very high negative correlations between soil temperature and biomass for all sites, indicating similar but opposite spatial patterns. For site A and B lower soil temperatures were related with annual grass patches, for plot C lower soil temperatures were mainly found under perennial grass tufts (Table 4). Cross-correlations of soil temperature with soil moisture further indicated that these lower soil temperatures were correlated with higher soil moisture at locations with a relatively high biomass for site A and B, but not for site C.

Discussion

We found a nested structure of vegetation patchiness consisting of four distinct levels (Figure 3) along the gradient of herbivore impact of transect 1 (Figure 2). We argue that the following characteristic spatial sequence (Figure 2) led to this nested structure. A spatially homogeneous part of the transect largely consisting of bare soil occurred close to the watering point at a distance of approximately 0–50 m. Vege-
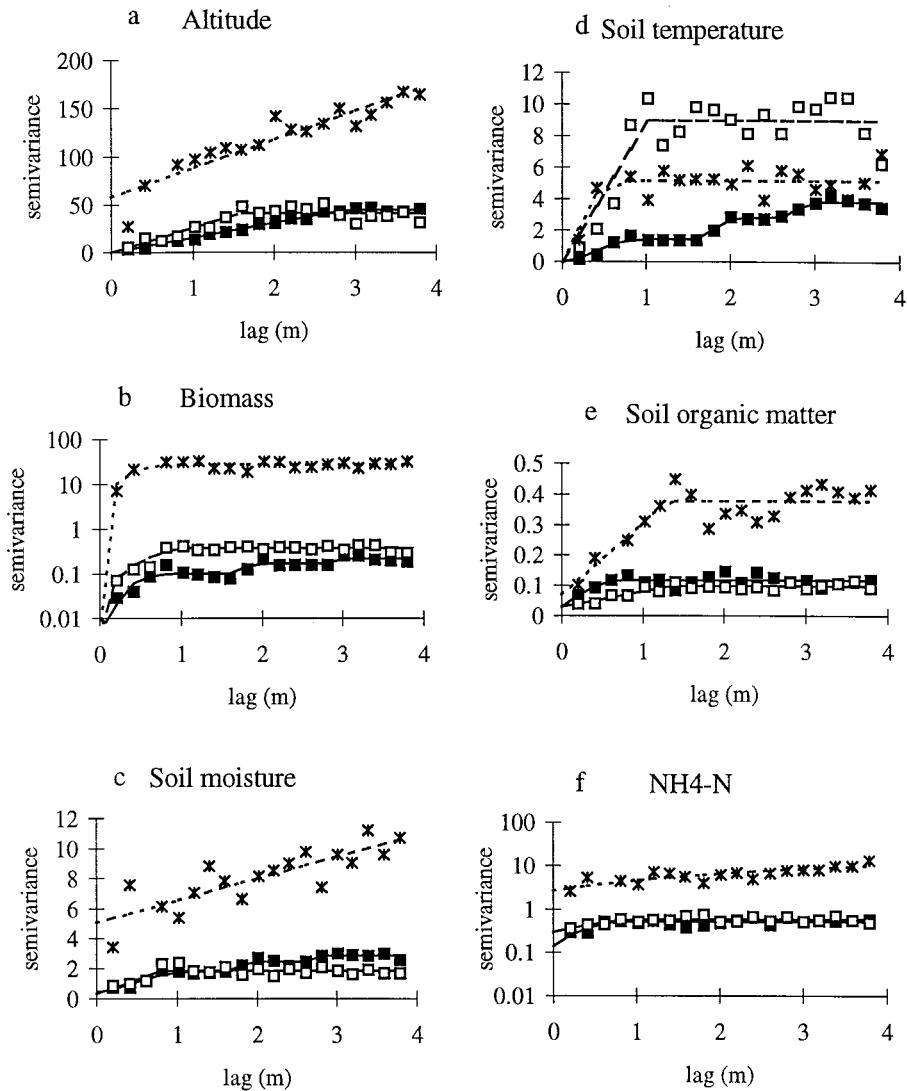
Figure 6. Semivariograms of the most important variables (according to PCA) (a) altitude, (b) biomass, (c) soil moisture, (d) soil temperature, (e) soil organic matter and (f) NH₄-N for site A (■), B (□) and C (∗). Lines represent optimal models. For parameters and types of optimal models for all variables, see Table 5. A log semivariance scale is used if semivariances of certain variables showed large differences between sites.

tated patches of co-occurring annuals and perennials with a scale of about 7.50 m (Table 1), alternating with bare soil, existed at a distance of approximately 50–130 m from the watering point. A continuous vegetation cover was present at a distance of approximately 130–180 m and further away from the watering point. Such characteristic spatial sequence and nested structure of vegetation patchiness was not found for transect 2, for which no significant gradient of herbivore impact was present. From this follows that the nested structure as well as the characteristic spatial

sequence may be attributed to the occurrence of a gradient of herbivore impact. We acknowledge, however, that we did not provide clear-cut evidence for this, due to lack of replication of watering points and transects with and without an underlying gradient of herbivore impact. Therefore, caution must be used when generalising these results. But still, on first inspection, our results are in line with our initial hypothesis that vegetated patches alternating with patches of bare soil would occur at intermediate herbivore impact.
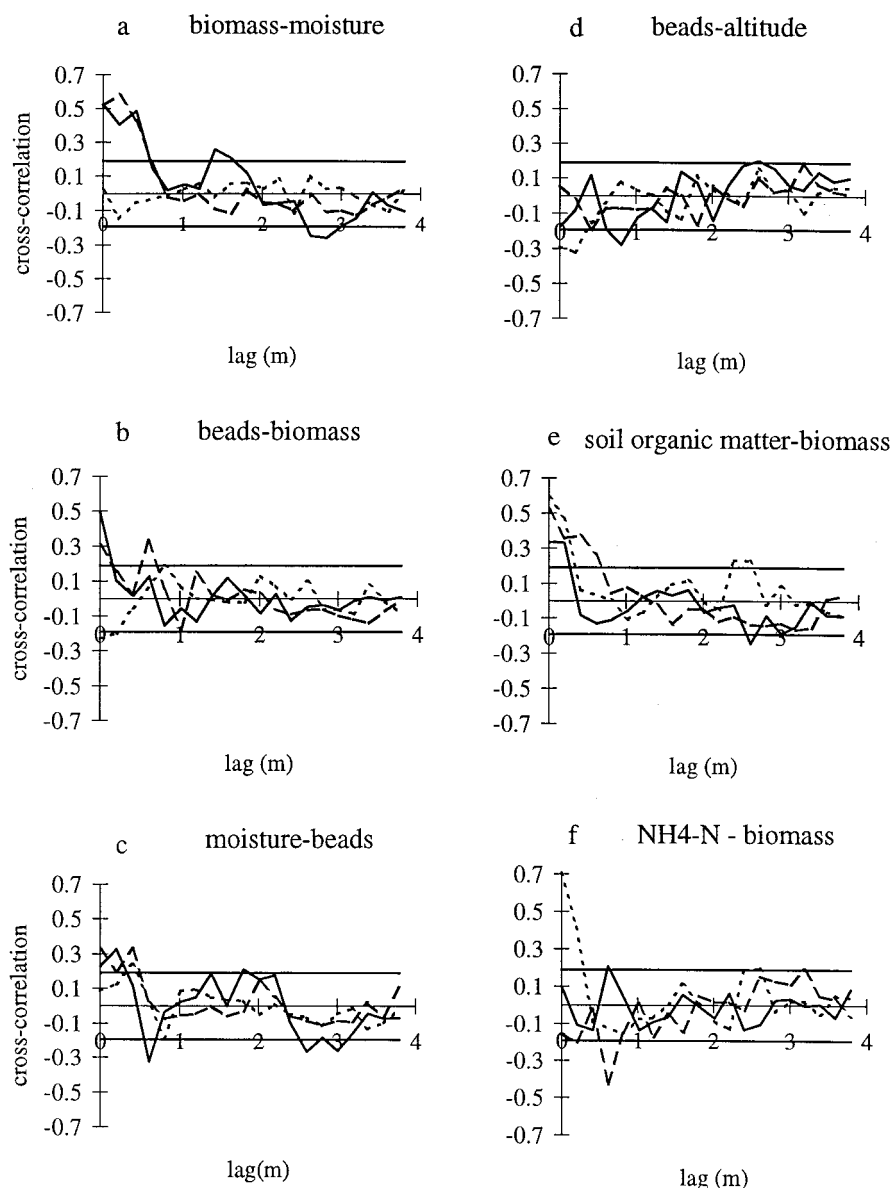
Figure 7. Cross-correlograms of (a) biomass - moisture, (b) beads - biomass, (c) moisture - beads, (d) beads - altitude, (e) soil organic matter - biomass and (f) NH_4-N - biomass for site A [—], B [– – –] and C [- - - -]. Confidence bounds indicate critical values of the correlation coefficient r for $\alpha = 0.05$ and $n = 105$, which is the number of pairs evaluated at lag distance $= 0$.

When analysing the data from the experimental sites along the gradient, however, we were surprised by the unexpected high degree of patchiness of vegetation and soil variables in case of low and high herbivore impact as well. In case of high (site A), intermediate (site B) and low (site C) herbivore impact, most variation of vegetation and soil variables was spatially explained, up to 100% for vegetation biomass and soil temperature (Table 5). But for low herbivore

impact (site C) this was clearly due to the presence of perennial grass tufts. The presence of perennial grass tufts determined the scale and degree of patchiness of biomass and to a certain extent also those of soil temperature, soil organic matter and NH_4-N (Figures 6, 7 and Table 5). These variables were important for explaining total variation within this site (Table 4). Redistribution of water after rain leading to higher soil

moisture if vegetation in present could not be detected (Figures 5, 7).

For high (site A) and intermediate (site B) herbivore impact, we found evidence that vegetated patches positively affected soil moisture through less run-off and higher infiltration of rainwater that could not infiltrate into the bare soil elsewhere (Figures 4, 7 and Table 4). For site A, however, it appeared that the occurrence of relatively high amounts of biomass was related with microdepressions ($r = -0.3$, $P < 0.05$). This, and the corresponding patchy structure of biomass, soil moisture and temperature with altitude (Figure 6 and Table 5), leads us to the conclusion that we could not exclude microrelief as an important factor contributing to vegetation and soil patterning within this site. For site B we could even exclude microrelief as an important factor contributing to vegetation and soil patterning, as these patterns were not overlapping. Thus, the vegetation could benefit from higher soil moisture if the soil is already vegetated. Alternatively, the vegetation could have difficulties colonising bare areas and becoming established due to lower soil moisture. Therefore, we conclude that in these cases a spatial pattern of vegetated patches alternating with bare soil could persist in time due to positive (self-reinforcing) plant-soil feedbacks, although a test of this would require a long-term study.

We found that perennial grass cover has a much stronger effect on infiltration capacity than annual grass cover (Figure 4). Apparently, with their extended root system, perennial grass tufts improve water infiltration much more effectively than annual grasses by funneling rain water via their basis into their own rhizospheres (Kelly & Walker 1976), stimulating biological activity, decreasing bulk density, thereby increasing plant available soil water (Table 2). Our data suggest that this is especially the case for perennials. It is well known that plant-induced soil changes are more pronounced for perennials than for annuals in semi-arid grasslands, although often attention is focussed primarily on nutrient cycling (Bolton et al. 1993; Vinton & Burke 1995; but see Tongway & Ludwig 1994, for the description of a larger set of resource regulation mechanisms including water cycling).

We propose that the differences of vegetation and selected soil variables between the sites A (high herbivore impact), B (intermediate herbivore impact) and C (low herbivore impact) was caused by the differences in herbivore impact. Grazing and trampling led to a relatively high coverage of bare soil, soil compaction and run-off. The availability of soil moisture was negatively affected by herbivore impact which can be explained by relatively high run-off and low infiltration for sites with a relatively low coverage of vegetation (Figure 4), combined with the effect of high soil evaporation due to relatively high soil temperatures for these sites. These effects of grazing and trampling are commonly found in semi-arid grazing systems (Elwell & Stocking 1976; Kelly & Walker 1976; Valentin 1985).

Further, it appeared that the availability of soil nutrients was negatively affected by herbivore impact. (The high amount of NO_3-N for plot B was probably due to local deposition of animal urine.) Generally, these results contradict those of Tolsma et al. (1987) who found higher amounts of soil nutrients, including nitrogen and phosphorus, in the vicinity of two boreholes (0–100 m) as compared to longer distances away. These authors attribute this effect to the transport of nutrients by cattle via dung from surrounding areas centripetally towards the watering points, and the deposition of urine. Although we did find an increase in faeces density with decreasing distance from the watering point, this was not in agreement with the distribution of soil nutrients. We attribute this to the effects of nutrient loss through soil erosion by run-off as a consequence of the relative high coverage of bare soil and to the relative low soil organic matter related to this; effects which were not apparent in the study of Tolsma et al. (1987).

Jackson & Caldwell (1993) and Ryel et al. (1996) found a spatial structure for NH_4-N and NO_3-N in a perennial sagebrush-wheatgrass steppe with typically a range of about 1 m and a proportion of structural variance of about 0.50, similar to our results. However, clear relationships between the location of perennial grass tufts and total soil nitrogen were not found by the above mentioned authors, while we found a clearly overlapping pattern of vegetation biomass, soil organic matter and NH_4-N due to the presence of perennial grass tufts of *Cymbopogon schoenanthus*. This was not the case for NO_3-N. The lack of significant cross-correlations between NO_3-N on the one hand and NH_4-N, vegetation biomass and soil organic matter on the other hand suggests no straightforward connection between the different, highly dynamic soil nitrogen pools (Stark 1994; Ryel et al. 1996). As instantaneous measurements of NH_4-N and NO_3-N reflect both nitrogen production and consumption, further conclusions could not be drawn about mineralisation or nitrification rates (Wedin & Tilman 1990).

Ryel et al. (1996) and Schlesinger et al. (1996) speculate that spatial patterns develop most rapidly for resources which are typically most limiting to plant growth. We found that soil water is important for explaining total variation if soil water is deficient. This was mainly the case for high and intermediate herbivore impact. Under these conditions, soil water also showed a clear patchy structure, overlapping with patterns of vegetation biomass. For low herbivore impact, soil water was higher and probably not limiting. Here, no patchy structures for this variable or overlapping patterns with vegetation biomass were found. Under these conditions, soil organic matter and NH_4-N took over as important variables for explaining total variation while spatial patterns of these variables were highly overlapping with vegetation biomass. In conclusion, although based on a snapshot in time, we think that our results support the hypothesis of Ryel et al. (1996) and Schlesinger et al. (1996).

By comparing the spatial distribution of soil nutrients in desert grasslands and shrublands, Schlesinger et al. (1996) argued that changes in the distribution of soil properties might be a useful index of overgrazing in semi-arid grasslands. Grazing and trampling creates spatial soil heterogeneity, this may lead to the invasion of grassland communities by desert shrubs, and these shrubs further localise soil fertility leading to even more soil heterogeneity. Our data indicates that the occurrence of perennial grass tufts leads to high plant-induced soil heterogeneity as well. Different functional plant groups (shrubs vs. perennial grass tufts vs. annual grasses) obviously induce different soil changes and spatial patterning. As the relative abundance of functional plant groups generally change with increasing herbivore impact, the effects of overgrazing on soil properties interact with the effects of different functional plant groups. Both factors should therefore be taken into account separately when determining the effects of overgrazing on soil heterogeneity.

Acknowledgements

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