

Link of vegetation with soil at a few metre-scale: herbaceous floristic composition and infiltrability in a Sudanian fallow-land

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Abstract – The link between vegetation and soil at a few meter-scale was studied in an old physiognomically homogeneous fallow-land (over 30 years) of anthropic Sudanian savanna with poor tree cover. Sampling was conducted systematically on a 60 m × 60 m surface, following a five-metre grid. Floristic relevés were made in quadrats (1 m × 1 m), in each corner of which infiltrability was measured by a method derived from the single-ring infiltrometer. Seventy four herbaceous species are present; the 156 relevés could be classified in seven floristic units, which have a clear link with the soil hydro-pedological characteristics at a few meter-scale. Among the 18 main species (present in at least 10 % of the 156 relevés) only four could be considered as indifferent to infiltrability, another eight preferred relatively high infiltrability microsites, and the last six preferred poor infiltrability microsites. The relatively high floristic richness of the site can be partly explained by the aptitude of various species to exploit one or another of the different microsites available. The results also suggest a certain structural and functional redundancy between species. © Elsevier, Paris

Savanna / herbaceous vegetation / small-scale heterogeneity / biodiversity / redundancy / soil infiltrability

1. INTRODUCTION

A large part of classical plant ecology studies are based on the 'homogeneous zone'¹ taken as the basic unit [4]. However, its homogeneity generally results from various smaller units which are juxtaposed and repeated. Our knowledge of this small-scale pattern is still incomplete, and it has mostly been studied using the mechanisms of species coexistence [5, 19, 22, 26, 37, 45, 48]. To what extent is this horizontal pattern determined by the physical heterogeneity of the environment, by the interactions between plants and by chance? What can its role be in the ecosystem's functional processes? In fact, few studies have been specifically devoted to the link between vegetation and

ecological factors at this scale [47]. It is well known that the soil's chemical and structural characteristics (besides being partly linked) deeply influence the savanna vegetation [2, 21]. Many studies have dealt with this problem at various scales. Regional and stationnal scales correspond to the notions of climatic area and habitat. The finer scales only retained attention more recently [18]. However, works related to soil structure [51] are fewer than those devoted to its chemistry [30, 31, 35, 39, 42, 50].

The hydric factor is one of the most important in plant ecology. Water availability is generally cited as the predominant factor which governs the savanna structure and functioning [14]. It depends above all on the climate of the considered region (yearly total and distribution of rainfall), but in a particular station, hydro-pedological features are extremely important. In fact, for a given quantity of water, the amount actually available to plants varies according to soil nature. How important the heterogeneity of soil features can be at a fine scale is still largely unknown [33]. In the present paper, we consider structural and floristic heterogeneity of the herbaceous layer of an old field savanna site, which is physiognomically homogeneous. A link is sought between vegetation and soil physical heter-

¹ The 'floristically homogeneous zone' is an intuitive concept; it qualifies a surface where:

- 1) ecological conditions are apparently uniform
- 2) one or more species are generally dominant (but sometimes there is no dominance)
- 3) floristic composition does not noticeably vary between the different parts.

Although the last criterion is the foremost one, the three reinforce each other [15, 20].

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ogeneity, through the study of its infiltrability features. This factor is of great ecological significance since soil physical characteristics affect water as well as nutrient availability through soil moisture-diffusion relationships. Diffusion of most nutrient ions is limited to the liquid phase, the diffusion rates being strongly affected by the volumetric water content of the soil. Water movement in soil is driven by water potential gradients rather than by water content gradients. However, at equal water potentials, fine-textured soils have greater volumetric water content than coarse-textured soils. The variability in texture, and therefore in moisture content, largely affects rates of nutrient diffusion, biological activity and thus heterogeneity in nutrient distribution [44].

2. MATERIAL AND METHODS

2.1 Region, study site and general sampling design

The Bondoukuy region (11° 51' N, 3° 45' W) in Burkina Faso (west Africa) belongs to the Sudanian regional center of endemism [49]; it is located at the boundary between the Sudanian woodland with abundant *Isoberlinia* and the Sudanian undifferentiated woodland. For centuries, human presence has deeply marked the region. The present main activity is cropping (cotton and cereals), partly with the ancestral practice of fallowing land but for increasingly shorter periods, and partly with regular cultivation on the best soils. The second activity is breeding cattle (mainly bovines) following an extensive system. The mosaic landscape consists of diverse cultivated areas and grazed fallow-lands. In this tropical climate consisting of one dry season followed by one four-to-five-month rainy season, the annual mean rainfall reaches 728 mm. The study site is representative of a situation very common to degraded poor shallow ferruginous soils [32], the most frequent soil type in the area. It is an homogeneous, over thirty years old, fallow, dominated by *Guiera senegalensis* and *Vitellaria paradoxa* (tree layer), *Andropogon pseudapricus*, *Loudetia togoensis*, and *Sporobolus festivus* (herbaceous layer). The tree crown cover is about 25 %. The indurated and shallow soil is sandy-silty at the surface and silty-sandy from 15 to about 40 cm depth. Presently, the study site is frequently disturbed by the strong grazing and collecting pressure from the neighbouring village. The sampling was conducted in systematic fashion over an area of 60 × 60 m (3600 m²); 156 sampling points were distributed in 12 lines of 13 points, following a 5-m grid.

2.2. Flora and vegetation structure

Floristic relevés were made at the end of October 1994, before the study of infiltrability that led to vege-

tation and soil disturbance. Since the phenological stage was then flowering or fructification, the herbaceous species had attained their maximum height. At each sampling point, a 1 m² surface, marked by a square frame lain on the soil, was studied. Each herbaceous species was given an abundance-dominance mark according to the Braun-Blanquet method. An analysis of the floristic structure was made through factor correspondence analysis on a relevés/species table [24, 29]. In each sampling unit, the average height of the herbaceous layer was easily estimated, since a few species were clearly dominant. When two layers were recognizable, the estimation was made on the top layer. The cover of the herbaceous layer cover was visually estimated using type figures, computer-calculated and drawn to minimize cover overestimation [6]. The ligneous component was less important and floristically rather poor. Ligneous species' presence - chiefly that of *G. senegalensis* individuals - was observed in the 156 sampling surfaces. A variable of value 1 in presence of ligneous species and value 0 in their absence was built up.

2.3 Infiltrability measurement and calculation

In the 156 sampling points, infiltrability was estimated between November 10-20, 1994. The test, derived from the single ring infiltrometer [1, 11], consists in measuring water volume infiltration inside a cylinder 15 cm in diameter. The result is a speed (mm per hour), which increases with infiltrability. Ring infiltrometers are harshly criticized [46] because they always give a by-excess value. There are three main reasons for this bias: i) the hydraulic charge in the ring is much higher than that provoked by rain; ii) the infiltration does not occur vertically under the ring: water migrates laterally towards the surrounding dry soil, so that the gravitational effect, compared with the capillary effect, is much higher than under natural rain; iii) in the classic method, the ring is pushed in the soil 10 cm deep to ensure waterproofness. This is an important source of soil disturbance and water can infiltrate along the ring's interior lining. In spite of all these imperfections, the ring infiltrometer method cannot be discarded when many replicates have to be rapidly done without using a lot of material and people. This method was readapted to minimize its most important defects. The main innovations consist in not pushing the ring into the soil and not working with a constant water pressure loading, but rather measuring continuously the infiltration of an 80 mm waterstrip along the ring inner wall. Measurements were made in the four corners of the square (1 m × 1 m) sampling-surface. Each replicate's location, determined in advance by a plan, was respected as strictly as possible. The vegetation inside the ring was carefully scissor-cut close to the soil, without dis-

turbing the soil surface. Waterproofness was ensured by a thick pure clay mud packed up to 5 cm around the ring by the use of a mould (a second ring, 35 cm in diameter), delicately placed. The ring was then filled with water up to 80 mm. The water height was read by the means of a little float sliding along a graduated ruler dipped into the water, since direct reading is made imprecise by the meniscus and the reflections that it provokes.

Readings were made at regular time intervals until the soil began to emerge or until the float touched the soil. If the sequence lasted more than 20 min, the test was terminated. In the opposite case, the ring was immediately refilled up to 80 mm, and a new measurement began and so on, until we obtained at least 20 min of consecutive measuring. The four replicates were considered either separately (geostatistical study), or together, to give a value which characterizes the sampling surface. For each replicate, we first calculated a collection of triplets I_h^t , where I is the infiltration speed taken under a load h at a time t spent since filling up the cylinder. This data processing is not intended to set a physical model to determine soil intrinsic characteristics, since the infiltration speed is not measured with great precision and an important number of experimental conditions also remain unknown. We simply seek to homogenize the data, by eliminating the most significant variations due to experimental conditions. The highest variation is a function of the hydraulic load

In a first approach, we consider that, for each 80 mm water height penetrating the soil, the infiltration speed is proportional to the load and we calculate I_{20}^t by linear interpolation of I in function of h . After two consecutive sequences having produced the value $I_{20}^{t_1}$ and $I_{20}^{t_2}$ respectively, with $t_1 < 30 \text{ min} < t_2$, one interpolates linearly in function of time the final value I_{20}^{30} used as the test result. If only one measurement was available, we used the only value I_{20}^t as the test result. When the values did not correspond to a simple infil-

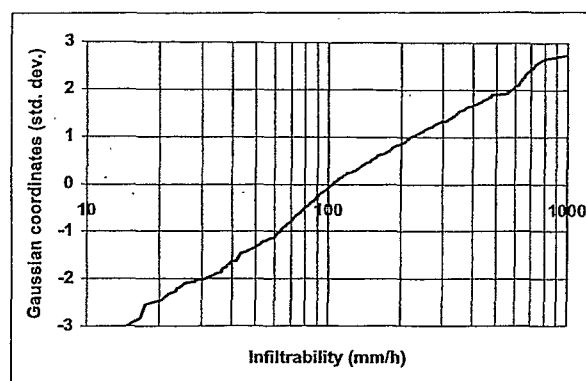
tration speed model proportional to the hydraulic charge and decreasing in time, the lowest infiltration speed of a 20 mm-water height was used as the result. These various interpolations permit the elimination of experimental conditions (at least partly) and supply results that can be compared with each other.

3. RESULTS

3.1. Infiltrability

The statistical characteristics of the 624 (156×4) replicates population are the following: the mean is $148 \text{ mm}\cdot\text{h}^{-1}$, the median is $105 \text{ mm}\cdot\text{h}^{-1}$, minimum and maximum are 13 and $1\,722 \text{ mm}\cdot\text{h}^{-1}$, respectively, and the 1st and 3rd quartile are 73 and $174 \text{ mm}\cdot\text{h}^{-1}$, respectively. The dissymmetrical distribution is shown in the form of a Henry graph: infiltrability is given in logarithmic coordinates on the X axis, the Y axis gives the experimental cumulate frequencies, expressed in Gaussian coordinates (figure 1). In such a graph, a log-normal distribution appears as a line, its abscissa at the 0 ordinate corresponds to the expectancy, and the steeper the slope the smaller the standard deviation. The in-depth analysis of the distribution is not detailed here, but the graph allows the adoption of a log-normal law as a first approximation. Let us simply notice that the variance is high and not constant: the measurements which correspond to the extreme values are less precise than those close to the median. A geostatistical analysis [35, 36, for applications in ecology] has been carried out on $\log I_{20}^{30}$. The results show that the studied variable is spatially structured with a spherical variogram, and has a range of 10 m. This result validates the sampling pattern used for the study, and allows the grouping of the four replicates in one unique value, calculated as e^M , where M is the median of the four replicates of $\log I_{20}^{30}$. This value has the dimension of an infiltration rate and is expressed in $\text{mm}\cdot\text{h}^{-1}$.

Figure 1. Henry graph showing the distribution of the infiltrabilities observed in a fallow-land site on indurated ferruginous soil (Bondoukuy, Burkina Faso).



3.2. Herbaceous flora and vegetation structure

3.2.1. Floristic richness and composition

Seventy four herbaceous species were observed in the study zone, with a mean specific richness of 7 species per sampling unit. The majority of the species (43 %) belong to the Poaceae family, 30 % to that of Papilionaceae, and 27 % to various other families (e.g. Rubiaceae, Compositae, Tiliaceae, Scrophulariaceae). Four species are found in more than 50 % of the relevés, often with coefficients of more than 1 or 2: *A. pseudapricus* (Poaceae), *S. festivus* (Poaceae), *Spermacoce stachydea* (Rubiaceae) and *L. togoensis* (Poaceae). Three other species are found in more than 25 % of the relevés: *Microchloa indica* (Poaceae), *Pennisetum pedicellatum* (Poaceae) and *Cassia mimosoides* (Caesalpiniaceae). The other species, about three quarters of the total number, are on the contrary present in less than 10 % of the relevés. The dominance of the four most abundant herbaceous exerts also at a very local scale. Inside each sampling surface (and inside the groups of relevés forming the floristic units described below), two or three of these species are always much more abundant than the others. The ligneous layer, less diverse with only a dozen species, is strongly dominated by *V. paradoxa* and chiefly by *G. senegalensis*.

3.2.2. Floristic units, cover and height


The correspondence factor analysis was applied to a relevés/herbaceous species table, where only the 37 species present in less than 90 % and more than 10 % of the relevés were taken into consideration. The eigen values of the first three axes are 0.4731, 0.3249, and 0.3848 and their contributions to the total inertia 9.1 %, 6.3 %, and 5.9 % (i.e. 21.3 %), respectively, which is acceptable for floristic data. Five variables (species) mainly contributed to the CFA axes constitution: they are by order of importance, the grasses *L. togoensis*, *P. pedicellatum*, *A. fastigiatus* and *M. indica*, and the Rubiaceae *Mitracarpus scaber*; 144 relevés out of 156 could be classified into seven different floristic units (table I and figure 2). The average cover of the herbaceous vegetation is rather high (71 ± 22 %) and relatively homogeneous (average variation coefficient on the mean of 31 %). Taken at the end of October, this cover reveals maximum herbaceous vegetation development in the year. Ranked according to increasing average cover, the seven floristic units appear as follows: IV (51 %), VI (59 %), III (62 %), I (73 %), VII (74 %), V (74 %), II (75 %). However, as can be seen through the comparison of averages (10 % limit unilateral test t [43]), the seven units show little cover difference (table II). Floristic unit IV, with the poorest cover, is completely different

Table I. Mean abundance-dominance coefficients of the main species in the seven floristic units defined on the basis of a correspondence analysis on herbaceous species/relevés table (156 × 37).


FLORISTIC UNIT / number of sampling points	I 23	II 18	III 9	IV 17	V 15	VI 12	VII 23
<i>Andropogon pseudapricus</i>	1.9 (0.9)	2.9 (1.0)	2.9 (1.0)	2.0 (1.0)	1.2 (0.8)	2.2 (0.9)	1.8 (0.9)
<i>Loudezia togoensis</i>	0.1 (0.1)	0.4 (0.3)	0.7 (0.4)	2.0 (0.9)	3.3 (1.0)	1.8 (0.8)	3.0 (0.9)
<i>Pennisetum pedicellatum</i>	1.3 (0.9)	0.4 (0.5)	0.1 (0.2)	0.1 (0.2)	0.3 (0.2)	0.2 (0.3)	0.1 (0.2)
<i>Andropogon fastigiatus</i>	0.7 (0.5)	0.1 (0.1)	0.1 (0.1)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)
<i>Microchloa indica</i>	0.3 (0.1)	0.4 (0.4)	1.1 (0.8)	0.2 (0.2)	0.0 (0.0)	0.7 (0.7)	0.3 (0.3)
<i>Mitracarpus scaber</i>	0.1 (0.1)	0.2 (0.4)	0.1 (0.1)	0.3 (0.7)	0.1 (0.2)	0.1 (0.2)	0.0 (0.0)
<i>Sporobolus festivus</i>	1.0 (0.7)	2.3 (0.9)	2.3 (0.9)	1.7 (0.9)	1.4 (1.0)	1.8 (1.0)	2.0 (0.9)
<i>Spermacoce stachydea</i>	0.3 (0.3)	0.7 (0.8)	0.5 (0.6)	0.6 (0.8)	0.7 (0.8)	0.6 (0.8)	0.1 (0.7)
<i>Cassia mimosoides</i>	0.3 (0.4)	0.2 (0.4)	0.2 (0.3)	0.1 (0.2)	0.3 (0.6)	0.2 (0.4)	0.1 (0.2)
<i>Setaria pallide-fusca</i>	0.1 (0.2)	0.1 (0.2)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)
<i>Stylochiton lancifolius</i>	0.1 (0.3)	0.1 (0.2)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.2)	0.1 (0.2)
<i>Indigofera stenophylla</i>	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.2)	0.1 (0.2)	0.1 (0.2)	0.1 (0.1)
<i>Biophytum umbraculum</i>	0.1 (0.3)	0.2 (0.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)
<i>Schwenckia americana</i>	0.2 (0.1)	0.2 (0.2)	0.1 (0.1)	0.1 (0.1)	0.2 (0.2)	0.1 (0.1)	0.1 (0.1)
<i>Cyperus rotundus</i>	0.3 (0.4)	0.1 (0.1)	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)
<i>Indigofera trichopoda</i>	0.1 (0.1)	0.2 (0.4)	0.1 (0.2)	0.1 (0.3)	0.1 (0.2)	0.0 (0.0)	0.1 (0.1)


Figured values correspond to the mean abundance-dominance coefficient of Braun-Blanquet (+ considered as 0.5); in brackets: the frequency of the species; in bold: the dominant of each unit. Species names: in bold the five species having strongly contributed to defining the first three axes of correspondence analysis.


1 m² sampling plots :

Infiltration :  1 replication at each corner of the plot.

Vegetation :  floristic group

 not classified

 : , sampling points for infiltrability

 1-7 floristic group of the vegetation sampling point


 0, sampling point which could not be classified

Figure 2. Spatial pattern of infiltrability and floristic groups.

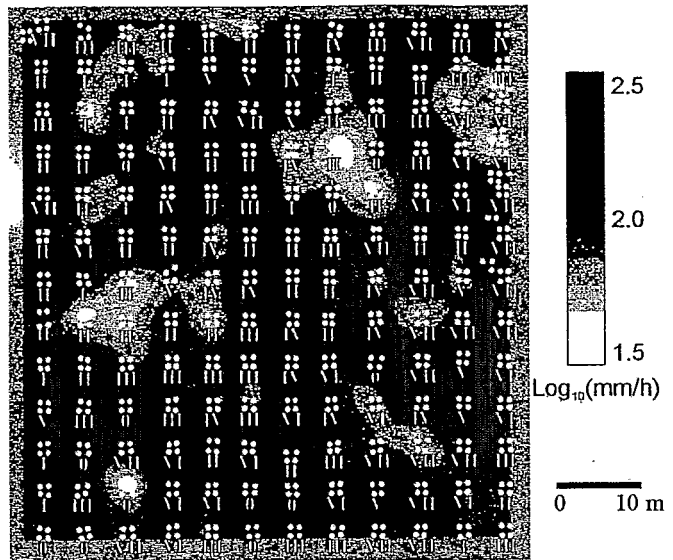


Table II. Cover means comparison between the seven herbaceous floristic units (unilateral *t*-test, limit 10 %).

	IV	VI	III	I	VII	V	II
IV	-						
VI	*	-					
III	NS	NS	-				
I	*	*	NS	-			
VII	*	*	NS	NS	-		
V	*	NS	NS	NS	NS	-	
II	*	*	*	NS	NS	NS	-

NS: non-significant difference
*: significant difference

from all the others, while unit VI is quite different. The mean height of the herbaceous cover is 141 + 49 cm and rather homogeneous (variation coefficient 35 %). Ranked according to increasing mean values of height, the floristic units come in the following order: IV (101 cm), VI (136 cm), VII (142 cm), II (148 cm), V (149 cm), I (155 cm), III (164 cm). However, the seven floristic units show little height difference (means comparison through a *t*-test, table III). Floristic unit IV, with the lowest mean height, distinguishes itself from all the others. Unit III, with the tallest mean height, is also different from most of the others.

3.2.3. Presence of ligneous plants and floristic units

Among the 156 unit areas, only 26 contain ligneous plants - mostly *G. senegalensis*. For each floristic unit,

Table III. Height means comparison between the seven herbaceous floristic units (unilateral *t*-test, limit 10 %).

	IV	VI	VII	II	V	I	III
IV	-						
VI	*	-					
VII	*	NS	-				
II	*	NS	NS	-			
V	*	*	NS	NS	-		
I	*	NS	NS	NS	NS	-	
III	*	*	*	NS	NS	NS	-

NS: non-significant difference
*: significant difference

the ratio of the relevés containing ligneous plants was calculated. Ranked according to increasing ligneous plants presence, they come in the following order: I, II, VII, V, IV, III, VI. Compared through a Chi square test with a continuity correction factor [43], only units I and VI differ from each other (table IV). So, at this scale, herbaceous and ligneous vegetation appear independent.

3.3 Infiltrability and vegetation

3.3.1. Presence of ligneous plants, herbaceous layer cover and height

The mean infiltrability of the 26 relevés with ligneous plants was compared with that of the 130 without ligneous plants through a unilateral *t*-test. The

Table IV. Ligneous presence proportions comparison between the seven floristic units (Chi square test with continuity correction factor, limit of 10 %).

	I	II	VII	V	IV	III	VI
I	-						
II	NS	-					
VII	NS	NS	-				
V	NS	NS	NS	-			
IV	NS	NS	NS	NS	-		
III	NS	NS	NS	NS	NS	-	
VI	*	NS	NS	NS	NS	NS	-

NS: non-significant difference
*: significant difference

Table V. Infiltrability means comparison between five cover classes (unilateral *t*-test, limit of 10 %).

	C1	C2	C3	C4	C5
C1	-				
C2	*	-			
C3	*	NS	-		
C4	*	NS	NS	-	
C5	NS	NS	NS	NS	-

NS: non-significant difference
*: significant difference

Table VI. Infiltrability means comparison between five height classes (*t*-test, limit of 10 %).

	H1	H2	H3	H4	H5
H1	-				
H2	NS	-			
H3	NS	NS	-		
H4	*	NS	NS	-	
H5	NS	NS	NS	NS	-

NS: non-significant difference
*: significant difference

values (153.7 ± 98.1 and 117.1 ± 56.38) differ in a significant way at the limit of 5 %. The presence of ligneous plant is clearly linked with higher infiltrabilities. Five classes with balanced number of relevés were created for the cover variable, and their mean infiltrabilities calculated (ordered by increasing values: 156.8, 118.1, 103.2, 119.0 and 118.0). On a 10 % limit *t*-test criterion, only the poorest cover class (class 1) differs from the others, with a higher mean infiltrability (table V). The two variables are weakly correlated. Five classes, with balanced number of relevés, were also created for the height variable, with

Table VII. Infiltrability means comparison between the floristic seven units (unilateral *t*-test, limit of 10 %).

FLORISTIC UNIT	VII	I	II	V	III	IV	VI
VII	-						
I	NS	-					
II	NS	NS	-				
V	*	*	NS	-			
III	*	*	*	*	-		
IV	*	*	*	*	NS	-	
VI	*	*	*	*	NS	NS	-

NS: non-significant difference
*: significant difference

their mean infiltrabilities calculated (ordered by increasing values: 136, 121, 117, 115, 118). On a 10 % limit *t*-test criterion, only classes 1 and 4 differ from each other (table VI). These two variables do not seem correlated either.

3.3.2. Herbaceous floristic units and species

The infiltrability means of the seven floristic units, classified by increasing order in table VII, were compared with each other. The floristic units III, IV and VI correspond to a higher infiltrability than the floristic units I, II, V and VII. The group with poorer infiltrability can be subdivided again: units VII and I correspond to a higher infiltrability than unit V, unit II is intermediate. So, five units have a clear indicator value: units I (dominated by *A. pseudapricus*, *P. pedicellatum* and *S. festivus*) and VII (dominated by *A. pseudapricus*, *L. togoensis* and *S. festivus*) correspond to the poorest values, units III (dominated by *A. pseudapricus*, *M. indica* and *S. festivus*), IV (dominated by *A. pseudapricus*, *L. togoensis* and *S. festivus*), and VI (dominated by *L. togoensis*, *S. festivus* and *A. pseudapricus*) correspond to the highest infiltrability values. The floristic heterogeneity we observed is clearly linked to the soil's hydropedological characteristics, that is to abiotic factors. The mean infiltrability of points where the main species are present was compared with that of points where the same species are absent (Student's *t*-test). Only the 18 species with a frequency of more than 10 % (or at least 16 presences among the 156 relevés) were taken into account (table VIII). Since the *t*-test probabilities show a break between 11.5 and 14.5 %, the means similitude limit was fixed at a 12 % level instead of the usual 10 % level (unilateral *t*-test). Only four species can be considered as indifferent to infiltrability. Most species are sensitive to the hydropedological characteristics of the substratum. Eight of them prefer relatively high infiltrability and six relatively low infiltrability

Table VIII. Herbaceous plants sensitiveness to infiltrability: *t*-test probabilities when the sampling surface infiltrability means are compared between the relevés where a species is present and the relevés where it is absent.

SPECIES	Probability (unilateral <i>t</i> -test %)	
<i>Spermacoce radiata</i>	44.1 %	
<i>Andropogon pseudapricus</i>	39.5 %	UNSENSITIVE
<i>Hackelochloa granulata</i>	20.9 %	
<i>Mitracarpus villosus</i>	14.5 %	
<i>Cassia mimosoides</i>	11.5 %	
<i>Loudetia togoensis</i>	10.3 %	
<i>Andropogon fastigiatus</i>	10.1 %	
<i>Sporobolus festinus</i>	8.9 %	
<i>Brachiaria distichophylla</i>	7.8 %	
<i>Indigofera stenophylla</i>	5.0 %	SENSITIVE
<i>Schwenckia americana</i>	3.3 %	
<i>Biophytum umbraculum</i>	2.8 %	
<i>Spermacoce stachydea</i>	2.3 %	
<i>Microchloa indica</i>	2.2 %	
<i>Cyperus rotundus</i>	0.9 %	
<i>Indigofera trichopoda</i>	0.2 %	
<i>Bulbostylis abortiva</i>	0.1 %	
<i>Pennisetum pedicellatum</i>	0.0 %	

Table IX. Sampling surfaces infiltrability mean values where a species is present and where it is absent: data relative to the fourteen herbaceous species which are the most sensitive to this factor (Bondoukuy, Burkina Faso).

INFILTRABILITY SPECIES	MEAN AND STANDARD ERROR	
	absent	present
<i>Cyperus rotundus</i>	118.4 ± 63.4	168.5 ± 78.9
<i>Pennisetum pedicellatum</i>	104.8 ± 43.7	161.1 ± 86.3
<i>Indigofera trichopoda</i>	117.4 ± 67.6	151.3 ± 52.0
<i>Indigofera stenophylla</i>	120.0 ± 66.2	145.2 ± 64.1
<i>Schwenckia americana</i>	119.7 ± 67.3	143.9 ± 56.9
<i>Cassia mimosoides</i>	118.3 ± 58.5	133.4 ± 79.6
<i>Spermacoce stachydea</i>	110.4 ± 42.3	129.1 ± 74.1
<i>Sporobolus festinus</i>	110.3 ± 37.7	124.8 ± 68.8
<i>Loudetia togoensis</i>	130.8 ± 80.4	116.9 ± 51.2
<i>Andropogon fastigiatus</i>	124.4 ± 68.7	111.8 ± 30.1
<i>Brachiaria distichophylla</i>	125.9 ± 70.1	111.3 ± 44.6
<i>Microchloa indica</i>	131.3 ± 73.1	111.1 ± 52.5
<i>Biophytum umbraculum</i>	125.2 ± 68.8	106.2 ± 32.7
<i>Bulbostylis abortiva</i>	129.1 ± 70.7	104.4 ± 45.3

(table IX). The mean infiltrabilities of the relevés where the sensitive species are present were compared afterward two by two through a unilateral *t*-test at limit of 10 % (table X). Three different groups of species appeared: the high and poor-infiltrability-preferring

species are clearly and totally different from each other, but there exists an intermediate group. *Cyperus rotundus*, *P. pedicellatum* and *Indigofera trichopoda* are very clearly linked to high infiltrabilities (table IX), followed by *I. stenophylla* and *Schwenckia*

Table X. Infiltrability means comparison between the sampling surfaces where a species is present and those where it is absent for the fourteen herbaceous species the most sensitive to this factor (unilateral *t*-test, limit of 10 %).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Group 1, low infiltrability														
1	<i>Cyperus rotundus</i>	-												
2	<i>Pennisetum pedicellatum</i>	NS	-											
3	<i>Indigofera trichopoda</i>	NS	NS	NS										
4	<i>Indigofera stenophylla</i>	NS	NS		-									
5	<i>Schwenckia americana</i>	NS	NS	NS	NS	-								
6	<i>Cassia mimosoides</i>	NS	*	NS	NS	NS	-							
Group 2, medium infiltrability														
7	<i>Spermacoce stachydea</i>	*	*	*	NS	NS	NS	-						
8	<i>Sporobolus festivus</i>	*	*	*	NS	NS	NS	NS	-					
9	<i>Andropogon fastigiatus</i>	*	*	*	*	*	NS	NS	NS	-				
Group 3 : high infiltrability														
10	<i>Biophytum umbraculum</i>	*	*	*	*	*	NS	NS	NS	NS	-			
11	<i>Brachiaria distichophylla</i>	*	*	*	*	*	NS	NS	NS	NS	NS	-		
12	<i>Loudetia togoensis</i>	*	*	*	*	*	NS	NS	NS	NS	NS	NS	-	
13	<i>Bulbostylis abortiva</i>	*	*	*	*	*	*	*	*	NS	NS	NS	NS	-
14	<i>Microchloa indica</i>	*	*	*	*	*	*	*	*	NS	NS	NS	NS	NS

NS : non-significant difference

* : significant difference

americana. The species clearly linked to poor infiltrabilities are *Bulbostylis abortiva*, *Biophytum umbraculum* and *M. indica*, followed by *Brachiaria distichophylla*, *Andropogon fastigiatus* and *L. togoensis*. Among the seven most abundant species, four prefer the microsites with relatively high infiltrability, two prefer the microsites with low infiltrability and one is indifferent.

4. DISCUSSION

4.1. Floristic richness and specific structure

The species particularly abundant in the study site are generally considered as linked to rather variable situations of disturbance and degradation: impoverished (and sometimes easily flooded), eroded, crusted skeletal, gravelly or overgrazed soils [3, 28, 34, 40]. The Sudanian savanna tree *V. paradoxa* is very common, except on easily flooded soils. Its dominance in sparse ligneous vegetation is a sign of cultivation; in fact this useful indigenous species is preserved during the clearing. The small *G. senegalensis* (Combretaceae) is very common in Burkina Faso's drier areas, but in the Sudanian zone, its abundance is considered a sign of overgrazing.

With 74 herbaceous species, the flora of the study site seems particularly rich. In fact, Devineau and Fournier [10] evaluated the homogeneous zone mean

richness between Bondoukuy and the Mouhoun river to only some twenty species, all types of vegetation included, from the young fallow-lands to uncultivated zones and from the most degraded environments to the best regenerated ones. For under six years old fallow-lands (younger than the study site), Hien [23] gave a mean estimate of 41 herbaceous species. The specific richness of our study site is similar to that of the Nazinga Game Ranch less anthropic Sudanian savannas studied by Fournier [12] in Burkina Faso with an average of 60 species. At the square meter scale, the richness is the same as in Nazinga where it reaches about 8 species [10, 12]. The high floristic richness of this anthropic site seems consistent with the scheme given by Grime [16, 17], where the maximum richness appears in mean stress and disturbance situations. While the high floristic richness of the site is unquestionable, it is difficult however to accept that it is really three times higher than other sites in the area. The difference partly results from the species registration methods employed. In the present study, systematic and careful relevés were made in previously delimited surfaces. In the other two studies, the list was established by walking through the whole 'homogeneous zone' and observing the species, which is quicker but certainly less accurate. Besides, for Hien's data [23], which were gathered between June and August, the relevés' seasonal period can come into consideration. But this is irrelevant for Devineau and

Fournier's data [10] gathered almost during the same period of the year (October). The taxonomic spectrum of the herbaceous vegetation of the study site slightly differs from that of most of the fallow-lands of the region. Papilionaceae, which generally never exceed 15 % [10, 23], are more numerous here. This feature of Sudanian savannas is often considered as representing a grazing degradation [7]. In fact this old fallow-land site on a shallow soil, near a village, is subjected to strong anthropic forces, especially to cattle grazing. One could also think that many species of this family, scarce and scattered, are often not listed in the botanical relevés less minutely conducted than the systematic ones applied here. The dominance of some grass species, as observed here, is usual in herbaceous vegetation [17, 18]. Such a specific structure, dominated by grasses, has already been described in Sudanian savannas [10, 12, 13].

4.2. Link between vegetation and soil heterogeneity

In the studied old fallow site, a small-scale spatial pattern has been revealed through independent methods. First, statistical analysis of the floristic data identified seven distinct floristic units with a few-metre pattern (figure 2). Secondly, the geostatistical analysis revealed patches of different soil infiltrability at about a ten-metre scale. Both types of heterogeneity are clearly linked: most of the floristic units correspond to a given range of infiltrability values. Moreover, the majority of the individual species is also distributed in relation to soil infiltrability. So, following the classic idea of ecological niche differentiation, one could think that species diversity can be partly explained by their specialization in exploiting different types of microsites and in sharing the environment. It is however unclear if the soil heterogeneity is the consequence or the cause of the vegetation pattern, since they undoubtedly positively interact. This point has already been stressed by several authors [2, 5, 44]. Let us examine the observed lognormal distributions of infiltrability: the method employed here gave the same type of distribution as in all preceding studies. This dissymmetrical distribution means that the factors capable of generating porosity in the soil are many. In a just abandoned field, poorly covered by vegetation with relatively few living organisms, porosity is low, with little variability in space, and is essentially due to the exclusive soil components mechanical assemblage [6]. The soil is compact and filters little. Later, when the soil is better covered by vegetation, as in our study site, the number of living organisms (roots, bacteria, earthworms, termites, ants, nematodes) increase the porosity and the heterogeneity. They mix the soil, and reorganize its components and hence contribute to maintaining a good infiltrability. Their positive interaction leads to the

emergence of fine-grain contrasts, even in a zone previously as homogeneous as an old field can be. It is well known that during secondary succession, the increasing cover of the vegetation and the related soil fauna enrichment develop simultaneously in a coalescent way around cores. The positive interaction between soil and living beings may generate or exaggerate local contrasts and lead to small-scale patterns such as those observed in the present study site. In Sudanese fallow-lands of Burkina Faso, a progressive 'improvement' of soil texture, and an increase of its heterogeneity, was described by de Blic and Somé [9]. It takes place at a very local scale, under individual grass tufts, through the succession of postcultural species. It clearly suggests a positive interaction between organisms and soil with increasing heterogeneity of the soil. So the number of interacting sources of porosity can generate the lognormal infiltrability distributions observed in our study site. In this hypothesis, the observed patches could be, to a large extent, the result of the activity of living organisms, rather than that of a pre-existing abiotic substrate heterogeneity. However, additional observations are necessary to specify how the pattern is generated, and if the localization of patches is permanent.

Our study shows that the herbaceous layer's height and cover, both relatively homogeneous, have little relation to either the floristic unit or the soil's infiltrability. The independence of height from floristic units and soil infiltrability should not be surprising since height estimates are based on the top layer. In fact the annual tall species *A. pseudapricus* and *L. togoensis* are often dominant, separately or together, whatever the specific structure. They have rather similar growth habit but differ in their soil infiltrability preferences as previously seen. However, the independence of cover and infiltrability needs to be more carefully considered, since it is usually accepted that a good herbaceous cover protects the soil against raindrop impact, and by doing so, limits soil surface encrusting and preserves its infiltrability [6]. In fact, in savannas, crusts develop early in the rainy season, when the soil is still poorly covered by vegetation. Unlike Sahelian regions where the growth period is shorter, the cover progressively establishes between May and September-October, with noticeable growth timing differences among species. So, the protective effect of the herbaceous cover is certainly more related to the rapidity of plant cover establishment than to its maximum level reached later in the season. The observed independence between the composition of the herbaceous layer and the presence of ligneous plants has also to be explained. We know there is a vertical sharing of the topsoil between herbs and trees (see references in [12]), trees having their roots distributed somewhat deeper (around 40 cm) than herbs (up to 30 cm). At the beginning of the rainy season when herbaceous

species germinate and establish (thus constituting assemblages described here as floristic groups), the water they can use is contained in the very upper layer of the soil. During the same period, trees have already been growing for several weeks, using the water they can find in the deeper soil layer. In fact during this period there is no or little interference between roots of either life forms.

4.3. Potential role of plant diversity

What can be the potential role of the observed plant diversity and patchiness in the functioning of the old field vegetation? Clearly, the function to consider here is producing herbaceous plant material per surface unit as efficiently as possible given the local constraints of the environment. In this respect, all the herbaceous species of our study site are redundant in their roles, any given species being able to replace another. This represents a first level of redundancy. However, the primary production function is fulfilled through a sharing of space (and resources) between different species, which seem to have specialized in exploiting a certain type of soil. This specialization represents a lower level of organization, where a certain redundancy is also visible. The grasses *A. pseudapricus* and *L. togoensis* are both tall and very abundant and supply the environmental physical structure for the whole herbaceous layer: they are structural species in the sense of Huston [27]. As primary producers, such structural species play a first rank role. Both of them have almost the same habit and the same growth features; they are found separately or together in the 1 m² sampling units. While *A. pseudapricus* seems indifferent to the soil infiltrability gradient (at least according to the studied site range of values), *L. togoensis* distribution clearly follows it (with a link to rather low infiltrability). This pattern can be interpreted as a redundancy in the spatial sharing of the environment at the local scale with an overlap between species; but since the habitat breadth of *A. pseudapricus* is larger than that of *L. togoensis*, the redundancy is only partial. The subordinate *A. fastigiatus* has also the same habit and growth features, but its range of preferred infiltrability values is slightly lower than that of *L. togoensis*. If more arid conditions would temporarily or permanently prevail, we can hypothesize that *A. fastigiatus* could become dominant and replace as main producer one or both of the other species, without noticeable change in the structure and functioning of the ecosystem. Other abundant species with similar habit seem specialized in exploiting different microsites. *M. indica* and *S. festivus* are both tufted short grasses reaching maturity in August, the former is annual in our area and the latter perennial. The first prefers microsites with rather poor infiltrability. Seghier et al. [41] already noticed that it was

more tolerant to water stress than *L. togoensis*. The second prefers microsites with rather high infiltrability. So, their function could be the same, but in different microsites. Mutual replacement could occur in the case of a change in environmental conditions. Most of the less abundant and smaller studied species also follow the soil infiltrability gradient. While their role is unclear, they could represent a pool of plants able to become dominant should climatic or other environmental conditions alter.

One notices that species which have similar preferences for infiltrability often differ from each other in morphological and developmental features. The four dominant and high infiltrability species have different life forms or different heights. *P. pedicellatum*, a rather tall annual graminoid, reaches maturity in September; *S. festivus*, a rather short perennial graminoid, reaches maturity in August; *S. stachydea*, a mean-height annual forb, reaches maturity in September and *C. mimosoides*, a mean height annual forb, reaches maturity in August or September. The two poor infiltrability-dominant species are annual graminoids: the tall *L. togoensis* reaches maturity in September and the shorter *M. indica* reaches maturity in August. These differences and other observations support the idea of temporal sharing. In fact, a preliminary morphological study showed a rather large diversity in the plants' root system: deep and taprooting (mostly forbs), rather fasciculate and superficial (mostly graminoids), and combined. Such morphological variation is usually understood to be a specialization in exploiting certain types of microsites or a different plasticity in the mode of exploiting the environment [18]. The preference of species for high or poor infiltrability sites should then be linked to their different abilities in exploiting resources in space and time. When plants germinate and establish at the beginning of the rainy season, availability of water and other resources are determining factors in Sudanian regions with contrasted climate. During this period, the various microsites obviously offer different environments. Hence, plant characteristics related to germination and early growth may also play an important role in spatial sharing. In a study of a Mediterranean herbaceous vegetation, Olsvig-Whittaker et al. [36] observed a strong seasonal trend in the environmental data which suggests the importance of timing in resource availability in such environments. The complexity of the organization revealed here, with regard to infiltrability, would certainly confirm this hypothesis if other factors were considered (infiltrability may be linked to many characteristics of the soil such as pH, texture and chemical richness). In fact, resource heterogeneity (i.e., microsite differentiation) seems generally very important on a small-scale. This pattern observed in a Mediterranean herbaceous vegetation by Olsvig-Whittaker et al. [36] was correlated with several environmental factors

(litter cover, soil salinity, nitrate level and soil moisture). Other factors, not considered here such as grazing, may also affect generation of the complex patterns observed. Many authors (e.g. [8]) believe that grazing pressure is a major determinant of biodiversity pattern because herbivores modify the competitive relations between species, suppressing certain species (sometimes to extinction) but allowing the ingress of grazing tolerant or avoided species. In conclusion, at the level of the whole herb layer, the functional redundancy of species regarding primary producer function is obvious. At a lower level of organization, there clearly exists a spatial and temporal sharing among species related to specialization. But this sharing and specialization seem incomplete and the idea of redundancy resurfaces.

5. CONCLUSION

Our study confirms the well known importance of hydro-pedological phenomena in determining the savanna vegetation structure, and highlights its rarely studied influence at a few metres-scale. However, the link observed here is obviously not a passive one: porosity and vegetation evolve and develop together. Moreover, their positive interaction probably generates (or exaggerates pre-existing) local contrasts such as those observed in the present study site, heterogeneity being to a large extent the result of the activity of living organisms. The small-scale pattern revealed by our study, where microsite differentiation plays a significant part in the vegetation structure, can thus be considered as the visible result of the interaction between plant and soil. A spatial sharing of environment between species or groups of species is obvious: it probably explains the high specific diversity of the herbaceous layer in this poor soil environment. This sharing may allow optimal use of resources and therefore, optimal productivity, but the results suggest also a structural and functional redundancy between species, the function of which could be to provide the system with resilience to respond to unpredictable perturbations.

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