

Soil seed bank and vegetation dynamics in Sahelian fallows; the impact of past cropping and current grazing treatments

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Abstract: The soil seed bank in a 5-y-old Sahelian fallow was studied through seed extraction and compared with germinations recorded either in controlled conditions, *ex situ* in a glasshouse, or in the field. The influence of phosphorus fertilizer and mulch application during the preceding crop period, and that of seasonal grazing regimes applied the last 2 y of fallowing, were assessed on the composition of the seed stock. *Cenium elegans*, *Fimbristylis hispida*, *Merremia pinnata* and *Phyllanthus pentandrus* accounted together for 75% of extracted seeds, 72% of *ex situ*, and 62% of *in situ* seedlings. Mulch treatment was correlated with the first axis of the canonical correspondence analyses performed on the seedling datasets. Mulch and phosphorus fertilizer treatments held similar responses, as they both favoured the seed bank of erect dicotyledons such as *P. pentandrus* and *Cassia mimosoides*. On the whole, the effects of grazing remained modest compared with the residual effects of past crop management practices. However, seedling densities increased as a result of dry-season grazing, while the soil seed bank decreased with wet-season grazing. Grazing also reduced the spatial heterogeneity of the seed bank rather than the overall number of species.

Key Words: annual plants, fallow, grazing, mulching, phosphorus fertilizer, rangelands, Sahel, seed bank, spatial heterogeneity, vegetation dynamics

INTRODUCTION

Sahelian semi-arid ecosystems spread over 6000 km from east to west and 400–600 km from north to south, in the south of the Sahara desert, between the 200 and 600 mm isohyets. Scattered shrubs, among which many *Acacia* and *Combretum* species, and a herbaceous layer, dominated by annual plants, characterize the vegetation of Sahelian rangelands and fallows. Annuals establish every wet season from seeds, which have to retain their viability through the long dry season (October to June). Annuals are favoured by: (1) the extreme dryness of the air during the arid dry season, that limits the role of perennials (Hiernaux 2001), (2) the regularity of the seasonal pattern of rainfall, that ensures yearly development of annuals. Most of them germinate with the first rains and the density of resulting seedlings depends on the density of viable seeds in the soil and on the competition between seedlings for resources driven by the soil moisture

regime, which is in turn a function of the early wet-season distribution of rainfall and redistribution by run-off (Cissé 1986, Hiernaux *et al.* 1994). Then, further plant growth and seed production are also controlled by the rainfall distribution and run-off during the rest of the wet season, which vary greatly in space and between years. As a result, floristic composition and productivity of rangelands may change greatly from year to year (Bremen & Cissé 1977). These spectacular changes come in support of the non-equilibrium model of vegetation dynamics (Behnke & Scoones 1993, Westoby *et al.* 1989) that denies significant impact of management, especially grazing, on vegetation dynamics (Ellis & Swift 1988). Besides, pastoral and agro-pastoral systems value this fluctuating resource by grazing cattle, sheep, goats and camels opportunistically under communal management (Graef & Haigis 2001). This implies livestock mobility and results in high spatial and temporal variation in grazing pressure which are thought to attenuate the impact of grazing on the herbage productivity and species composition through decoupling livestock and range resources (Hiernaux 2000). Studies have described the

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Table 1. Outline of the four experimental treatments in the 16 selected plots.

Plots	A4	A9	B12	C1	C7	D1	D3	D12	E3	E6	E12	F8	F9	G6	G11	H5
CR ¹	0	1	0	1	0	0	1	1	1	0	0	1	1	1	0	0
SSp ²	0	0	0	0	1	1	0	1	0	0	1	1	1	1	0	1
DSG ³	1	0	0	1	0	1	1	0	1	1	0	0	0	1	0	1
WSG ⁴	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0

¹ CR: Crop Residues broadcast from 1991 to 1996, 0: without, 1: 2000 kg CR ha⁻¹.

² SSp: Single Superphosphate broadcast from 1991 to 1996, 0: without, 1: 13 kg SSp ha⁻¹.

³ DSG: Dry-Season Grazing from 1999 to 2002, 0: without, 1: 0.25 Tropical Livestock Unit ha⁻¹.

⁴ WSG: Wet-Season Grazing from 2000 to 2002, 0: without, 1: 0.25 Tropical Livestock Unit ha⁻¹.

impact of past cropping practices and successive grazing treatments on the fallow vegetation (Fournier *et al.* 2000, Gérard *et al.* 2001, van de Koppel *et al.* 1997), but not related them to the composition of the soil seed bank. The objective is thus to analyse the dynamics of Sahelian annual vegetation by assessing the influence of past crop and current grazing management on the soil seed bank and seedling population in a 5-y-old fallow. Three hypotheses that follow the non-equilibrium model are tested on the composition of the seed bank and seedling populations: (1) the residual effects of mulching with millet stalks and of applying phosphorus fertilizer, performed when the field was cropped, are not significant after 5 y of fallow; (2) the effects of 2 y of seasonal grazing at moderate stocking rate are not significant on species composition nor (3) on the spatial heterogeneity (beta diversity).

STUDY SITE

The study was conducted at the ICRISAT Research Centre, located 45 km south of Niamey in the south-west of Niger (13°15'N, 2°18'E). The climate is semi-arid tropical with a long dry season from October to late May alternating with a 4-mo wet season. If the rainy season is highly predictable on a regional scale, the rainfall pattern is erratic both spatially and temporally on local scales (Lebel *et al.* 1997). The spatio-temporal pattern and volume of the first rains influence germination, favouring some species to the detriment of others (Breman *et al.* 1982, Cissé 1986). On average from 1982 to 1992, the mean annual rainfall at Icrisat-Sadoré was 560 mm (Sivakumar *et al.* 1993), providing 100 growing days (Warren *et al.* 2001). The average monthly minimum and maximum temperatures are 16 and 42 °C. Soil of the Research Centre has been described as 'psammentic Paleustalf, sandy, siliceous, isohyperthermic' in the USDA system (West *et al.* 1984); they are very sandy (92–98%), poor in organic compounds, acid (pH 4.5–5), and poor in nutrients with concentrations of 2.8 mg kg⁻¹ for P_{bray}, 2.3 g kg⁻¹ for C_{org}, and 5 mg kg⁻¹ for N_{min}. (Gérard *et al.* 2001). Water infiltration is fast (Kumar *et al.* 2002) facilitating rapid germination and plant growth. Put to fallow in 1982, a

1-ha field was cleared in 1991 to conduct a millet crop experiment aimed at measuring the effect of combined application of crop residue and phosphorus fertilizer on the pearl-millet yield under a factorial design with 96 plots of 10 × 10 m (see Buerkert *et al.* 1996). In 1997, the field was turned into fallow that remains protected from external interventions such as grazing, logging and burning. Then, four different cattle grazing treatments initiated in the dry season of 2000 have been applied (dry season alone, wet season alone, combined wet and dry, and protection from grazing) to each quarter of the field. Stocking rates applied in wet and in dry season were 0.25 Tropical Livestock Unit (TLU) ha⁻¹. For this study, 16 plots were sampled, four in each grazing treatment block selected in the more contrasting past agronomic treatments combining: 0 or 2000 kg ha⁻¹ mulch of millet stalks, 0 or 13 kg P ha⁻¹ of broadcast simple super-phosphate. Unfortunately, a sampling error impeded perfect factorial arrangement (Table 1).

METHODS

Data collection

In each of the 16 plots, soil seed banks were sampled in eight quadrats (1 m²) systematically placed along the diagonals of the plot. In each quadrat, soil was sub-sampled over either 20 × 20 cm (germinations) or 10 × 10 cm (extracted seeds) by 2 cm deep. The soil seed bank was investigated in three different ways: (1) Counting seeds extracted from soil sample (128 samples of 10 × 10 × 2 cm) in two steps: first by sieving (1 mm), then extracting by flotation of the residue in a glucose solution (1.2 g cm⁻³) later filtered, seeds being counted on the filter extract using a binocular microscope, (2) pot germination *ex situ* in glasshouse (128 samples of 20 × 20 × 2 cm) at 35 °C, watered every 3 d from 30 April to 19 July with two 12-d dry spells (30 May–10 June; 26 June–8 July) to optimize the germination of some species (Héroult & Hiernaux 2003), (3) *in situ* monitoring of seedlings (128 couples of 20 × 20 cm quadrats) with observation after each rainfall from 2 July 2001 to

26 July 2001. Counted seedlings (2 and 3) were removed to avoid double counts. In a complementary experiment (plots B12 and D12), soil was sampled at three depths (0–2, 2–4, 4–6 cm) to estimate the vertical distribution of the seed bank. Plant nomenclature follows Hutchinson & Dalziel (1954–1972).

Statistical analyses

To avoid risks of 'pseudo-replication' (Hurlbert 1984) the sampling units considered in statistical analysis were not the quadrats within plots but their sum.

Canonical correspondence analyses

Canonical correspondence analysis (CCA) was used to assess how much of the variation of the seed bank composition could be explained by the interaction between the past cropping and the current grazing treatments. Simultaneous ordinations of plots and treatments were performed using seed or seedling densities per species and plot (ter Braak 1986). Treatments were converted into dummy variables and plot scores are linear combinations of variables (Palmer 1993). The ratio of the inertia of CCA over the inertia of a correspondence analysis, called multivariate squared correlation (MSC), provides an evaluation of the quality of the model (Sabatier *et al.* 1989). MSC value was compared with the expected value, under the null hypothesis (no relationship between seed or seedling densities and treatments), which is equal to the ratio of the number of independent variables over that of independent samples (Lebreton *et al.* 1991). CCAs were performed using Pc-Ord (McCune & Mefford 1999).

Analyses of variance

Influences of grazing and past cropping treatments were assessed by performing analyses of variance (General Linear Model procedure) using the software Statistica. Only one interaction term exhibited significance and was retained in the model:

$$\text{Response} = \text{DSG} + \text{WSG} + \text{CR} + \text{SSp} + \text{DSG} \times \text{WSG} + \varepsilon$$

With: DSG = Dry season grazing; WSG = Wet season grazing; CR = Crop residue application; SSp = Phosphorus application; ε = residual term.

Analyses of variance were performed separately on the number of species and on the total number of seeds or seedlings by plot, as well as on seed and seedling densities for graminoids, legumes and other dicotyledons or for groups based on seed maximum length (following Bille

1972): small-sized seeds (< 1 mm), medium-sized seeds (1–2 mm), large-sized seeds (> 2 mm).

Heterogeneity assessment

The heterogeneity or beta diversity of the species composition was calculated between plots within each grazing treatment block using Detrended Correspondence Analysis (DCA), performed with Pc-Ord (McCune & Mefford 1999). Beta diversity was calculated as the length of the gradient on the first axis of the DCA for the four plots within each grazing block (Hill 1979).

RESULTS

Composition of the seed bank

Fifty-seven species were observed at least once with one of the three methods. Only species recorded more than four times on average per plot were retained in Table 2. Four species: *Ctenium elegans*, *Fimbristylis hispidula*, *Merremia pinnata* and *Phyllanthus pentandrus* predominated, accounting together for 75%, 72% and 69% of the overall extracted seeds, germinations *ex situ* and *in situ* respectively. *Phyllanthus pentandrus* dominated the extracted seeds while *C. elegans* dominated the seedling densities. Annuals provided most of the seeds and seedlings, *Aristida sieberiana* being the only perennial present. About 90% of the extracted seeds occurred in the upper 2 cm of the soil. *Ex situ* germinations were less concentrated on the surface with on average 73%, 12% and 15% of the seedlings at respectively 0–2, 2–4 and 4–6 cm.

Ordinations

The eigenvalues of the first axis of the three CCAs were markedly higher than those of the following axes (Table 3) indicating that the first axis contributed chiefly to explain species composition. For extracted seeds, the first axis was strongly correlated with dry-season grazing ($r = 0.865$) and the second axis with wet-season grazing ($r = 0.882$) (Figure 1). The MSC explained 36.8% of the variation compared to the null hypothesis value of 25% (Table 3). For the germinations *in* and *ex situ*, the spatial arrangement of explanatory variables and plots was more structured than for seeds with 52 and 49% of the variance explained by the first two axes and MSC reaching 50%. The first axis was strongly correlated with mulching ($r = -0.914$ for *ex situ* and $r = -0.939$ for *in situ*). For *ex situ* germinations, the second and third axes were slightly correlated with dry-season grazing ($r = -0.677$ and $r = 0.730$ respectively). For *in situ* germinations,

Table 2. Mean densities (\pm SD) of the extracted seeds (top 2 cm) and of the seedlings *in-* and *ex situ*.

	Extracted seed bank (seeds m ⁻²)	<i>Ex situ</i> germination (seedlings m ⁻²)	<i>In situ</i> germination (seedlings m ⁻²)
Graminoids			
<i>Aristida sieberiana</i>	–	21 \pm 25	–
<i>Ctenium elegans</i>	814 \pm 923	898 \pm 717	302 \pm 293
<i>Digitaria gayana</i>	112 \pm 112	42 \pm 77	19 \pm 20
<i>Eragrostis tremula</i>	–	40 \pm 27	11 \pm 11
<i>Fimbristylis hispidula</i>	1041 \pm 1612	130 \pm 124	122 \pm 120
Legumes			
<i>Alysicarpus ovalifolius</i>	60 \pm 101	34 \pm 33	25 \pm 27
<i>Cassia mimosoides</i>	202 \pm 296	188 \pm 143	19 \pm 21
<i>Indigofera strobilifera</i>	–	–	7 \pm 6
<i>Tephrosia gracilipes</i>	–	–	9 \pm 31
<i>Zornia glochidiata</i>	350 \pm 1146	17 \pm 48	–
Non-legume dicotyledons			
<i>Ceratotherca sesanoides</i>	222 \pm 331	74 \pm 88	14 \pm 16
<i>Gisekia pharnacoides</i>	–	–	18 \pm 35
<i>Hibiscus</i> spp.	172 \pm 139	43 \pm 46	41 \pm 35
<i>Jacquemontia tannifolia</i>	103 \pm 130	28 \pm 31	21 \pm 28
<i>Merremia pinnata</i>	1295 \pm 0789	125 \pm 101	76 \pm 79
<i>Mitracarpus scaber</i>	98 \pm 129	54 \pm 81	7 \pm 8
<i>Phyllanthus pentandrus</i>	1880 \pm 2110	507 \pm 344	166 \pm 107
<i>Waltheria indica</i>	52 \pm 101	–	27 \pm 31
Other species	248 \pm 569	92 \pm 171	80 \pm 119
Total	6648 \pm 3859	2291 \pm 0603	963 \pm 345

Table 3. Results of the Canonical Correspondence Analyses: effects of current grazing and past agricultural treatments on the extracted seed bank, germinations *ex situ* and *in situ*.

Analysis	Inertia ¹	Axis 1 ²	Axis 2 ²	Axis 3 ²	MSC ³
Extracted seed bank					
CA	1.026				
CCA	0.378	26.8	6.1	3.9	36.8
Germinations <i>ex situ</i>					
CA	0.848				
CCA	0.481	40.9	11.1	4.7	56.7
Germinations <i>in situ</i>					
CA	0.975				
CCA	0.525	38.4	11.0	4.3	53.9

¹ Inertia = sum of eigenvalues.

² % contribution to inertia.

³ MSC = (inertia of CCA/inertia of CA) \times 100; it provides an indication of the proportion of the variance accounted for.

the second axis was correlated with dry-season grazing ($r = -0.826$), whereas the third was tied to wet-season grazing ($r = 0.841$).

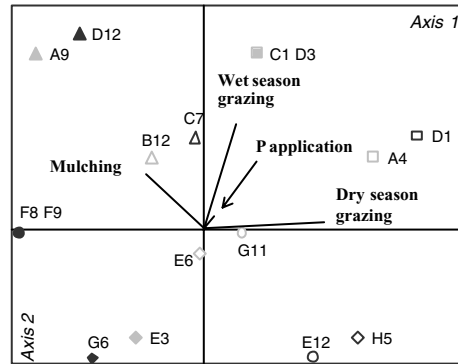
Extracted seeds

Thirteen species had more than 4 seeds per plot on average, and *P. pentandrus* seeds were the most abundant with 1880 seeds m⁻² (Table 2). Dry-season grazing did not influence the abundance of seeds per species group, nor the number of species (Table 4). Wet-season grazing

led to a decrease of seed densities, especially those of non-legume dicotyledons. These trends were explained by density changes of a few species, mostly by the drop of *P. pentandrus* and *Hibiscus* spp. (*H. asper* plus *H. sabdariffa*) seeds. Crop residue application decreased markedly the density of all graminoids; this was mainly due to a reduction in *C. elegans*. Conversely, non-legume dicotyledons benefited from it. While the number of species diminished following crop residue application, it increased strongly following the application of fertilizer that enhanced the seed bank of dicotyledons and large-seeded annuals.

Ex situ germinations

Fourteen species had more than 4 seedlings per plot on average, and *C. elegans* was the most abundant with 898 seedlings m⁻² (Table 2). In general, the responses of species groups to grazing treatments were weak, while the residual effect of past cropping treatments led to contrasting effects (Table 4). Wet-season grazing increased the germination density of grasses such as *C. elegans*, while the drop of *C. mimosoides* germinations explained the decrease of legumes. Crop residue application resulted in a strong density drop in graminoids, mostly *C. elegans* and *F. hispidula*, and an increase of all dicotyledons. *Fimbristylis hispidula* also explained the drop among small-seeded species.



(a) Extracted seed bank

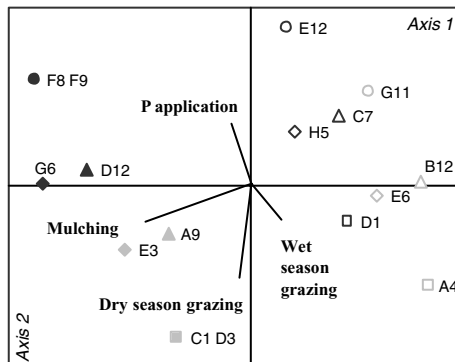
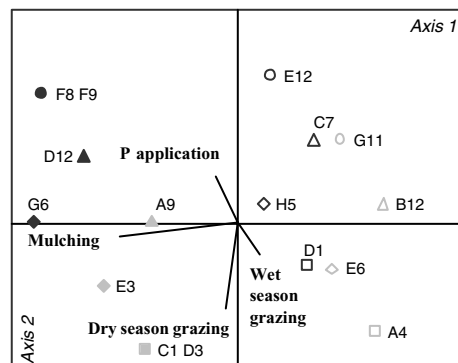
(b) Germinations *ex situ*(c) Germinations *in situ*

Figure 1. Canonical Correspondence Analyses of the effects of past agricultural and current grazing treatments on (a) seed bank composition, germinations (b) *ex situ* and (c) *in situ*. Labels and symbols refer respectively to plots (Table 1) and treatments (●: without grazing; ▲: wet-season grazing; ◆: dry-season grazing; ■: year-round grazing; empty symbols: without mulching; filled symbols: mulching; grey symbols: without phosphorus application; black symbols: phosphorus application).

Dicotyledon densities were greatest on plots fertilized in the past.

In situ germinations

Sixteen species had more than 4 seedlings per plot on average and *C. elegans* was the most abundant

with 302 seedlings m^{-2} (Table 2). Dry-season grazing enhanced the seedling density of several dicotyledons, and consequently, the total seedling density (Table 4). It also enhanced the number of species. Seedlings responded less to wet-season grazing and interaction between wet- and dry-season grazing was only significant for *Hibiscus* spp. seedlings, which decreased substantially when grazed in both seasons. The density of graminoid seedlings decreased whereas that of non-legume dicotyledons was enhanced following mulching, mostly because of changes in *C. elegans* and *P. pentandrus*. The decrease of *C. elegans*, *Digitaria gayana* and *Eragrostis tremula* densities also explained the response of graminoids to past fertilization while the seedling density of several dicotyledons was enhanced.

Vegetation heterogeneity and grazing treatments

The beta diversities of species composition calculated for the seed bank and seedling populations were highest in the ungrazed block (Table 5). The length of the gradient along the first axis of a DCA performed on the extracted seed dataset was shorter under grazing and shortest for wet-season grazing. For *ex situ* and *in situ* germinations, beta diversity was the lowest under year-round grazing and intermediate under single-season grazing. Globally, grazing tended to homogenize seed bank composition between plots.

DISCUSSION

Soil seed bank and seedling populations

Observations on the vertical distribution of the seed bank confirmed literature reports that the majority of seeds are located in the topsoil (Carrière 1989, O'Connor & Pickett 1992). The wider vertical spread of *ex situ* germinations is less significant as some of the seeds from deep layers that germinated when the soil layer was laid on the surface of a pot would not have germinated *in situ* either because of the unfavourable biotic environment created by the seedlings germinating earlier from the upper layer of soil (Inouye 1980) or because they would fail to reach the soil surface (Schafer & Chilcote 1969).

The average seed density was relatively low compared with other data on Sahelian fallow and rangeland vegetation (Bille 1977, Carrière 1989, Gaston 1976). Direct counting of extracted seeds overestimates seed densities because it includes inviable diaspores (Gross 1990). Even if the mechanisms of dormancy are not known for all Sahelian species (Elberse & Breman 1989), dormancy is generally broken at the end of the dry season (Granier & Cabanis 1974, Miège & Tchoumé 1963) and

Table 4. The least-square means of extracted seed bank densities (seeds m⁻²), of *ex situ* seedling densities (seedlings m⁻²), and of *in situ* seedling densities (seedlings m⁻²) in total and per species groups, and that of species number, resulting from the variance analysis performed with the model: Dependent variable = DSG + WSG + CR + SSp + DSG × WSG + ε.

	Dry-season grazing DSG (0.25 TLU ha ⁻¹)			Wet-season grazing WSG (0.25 TLU ha ⁻¹)			Crop residue application CR (2000 kg ha ⁻¹)			Phosphorus application SSp (13 kg P ha ⁻¹)		
	without	with	P	without	with	P	without	with	P	without	with	P
<i>Extracted seed bank</i>												
Total seed number	7269	6028	ns	8226	5070	*	7427	5870	ns	4791	8506	***
Graminoids	2361	1574	ns	1975	1959	ns	3566	369	***	1917	2017	ns
Legumes	902	322	ns	992	231	ns	780	444	ns	153	1070	*
Other dicotyledons	3708	3936	ns	4981	2663	**	2742	4902	***	2505	5139	***
Small-sized seeds	1441	839	ns	1408	872	ns	1997	283	*	717	1562	ns
Medium-sized seeds	4358	4766	ns	4194	4930	ns	4194	4930	ns	3750	5373	ns
Large-sized seeds	536	291	ns	602	225	ns	342	484	ns	142	684	*
Species number	7.03	6.20	ns	6.05	7.19	*	7.06	6.17	*	6.04	7.20	**
<i>Ex situ seedlings</i>												
Total seedling number	2076	2507	ns	2236	2347	ns	2631	1952	**	2343	2240	ns
Graminoids	980	1304	ns	915	1369	*	1818	466	***	1387	897	ns
Legumes	229	249	ns	316	161	*	159	318	***	178	300	*
Other dicotyledons	778	915	ns	945	748	ns	571	1122	***	732	961	*
Small-sized seeds	237	209	ns	269	177	ns	357	89	**	188	258	ns
Medium-sized seeds	1588	2110	*	1777	1921	ns	2038	1660	ns	1959	1739	ns
Large-sized seeds	78	78	ns	72	84	ns	71	84	ns	53	103	*
Species number	9.08	9.48	ns	9.37	9.19	ns	9.47	9.09	ns	9.06	9.50	ns
<i>In situ seedlings</i>												
Total seedling number	830	1147	**	909	908	ns	1226	750	***	1053	923	ns
Graminoids	408	543	ns	392	559	ns	833	117	***	596	354	**
Legumes	46	73	ns	61	58	ns	46	72	ns	54	65	ns
Other dicotyledons	331	497	***	414	414	ns	308	519	***	370	458	ns
Small-sized seeds	96	83	ns	84	95	ns	162	17	***	106	73	*
Medium-sized seeds	326	513	*	400	439	ns	496	343	*	459	379	ns
Large-sized seeds	51	29	ns	44	37	ns	34	47	ns	19	61	*
Species number	9.25	10.12	**	9.84	9.53	ns	10.08	9.30	ns	9.48	9.89	ns

ns P > 0.05; * 0.01 < P < 0.05; ** 0.001 < P < 0.01; *** P < 0.001.

Table 5. Changes in beta diversity* with regard to the variables dry-season grazing and wet-season grazing.

	Length of the gradient		
	Extracted seed bank	Germination <i>ex situ</i>	Germination <i>in situ</i>
Without any grazing	2.30	1.68	2.50
Dry-season grazing	1.92	1.44	1.63
Wet-season grazing	1.60	1.54	1.66
Dry + Wet-season Grazing	1.67	1.28	1.52

* Beta diversity estimation is based on the first axis scores of a Detrended Correspondence Analysis (Standard Deviation units along the first axis).

would thus only explain a portion of the discrepancy between seed stock and *ex situ* seedling densities. The discrepancy between *ex situ* and *in situ* germination densities may be explained by the loss of seedlings due to herbivores (insects, rodents, lizards) just prior to counting, or due to failed germinations because of insufficient soil water availability (Elberse & Breman 1990). Indeed in the field, the topsoil layer dries out very quickly after a rain event, because of wind and of direct insolation,

while continuously wet substrate and constant relative air humidity were artificially maintained under glasshouse.

The low proportion of grass seeds and seedlings could result from the grasshopper outbreak in 1998 which specifically eradicated grass seedlings (Hiernaux 1998). Common weeds in millet fields such as *E. tremula*, *Mitracarpus scaber* and *Jacquemontia tamnifolia* contributed little to the seed bank. Indeed, to persist in a crop field, weeds must have some germinations late enough to occur after weeding as has been observed for *E. tremula* (Héroult & Hiernaux 2003). As the fallow gets older, late germination becomes disadvantageous due to the intense competition from early germinating species. In this particular field, *P. pentandrus* was the dominant weed in 1996, the last year of cropping (Gérard *et al.* 2001), and in 1997. It was still abundant in 1998, but was not recorded as dominant in any of the plots from 1999 onwards. Still in 2001, *P. pentandrus* contributed to 28.3, 22.1 and 17.2% of the seed, *ex situ* and *in situ* seedling densities respectively. This large seed stock was thus likely established in the early years of fallow if not during the cropping period. A fraction of its soil seed bank would

thus be less transient than thought from the high rates of germination observed with most species (Carrière 1989, Elberse & Breman 1989).

Influence of cropping practices

The effect of mulching on crop yields, even applied in limited amount such as 500 kg dry matter ha⁻¹, is recognized by Sahelian farmers and has been measured by agronomists (Bationo & Mokwunye 1991, Sterk & Spaan 1997). In this particular field, application of millet stalks as mulch increased millet yields, lessened soil deflation by wind, and prevented soil surface crusting (Buerkert *et al.* 1997). These differences in soil surface features are still visible after 5 y of fallowing. Measures of the vegetation biomass and composition during the first 3 y of fallowing demonstrated that the residual effect of past mulching prevailed over the residual effect of fertilisation (Gérard *et al.* 2001). Yields on past-mulched plots were twice those of non-mulched plots, and species composition was dominated by dicotyledons such as *P. pentandrus*, *H. sabdariffa*, *C. mimosoides* and *Ceratotherca sesamoides*. The soil seed banks sampled 2 y later for this study still reflect this trend. The protocol does not permit us to separate the effects of changes of soil properties from the carry-over effect through the soil seed bank (supposing a limited radius of dispersion for most seeds), nor from the indirect effect due to the higher herbage mass on the plots mulched, which in turn produces more litter and thus, perpetuates the mulch treatment. However, passed mulching comes in first to explain the differences in seed and seedling densities between plots for species groups, as demonstrated by the analyses of variances (Table 4), or for vegetation communities, as demonstrated by its leading contribution to the first axis of the three CCAs.

Broadcast application of 13 kg P ha⁻¹ of phosphate fertilizer explained an average increase in yield by 96% of the millet cropped in 1995 and 1996 in that field (Muehlig-Versen *et al.* 1998). The residual effect of this fertilizer 2 y after crop abandonment still explained a 14% increase of standing matter yield of the fallow (Gérard *et al.* 2001). In 2001, the residual effect of the fertilizer was still perceptible (Table 4) although difficult to separate from that of mulch, as they are similarly oriented. Anyway, residual effects of mulch and fertilizer invalidate hypothesis 1.

Influence of the grazing treatments

Globally, the effects of grazing on both soil seed bank and seedling establishment were modest compared with the residual effect of soil amendments as indicated by the lower rank of the grazing variables in explaining

CCA axis. Thus, hypothesis 2 is partly invalidated. However, the density of *in situ* seedlings and the number of germinating species increased as a result of dry-season grazing, while seed density in the topsoil was not affected. The increase in density of seedlings could thus result from trampling that triggered seed germination (Granier & Cabanis 1974) either because it removed seed dormancy by physically altering the seedcoats, or because it improved the conditions for germination by breaking the soil surface crust (Hiernaux *et al.* 1999) and thus enhancing water infiltration (Casenave & Valentin 1992). Wet-season grazing decreased seed densities confirming the observations by Grouzis (1992) in other Sahelian rangelands. Moreover, wet-season grazing increased the species richness of the extracted seed bank. This conflicts with the report of higher species richness with protection from grazing observed by Hiernaux (1998). However, the size of the sample used for seeds and seedlings is much smaller than those used to assess plant communities, and the stocking rate applied in the trial was low enough to create more micro-habitats than to level them out. Globally, wet-season grazing had less influence than had dry-season grazing as indicated by the CCA outputs in which dry-season grazing always associates with the second axis whereas wet-season grazing only associates with the third axis for *in situ* seedlings. Besides, grazing reduced the heterogeneity of seed and seedling composition between plots (Table 5). This argues against hypothesis 3 and extends the effect of grazing observed on herbaceous communities (Hiernaux 1995) to soil seed banks and seedling populations.

Conclusions

The inferences made in the discussion on, for example, the processes of the grazing and trampling effects, remain hypothetical. However, the assessment of the soil seed bank demonstrated the persistence of the influence of past crop management, and that of seasonal grazing, not only on species composition, but also on its spatial distribution with a homogenizing effect of grazing. Further research could aim to monitor and model inter-annual changes in soil seed bank during the whole fallow period. Indeed, previous studies have called attention to dramatic year-to-year fluctuations in productivity, and species composition of the Sahelian rangelands and fallows (Breman & Cissé 1977) reflecting interplays between short-life cycles, diversity in seed dispersal and germination properties (Héroult & Hiernaux 2003), and unpredictable rainfall pattern within the rainy season. This behaviour conforms to the non-equilibrium model of vegetation dynamics. However, contrary to what is expected from that model, this study demonstrated that the species composition was also determined by agricultural management, with

the residual effect of extensive crop management and moderate grazing treatments, both having a consistent impact on the composition of the soil seed bank and on resulting seedling populations.

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