



# Comparison of aboveground vegetation and soil seed bank composition at sites of different grazing intensity around a savanna-woodland watering point in West Africa

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## Abstract

Grazing removes a plant's aboveground vegetative and reproductive tissues and can modify the soil seed bank, potentially impacting the restoration of preferred species. Knowledge about aboveground vegetation and species composition of soil seed bank and the processes that contribute to vegetation recovery on and surrounding watering points subjected to grazing is lacking. Successful restoration strategies hinge on addressing these knowledge gaps. We assessed the effects of livestock grazing on aboveground vegetation and soil seed bank characteristics along a river bank and surrounding areas subject to different grazing intensities and draw implications for restoration. Plots (50 × 50 m) were established along five transects representing differing levels of grazing intensity. Soil samples were taken from three layers within each plot to determine soil properties and species composition of soil seed bank using the seedling emergence method. Heavy grazing resulted in the disappearance of perennial grasses, a reduction in species diversity and a decrease in soil nutrients with increased soil depth. Overall, the similarity between the extant aboveground vegetation and flora within the soil seed bank was low. The soil seed bank was dominated by herbaceous species and two woody species, suggesting that many woody species are not accumulating in the soil. With increasing soil depth, the seed density and richness declined. Canonical correspondence analyses (CCAs) showed that emerged seedlings from the soil seed bank were significantly influenced by soil carbon, organic matter, total nitrogen, total potassium and soil cation exchange capacity. This finding suggests that current grazing practices have a negative impact on the vegetation surrounding watering points; hence there is a need for improved grazing management strategies and vegetation restoration in these areas. The soil seed bank alone cannot restore degraded river banks; active transfer of propagules from adjacent undisturbed forest areas is essential.

**Keywords** Ecosystem disturbance · Grazing intensity · Restoration · Seed density · Semi-arid ecosystem · Vegetation and soil degradation

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## Introduction

Riparian environments in arid and semi-arid areas experience different forms of soil and vegetation degradation and this threatens the livelihoods of millions of people (Holmes et al. 2008; Jansen et al. 2007). This degradation can be attributed to many factors including climate change (Fuhlen-dorf et al. 2001), but overgrazing is thought to play a major role (Allsopp et al. 2007; Strauch et al. 2009). Increasing grazing pressure beyond a certain threshold often leads to irreversible effects on the integrity of fragile riparian ecosystems. Changes in species richness and diversity, and vegetation structure are common responses to increased grazing pressure (Eldridge and Whitford 2009). Impacts of grazing on the aboveground vegetation community involve

the removal of plant parts from groundcover vegetation, shrubs and saplings, and damage through trampling. This may lead to erosion, local disappearances of forage species, and changes in species functional groups (James et al. 1999).

Water points are concentrators in grazed areas, drawing in large numbers of domestic and wild animals, especially during the dry season. This creates gradients of vegetation and soil degradation in the surrounding landscape (Manthey and Peper 2010). Vegetation trampling and associated ecosystem degradation generally decrease exponentially outwards from the water points (Eldridge and Whitford 2009). These changes to vegetation create an ecological phenomenon named the “piosphere” effect (Todd 2006). The “piosphere” is the zone of ecological impact focused around livestock watering points, and it provides a good context for studying livestock impacts on soil and vegetation (Andrew 1988; Lian et al. 2015; Thrash 2000). Grazing pressure over increasing distances from watering points may induce changes in the availability of propagules (soil seed bank, seed rain, and seedling, sapling and re-sprouting banks) and regeneration characteristics of the vegetation, and this can affect the composition, abundance and spatial distribution of the above-ground vegetation.

The soil seed bank comprises all viable seeds present on or in the soil and associated surface litter, and is considered crucial for the persistence of many species of flora following ecosystem disturbance (Fenner and Thompson 2005). The soil seed bank density, persistence and viability are important for driving ecosystem regeneration, particularly for ecosystems subject to regular disturbances (Bakker et al. 2005; Qian et al. 2016; Savadogo et al. 2017). A ‘healthy’ soil seed bank, in which all of an ecosystem’s flora are adequately represented, is vital for the conservation of individual species as well as plant communities (Fisher et al. 2009).

Evidence of grazing impacts on the size, richness and composition of soil seed banks is contradictory (Kinloch and Friedel 2005a). The effect can be strongly shaped by the historical grazing intensity, and by the species-specific sensitivity to this disturbance. Some studies have suggested positive responses of seed abundance to grazing (Navie et al. 1996), while others have found neutral effects (Kinucan and Smeins 1992; Meissner and Facelli 1999) or negative responses with increasing grazing pressure (Bertiller 1996). Grazing can affect seed production through the direct consumption of flowers and immature seeds or by reducing a plant’s ability to produce seeds (Hoshino et al. 2009; Sternberg et al. 2003). Thus, seed numbers of palatable species such as perennial grasses and legumes decrease in the soil seed bank at the benefit of annual weeds or ruderal species (Bertiller 1996). Also, weeds are spread by the movement of stock, either in their faeces or by attachment to the animal and these species can modify vegetation in areas of high grazing intensity close to watering points. Structural changes in the

environment associated with grazing-induced degradation due to the trampling may lead to changes in the prevailing micro-environmental conditions which prevent germination. This may reduce the number or quality of favorable micro-sites available to retain seeds (Kinloch and Friedel 2005b), thereby decreasing the possibilities of their incorporation into the soil seed bank.

In Burkina Faso, most savanna-woodlands are legally or illegally grazed (Savadogo 2009). These ecosystems are characterized by a lack of rivers and other surface water during the dry season. The Mouhoun River is Burkina Faso’s only permanent river, running through some of the country’s forests and protected areas. Its banks are often the most productive parts of the landscape, supporting a higher quality and more diverse forage than surrounding areas. In the dry seasons, stock are attracted to the cooler microclimates that characterize the river bank areas and may spend extended periods grazing or loafing in the shade (Savadogo 2009). These effects of presence of the grazers are exacerbated during drought years, when water becomes scarce. The uncontrolled access of an increasing number of livestock onto river bank areas can degrade the vegetation, increase erosion, change the floral communities by way of preferential grazing, and lead to invasion by exotic weeds. Over time, such disturbances can lead to extended bare patches and a shift in species composition from predominantly palatable perennials towards unpalatable annuals. Today, the observed reduced vegetation cover, particularly that of perennial grasses, strongly affects hydrological processes such as by increasing runoff and soil erosion (Savadogo 2009). Together these processes are assumed to lessen the capacity of the system to maintain a soil seed bank suitable for vegetation regeneration. Therefore, to inform management decisions about the conservation and restoration of biodiversity along river banks, research attention should be paid to understanding the potential of soil seed banks to contribute to the regeneration of plant cover following disturbance. An evaluation of the spatial pattern of buried viable seeds is of practical importance in conservation as it can provide an indication of the recovery potential and turnover of seeds (Solomon et al. 2006). In West Africa, many studies on the impacts of grazing on savanna-woodland dynamics are restricted to the aboveground vegetation community (Savadogo et al. 2008; Scheiter and Savadogo 2016); little is documented about grazing impacts on the diversity of the soil seed bank and its relation to the aboveground vegetation (Savadogo et al. 2017), particularly surrounding watering points where the vegetation is becoming increasingly degraded.

This study was undertaken to generate knowledge to support the restoration of degraded river banks and associated riparian areas in West African savanna-woodlands. Specific objectives were to: (1) evaluate the influence of grazing

intensity on river bank species compositions and vegetation structure, (2) determine the effects of grazing intensity on the soil seed bank, (3) better understand the relationship between the soil seed bank and aboveground vegetation, and (4) evaluate the river bank vegetation restoration potential based on the soil seed bank. We assessed the aboveground vegetation and compared this with the emergence of seedlings from soil samples taken at different depths from sites representing five different levels of grazing intensity. Relationships between the aboveground vegetation and soil seed bank and possible sources of dissimilarity in seedling emergence are discussed. The paper concludes by pointing to actionable implications for river bank restoration.

## Materials and methods

### Site description

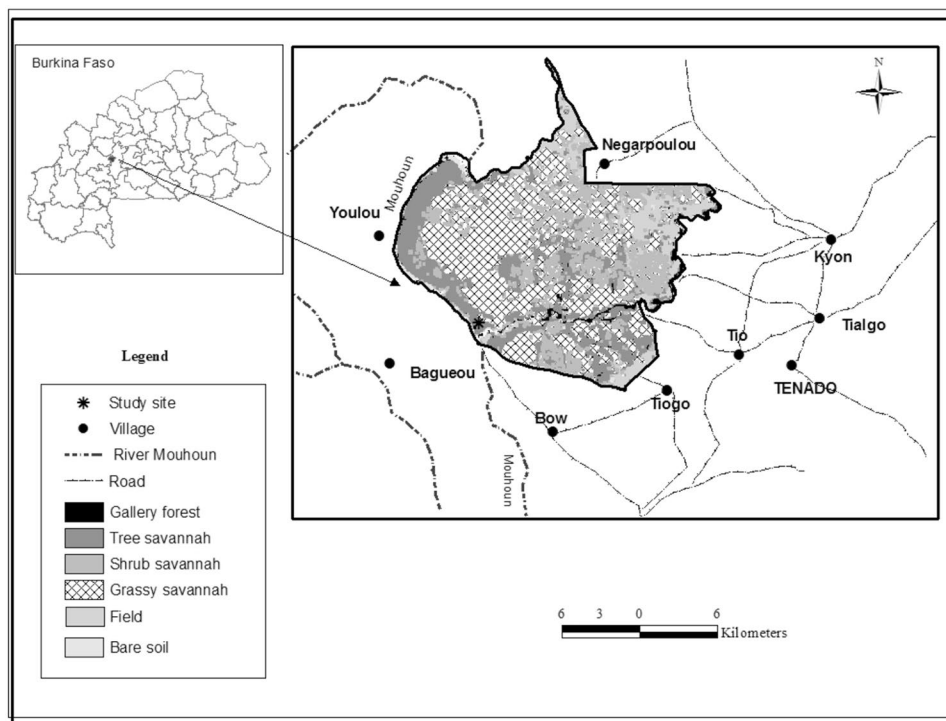
The study site is in Tiogo State Forest (SF) Reserve (12°13'N, 2°42'W, 300 m.a.s.l.) in Burkina Faso, West Africa (Fig. 1). Tiogo SF covers 30,000 ha and borders the Mouhoun River along its western boundary. The site has a unimodal rainy season, which lasts for about 6 months each year from May to October. The mean annual rainfall for the last decade was  $862 \pm 121$  mm and the number of rainy days per annum was  $64 \pm 8$ . Mean daily minimum and maximum temperatures ranged from 16 to 32 °C in January (the coldest month) and from 26 to 40 °C in April (the hottest month).

The most frequently encountered soils along the Mouhoun River are lateritic or hydromorphic. Gallery forest occurs along the floodplains and the tree species are mainly evergreen. The most common tree species are *Mitragyna inermis* (Willd.) K. Schum., *Vitex chrysocarpa* Planch., *Syzygium guineense* Guill. & Perr., *Acacia seyal* Delile, *Pterocarpus santalinoides* L'Hér. Ex DC. and *Acacia polyacantha* Willd (Savadogo et al. 2007b), while the main grass species is *Vetiveria nigriflora* Stapf.

### Experimental design

The experimental area comprised a zone along the Mouhoun River bank that is frequently grazed by cattle, sheep and goats. The site was selected based on information gathered from local agro-pastoralists and corroborated with preliminary field observations. Transects were placed along the watering point (Mouhoun River bank), to evaluate grazing intensity on soil seed bank and aboveground vegetation. Survey plots were installed along five parallel straight-line transects set at right angles from the river bank with each transect representing a different level of grazing pressure (Fig. 2). It was assumed that grazing pressure decreases as one moves away from the river. Also, since livestock gather around the watering-points to rest and drink, we expected to find that seeds were frequently transported to the area in the immediate vicinity of the watering-point, hence some seeds produced by plants further away might be dispersed, deposited closer to watering-points and finally become

Fig. 1 Study site location

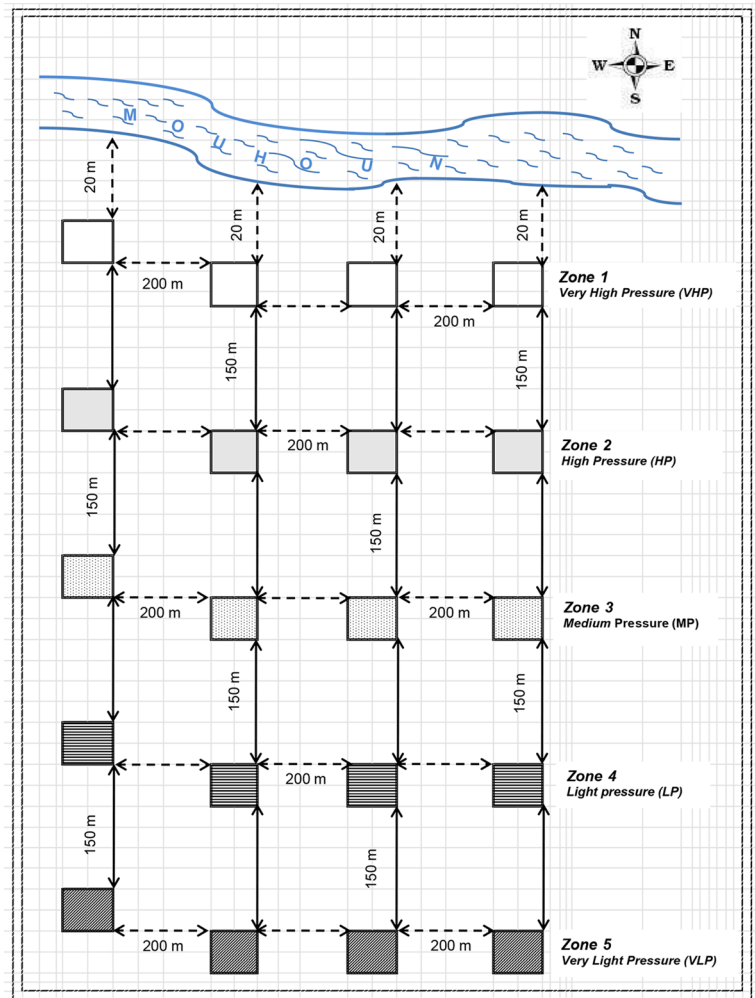


Source : Image Landsat 2013 - BNDT

July 2015

Author : NABALOU M.

Fig. 2 Experimental design



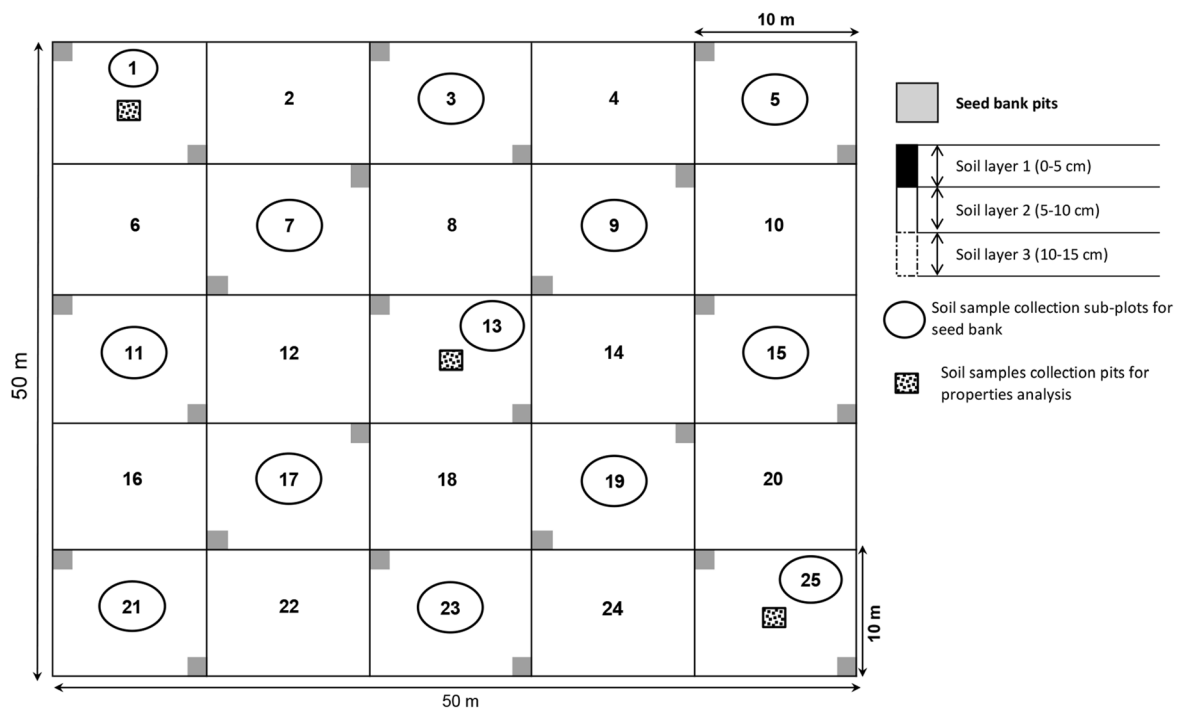
a component of the soil seed bank. Following Brits et al. (2002), the area around the watering point was divided into five levels of grazing pressure: very high pressure (VHP), high pressure (HP), medium pressure (MP), light pressure (LP) and very light pressure (VLP). Each transect contains four plots representing four replicates of a level of grazing pressure, giving a total of 20 plots. The plots cover an area of 2500 m<sup>2</sup> (50 m × 50 m) and are located 200 m apart along each transect. Neighboring transects were separated by a distance of 150 m. The first level of grazing pressure (i.e. very high pressure) is installed 20 m from the river bank. The same design was repeated at four different locations along the river.

## Soil sampling

### Analysis of soil properties

Samples for the analysis of soil properties were collected using an auger at three locations along the diagonal within each 50 m × 50 m plot (Fig. 3). The sample pit dimensions

were 10 cm × 10 cm at three different depths (0–5, 5–10, 10–15 cm). In total, 720 soil samples were obtained: 20 plots × 3 quadrats × 3 depths × 4 locations. Soil samples from the same depth were pooled for each plot and bagged, labelled and transported to the Soil Sciences Laboratory of the Institute of Environment and Agricultural Researches, INERA (Burkina Faso). The soil samples were air-dried and sieved through 2 mm mesh. Soil organic matter and soil carbon were determined after oxidation of organic matter following the procedures described by Walkley and Black (1934); soil pH was determined using a glass electrode connected to a digital ion analyzer (Digital pH/mv Meter, Model 701A); total N (N<sub>tot</sub>) was determined using the Kjeldahl procedure; available potassium (K) was extracted using atomic absorption spectrometry; available P was extracted using a Bray-1 extract as described by Olsen and Dean (1965); and soil cation exchange capacity was measured using the protocol described by Metson (1956).



**Fig. 3** Layout of sampling design employed for assessing the soil seed bank, natural regeneration and aboveground vegetation

### Soil seed bank assessment

For soil seed bank evaluation, each 50 m × 50 m plot was further divided into 25 subplots of 10 m × 10 m dimensions (Fig. 3). To investigate the composition, density and vertical distribution of the viable soil seed bank, soil samples were taken at the end of the rainy season when seeds persisting from the previous growing season could still germinate and seed dispersal in the current season was peaking. The samples were taken by hammering a hollow 15 cm × 15 cm square metal frame into the soil in two opposite corners of 13 out of the 25 subplots to obtain a representativeness of the plot (Fig. 3). Three soil layers (0–5, 5–10 and 10–15 cm) were collected using a sharp knife, following the procedure used by Kennarda et al. (2002). In the field, samples were kept in separate bags, shaded and air-dried to prevent damage from heat and mold. The soil samples were subsequently transferred into plastic bags and transported to the greenhouse for investigation. In total, 1560 soil samples (20 plots × 13 subplots × 3 depths × 2 corners) were collected from across the five grazing pressure transects at four locations. Soil cores for each depth per plot were mixed to obtain 60 composite samples (20 plots × 3 layers).

To assess the species composition of the soil seed bank, we used the seedling emergence method because of its ability to determine the viable fraction of readily-germinable seeds (Espeland et al. 2010). This fraction is the soil seed bank component that is most important for vegetation

restoration. The composite soil samples were thinly spread into polypropylene trays arranged in a tunnel greenhouse that provided the ideal uniform conditions for germination. The dimensions of each tray were 28 cm × 11 cm × 6 cm. The trays were kept continuously moist by daily watering and monitored over a 4-month period. Additionally, 20 trays containing sterilized sand were randomly placed throughout the greenhouse to determine if there was any airborne contamination. During the trial, no species germinated in the control trays, indicating no airborne seed contamination. All trays were checked for seedlings once a week. The emerging seedlings were identified, counted, recorded and discarded. During the trial, soil samples were stirred each week to bring any non-germinated seeds to the surface. At the end of the 4-month trial, the total number of emergent seedlings was used as the measure of soil seed bank viability.

### Sampling aboveground vegetation

To compare plant species represented in the soil seed bank and the aboveground vegetation, the composition and density of woody plants were assessed in each plot. All trees and shrubs were measured [their diameter at breast height (dbh) was measured by cross-calipering, and their height was measured using a graduated pole], identified and counted in the plots of 50 m × 50 m and the herbaceous layers were inventoried for all species in each of the 10 m × 10 m subplots. Individuals of woody species were classified as mature



trees and seedlings according to their dbh and height. Identification of plant species and families followed Hutchinson et al. (1954).

### Species composition in the aboveground vegetation

To compare species diversity in the aboveground vegetation of each level of grazing intensity, we calculated the number of species, Shannon's measure of evenness, Margalef's index, Simpson's index, Shannon-Wiener information and Fisher's diversity index (Krebs 1999). These indices are widely employed to measure biological diversity. To evaluate  $\beta$ -diversity (dissimilarity between species composition at each level of grazing intensity), similarity indices were computed based on species presence/absence data. The values potentially vary between 0 and 1, and a value close to 1 indicates a high similarity between the level of grazing intensity, and hence low  $\beta$ -diversity (Krebs 1999). Also, the spatial distribution of seedlings for each species in the different levels of grazing intensity was obtained by calculating the standardized Morisita index (Ip) (Krebs 1999). The standardized Morisita index was modified from the Morisita index of dispersion with a range from  $-1$  to  $+1$  and confidence intervals between  $-0.5$  and  $0.5$ . If the standardized Morisita index was between  $-0.5$  and  $+0.5$ , the seeds were randomly distributed. Values greater than  $0.5$  indicated seedlings were clumped, and values less than  $-0.5$  indicated seeds were uniformly distributed.

### Statistical analysis

The calculated parameters for the species composition and vegetation structure were first subjected to one-way analysis of variance to test the difference among plots associated with differences in their level of grazing intensity. When a significant difference was detected, a pair-wise comparison was made using Tukey's test at the 5% level of significance. Changes in soil seed bank density and species richness between the different levels of grazing intensity and soil depth were tested using a generalized linear model (GLM). The number of germinated seeds and species richness per plot and soil sampling layer were first aggregated by plot and then converted to densities. To determine the vertical distribution of seeds associated with each level of grazing intensity, numbers of germinated seeds from each layer from each plot assigned to that level of grazing intensity were combined to determine the corresponding density at each soil sample depth.

Prior to analysis, data exploration was performed following the protocol described by Zuur et al. (2010). Since the values were count data, we used a GLM with a Poisson distribution to account for the associated non-normal errors and increasing variance with increasing averages that are

associated with count data (Crawley 2005). The linear model used was as follows:

$$N_{isk} \sim P(\exp(\mu + \alpha_s + \beta_k + \gamma_{sk})),$$

where  $N_{isk}$  is the seedlings count per unit area  $s$  in plot  $i$  at site  $k$ ,  $P$  denotes the Poisson distribution,  $\mu$  is the overall mean,  $\alpha$  the effect of grazing pressure,  $\beta$  the effect of depth of soil sampling and  $\gamma$  the interaction between the two factors. Examination of the residues revealed wide dispersion (the dispersion coefficient was always  $> 2.4$ ), so the results were reviewed using penalized quasi-likelihood with Poisson errors. The GLM was performed using the statistical software R (R Development Core Team 2012).

Relationships between species composition and the soil seed banks and aboveground vegetation were tested by non-metric multidimensional scaling (NMDS). We calculated similarity matrices using the Bray Curtis coefficient, and all ordinations were based on species presence/absence data. Correlations between species composition of the soil seed bank and soil chemical properties were explored by means of Canonical Correspondence Analysis (CCA) using CANOCO 4.5 (Ter Braak and Smilauer 2002). Each variable was tested in a single model to determine whether it significantly influenced the soil seed bank. All significant variables were then used in one model to determine their collective influence on the soil seed bank. The statistical significance of the CCA results were tested using a Monte Carlo unrestricted permutation test under a full model with 999 random permutations (Leps and Smilauer 2003).

## Results

### Species diversity and composition of the aboveground vegetation

In total, the plots contained 44 tree species belonging to 19 families, 32 genera and three life forms (i.e. mesophanerophyte, microphanerophyte or nanophanerophyte) (Table S1), and 77 herbaceous species representing 17 families and 36 genera (Table S2). There was no significant difference between grazing intensity in terms of the number of families and genera as well as average dbh (Table 1). However, the average tree density increased ( $P < 0.05$ ) as the grazing intensity decreased (Table 2). According to Margalef's index of species richness, the very light pressure sites were the most diverse, followed by the medium pressure and very high pressure sites. Shannon's measure of evenness did not differ between the different levels of grazing intensity. Shannon-Wiener's information index indicated that the least disturbed sites were the most diverse (Table 2). Herbaceous species evenness and dominance were also affected by the levels of grazing intensity. Accordingly, the lightly grazed

**Table 1** Summary of the species composition and structural characteristics of trees with diameter at breast height (dbh)  $\geq 5$  cm at each level of grazing intensity [for each parameter, means with different letters are significantly ( $P < 0.05$ ) different based on Tukey's HSD test]

	Grazing intensity				
	Very high pressure	High pressure	Medium pressure	Light pressure	Very light pressure
Families (number)	7a	8a	7a	13a	13a
Genera (number)	10a	10a	12a	19a	22a
Species (number)	14a	12a	15a	28a	31a
Average dbh	2.56 $\pm$ 6.34a	4.54 $\pm$ 11.91a	1.80 $\pm$ 4.09a	1.92 $\pm$ 4.66a	2.8 $\pm$ 7.67a

**Table 2** Diversity measures for trees with diameter at breast height (dbh)  $\geq 5$  cm at the five levels of grazing intensity [for each parameter, values with different letters are significantly ( $P < 0.05$ ) different based on Tukey's HSD test]

Diversity measures	Grazing intensity				
	Very high pressure	High pressure	Medium pressure	Light pressure	Very light pressure
Number of individuals recorded (N)	80 $\pm$ 8.11c	181 $\pm$ 38.60b	318 $\pm$ 41.27ab	324 $\pm$ 18.79ab	359 $\pm$ 20.20a
Total number of species recorded (S)	14	12	15	28	31
Rate of species increase per individual enumerated (S/N)	0.18	0.07	0.05	0.09	0.09
Margalef's index of species richness. $DMg=(S-1)/\ln N$	2.96a	2.11a	2.42a	4.67b	5.09b
Shannon's measure of evenness. $J'=H'/\ln S$	0.32a	0.18a	0.25a	0.33a	0.32a
Shannon-Wiener index. $H'=-\sum p_i \log_2 p_i$	0.86a	0.45b	0.69a	1.11c	1.11c
The reciprocal of Simpson's index. $1/l = \sum S_i(n_i - 1)/N_i(N_i - 1)$	4.87a	1.71b	3.30c	7.93d	7.85d
Fisher's index of diversity $a=N(1-x)/x$ x is the log series parameter	0.40a	0.91a	1.60b	1.63b	1.80b

sites had a higher species richness than the heavily grazed sites at  $P < 0.05$ . The higher grazing intensity significantly reduced the herbaceous species evenness and Shannon's index in the heavily grazed sites, although there was no significant difference among the other three levels of grazing intensity at  $P > 0.05$ .

The reciprocal of Simpson's concentration index ( $1/l$ ) showed that light pressure sites were the most diverse (7.93) followed by the very light pressure sites (7.85). The high pressure sites were the least diverse (1.71). The Simpson's dominance index was higher for the very high pressure sites because of the high importance values of a few species. Fisher's diversity index also identified the very light pressure sites as the most diverse (1.80) and the very high pressure sites as the least diverse (0.40). Fisher's alpha value calculated from each level of grazing intensity indicated that plant species diversity was significantly different. Overall, most measures showed that the level of diversity decreased in the following order: very light pressure > light pressure > medium pressure > high pressure > very high pressure. Morisita-Horn's, Jaccard's and Sorensen's indices of similarity ranged from 3 to 88%, 13 to 50%, and 22 to 68%, respectively. In general, these indices showed that there is

similarity between the first two levels of grazing intensity (i.e. very light pressure, light pressure) and also between the last two levels of grazing intensity (i.e. high pressure, very high pressure) (Table 3).

### Seedling population and distribution pattern

Overall, seedling populations decreased significantly with the increase in grazing intensity ( $P < 0.05$ ). The results showed that regeneration is highest on very light pressure sites, with an average density of  $955 \pm 231$  small individuals/ha (Table S3A). Species showing trends of decreasing number of seedlings with proximity to water significantly outnumbered those showing increasing trends. Seedling population density was lowest on the very high pressure sites with an average density of  $98 \pm 12$  individuals/ha.

Species that had the highest density of small individuals throughout the plots were *Combretum nigricans* Leprieur ex Guill. & Perr., *Combretum micranthum* G.Don, *Feretia apodanthera* Delile, *Combretum glutinosum* Guill. & Perr., *Boscia senegalensis* Hochst. Ex Walp., *Crossopteryx febrifuga* Benth., *Grewia mollis* Juss. and *Detarium microcarpum* Guill & Perr. The spatial distribution of seedlings for

**Table 3** Morisita-Horn, Jaccard and Sorensen indices of similarity between each level of grazing intensity

Index of similarity	Grazing intensity	Very high pressure	High pressure	Medium pressure	Light pressure	Very light pressure
Morisita-Horn	Very high pressure	1				
	High pressure	0.71	1			
	Medium pressure	0.05	0.03	1		
	Light pressure	0.11	0.08	0.31	1	
	Very light pressure	0.23	0.11	0.18	0.88	1
Jaccard	Very high pressure	1				
	High pressure	0.37	1			
	Medium pressure	0.32	0.26	1		
	Light pressure	0.27	0.21	0.39	1	
	Very light pressure	0.21	0.13	0.31	0.51	1
Sorensen	Very high pressure	1				
	High pressure	0.54	1			
	Medium pressure	0.49	0.42	1		
	Light pressure	0.43	0.35	0.56	1	
	Very light pressure	0.34	0.22	0.48	0.68	1

each tree species in the different levels of grazing intensity was obtained by calculating the standardized Morisita index ( $I_p$ ). For the majority of the species, both the mean and confidence interval for Morisita's index were greater than 0.5, indicating the seedlings of all species were clumped. Approximately 47–88% of the species in each level of grazing intensity had a clumped distribution and few species had a uniform distribution, especially in the very high pressure and very light pressure sites. Many seedlings that were absent in the high disturbance sites were found in the least disturbed sites with a clumped or uniform distribution. Certain species exhibited clumped then uniform distribution or the reverse as grazing intensity increased (Table S3B).

### Species composition and density in the soil seed bank

A total of 3948 native seedlings belonging to 30 species, comprising 21 genera and 13 families (Table S4) germinated from the soil samples. The soil seed bank was dominated by members of the Poaceae family, primarily annual and short-lived perennial grass species. Annual grass species were abundant and represented 87% of the seedlings, while the density of other functional groups was small and

fluctuated only slightly with the different levels of grazing intensity. The perennial grass species *Achyranthes aspera* L., *Andropogon fastigiatus* SW., *Andropogon gayanus* Kunth, *Sida acuta* Burm. f., *Sida alba* L. and *Sida rhombifolia* L. were mainly found in soil samples from the lowest grazing intensity sites. Only two woody species (i.e. *Balanites aegyptiaca* Delile and *Mitragyna inermis*) were observed. *Schoenefeldia gracilis* Kunth, *Loudetia togoensis* (Pilg.) C.E.Hubb. and *Cassia mimosoides* L. were three herbaceous species found in soil samples from all sites. In terms of species richness, soil samples from the very light pressure sites contained the highest number of species (25 species belonging to 18 genera and 10 families) followed by the light pressure (23 species belonging to 15 genera and 9 families) and medium pressure sites (14 species belonging to 10 genera and 5 families). Samples from the high pressure and very high pressure sites both had 9 species belonging to 6 families and 9 and 6 genera, respectively (Table S4).

Among the 30 identified species, a very large variation in their seed density in the soil seed bank was observed across the sites. The GLM with Poisson distribution analysis of the soil seed bank density and species richness showed that these decreased significantly ( $P < 0.0001$ ) with the increase in grazing intensity (Table 4). Density of germinated

**Table 4** Results of the generalized linear model analysis of density of species and species richness

Parameters	Density			Richness		
	df	F	P	df	F	P
Sources of variation						
Grazing pressure (G)	4	1832.466	<0.0001*	4	175.378	<0.0001*
Depth (D)	2	232.688	<0.0001*	2	1.402	0.4959
G × D	8	159.448	<0.0001*	8	16.276	0.0386*



seedlings was significantly highest in the soil seed bank sampled from the low-intensity grazing plots and lowest in the high-intensity grazing plots. The mean soil seed bank densities were estimated at 24.80, 59.52, 71.10, 88.07 and 191.70 seeds  $L^{-1}$  for the very high pressure sites through to the very light pressure sites respectively (Fig. 4). The species richness increased significantly when the grazing intensity decreased. Also, grazing intensities and their interaction with soil depth had a significant effect ( $P < 0.05$ ) on soil seed bank richness (Table 4).

### Relationship between the soil seed bank and aboveground vegetation

A comparison of the soil seed bank and aboveground vegetation indicated a lack of correspondence, particularly for ligneous species. 42 woody species and 28 herbaceous species recorded in the aboveground vegetation were absent in the soil seed bank. The results of the Non-metric multidimensional scaling (NMDS) ordination based on presence/absence data ( $k=2$ , nonmetric fit:  $r^2=0.937$ ) showed a clear clustering between species composition of the aboveground vegetation and the soil seed bank (Fig. 5), indicating a low similarity. Many species of the aboveground vegetation were absent in the soil seed bank. A number of species found in the soil seed bank were not found in the aboveground

vegetation. The species that occurred in both the soil seed bank and aboveground vegetation displayed a relatively clear pattern. Species found in the aboveground vegetation are grouped (in Fig. 5) at the left-hand side of the first axis and in the middle range of the second axis except for a few outliers. Herbaceous species that were present in the soil seed bank and aboveground vegetation are clustered in the center of the second axis and along the first axis. There was no co-occurrence of ligneous species in the soil seed bank and aboveground vegetation. The vegetation of the herbaceous layer contained species that were not detected in the soil seed bank.

### Relationship between grazing intensity, soil chemical properties and soil seed bank

The study site's soil characteristics are provided in Table 5. The soil was acidic ( $pH < 7$ ) at all grazing intensities and depths. Grazing significantly influenced soil chemical factors in terms of organic matter, carbon, nitrogen, phosphorus, potassium and cation exchange capacity ( $P < 0.05$ ). The values of soil chemical factors decreased with soil depth and the level grazing intensity. The topsoil at sites with a higher grazing intensity contained more nitrogen and phosphorus, and had a higher cation exchange capacity than the lower-intensity grazed sites. The CCAs showed that the emerged

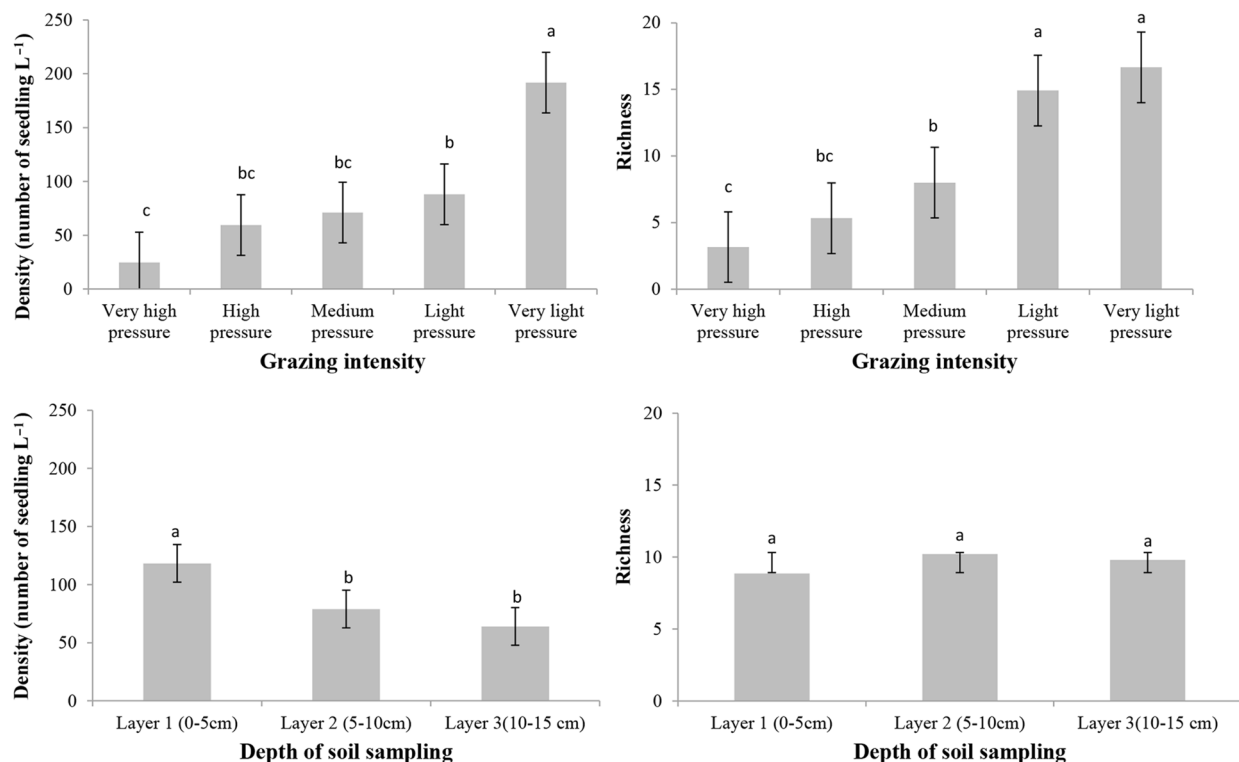
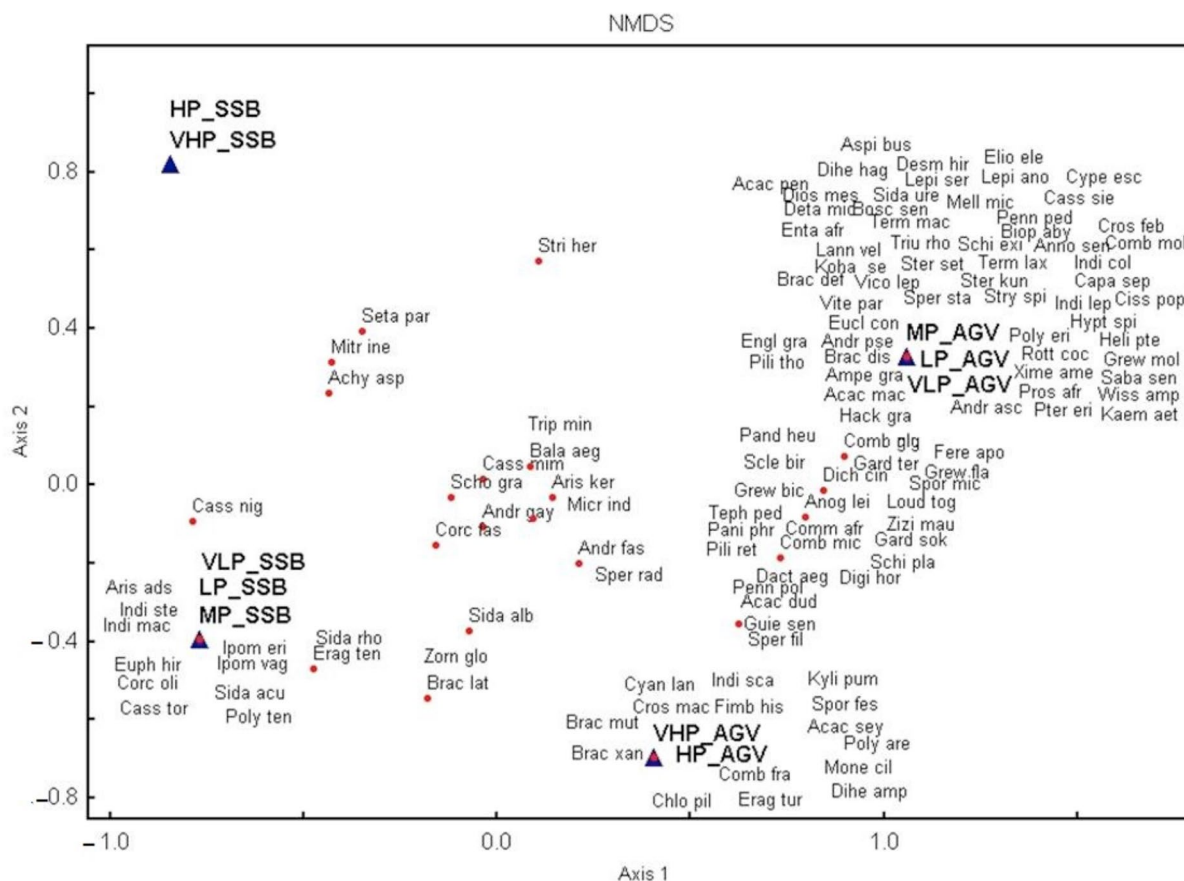


Fig. 4 Effects of grazing intensity and depth of sampled soil on the soil seed bank density and richness



**Fig. 5** Ordination (NMDS) based on species composition of the aboveground vegetation at different levels of grazing intensity and the soil seed bank (based on seedling emergence from soil samples). Stress value = 7.55 ( $K=2$ , nonmetric fit = 0.937). Ordination based on Sorensen (Bray-Curtis) similarity of the presence/absence of all taxa. The label of the most species onto the ordination was constituted by the first four letters of the genera and the three letters of species

( $r^2=0.744$  and  $P=0.001$ ). Notes: very high pressure (VHP); high pressure (HP); medium pressure (MP); light pressure (LP) and very light pressure (VLP) are the five different levels of grazing intensity. SSB and AGV are the soil seed soil bank (emerged seedlings from soil samples) and aboveground vegetation (herbaceous and woody species present in extent vegetation), respectively

seedlings from soil seed bank was significantly influenced by soil carbon, organic matter, total nitrogen, total potassium and soil cation exchange capacity ( $P < 0.05$ ) (Table 6). Combined, these five variables significantly accounted for the composition of the soil seed bank. The CCAs show the changes in the species composition of the soil seed bank according to the five variables (Fig. 6). Soil K and cation exchange capacity had similar effects on the species composition. The soil pH, C/N ratio and P did not influence the composition of the soil seed bank.

## Discussion

### Aboveground vegetation in relation to grazing intensity

Our findings suggest that species richness in the herbaceous layer, and vegetation structure and species composition were influenced by the level of grazing intensity adjacent to the riparian area. Our results are largely consistent with previous studies (e.g. Ameha et al. 2008; Jawuoro et al. 2017; Todd 2006) that have found standing herbaceous vegetation to be negatively associated with grazing pressure. Indeed, trampling and defoliation observed near the water points could hamper herbaceous seed germination and plant growth and development, and hence significantly lower grass species diversity, richness and evenness. Hoof action could have led to soil compaction, hindering infiltration of water (Savadoغو et al. 2007a; Thrash 1997) and consequently reducing plant

**Table 5** Summary of soil characteristics at the different levels of grazing intensity (mean  $\pm$  SD) [means of each soil parameter with different letters are significantly ( $P < 0.05$ ) different based on Tukey's HSD test]

Grazing intensity	Depth	Soil pH (H <sub>2</sub> O)	Soil pH (KCl)	Organic matter (%)	Carbon (g kg <sup>-1</sup> )	Nitrogen (g kg <sup>-1</sup> )	Phosphorus (mol kg <sup>-1</sup> )	Potassium (mol kg <sup>-1</sup> )	Cation exchange capacity (mmol kg <sup>-1</sup> )
Very high pressure	0–5 cm	5.61 $\pm$ 0.02a	4.57 $\pm$ 0.05b	19.05 $\pm$ 0.08c	11.05 $\pm$ 0.02c	1.25 $\pm$ 0.007a	1.93 $\pm$ 0.04c	22.75 $\pm$ 0.02a	82.10 $\pm$ 2.8a
	5–10 cm	6.08 $\pm$ 0.02b	4.85 $\pm$ 0.05c	11.22 $\pm$ 0.12b	6.53 $\pm$ 0.03b	0.80 $\pm$ 0.02a	1.54 $\pm$ 0.05b	21.90 $\pm$ 0.09a	88.61 $\pm$ 1.5b
	10–15 cm	5.8 $\pm$ 0.02c	3.84 $\pm$ 0.04a	7.33 $\pm$ 0.15c	4.21 $\pm$ 0.10a	0.40 $\pm$ 0.0010	1.35 $\pm$ 0.08a	20.62 $\pm$ 1.15	89.86 $\pm$ 0.8b
High pressure	0–5 cm	5.94 $\pm$ 0.07b	5.09 $\pm$ 0.17a	17.95 $\pm$ 0.13c	10.38 $\pm$ 0.09c	0.79 $\pm$ 0.05a	1.08 $\pm$ 0.01b	24.87 $\pm$ 0.08c	87.32 $\pm$ 0.3c
	5–10 cm	5.54 $\pm$ 0.11a	4.57 $\pm$ 0.06b	11.82 $\pm$ 0.04b	6.8 $\pm$ 0.09b	0.64 $\pm$ 0.05a	0.67 $\pm$ 0.03 a	21.90 $\pm$ 0.08b	57.10 $\pm$ 0.2b
	10–15 cm	5.80 $\pm$ 0.02b	4.64 $\pm$ 0.05b	10.16 $\pm$ 0.05a	5.23 $\pm$ 0.58a	0.62 $\pm$ 0.006a	0.70 $\pm$ 0.01 a	20.83 $\pm$ 0.01a	46.65 $\pm$ 1.5a
Medium pressure	0–5 cm	6.13 $\pm$ 0.02b	5.33 $\pm$ 0.03c	15.65 $\pm$ 0.04c	9.08 $\pm$ 0.01b	1.04 $\pm$ 0.005a	1.17 $\pm$ 0.02 c	16.95 $\pm$ 0.00c	60.66 $\pm$ 0.5c
	5–10 cm	5.79 $\pm$ 0.09a	4.6 $\pm$ 0.09b	9.05 $\pm$ 0.16b	5.21 $\pm$ 0.04a	0.54 $\pm$ 0.009a	0.69 $\pm$ 0.01 b	13.92 $\pm$ 0.00a	38.94 $\pm$ 1.0b
	10–15 cm	5.8 $\pm$ 0.01a	4.23 $\pm$ 0.02a	8.93 $\pm$ 0.05a	5.18 $\pm$ 0.03a	0.49 $\pm$ 0.005a	0.65 $\pm$ 0.00a	14.96 $\pm$ 0.00b	32.93 $\pm$ 0.1a
Light pressure	0–5 cm	5.77 $\pm$ 0.06b	4.92 $\pm$ 0.05b	12.3 $\pm$ 0.02c	7.11 $\pm$ 0.03c	0.62 $\pm$ 0.01a	0.95 $\pm$ 0.02c	15.98 $\pm$ 0.00c	47.92 $\pm$ 0.1c
	5–10 cm	5.62 $\pm$ 0.02a	4.36 $\pm$ 0.00a	7.72 $\pm$ 0.01a	4.45 $\pm$ 0.04a	0.41 $\pm$ 0.001a	0.61 $\pm$ 0.00a	13.97 $\pm$ 0.00a	28.96 $\pm$ 0.5a
	10–15 cm	5.73 $\pm$ 0.03ab	4.39 $\pm$ 0.00a	9.13 $\pm$ 0.11b	5.31 $\pm$ 0.02b	0.55 $\pm$ 0.01a	0.67 $\pm$ 0.00b	14.92 $\pm$ 0.00b	30.94 $\pm$ 0.5b
Very light pressure	0–5 cm	5.69 $\pm$ 0.04a	4.68 $\pm$ 0.26a	14.73 $\pm$ 0.13c	8.48 $\pm$ 0.09b	0.70 $\pm$ 0.00a	1.45 $\pm$ 0.00b	12.93 $\pm$ 0.00a	48.87 $\pm$ 0.2b
	5–10 cm	5.62 $\pm$ 0.13a	4.71 $\pm$ 0.03a	9.92 $\pm$ 0.04b	5.67 $\pm$ 0.14a	0.55 $\pm$ 0.01a	1.03 $\pm$ 0.00a	12.86 $\pm$ 0.00a	41.53 $\pm$ 0.5a
	10–15 cm	5.71 $\pm$ 0.02a	4.27 $\pm$ 0.16a	9.64 $\pm$ 0.05a	5.51 $\pm$ 0.06a	0.46 $\pm$ 0.07a	1.07 $\pm$ 0.00a	14.24 $\pm$ 0.00b	44.31 $\pm$ 2.5a

**Table 6** Canonical correspondence analysis (CCA) results

CCA model	<i>P</i>	<i>F</i>	Eigen value first axis	Species-environment correlations
pH water	0.0500	1.877	0.163	0.761
pH Hcl	0.8380	0.568	0.054	0.560
Carbon (C)	<b>0.0020</b>	<b>4.454</b>	0.330	0.883
Organic matter (OM)	<b>0.0020</b>	<b>4.246</b>	0.319	0.870
Total nitrogen (Nt)	<b>0.0020</b>	<b>4.613</b>	0.339	0.898
C/N	0.0560	1.719	0.151	0.671
Phosphorus (P)	0.3200	1.124	0.103	0.589
Total potassium (Kt)	<b>0.0020</b>	<b>4.921</b>	0.355	0.914
Cation exchange capacity (CEC)	<b>0.0020</b>	<b>4.611</b>	0.339	0.887
C + OM + Nt + Kt + CEC	<b>0.0020</b>	<b>4.048</b>	0.402	0.955

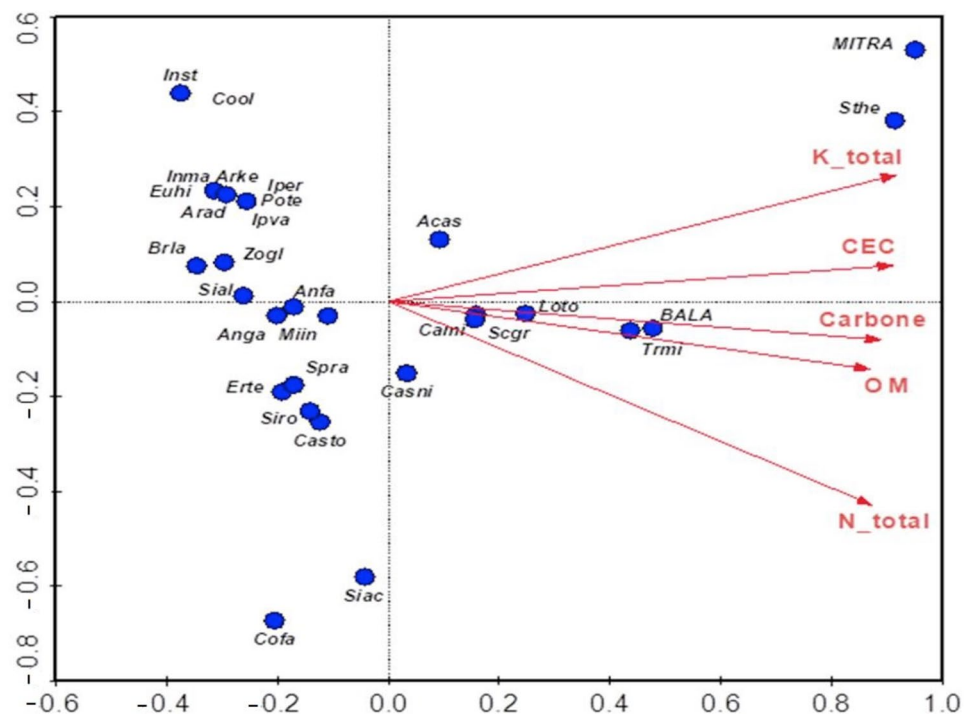
Significant relationships are indicated in bold

growth and reproduction. The high levels of grazing intensity were observed to encourage the succession of annuals and unpalatable species (less desirable forbs and annual grass) over palatable perennial species.

Our results also demonstrate that there was no difference in species richness, and that grazing intensity had relatively little effect on species composition of mature tree individuals. The difference between each level of grazing intensity was not significant in terms of Shannon's measure of evenness and the Shannon-Wiener index. The Shannon-Wiener

index values (0.45–1.11, Table 2) were comparatively low compared to the findings of Savadogo et al. (2007a, b) who found values ranging from 1.33 to 4.34 in different landscape patches of Tiogo SF. Such differences could be explained by the focus of our fieldwork on grazing intensity adjacent to the river where the ecosystem presented a spatial heterogeneity characterized by disturbance effects. Nevertheless, most indices showed that the least disturbed sites (medium pressure, light pressure and very light pressure) were more diverse than the more heavily disturbed sites. Morisita,

**Fig. 6** Ordination of canonical correspondence analysis (CCA). The ordination displays species and significant variables: carbon, organic matter (OM), N-total, K-total and cation exchange capacity (CEC)



Jaccard and Sorensen indices were low, except between the light pressure and very light pressure sites (Table 3). This low similarity between different levels of grazing intensity might mirror the habitat conditions in the riparian areas (Jansen et al. 2007).

### Density and spatial distribution of seedling populations

There was a significant difference in the numbers of seedling within plots subject to different levels of grazing intensity. The number of seedlings was significantly higher at sites with the least grazing intensity. Regeneration was highest at the light pressure sites, which is an indication of ongoing natural seedling recruitment. The lower proportions of seedlings at the sites subject to high grazing intensities shows a restricted recruitment of tree seedlings, presumably due to livestock impacts. That is, tree seedlings are being grazed and browsed or trampled by livestock, leading to failure in their regeneration patterns. Species that had the highest density of natural regeneration throughout the study sites could be an indication of their adaptability to grazing impacts. We could concur with Honu and Dang (2002) that these tree seedlings have an ability to survive unfavorable conditions or that the species are tolerant to grazing disturbance. These species—*Combretum nigricans*, *C. micranthum*, *F. apodanthera*, *C. glutinosum*, *B. senegalensis*, *C. febrifuga*, *G. mollis* and *D. microcarpum*—may therefore be worthy of consideration in future restoration programs in semi-arid ecosystems.

### Characteristics of the soil seed bank and its relationships with aboveground vegetation and soil chemical properties

The increase in soil seed bank density with increasing distance from the watering point was most likely due to these locations providing a greater opportunity for seed production under conditions of lower grazing intensity. The intensive grazing close to watering points could be one of the most important causes of variation in soil seed bank. There are several mechanisms whereby livestock grazing can affect plant communities. Grazers can remove biomass which might result in a reduction of the seed production capacity of plants, physically damage plants by trampling, creating vegetation gaps, and altering plant reproductive output (Paruelo et al. 2008). Consequently, the contribution of seeds to the soil seed bank can be reduced by intensive grazing. In addition, trampling by livestock may have detrimental effects on the structure of the upper soil layer by destroying soil aggregates (Eldridge and Whitford 2009; Risch et al. 2007).

The abundance of annual species in the soil seed bank suggests that the grazing of perennial grasses was resulting in their progressive replacement by annual species (Klintonberg and Verlinden 2008; Tessema et al. 2016). Indeed, Metzger et al. (2005) reported that areas with a high animal density are characterized by the abundance and a remarkable recovery rate of annuals. Similar to our findings, other authors have suggested that an increase in annuals and a reduction in perennials around water points is not the result of intensive grazing alone, but other factors such as nutrient

accumulation from faeces deposition, increased moisture availability, and compacted and eroded soils from animal trampling (Jauffret 2001; Tarhouni et al. 2010; Todd 2006). The families most commonly represented in the soil seed banks were Poaceae, Leguminosae and Convolvulaceae. This is consistent with the findings of De Andrade and Miranda (2014) and Savadogo et al. (2017). The presence of *Loudetia togoensis* is common to disturbed sites. Also, the presence of species of the genera *Aristida*, *Brachiaria*, *Eragrostis*, *Panicum* and *Digitaria* are dominant in grazed areas. The presence of species such as *Achyranthes aspera* is to be expected, because they possess seeds which attach to animals and become dispersed over long distances (Teketay 1996). Several studies have reported that herbaceous species are more abundant than woody species in soil seed banks (Dreber and Esler 2011; Erfanzadeh and Hosseini Kahnij 2015; Savadogo et al. 2017; Tessema et al. 2016). It is probable that tree seeds buried at depth may remain dormant or be consumed by the soil fauna (Elberse and Breman 1989). The recruitment of tree seedlings is only possible when the appropriate environmental conditions coincide with seed-fall (Higgins et al. 2000).

The fodder species *Balanites aegyptiaca* was present at all the sites of different grazing intensity, especially in the immediate vicinity of the water point (i.e. very high pressure and high pressure sites). This may be explained by the fact that livestock remain around the water point for long periods to drink and rest, resulting in high depositions of faeces that would contain the seeds of fodder species. The passage of many woody seeds, particularly legumes, through the gut of ruminants also helps to break their dormancy and thereby support an increased rate of germination (Razanamandranto et al. 2004). Livestock therefore play a major role in maintaining the biodiversity of grassland vegetation through the spatial and temporal dispersion of readily-germinating seeds in their manure (Woldu and Saleem 2000). The presence of *Mitragyna inermis* (characteristic species of the gallery forest) can be largely explained by its water dispersal mechanism; whereby the seeds floating on the surface of water are deposited around the vicinity of water points (i.e. hydrochorous seed dispersal). The presence of this species has also been recorded in the study by Diawara (2012) in the Tiogo SF. Our findings are in accordance with Rouw et al. (2014) who concluded that woody species contribute less to enrichment of the soil seed bank in tropical dry forests and that the lack of viable woody species seeds in the soil seed bank can be explained by many factors such as predation by frugivorous fauna and insects, and their long dormancy period.

The densities and number of species were highest in the first soil layer at all levels of grazing intensity and they gradually decreased with increasing depth (Fig. 4). This is similar to the results of Teketay (1996) and Diane and Pàez

(2000). The species densities and richness were also highest in the least disturbed sites (i.e. light pressure and very light pressure) and this is consistent with the findings of Looney and Gibson (1995), Erfanzadeh et al. (2016) and Tessema et al. (2016). Similarity indices indicated that there were low similarities in species composition of the soil seed bank at the different levels of grazing intensity. The effects of grazing on the similarity between the soil seed bank and aboveground vegetation are debatable: certain authors have reported that grazing can increase the similarity (Unger and Woodell 1996), decrease it (He and Ne'eman 2012), or have no effect (Peco et al. 1998). These contrasting findings may be due to the grazing regime, environmental conditions or the spatial distribution of the species. In our case, Jaccard's coefficient values for the similarity between the species composition of the soil seed bank and aboveground vegetation were low, because many species of the aboveground vegetation were absent in the soil seed bank (61 species). This dissimilarity is probably related to the relatively faster succession of aboveground vegetation compared to the soil seed bank (Karlik and Poschlod 2014). The low similarity between the soil seed bank and aboveground vegetation across different landscape patches was linked to effects of the grazing disturbance which can decrease the floristic richness and seriously alter the soil seed bank. This is a key reason why certain species are absent from the soil seed bank or that their emergence capacity is reduced. This result is consistent with the findings of Tessema et al. (2016) who reported a low mean similarity between the soil seed bank and aboveground vegetation, indicating an effect of heavy grazing.

Similarity between the soil seed bank and aboveground vegetation was generally low at all of the different levels of grazing intensity (Fig. 5). This was due to the fact that many species present in the aboveground vegetation were absent from the soil seed bank. This finding is consistent with several studies that also compared seedlings of the soil seed bank with the aboveground vegetation (Erfanzadeh and Hosseini Kahnij 2015; Savadogo et al. 2017). Grazing significantly influenced soil chemical factors in terms of phosphorus, organic matter, carbon, nitrogen, potassium and cation exchange capacity ( $P < 0.05$ ). This finding is consistent with the results of Hoffmann et al. (2016) who stated that grazing changed the distributions of most topsoil parameters at the plot scale, and strongly altered the stocks and spatial distribution of soil organic carbon. The CCA showed that the soil seed bank was significantly influenced by soil carbon, organic matter, total nitrogen, total potassium and soil cation exchange capacity ( $P < 0.05$ , Fig. 6). Hegazy et al. (2009) and Ma et al. (2015) have also demonstrated significant associations between the soil seed bank composition and edaphic factors such as  $\text{CaCO}_3$ , electrical conductivity, organic carbon and soil texture.



## Conservation implications for riparian areas

Our findings suggest the control of grazing herds around watering points is necessary to allow riparian ecosystems to conserve and replenish their soil seed bank density (and richness). Annual and perennial herbaceous species are the main species colonizing sites impacted by grazing along the Mouhoun River. If grazing pressure is maintained at moderate levels, these herbaceous species can help mitigate erosion at the site through their ability to provide ground-cover and accumulate organic matter. They can also help to improve soil fertility and enrich the soil seed bank by creating conditions (i.e. micro-habitats) conducive to the entrapment of tree seeds. In the long-term, the process of ecosystem auto-repair can facilitate the progressive replacement of annual species with perennial herbaceous and woody species. However, given the lack of tree seeds in the soil seed bank, such natural restoration will be very slow and likely limited at highly disturbed sites such as in the immediate vicinity of rivers where there is often bare soil and low soil seed bank densities (Savadogo et al. 2017). The fact that seeds of most of the savanna-woodland's dominant tree species do not accumulate in the soil seed bank highlights the importance of vegetative propagation for these species and the critical nature of ensuring the retention of mature individuals (Teketay 1996).

The lack of tree seeds in the soil seed bank means human interventions will be essential to accelerate forest recovery in many highly-disturbed savanna-woodland ecosystems. Essential actions will include reducing the frequency and/or intensity of anthropogenic disturbances by establishing firebreaks and fences to restrict the spread of wildfires and protect young regrowth (Savadogo 2007), mulching of bare soils to facilitate soil building and improved conditions for soil seed bank accumulation and regeneration, and strategic plantings of locally-native tree and shrub species. Careful selection of the species for planting will help to improve herbaceous and ligneous species richness and facilitate the conservation of local biodiversity. Grazing pressures will also need to be moderated because this disturbance can seriously affect the quantity and quality of soil nutrients that can influence seedling regeneration. The design and application of successful restoration strategies will also require collaboration between many stakeholders, including local communities, ecologists, NGOs and government decision-makers.

## Conclusion

Irrespective of the level of grazing intensity, herbaceous species are the main component of the soil seed bank around water points. This finding suggests that the restoration of grazing-impacted areas along watercourses will therefore be

difficult to achieve from local seed banks. Such restoration will require human interventions such as planting seedlings and creating favorable conditions to improve soil seed bank accumulation and seedling germination and growth of some target species. However, further research is required to better understand the effects of micro-habitats and different land-uses on the soil seed bank composition and its potential to contribute to the restoration of savanna-woodlands.

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