Relationships between soil seed banks and above-ground vegetation along a disturbance gradient in the W National Park trans-boundary biosphere reserve, West Africa

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Abstract

Aims

Vegetation succession depends on the availability of suitable prop-agules in the soils, thus knowledge of soil seed banks is essential for formulating effective strategies for restoring the vegetation of degraded sites. The W National Park, the only trans-boundary biosphere reserve in West Africa, is being extensively fragmented and degraded in recent decades. The aims of this study were to assess the reserve's soil seed banks, their relationships with standing vegetation and bundle of disturbances and their potential significance for vegetation restoration.

Methods

The size and composition of the above-ground species vegetation were assessed in nine plots of 1 ha each representing a range of habitats with differing disturbance severity (low, intermediate and high). A total of 702 soil samples were taken from three layers (0–3, 3–6 and 6–9 cm) and soil seed bank was analyzed using the seedling emergence technique.

Important Findings

Generally, seeds of non-woody taxa dominated in samples from all soil depths and habitats of all disturbance severities. The mean soil seed density was 17.8, 24.4 and 26.3 seeds/dm^3 in samples from the least, intermediate and most disturbed sites, respectively, and highest in the upper soil layers in all cases. The results indicate that there is limited potential for restoring woody vegetation solely from soil seed banks, and that woody species in the region rely more on recently shed seeds trapped in the standing dead biomass and litter on the ground than soil seed banks for regeneration. Thus, human intervention is needed to accelerate forest recovery, mainly through alleviating anthropogenic impacts on the ecosystem (for instance, avoiding destruction of new seeds by intense fire), and site manipulation to improve environmental conditions for seedling establishment and growth. Other ways of restoring forests than through the soil seed bank (e.g. sowing seeds collected elsewhere, and planting tree seedlings) could also be relevant.

Keywords: disturbance, savanna–woodland restoration, regeneration, seed bank, vegetation degradation, West Africa

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INTRODUCTION

Tropical savanna is subject to various forms of soil and vegetation degradation, due to diverse disturbances, such as fire, wood cutting, grazing and climatic change (Savadogo *et al.* 2008). In recent decades, these disturbances (mainly anthropogenic) have increasingly altered the structure of savanna ecosystems. Disturbances can be classified according to their severity, duration and frequency (White *et al.* 1985). Disturbances are ubiquitous, inherent (inbuilt), unavoidable and affect all levels of biological organization from individuals to ecosystems and landscapes with different consequences and mechanisms at each hierarchical level (Rykiel 1985). An inherent disturbance is a type of disturbance integral to a given forest ecosystem (Perera *et al.* 2004), which can be autogenic (arising from within) and allogenic (arising from outside the system). Disturbances create gaps with distinctive characteristics, leading to changes in local environment and biotic conditions, triggering recruitment processes of different species groups. During recovery after disturbance plants that grow may originate from four types of sources (Garwood 1989): seedling banks and advance regeneration (seedlings and saplings already present); vegetative reproduction (from stems and roots sprouting), seed rain (seeds dispersed by biotic and abiotic agents from neighboring sites) and soil seed banks. Soil seed banks are defined as the mature viable seed stocks present on soils' surfaces, or buried in the soil, duff or litter (Garwood 1989; Swaine 2001). They are important determinants of the initial floristic composition following disturbance (Hopkins *et al.* 1984; Pakeman *et al.* 2005) as they can serve as 'succession primer' for secondary regrowth in abandoned or degraded sites, depending on the frequency and severity of previous disturbance. Seed bank density and diversity strongly influence the composition of vegetation that develops and its rate of development (Thompson *et al.* 2003). Thus, knowledge of seed banks, and their relationships with standing vegetation and disturbances, is essential for both understanding community dynamics and formulating appropriate strategies for restoring vegetation (Kassahun *et al.* 2009; Snyman 2004; Solomon *et al.* 2006). Restoring degraded sites can be challenging and costly, because it often requires reintroduction of desirable vegetation by direct seeding or planting seedlings. However, it may be possible to avoid such costly means if sufficient seeds of desirable native ground cover species are present in the seed bank (Cohen *et al.* 2004). The seed stock depends on the balance between inputs and outputs, and hence on component species' temporal patterns of seed dispersal and germination parameters (Martins *et al.* 2007) under relevant disturbance regimes.

Disturbance may have various effects on seed banks. For instance, densities of seed and seedling banks and their species richness have been found generally lower at grazed sites than at ungrazed sites (Ma *et al.* 2010; Mayor *et al.* 2003). Accordingly, under heavy grazing, impoverishment of aboveground vegetation and seed banks may strongly restrict recovery of the vegetation (Kinloch *et al.* 2005; Snyman 2004; Tessema *et al.* 2012). However, Meissner and Afacelli (1999) found that grazing had no impact on total soil seed density in shrub land in southern Australia, and several studies have even found positive correlations between seed density and grazing intensity (Navie *et al.* 1996). The relationships between grazing and seed bank parameters may be complex, and heavily influenced by diverse factors, including stand species pool, site characteristics and climatic conditions.

Fire regimes in savanna also strongly affect seed bank dynamics in various ways. Notably, their occurrence interacts with reproductive phenology, e.g. fires that are synchronized with seasonal peaks in seed dispersal will influence the survival and germination of the largest numbers of seeds. Post-fire climatic conditions also influence seed germination, and thus seed bank dynamics (Whelan 1995); e.g. fire may induce a flush of seedlings from the soil seed bank during the following season (Snyman 2015). Fire can also act either independently or interactively with grazing disturbances (Savadogo *et al.* 2008). The simultaneous occurrence of several types of disturbance, if exerted in a bundle, will cause even stronger and more practically important changes in status and trend (negative in some cases and positive in others) of various ecosystem characteristics (Belsky 1992; Valone 2003). Generally, the co-occurrence of a number of disturbance factors has a synergistic effect on savanna ecosystem both in time and space (McNaughton 1983). The spatial distributions of seed banks, seeds' persistence in soil, effects of environmental factors on seed bank and similarities between seed bank species and standing vegetation have been described in many ecosystems (Luzuriaga *et al.* 2005; Teketay *et al.* 1999). However, very few studies have addressed the regenerative potential of seed banks in the West African savanna, although many degraded areas in diverse ecosystems have been restored using soil seed banks recently (Augusto *et al.* 2001; Li *et al.* 2008). Thus, there is a clear need to explore the potential for exploiting them to restore disturbed patches within protected areas in the savanna–woodlands. Furthermore, insufficient investment in protected areas and increases in tree products exploitation are resulting in so-called 'paper parks' with ineffective or insufficient management and progressive degradation of the resources theses reserves were established to protect (Myers 1994; Pare *et al.* 2010). This increases the urgency of exploring any possibilities for reducing costs associated with their effective management, particularly establishing desirable vegetation by means of existing seed bank.

Hence, the overall objective of this study was to acquire fundamental knowledge of seed banks to facilitate the management and conservation of flora and habitats of the savanna–woodlands, particularly the W National Park in Burkina Faso. Specific aims were to evaluate: vegetation composition and structure along a disturbance severity gradient; severity-related effects of disturbance on soil seed banks' importance, diversity and vertical distribution and the relationship between soil seed banks and standing vegetation.

Based on the findings, management recommendations are presented for conservation and restoration efforts. Therefore, in this study we have attempted to test the hypotheses that (i) variation in stand structure, spatial dispersion and regeneration of tree species in disturbed patches is related to the intensity of a bundle of inherent disturbances; (ii) seed bank density and composition vary among disturbed stands, and the variation is related to the intensity of a bundle of inherent disturbances and vertical seed distribution (i.e. seeds on soil surface or buried); (iii) the relationship between viable soil seed bank species composition and above-ground vegetation differ under varying site disturbance history.

MATERIALS AND METHODS

Study site description

The study was conducted in the W National Park, located in the Sudanian zone of Burkina Faso, between latitude 11°54′ and 12°35′N, and longitude 1°46′ and 2°23′ E. The name 'W' comes from the W-shaped bends in the bordering Niger River, which constitutes the natural boundary between Niger, Burkina Faso and Benin. W National Park includes wetlands and elevated plains, but is mostly covered by wooded savanna. It contains a wide range of plants characteristic of West African savanna–woodland and the largest population of mammalian herbivores in the region. W National Park is one of the most important UNESCO-MAB trans-boundary (Benin, Burkina Faso and Niger) Biosphere Reserves in West Africa.

The park is located in a region that has a tropical climate with average annual rainfall of 750–1000 mm, annual mean temperatures of 26–29°C, and rainy seasons from May to October alternating with dry seasons from November to April. The vegetation is composed of a mosaic of various types of savanna (woodland, grass-, shrub and tree savanna) (Fontes and Guinko 1995). The seed dispersal of both woody and herbaceous species at the site occurs between November and March. Beyond this period, the W National Park will be subject to late fires with potential negative consequences on plant phenology and also on the accumulated seeds on the surface and in the first layers.

The main soil types are Luvisols, Lixisols and Leptosols. The farming system around the study area consists of alternating cycles of cultivation and fallows. This lead to the occurrence of various disturbance agents in the park system since it is managed by the state with relaxed protection. The major disturbances include extensive livestock grazing and harvesting of various natural products, namely fuel wood, thatching materials, poles for construction, edible and medicinal plants. Fires are also used to clear fallows for cultivation and to prepare fields for sowing at the end of the dry season. Livestock grazing and fuel wood extraction are prohibited in W National Park, while prescribed early fire is recommended as a management tool. However, since the rural population highly depends on these forests for their subsistence needs, the strict protection is still not feasible.

Sampling

Initially, variation in the vegetation in the entire park was evaluated in a reconnaissance field survey. Based on the acquired information and satellite images, nine 1-ha sites were selected, three located in accessible areas close to the villages Kabougou, Kondio and Tapoa-Djerma and hence designated Kabougou 1–3, Kondio 1–3 and Tapoa-Djerma 1–3 (Fig. 1). The selected sites had visible signs of biotic disturbance, including fire scars, removal of ground cover by grazing animals (wildlife and livestock) and vegetation disturbance by local people through the collection of grasses, cutting and lopping of trees and shrubs for fodder and fuel wood and dead stumps. Other natural disturbances included soil erosion and rocky or hard-pan erosive shallow soils and termite mounds. The variability provided opportunities for examining effects of bundle of disturbance with a wide range of severity on vegetation diversity, seedling composition and soil seed banks.

Before detailed inventories and collection of soil samples from the 1-ha sites, they were ranked according to the severity of disturbance present using disturbance impact factors (DIFs). The DIFs were obtained using methods presented by Sagar *et al.* (2003) and Sapkota *et al.* (2009), with modifications, based on relative impacts of major disturbance sources or indicators. The DIF was derived from the relative impact of major disturbance sources or indicators for each site. DIF values for cutting and lopping and dead stump were obtained from estimates of relative densities of disturbed individual defined as the ratio of total disturbed density of saplings and trees to their total density at the respective site. The site with the lowest values of cut stump, lopped individuals or standing dead tree stump was assigned an impact factor of 1. For other stand, the relative impact factor was calculated as the ratio of the relative disturbed density of the respective stand to that of the site with the lowest value; e.g. number of cut, lopped and dead stump at Kondio 1 was the lowest, e.g. 10 and for Kabougou 1 it was 22. The impact for cutting for Kondio was assigned 1 and that of Kabougou was 2.2 (22/10). The relative impact factors of other disturbances, herbivory and termites mound were determined through visual estimation of the area (bare ground, rocky or hard-pan erosive shallow soils area within the plot) and counting (foot path, animal feces, fire scars and termites' mound). The stand with the lowest number of cases/ area was assigned 1 and proportionally higher values to the other sites. The impact factors for each disturbance source or indicator were then summed and each site was finally assigned a disturbance severity level of I (least disturbed), II (intermediately disturbed) or III (heavily disturbed) (Table 1).

Soil seed bank analysis

For soil seed bank sampling and surveying the vegetation at the sites, each of the nine 1-ha plots was first divided into 25 numbered 20×20 m subplots (Fig. 2). To investigate the composition, density and vertical distribution of the viable soil
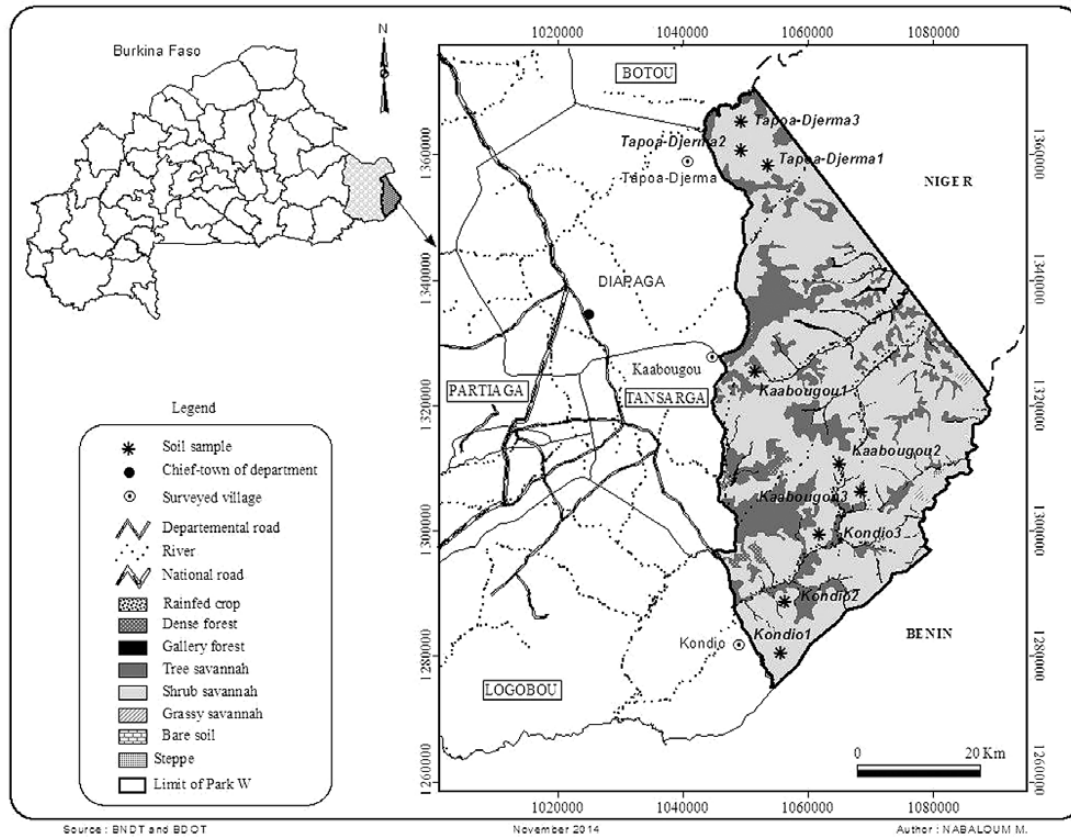
Figure 1: study site location.

Table 1: estimated disturbance impact factors (DIFs) for each site

Source of impact	Sites								
	Kon1	Kon2	Kon3	Kab1	Kab2	Kab3	Tap3	Tap2	Tap1
Cutting and lopping	2	5	2	4	1	2	1	1	3
Dead stumps	1	4	2	3	2	1	1	1	4
Fire	2	5	3	5	1	3	3	3	7
Grazing (animal feces)	2	4	5	6	1	3	4	1	4
Scraping	1	4	3	3	3	1	2	3	3
Foot path	2	4	4	5	2	3	3	1	4
Termite mounds	2	8	3	6	1	2	3	1	7
Bare ground and rocks	1	7	3	5	1	4	6	3	6
Soil erosion	2	3	2	3	1	3	2	3	4
Total	15	44	27	40	13	22	25	17	42
Assigned disturbance severity level	I	III	II	III	I	II	II	I	III

Abbreviations: Kab1–3 = Kabougou 1–3; Kon1–3 = Kondio 1–3; Tap1–3 = Tapoa1–3.

seed bank, soil samples were taken from every second sub-plot at the end of the rainy season (November–December), when seed persisting from the previous growing season could still germinate and seed dispersal in the current season was peaking. Thus, the samples may have contained both transient and persistent seed. The samples were taken by hammering a hollow 15×15 cm square metal frame into the soil in opposite corners of 13 subplots to obtain a representation of the plots. Three soil layers (0–3, 3–6 and 6–9 cm) were collected, following procedure used by Kennarda *et al.* (2002) using a sharp knife. The litter layer was included with the soil samples, because it may contain a high number of seeds. In the field, samples were kept in separate bags, shaded and air-dried to prevent damage from heat and mold. The soil samples
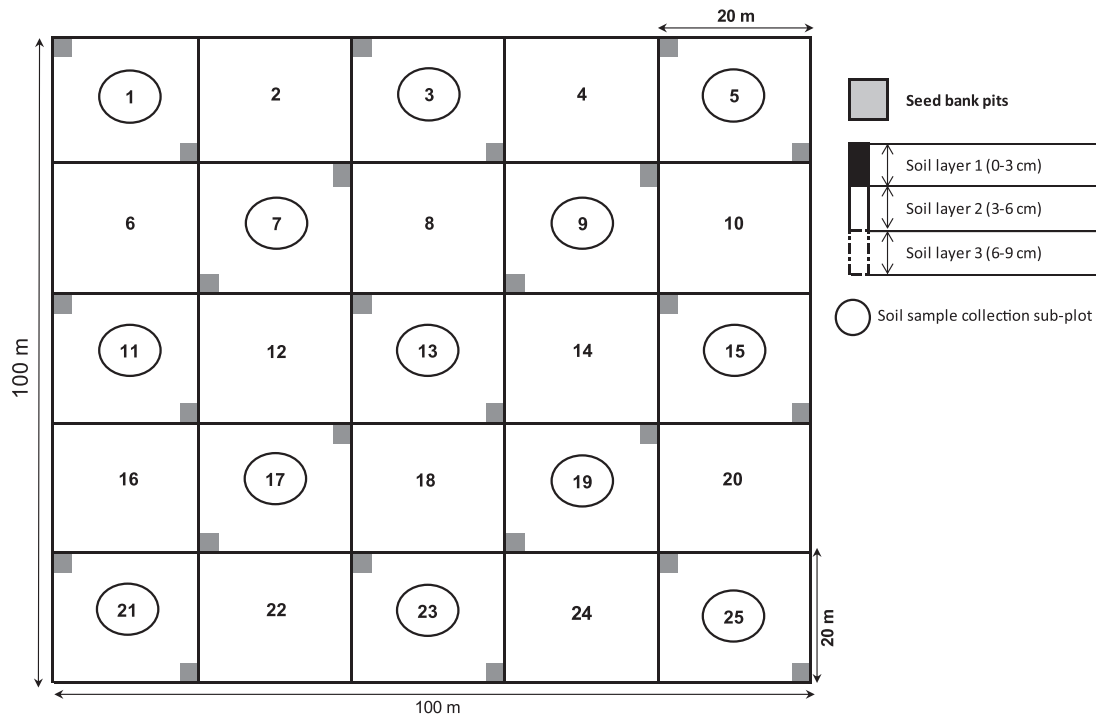
Figure 2: layout of sampling design employed for assessing the soil seed bank, natural regeneration and above-ground vegetation.

were transferred into plastic bags and transported to the greenhouse of the Institute of Environment and Agricultural Research at Saria research station (12°16′N and 2°09′W) for seed bank analysis. Soil cores for each depth were mixed to obtain a composite sample (Kassahun *et al.* 2009) before estimating the composition of soil seed banks.

Two main approaches are being used to elucidate seed bank components—extraction techniques and germinability assays. The utility of these approaches varies with community type and habitat although a common theme is the quest for an efficacious method (Price *et al.* 2010). The extraction method (through 'rinsing', sieving, flotation in a salt solution or other high specific gravity liquid, or a combination of both) is regarded as providing a better quantitative estimate of total seed bank densities (Brown 1992). However it is not commonly used as it is time consuming, ineffective at finding small seeded species and may overestimate the viable seed bank by including non-viable seeds (Baskin and Baskin 1998). In contrast, the seedling emergence method, though it can dramatically underestimate the density of the seed bank due to errors associated with seed dormancy and specific environmental requirements for germination (Wright and Clarke 2009), is commonly used and gives a good indication of the readily germinable seed bank.

For the assessment of the composition of the seed banks, we therefore used the seedling emergence method because of its ability to determine the viable fraction of readily germinable seeds (Espeland *et al.* 2010). This will allow us to provide a good perspective for managers in using *in situ* seedbanks as opposed to sowing seed as source material for vegetation restoration efforts. Coarse stones and vegetative material (root and plant fragments) were removed and composite soil samples were spread in a thin layer in polypropylene trays, arranged in a tunnel greenhouse that provided ideal and uniform conditions for germination of viable seeds. The greenhouse was equipped with two irrigation lines, controlled by a micro-sprinkler system with a flow rate of 90 L/h. The seed trays were kept continuously moist by watering daily. The trays were placed on pallets inside the greenhouse to avoid contact with any source of contamination. Average minimum temperatures during the 4 months study were 26.2 ± 1.3 and $25.5°C \pm 5.9°C$ inside and outside the glasshouse and the average relative humidity was 31.6 ± 11.5. Every week, all seed trays were checked for emerging seedlings. The emerging seedlings were identified, counted, recorded and removed. Those that were difficult to identify were retained in the trays until they had been identified. During this observation phase, to facilitate the growth of seedlings a solution of fertilizer nutrients (Blomstra Växtnäring, Cederroth Corporation, Sweden) was added to the substrate. Soil samples were maintained for 4 months, which was deemed sufficiently long to avoid significant underestimation of the persistent seed bank. During this period, soil samples were stirred five times to bring any non-germinated seeds to the surface. The total number of seedlings that emerged was used as the measure of viable seeds in the seed bank.

Sampling above-ground vegetation

In order to compare plant species represented in the soil seed banks and the existing above-ground vegetation, the composition and density of woody plants were assessed in each 1-ha plot, as follows. All trees and shrubs were identified and counted, their diameter at breast height (dbh) was measured by cross-calipering and their height was measured using a graduated pole. Individuals of tree species were classified as mature trees if their dbh > 2.5 cm and height > 1.5 m and seedlings otherwise. Species in the herbaceous layer were recorded within the sets of 25 (20×20 m) quadrats mentioned above. Identification of species and families of plants follows Hutchinson *et al.* (1954).

Analyses

Vegetation species composition

To examine the relationship between diversity and disturbance severity, for each 1-ha plot we calculated Shannon's measure of evenness and Margalef's, Simpson's, Shannon–Wiener information and Fisher's diversity indices, which are widely employed to measure biological diversity (Krebs 1999). To evaluate β-diversity (similarity between plots of differing disturbance severity), Jaccard's similarity index was computed based on the presence/absence data of the species. It potentially varies between 0 and 1, and a value close to 1 indicates high similarity between patches, and hence low β-diversity (Krebs 1999).

Density and spatial distribution of seedling populations

The spatial distribution patterns of the seedling populations within each 1-ha plot were analyzed using the standardized Morisita's index (I_p), since it is relatively independent of population density (Krebs 1999). First, the Morisita's index was computed as:

$$I_d = n \left(\sum x^2 - \sum x \right) \ / \ \left[\left(\sum x \right)^2 - \sum x \right]$$

where I_d is Morisita's index of dispersion, n is the sample size and $\sum x$ and $\sum x^2$ are sums of the quadrat counts and squares of quadrat counts, respectively. Then two critical values for Morisita's index were calculated using the following formulas:

$$\text{Uniform index}: \ M_u = (\chi^2_{0.975} - n + \sum x_i) \ / \ \left(\sum x_i - 1 \right)$$

$$\text{Uniform index}: \ M_c = (\chi^2_{0.025} - n + \sum x_i) \ / \ \left(\sum x_i - 1 \right)$$

where $\chi^2_{0.975}$ and $\chi^2_{0.025}$ are values of chi-squared with (n − 1) degrees of freedom that have 97.5 and 2.5% of the area to the right, respectively; x_i = a set of counts of organisms in a set of quadrats and n = number of quadrats. Finally, the standardized Morisita's index was calculated using the relevant formula of the following four:

i) $\ I_p = \ 0.5 + 0.5 \left(I_d - M_c \right) \ / \ \left(n - M_c \right);$ when $I_d \geq M_c > 1.0$

ii) $\ I_p = \ 0.5 \left(I_d - 1 \right) \ / \ \left(M_u - 1 \right);$ when $M_c \geq I_d > 1.0$

iii) $\ I_p = \ - 0.5 \left(I_d - 1 \right) \ / \ \left(M_u - 1 \right);$ when $1.0 > I_d > M_u$

iv) $\ I_p = \ - 0.5 + 0.5 \left(I_d - M_u \right) \ / \ M_u;$ when $1.0 > M_u > I_d$

The standardized Morisita's index of dispersion (I_p) ranges between −1 and +1. Values of 0, > 0 and < 0 indicate a random dispersion pattern, a clumped pattern and a uniform pattern, respectively.

Statistical analysis

The calculated parameters for the vegetation composition and structure were first analyzed with a nested ANOVA considering sites as a random factor and disturbance levels as a fixed factor nested within sites. The models were fitted using the function 'aov' from the 'stats' package in R software (R Development Core Team 2012). When a significant difference was detected, a pair-wise comparison was made using Tukey's test at the 5% level of significance.

Changes in seed bank density and species richness along the disturbance gradient and with 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 disturbance level, numbers of germinated seeds from each layer from each plot assigned to that disturbance level were combined to determine the corresponding density at each soil sample depth. This density was calculated using the following formula: Density = 100 × cumulative total number of seedlings/volume. 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 (Crawley 2005).

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

where N_{isk} is the number of seedlings per unit area s in plot i at site k, P denotes the Poisson distribution and μ, α and β are parameters. Disturbance severity level and depth of soil sampling were considered as explanatory variables in the GLM. 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. GLM was performed using the stats package in R statistical software (R Development Core Team 2012).

To compare the similarity in species composition between the soil seed banks and standing vegetation, sampling sites were ordinated by multivariate analysis. The species emerging from the soil seed banks and species in the above-ground vegetation were ordinated by detrended correspondence analysis (DCA) using

the presence/absence data. Correlations between seed bank composition and environmental parameters (disturbance level and soil depths) were investigated by Canonical Correspondence Analysis calculated using CANOCO 4.5 (Ter Braak *et al.* 2002). The statistical significance of the CCA results was tested using a Monte Carlo unrestricted permutation test under a full model with 999 random permutations (Leps *et al.* 2003).

RESULTS

Vegetation composition and species diversity

In total, 44 woody species belonging to 13 families, 33 genera and three life forms (mesophanerophyte, microphanerophyte or nanophanerophyte) were encountered during the inventories at the three study sites (Table S1, see online supplementary material), and 35 herbaceous species representing 14 families (Table S2, see online supplementary material). Disturbance severity did not influence the composition of woody vegetation in terms of numbers of families, genera and species, or the average dbh of mature trees (Table 2). To allow comparison of diversity between disturbance levels, several diversity measures were computed, but no significant disturbance-related differences in them were observed (Table 3). However, most diversity measures tended to decrease when disturbance

severity decreased. Jaccard's similarity index, which expresses the similarity in terms of the presence or absence of common or different species of vegetation types, showed that vegetation in plots with different levels of disturbance were relatively similar, with values ranging from 18% (between disturbance levels II and III) to 30% (between disturbance levels I and II).

Seedling bank and distribution pattern

Numbers of recruited seedlings decreased significantly with increasing disturbance severity ($P < 0.05$). Regeneration of trees was highest on disturbance level I and lowest on disturbance level III, with respective average densities of 206 ± 61 and 64 ± 9 small individuals/ha. Spatial distributions of seedlings of each species at the three levels of disturbance were obtained from the calculated standardized Morisita's index (I_p), which ranged from 0.23 to 1, showing that all species at each level of disturbance had a 'clumped dispersion' pattern (Fig. 3). For disturbance levels I, II and III, the species with the highest Morisita indices were respectively *Balanites aegyptiaca* (0.93), *Feretia apodanthera* (1.00) and *Guiera senegalensis* (1.00), while those with the lowest indices were *Piliostigma reticulatum* (0.23), *Sclerocarya birrea* (0.23) and *Pterocarpus erinaceus* (0.45), respectively. In terms of seedling species richness, seedlings representing 25, 22 and 23 species were detected in plots assigned to disturbance severity levels I–III, respectively.

Seed bank botanical composition and density

The seedlings that germinated from samples of all three soil layers collected from plots assigned to all three disturbance levels were all herbaceous, belonging to 35 species from 29 genera and 15 families (Table S2, see online supplementary material). Of those 35 species, only five are perennial (*Achyranthes aspera*, *Schizachyrium platyphyllum*, *Hyparrhenia rufa*, *Sida acuta* and *Sida rhombifolia*) the others being annuals. In terms of functional groups, forbs were the largest group, represented by 40% of the species. Grasses were the next most abundant group, comprising just over 30% of the total taxa (Table S2, see online supplementary material). There was no significant difference in species richness with respect to disturbance severity ($P > 0.05$);

Table 2: summary of the species composition and structural characteristics of trees ≥ 5 cm dbh at each disturbance level

	Disturbance severity		
	I	II	III
Families (number)	$7 \pm 1.00a$	$8 \pm 1.00a$	$8 \pm 0.00a$
Genera (number)	$10 \pm 3.00a$	$11 \pm 2.00a$	$10 \pm 0.00a$
Species (number)	$12 \pm 3.00a$	$13 \pm 2.00a$	$12 \pm 0.00a$
Average dbh (cm)	$9.67 \pm 0.88a$	$11.00 \pm 2.18a$	$12.00 \pm 1.73a$

For each parameter, means with different letters are significantly ($P < 0.05$) different based on Tukey's HSD test.
Abbreviations: dbh = diameter at breast height.

Table 3: diversity measures for trees with dbh ≥ 5 cm at the three levels of disturbance severity

Diversity measures	Disturbance severity		
	I	II	III
Number of individuals recorded, N	$77 \pm 9.00a$	$67 \pm 21.00a$	$63 \pm 11.00a$
Total number of species recorded, S	$12 \pm 3.00a$	$13 \pm 2.00a$	$12 \pm 0.00a$
Rate of species increase per individual enumerated, S/N	$0.18 \pm 0.06a$	$0.21 \pm 0.08a$	$0.26 \pm 0.03a$
Margalef's index of species richness, DMg = (S − 1)/lnN	$2.74 \pm 0.65a$	$2.95 \pm 0.35a$	$2.99 \pm 0.09a$
Shannon's measure of evenness, J′ = H′/lnS	$0.25 \pm 0.14a$	$0.28 \pm 0.01a$	$0.34 \pm 0.03a$
Shannon-Wiener index, H′ = −Spi log2 pi	$0.65 \pm 0.25a$	$0.72 \pm 0.06a$	$0.88 \pm 0.04a$
The reciprocal of Simpson's index, 1/l =Sni (ni − 1)/ Ni (Ni − 1)	$5.03 \pm 5.15a$	$3.35 \pm 0.65a$	$6.5 \pm 1.56a$
Fisher index of diversity a = $N(1 − x)/x$ x is the log series parameter	$4.53 \pm 1.48a$	$5.48 \pm 1.34a$	$6.01 \pm 0.88a$

Abbreviation: dbh = diameter at breast height.

the plots assigned to disturbance level I had 25 species (belonging to 21 genera and 8 families), followed by level II (23 species belonging to 20 genera and 11 families) and III (17 species
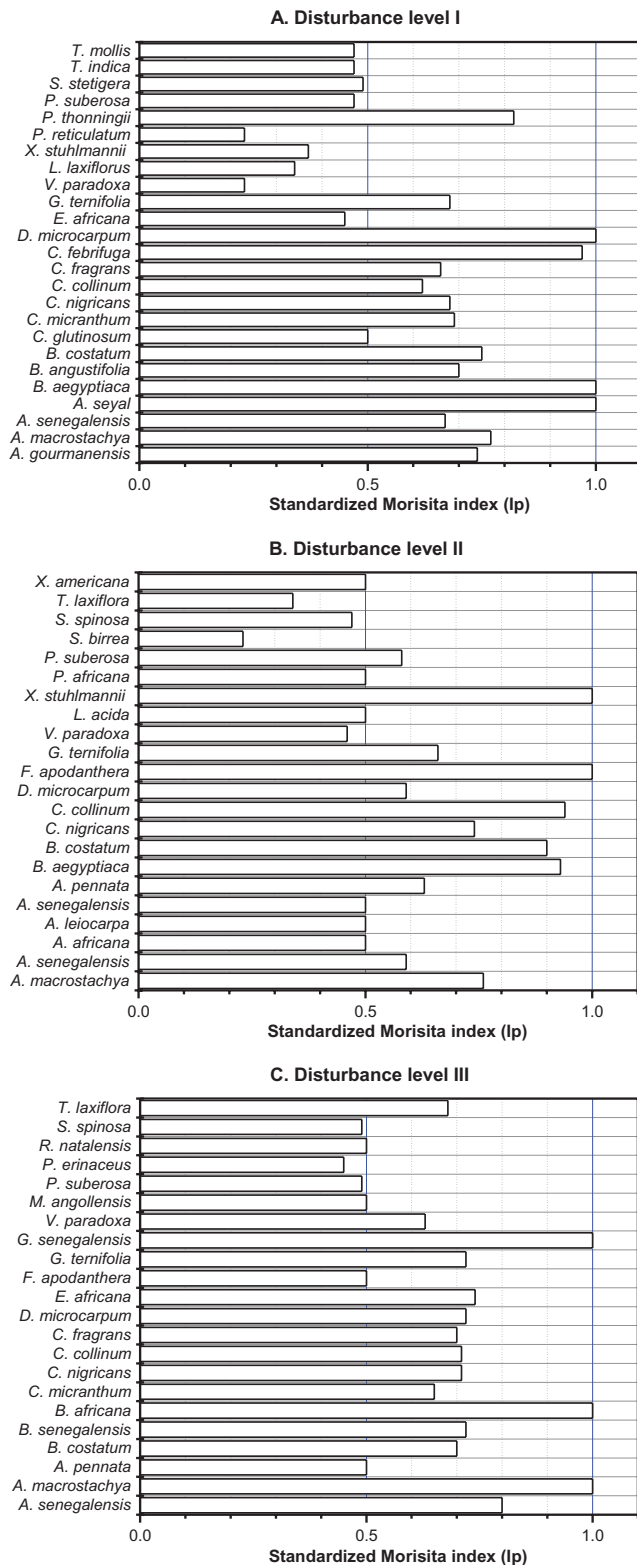
A. Disturbance level I

B. Disturbance level II

C. Disturbance level III

Figure 3: spatial distribution of the seedling population at each disturbance level.

belonging to 14 genera and 8 families) (Table S2, see online supplementary material). At each disturbance level, the family represented by the highest number of species was Poaceae (12, 7 and 5 species at disturbance levels I–III, respectively). The two most represented families at all disturbance levels (Poaceae and Fabaceae) accounted for 68.6% of all germinated seeds. At the site level, the seed bank and above-ground community composition moderately differed, across disturbance levels and depths of sampled soil. Values of Jaccard's similarity index ranged between 20 and 38%, reflecting a lack of common species between the standing vegetation and the seed banks.

In total, 2300 seeds germinated from all soil samples. The analysis of seed bank species richness using the GLM showed that no tested variable had a significant effect (Table 4). However, seed bank density decreased highly significantly ($P < 0.001$) with increasing soil depth but was not varying between gradient of disturbance (Fig. 4). Further, a small number of species dominated the pool of germinated seeds across the disturbance gradient. Half of the emerged seedlings represented just four species (out of 35): *Loudetia togoensis*, *Hyparrhenia rufa*, *Spermacoce radiata* and *Cassia mimosoides*.

The total variance (sum of eigenvalues) of species composition among quadrats obtained from the DCA of the presence/absence data matrix was 2.785 (Fig. 5). The first two axes contributed 31.7% of that variation. Soil seed bank and standing vegetation were relatively clearly clustered. The species that occurred in both the standing vegetation and seed bank displayed a relatively clear pattern. Species found in the aboveground vegetation are grouped at the left hand side of the first axis and in the middle range of the second axis except some few outliers as (AGS *Anogeissus leocarpa*, FER *Feretia apodanthera* and Bala *Balanites aegyptiaca*). Herbaceous species that were present in seedbank and vegetation are clustered in the centre of the second axis and along the first axis. There was no co-occurrence of ligneous species in the vegetation and soil seed banks. The vegetation of the herbaceous layer contained one species (*Andropogon gayanus*) that was not detected in the seed bank. Some species (e.g. *Cassia nigricans*,

Table 4: results of Generalized Linear Model analysis of species richness (A) and density (B)

	df	ER	df.E.R.	F	P (>F)
A:					
Null			26	16.319	
Disturbance severity (D)	2	0.654	24	15.665	0.721
Depth of soil sampling (P)	2	1.912	22	13.753	0.384
D × P	4	1.931	18	11.822	0.748
B:					
Null			26	503.75	
Disturbance severity (D)	2	16.356	24	487.4	<0.001
Depth of soil sampling (P)	2	204.611	22	282.78	<0.001
D × P	4	32.193	18	250.59	<0.001

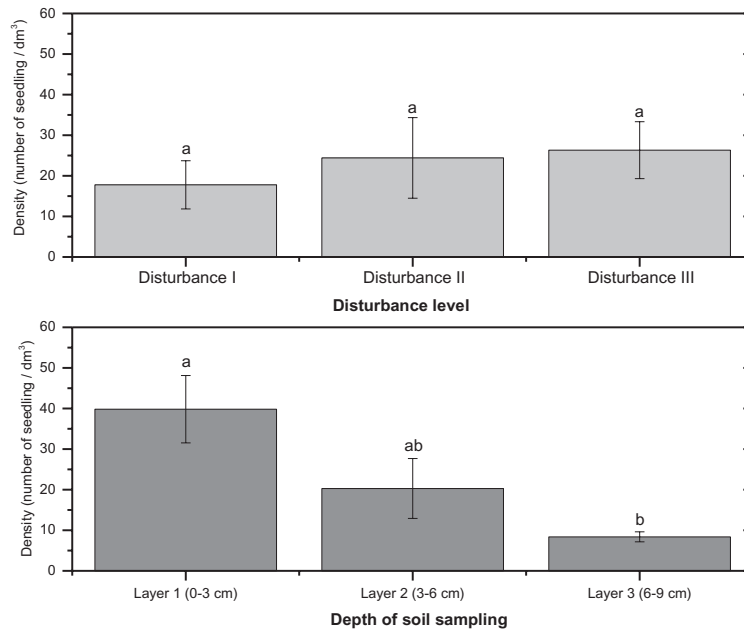Abbreviations: E.R. = residual error; df = degree of freedom.

Figure 4: main effects of disturbance gradient and depth of sampled soil on soil seed bank density.
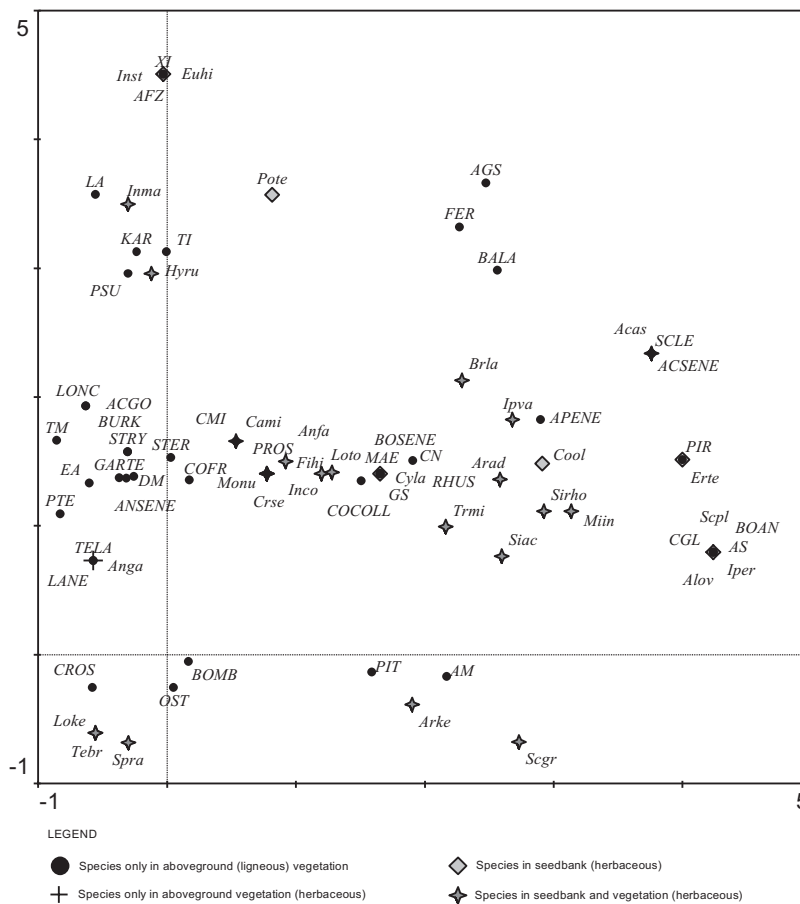

Figure 5: results of detrended correspondence analysis of the aboveground vegetation and the soil seed bank data obtained from the three study sites. First axis: λ = 0.517; percentage variance explained = 18.6%, gradient length 2.97. Second axis: λ = 0.365; cumulative variance explained = 31.7%, gradient length 2.90.

Corchorus olitorius, *Cyanotis lanata*, *Eragrostis tremula*, *Indigofera stenophylla*, *Ipomoea eriocarpa*, *Lepidagathis anobrya*, *Polycarpea tenuifolia*, *Zornia glochidiata*) that were present in the seedbank were not recorded in the vegetation. The ordination diagram based on CCA of the soil seed bank composition with respect to environmental variables (disturbance gradient and depth of sampled soil) is illustrated in Fig. 6. The first two axes had eigenvalues of 0.273 and 0.242, respectively, showing that not much floristic variation was explained by the environmental variables. The cumulative percentage of variance of species-environment relation was 63%. The Monte Carlo permutation tests indicated that the CCA for the seed bank was not significant (499 random permutations, $P = 0.064$, $F = 1.35$). The ordination vectors indicated that disturbance level II, and both 0–3 cm and 6–9 cm soil depths, were strongly correlated with the ordination axes, and thus with the community variation shown by the diagram. However, the CCA biplot showed a relatively low association between species and any particular environmental factor.

DISCUSSION

Floristic composition and characteristics of the vegetation

We observed much lower species richness than values recorded in previous studies of sites in W National Park and Arly National Park, which is also in Burkina Faso (Ouédraogo *et al.* 2006), possibly because we focused on degraded areas where sensitive species may have been eliminated. Members of the Combretaceae, Caesalpiniaceae, Mimosaceae and the Rubiaceae were recorded at sites representing every disturbance level. According to Fontes and Guinko (1995), these families are typical in the North Sudanian zone and most woodland mosaics. At the study sites, frequent and fluctuating disturbances act simultaneously and may have various effects, and other investigations have documented changes in vegetation structure and composition due to disturbance of tropical ecosystems (Pandey *et al.* 1999). However, analyses of variance of the entire woody vegetation revealed no significant disturbance-related differences in terms of Margalef, Shannon and Simpson's reciprocal or Fisher alpha indices, density, basal area or species richness. These results are not consistent with the intermediate disturbance hypothesis (IDH) for ecological succession, as described by Connell (1978), which holds that diversity or richness is maximized at intermediate frequencies and/or intensities of disturbance or environmental change. The species richness of a site subject to disturbance depends on the differential responses of species; some species may tolerate the disturbances, while others may become locally extinct (Sagar *et al.* 2003). According to the Jaccard's index values, the similarities in species
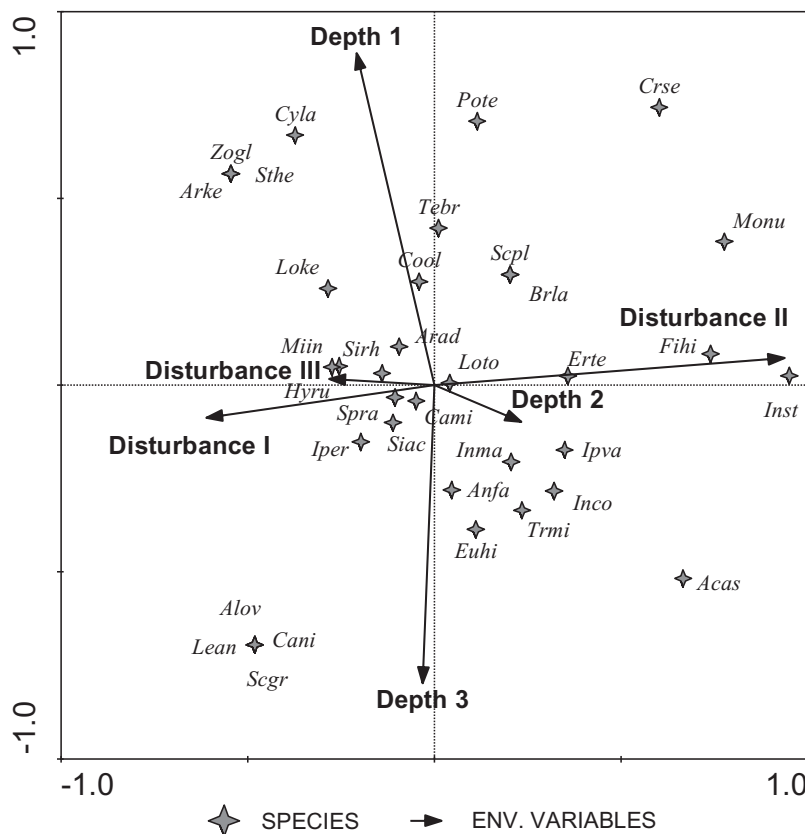
Figure 6: triplot from a CCA of species to environmental variables (disturbance level and depth of soil sampling). The species are listed by the first four letters of the genus and the specific epithet.

composition between the different levels of disturbance are low, except between disturbance levels I and II (for which we obtained a similarity index of 30%). The low similarity presumably reflects differences in habitat conditions (particularly stresses).

Density and spatial distribution of seedling populations

Patterns of tree regeneration following natural or anthropogenic disturbances are determined by interactions between the disturbance regime (i.e. intensity, frequency, scale) and species' traits (i.e. life history, physiology and behavior) (Pickett and White 1985). Modes of regeneration, i.e. from sprouts, seedling banks or seed banks may influence the success or dominance of a species in successional communities. Consequently, shifts in species composition following disturbances can arise from differences in species-specific modes of persistence through these disturbances. Within the studied plots there were relatively high numbers of juveniles (individuals with dbh < 2.5 cm), indicating that the vegetation could recover if these seedlings can avoid (or tolerate) stresses during their critical stages of development and reach higher diameter and height classes. A relatively high density of seedlings was observed in plots of disturbance severity level I, probably because of the relatively low trampling and browsing pressure (Brits *et al.* 2002). Thus, woody regeneration should be hindered less, and small individuals should have higher chances of developing to maturity than at sites with more severe disturbance. Variations in species' propagation strategies may also contribute to the high densities (Baskin and Baskin 1998). The abundance of juveniles of some species in plots with all three disturbance levels (*Combretum collinum*, *Combretum nigricans*, *Detarium microcarpum*, *Gardenia erubescens* and *Terminalia laxiflora*) may be related to coping mechanisms or intrinsic factors they have evolved that permit them to cope with several disturbances simultaneously.

The standardized Morisita's index value varied depending on the species and exceeded 0.5 for 98% of the recorded species. However, in contrast to previous findings (Sagar *et al.* 2003), none of the species dispersion patterns changed with changes in disturbance severity. Overall, the seedling populations of all species examined displayed clumped distributions at all three disturbance levels. This distribution pattern probably reflects the dominance of clonal propagation in the area, but also by low dispersion capacity, distribution of resources and facilitation among individuals which allows many plant species to persist in disturbance-free periods and is promoted by the disturbances that frequently occur in most African savanna ecosystems (Bognounou *et al.* 2010; Ky-Dembele *et al.* 2007). Accordingly, a substantial proportion of species detected in the survey have been identified as resprouters, although they also regenerate by seeds under certain circumstances. These include *Acacia macrostachy*a, *Azadirachta indica*, B. *ferruginea*, *D. cinerea*, *D. mespiliformis*, *P. biglobosa*, *P. erinaceus*, *S. latifoliu*s, *V. paradoxa*, *I. doka*, *Lannea velutina*, *Xeroderris*

stuhlmannii, *P. suberosa*, *D. microcarpum* and *Pseudocedrela kotschyi*. However, the transition from juvenile to sapling and adult stage depends on many abiotic and biotic factors, such as amount of rainfall, soil properties or hydrology and other anthropogenic disturbances (Kozlowski 2002; Sagar *et al.* 2003). Similarly, recruitment of species from the soil seed bank for regeneration is likely to be influenced by numerous factors related to the surrounding (standing) vegetation, the age of the forest stand (successional time), forest edge effects, soil conditions and the nature of disturbance events.

Seedbank richness and density

In total, 2300 seeds belonging to 35 species, 29 genera and 15 families were found after incubating soil samples for four months. The most common families were Poaceae (51.33%) followed by Fabaceae (20.67%). The results from the soil seedbank assessment provide some support for Huston's dynamic-equilibrium model, but do not support the intermediate-disturbance hypothesis. Our analyses show that species richness and species density may display opposite responses to disturbance, and that certain species of the Poaceae family *Aristida*, *Eragrostis*, *Schizachyrium* and Malvaceae family *Sida* commonly germinate following disturbance. Similarly, De Andrade and Miranda (2014) found that Poaceae (64%) are often the most abundant species following fire in savanna, and Li *et al.* (2014) noted that *Eragrostis pilosa* is one of the five most common annual species in the soil seed bank.

The numbers of species and densities we recorded were high compared with those obtained by Diawara (2012) in two Sudanian savanna–woodlands in the Centre West region of Burkina Faso. Our soil seed banks were dominated by herbaceous species, implying that herbaceous species have better chances of establishing from the soil seed banks following disturbance than tree species. Previous research has shown that existence and persistence of seeds in the soils are partially influenced by seed production and intrinsic attributes of seeds (Luzuriaga *et al.* 2005). The fact that most of the dominant tree species were not found germinating from our soil samples suggests that their regeneration from seeds may have been prevented by different type of dormancy (e.g. mechanical) that was not broken during the length of the study (Bewley *et al.* 1994). This points to one of the weaknesses of the seed germination method used in this study which ignores the plant species with dormant seeds (Price *et al.* 2010). For instance, the woody species might have been ignored because of this methodology defect.

Other studies using the seedling emergence method with other mean of releasing dormancy in relatively similar environment indicate that perennial species may contribute in the species richness of the soil seed bank (Fisher *et al.* 2009). However, as our study focused on readily viable seed for *in situ* restoration of vegetation, we simulated natural habitat conditions for seedbank and no soil pre-treatment has been used to break dormancy of dormant woody seeds. This may explain that no woody species was found. The dominance of

herbaceous species could be attributed to ease of dispersal by various agents, such as wind and water, because of their light weight. These results are consistent with findings by Baskin and Baskin (1998) and Martins and Engel (2007) that seeds of herbaceous weeds and forbs dominate the soil seed banks in dry and/or seasonal ecosystems, while few tree species produce long-lived seeds that can accumulate in the soil. The depletion of woody plants by disturbance opens up resources that are exploited by other life forms, and the germination of perennial species, despite their low richness, can improve ecosystem resilience after disturbance. According to Caturla et al. (2000) and De Andrade and Miranda (2014), these species are capable of maturing after disturbance, thus allowing them to successfully add to the seed bank. Perennial graminoids may also be promoted by their resprouting capacity, and their sexual reproduction is enhanced post-fire. The post-fire recruitment increases genetic variability and contributes to the persistence of plant populations.

We conclude that annual and perennial forbs, and graminoids, can benefit from the reductions in competition with perennial vegetation that follow disturbance. The dominance of *Loutedia togoensis*, which is a competitive species (Seghieri et al. 1995), is favored by grazers avoiding it after it flowers. However, the grazing intensity and the time of the year when grazing occurs are all potentially important factors that vary from 1 year to another. In addition, some species, such as *Achyranthes aspera*, have seeds that stick to animals and are dispersed over long distances, while most herbaceous species are dispersed by wind (Teketay 1996).

Distribution of seeds in the soil profile

The analysis of seeds' vertical distribution in the soil showed that seed densities were generally highest in the upper 3 cm of soil and gradually decreased with increasing depth, in accordance with previous reports (Teketay 1996). According to Putwain and Gillham (1990) the predominance of soil seed (herbaceous and other sedge species) in the top 5 cm layer, is due to high litter accumulation. Conversely, the ability of seeds to germinate decreases with increasing soil depth (Baskin and Baskin 1998), as evidenced by the decreasing densities of germinable seeds in deeper soil layers.

There were low similarities in species composition of the soil seed banks at the three study sites, possibly due to variation in the intensity and types of disturbances between them. Jaccard's coefficients of similarity also indicate that there was very little similarity between above-ground and soil seed bank flora at all three sites, as reflected in the ordination diagram. This result is consistent with findings of other soil seed bank studies in tropical regions (Lemenih et al. 2005; Wassie et al. 2006). One of the main reasons for the disparity between above-ground vegetation and soil seed bank flora is probably that seeds of the woody plant species present in the above-ground flora, after dispersal, germinate during the first period with favorable environmental conditions. These species have transient seeds that only survive for a short period in soils,

in contrast to long-lasting herbaceous seeds. For each soil depth, the Jaccard similarity index indicated low similarity between the three levels of disturbance, corroborating findings by Dreber (2010) and Salazar et al. (2011). The variation in seed density in the three successive soil layers may indicate differences in terms of seed longevity in the soil, mode of seed dispersal and seed predation.

Dissimilarity between the seed bank and above-ground vegetation

A particular feature of the soil seed banks was their lack of close association with the standing vegetation. No tree species' seeds were encountered in the soil seed banks examined in this study. Even the understory species component of the vegetation was not closely related to the soil seed bank. The pattern of species representation also differed from site to site. Comparisons of the soil seed bank species and seedling species in the degraded areas examined in this study showed that they had little correlation. The fact that the seed bank characteristics in this study represents for a short time periods within the year of investigation, a few plant species with transient seed banks at other time periods may have been missed in the samples we took; thus emphasizing the dissimilarities between our soil seed bank and standing vegetation. However, the current result is consistent with Hopfensperger (2007) review on the relationship between above and below-ground species which revealed low similarity between seed bank and vegetation composition. DCA analysis revealed that woody species were far more abundant among seedling populations in disturbed areas than in the seed banks, indicating that their regeneration stemmed from formerly suppressed understory seedlings. However, as found in the present study, much of the recent evidence from forest seed bank studies suggests that the flora of soil seed banks is not closely associated with the standing vegetation (Mukhongo et al. 2011). Disturbed habitats generally have less relation between the species present in the seed bank and the vegetation (Tessema et al. 2012; Wellstein et al. 2007).

The results from the soil seed bank study revealed that there were large quantities of seeds of herbaceous species, but no woody species were detected in the germinable seed bank. This is consistent with findings in several studies (Lemenih et al. 2005; Wassie et al. 2006) of high proportions of viable seeds of herbaceous species and low proportions of woody species in the soil seed bank. The former is probably due to the ability of grasses, sedges and herbaceous plants to produce numerous small, persistent seeds, while the lack of woody species is due to the relatively short residence time of seeds of most woody savanna species. According to Teketay (1996), most of the tree species produce seeds that germinate within a few days or weeks after dispersal and do not form large soil seed banks. Other factors that probably contribute to the difference in composition of seed banks are that the seeds of large woody species are heavily predated and decompose rapidly (Teketay 1996). Moreover, because of their large size

they cannot be easily incorporated into the soil seed bank and thus remain on the surface. Thus, they will be affected by surface fire set by the local people to create space for grazing land. They are therefore also exposed to other severe stresses. Furthermore, due to their fruiting behavior some tree species produce seed infrequently.

Restoration perspectives

The results strongly indicate that disturbed areas of National Park W have large populations of buried seeds of herbs, grasses and sedges. Considering that savanna is dominated by herbaceous species and that the studied sites are subject to a range of disturbances, the results also provide strong indications of the general succession of savanna vegetation. After severe disturbance, the grass species establish first, cover the soil and protect it from erosion, allowing colonization of the soil by mites and other invertebrates that help to improve the soil properties. The results also indicate that restoration of disturbed sites from the soil seed bank may be limited by the lack of sufficient viable tree seeds in the soil for restoring previous plant community structures and functions. The high abundance of herbaceous seeds may drive ecological restoration towards savanna-type vegetation rather than a transition to perennial cover. However, the herbaceous seed bank might play an important role in early stages of the successional process in degraded areas by fostering the growth of small vegetation patches capable of trapping tree seeds dispersed into the site. Accordingly, seed-bank densities are higher in vegetated patches than in bare soil patches in many vegetation types ([Marone *et al.* 2004](#); [Pugnaire *et al.* 2000](#)). Nevertheless, reliance on the seed bank does not seem to be a good strategy for restoring degraded areas in the studied reserve, so human intervention is probably needed to accelerate forest recovery. Key actions are likely to include alleviation of anthropogenic impacts in the ecosystem, site manipulation to improve environmental conditions for seedling establishment and growth, and possibly seed or seedling addition.

Conclusions and management implications

The overall objective of this study was to generate knowledge that could facilitate efforts to improve the management and restoration of degraded areas in the focal natural reserve and similar ecosystems. The results indicate that there is low diversity of woody species in the degraded areas, which are dominated by species of the Combretaceae, Caesalpiniaceae, Mimosaceae and Rubiaceae. Also, no significant differences between disturbance levels were detected in terms of density, diversity and other structural parameters of the vegetation.

Although no significant differences were found between plots with different disturbance levels in terms of species richness, the calculated Jaccard's indices showed dissimilarity between them. Overall, seedling populations of all species examined displayed clumped distributions at all sites. Seed densities in the soil also decreased with increases in depth at all sites. In addition, the dominant vegetation life form differed between the standing vegetation and the soil seed bank life forms at all three sites. The study showed that the soil seed bank could contribute, at least in this study area, to the recolonization of degraded sites with herbaceous species. However, restoration of native forest flora, particularly of woody species in degraded habitat types of this biosphere reserve, may be difficult if it is to rely on natural processes. Therefore, intervention is crucial to enhance the regeneration of poorly represented species through planting seedlings and providing an external supply of tree propagules. Nevertheless, studies should continue in other local habitats to improve understanding of the role of the soil seed bank in the recolonization of disturbed areas and constraints on natural regeneration. Also, since seed bank sampling on a single period may miss transient species, seasonal seed bank dynamics should be followed in future studies.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Plant Ecology online*.

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