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**Herbaceous seeds dominates the soil seed bank after long-term prescribed fire, grazing
and selective tree cutting in savanna-woodlands of West Africa**

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Abstract

The soil seed bank (SSB) is an important source of resilience for plant communities subjected to disturbances. This study aimed to identify characteristics of the SSB, its relationship with aboveground vegetation (AGV), and its significance for restoration of vegetation in West African savanna-woodlands. Data were collected from two long-term factorial experiments established in 1992 in Burkina Faso to examine the long-term ecological effects of grazing, early fire, selective tree cutting on savanna-woodland ecosystem. A total of 1,920 soil samples were taken from three soil layers (i.e. 0-3 cm, 3-6 cm and 6-9 cm) and the SSB was assessed using the seedling emergence technique. The emerged seedlings were dominated by non-woody taxa. Only two woody species that were *Flueggea virosa* and *Mitragyna inermis* emerged, showing that woody species feature little in the SSB. The SSB density and richness decreased significantly with soil depth. Non-metric multidimensional scaling (NMDS) ordination indicated a lack of correspondence between the AGV and SSB. The results suggest site-specific responses to disturbance also following long-term disturbance, the SSB will be ineffective in regenerating the remnant vegetation of West African savanna-woodlands. Hence, ensuring the resilience of West African savanna woodland ecosystems will require targeted introductions (i.e. planting and seeding) of indigenous species and a reduction in on-going disturbances.

Keywords: disturbance ecology; plant functional types; regeneration; seed bank; species richness

Introduction

Ecological resilience is defined as the capacity of a system to return to its original state after disturbance events (Holling, 1973), therefore it is important for maintaining desired ecosystem functions (Myers-Smith et al., 2012; Todman et al., 2016). Savanna ecosystems experience different forms of soil and vegetation degradation due to different kinds of disturbance and their changing regimes including wood cutting, conversion into cultivated land for subsistence farming, uncontrolled livestock grazing often under high degree of intensity and climatic variations (Scheiter and Savadogo, 2016). Moreover fires frequency and extend of burnt areas has increased (Caillault et al. 2014; Larris, 2002). These disturbances can affect established vegetation, decrease plant biomass, survival and seed production, and affect the livelihoods of many local forest-dependent people (Scheiter et al., 2019). Disturbances can also create gaps with distinctive characteristics, leading to potentially positive changes in local environmental and biotic conditions that can trigger the recruitment process of different species groups. During recovery after disturbance events, plants that grow may originate from four types of sources: seedling banks and advanced regeneration (i.e. from seedlings and saplings already present); vegetative reproduction (i.e. from stem and root sprouting); seed rain (i.e. from seeds being dispersed by biotic and abiotic agents from neighboring sites); and the soil seed bank (SSB) (Garwood, 1989).

The SSB is defined as the mature viable seed stock existing at the soil surface, or buried in the soil, in a specific moment and place (Swaine, 2001; Walck et al., 2005). The SSB density and diversity are important for determining the likely initial floristic composition following disturbance and its trajectory during the restoration phases (Thompson et al., 2003). A high SSB density and diversity (woody and perennial grass species) could accelerate the ecosystem

recovery following disturbance. Thus, the pool of lived seeds in the soil ensures the continual occupation of an ecosystem and also serves as a gene pool (Mcgraw et al., 1991).

Seed stock depends on the balance between inputs and outputs, and on seed bank strategies, due to germination behavior and temporal patterns of seed dispersal (Dalling et al., 1998; Martins and Engel, 2007). Therefore, determining the quantity of seed available in the SSB gives valuable insight into both the vulnerability of a species to local extinction (absence of a species in the SSB) (O'Connor and Pickett, 1992), and the likelihood of species maintenance and/or invasion (increasing dominance of a species in the SSB) (DiTomaso, 2000). Similarly, the composition of the SSB becomes a crucial indicator of possible successional trends (Snyman, 2004) and the long-term survival and resilience of plant populations (Dreber et al., 2011; O'Connor and Pickett, 1992). In savanna communities, single or multiple disturbance agents acting independently or interactively commonly influence the SSB.

Grazing is common in this system and the effects of grazing on SSBs and aboveground vegetation (AGV) are related to its intensities and climatic conditions. Heavy grazing involves the removal of plant parts from ground cover vegetation, shrubs and saplings, and damage through trampling. Under heavy grazing, impoverished AGV and SSBs may become limiting factors for vegetation recovery (Sternberg et al., 2003, Tessema et al., 2012).

Compared to grazed sites, the SSB at un-grazed sites typically possesses a greater number of species and a higher species density (Mayor et al., 2003). Indeed, previous studies carried out in savanna-woodlands found that lightly grazed sites have higher species richness than heavily grazed sites and that species richness may increase significantly (Sanou et al., 2018).

Fire is an important and frequent disturbance factor that affects savanna ecosystems, by exerting a large influence on the composition and density of SSBs (Auld and Denham, 2006; Keeley and Fotheringham, 2000). It has also a direct effect on vegetation that can indirectly

89 affect the richness and abundance of soil seed bank. The influence of fire on the SSB and
90 herbaceous vegetation layer mainly depends on its intensity, frequency and season (Cox and
91 Allen, 2008; Lipoma et al., 2018; Minor et al., 2017). Fire opens up spaces in plant
92 communities that can be occupied either by the re-sprouting of established plants or by the
93 establishment of new plants from seed (Whelan, 1995) particularly for obligate seeders. The
94 season of fire can influence SSB dynamics by interacting with reproductive phenology, and
95 fires that are synchronized with seasonal peaks in SSB density will influence the survival and
96 germination of a greater number of seeds. Smoke can act as a cue to break dormancy in the
97 SSB, suggesting that fire favours germination of plants that have evolved a fire-tolerant life-
98 history strategy (Liyanage and Ooi, 2017; Ren and Bai, 2016).

99 Canopy gaps created by single or multiple tree deaths due to selective cutting and natural
100 mortality provide more light, space and nutrients for the establishment and growth of
101 herbaceous and woody species. These favorable conditions facilitate germination of the SSB
102 and contribute in the recolonization process. Selective tree cutting reduces seed production
103 through the harvesting of mature plants, thereby impoverishing the SSB. In savanna-
104 woodlands, the canopy gaps can also create unfavorable thermal conditions and favour the
105 growth of drought-tolerant species, thereby contributing to competitive exclusion processes
106 (Savadojo et al., 2009; Wiegand et al., 2006).

107 In sum, the frequent disturbances factors in savanna-woodlands that are fire, grazing and
108 selective cutting and their co-occurrence in time and space have not only negative effects on
109 these ecosystems but they can show beneficial effects depending on their intensity and timing
110 suggesting their possible use as management tools with due caution to the control of their
111 implementation conditions. Most ecologically based disturbance management policies in
112 West African savanna recommend annual early fire (Zida et al., 2007) and selective tree

cutting of 50% of the merchantable standing volume on a 20-year rotation period. Light to moderate livestock grazing has been recommended (Zida et al., 2007; Savadogo et al. 2007) as it can increase plant diversity, increase ground cover and assist the re-establishment of desirable grass, forbs and shrubs. Unfortunately, these management prescriptions are not driven by data of long-term observations particularly on SSB.

In this study, we assessed the AGV and compared this with the emergence of seedlings from soil samples taken at different depths from plots subjected to long-term fire, grazing, selective tree cutting. Relationships between the AGV and SSB and possible sources of dissimilarity in seedling emergence are discussed. We hypothesized that: (1) SSB richness and density on 20-year-old undisturbed sites would be greatest and reflect a long vegetation history because of long-term accumulation and (2) in contrast, in repeatedly disturbed communities, SSB diversity would be negatively affected and could not potentially be regarded as a sole source for restoration. The paper concludes with a perspective on appropriate restoration management of disturbance agents to improve the resilience of savanna-woodlands.

Materials and methods

Site description

The experimental sites are located on flat terrain in Laba (11°40' N, 2°50' W) and Tiogo (12°13' N, 2°42' W) State Forests in Burkina Faso, West Africa (Fig. 1). Both sites are at an altitude of 300 m a.s.l. The Laba and Tiogo State Forests were delimited by the colonial French administration in 1936 and 1940, and cover 17,000 ha and 30,000 ha, respectively. Both forests are located along Burkina Faso's only permanent river (Mouhoun River). Phytogeographically, the study sites are situated in the Sudanian regional centre of endemism in the transition from the north to the south Sudanian Zone (Fontès and Guinko, 1995). The vegetation type at both sites is savanna-woodland, characterized by a closed tree canopy with

several woody strata and a sparse grass layer subject to sporadic and patchy fire. The annual grasses are *Andropogon pseudapricus* Stapf. and *Loudetia togoensis* (Pilger) C.E. Hubbard and the perennial grasses are *Andropogon gayanus* Kunth. (dominant in Tiogo) and *Andropogon ascinodis* C.B.Cl. (dominant in Laba). The main forb species are *Borreria radiata* DC., *Borreria stachydea* (DC.) Hutch. & Dalz., *Cochlospermum planchonii* Hook.f. and *Wissadula amplissima* L.. Species in the families Fabaceae and Combretaceae dominate the woody vegetation component at both sites.

The experimental sites have a unimodal rainy season which lasts for about 6 months each year, from May to October. The mean (\pm SE) annual rainfall during the period 1992-2016 was 916 ± 150 mm for Laba and 842 ± 148 mm for Tiogo, and the number of rainy days per annum was 62 ± 15 and 61 ± 11 for Laba and Tiogo, respectively. Mean daily minimum and maximum temperatures are 16°C and 32°C in January (the coldest month), and 26°C and 40°C in April (the hottest month), yielding an aridity index of 3.5 for Laba and 3.7 for Tiogo. The most frequently encountered soils are Lixisols (Driessen et al., 2001). The soil at Laba is a shallow (< 45 cm depth) silty-sand, while it is mainly a deep (>75 cm) silty-clay at Tiogo. These differences on the phytogeographical location, the rainfall, and the types of soil between the both sites justified the choice of carrying out this study where the same factorial experiment comprising the same disturbances were applied 20 years ago.

Experimental design

Data were collected from part of a large factorial experiment (Savadogo et al. 2007) established in each of the two State Forests to examine the long-term ecological effects of selective cutting, early fire, grazing on savanna-woodland ecosystems. In this large factorial experiment, each experimental site (18 ha) was divided into eight half-blocks (2.25 ha) of which four were fenced to exclude livestock (hereafter referred to as non-grazed plots) while

the other four were open for grazing (hereafter referred to as grazed plots). Each half-block was further divided into nine plots of 0.25 ha (50 m × 50 m), separated from each other by 20–30 m perimeter and inter-plot fire-breaks and fence in order to avoid fire propagation and browsing in the unburnt and ungrazed plots, respectively. In total, each experimental site comprised four repetitions (blocks) of 18 treatment plots (50 m × 50 m) yielding a total of 72 plots. For the current study, we only considered four combined treatments namely control (no cutting, no fire, no grazing), early fire (no cutting, no grazing), grazing (no cutting, no fire), and selective cutting (no fire, no grazing) which were randomly assigned to four plots within each block (Fig. 2).

Selective cutting in the plots was conducted in December 1993 at Tiogo and in January 1994 at Laba and there has not been any other follow-up cutting. The selective cutting treatment involved removing 50% of the basal area at stump level. Except for the protected species, individual trees were cut according to the following size criteria: > 30 cm butt diameter for timber species, > 14 cm diameter at stump level for poles and fuelwood species, and > 8 cm diameter at stump level for fuelwood and other use species (Sawadogo et al., 2002). The prescribed early fire began in 1993 and was applied at the end of the rainy season each year (October–November) when the grass layer humidity was approximately 40%. The grazed plots at both study sites were open for grazing mainly by livestock (a mixed herd of cattle, sheep and goats) but also wild animals. The livestock carrying capacity in Laba State Forest is 1.0 tropical livestock unit ha⁻¹ (TLU ha⁻¹) and in Tiogo, it is 1.4 TLU ha⁻¹. But the grazing pressure applied at both sites was about half of this capacity (Sawadogo et al., 2005).

Soil seed bank (SSB) assessment

At each of the Laba and Tiogo experimental sites, soil samples for the SSB assessment were taken from 16 plots of 50 × 50 m (i.e. four plots for each treatment mentioned above: selective cutting, early fire, grazing and control). Each of the plots was divided into 100 subplots of 5 × 5 m, and then 20 subplots were considered in a systematic manner for soil sampling (Fig. 3). The soil samples for the SSB analyses were taken at the end of the rainy season (November –December 2013). At that time, the persistent seed bank from the previous growing season still has the potential to germinate, while the timing also coincided with peaks of current season seed dispersal. Thus, the samples may contain both transient and persistent seeds.

To investigate the composition, density and vertical distribution of the viable SSB, soil samples were taken by hammering a hollow 25 × 25 cm square metal frame into the soil in the opposite corners of each of the 20 selected subplots. The depth of the soil was stratified into three layers, being 0-3 cm, 3-6 cm and 6-9 cm (Kennarda et al., 2002; Savadogo et al., 2017a; Sileshi and Abraha, 2014) using a sharp knife. The litter layer was included with the soil samples, because it may contain a high number of seeds. In total, 1,920 soil samples (20 seed bank pits × 16 plots × 3 soil layers × 2 sites) were collected in the field and air-dried to prevent damage from heat and mould. The soil samples were transferred into plastic bags and transported to the greenhouse of the Institute of Environment and Agricultural Research at Saria Research Station for SSB determination.

From each of the sampled quadrats, soil cores from each sampling depth level were mixed to obtain a composite sample (Kassahun et al., 2009) before being placed into germination trays. We used the seedling emergence method because of its ability to quantitatively and qualitatively determine the viable fraction of readily germinable seeds (Espeland et al., 2010),

which is the component of the SSB most important for restoration management. The composite soil samples were spread in a thin layer in 384 polypropylene trays and arranged in a tunnel greenhouse where an ideal and uniform condition for germination of viable seeds was provided. Twenty trays containing sterilized sand were also randomly placed throughout the greenhouse to determine if there was any airborne continuation. The trays were kept continuously moist by daily watering and monitored over a 4-month period in order to avoid an underestimation (below 4 months) and overestimation (beyond 4 months) of the persistent SSB (Brown, 2011). During the experimentation, no species germinated in these control trays, indicating no airborne seed contamination. Every week, all trays were checked for emerging seedlings that were counted, identified and discarded. Those in the juvenile stage that were difficult to identify were retained for longer in trays until their determination. During this period, the soil samples were stirred five times to bring any non-germinated seeds to the surface. Temperature was maintained close to outdoor ambient conditions. Additionally, locations of the trays in the greenhouse were reorganized in each week in order to minimize micro-climatic differences (light and temperature conditions in the greenhouse).

Assessment of aboveground vegetation (AGV)

The sixteen plots of 50 m × 50 m for monitoring the SSB were also used to compare the SSB species with the AGV. All trees within the sixteen plots were identified and counted. The herbaceous layer was inventoried at a period where herbaceous species are easily identifiable, and it is the flowering stage of most herbaceous species using the line interception method (Levy and Madden, 1933). Also, all species present within the plots were recorded. Identification of species and families of the AGV used *The Plant List* (www.theplantlist.org).

Data analysis

The calculated parameters for the SSB composition were first analyzed with ANOVA considering the block as a random factor and the treatments applied as a fixed factor for each site. The models were fitted using the function ‘aov’ from the ‘stats’ package in R software. When a significant difference was detected, a pair-wise comparison was made using Tukey’s test at the 5% level of significance. To detect the effects of treatments (fire, grazing and selective cutting) and depth of soil sampling on the SSB in terms of density, composition and richness, the data were analyzed according to the following procedure. The number of germinated seeds and species richness both per plot and the soil sampling layer were first aggregated by plot and then converted into density (number of seedlings/dm³). To determine the vertical distribution of seeds in each treatment, the numbers of seedlings from each similar layer were combined to determine the density of each soil sample depth concerned. The density of seedlings (number/square meter of soil) was calculated using the following formula: Density = 100 × (cumulative total number of seedlings) / (volume of soil by polypropylene tray). Prior to analysis, data exploration was performed following the protocol described by Zuur et al. (2010). Since it was count data, we used a Generalized Linear Model (GLM) with a Poisson distribution to account for non-normal errors and increasing variance with increasing averages that are associated with count data. The GLM used in R statistical software 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, μ is the overall mean, α the effect of the treatment, β the effect of depth of soil sampling, and γ the interaction between the treatment and the depth of soil sampling. Disturbance factors and depth of soil sampling were considered as explanatory variables in the GLM. Examination of the residues revealed wide dispersion, so the results were reviewed

using penalized quasi-likelihood with Poisson error. GLM was performed using the stats package in R statistical software.

To evaluate β -diversity (similarity between treatments), Jaccard's coefficient of similarity index was computed based on presence/absence data of the species. Relationships between the species composition of the SSBs and AGV were tested by non-metric multidimensional scaling (NMDS). We calculated similarity matrices using the Bray Curtis coefficient, and the ordination was based on presence/absence of all taxa. The statistical significance of the NMDS results was tested using the permutation multivariate ANOVA with the software PC-ORD version 6.

Results

SSB composition

In total, 38 species belonging to 34 genera and 10 families emerged from the soil samples (Table 1). In terms of species richness, the experimental sites at Tiogo State Forest had a higher number of species (i.e. 35 species belonging to 32 genera and 10 families) than those at Laba (i.e. 24 species belonging to 22 genera and 8 families). The results indicated that, irrespective of the treatment, the two sites have 8 families and 21 species in common. Of these species, Poaceae comprised the largest family, with nearly 46% of the total species. Fabaceae and Malvaceae are common families in the plots subjected to early fire.

Of the 38 species that emerged from the soil samples, 95% were annuals. Only two tree species that were *Flueggea virosa* (Roxb. ex Willd.) Baill. and *Mitragyna inermis* (Willd.) O. Ktze. germinated from soil samples taken in the control and the grazed plots at Laba, respectively. At Tiogo, only *Flueggea virosa* was recorded in soil samples from the burnt and

grazed plots. Also, no perennial herbaceous species were encountered during the observation phase in the greenhouse. In terms of functional groups, the graminoid group was the largest group at both sites, represented by 58% of the species, followed by forbs (37%) and trees (5%).

Effects of treatments on SSB richness and density

The analysis of SSB species richness using the GLM with Poisson distribution showed that treatments and their interaction with soil depth had an insignificant effect ($P > 0.05$) on SSB richness (Table 2). Seed bank richness significantly decreased with increasing soil depth at the Laba sites ($P = 0.021$). Also, SSB richness at Tiogo site was higher from all upper soil layers than those of Laba (Fig. 4).

The analyses of SSB density indicated that the applied treatments and depth of soil sampling had a significant effect ($P < 0.05$) at both sites (Table 3). Like the richness, SSB density was the highest for soil samples taken from the surface layer and decreased significantly with increasing depth (Fig. 4). Thus, the deepest soil layers (i.e. 3-6 cm and 6-9 cm) had the lowest seed density. In addition, the seed densities at Tiogo were higher than those at Laba in all treatments and soil depths (Fig. 4 & 5). The seed densities within the SSBs were significantly different under different disturbance factors. The soil samples from the grazed plots at Laba had more seeds (270 seedlings/dm³) than the other three treatments (control, early fire and selective cutting), which had very similar values. In contrast, at Tiogo, the plots subjected to early fire had the highest density (720 seedlings/dm³), followed by the selective cutting (390 seedlings/dm³), grazing (354 seedlings/dm³) and control plots (180 seedlings/dm³), (Fig. 5).

The interaction between the variables (treatment \times depth of soil sampling) was not significant at Laba (Table 3), while it was marginally significant at Tiogo for SSB density ($P = 0.045$).

Similarity between the composition of the SSB and relationship between the AGV and SSB

Jaccard's index was calculated to evaluate similarity for species composition of the SSBs between the both sites. Thus, when comparing species composition of the grazed plots and the annually burnt plots, we observed that, unlike the plots at Tiogo, the plots at Laba were similar. This was indicated by the highest value of the Jaccard similarity index (i.e. $C_j = 0.62$) (Table 4). The plots that were subject to selective cutting had the lowest similarity to the species pools of the grazed and control plots at Laba (i.e. C_j values were 0.25 and 0.27 respectively). However, at Tiogo we observed a low species pool similarity between the different treatments (Table 4).

The comparison of the SSB composition at the both sites and their AGV revealed a little correspondence between them, particularly for ligneous species (Fig.6). Up to 97% of woody species and 36% of herbaceous species recorded in the AGV were absent in the SSB. The SSBs at the both sites partially reflect the floristic composition of their AGV. The results of the Non-metric multidimensional scaling (NMDS) showed a clear clustering between the SSBs of both sites submitted to the same treatments and the species composition of their AGV, suggesting a low similarity between the AGV and the SSB. In contrast, the species composition of the AGV at the both sites presented the relative high similarity than the species of the SSBs. The fit of the treatments onto the plots was statistically significant according to permutation multivariate ANOVA ($r^2 = 0.802$, $P = 0.00128$), which revealed that the different treatment affected the floristic composition of the SSB.

330

331 **Discussion**

332 **Botanical composition of the SSB**

333 Our encountered SSB richness was higher than that found by Savadogo et al. (2017). They
334 found that emerged seedlings from SSB samples taken from disturbed sites in the W National
335 Park comprised 35 species from 29 genera and 15 families, with the dominant family being
336 Poaceae (51%). Poaceae (45%), Cyperaceae and Fabaceae (18%) were the most common
337 families found at both of our study sites. Their predominance in the SSB composition could
338 be explained by the fact that they contain the highest number of dispersal mechanisms
339 (dyszoochory, epizoochory, endozoochorie, anemochory, hydrochory and autochorie, which
340 are all long-distance dispersal mechanisms) (Zerbo et al., 2017). According to Zizka *et al.*
341 (2015), Poaceae and Fabaceae are the most common families in West African savanna regions
342 that are frequently disturbed. Also, Fabaceae and Malvaceae were found to be common
343 families in the plots subjected to fire at both of our study sites. Keeley and Fotheringham
344 (2000) note that species from Fabaceae, Rhamnaceae, Malvaceae, Sterculiaceae, Cistaceae
345 and Convolvulaceae are widespread in many fire-prone ecosystems. This situation may be
346 explained by the fact that the species of these families require fire to break their seed
347 dormancy. This is an indication of their adaptability to disturbance impacts, making them
348 worthy of consideration for rehabilitation programs in tropical savanna ecosystems.

349

350 Most species in the SSB flora (i.e. up to 95% of emerged seedlings) were herbaceous species,
351 and there was little evidence of woody species. This finding is in line with several studies
352 carried out in African savanna-woodlands that have reported a predominance of herbaceous
353 species rather than woody species in the SSB, and added that the abundance of annual species

is due to grazing impacts (Dreber and Esler 2011, Savadogo et al. 2017). The high density of herbaceous species' seeds in the SSB may be related to species traits. Such traits include: (1) herbaceous species produce numerous small and long-lived seeds that, compared to larger seeds, have a better chance of escaping predation by granivores, and (2) seeds of herbaceous species progressively accumulate in large quantities in the soil and can remain viable in the soil for much longer than other seed types (Arnolds et al., 2015; Martinez-Ghersa et al., 2000). The ability of herbaceous plants to quickly colonize disturbed sites is also because they usually have small seeds which can pass through litter faster, thereby reaching the humus and mineral soil layer in a shorter time than larger seeds that are more prone to predation (Egawa and Tsuyuzaki, 2013). Thus, compared to tree species, herbaceous species have better chances of recovery from the SSB on disturbed sites (Bernhardt and Ubel, 2000). Also, as seed size and longevity are often negatively correlated, this could be the main factor for the scarcity of tree seed and perennial herbaceous species in SSBs (Bossuyt et al., 2002).

Furthermore, the absence of perennials in the SSBs is probably due to the fact that annual production of perennial seeds is generally low and their longevity is also limited (Ford, 2015). Other explanatory factors may relate to the applied disturbance treatments at both sites being the sources of the prominence of annual species. According to Savadogo et al. (2008), disturbance factors such as fire tend to reduce the abundance of perennial grasses. Several studies have reported that herbaceous species typically dominate the SSB, with only a few tree species being capable of accumulating long-lived seeds in the soil (Kunz and Martins, 2016; Mukhongo et al., 2011; Oke et al., 2006). According to Hanley et al. (2003), smaller-seeded species are more tolerant of the higher temperatures frequently experienced nearer the soil surface during fire. Thus, small-seeded herbaceous species are likely to benefit from their

ability to emerge from deeper within the soil profile (Hanley et al., 2003). Also, the lack or insufficiency of woody species in SSB taxa is due to their high vulnerability to disturbance factors and predation (Elberse and Breman, 1989; Obiri et al., 2005; Rouw et al., 2014). Furthermore, the insufficiency of tree species from the soil samples indicates that their regeneration from seeds may have been prevented by different types of dormancy that were not broken during the length of the study. It may also be due to the seed germination and single time of soil sampling methods used in this study leading to the exclusion of plant species with dormant seeds. Thus, these latter two factors highlight some limitations of the study's methodology. To bridge these limitations, further studies combining the use of the seedling emergence method with other means of releasing the dormancy of woody species' seeds and the collection of soil samples at two or more separate times are needed.

The fact that herbaceous taxa were the major constituent of the germinable seed bank is in contrast with the findings of Leckie et al. (2000) and De Andrade and Miranda (2014), who found that SSBs were dominated by seeds of woody species. Notwithstanding this, several studies have found evidence that woody species commonly contribute little to SSBs in tropical savannas (Lipoma et al. 2018; Rouw et al. 2014). *Mitragyna inermis* was recorded in our control plots and *Flueggea virosa* germinated from our burnt and grazed sites, indicating the effects of fire and grazing breaking the dormancy of seeds of certain species, particularly for fodder species. Dispersal via endozoochory is a trait related to herbivore tolerance, and its frequency is potentially higher in plants with grazing-tolerant life histories (Anderson et al., 2014). Hence, grasses are the dominant functional type germinating from the faeces of grazing animals (Shen et al., 2007). In our study, grasses were the dominant functional group observed in the SSB samples taken from both sites. The dominance of grasses is due to the

fact their seeds are primarily wind dispersed or via epizoochory (Perera, 2005). According to Bocksberger (2012), these species' predominance in the Sudanian zone could be explained by grazing pressure, which favors the dispersal of annual or small-sized herbaceous species. We can therefore concur with Dreber et al. (2011) that disturbances such as moderate grazing tend to favor the establishment of annual grasses over other functional groups.

For the deep silty-clay soil at Tiogo, the high germination rate on plots which were annually burnt could be explained by the fact that early fire favors the development of grasses (Mbaye and Ickowicz, 1998) and some forbs (Dayamba et al., 2010). Germination of forbs such as *Borreria scabra* is strongly stimulated by smoke because it releases the physical dormancy of the species' seed. However, fires at very regular intervals may cause a decrease in the germination rate of woody species, probably because of a reduction in their seed in the SSB, thus giving greater opportunity for the establishment of herbaceous species (Duguy and Vallejo, 2008).

Effects of treatments on SSB density and richness

The density and viability of the SSB depends on annual seed production, seed rain and material accumulation on the soil surface, resulting in changes in seed germination rates along the soil profile (Bonis and Lepar, 1994). Therefore at both of our study sites, including the applied treatments, the assessment of the seeds' vertical distribution in the soil showed that seed densities were highest in the first three inches of soil and declined with depth (Fig. 4). This finding is consistent with studies in East and West African savanna-woodlands, where the authors have found that the highest numbers of seeds are located in the upper soil layer (Hérault and Hiernaux 2004; Savadogo et al. 2017; Teketay 1996). In addition, the

predominance of soil seed in the upper 3 cm layer is mainly due to high litter or organic matter accumulation, but it is also well-established that the ability of many seeds to germinate decreases with increasing soil depth (Baskin and Baskin, 1998; Getachew et al., 2004; Putwain and Gillham, 1990).

Our results showed no significant effect of treatment on species richness, while it was the opposite for the SSB density at Tiogo (Tables 3 & 4). These results on the effect of applied treatment on SSB densities and richness concur with previous studies (Lipoma et al. 2018; Savadogo et al. 2017) that indicate both disturbance and seed depth affect the survival and germination probability of seeds in the SSB, which in turn affects population dynamics. The long-term effects of disturbances tend to eliminate the intolerant species to these disturbances decreasing the species richness of the SSB. Seed densities were higher at the sites subjected to grazing and early fire compared to the other treatments. The site-specific responses, could be explain by the types and structure of plant community present and their interaction with site specific ecological factors, such as soil and precipitation (Belsky et al. 1992). These results confirmed the findings of previous studies which have reported that moderate grazing increases seed numbers and species numbers (Dreber and Esler, 2011; Unger and Woodell, 1996) and that early fire permits the germination of grasses. Keeley and Fotheringham (2000) added that many species accumulating in SSBs are triggered to germinate by fire-related cues, such as heat shock. Generally, compared to late fire, early fire is of a low intensity and severity due to the high moisture content of fuels (Nikiema et al., 2005; Savadogo, 2007). Early fire therefore has a minor impact on seed viability while also removing litter cover thereby creating favorable conditions for germination and favoring tillering (Whelan, 1995). Also, Adkins and Peters (2001) added that germination of many herbaceous species is stimulated by smoke released during burning. These findings indicate that even if fire impacted on SSB density and

richness through smoke and soil heat, the high seed density was found in the plots subjected to early fire. As van der Valk and Pederson (1989) point out, prescribed burning may be used as a tool for the forest management prescriptions.

Grazers play an important role in seed dispersal, germination, SSB composition, enabling species' colonization of grazed sites, amelioration of soil condition by enhancing water infiltration, and through the localized fertilization effects of dung and urine (O'Connor and Pickett 1992; Savadogo et al. 2009). Both grazing and fire influence the amount of seed that sets and the conditions under which seed can emerge (O'Connor and Pickett, 1992). The highest number of seedlings found in the plots subjected to selective tree cutting at Tiogo compared to control plots, indicates that selective removal of trees can favor seed germination by opening up the tree canopy (i.e. creating space and increasing the availability of light) and reducing competition for water and nutrients (Frost et al. 1986; Savadogo et al. 2009).

Based on the SSB densities at Tiogo, the control plots (not subjected to any disturbance treatment) have the lowest values (Fig. 5). This result corroborated the findings of Savadogo et al. (2017) who found the lowest value of seed density in the least disturbed sites compared to intermediately and heavily disturbed sites. At Tiogo, the plots subjected to early fire had the highest density followed by the selective cutting treatment. This result showed that selective cutting creates favorable environmental conditions for buried seeds to germinate. This is consistent with other works that have argued that logging activities can positively impact the regeneration of certain species by opening up the canopy, reducing competition for resources such as water and nutrients, and favoring their seed germination (Dohu et al., 2018; Setterfield et al., 2005).

Similarity between the SSBs and AGV

The Jaccard similarity coefficient indicates a low similarity between the SSBs in the plots subjected to different treatments (Table 4). This result is consistent with those of Masunga et al. (2013), who found differences in plant species composition between their study's treatments (fire not grazing, grazing not fire, control [no fire and grazing], fire + grazing). Lipoma et al. (2018) also found a high dissimilarity between burnt and unburnt sites. Dreber and Esler (2011) reported a low similarity between their control plots and those subjected to disturbance, suggesting a preferred ecological niche of the species of their study according to spatial heterogeneity and disturbance. The spatial heterogeneity and disturbance reported in our study was created by 20-years of early fire, grazing and selective tree cutting, and this affected species richness, abundance and diversity of SSBs. The results of our NMDS ordination that evaluated the similarity between AGV and SSB through the Bray Curtis coefficient showed that the both vegetation shared few herbaceous and woody species, indicating little reflectance of the AGV in the SSBs. This supports the idea that most of the seeds in the soil come from outside of a stand via different dispersal mechanisms: seeds were dispersed over long distances, or large seeds and seeds with a large surface and volume are less likely to be incorporated into the soil (Bekker et al., 1998). In terms of the latter, Wang et al. (2009) argue that seed size may be another factor responsible for the scarcity of many aboveground species in SSBs, thus increasing the dissimilarity between the SSB and the AGV.

The low resemblance between the SSB and the AGV found in this study did not corroborate with the findings of Looney and Gibson (1995). These authors found through DCA ordination that the SSB and AGV were highly correlated. Many authors have tried to explain the

dissimilarity between the SSB and AGV. For example, Sileshi and Abraha (2014) argued that the persistent SSB is not capable of restoring all species of the extant vegetation. Li et al. (2017) reported that the great difference between the composition of vegetation and the SSB is possibly due to three main reasons: (1) the proportion of annuals and perennials in the SSB and the vegetation differs because perennial species are commonly lacking in the SSB, (2) many of the seeds in the SSB possibly fail to germinate during germination experiments due to differences in environmental conditions between the greenhouse and the field, and (3) different dispersal patterns lead to species differences between the SSB and the vegetation. Douh et al. (2018) reported that the floristic composition of the SSB somewhat depends on seed rain, which varies according to the seasonal phenology. Nevertheless, the emergence of annual herbaceous species could provide groundcover after disturbance events.

Conclusions

Our evaluation of viable seeds in the SSB at disturbed sites has provided valuable insights into the site-specific responses to disturbance, which accentuates the importance of landscape-scale approaches to understand the impacts of disturbances on composition and density of soil seedbank in savanna ecosystems. Our results demonstrated that 20 years of livestock grazing, prescribed early fire and selective tree cutting has induced changes in the SSB community, characterized by the relative abundance of annual herbaceous species. This situation highlights the slow and limited potential of the SSB to support the regeneration of savanna-woodlands characterized by predominant disturbances. The annuals are the pioneers that could provide groundcover after disturbance events. However, the high dissimilarity between the AGV and the SSB and the absence of perennial species in the SSB indicates that soil seed bank alone cannot restore the ecosystems. Human interventions such as alleviating the

disturbances, site manipulation in order to improve environmental conditions for seedling establishment and growth, the addition of seeds and seedlings of target species or the active transfer of propagules from adjacent undisturbed forest areas are needed to improve resilience of savanna-woodlands.

Contributions of the authors

DZ, PS and LS conceived the ideas of this research. LS, SD and DZ collected the data. LS and PS performed the data analysis. DZ, PS, and LS identified together the emerged seedlings and wrote the manuscript with valuable contributions from AT. All authors improved and approved the manuscript.

Compliance with ethical standards

This study does not infringe on any bioethical principles and no damage to biodiversity was inflicted carrying out this study

Conflicts of interest

The authors declare that they have no conflict of interest.

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Figure captions

Figure 1: Study site location showing the State Forests of Laba and Tiogo in Burkina Faso, West Africa.

Figure 2: Experimental design showing the four applied treatments at the two studied sites.

Figure 3: Layout of the sampling design employed for assessing the soil seed bank (SSB) and above-ground vegetation (AGV).

Figure 4: SSB density and richness according to depth of sampled soil at the Laba and Tiogo sites. Means \pm SE with different letters are significantly ($P<0.05$) different based on Tukey's HSD test.

Figure 5: Main effect of disturbances on the SSB density at the Laba and Tiogo sites. Means \pm SE with different letters are significantly ($P<0.05$) different based on Tukey's HSD test.

Figure 6: Ordination (NMDS) based on species composition of the AGV under different treatments and seedlings that emerged from the SSB samples.

Abbreviations: Laba and Tiogo are the two studies sites. The letters added to the Laba or Tiogo design – F (Fire), C (Cutting), Cntrl (Control), P (Grazing), respectively.

Figure 1

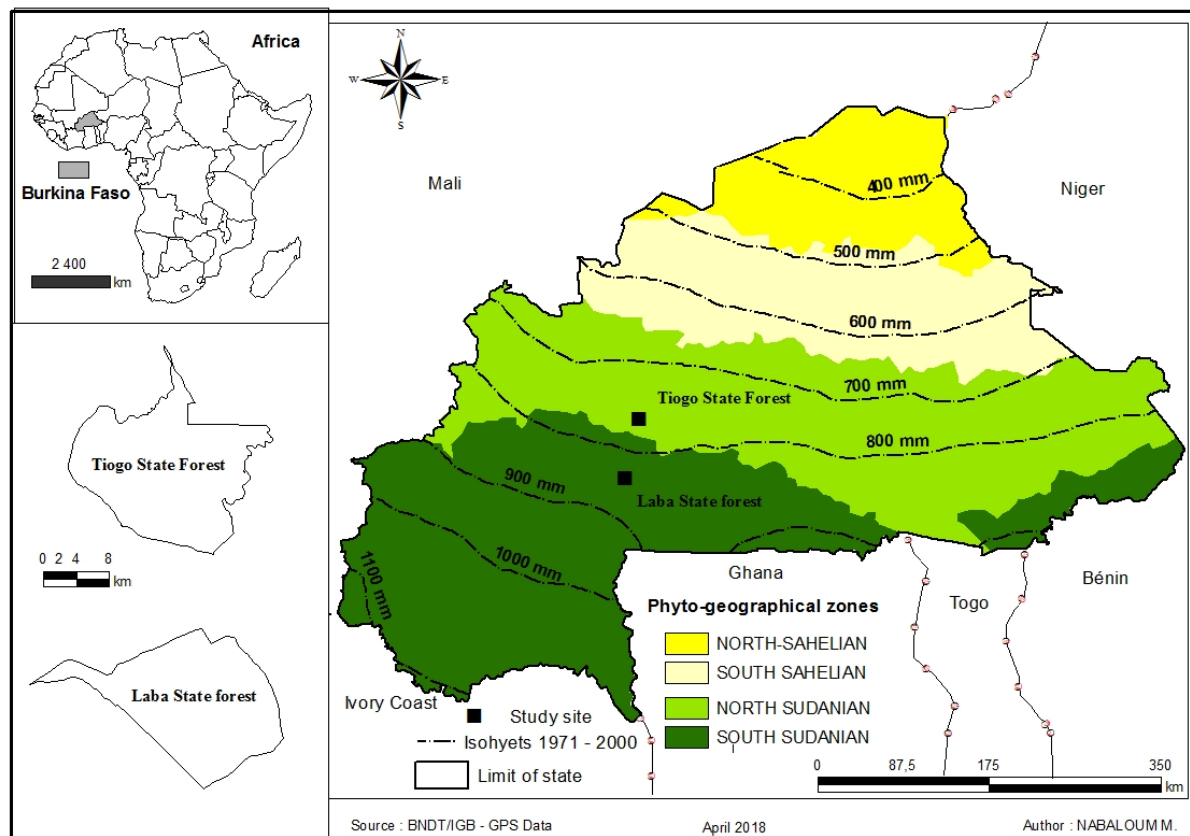


Figure 2

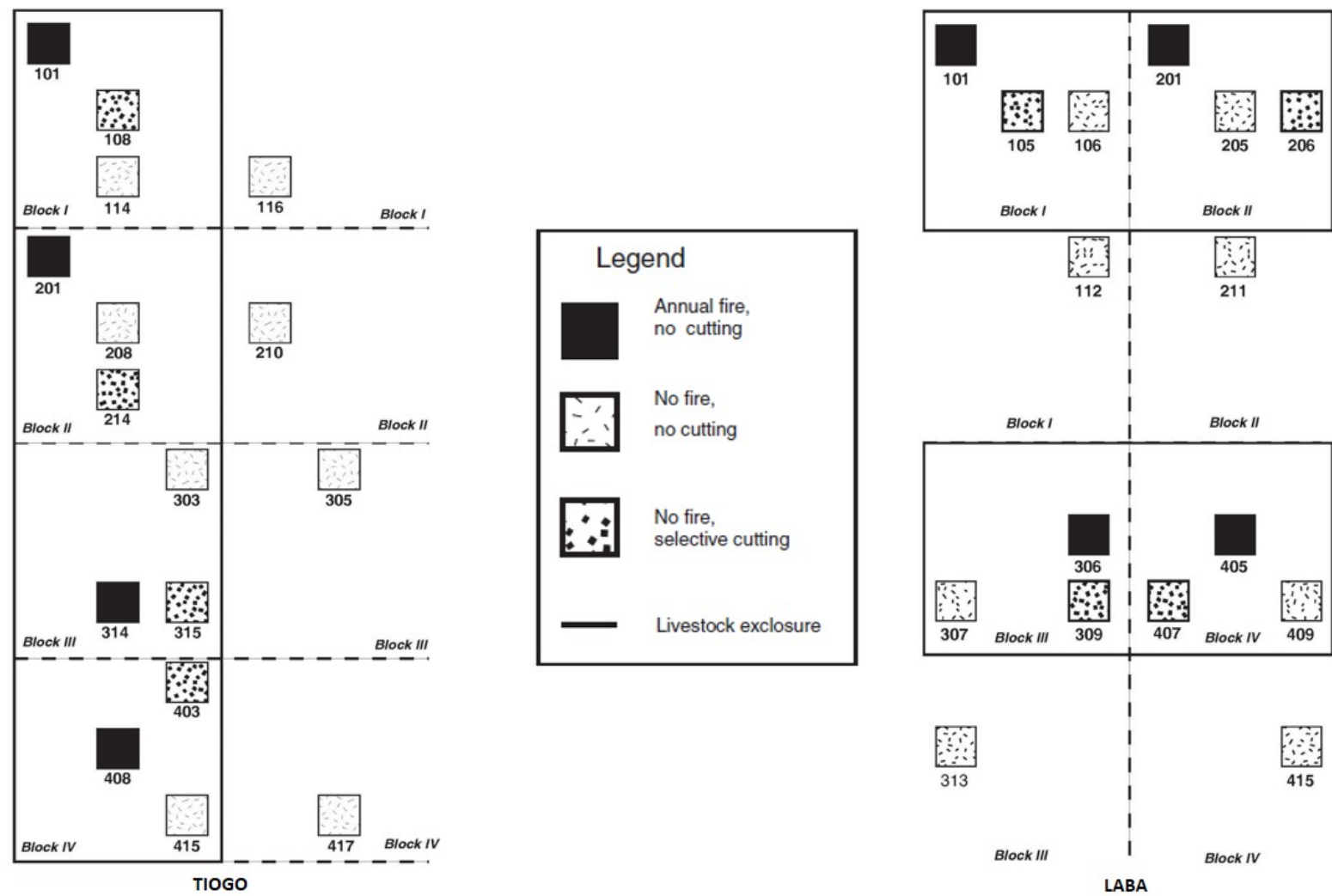


Figure 3

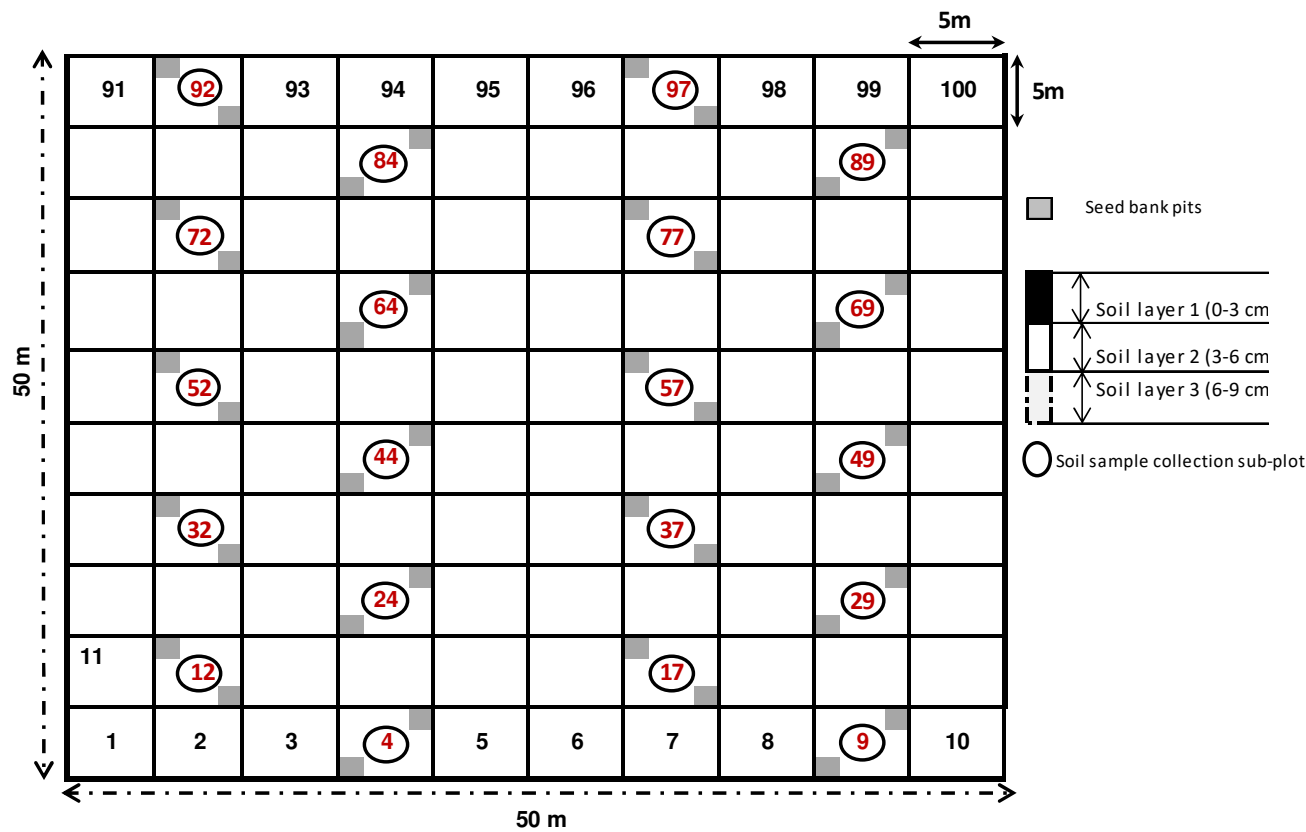


Figure 4

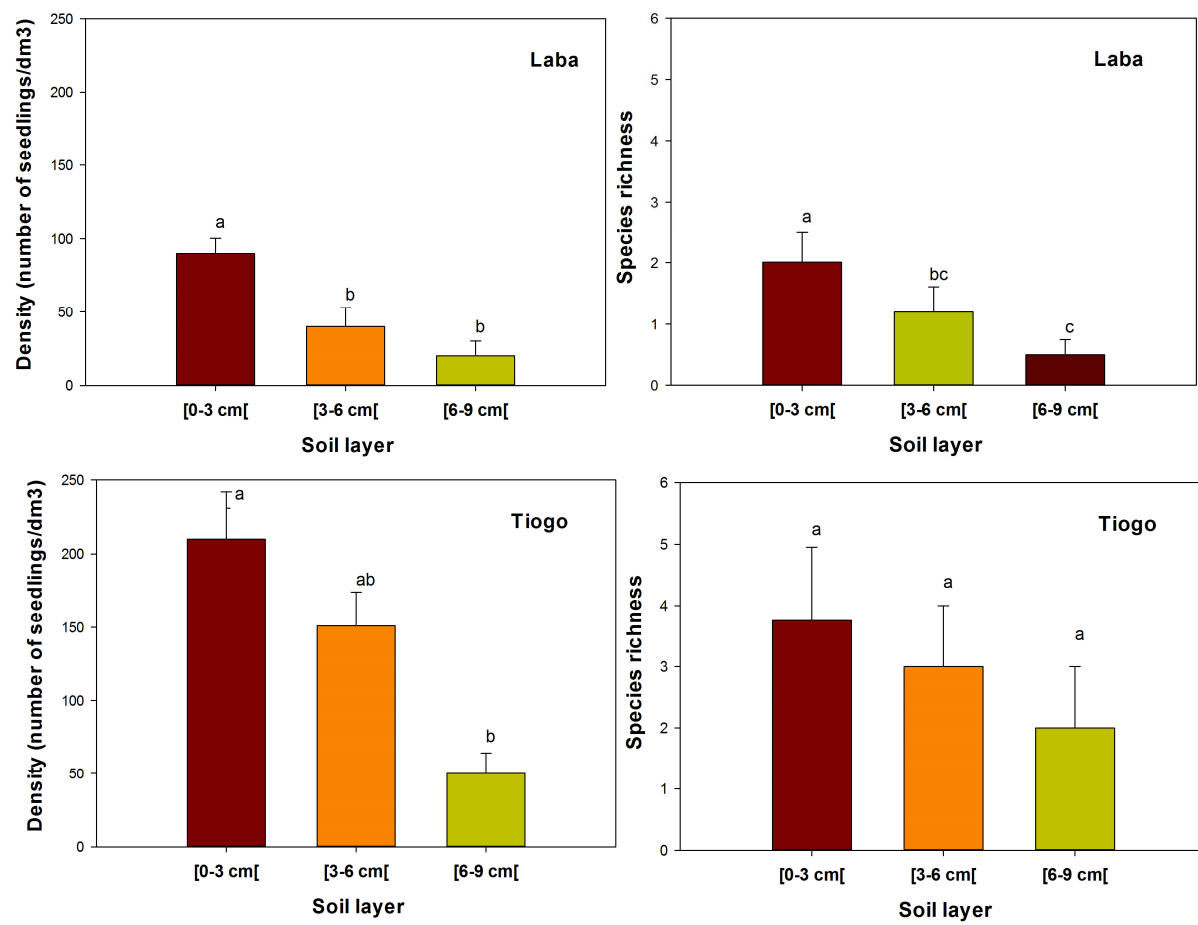


Figure 5

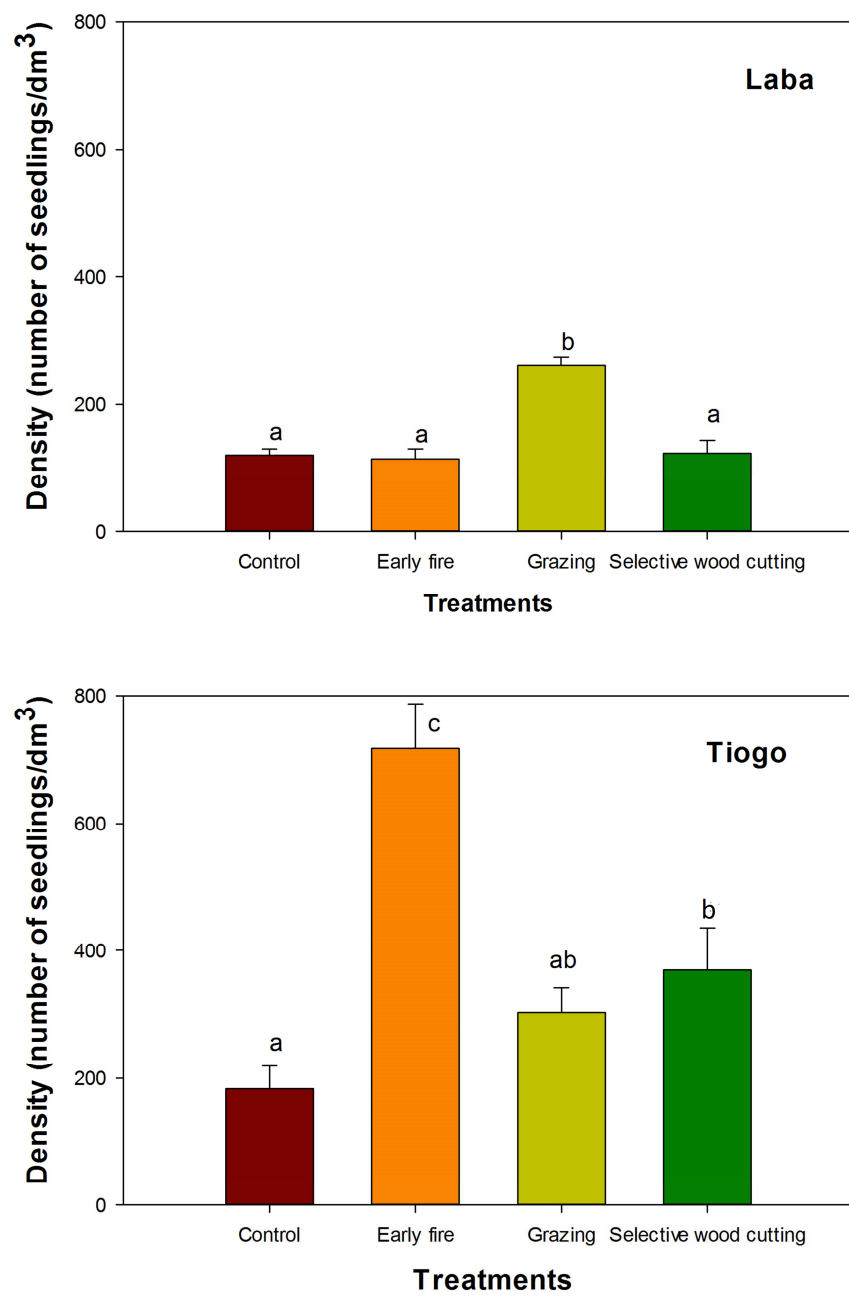


Figure 6

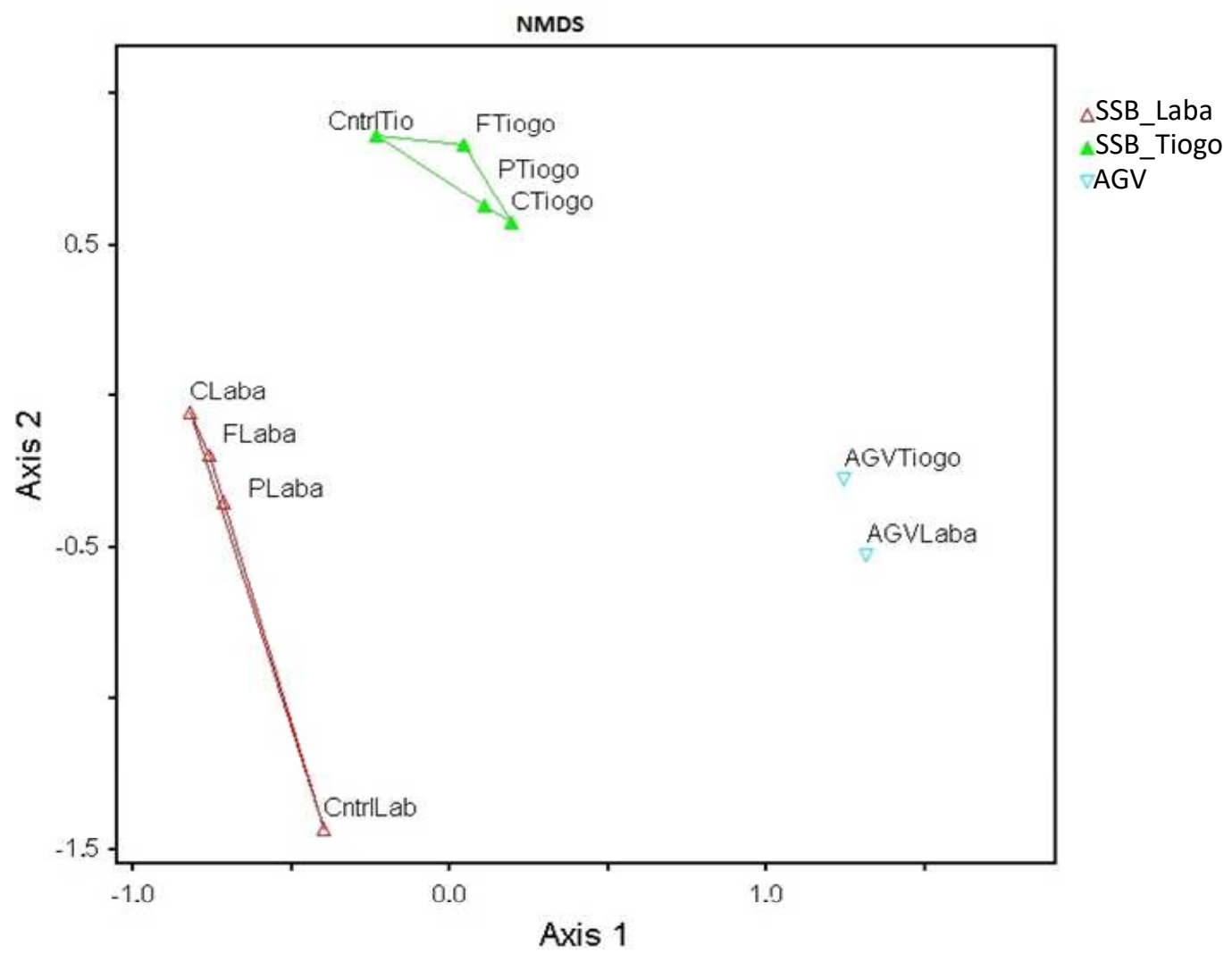


Table 1: Identified species in soil seed bank (SSB) samples from Laba and Tiogo State Forests according to different treatments: Selective cutting (SC), Fire (F), Control (C) and Grazing (G) The digits next to the names of species express the presence (1) or absence (0) of the species. The woody species that emerged from soil samples are in bold face and mph is microphanerophyte.

Species	Families	Life form	Functional group	Laba				Tiogo			
				SC	F	C	G	SC	F	C	G
<i>Acroceras amplexans</i> Stapf	Poaceae	Annual	Graminoid	0	0	0	0	0	0	1	1
<i>Amaranthus viridis</i> L.	Amaranthaceae	Annual	Forb	0	0	0	0	0	0	0	1
<i>Andropogon pseudapricus</i> Stapf	Poaceae	Annual	Graminoid	0	0	0	1	0	1	1	1
<i>Aristida kerstingii</i> Pilg.	Poaceae	Annual	Graminoid	0	0	0	0	0	1	1	0
<i>Aspilia bussei</i> O.Hoffm. & Muschl	Asteraceae	Annual	Forb	0	0	0	0	0	0	1	0
<i>Borreria stachydea</i> (DC.) Hutch. & Dalziel	Rubiaceae	Annual	Graminoid	1	0	0	0	0	0	1	1
<i>Brachiaria distichophylla</i> (Trin.) Stapf	Poaceae	Annual	Graminoid	0	1	0	1	1	1	1	1
<i>Brachiaria lata</i> (Schumach.) C.E.Hubb	Poaceae	Annual	Graminoid	1	0	0	1	0	1	0	0
<i>Cassia mimosoides</i> L.	Fabaceae	Annual	Forb	0	1	0	0	0	1	1	0
<i>Corchorus tridens</i>	Malvaceae	Annual	Forb	0	1	0	0	1	1	0	0
<i>Cyanotis lanata</i> Benth.	Commelinaceae	Annual	Forb	0	0	0	1	0	1	1	0
<i>Cyperus difformis</i> L.	Cyperaceae	Annual	Graminoid	1	1	0	1	1	1	1	0
<i>Digitaria argillacea</i> (Hitchc. & Chase) Fernald	Poaceae	Annual	Graminoid	0	0	0	0	0	0	1	0
<i>Digitaria horizontalis</i> Willd.	Poaceae	Annual	Graminoid	1	0	0	0	0	1	0	0
<i>Diheteropogon amplexans</i> (Nees) Clayton	Poaceae	Annual	Graminoid	0	1	1	1	1	1	1	1
<i>Diheteropogon hagerupii</i> Hitchc.	Poaceae	Annual	Graminoid	0	0	1	0	0	0	0	0
<i>Elionurus elegans</i> Kunth	Poaceae	Annual	Graminoid	0	0	0	0	0	1	0	0
<i>Bulbostylis hispidula</i> (Vahl) R.W. Haines	Cyperaceae	Annual	Graminoid	0	0	1	0	1	0	1	0
<i>Flueggea virosa</i> (Roxb. ex Willd.) Baill	Phyllanthaceae	Perennial	mph	0	0	0	1	0	1	0	1
<i>Hackelochloa granularis</i> (L.) Kuntze	Poaceae	Annual	Graminoid	0	1	1	0	0	1	0	1
<i>Indigofera colutea</i> (Burm.f.) Merr.	Fabaceae	Annual	Forb	0	1	1	0	0	1	0	0
<i>Loudetia togoensis</i> (Pilg.) C.E.Hubb	Poaceae	Annual	Graminoid	0	1	0	1	0	1	0	0
<i>Mariscus squarrosus</i> (L.) C.B. Clarke	Cyperaceae	Annual	Graminoid	0	0	0	0	1	0	0	0
<i>Microchloa indica</i> (L.f.) P.Beauv.	Poaceae	Annual	Graminoid	0	1	1	1	0	1	1	1
<i>Mitragyna inermis</i> (Willd.) K.Schum.	Rubiaceae	Perennial	mph	1	0	0	0	0	0	0	0
<i>Mollugo nudicaulis</i> Lam.	Molluginaceae	Annual	Forb	0	1	1	1	1	1	0	0
<i>Pandiaka angustifolia</i> (Vahl) Hepper	Amaranthaceae	Annual	Forb	0	0	0	0	0	0	1	0
<i>Pennisetum pedicellatum</i> Trin	Poaceae	Annual	Graminoid	0	0	0	1	0	1	1	1
<i>Phyllanthus amarus</i> Schumach. & Thonn	Phyllanthaceae	Annual	Forb	0	0	0	0	1	1	1	1
<i>Phyllanthus maderaspatensis</i> L.	Phyllanthaceae	Annual	Forb	1	0	0	0	0	0	0	0
<i>Rottboellia cochinchinensis</i> (Lour.) Clayton	Poaceae	Annual	Graminoid	0	0	0	0	0	1	1	1
<i>Schizachyrium platyphyllum</i> (Franch.) Stapf	Poaceae	Annual	Graminoid	0	0	0	0	0	1	0	0

<i>Setaria pumila</i> (Poir.) Roem. & Schult.	Poaceae	Annual	Graminoid	1	0	1	0	1	1	1	1
<i>Tephrosia pedicellata</i> Baker	Fabaceae	Annual	Forb	0	1	1	1	0	1	0	1
<i>Triumfetta rhomboidea</i> Jacq.	Malvaceae	Annual	Forb	0	0	0	0	0	0	0	1
<i>Pentanema indicum</i> (L.) Y. Ling	Asteraceae	Annual	Forb	0	0	0	0	1	1	0	1
<i>Wissadula rostrate</i> (Schumach) Hook. f.	Malvaceae	Annual	Forb	0	0	0	0	1	1	0	1
<i>Zornia glochidiata</i> DC.	Fabaceae	Annual	Graminoid	0	1	1	1	1	1	1	1

Table 2: Results of the Generalized Linear Model (GLM) analysis of the species richness from the germinable SSB at Laba (A) and Tiogo (B) State Forests. The values of probability in bold face are significant.

A. Laba					
	Df	Residual error (E.R.)	Df E.R.	F	Pr (> F)
Null			47		
Treatment (T)	3	9.563	44	4.712	0.084
Sampling depth (D)	2	15.500	42	2.403	0.015
T×D	6	8.000	36	1.005	0.437
B. Tiogo					
Null			47		
Treatment (T)	3	40.750	44	2.362	0.087
Sampling depth (D)	2	26.542	42	2.308	0.114
T×D	6	3.625	36	0.105	0.996

Table 3: Results of the GLM analysis of seed density from the germinable SSB at Laba (A) and Tiogo (B) State Forests. The values of probability in bold face are significant.

A. Laba					
	Df	Residual error (E.R.)	Df E.R	F	Pr (> F)
Null			47		
Treatment (T)	3	23	44	3.259	0.033
Sampling depth (D)	2	37.13	42	7.893	0.001
T×D	6	24.31	36	1.722	0.144
B. Tiogo					
Null			47		
Treatment (T)	3	189.04	44	2.751	0.050
Sampling depth (D)	2	195.58	42	4.270	0.022
T×D	6	62.06	36	.452	0.045

Table 4: Jaccard's coefficient of similarity for species composition of the SSB between Laba (A) and Tiogo (B) State Forests. The value of Jaccard's index of similarity in bold face is highest.

Sites		Control	Selective cutting	Early fire	Grazing
A. Laba	Control	1			
	Selective cutting	0.27	1		
	Early fire	0.33	0.42	1	
	Grazing	0.35	0.25	0.62	1
B. Tiogo	Control	1			
	Selective cutting	0.24	1		
	Early fire	0.32	0.38	1	
	Grazing	0.35	0.41	0.44	1