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Influence of Grazing on Soil Seed Banks Determines the Restoration Potential of Aboveground Vegetation in a Semi-arid Savanna of Ethiopia

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ABSTRACT

Species composition, number of emerging seedlings, species diversity and functional group of the soil seed banks, and the influence of grazing on the similarity between the soil seed banks and aboveground vegetation, were studied in 2008 and 2009 in a semi-arid savanna of Ethiopia. We tested whether the availability of persistent seeds in the soil could drive the transition from a degraded system under heavy grazing to healthy vegetation with ample perennial grasses. A total of 77 species emerged from the soil seed bank samples: 21 annual grasses, 12 perennial grasses, 4 herbaceous legumes, 39 forbs, and 1 woody species. Perennial grass species dominated the lightly grazed sites, whereas the heavily grazed sites were dominated by annual forbs. Heavy grazing reduced the number of seeds that can germinate in the seed bank. Species richness in the seed bank was, however, not affected by grazing. With increasing soil depth, the seed density and its species richness declined. There was a higher similarity in species composition between the soil seed bank and aboveground vegetation at the lightly grazed sites compared with the heavily grazed sites. The mean similarity between the seed banks and aboveground vegetation was relatively low, indicating the effect of heavy grazing. Moreover, seeds of perennial grasses were less abundant in the soil seed banks under heavy grazing. We concluded that restoration of grass and woody species from the soil seed banks in the heavily grazed areas could not be successful in semi-arid savannas of Ethiopia.

Key words: functional group; grass species; grazing pressure; savannas restoration; seed banks; vegetation degradation.

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A CONTINUOUS GRASS LAYER BENEATH WITH A DISCONTINUOUS LAYER OF TREES AND SHRUBS are typical features of semi-arid savannas (Van de Koppel & Prins 1998, Van Langevelde *et al.* 2003). The balance between trees and grasses, however, is often highly disturbed due to heavy grazing and poor management (Pugnaire & Lazaro 2000, Van Auken 2000). The disappearance of good fodder grasses and browse species are serious challenges, threatening the livelihoods of millions of people in semi-arid savannas worldwide (Oba *et al.* 2000, Harris 2010). Increasing the grazing pressure beyond a certain threshold, often leads to irreversible effects. At high grazing pressures, perennial grasses are replaced by annual herbs, which could trigger a vegetation collapse from which recovery to the grassland state is extremely difficult, even if the grazing pressure is greatly reduced (Rietkerk *et al.* 1996, Van de Koppel *et al.* 1997). The recovery of species that disappeared from the aboveground vegetation heavy grazing can, however, be facilitated by the soil seed banks (Baker 1989, Leck *et al.* 1989, de Villiers *et al.* 2003). In this study, we tested whether the availability of seeds in the soil could 'kick-start' the recovery of the vegetation and accelerate the transition from a degraded state to vegetation with a perennial grass cover.

Similarities between the soil seed banks and aboveground vegetation have been previously reported (Leck & Graveline 1979, Henderson *et al.* 1988, Levassor *et al.* 1991), although several studies show poor similarities of species composition between the soil seed banks and aboveground vegetation (Bakker & Berendse 1999, de Villers *et al.* 2003, Lemenih & Teketay 2006, Solomon *et al.* 2006). This dissimilarity is characterized by more frequent occurrence of perennial grasses and woody plants in the aboveground vegetation (Abule *et al.* 2005, Tessema *et al.* 2011a), and more annual forbs in the soil seed bank (Solomon *et al.* 2006, Hopfensperger 2007). Such dissimilarities can be caused by species differences in seed dormancy and germination rates (Baskin & Baskin 2004, Scott *et al.* 2010, Tessema *et al.* 2011b), caused by either embryonic dormancy or impermeable seed coats or both (Baskin & Baskin 2004). For instance, Mott (1978) and McIvor and Howden (2000) reported that the seeds of most grass and woody species in tropical savannas are dormant following seed fall in the late wet season, but overcome this dormancy during the late dry season when soil temperatures increase. These differences in species composition, number of species and germination success of the soil seed bank down the soil profile might be attributed due to differences in soil texture and other soil quality parameters (Hopkins & Graham 1983), under influence of grazing (Moussa *et al.* 2009, Tessema *et al.* 2011a).

Vegetation studies in communal grazing systems of semi-arid African savannas are mostly restricted to the aboveground vegetation, and often ignore the role that soil seed bank could play in the restoration of degraded vegetation after heavy grazing

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(de Villiers *et al.* 2003, Solomon *et al.* 2006, Hopfensperger 2007, Kassahun *et al.* 2009). Indeed, knowledge about the factors and mechanisms that contribute to the recovery of vegetation, and information on the species composition of soil seed banks, are either minimal or lacking in semi-arid savannas (Hopfensperger 2007). We therefore studied the effect of light and heavy grazing on the soil seed bank and aboveground vegetation in an experimental setup in a semi-arid savanna of Ethiopia, and tested the following predictions: (1) as the soil seed bank serves to return to the original light grazing situation, we expect the number of emerging seedlings and number of species (species richness) in the soil seed banks are similar between the light and heavy grazing sites; and (2) the soil seed bank samples are more similar than the aboveground vegetation samples, but the similarity in species composition between the soil seed bank and aboveground vegetation is highest under light grazing.

METHODS

STUDY AREA.—The study was conducted in two semi-arid locations: Awash National Park (ANP: 9°20′ N, 40°20′ E, 960–1050 m asl); and Abernosa Cattle Breeding Ranch (ACBR: 7°47′ N, 38°40′ E, 1660–1740 m asl), both located in the Ethiopian Rift Valley. The two locations were selected because both areas are rangelands occupied by pastoralists and it was possible to contrast a heavy grazing condition with a light grazing at both locations.

The ANP was established in 1966, covers about 756 km^2 and is located 225 km east of Addis Ababa. The mean annual rainfall (1989–2008) of ANP was 512 mm (Tessema *et al.* 2011a), ranging between 277 mm and 653 mm, and was highly variable among years (coefficient of variation [CV] = 103%). Its main rainy season is from July to September, with a short rainy season from February to April. The mean daily minimum and maximum temperatures are 18°C and 34°C, respectively (Tessema *et al.* 2011a). The vegetation of the ANP has been described as an *Acacia* shrub land and open grassland (Abule *et al.* 2005).

The ACBR covers about 23 km^2, and is located 175 km south of Addis Ababa. It has a bimodal rainfall through the year; the main rain season is from July to October and the short rain is from March to April, with a short dry spell in May and June. The long dry period is from November to February. The average annual rainfall of ACBR was 734 mm (346–959 mm; CV=116%; Tessema *et al.* 2011a). The mean minimum and maximum temperatures are 14°C and 28°C, respectively. The ranch was established about 40 yr ago by fencing the woodland, and paddocks were established for rotational grazing.

The vegetation is open *Acacia* woodland dominated with grasses (Argaw *et al.* 1999). Inside the ranch, the trees are protected from cutting and the vegetation is dominated by tall grasses (*e.g., Hyparrhenia, Chloris, Cenchrus, Panicum* and *Sporobolus* spp.) with scattered trees (*e.g., Acacia* and *Balanites* spp.).

SELECTION OF SAMPLING SITE.—Light and heavy grazing sampling sites were systematically identified inside and outside the ANP and ACBR, based on the history and intensity of livestock grazing according to previous studies (Argaw *et al.* 1999, Abule *et al.* 2005, Tessema *et al.* 2011a). Four sampling sites in each light and heavy grazing area in each location were selected, using a stratified sampling procedure.

SAMPLING OF ABOVEGROUND VEGETATION.—To compare the soil seed bank species with the aboveground vegetation, the herbaceous species composition was assessed using 1-m^2 quadrats during the flowering stage of herbaceous species in September 2008. Twenty quadrats were randomly recorded in each sampling site under light and heavy grazing pressures, totaling 320 (2 locations × 2 grazing pressures × 4 sampling sites × 20 quadrats). The species were classified into grasses (annual or perennial), herbaceous legumes and forbs to determine the contribution of each functional group. Individual plants were counted to determine the abundance of each species. The woody species composition (trees and shrubs >1 m height) and their density were recorded in a sample area of 100 m × 100 m at each site under heavy and light grazing sites in both locations. Three of these 1-ha plots were assessed for woody species per site, yielding a total of 48 ha (two locations × two grazing pressures × four sampling sites × three quadrats), but samples were pooled across sites. For further details, the aboveground vegetation composition was described in Tessema *et al.* (2011a).

SOIL SEED BANK STUDY.—Soil samples for the soil seed bank study were collected at the end of October 2008, at the end of the growing season (after seed production) at the same locations as the aboveground vegetation sampling. The samples serve as an indication of viable seeds not germinated in the soil over the season. Twenty 1-m^2 soil samples were collected in each sampling site at two soil depths (0–5 cm and 5–10 cm), yielding a total of 640 samples in both locations (2 locations × 2 grazing pressures × 4 sample sites × 20 subsamples × 2 soil depths). The soil samples from the same soil depth in each sampling site were pooled and mixed to form one composite soil sample for each of the two depths for each of the 16 sampling sites. Finally each of the 32 (two locations × two grazing pressures × four sample sites × two soil depths) composite soil samples was divided into three equal parts, out of which one was randomly chosen for the soil seed bank germination study. The composite soil samples were analyzed for texture and soil nutrients using standard procedures and the findings were reported in Tessema *et al.* (2011a).

The number of seedlings of different species emerging from the soil samples was used as a measure of the number of viable seeds in and the composition of the seed bank (Roberts 1981). The emergence method is more appropriate than actual identification of seeds (Gross 1990, Espeland *et al.* 2010), because it determines the relative abundance of viable seeds that can germinate, and excludes the nonviable seeds (Poiani & Johnson 1988). The soil was thoroughly mixed after removal of all root and plant fragments, and spread over sand in plastic pots to a depth of 20 mm. Five pots (area = 0.065 m^2) were used per composite soil sample per soil depth, totaling 160 pots. The pots were placed at random in the greenhouse at Haramaya University of Ethiopia, with no artificial light supplied. The greenhouse temperature ranged from 19–22°C during the day to 10–12°C at night. Pots were examined every 3 d for the first 2 mo and thereafter weekly until the end of the experiment. Seedlings started to emerge after 1 wk, and those seedlings that were readily identifiable counted, recorded and discarded. Those difficult to identify at the seedling stage were first counted, but maintained in the pots until they were identified. Each pot was hand watered regularly until saturated. The soil sample incubation was done for a period of 6 mo (November 2008–April 2009), since the number of emerging seedlings, particularly grasses and forbs declined considerably after 6 mo. Plant nomenclature follows Cufodontis (1953–1972), Fromann and Persson (1974) and Philips (1995).

DATA ANALYSES.—The density of seeds (number of emerged seedlings), number of species (species richness), species composition and functional group (grasses, herbaceous legumes, forbs and woody species) were recorded. Species diversity was calculated using the quadratic entropy diversity index (Q): $\Sigma\Sigma d_{ij}P_iP_j$, where d_{ij} and P_iP_j represents the dissimilarity and the relative abundance between species i and j, respectively (Ricotta & Szeidl 2006, Ricotta & Marignani 2007). To test for differences in number of emerged seedlings, species richness and functional group in the soil seed banks a general linear model (GLM) was applied, PASW (v.17), with location, grazing pressure, soil depth and their interactions as independent factors. Dependent proportional data were arcsine transformed to meet the assumption of normality and homogeneous variances.

The Jaccard's coefficient of similarity (Magurran 2004) was used to test for similarities in species composition of the soil seed banks between locations and grazing pressures as well as between the soil seed banks and aboveground vegetation. To compare the similarity in species composition between the soil seed banks and aboveground vegetation, ordination of sampling sites under the light and heavy grazing pressures was carried out by multivariate analysis (CANOCO 4.5, ter Braak 1997). The species emerging from the soil seed banks and species composition in the aboveground vegetation in 16 sampling sites was ordinated by a correspondence analysis (CA) on presence/absence data. Moreover, a canonical correspondence analysis (CCA) was conducted to determine the correlation between the species germinated in the soil seed banks and the soil parameters per study location under the light and heavy grazing sampling sites.

TABLE 1. *Effect of light and heavy grazing on number of species and number of emerging seedlings (seed density) in the soil seed bank samples at two locations in a semi-arid savanna of Ethiopia, with statistical results of the general linear model (*F, P, $R^2_{adjusted}$*).*

	Mean ± 95% CL	
	Number of species (n/m²)	Seed density (n/m²)
Abernosa Cattle Breeding Ranch		
Light grazing		
5 cm	8.1 ± 0.7	4291.6 ± 1046.3
10 cm	5.5 ± 0.8	2115.4 ± 423.8
Heavy grazing		
5 cm	7.9 ± 3.2	2162.5 ± 618.6
10 cm	5.5 ± 2.6	1149.5 ± 288.0
Awash National Park		
Light grazing		
5 cm	5.0 ± 0.5	1509.5 ± 381.2
10 cm	2.9 ± 0.2	345.5 ± 120.8
Heavy grazing		
5 cm	3.0 ± 1.0	257.2 ± 80.5
10 cm	1.3 ± 0.4	44.7 ± 65.9
Location (LOC)		
F (df = 1, 24)	44.72	113.350
P	< 0.001	< 0.001
Grazing pressure (GP)		
F (df = 1, 24)	2.85	42.490
P	0.10	< 0.001
Soil depth (SD)		
F (df = 1, 24)	16.25	40.980
P	< 0.001	< 0.001
LOC × GP		
F (df = 1, 24)	2.41	5.001
P	0.13	0.040
LOC × SD		
F (df = 1, 24)	0.27	6.871
P	0.61	0.020
GP × SD		
F (df = 1, 24)	0.09	9.492
P	0.62	0.011
LOC × GP × SD		
F (df = 1, 24)	0.01	0.030
P	0.967	0.875
$R^2_{adjusted}$	0.66	0.874

RESULTS

NUMBER OF EMERGED SEEDLINGS.—The lightly grazed sites had a higher number of emerged seedlings (2061 seeds/m²) in the soil seed bank compared with the heavily grazed sites (1302 seeds/m²). There were also site-specific differences, as the number of emerged seedlings at ACBR was higher than those at ANP (2807 and 557 seeds/m², respectively; Table 1). As expected, the upper soil layer had more emerged seedlings compared with the deeper soil layer in both locations (Table 1). More seedlings emerged from the upper soil layers than the deeper soil layers under the lightly grazed sites compared with the heavily grazed sites (interaction term of grazing pressure × soil depth; Table 1). The full model explained together 87 percent of the variation in germinated seed density.

NUMBER OF SPECIES AND SPECIES COMPOSITION.—Of the 77 soil seed bank species, 33 were grasses (21 annual and 12 perennial grasses), 4 herbaceous legumes, 39 annual forbs and 1 *Acacia* spe-

TABLE 2. *Effect of light and heavy grazing on number of emerging seedlings (n/m²) for the different functional group from the soil seed bank samples at two locations in a semi-arid savanna of Ethiopia, together with results (F, P, $R^2_{adjusted}$) of the general linear model that tested for differences in location, grazing pressure and soil depth and their interactions.*

	Functional group (Mean ± 95% CI)				
	Annual grass	Perennial grass	Total grass	Herbaceous legume	Annual forbs
Abernosa Cattle Breeding Ranch					
Light grazing					
5 cm	1458.4 ± 87.8	1172.5 ± 61.9	2630.8 ± 111.8	169.0 ± 31.4	1491.8 ± 77.2
10 cm	796.1 ± 87.8	626.5 ± 61.9	1422.6 ± 111.8	60.7 ± 31.4	632.1 ± 77.2
Heavy grazing					
5 cm	911.8 ± 87.8	413.9 ± 61.9	1325.7 ± 111.8	27.7 ± 31.4	809.1 ± 77.2
10 cm	300.5 ± 87.8	293.1 ± 61.9	593.6 ± 111.8	26.6 ± 31.4	529.4 ± 77.2
Awash National Park					
Light grazing					
5 cm	408.1 ± 87.8	748.7 ± 61.9	1156.8 ± 111.8	84.3 ± 31.4	268.4 ± 77.2
10 cm	132. ± 87.8	95.1 ± 61.9	224.3 ± 111.8	11.1 ± 31.4	108.1 ± 77.2
Heavy grazing					
5 cm	103.8 ± 87.8	55.0 ± 22.3	125.9 ± 111.8	6.7 ± 31.4	124.6 ± 77.2
10 cm	5.8 ± 87.8	27.4 ± 14.7	60.8.3 ± 111.8	3.1 ± 31.4	41.6 ± 77.2
Location (LOC)					
F (df = 1, 24)	129.484	81.350	194.224	4.041	178.727
P	< 0.001	< 0.001	< 0.001	0.046	< 0.001
Grazing pressure (GP)					
F (df = 1, 24)	35.404	111.981	110.904	8.634	20.778
P	< 0.001	< 0.001	< 0.001	0.004	< 0.001
Soil depth					
F (df = 1, 24)	44.284	54.470	86.398	4.387	40.075
P	< 0.001	< 0.001	< 0.001	0.038	< 0.001
LOC × GP					
F (df = 1, 24)	6.102	3.561	8.842	1.019	6.936
P	0.015	0.061	0.003	0.314	0.009
LOC × SD					
F (df = 1, 24)	13.213	0.054	8.897	0.133	16.847
P	0.357	0.816	0.003	0.716	< 0.001
GP × SD					
F (df = 1, 24)	0.854	39.909	18.069	3.949	9.052
P	0.357	< 0.001	< 0.001	0.049	0.003
LOC × GP × SD					
F (df = 1, 24)	0.263	2.136	1.532	0.176	5.301
P	0.609	0.146	0.218	0.673	0.023
R^2_{adjusted}	0.585	0.643	0.726	0.088	0.630

cies germinated (Table S1). The number of species at ACBR and ANP was similar (59 and 58 species, respectively). Ten grass species (five perennial and five annuals) were found only in the lightly grazed sites and were totally absent from the heavily grazed sites. Only one perennial grass species (*Belpharis ciliaris*), however, was found only at the heavily grazed sites, and these sites were dominated by annual forbs (Table S1).

The average number of emerged species (species richness) in the soil seed bank was higher at ACBR (Table 1) than at ANP with a mean of 6.8 and 3.1 species/m², respectively (Table 1). More species emerged from the upper soil layer than the deeper soil layer (8 and 3.8 species/m², respectively; Table 1).

The light and heavy grazing sites at ANP had a higher soil seed bank species diversity index (Q = 0.85 and 0.53, respectively) compared with both the lightly and heavily grazed sites of the soil seed bank at ACBR (Q = 0.450 and 0.395, respectively). In the aboveground vegetation, both at ACBR and ANP, the light grazing sites had a higher species diversity index (Q = 0.40 and 0.34, respectively) than the heavily grazed sites (Q = 0.33 and 0.27, respectively; Table 2).

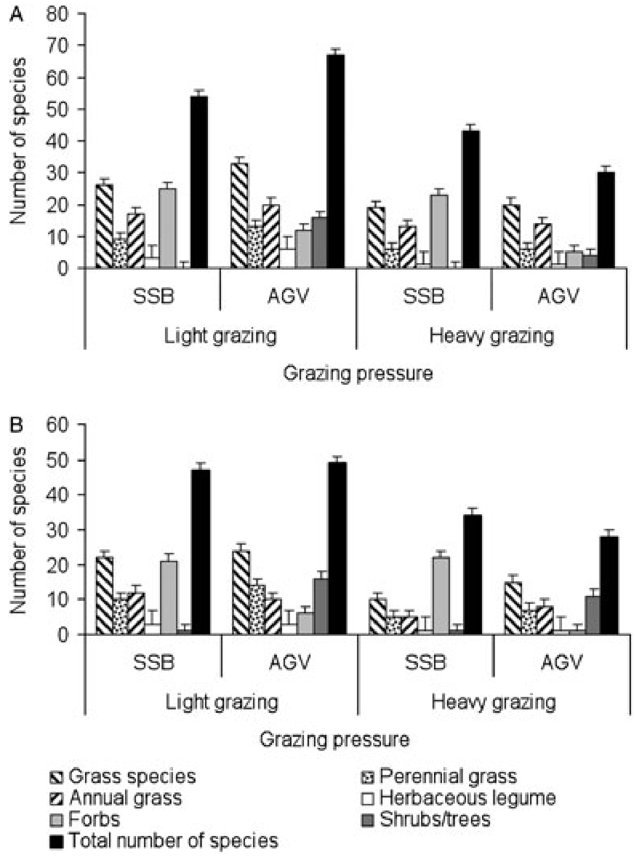

FIGURE 1. Number of species recorded in the soil seed banks (SSB) and aboveground vegetation (AGV) with their functional group under light and heavy grazing conditions at Abernosa Cattle Breeding Ranch (A) and Awash National Park (B) in a semi-arid savanna of Ethiopia.

The CCA ordination results showed a clear separation of the sampling sites for the soil parameters, as the light grazing sites are separately clustered from the heavy grazing sites in each location, with a high correlation between the soil seed bank species and the soil parameters on the first and second ordination axis (Figs. S1A and B). The first and second axis explained together 93 and 77 percent of the total variation at ACBR and ANP, respectively. The relation between the species ordination and the soil parameters was location specific. Sand, total nitrogen, organic carbon, phosphorous, cation exchangeable capacity, magnesium, calcium and pH had dominant effects on lightly grazed sites at ACBR, whereas silt, clay, electrical conductance and potassium were strongly correlated with the heavily grazed sites (Fig. S1A). Similarly, silt, clay, total nitrogen, organic carbon, potassium, cation exchangeable capacity, magnesium, calcium and pH had dominant effects on the lightly grazed sites at ANP, whereas only sand and phosphorous were important on the heavily grazed sites at ANP (Fig. S1B).

FUNCTIONAL GROUP.—The number of emerged seedlings for total grass, annual grass, perennial grass, herbaceous legumes and annual forbs were higher ($P < 0.001$) at ACBR than ANP (Table 2). Light grazing had a higher ($P < 0.001$) number of emerged seedlings for total grass, annual grass, perennial grass, herbaceous legumes and annual forbs than the heavily grazed sites (Table 2). The upper soil layers produced more seedlings of annual grasses, perennial grasses, herbaceous legumes and annual forbs compared with the lower soil layers (Table 2).

SIMILARITY BETWEEN THE SOIL SEED BANKS AND ABOVEGROUND VEGETATION.—The total number of germinated species in the soil seed bank was lower than the total number of species recorded in the aboveground vegetation under light grazing (Figs. 1A and B). The total number of germinated species in the soil seed bank was, however, higher than the number of species identified in the aboveground vegetation under heavy grazing. The total number of annual and perennial grass species emerged from the soil seed bank was lower than the total number of grass species recorded in the aboveground vegetation both under light and heavy grazing (Figs. 1A and B). In a similar fashion, the total number of woody species recorded in the soil seed bank was lower than the soil seed bank under light and heavy grazing (Figs. 1A and B). The total number of annual forbs was, however, considerably higher (> 50%) in the soil seed bank than the aboveground vegetation, where the annual forbs contributed only 26 percent.

The lightly grazed sites had a higher ($F_{2,979} = 4.10$; $P < 0.02$; $R^2 = 0.68$) Jaccard's coefficient of similarity than the heavily grazed sites both in the soil seed bank and aboveground vegetation (Table 3). The mean similarity in species composition of the aboveground vegetation was relatively high at 0.41, and ranged from 0.22 (between samples collected from the heavy grazing sites at ACBR and heavy grazing sites at ANP) to 0.70 (between samples collected at different light grazing sites at ANP). However, the mean similarity in species composition of the soil seed bank samples was relatively lower at 0.289, and ranged from 0.196 (between samples from light and heavy grazing sites at ANP) to 0.43 (between samples collected from light grazing sites at ACBR; Table 3). Hence, the similarity coefficient of the soil seed bank was lower ($F_{2,979} = 374.72$; $P < 0.001$) than that of the aboveground vegetation (Table 3). The mean similarity coefficient between the soil seed bank and aboveground vegetation was relatively low (0.13; Table 3), but this was, as predicted, higher at light grazing sites than at heavy grazing sites for both locations ($F_{4,979} = 18.01$; $P < 0.001$; Table 3).

The CA ordination separated the soil seed bank and aboveground vegetation composition along the first ordination axis (Fig. 2). Moreover, the CA ordination result showed that the 16 soil seed bank sampling sites could already be separated on the first two axes, distinguishing both the light and heavy grazing sites and the two locations (Fig. 2). Indeed, the soil seed bank samples were clustered together, and the aboveground vegetation samples were more heterogeneous, clustered in two separate groups.

TABLE 3. *Mean Rao's quadratic diversity index (Q) and mean Jaccard's coefficient of similarity (*N *= 160) for species composition, comparing the soil seed banks and aboveground vegetation under light (LG) and heavy grazing (HG) at Abernosa Cattle Breeding Ranch (ACBR) and Awash National Park (ANP) in a semi-arid savanna of Ethiopia.*

		Soil seed banks (SSB)				Aboveground vegetation (AGV)			
		ACBR		ANP		ACBR		ANP	
	Q	LG	HG	LG	HG	LG	HG	LG	HG
SSB									
ACBR									
LG	0.450	—							
HG	0.395	0.395	—						
ANP									
LG	0.847	0.258	0.210	—					
HG	0.532	0.230	0.243	0.196	—				
AGV									
ACBR									
LG	0.399	0.184	0.184	0.087	0.187	—			
HG	0.326	0.151	0.199	0.076	0.156	0.343	—		
ANP									
LG	0.341	0.101	0.123	0.071	0.144	0.353	0.220	—	
HG	0.274	0.073	0.094	0.062	0.169	0.225	0.219	0.422	—

DISCUSSION

Number of emerged seedlings.—The results suggest that grazing had a major impact on the soil seed banks in semi-arid savannas of Ethiopia, with a larger quantity of emerged seedlings at the lightly grazed sites. Solomon *et al.* (2006) also observed more seedlings of grass species at lightly grazed areas compared with heavily grazed ones. Seed survival on the inflorescence of the plant is adversely affected by continuous heavy grazing, leading to smaller seed banks (Abule *et al.* 2005, Tessema *et al.* 2011a). It is known that the seed production capacity of grasses and their ultimate contribution of seeds to the soil seed bank can be reduced under grazing (Solomon *et al.* 2006, Kassahun *et al.* 2009). Therefore, the seed buffer provided by the soil seed bank is reduced under heavy grazing.

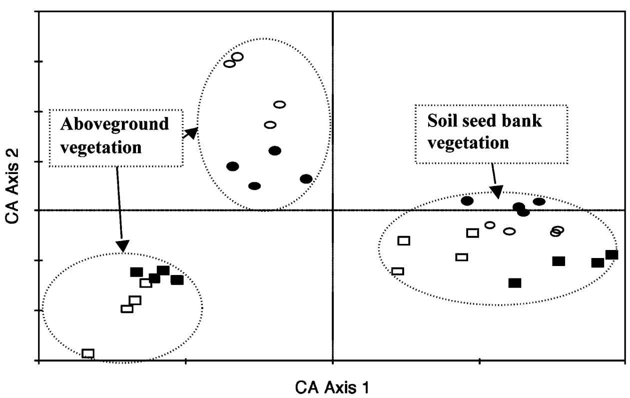

FIGURE 2. Ordination diagram of the 16 sampling sites for the soil seed bank species and aboveground vegetation under two grazing pressure (filled symbols represent heavily grazed sites and open symbols represent lightly grazed sites) at two locations (circles represent Abernosa Cattle Breeding Ranch and squares represent Awash National Park) by a correspondance analysis (CA) in a semi-arid savanna of Ethiopia.

Only one woody species seed emerged from the soil seed banks, out of the 27 woody species reported in the aboveground vegetation (Tessema *et al.* 2011a). Previous soil seed bank studies have shown that the seeds of woody species are rare compared with herbaceous species in various tropical ecosystems (Wassie & Teketay 2006, Solomon *et al.* 2006), which is in agreement with our findings. A lack of woody species seeds in the soil seed bank suggests that the regeneration of such species would be inhibited by the loss of mature individuals in the aboveground vegetation (Wassie & Teketay 2006).

The number of emerged seedlings in the soil seed bank at ACBR was higher than ANP, which might be due to differences in rainfall, as rainfall is higher at ACBR than ANP. Higher rainfall in tropical environments promotes rapid growth of herbaceous species, leading to higher seed production and larger seed banks. The number of emerged seeds in both locations was within the ranges reported for East African savannas (Skoglund 1992, Solomon *et al.* 2006). The number of seeds emerged in the soil seed banks, however, depends on the characteristics of the study sites (Meissner & Facelli 1999, Kinloch & Friedel 2005), with lower seed densities in drier areas (Skoglund 1992).

The influence of soil depth on seed density was consistent at both sites and at the two grazing pressures, decreasing with increasing soil depth. Young (1985) indicated that seeds of tropical vegetation are generally more abundant near the surface. The observed vertical distribution in seed density might be associated with changes in soil structure due to heavy grazing (Hopkins & Graham 1983). According to Skoglund (1992), recruitment from the seed bank is restricted to periods with favorable conditions of soil parameters controlling seed germination. The presence of bare soil and the sand content tend to increase under heavy grazing (Abule *et al.* 2005, Tessema *et al.* 2011a), and may therefore indirectly decrease seed germination through a reduction of the soil moisture content. Hence, soil parameters not only influence the aboveground vegetation species composition, but probably also the composition of the soil seed banks and the seed germination.

SPECIES COMPOSITION.—Lightly grazing sites had a higher species diversity index in the soil seed banks compared with heavily grazed sites, indicating that grazing has reduced the species diversity not only in the aboveground vegetation but also in the soil seed banks, a result that has also been obtained in Australia and South Africa (Snyman 2004, Kinloch & Friedel 2005). The number of species and species composition on heavily grazed areas often do not revert to that of lightly grazed areas after rainfall, indicating that the species composition on the heavily grazed areas has undergone persistent changes (Abule *et al.* 2005, Kassahun *et al.* 2009). Besides grazing, differences in flowering time, and the influence of wind can also contribute to the differences in species composition (Snyman 2004). This study confirmed that heavy grazing reduced the number of emerging species and changed the species composition in the soil seed bank species, indicating that heavy grazing caused a persistent reduction in annual and perennial grasses not only in the aboveground vegetation but also in soil seed banks.

FUNCTIONAL GROUPS.—Lightly grazed sites were strongly dominated by perennial grass species, whereas the heavily grazed sites were covered by annual forbs in the soil seed banks. According to Solomon *et al.* (2006), out of the total 44 species germinated in the soil seed bank of semi-arid rangelands of southern Ethiopia, 25 percent were grasses and 75 percent were forbs. Soil seed banks usually contain more annuals than perennials, more forbs than grasses, and more weeds when highly disturbed (Rice 1989, Sternberg *et al.* 2003). The colonization of annual species on heavily grazed sites indicates that heavy grazing reduces the performance and seed production of the perennial grass component, thereby favouring annual forbs and increasing their seed contribution to the soil seed banks (Solomon *et al.* 2006). Annuals are more abundant in soil seed bank than perennials owing to their high reproductive output (Sternberg *et al.* 2003, Scott *et al.* 2010) and because perennial grasses often propagate vegetatively (O'Connor 1994, 1996).

SIMILARITY BETWEEN SEED BANKS AND ABOVEGROUND VEGETATION.—The similarity in species composition between the soil seed banks and aboveground vegetation was relatively low, but was higher for lightly grazed sites than for the heavily grazed sites. Low similarity in species composition between the soil seed banks and aboveground vegetation was also reported in natural forests (Lemenih & Teketay 2006), church forests (Wassie & Teketay 2006) and in *Acacia* woodlands (Argaw *et al.* 1999). Previous studies (Thompson & Grime 1979, de Villers *et al.* 2003) also reported poor correlations between species in the soil seed banks and standing vegetation, with similarity often not more than 50–60 percent (Bekker *et al.* 1997, Bakker & Berendse 1999). Others, however, report much higher similarity (Leck & Graveline 1979, Henderson *et al.* 1988, Levassor *et al.* 1991). The low similarity between the soil seed banks and aboveground vegetation in terms of palatable perennial grasses might reflect overgrazing the aboveground vegetation, as higher similarity is generally reported only for well-managed plant communities (Rice 1989, Hopfensperger 2007).

CONCLUSION

The number of species and emerging seedlings in the soil seed banks were higher at the lightly grazed sites than at the heavily grazed sites. We found low similarity in species composition between seed banks and aboveground vegetation, which could be attributed to the impact of heavy grazing. In addition, we observed two states in the soil seed banks as a result of grazing. The first state, typical of sites under light grazing, was characterized by greater abundance of seeds of annual and perennial grass species. The second was typical for heavy grazing, with few grass seeds, but characterized by seeds of annual forbs. We conclude that the seeds of grass species available in the soil seed banks are unable to rapidly drive the transition from degraded conditions to perennial grass cover that represents better fodder value in semi-arid savannas.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *List of species in the soil seed banks andaboveground vegetation, relative abundance with their life formsand functional groups under light and heavy grazing conditions attwo locations in semi-arid savannas of Ethiopia.*

FIGURE S1. Ordination diagram of the sampling sites × soil parameters under two grazing pressures at Abernosa Cattle Breediong Ranch, and Awash National Park by a Canonical Correspondance Analysis in a semi-arid savanna of Ethiopia.

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