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Research article

Changes in grass plant populations and temporal soil seed bank dynamics in a semi-arid African savanna: Implications for restoration

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ABSTRACT

The re-colonization or recovery of grass species after disappearance due to heavy grazing depends on the presence of persistent soil seed banks that might be accumulated over time from the aboveground vegetation. Moreover, successful plant recruitment is a function of seed production, seed germination and seedling survival, which can be mechanistically understood through studying the life cycle processes of grass species populations under field conditions. Therefore, we studied the number of germinable seeds, species richness and life-forms in the soil seed banks under light and heavy grazing conditions, and the changes in grass species populations in a semi-arid savanna of Ethiopia. Accordingly, a total of 103 species (15 perennial and 29 annual grasses, 6 legumes, 52 forbs and 1 woody species) emerged from the soil samples collected. Lightly grazed sites had a higher seed density compared with heavily grazed sites. The seed density increased over the first three months of soil sampling and decreased thereafter. Perennial grasses dominated the light grazing sites, whereas annual species dominated the heavily grazed sites, indicating that perennial grasses were replaced by annual species in the soil seed bank through grazing. The mean mortality rate from the seedling stage to adult plants was 65%. The seed-to-seedling stage was found to be the most critical transitional stage for grass survival. High seedling mortality in the aboveground vegetation and depletion of seeds in the soil seed banks as a result of sustained heavy grazing can lead to local extinction and disappearance of perennial grasses in semi-arid Ethiopian savannas.

1. Introduction

Tropical savannas cover about 20% of the world's land surface (Scott et al., 2010). However, arid and semi-arid rangelands in savannas experience different forms of vegetation degradation (Harris, 2010), as a result of continuous heavy grazing (Valone and Sauter, 2004). The disappearance of good fodder grasses are major challenges in semi-aid savannas for both wild and domestic herbivores (Prins, 1988; Angassa and Oba, 2010; Tessema et al., 2011). The structure and composition of savanna vegetation is highly resilient to disturbances, such as herbivory and fire (van Langevelde et al., 2003), as the majority of plants exhibit adaptive traits that enable them to persist (Sarmiento, 1992; O'Connor, 1994). Hence, grasses establish by the expansion and subsequent fragmentation of vegetative parts (i.e., tillers, rhizomes or stolons), or establish from the soil seed banks (O'Connor, 1996; Snyman, 2004; Solomon et al., 2006). These seeds survived in the soil seed banks can bridge the gap between seed production and seed germination (Williams et al., 2005; Scott et al., 2010; van Langevelde et al., 2016).

Heavy grazing reduces seed production of grass species by affecting the allocation of resources for reproduction through reducing active surface areas for photosynthetic processes, as well as through direct removal of flowers and seeds (O'Connor and Pickett, 1992; Hoshino et al., 2009). Thus, perennial grass species that reproduce only from seeds and are palatable to herbivores and with a low seed output potentials and short seed longevity might disappear in the system due to sustained heavy grazing (O'Connor, 1991, 1994, 1996). Subsequently, depletion of the soil seed bank could follow, due to lack of seed production from the established plants (O'Connor and Pickett, 1992; Snyman, 2004). Moreover, perennial grasses can also be rapidly disappeared after germination from the systems as results of heavy grazing, or under erratic rainfall regimes, or during prolonged dry periods, all of which are typical features of semi-arid savannas. Therefore, continuous heavy

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grazing could trigger the disappearance of perennial grass species both in the aboveground vegetation (O'Connor, 1994; Angassa and Oba, 2010; Tessema et al., 2011) and in the soil seed banks (Solomon et al., 2006; Tessema et al., 2012; van Langevelde et al., 2016)). The re-colonization of perennial grass species after disappearance due to heavy grazing depends primarily on the presence of persistent soil seed banks (Baskin and Baskin, 2004; Snyman, 2004; van Langevelde et al., 2016)) that are accumulated over time from the aboveground vegetation (Kinucan and Smeins, 1992; O'Connor, 1991, 1994), as well as by the survival of standing plants that could supply new seeds in to the soil (O'Connor, 1991; Veenendaal et al., 1996; Gibson et al., 2002).

The ability of grass species to survive under the influence of grazing can be understood mechanistically through studying the life cycle processes of the grass species populations (Snyman, 2004; Scott et al., 2010), such as number of seeds in the soil seed banks, number of seedlings and established plants, as well as number of flowering and seed setting matured plants of the standing populations (O'Connor, 1996; Veenendaal et al., 1996; Scott et al., 2010). Hence, studies into the temporal dynamics of soil seed banks (Kassahun et al., 2009; Dreber and Esler, 2011), and survival of grass plants (O'Connor, 1994, 1996; Zimmermann et al., 2010) help to understand and facilitate the conservation, management, and restoration of grass species in semi-arid savannas (Snyman, 2004; Tessema et al., 2011). However, knowledge on temporal soil seed bank dynamics under contrasting grazing regimes, as well as the rate of change in grass plant populations at various growth stages is either minimal or lacking in semi-arid African savannas. In this research, we addressed the following research questions: (i) do grazing intensity affect seed density and species richness in the soil seed bank overtime? (ii) are effects of grazing intensity similar across life-forms? and (iii) which growth stage is most critical to the survival of grass plants in semi-arid African savannas?

2. Materials and methods

2.1. Description of the study areas

The study was conducted in two semi-arid locations: the Abernosa Cattle Breeding Ranch (ACBR: 7°47′N, 38°40′E, 1660–1740 masl) and Awash National Park (ANP: 9°20′N, 40°20′E, 960–1050 masl) of Ethiopia (Fig. 1;Tessema et al., 2012). The distance between the ACBR and ANP is about 200 km, located in the upper and middle Rift Valley of Ethiopia, respectively, typical of semi-arid savannas characterized by low rainfall and long dry seasons. The mean annual rainfall (1989–2008: Tessema et al., 2011, 2012) of ANP was 512 mm, and was highly variable among years, with a main rainy season from July–October and a short rainy season from February–April. The mean daily minimum and maximum temperatures were 18 °C and 34 °C, respectively (Tessema et al., 2011, 2012). The ACBR has a bimodal rainfall; the short rains fall from February–April, followed by a short dry spell in May and June, and the main rainy season from July to October, with a long dry period from November to January. The average annual rainfall of ACBR was 734 mm (Tessema et al., 2012, 2012). The mean minimum and maximum temperatures were 14 °C and 28 °C, respectively.

2.2. Selection of sampling sites

Light and heavy grazing sites were systematically selected inside and outside the ANP and ACBR, based on the history and intensity of livestock grazing (Mekuria et al., 1999; Abule et al., 2005; Tessema et al., 2011), using a stratified sampling procedure. In ANP, the light grazing sites were browsed by few wild herbivores, e.g., east African Oryx (*Oryx beisa*), soemmerring's Gazelle (*Nanger soemmeriingii*), dik-dik (*Madoqua kirkii*), lesser kudu (*Tragelaphus imberbis*) and greater kudu (*Tragelaphus strepsiceros*), and grazed intermittently by livestock. The vegetation of the ANP was described as an *Acacia* shrub land and open grassland (Tessema et al., 2011, 2012), and the vegetation cover and the composition are therefore in good condition every year. The heavy grazed sites are nearby open grasslands, just outside the border of the park, and the former excellent grass cover that used to provide soil cover vanished, due to continuous heavy grazing by cattle, small ruminants, donkey and camels, as well as a few wildlife species (Abule et al., 2005; Tessema et al., 2012). In ACBR, the light grazing sites are fenced to control overgrazing by livestock of neighbouring communities, and only the Borana cattle, owned by the ranch, graze the paddocks in rotation, and the herbaceous vegetation is in good condition with a dense basal cover. The vegetation is open *Acacia* woodland dominated with grasses. Inside the ranch, the trees are protected from cutting and the vegetation is dominated by tall grasses (e.g., *Hyparrhenia rufa*, *Chloris radiata*, *Cenchrus ciliaris*, *Panicum coloratum* and *Sporobolus pyramidalis*) with moderately closed canopy of upper storey trees (e.g., *Acacia tortilis*, *A. seyal* and *Balanites aegyptiaca*). The heavy grazing sites outside the ranch are grazed throughout the year and are dominated by short annual species, with a high percentage of bare soil (Tessema et al., 2011, 2012).

2.3. Sampling procedures for the estimation of soil seed banks

The soil seed bank study covered 9 months, during which soil samples were collected 7 times, in October, November and December 2010 (long dry season), January and March 2009 (short rainy season), and in May and June 2009 (short dry season), in light and heavily grazed sites at both locations. Soil samples were collected in 4 sampling sites (10 m × 10 m) divided into 17 sampling quadrats (1 m × 1 m) sampled at the center, horizontal, vertical and diagonal directions (Fig. 2), at two soil depths (0–5 and 5–10 cm), yielding a total of 544 subsamples (2 locations × 2 grazing pressures × 4 sampling sites × 17 quadrats × 2 soil depths). The soil samples from the same soil depth in each sampling site were mixed to form one composite soil sample for each of the 4 sampling sites. Finally, each of the 32 (2 locations × 2 grazing pressures × 2 soil depths × 4 sampling sites) composite soil samples was divided into three equal parts, out of which one was randomly chosen for the soil seed bank germination study. The two soil depths were used to evaluate the depth distribution of seeds in the soil seed banks as a result of trampling by livestock during grazing.

The seedling emergence method was used to estimate seed density and species composition of the composite soil samples during the soil seed bank study (Roberts, 1981). The emergence method is more appropriate than actual identification of seeds (Gross, 1990; Page et al., 2006) because it determines the number of viable seeds that can germinate, by excluding the non-viable seeds (Poiani and Johnson, 1988; Page et al., 2006). The soil was thoroughly mixed after removal of all root and plant fragments, and soil samples were 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, totaling 160 pots (2 locations × 2 grazing pressures × 2 soil depths × 4 sampling sites × 5 replications). The pots were placed at random in the greenhouse at Haramaya University, Ethiopia, without artificial light. Each pot was hand-watered regularly until saturated. The greenhouse temperature was 19–22 °C during the day and 10-12°C during night. Pots were examined every 3 days for the first 2 months, and thereafter weekly until the end of the experiment. Seedlings started to emerge within one week, and

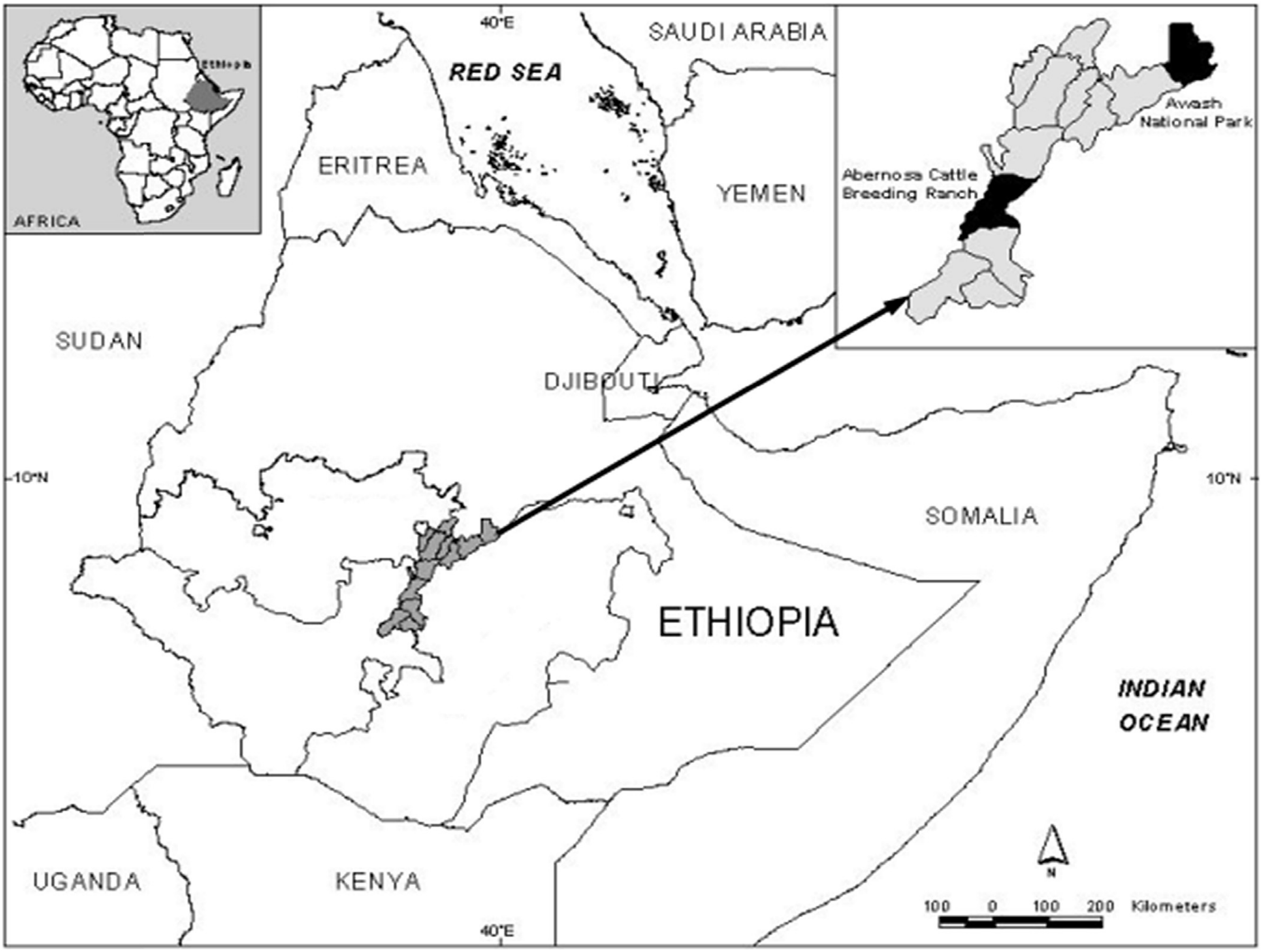

Fig. 1. Location of the study areas, Abernosa Cattle Breeding Ranch (7°47′N, 38°40′E) and Awash National Park (9°20′N, 40°20′E) in a semi-arid savanna grazing systems of Ethiopia.

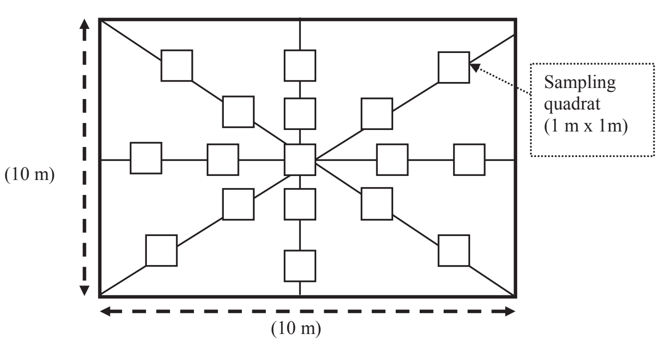

Fig. 2. Diagram illustrating quadrat position in a 10 m × 10 m sampling site for recording the number of seedlings, established plants, flowering plants and seed setting plants of grass species in a semi-arid savanna of Ethiopia.

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 identified. The first soil samples (for October) were incubated in November 2008, and the soil sample incubation for other months was repeated consecutively, according to the near-monthly sampling schedule in the field, for a period of six months. Plant nomenclature follows Cufodontis (1953–1972), Fromann and Persson (1974), and Philips (1995).

2.4. Monitoring growth stages of grass species

A 50 m × 100 m heavily grazed site was fenced both at ACBR and ANP, for monitoring the different growth stages of grass species, so grazing by large herbivores was excluded. Only those tufted grasses that producing tillers were recorded during the study, by excluding prostrate grasses, propagated by rhizomes and/or stolons, since tufted grasses are mostly dependent on seed production for their survival and are expected to contribute more to the soil seed bank formation than prostrate grasses in semi-arid areas. Within the fenced area in each location, 4 (four), 10 m × 10 m sampling site was used to record plant density (number of individuals) of different grass species with respect to their growth stages in 17 quadrats (1 m × 1 m) at the center, and at the horizontal, vertical and diagonal axes (Fig. 2), yielding a total of 136subsamples (2 locations × 4 sampling paddocks × 17 sample quadrats). Plant density was recorded at the appropriate time of each growth stage. The study used a key-stage analysis (Yamamura, 1999; Oli and Bruna, 2005), widely used to analyze life table data, and aimed at finding the growth stage that is largely responsible for the observed changes in plant populations (Sibly and Smith, 1998; Zimmermann et al., 2010).

2.5. Data analyses

A Generalized Linear Model (GLM) was applied to test for differences in number of germinated seeds (seed density), species richness and life-forms in the soil seed banks, using PASW (version 17), with location, grazing pressure, months, soil depth and their interactions as independent factors. Tukey-HSD test was employed for mean separation at $P \leq 0.05$. Dependent proportional and/or count data were transformed to meet the assumptions of normality and homogeneity of variance.

The key stage analysis in our study included number of germinated seeds in the soil seed bank (NSSSB), number of seedlings (NSL), number of established plants (NEP), number of flowering plants (NFP) and number of seed setting and matured plants (NSSP) of the grass species. The K-stages between the soil seed bank and aboveground vegetation involve four transitions, indicated as: NSSSB-►NSL-►NEP-►NFP-►NSSP. A Generalized Linear Model (GLM) was also applied using PASW (version 17), with location and growth stages and their interactions as independent factors, to test for differences between various growth stages of grass plants. Moreover, the K-value for each transition was designated as k_1, k_2, k_3 and k_4. The total K value for the whole life-table, describing the transition from the soil seed bank to the aboveground vegetation was calculated as $K_{total} = k_1 + k_2 + k_3 + k_4$ (Newton, 1988; Begon et al., 1996; Sibly and Smith, 1998). The k-value for each transition was calculated using the formula (Sibly and Smith, 1998): $k_1 = \log$ (NSSSB/NSL); $k_2 = \log$ (NSL/NEP); $k_3 = \log$ (NEP/NFP); $k_4 = \log$ (NFP/NSSP), with $K_{total} = \log$ (NSSSB/NSSP). To find the key stage, each k value was plotted as the independent variable against the total K value, using regression analysis; the k value with a slope nearest to unity was considered as the key stage (Begon et al., 1996; Yamamura, 1999), indicating the critical transition (growth stage) in the life cycle of grass species.

3. Results

3.1. Seed density in the soil seed banks

The lightly grazed sites had a higher total seed density (1849 seeds m^{-2}) from the soil seed bank samples compared with the heavily grazed sites (1164 seeds m^{-2}), with on average a higher seed density at ACBR (2045 seeds m^{-2}) than at ANP (968 seeds m^{-2}; Table 1). The top soil layer had a higher seed density (2244 seeds m^{-2}) compared with the deeper soil layer (769 seeds m^{-2}) both at two study locations and grazing pressures. The light grazing sites had a higher seed density than the heavy grazing sites both at ACBR and ANP (location × grazing pressure interaction effect; Table 1).

The months of soil sampling had a significant ($F_{6,\ 270} = 6.758$; $P < 0.010$; entire model $R^2_{adjusted} = 0.540$) effect on total number of seeds from the soil seed banks. The total number of seeds increased over the first three months until December, and decreased thereafter (Fig. 3a & 3b). The light and heavy grazing sites showed a similar trend over time, except that the total number of seeds was higher under the light grazing than the heavily grazing sites (Fig. 3).

3.2. Species richness and species composition in the soil seed banks

A total of 103 plant species emerged from all soil samples throughout the 9 months study (Appendix A and B). The number of emerged species at ACBR and ANP was 82 and 87 species, respectively (Appendix A). The total number of species emerged at the light grazing sites was 91 species (28 annual and 12 perennial grasses, 6 herbaceous legumes, 44 forbs and 1 woody species), decreasing to 82 species at heavy grazing (23 annual and 11 perennial grasses, 5 herbaceous legumes, 42 forbs and 1 woody species) (Appendix A).

Location had a significant effect on the number of emerged species in the seed banks (Table 1). The number of emerged species was higher at ACBR (6.9 species m^{-2}) than ANP (5.7 species m^{-2}; Table 1). Similarly, the upper soil layer had more number of emerged species (7.8 species m^{-2}) than the deeper soil layer (4.8 species m^{-2}). Time (months) had a significant effect on the number of emerged species in the soil seed banks (Fig. 3c and 3d), as species richness was lower in October compared to other months, and was similar across grazing regimes (Table 1).

3.3. Seed density according to life-form groups in the soil seed banks

The seed density for annual grass, perennial grass, herbaceous legumes and annual forbs in the seed banks were higher at ACBR than at ANP (Table 1). The light grazing sites had higher seed density for total grasses, annual grasses, perennial grasses and herbaceous legumes compared with the heavily grazed sites both at ACBR and ANP (Table 1). However, grazing pressure had no significant effect on the number of annual forbs that emerged from the soil. The top soil layer had more seed density for total grasses, annual grasses, perennial grasses, herbaceous legumes and annual forbs than deep soil layer (Table 1).

Time of soil sampling had a significant effect on the seed density for different life-forms, in that the number of emerged annual and perennial grass seedlings increased until the 3 months (December) of the soil sampling, and decreased thereafter, both under light (Fig. 4a and 4c) and heavy grazing (Fig. 4b and 4d). The number of emerging perennial grass seedlings was low, and was even lower than that of annual forbs under heavy grazing. The number of emerged herbaceous legume seedlings increased until 4 months (January) of soil sampling and decreased thereafter for both grazing regimes (Fig. 4e and 4f). Time of sampling had no effect on the number of emerging annual forb seeds both under light or heavy grazing sites (Fig. 4g and 4h), as the number of seedling density remained stable over time.

3.4. Growth stages analysis of grass species

Location had a highly significant ($F_{1,\ 160} = 155.301$; $P < 0.001$) effect on the number of individuals over the different growth stages, with higher values at ACBR than ANP (Fig. 5). Similarly, there was a highly significant effect of the different growth stages on the number of plants ($F_{1,\ 160} = 155.301$; $P < 0.001$; whole model $R^2_{adjusted} = 0.671$). As expected, the number of seeds in the soil seed banks was higher than the number of seedlings, number of established plants, number of flowering plants and number of seed setting plants (Fig. 5), indicating that there were high rate of change in grass plant populations from the seedlings stages until the grass plants reached the seed setting stage. The total rate of change in grass plant populations, recorded from the seedling stage until the plants reached the seed setting stage, were 60% and 69% at ACBR and ANP, respectively. In addition, the growth stage from seeds-to-seedlings (k_1) could best explain the variation in the total rate of change in grass plant populations (K_{total}) compared with other growth stages ($F_{1,\ 32} = 86.177$; $R^2 = 0.729$; Fig. 6a). Moreover, the seed-seedling transition had a higher slope, close to unity (0.815), larger than the other growth stages, indicating that this stage is the most critical transitional stage in the life cycle of grass species. The transitions from established plants to flowering and from flowering

Table 1
Number of species, total seed density and seed density over the different life-forms (grasses, herbaceous legumes and forbs) from the soil seed bank samples under light and heavy grazing at two locations in a semi-arid savannas of Ethiopia, with statistical results of the GLM (F, P, $R^2_{adjusted}$; N = 544).

	Number of species (n m^{-2})	Seed density (mean ± 95% CI)					
		Life-forms (n m^{-2})					Total seed density
		Annual grasses	Perennial grasses	Total grass	Herbaceous legumes	Annual forbs	
Abernosa Cattle Breeding Ranch							
Light grazing							
5 cm	8.5 ± 0.4	1453.3 ± 92.2	1139.8 ± 68.1	2593.1 ± 145.3	169.2 ± 31.0	929.7 ± 71.3	3692.0 ± 153.4
10 cm	5.5 ± 0.4	493.1 ± 92.2	362.8 ± 68.1	856.0 ± 145.3	40.5 ± 31.0	376.6 ± 71.3	1273.0 ± 165.3
Heavy grazing							
5 cm	8.2 ± 0.4	856.4 ± 92.2	478.7 ± 68.1	1335.1 ± 145.3	76.6 ± 31.0	718.3 ± 71.3	2130.0 ± 148.3
10 cm	4.3 ± 0.4	341.1 ± 92.2	169.8 ± 68.1	510.9 ± 145.3	24.1 ± 31.0	513.1 ± 71.3	1048.1 ± 139.6
Awash National Park							
Light grazing							
5 cm	7.5 ± 0.4	616.8 ± 92.2	485.3 ± 68.1	1102.1 ± 145.3	347.1 ± 31.0	541.7 ± 71.3	1990.9 ± 153.4
10 cm	4.4 ± 0.4	118.0 ± 92.2	90.2 ± 68.1	208.2 ± 145.3	69.6 ± 31.0	92.5 ± 71.3	370.3 ± 165.3
Heavy grazing							
5 cm	6.9 ± 0.4	407.7 ± 92.2	286.6 ± 68.1	694.3 ± 145.3	54.1 ± 31.0	417.2 ± 71.3	1165.6 ± 148.3
10 cm	3.6 ± 0.4	82.2 ± 92.2	84.0 ± 68.1	166.2 ± 145.3	18.4 ± 31.0	138.0 ± 71.3	322.6 ± 139.6
Location (LOC)							
F (df = 1, 270)	19.871	54.188	38.481	57.422	4.144	44.665	77.937
P	<0.001	<0.001	<0.001	<0.001	0.043	<0.001	<0.001
Grazing pressure (GP)							
F (df = 1, 270)	1.727	14.532	30.792	25.195	26.644	0.581	30.458
P	0.019	<0.001	<0.001	<0.001	<0.001	0.446	<0.001
Soil depth (SD)							
F (df = 1, 270)	119.923	77.790	77.283	94.402	31.705	54.303	141.033
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Time							
F (df = 1, 270)	28.413	7.280	7.608	5.179	9.099	0.228	6.758
P	<0.001	0.007	0.006	0.024	0.003	0.633	0.010
LOC × GP							
F (df = 1, ,270)	0.080	3.738	11.006	7.737	7.176	0.001	4.517
P	0.777	0.054	0.001	0.006	0.008	0.984	0.034
LOC × SD							
F (df = 1, 270)	0.017	6.324	6.163	7.550	2.258	0.022	3.873
P	0.898	0.013	0.014	0.006	0.134	0.882	0.050
GP × SD							
F (df = 1, 270)	0.054	5.623	12.119	9.835	13.119	6.591	17.247
P	0.817	0.018	0.001	0.002	<0.001	0.011	<0.001
LOC × GP x SD							
F (df = 1, 270)	0.192	1.085	1.901	1.709	3.553	0.777	1.053
P	0.662	0.298	0.169	0.192	0.061	0.379	0.306
R^2 *adjusted*	0.368	0.397	0.453	0.467	0.247	0.271	0.536

to seed setting stages had lower slopes (<0.269), so these stages are less important for the overall plant rate of change in grass plant populations in the study areas.

4. Discussion

4.1. Soil seed bank response to grazing intensity

Soil seed banks of a semi-arid savanna of Ethiopia varied with grazing regimes, with seed density being greater at the light grazing than at the heavy grazing site. Accordingly, the density of soil seed bank composition is strongly influenced by surrounding plant communities (Kinucan and Smeins, 1992; Kassahun et al., 2009; Dreber and Esler, 2011), shaped by the severity of grazing over extended time periods (Kinloch and Friedel, 2005; Solomon et al., 2006). However, Dreber and Esler (2011) and Snyman (2004) reported that long term heavy grazing increased germinable seed densities in the seed banks in semi-arid rangelands of southern Africa, which is contrary to our findings. In this case, heavy grazing might favour small-seeded annual forbs and weed species in the soil seed banks (Solomon et al., 2006; Kassahun et al., 2009; Scott et al., 2010; Tessema et al., 2012).

Time of soil sampling had a significant effect on total number of germinated seeds in the soil seed banks, as the total seed density increased over the first 3 months of sampling, and decreased thereafter. Previous studies (Williams et al., 2005) also reported that temporal variations in the germinable soil seed bank composition are common features of semi-arid savanna vegetation. Similarly, the total density of germinable seeds in the soil seed banks in northern Australia was much higher in early dry season compared with the late dry season (Scott et al., 2010). The higher seed density from the seed banks early in the dry season might be due to the deposition of seeds into the soils from the previous year seed production, whereas lower seeds at the late dry season in the soil seed banks might be associated with the germination of seeds, particularly perennial grasses, early in the dry season immediately after seed dispersal, as well as seed predation and mortality over time due to biotic and abiotic factors in semi-arid savanna ecosystems (Onaindia and Amezaga, 2000).

The temporal variations in the soil seed banks of semi-arid ecosystems could be associated with the depletions of seeds in the soil after initial seed dispersal (Scott et al., 2010; Tessema et al., 2012), and/or due to differences in longevity and germination of seeds of various species in the soil seed banks (Baskin and Baskin, 2004). According to previous studies (Mott, 1978; McIvor and Howden, 2000), the seeds of most grass species in tropical savannas are found to be dormant following initial seed dispersal but overcome this dormancy immediately in the middle of the dry

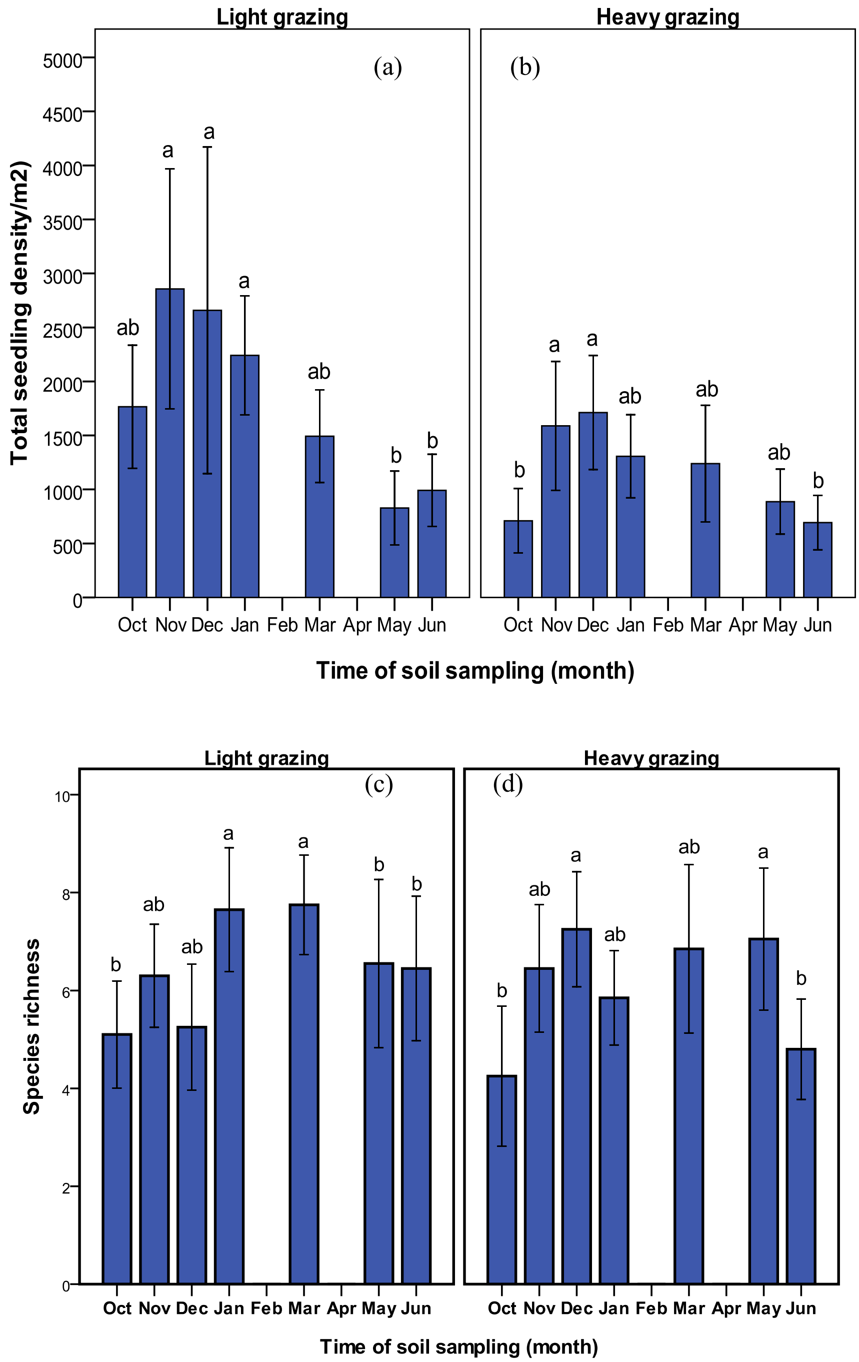

Fig. 3. Total number of seeds (n m^{-2}; a & b) and number of species (n m^{-2}; c & d) from the soil seed banks under light (LG) and heavy grazing (HG) sites over time (months) in a semi-arid Ethiopian savanna (N = 544).

season when soil temperature increases. Thus, perennial grasses, with a low seed producing ability and limited seed longevity might become locally extinct in the soil seed banks of semi-arid African savannas as a result of sustained heavy grazing.

4.2. *Effect of grazing intensity on species richness in soil seed banks*

The number of species emerged from the soil seed banks at the lightly grazing sites was higher than the heavy grazing sites in a semi-arid savanna of Ethiopia. According to Snyman (2004) the number of species from the soil seed banks in South Africa declined as a result of sustained heavy grazing. However, the number of species emerged from the soil seed banks is reported to increase with grazing intensity (Dreber and Esler, 2011), which is contrary to our results. According to Kinloch and Friedel (2005) and Kassahun et al. (2009) variability between soil sampling sites rather than grazing intensity can be the main cause of variation in species richness in semi-arid savannas. The higher number of species emerged from the soil seed banks at the degraded conditions may be related to heavy grazing that could provide opportunities for more annual species to re-colonize bare soil and eroded patches (Landsberg et al., 2002). Moreover, the time of soil sampling had a significant effect on species richness from the soil seed banks, as the number of species increased until the end of the soil sampling

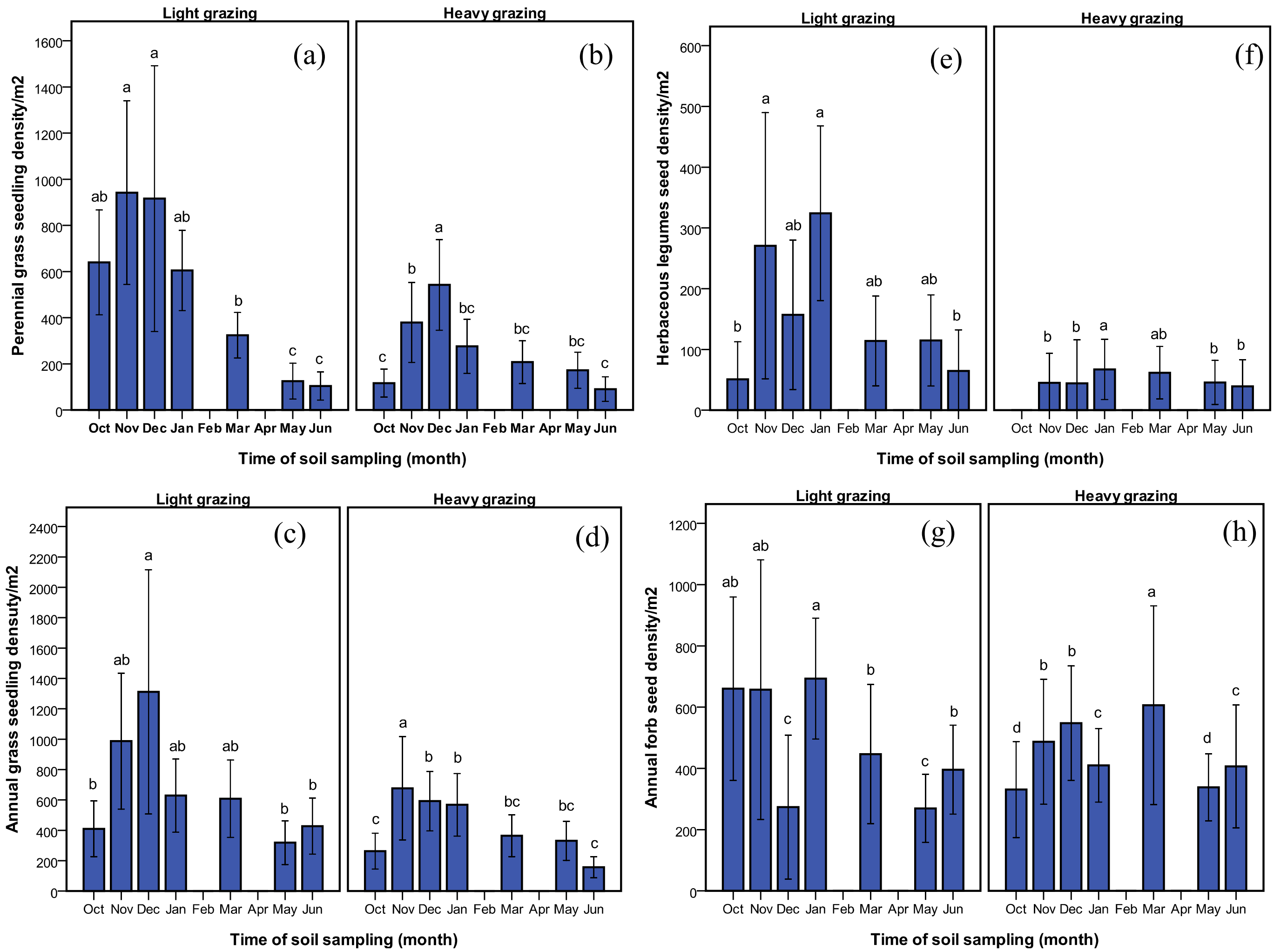

Fig. 4. Seed density (n m^{-2}) for different life-forms of herbaceous species recovered from the soil seed banks: perennial grasses (a & b), annual grasses (c & d), herbaceous legumes (e & f) and annual forbs (g & h) under light (LG) and heavy grazing (HG) sites over time (months) in a semi-arid savanna in Ethiopia (n = 544).

under the light grazing sites, whereas at the heavy grazing sites, the species showed an increasing trend and decreased thereafter.

4.3. Patterns of seed density between life-forms in the soil seed banks

Under the light grazing, perennial grasses dominated, while the heavily grazed sites were dominated by annual forbs in the present study. This indicates that palatable perennial grass species, with good fodder value, are replaced by annual species in the seed banks associated with heavy grazing. According to Dreber and Esler (2011), heavy grazing favours annuals in the soil seed banks since they tolerate heavy grazing and trampling through various adaptive mechanisms, which become easily buried in the soil. Similarly, temporal variation in soil seed banks in semi-arid African savannas could also be due to differences in phenology of herbaceous species in response to grazing (O'Connor and Pickett, 1992; Snyman, 2004).

4.4. Changes in grass plant populations according to growth stages

According to Scott et al. (2010) the resilience of grass dominated plant population in relation to disturbances, such as sustained heavy grazing, can be interpreted mechanistically through an examination of life-cycle processes. We found a decrease of 65% in grass plant populations from the seedling stage until the grass plants reached the seed setting stage in the present study. This result is in line with Lauenroth and Adler (2008) who reported mortality rates of grass plant population between 37% and 70% in the Great Plains, whereas Zimmermann et al. (2010) reported a lower mortality rate (31%) in semi-arid north-central Namibia. The present study showed that the growth stage from seeds-to-seedlings (k_1) could best explain the variation in total rate of change (K_{total}) in grass plant populations compared with the establishment, flowering and seed setting stages, indicating that this stage is the most critical transitional stage in the life cycle of the grass species. O'Connor (1994) and Oliva et al. (2005) indicated that smaller individuals are more likely to die than larger ones as a result of trampling ()during heavy grazing (Milton and Dean, 2000; Hodgkinson and Müller, 2005).

According to Snyman (2004) successful seedling recruitment is defined as a seedling that survives at least one growing season or up to the flowering and seed setting stages. However, seedling establishment and subsequent survival of grass species are strongly affected by temporal variation in rainfall distributions in semi-arid African savannas (Veenendaal et al., 1996). In most semi-arid savannas, grass seedling mortality is likely to be expected because of insufficient and erratic rainfall (Andrew and Mott, 1983; Veenendaal et al., 1996). For instance, a minimum amount of

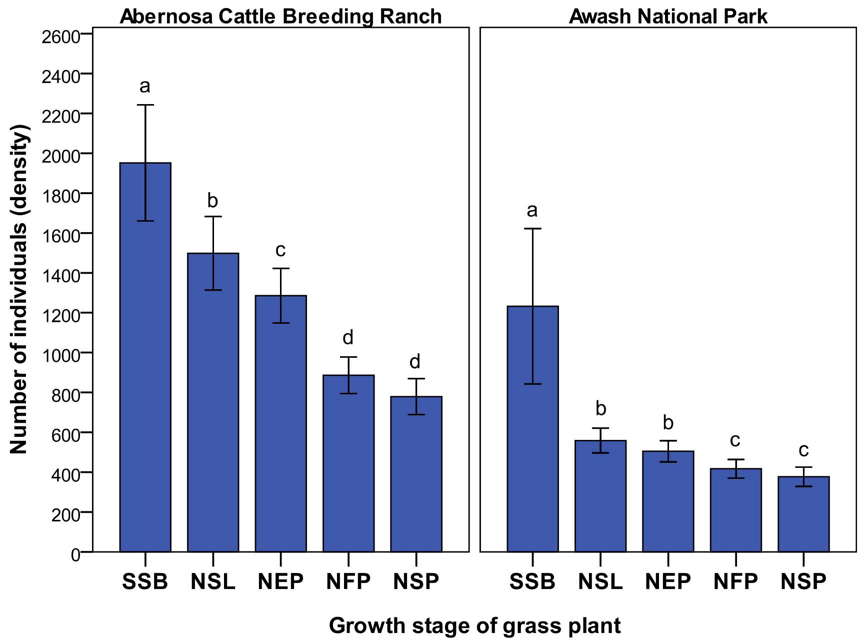

Fig. 5. The survival of grass plants at various stages (SSB = number of seeds in the seed banks, NSL = number of seedlings, NEP = number of established plants, NFP = number of flowering plants, NSP = number of seed setting plants) at Abernosa Cattle Breeding Ranch and Awash National Park in a semi-arid savanna of Ethiopia (n = 136).

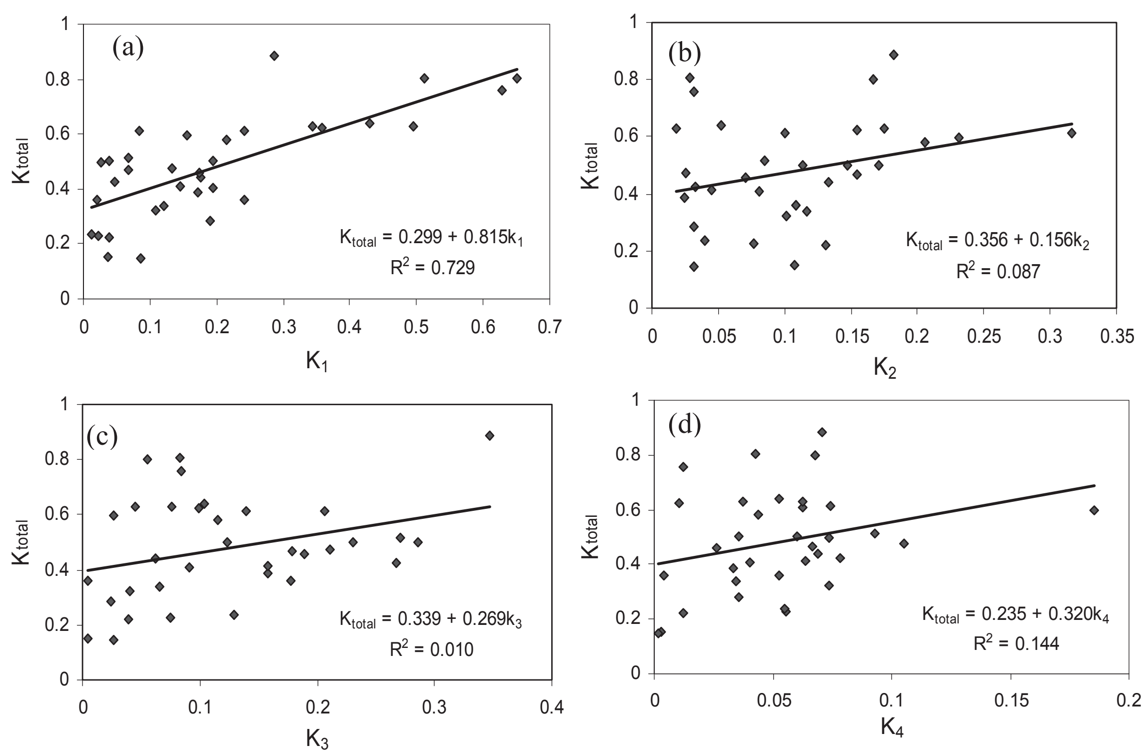

Fig. 6. The contribution of each growth stage [(k_1 = log (number of seeds in the seed banks/number of seedlings; a), k_2 = log (number of seedlings/number of established plants; b), k_3 = log (number of established plants/number of flowering plants; c), k_4 = log (number of flowering plants/number of seed setting plants; d)] to the total rate of change in grass plant populations ($K_{total} = k_1 + k_2 + k_3 + k_4$) in a semi-arid savanna of Ethiopia (n = 136).

15–25 mm rainfall is reported to trigger germination of grass species in semi-arid savannas (Andrew and Mott, 1983; Elberse and Breman, 1990), since tropical perennial grasses usually break their dormancy immediately after seed dispersal (Tessema et al., 2016). Therefore, a single rainfall event, especially early in the dry season, could initiate a cohort of seedlings, and followed by a long dry spell, cause a high seedling mortality in grass species, which is a typical feature of semi-arid savannas. Thus, exclusion from grazing in the early germination stage and/or the supply of water (i.e., irrigation) is good options to facilitate the transition from seedling-to-established plants in semi-arid African savannas. However, the transitions from established plants to flowering and from flowering to seed setting stages are less important for the species' permanent establishment, so that rotational grazing, especially later in the growing season, could still be used to exploit these grasslands.

5. Conclusions

In our study, the seed density from the soil seed banks, showed varying response to grazing regimes, as the light grazing sites had a higher seed density than the heavy grazing sites. Similarly, the soil seed bank compositional variation reflected the grazing history, as the lightly grazed sites were characterized by long-lived, perennials, whereas the heavily grazed sites by short-lived, forb species. Moreover, the seed density from the seed bank increased in the long dry season, immediately after initial seed dispersal, and declined thereafter both at the light and heavy grazing conditions. In addition, the mortality rate from the seedling stage until the grass plants reached the seed setting stage was of 64.5%. Hence, perennial grasses, characterized by a higher germination and lower longevity, can easily be eliminated in semi-arid African savannas due to sustained heavy grazing. We concluded that depletion of seeds in the soil over time as a result of heavy grazing coupled with high seedling mortality considerably decrease the density of perennial grasses both in soil seed banks and aboveground vegetation in semi-arid African savannas. Therefore, seedling survival and subsequent establishment are critical processes determining the successful recovery, growth and long-term persistence of grass species populations under the influence of heavy grazing in semi-arid ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jenvman.2016.07.057.

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