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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